INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

THE APPEARANCE OF STOCHASTIC CONTROL IN

FISH COMMUNITIES ON CORAL REEFS:

A HIERARCHICAL APPROACH TO

SYSTEM ORGANIZATION

By

NIGEL WALTHO, B.SC.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfilment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

ORGANIZATION OF FISH COMMUNITIES ON CORAL REEFS

DOCTOR OF PHILOSOPHY (1997)　　　　　　　　　　McMaster University

(Biology)　　　　　　　　　　　　　　　　　　　　　Hamilton, Ontario

TITLE:　　　　　The Appearance of Stochastic Control in Fish Communities on

　　　　　　　　Coral Reefs:　a Hierarchical Approach to System Organization

AUTHOR:　　　　Nigel D. Waltho　　B.Sc. (McMaster University)

SUPERVISOR:　　Dr. Jurek Kolasa

NUMBER OF PAGES:　xxv, 170

ABSTRACT

Species membership and population densities of fish communities on coral reefs are highly variable both spatially and temporally across many scales. Several models of stochastic control (i.e., organizing processes that produce these highly variable patterns) have been proposed. These models of stochastic control include: a lottery for available habitat sites, limited recruitment, and opportunistic predation. Although these models of stochastic control differ from each other in their organizing processes, they are similar in that they share two implicit assumptions. First, there is only one level or scale of system organization; second, there is only one significant organizing process.

Recent developments in community ecology, however, suggest that the organization of fish communities on coral reefs is complex (i.e., involves *multiple* levels of system organization). The heuristic value of a multi-level system of organization is that patterns that appear under stochastic control can, at least theoretically, be broken down or decomposed into a series of simpler, non-stochastic patterns.

If fish communities on coral reefs are indeed complex as in the above sense, then we need to re-evaluate the supposed single-level stochastic control in these systems. The purpose of this thesis, therefore, is to test the null hypothesis that fish communities on coral reefs are dependent on single-level stochastic processes as has been suggested. The alternative hypothesis is the appearance of stochastic control is a blend of patterns due to multiple levels of system organization. The method I use to test this is conceptually

straightforward. The first step is to divide the species membership into several groups. In the second step, for each species group I determine the correlation between species distributions and, for example, some attribute of the habitat template. If the organization of fish communities on coral reefs is dependent on stochastic processes acting within a single level, then independent of how the species are divided into groups, the correlation for all species groups should be similar. I found that:

- when the species are divided into groups based on similarities in the number of patch reefs a species is found, then significant differences occur among groups in correlation between species distributions and habitat attributes,

- specifically, for each habitat attribute tested there exists a trend of increasing correlation (or decreasing correlation—depending on the habitat attribute) from species found on most patches to species found on few patches.

This suggests that the previous models of single-level stochastic control (e.g., habitat lottery, limited recruitment, and predation) are incomplete because they do not consider consequences due to differences in species' distributions and densities. Instead these results suggest that the structure and organization of fish on coral reefs incorporate a mixture of stochastic and non-stochastic processes that occur (a) simultaneously within the community, and (b) differentially between the species. This implies that fish communities on coral reefs are complex concerning their basic structure, and that unless a community level pattern is decomposed into its component elements, the conclusions made about the nature of these communities can be misleading.

Acknowledgments

Many individuals contributed their time, energies, and support to the development and completion of this thesis. To each individual I say thank you, for without your support the task of completing this document would have been much more difficult, and in some cases, impossible to achieve. Foremost, I thank Jurek Kolasa for his years of contribution and patience in guiding me to a successful conclusion, and for the opportunities created during these years. I similarly thank Mike Risk and Dave Rollo who combined, provided further guidance and new and different experiences. As the core team responsible from the initiation of the Ph.D. to its completion I congratulate you each on a job well done.

A number of individuals contributed towards the data collection. Some were fortunate to develop a suntan during work in Jamaica, and others no doubt, contemplated their sanity moments before plunging through the ice in Sharbot Lake, Ontario. To all divers I thank you each for your help during these times, and overall enthusiasm in the project: Mark Allan, Patti Allan, Ron Allan, Karen Barnes, Jen Beecker, Keith Browne, Steve Connor, Aria Johnson, Matthew Jones, Tanya Kaczanowski, Liz Kernagham, Bruce King, Sandra Kittel, Mike Kolasa, Susan LaFlair, Kathy Lankester, Tara Lunn, Venessa McCracken, Mike Nowacki, Paul Roth, Kristi Sebalj, John Shannon, Brandy Strelec, Steve Varieur, Doug Wishart, and Dave Yarmand.

I further wish to extend my deepest appreciation towards my family and close friends who made it possible to tackle and complete the Ph.D. in such a positive environment: my family Maureen and Alan Waltho, Derek Waltho, and Andrea and Glenn Atkins; and my close friends Ron Allan, Gitanjali Canaran, Bruce King, Jane Kinney, Jurek Kolasa, Sue LaFlair, Mike Nowacki, and John Shannon. A toast to each!

v

TABLE OF CONTENTS

SECTION I

SECTION II

SECTION III

SECTION IV

SECTION V

SECTION VI

SECTION VII

LIST OF TABLES

SECTION II

Ambiguity in the Sampling window: Reef Fish Stability Revisited (Waltho N.D., and J. Kolasa. A manuscript prepared for publication in Bull. Mar. Sci.)

SECTION IV

Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models (Waltho N.D., and J. Kolasa 1996. Env. Biol. Fishes 47:255-267)

SECTION V

Coral reef fish and hierarchical community organization - the habitat dimension

model (Waltho N.D., and J. Kolasa 1996. A manuscript prepared for

publication in Ecology)

LIST OF FIGURES

SECTION I

GENERAL INTRODUCTION

SECTION II

Ambiguity in the Sampling window: Reef Fish Stability Revisited (Waltho N.D.,

and J. Kolasa. A manuscript prepared for publication in Bull. Mar. Sci.)

SECTION III

Organization of instabilities in multi-species systems, a test of hierarchy theory

(Waltho N.D., and J. Kolasa 1994. Proc. Nat. Acad. Sci. 91:1682-1685)

SECTION IV

Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models (Waltho N.D., and J. Kolasa 1996. Env. Biol. Fishes 47:255-267)

SECTION V

Coral reef fish and hierarchical community organization - the habitat dimension model (Waltho N.D., and J. Kolasa 1996. A manuscript prepared for publication in Ecology)

SECTION VI

GENERAL DISCUSSION AND SUMMARY

PREFACE

The organization of ecological communities (i.e., how species and individuals arrange themselves in space and time) is of considerable interest to ecologists. This is because an understanding of community organization can, for example, contribute to more accurate predictions of community structure and behaviour at some later time or place. However, to develop a good understanding of community organization two criteria must be met. The first criterion is to identify the community and its components. Inaccuracies here can lead to misrepresentations of the true community, and therefore a weakening in the confidence of the predicted outcome. The second criterion is to identify the mechanism that develops and maintains the community's internal structure. It is necessary to assume that such a mechanism occurs because without such, the arrangement of community components is random and any prediction of community structure or behaviour is trivial.

I expect that a good understanding of fish communities on coral reefs will provide similar benefits. However, this has proven problematic for several reasons. Foremost, the definition of what a fish community is remains unclear. It has implied a description involving the presence or absence of species, species relative or absolute abundance, or even type of species included in the species membership (e.g., genetic versus ontological species, or transient versus resident species). Furthermore, there is no consensus as to the mechanism (best known as *assembly process* as it is not unreasonable to think of the community structure as a product of the accumulation or assembly of species through

time) that develops and maintains the community structure. Several assembly processes have been hypothesized; each requires a different generic type of community behaviour by which all species respond (e.g., interspecific competition and niche specialization, competition for limited habitat space, recruitment limitation, and opportunistic predation). This singular view of community organization has, in part, impeded the ability to attain a good understanding of reef fish organization as various ecologists identify themselves almost exclusively with one reef model or another.

To improve our understanding of fish communities on coral reefs new conceptualizations, methodologies, and data, are required. One promising area of research includes developments in ecological theory that recognize and draw attention to the fact that ecological communities are complex in that they consist of *multiple levels* of organization. It is possible that in a multi-level system different species respond to different assembly processes at separate levels of organization. If fish communities respond to such a structure then it is possible that the previously hypothesized views of community organization may be incomplete, or furthermore, even incorrect.

The purpose of this thesis, therefore, is to derive a better understanding of the organization of fish communities on coral reefs. Specifically, I aim to show that fish communities on coral reefs are indeed multi-level structures, and that for each level a different assembly process dominates.

The thesis is divided into six Sections. In Section 1, the General Introduction, I review the previous models of fish community organization, and provide an explanation why I find these models are incomplete. Sections 2 to 5 are presented as journal articles.

Each of these Sections begins, however, with a description of the article's rationale and objectives. For articles that are reprinted from previously published sources, I provide a formal acknowledgment of the source immediately before the reproduced article.

The first of these journal articles is a manuscript submitted to the Bulletin of Marine Science, entitled "*Ambiguity in the sampling window: reef-fish stability revisited*" (Section 2). In this manuscript I examine issues that make the definition of community membership and its population densities technically difficult to determine, and provide a solution.

Section 3 contains the second article, entitled "*Organization of instabilities in multispecies systems, a test of hierarchy theory*", published in The Proceedings of the National Academy of Sciences, USA (Waltho & Kolasa 1994 Proc. Natl. Acad. Sci. 91:1682-1685). In this manuscript I determine if fish communities on coral reefs are indeed organized as multi-level structures.

In Section 4 and 5, I test attributes of the habitat template that limit the stochastic control of fish membership and distribution on coral reefs. Section 4 contains the third article, entitled "*Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models*", published in Environmental Biology of Fishes (Waltho & Kolasa 1996 Environ. Biol. Fishes 47:255-267). Section 5 contains the fourth article, entitled "*Coral reef fish community patterns in a hierarchy of dimensions*" submitted to the journal Ecology.

Section 6 is the General Discussion of my thesis. In this Section I consolidate the results made from within this thesis (with those made from prior studies and subsequent

observations) to develop a model of multi-level organization of fish communities on coral

reefs.

CLARIFICATIONS OF CONTRIBUTIONS

Works presented in Sections 2 to 5 are in the form of four journal articles. For each article I am the senior author, and J. Kolasa is the contributing author. For each article I was fully responsible for developing the original ideas, designing the experimental procedures, and collecting and analyzing the data. Except for the article in Section 3, I was also fully responsible for writing the initial versions of each manuscript. Much of the subsequent development of all manuscripts was a collaborative effort between J. Kolasa and myself.

SECTION I

GENERAL INTRODUCTION

1

General Introduction

1.1 Models of Community Organization in Fish on Coral Reefs

The community organization of fish on coral reefs (i.e., how fish arrange themselves in space and time) is of interest to many disciplines. By understanding the community organization and how these communities emerge it should be possible to make more accurate and precise predictions of community appearance and behaviour at different locations or times. The ability to make accurate and precise predictions is of heuristic value for many reasons. One reason is that it should be possible to develop more efficient and sustainable fishery and management policies for, for example, people dependent on the reefs for protein. However, independent of *effective management*, our understanding of fish communities on coral reefs is hampered by issues of inadequate definitions, conceptualization, methodology, and data. These issues are in great need for refinement. The purpose of this thesis is to advance new answers to these issues, and thereby, to improve our understanding of fish organization on coral reefs.

The definition of fish community is inadequate primarily because it does, and continues to vary according to the choice and use of the following parameters:

- numerical resolution (e.g., species presence or absence, species ranking according to abundance, or absolute abundance of species),

- spatial scale (e.g., the single patch reef, large reef platforms, or geographic range of the species),

- temporal scale (e.g., an instant in time, decades, to even a millennium), and

- selection criterion used to include species in the community (e.g., resident species versus transient species, functional groups, or various behavioral and morphological types).

As there are many possible permutations of these parameters, an accepted one-and-only definition of what consists a fish community is tenuous at best. In general, therefore, studies of fish communities on coral reefs subscribe to their own definitions. Meaningful comparisons of results and conclusions made between studies, therefore, are rare.

The current understanding of fish organization on coral reefs is also subject of debate. Four models of community organization have been proposed (see below); each model stresses a different assembly process as dominant in affecting the community structure. However, despite the emphasis on different assembly processes, the models are similar to each other in that they share two implicit assumptions. The first assumption is that only *one* assembly process (or family of processes such as those in the dynamic equilibrium between immigration and emigration rates) contributes to the observed species membership and population densities. This means that each model requires a generic type of community behaviour by which all species respond. The second assumption is that species in the community membership respond to the assembly process within a *single* level of organization (i.e., within the same spatio-temporal scale or habitat resolution).

This suggests there is only *one* level of community organization. These four models I now outline.

1.1.1 Interspecific Competition and Niche Specialization

Coral reef fish exist in a resource limited environment. It was thought, therefore, that high species diversity normally observed in fish communities is a result of interspecific competition and niche specialization. Specifically, juvenile and adult individuals were thought to compete between species for the limited resources. Thus, species evolved as habitat specialists (species with narrow niche requirements) to minimize the competitive stresses of interspecific competition. With narrow niche requirements it is possible to maximize species packing, and thus, generate the high species density observed (Hiatt & Strasburg 1960, Smith & Tyler 1972, Ehrlich 1975, Goldman & Talbot 1976, Connor & Simberloff 1979, Connell 1980, Gladfelter et al. 1980, Jackson 1981, Hay 1991, Hobson 1991). Choat and Bellwood (1991, and references within) show that in such an environment stresses from *intra*-specific competition may limit population abundances to below carrying capacities. Therefore, any disturbance such as local fishing pressure is minimal because populations quickly restore themselves to their former abundances. As long as the resource supply remains stable the communities always return to equilibrium following a perturbation (Fig. 1.1).

1.1.2 Lottery Hypothesis

Subsequent to the introduction of the Interspecific Competition and Niche Specialization model two new observations were made that initiated a general paradigm shift in how most ecologists think fish communities on coral reefs are now organized. These two observations are:

- most fish have a bipartite life strategy living first as a pelagic larvae for a few weeks, and then as a sedentary reef-oriented juvenile and adult lasting a few years,

- the juvenile and adult reef-oriented fish communities are highly variable in species membership and population densities.

These two observations "forced" ecologists to consider models of stochastic control (i.e., models that prescribe high variability), as alternatives to the preceding deterministic model. Three models of stochastic control were developed. The Lottery Hypothesis is the first of these three models.

The Lottery Hypothesis suggests that species composition and population densities are determined by competition between *recruiting individuals* for available habitat sites (Sale 1974, 1975, 1977, 1978, 1980, and Talbot et al. 1978). Although there may be restrictions upon which species can successfully recruit to a specific habitat site (or ecological space), it is assumed that the species membership is essentially interchangeable within a guild (Williams 1983, 1986). This means that several different species may occupy the same habitat site, but it is a lottery as to which species will be successful at any given time. The Lottery Hypothesis relies, in part, in the knowledge that recruitment success is independent of the adult fecundity in the area. Adult composition, therefore,

and in contrast to the preceding Interspecific Competition and Niche Specialization model, is highly variable. Any disturbance to the system is mitigated by the stochastic outcome of this lottery independent of the current occupants (Fig. 1.2).

1.1.3 Recruitment-Limitation Hypothesis

The Recruitment-Limitation Hypothesis is the second of the three stochastic models. The Recruitment-Limitation Hypothesis suggests that species composition and populations densities on reefs are not determined by a "lottery" for available habitat sites (as in the above Lottery Hypothesis). Instead, species composition and population densities are determined by the availability of recruits settling after the pelagic stage (Victor 1983, 1986, Wellington & Victor 1988, Doherty & Williams 1988a,b, Jones 1990, Robertson et al. 1990, Sale et al. 1994). The key issue is that almost 100% mortality of fish occur during the oceanic plankton stage. In essence then, any larval recruit that makes it back to the reef habitat after its pelagic stage has a relatively good chance to settle. This means that the availability of recruits is low and stochastic both spatially and temporally. The organization of fish communities on coral reefs, therefore, remains highly variable because of the stochastic outcome of recruit availability independent of the current occupants (Fig. 1.3).

1.1.4 Predation Hypothesis

The Predation Hypothesis stresses *post-settlement* stochastic processes as dominant in organizing fish communities on coral reefs (as compared to *pre-settlement* stochastic processes as in the Lottery Hypothesis and the Recruitment Limitation models above). Specifically, the Predation Hypothesis suggests that non-selective piscivory on the reefs themselves is primarily responsible for the highly variable community density patterns (Jones 1991, Hixon 1991, Hixon & Menge 1991, Buchheim & Hixon 1992). High predation pressure from piscivorous reef fish (and anemones, cone shells, mantis shrimps, sea stars, sea snakes, and sea birds) on new recruits, juveniles, and adults results in such low species abundance that constraints imposed by resource limitation, or competition for habitat space, or availability of recruits, are negligible. Since most reef predators are non-selective, predation pressure structures a prey assemblage by altering the absolute and relative abundance of species, and thereby affecting the distributions and the local diversity of the prey. Assuming that species abundances are limited by recruitment initially, the result of such a high non-selective predation pressure is also a species assemblage that also appears highly stochastic both spatially and temporally (Fig. 1.4).

1.2 TOWARDS A MULTI-LEVEL MODEL OF COMMUNITY ORGANIZATION

Each of the four preceding models of community organization differs in that each stresses a different assembly process as responsible for affecting species membership and population densities. However, the four models are similar to each other in that they share

the same two implicit assumptions (i.e., *one* assembly process affects community organization, and all species respond to the assembly process within a *single* level of organization). Although these assumptions were never explicitly stated, I assume they must have been used for two reasons.

The first is that the experimental designs and statistical analyses associated with these models do not differentiate among members of the fish community. Out-liers, that are fish species that do not appear to fit within the experimental model, have been dropped from the species membership (e.g., transient species).

The second reason is that the concept of *multi-level* ecological systems has only recently been introduced to ecology, and therefore, was unavailable during the development of the four models (Allen & Starr 1982, Allen & Wyleto 1983, Eldredge & Salthe 1984, Mauer 1985, O'Neill et al. 1986, Kolasa 1989, Kotliar & Wiens 1990, Collins and Glenn 1991, Thorhallsdottir 1991, Bock & Ricklefs 1993, Sagova & Adams 1993, Wu & Loucks 1995).

The concept of multi-level ecological systems is that there are *multiple levels* of community organization within each system, and that for *each level* a single generic type of community response occurs. Further, species can only occur at one level at a time. This means that each level contains only a partial collection of the species membership, that is, the total species membership is found only when all levels are combined. This multi-level approach is parallel (at least conceptually) to a model of a complex wave pattern that can be decomposed into a series of simple harmonics—each with a specific amplitude and period.

The concept of multi-level organization is not foreign to the study of fish communities on coral reefs. A series of preliminary observations suggest that multiple levels and multiple assembly processes are, in fact, how fish communities are organized (Hanski 1982, Kaufman 1983, Williams 1985, Jones 1986, Sano et al. 1987, Wellington & Victor 1988, Kareiva 1990, Hixon 1991). However, these studies are limited to two-level models, or to select species only. To date, no study occurs that includes all species in the species membership and is observer independent as to the number of levels in the community organization (both of which I attempt to correct for in this thesis).

If fish communities on coral reefs are composed of multiple levels of organization, then it is possible that the high variation observed (in species membership and population densities) occurs from several assembly processes operating each on a different subset of species—as compared to a single stochastic process operating on all species at once. The purpose of the thesis, therefore, is to further our understanding of fish organization on coral reefs from a multi-level conceptualization of community organization. I aim to achieve this goal in two steps.

In Step 1, I determine if fish communities on coral reefs do indeed comprise of multiple levels of organization (Section 3). The criterion I use to assign species to their respective levels is derived from one of the tenets of Hierarchy Theory. The tenet states that system components (i.e., the species) can be placed into their respective levels according to the *magnitude of their relative variation* (Kolasa & Pickett 1989, O'Neill et al. 1989, Pickett et al. 1989, Allen & Hoekstra 1992). Specifically, system components with similar magnitudes of relative variation (to the criterion of interest) are associated

within the same level: system components with significantly different magnitudes of relative variation are placed at different levels. Furthermore, the order of the levels is such that lower levels contain system components with the greater magnitudes of relative variation, and higher levels contain system components with the smaller magnitudes of relative variation. The implicit assumption made is that *high variation is associated with organizing processes (i.e., assembly processes) that function or operate on small spatial and temporal scales, and low variation is associated with organizing processes that operate on larger spatio-temporal scales.*

On the assumption that fish organization is indeed a multi-level phenomenon, then I propose that one of three possible models (outlined below) describes the dynamics of the assembly processes involved. Step 2, therefore, aims to determine the model that most accurately describes the assembly processes involved that organize fish on coral reefs in a multi-level system (Sections 4 to 6). The three possible models include:

- multiple non-stochastic assembly processes acting simultaneously—albeit each at a different level or scale of the coral reef template, or

- a mixture of stochastic and non-stochastic processes operating as above, or

- multiple stochastic processes operating as above.

FIGURE 1.1 INTERSPECIFIC COMPETITION AND NICHE SPECIALIZATION

Species evolved specialized niche requirements to reduce competition for limited resources. Because of this and the assumed readily available local supply of recruits, the community can quickly restore itself to its prior structure following any local disturbance.

FIGURE 1.2 LOTTERY HYPOTHESIS

Species settle onto reefs according to the chance probability that a habitat site is available

at the time of recruit availability. If a specific recruit is not present at the time of habitat

availability, then another recruit from a different species may move in to occupy the site.
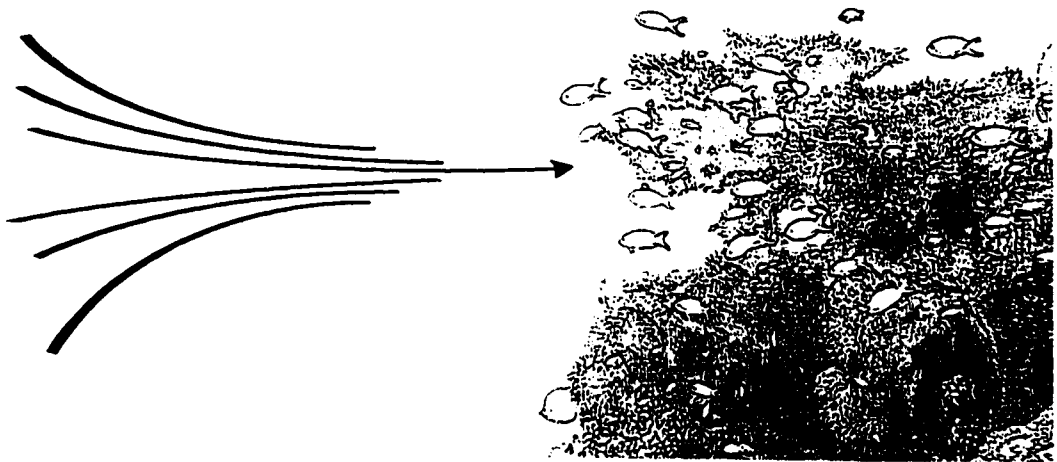
FIGURE 1.3 LIMITED RECRUITMENT

Species membership and population densities are dependent on the stochastic supply of recruits settling from the pelagic larval stage.
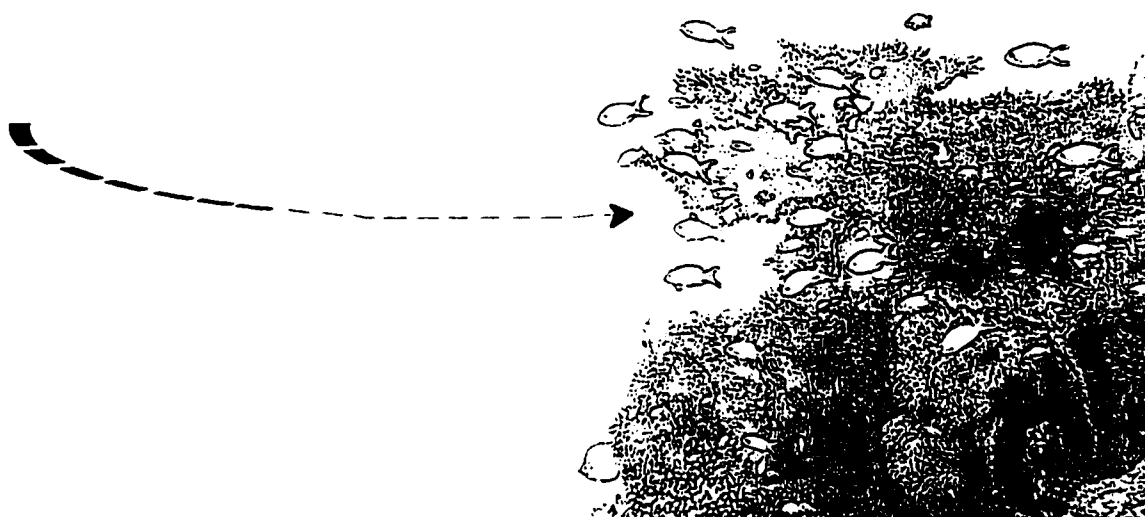
FIGURE 1.4 OPPORTUNISTIC PREDATION

The high variability of species membership and populations densities is not due to *pre-settlement* processes, but is due to *post-settlement* processes such as opportunistic predation. Specifically, species density patterns developed at the time of recruitment are significantly altered by continuous, non-selective predation.
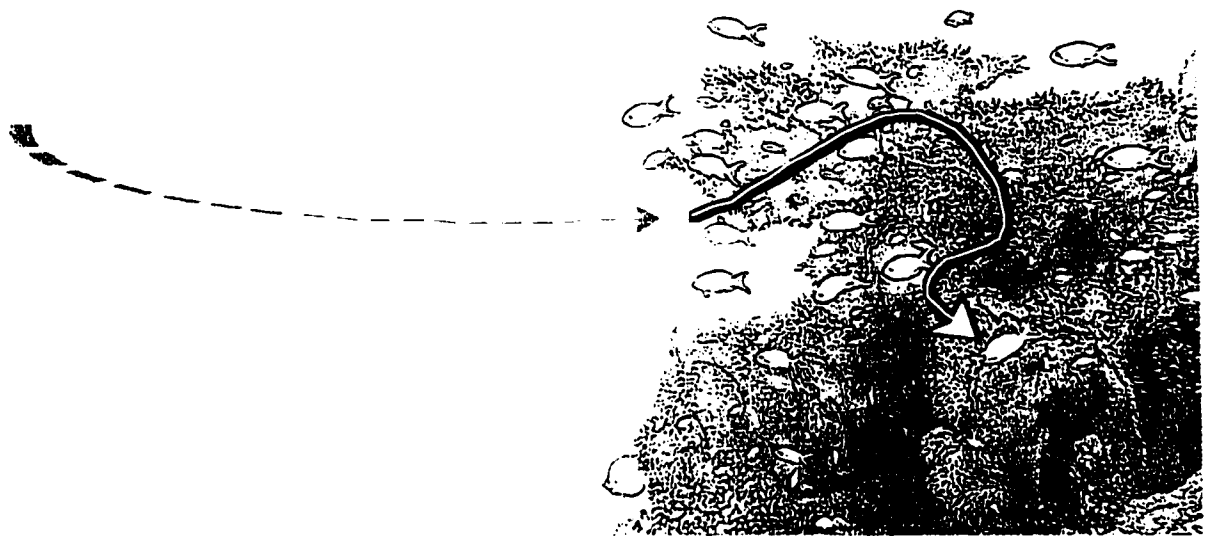
SECTION II

AMBIGUITY IN THE SAMPLING WINDOW: REEF FISH STABILITY REVISITED

2

Ambiguity in the Sampling window: Reef Fish Stability Revisited

2.1 RATIONALE AND OBJECTIVES

The focus of this thesis is to determine if the supposed stochastic determination of fish community structure on coral reefs can be better explained by a multi-level model of community organization as compared to a single-level model. However, field and analytical methods used in reef fish studies are inadequate to make such an assessment. Field methods, especially those developed for enumerating fish, are biased in numerous ways (cf. references within this Section). For example, studies that have focused at the scale of single patch reefs have assumed these fish assemblages to exist in relative isolation because they are surrounded by exposed habitat of sand and/or seagrass. Since some species are particularly adept at travelling though this exposed environment, fishes were generally categorized into one of two groups—transient and resident. In many studies of community organization, transient species were dropped from analyses. There are advantages to this approach because it helps standardize and simplify sampling protocols. Conversely, to include all species in the sampling protocol is problematic because:

- a positive correlation exists between the duration of sampling and species richness (the number of species present), and

• a positive correlation exists between the duration of sampling and species abundance (the number of individuals present).

The correlations mean that the longer an observer records fish on a particular site the greater the species richness (number of species) and species abundance (numbers of individuals) observed as fish enter and leave the site. Since an instantaneous count is impossible to achieve, the observer must spend time enumerating the fish. The question remains—how long this enumeration should last on a particular site? If the sampling protocol is designed such that transient species are not included in the analysis, then this problem is of lesser concern. However, for this thesis it is necessary to include all species in the sampling protocol, and therefore, necessary to confront the issue of sampling duration. The purpose of this Section is to resolve this problem.

2.2 TITLE PAGE

AMBIGUITY IN THE SAMPLING WINDOW: REEF FISH STABILITY REVISITED (A manuscript for Bull. Marine Science)

NIGEL D. WALTHO and JUREK KOLASA

Department of Biology, McMaster University, 1280 Main St. W.,

Hamilton Ontario, Canada, L8S 4K1

Tel. (905) 525 - 9140 Ext. 23100

Fax (905) 522 - 6066

2.3 ABSTRACT

The dichotomy that exists between coral reef-fish ecologists concerning assemblage stability (i.e., in terms of species membership and population densities) is well established. One view is that assemblages are stable structures due to deterministic assembly processes such as competition and niche specialization. A second view is that assemblages are highly variable as a result of stochastic assembly processes such as limited recruitment and opportunistic predation. However, independent of the assembly process (or processes) involved, it is reasonable to assume that differences in the methods used by the researchers may also contribute to this dichotomy. We propose, therefore, that one domain of sampling methodology—the sampling window (i.e., the duration of sampling one statistical replicate)—may have significant effects on the interpretation of reef-fish stability. We test this assumption by examining the frequency of site similarities as a function of sampling window for spatially isolated reef fish assemblages (N=12 sites). Our results show that the longer the duration of the sample window, the greater the implied stability of reef fish assemblages. This suggests that the dichotomy that exists between the two schools could be due, in part, to non-standardized sample windows. We therefore introduce a procedure to help remove the subjectivity in determining the sampling window for field studies, thus minimizing experimental biases. The procedure involves an initial pilot field-study.

2.4 INTRODUCTION

Processes that organize coral reef fish assemblages can be considered from two points of view. The first is that species have evolved precise habitat requirements to reduce competition for limited resources. Reduced competition prevents competitive exclusion and thereby encourages community stability. Reef fish assemblages, therefore, are considered ordered, deterministic, and relatively constant through time (Smith & Tyler 1972, 1975, Smith 1973,1978, , Gladfelter and Gladfelter 1978, Gladfelter et al. 1980, Anderson et al. 1981, Ogden and Ebersole 1981, Shulman et al. 1983, Shulman 1984, Eckert 1985, Walsh 1985). The second point of view suggests factors such as habitat availability, recruitment limitation, and predation and other small scale disturbances are commonplace. Through these small scale disturbances critical habitat space is made available. These new spaces are colonized during chance recruitment from the available larval pool. Since predation and successful recruitment varies unpredictably on both spatial and temporal scales, assemblage stability can not be achieved (Sale 1977, 1980a, 1980b, Russel et a. 1974, Sale and Dybdahl 1978, Williams 1980, Robertson et al. 1981, Doherty 1983, Victor 1986, Wellington and Victor 1985, Sale and Douglas 1984, Bohnsack 1989).

Some researchers have proposed that these two views represent endpoints of a continuum between deterministic and stochastic philosophies, and the correct explanation lies somewhere between the two (e.g., Brock et al. 1979, Clarke 1988). The attraction towards one end of the continuum versus the other depends on a number of criteria: (a) priori assumptions (Hixon and Beets 1989, Kareiva 1990), (b) spatial scale (Brock et al.

1979, Alevizon et al. 1985b, Hatcher et al. 1987, Brock and Norris 1989), (c) sampling

methodology (Sale and Sharp 1983, Thresher and Gunn 1986, Galzin 1987b), (d)

sampling frequency (Bohnsack 1983), (e) sampled species (Kimmel 1985), and (f)

taxonomic resolution (Galzin 1987b, Rahel 1990). One domain that has not been

evaluated (in terms of its relative significance to either deterministic or stochastic

processes) is how the sampling window (the duration required to sample one statistical

replicate) affects the composition and abundance of patch reef fish assemblages. Most

studies appear to consider this factor lightly (with exceptions of DeMartini and Roberts

1982, Fowler 1987, and Greene and Alevizon 1989). For example, in a series of articles

(N=36, published between 1976 and 1992: each addressing the structure or stability of

coral reef-fish assemblages), only one half of them (N=18) specify the sampling period

used. Further, only 5 of these articles explained criteria used to determine the length of

this period. In each case, the determining criterion was arbitrary-based. Sale and Douglas

(1981) clearly acknowledge this, "The time required to inspect the reef varies with water

clarity and with reef size. It is rarely less than 10 minutes or more than 40 minutes, but we

have no objective criteria for determining when the data collected are complete."

We suggest that subjective means (or conversely, the lack of any empirical

methods) currently used to define duration of the sampling window is an inherent

weakness that complicates interpretation of the results from one study to the next. This

weakness could influence how one perceives the distribution, and ultimately the stability

and organization of reef-fish assemblages. Consider, for example, patch sites either

spatially or temporally isolated. We argue that at such sites species composition and

species abundances become more similar with increased sampling window because of the higher proportions of transient herbivores observed. The inference made here is similarity of species structures among sites generate appearances of deterministic community structures (Sale and Guy 1992).

We test this hypothesis by determining the number of significant assemblage correlations between sites, as a function of sampling time. The null model we propose specifically states that the count of significant correlations remains constant. If our alternative hypothesis is correct, that is, the count of significant correlations is proportional to sampling window, then several questions arise. First, how does the relationship vary between sites—is it constant or highly variable? Second, are the effects specific to transient fish species relative to resident species (Sale and Douglas 1981, Brock 1992, Kareiva 1990)? Finally, how does one determine the appropriate sampling window for future studies? We explore these questions, and provide a possible solution to the latter most. The solution requires an initial pilot study followed by empirical interpretations.

2.5 MATERIALS AND METHODS

A portable frame, made with polyvinyl household tubing and polypropylene twine, was used to delineate a 9m^2 quadrat. The quadrat was placed on a continuous section of back-reef coral (approximate dimensions 50m X 20m) in Discovery Bay, Jamaica. A minimum of two hours was allowed following quadrat placement for fish habituation.

Censusing by SCUBA divers was then initiated subsequent to a further 15 minute "fish-diver" habituation. Species abundances were censused sequentially for 5, 10, 15, 20, and 30 minute long sampling windows. Each observer positioned themselves peripherally to the quadrat during this time. If the need arose to identify species from better angles, the observer would either lean into the quadrat or swim along the outside perimeters to a different location.

To the observers' best abilities, individual fish were counted once during each sampling window. We acknowledge that this can not be verified without a marking or removal program, or a priori knowledge of assemblage composition (e.g., Greene and Alevizon 1989). Each sampling window started anew, that is, none of the assemblage data was carried from one census to the next. This is in direct contrast to the "species-time" techniques employed by others (e.g., DeMartini and Roberts 1982, Kimmel 1985, Greene and Alevizon 1989).

We accept the view that fish species have a range of "affinities" to patch reefs (Kareiva 1990) and thus cannot be classified as only resident or transient. This is in contrast to many studies (e.g., Sale and Douglas 1981, Brock 1992) that choose to sample resident species only, having defined "resident" on some subjective criterion. Consequently, we adjusted our methods to record all fish individuals that swam within the quadrat boundaries during the census interval, irrespective of how long they remained.

The above protocol was applied to twelve sites. Each site was randomly chosen from the continuous section of the back-reef coral. Sites contained a minimum 75% coral

cover (dead and alive), the remainder being sand. Depth from the water surface to the highest reef node ranged from 3 to 6m.

We assume that no site comprises a species assemblage that is significantly less similar to any other site. Specifically, we assume that no site harbours an assemblage structure that could be viewed as a statistical out-lier. It is necessary to make this assumption so data from all 12 sites can be used for further statistical analyses. To test this assumption we use the Sign test (SYSTAT) to examine similarities between sites in the presence and absence of species (available species pool = 36 species, mean number of species per site = 14.5, standard deviation in number of species per site = 2.7). Our results show that each site is similar to at least 8 other sites. We therefore accept all 12 sites to test our null hypothesis that there is no relation between the count of assemblage similarities and the sampling window duration.

2.6 RESULTS

We test our null hypothesis that there is no relationship between the count of assemblage similarities and the sampling window duration. From loglinear regression, we find that the relationship is positive and highly significant (Fig. 2.1., $r^2 = 0.999$, P < 0.001, SYSTAT). This relationship suggests that under theoretical conditions (i.e., the relationship holds when extrapolated to the maximum number of correlations), all sites from this study will be significantly correlated with each other when the sampling window is 58 minutes.

We further examine (all tests done in SYSTAT) assemblage trends in response to sampling window at two levels of resolution; (a) community (site richness and total site abundance), and (b) population (species abundances). At the resolution of the community, we find site richness increases as a function of sampling window (Table 2.1., column "Mean Site Richness"), though the rate of increase depends on site location (Fig. 2.2.). Total site abundances show a similar trend.

At the population resolution, species abundances increase with sampling window. The rate of increase is also site-dependent. However, the "species abundances—sampling window period" relationship is not a general trend for all species. The trend is significant for only 19 species (Table 2.2.). Cluster analysis (single linkage) for these 19 species versus the remaining 17 failed to differentiate between resident and transient species (Sale and Douglas 1981, Brock 1992).

2.7 DISCUSSION AND CONCLUSIONS

The finding that site similarity increases with lengthening of sampling time is relevant to the perception of spatial patterns in fish community composition, structure, and stability. Using our data as an example, field studies conducted with 5 minute sample windows may lead to a conclusion that stochastic processes are most likely responsible for structuring the community. Conversely, field studies sampling with a 30 minute window will likely fail to support or refute stochastic processes as a predominant factor. Extrapolation of the number of significant correlations and sampling window to the

theoretical limit (N=66 correlations) is obtained when a window width of 58 minutes is reached. At this point the most likely conclusion would be that processes structuring reef-fish assemblages are deterministic. We therefore suggest that our perception of reef-fish assemblage dynamics is, amongst other factors (e.g., Andrew and Mapstone 1987), a function of the sampling window used for recording fish presence and abundances.

Since we use all fish species observed these results may seem intuitive. For example, if we were to assume that an observer quickly records all available resident individuals, then any further increase in sampling window would inflate only the abundances of transient species. Since transient species represent a small number of overall fish species relative to resident species (Sale and Douglas 1981), the transients will add to each of the sites in increasingly greater proportions (relative to the resident species). With each incremental increase in sampling window it can only be expected that similarity between sites will increase.

Our data do not support this premise. According to the traditional definitions of "resident" and "transient" species, just as many species from both species types do and do not show significant relationships between their species abundances and sampling window (Table 2.2.). For the resident species this contradicts the expected result (Sale and Douglas 1981). We suggest that for our individual "resident" species, the relationships between abundance and sampling window that occur are due, at least in part, to habitat complexity. We hypothesize that the more structurally complex the habitat is (a) the greater the chance that not all resident individuals will be observed within short sample

windows, and (b) the higher the risk of individual duplications (triplication?) with longer sample windows.

The important issue is to remove the element of ambiguity (i.e., the guesswork when a site observation is complete) from field studies. Sampling windows must be determined empirically, not subjectively, to (a) maximize the precision and accuracy of field methods, and (b) enable informative comparisons between studies (Kimmel 1985, Thresher and Gunn 1986, McCormick and Choat 1987, Fowler 1987). Since the actual assemblage composition and structure are not known, estimating the reliability of sampling protocol necessitates a pilot study. We suggest that the observer selects a sample of quadrat sites typical of the habitat structure to be expected for the main study. For each quadrat site, record the assemblage structure sequentially along a series of sample window widths. Plot the total abundance (or richness) from each sample quadrat as a function of the sample window. The point along the sample window axis where the variance between sample quadrats is the least identifies the sampling window for the main study.

The empirically derived sampling window is specific to the skill level of the observer, habitat complexity of the field site, and overall species richness and abundances in the community. Each of these parameters introduces an element of variance that collectively can be standardized. For example, consider the skill level of an observer. No two observers record assemblage structures accurately and precisely in exactly the same manner. Differences may be due to relative training (Sale and Sharp 1983, Thresher and Gunn 1986), and one's own search and recognition patterns. The pilot study entitles each observer to obtain their own sampling window. Variance in recorded assemblage

structure would therefore be minimized. Further, the empirically derived sample window is characteristic to both habitat complexity and fish species richness of the location. Both increased habitat complexity and higher species richness impart longer sampling windows. An empirically derived sampling window as described has the advantage that precision of community structures obtained from either structurally diverse habitats, or different species assemblages, is standardized.

The disadvantages of the pilot study are purely financial. Since an observer's skills change with time, and it is presumptuous to assume all field locations have the same degree of habitat complexity and community richness, it is therefore necessary to repeat the pilot study for all field locations during an individual's career. The financial costs can not be estimated. The apparent trade-off is between greater precision versus costs incurred. The more sample pilot quadrats used to derive empirically a sample window, the more precise the recorded assemblage structure – but also the more costly the study.

2.8 ACKNOWLEDGMENTS

2.9 REFERENCES CITED

Ambrose R.F., and S.L. Swarbrick (1989) Comparison of fish assemblages on artificial and natural reefs off the coast of southern California.

Andrew N.L., and B.D. Mapstone (1987) Sampling and the description of spatial pattern in Marine Ecology. Oceanogr. Mar. Biol. Ann. Rev. 25:39-90.

Bohnsack J.A. (1983) Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs 1:223-228.

Bohnsack J.A. (1989) Are high densities of fish at artificial reefs the result of habitat limitation or behavioral preferences? Bull. Mar. Sci. 44(2):631-645.

Brock R.E. (1982) A critique of the visual census methods for assessing coral reef fish populations. Bull. Mar. Sci. 32(1):269-276.

Brock R.E., and J.E. Norris (1989) An analysis of the efficacy of four artificial reef designs in tropical waters. Bull. Mar. Sci. 44(2):934-941.

Brock R.E., C. Lewis, and R.C. Wass (1979) Stability and structure of a fish community on a coral patch reef in Hawaii. Mar. Biol. 54:281-292.

Clarke R.D. (1988) Chance and order in determining fish-species composition on small coral patches. J. Exp. Mar. Biol. Ecol. 115:197-212.

Fowler A.J. (1987) The development of sampling strategies for population studies of coral reef fishes. A case study. Coral Reefs 6:49-58.

Galzin R. (1987) Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. Mar. Ecol. Prog. Ser. 41:129-136.

Galzin R. (1987) Structure of fish communities of French Polynesian coral reefs. II. Temporal scales. Mar. Ecol. Prog. Ser. 41:137-145.

Gladfelter W.B., J. Ogden, and E.H. Gladfelter (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61(5):1156-1168.

Godwin J.R., and R.K. Kosaki (1989) Reef fish assemblages on submerged lava flows of three different ages.

Goldman B., and F.H. Talbot (1976) Aspects of the ecology of coral reef fishes. In: Jones OA, Endean R (eds) Biology and Geology of Coral Reefs, VIII, Biology 2. Academic Press N.Y. pp. 125-154.

Greene L.E., and W.S. Alevizon (1989) Comparative accuracies of visual assessment methods for coral reef fishes. Bull. Mar. Sci. 44(2):899-912.

Hatcher B.G., J. Imberger, and S.V. Smith (1987) Scaling analysis of coral reef systems: an approach to problems of scale. Coral Reefs 5:171-181.

Hixon M.A., and J.P. Beets (1989)   Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. 44(2):666-680.

Kaufman L.S. (1983) Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica.

Kimmel J.J. (1985) A new species-time method for visual assessment of fishes and its comparison with well established methods. Env. Biol. Fishes 12(1):23-32.

Maurer B.A. (1990) The relationship between distribution and abundance in a patchy environment. Oikos 58:181-189.

McCormick M.I., and J.H. Choat (1987) Estimating total abundance of a large temperate - reef fish using visual strip-transects. Mar. Biol. 96:469-478.

Ogden J.C., and J.E. Ebersole (1981) Scale and community structure of coral reef fishes: a long term study of a large artificial reef. Mar. Ecol. Prog. Ser. 4:97-103.

Rahel F.J. (1990) The hierarchical nature of community persistence: A problem of scale. American Naturalist 136:328-344.

Sale P.F. (1977) Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337-359.

Sale P.F. (1980) The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18:367-421.

Sale P.F., and B.J. Sharp (1983) Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37-42.

Sale P.F., and J.A. Guy (1992) Persistence of community structure: what happens when you change taxonomic scale? Coral Reefs 11:147-154.

Sale P.F., and W.A. Douglas (1981) Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. Env. Biol. Fishes. 6:333-339.

Sale P.F., and W.A. Douglas (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecology 65(2):409-422.

Sale P.F., and W.J. Steel (1986) Random placement and the distribution of fishes among coral patch reefs. Mar. Ecol. Prog. Ser. 28:165-174.

Sale P.F., and W.J. Steel (1989) Temporal variability in patterns of association among fish species on coral patch reefs. Mar. Ecol. Prog. Ser. 51:35-47.

Sale P.F., P.J. Doherty, G.J. Eckert, W.A. Douglas, and D.J. Ferrell (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. Oecologia (Berlin) 64:191-198.

Smith E.P., K.W. Pontasch, and J. Cairns (1989) Community similarity and the analysis of multispecies environmental data: a unified statistical approach. Wat. Res. 24(4): 507-514.

Smith G.B. (1979) Relationship of eastern Gulf of Mexico reef fish communities to the species equilibrium theory of insular biogeography. J. Biogeog. 6:49-61.

Thresher R.E., and J.S. Gunn (1986) Comparative analysis of visual census techniques for highly mobile, reef associated piscivores (Carangidae). Env. Biol. Fishes 17(2):93-116.

Victor B.C. (1984) Coral reef fish larvae: patch size estimation and mixing in the plankton. Limnol. Oceanogr. 29:1116-1119.

Walsh W.J. (1983) Stability of a coral reef fish community following a catastrophic storm. Coral Reefs 2:49-63.

.

TABLE 2.1. MEAN SITE RICHNESS AS A FUNCTION OF SAMPLING WINDOW

Site richness as a function of sampling window—standard errors are provided (in loglinear regression mean site richness increases directly with sample window: $r^2 = 0.979$, $P < 0.001$, DF = 4, SYSTAT).

Sampling Window (min.)	Mean Site Richness (± SE)
5	8.25 ± 0.13
10	10.00 ± 0.16
15	11.58 ± 0.14
20	12.33 ± 0.17
30	14.5 ± 0.21

TABLE 2.2. SPECIES ABUNDANCE TRENDS AS A FUNCTION OF SAMPLING WINDOW

Species abundances as a function "Sample Window" and "Site" where;

Log(Species abundance) = Log(sample window) + site

and n = 60 for each species (i.e., 5 sample windows * 12 sites, ANCOVA, DF = 12, SYSTAT). Bullets "•" indicate those species that are significant at P < 0.05.

Family	Species	Common name	r^2	P sample window		P site	
Acanthuridae	Acanthurus bahianus	Surgeon	0.364	0.005	•	0.110	
	A. coeruleus	Blue Tang	0.527	0.006	•	0.001	•
Apogonidae	Apogon binotatus	Barred Cardinal	0.443	0.001	•	0.047	•
Aulostomidae	Aulostomus maculatus	Trumpet	0.417	0.088		0.007	•
Chaetodontidae	Chaetodon capistratus	Foureye Butterfly	0.296	0.101		0.148	
Holocentridae	Holocentrus adscensionis	Squirrel	0.827	0.001	•	0.001	•
	H. rufus	Longspine Squirrel	0.510	0.004	•	0.001	•
	Myripristis jacobus	Black Squirrel	0.231	0.104		0.431	
	Neoniphon marianus	Longjaw Squirrel	0.380	0.779		0.011	•
	Sargocentron coruscus	Reef Squirrel	0.568	0.003	•	0.001	•
	S. vexillarius	Dusky Squirrel	0.274	0.640		0.131	
Labridae	Bodianus rufus	Spanish Hogfish	0.399	0.221		0.009	•
	Thalassoma bifasciatum	Bluehead Wrasse	0.622	0.007	•	0.001	•
Mullidae	Pseudupeneus maculatus	Spotted Goatfish	0.877	0.062		0.001	•
Pomadasyidae	H. carbonarium	Caesar Grunt	0.855	0.161		0.001	•
	H. flavolineatum	French Grunt	0.653	0.974		0.001	•
	H. striatum	Striped Grunt	0.231	0.104		0.431	
Promacentridae	Stegastes diencaeus	Longfin Damselfish	0.321	0.215		0.067	
	S. fuscus	Dusky Damselfish	0.755	0.001	•	0.001	•
	S. leucostictus	Beaugregory Damselfish	0.759	0.001	•	0.001	•

Family	Species	Common Name					
	S. planifrons	Threespot Damselfish	0.788	0.001	•	0.001	•
	S. variabilis	Cocoa Damselfish	0.363	0.418		0.020	•
	Scarus iserti	Striped Parrot	0.569	0.007	•	0.001	•
Scaridae	Sparisoma taeniopterus	Princess Parrot	0.58	0.001	•	0.001	•
	S. aurofrenatum	Redband Parrot	0.601	0.009	•	0.001	•
	S. chrysopterum	Redtail Parrot	0.231	0.104		0.431	
	S. viride	Stoplight Parrot	0.617	0.001	•	0.001	•
Serranidae	Hypoplectrus aberrans	Yellowbelly Hamlet	0.9	0.014	•	0.001	•
	H. chlorurus	Yellowtail Hamlet	0.303	0.562		0.076	
	H. guttavarius	Shy Hamlet	0.417	0.088		0.007	•
	H. indigo	Indigo Hamlet	0.537	0.010	•	0.001	•
	H. nigricans	Black Hamlet	0.625	0.021	•	0.001	•
	H. puella	Barred Hamlet	0.719	0.011	•	0.001	•
	H. unicolor	Butter Hamlet	0.716	0.325		0.001	•
	Hypoplectrus sp.	Masked Hamlet	0.602	0.107		0.001	•
	Canthigaster rostrata	Sharpnose Puffer	0.423	0.085		0.006	•

FIGURE 2.1. PEARSON CORRELATIONS

Count of significant Pearson site correlations (Bonferroni P < 0.05) as a function of sampling window (loglinear regression r^2 = 0.999, P < 0.001, DF = 4, SYSTAT). Pearson correlations are generated from species abundance data.
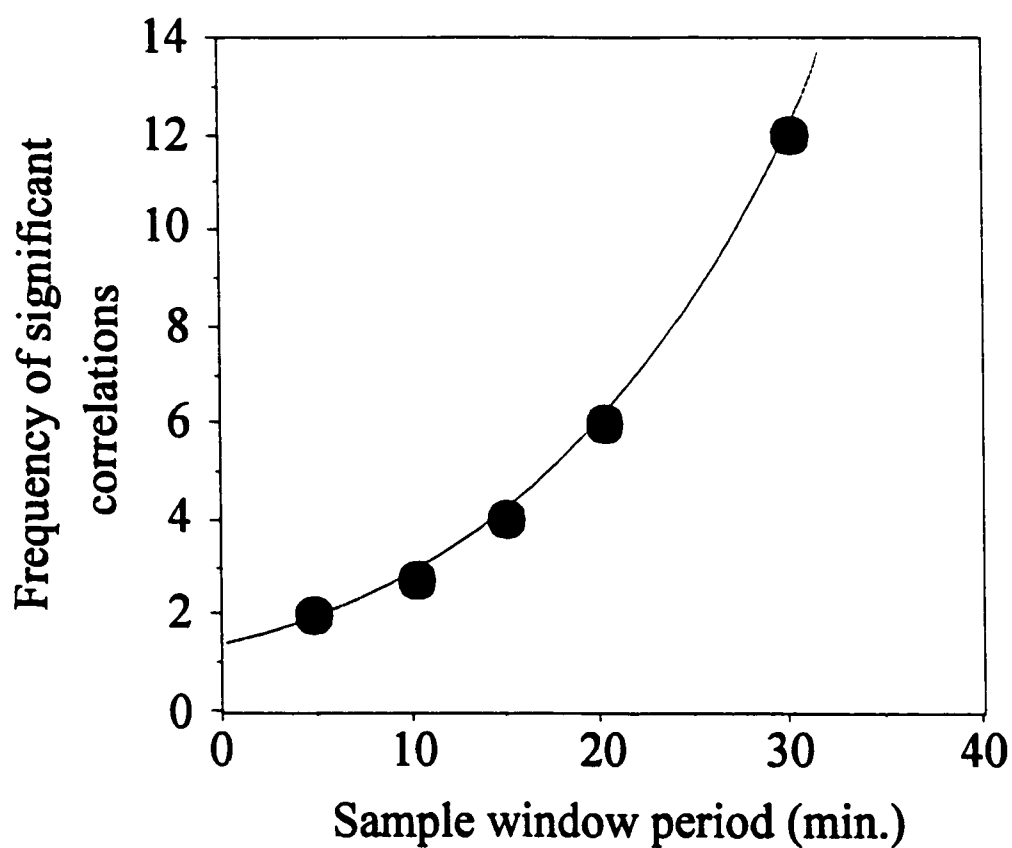
FIGURE 2.2. SITE RICHNESS

Site richness as a function of sampling window (curve-linear regression, TableCurve 2D). Nine of these regressions are significant at $P < 0.05$ (mean $r^2 = 0.906$, standard deviation of $r^2 = 0.041$). In log transformed ANCOVA, that is;

Log(Richness) = Log(sample window) + site

both "sample window" (DF = 1) and "site" (DF = 11) are significant at $P < 0.001$ (SYSTAT).
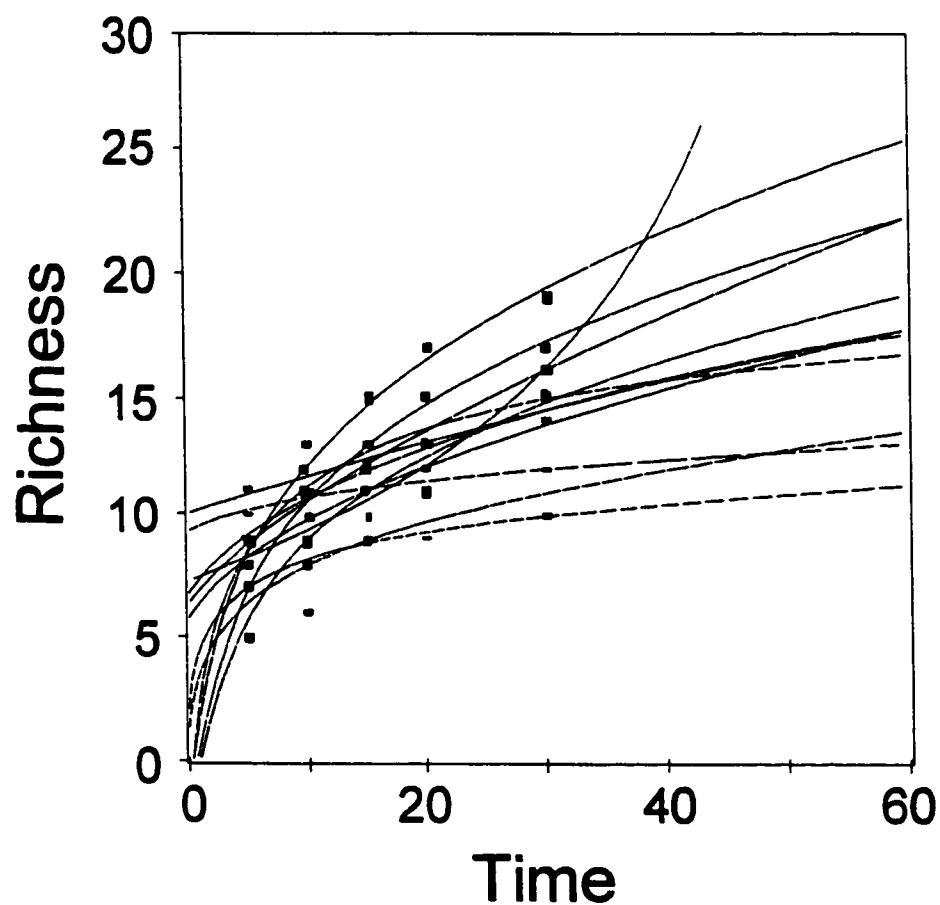
SECTION III

ORGANIZATION OF INSTABILITIES IN MULTI-SPECIES SYSTEMS,
A TEST OF HIERARCHY THEORY

3

Organization of instabilities in multi-species systems, a test of hierarchy theory

3.1 RATIONALE AND OBJECTIVES

The goal of this thesis is to determine if the organization of fish on coral reefs (i.e., how species and individuals arrange themselves in space and time) can be better explained by a mixture of processes functioning at different levels of the habitat template, as compared to a single stochastic process operating unequivocally throughout. The purpose of this Section in particular, therefore, is to show that fish communities on coral reefs can indeed be organized into multi-level structures. I test this proposition by applying one of the tenets of Hierarchy Theory (Kolasa and Pickett 1989, Pickett et al. 1989, Allen & Hoekstra 1992) to data collected in the back reef of Discovery Bay, Jamaica. Specifically, species can be organized into their respective levels according to the magnitude of their *relative variation* along one or a combination of several ecological dimensions. Species that are shown to have relatively high variation are placed in the lower levels of the community structure. These species are suspected to be constrained by assembly processes that function or operate on small spatial and temporal scales. Species that are shown to have relatively low variation are placed into the higher levels of the community organization, constrained by assembly processes that function or operate on larger spatio-

temporal scales. The implicit assumption made is that high variation is associated with organizing processes that function or operate on small spatial and temporal scales, and low variation is associated with organizing processes that operate on larger spatio-temporal scales.

3.2 LETTER OF CONSENT

Letter of consent from the National Academy of Sciences, USA, granting permission to include the published journal article (Waltho and Kolasa 1994) as part of the present thesis. It should be made clear though, that several areas have been slightly modified to reflect the standards set by the Ph.D. requirements.

McMASTER UNIVERSITY
Department of Biology
1280 Main Street West,
Hamilton, Ontario, Canada L8S 4K1
Telephone: (905) 525-9140
Fax: (905) 522-6066

JUL 0 9 1997

'OCELL-···⊔⊔S OFS1'
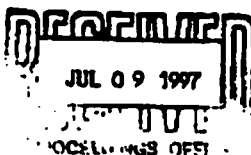
May 20, 1997

Managing Editor
PNAS
2101 Constitution Ave. NW
Washington, DC 20418

Dear Diane Sullenberger

I am completing a Ph.D. thesis at McMaster University (Ontario, Canada) entitled "The Appearancy of Stochastic Control in Coral Reef Fish Communities: a Hierarchical Approach to System Organization". I would like your permission to reprint the following journal article in my thesis.

Waltho N.D., and J. Kolasa (1994) Organization of instabilities in multispecies systems, a test of hierarchy theory. Proc Natl Acad Sci USA 91:1682-1685.

Please note that I am the senior author of this work.

I am also requesting that you grant an irrevocable, non-exclusive licence to McMaster University and the National Library of Canada to reproduce this material as a part of the thesis. Proper acknowledgment of your copyright of the reprinted material will be given in the thesis.

If these arrangements meet with your approval, please sign where indicated below and return this letter to me in the enclosed envelope. Thank you very much.

Sincerely,

Nigel Waltho
(Ph.D. candidate)

email: nwaltho@yorku.ca

....

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE

National Academy of Sciences, USA
Washington DC
20418 USA

Authorized by: _____

Title: _____

Date: _____

Signature: _____

Permission granted. Please cite full journal reference and "Copyright (year) National Academy of Sciences, U.S.A."

Diane M. Sullenberger, Managing Editor
848 for bHS 7/7/97

3.3 TITLE PAGE

ORGANIZATION OF INSTABILITIES IN MULTISPECIES SYSTEMS, A TEST OF HIERARCHY THEORY. PROC. NAT. ACAD. SCI. 91:1682-1685 (1994)

NIGEL D. WALTHO and JUREK KOLASA

Department of Biology, McMaster University, 1280 Main St. W.,

Hamilton Ontario, Canada, L8S 4K1

Tel. (905) 525 - 9140 Ext. 23100

Fax (905) 522 - 6066

3.4 ABSTRACT

The hierarchy theory predicts that system components functioning at lower levels of hierarchy operate or change at higher rates than the components at the level(s) above. If this prediction is correct, then interpretation of stability in complex ecological systems may be in need of revision. We test the prediction using a model of hierarchical structure of habitat and a coral reef fish community. We found that the variability of ecological range and abundance increases exponentially from habitat generalists (high in hierarchy) to specialists (low in hierarchy), as postulated by the hierarchy theory. Our result suggests that community stability is a composite property and should be evaluated by considering the hierarchical structure of that community.

3.5 INTRODUCTION

Although the hierarchy theory, HT, provides a framework for examination of (a) macropatterns and (b) general structure and mechanisms organizing multispecies assemblages (1-5), almost no empirical tests of the theory are available (6-8). Structure and organization of such systems are intricately linked to the idea of stability. Stability of multispecies communities has been attributed to factors such as environmental constancy, habitat heterogeneity, productivity or food web attributes. This has become one of the most discussed issues in theoretical and applied ecology (9). Some have recently suggested that whether communities are stable or not is a matter of spatial or temporal scale at which data are collected (10) or aggregated (11).

If communities are organized hierarchically as many have recently suggested (3,10-12), then we may expect species to respond to the environmental template in accordance with the constraints due to their position in the hierarchy. The measures and interpretation of stability could be further affected depending on the specific behavior of individual levels. Thus, understanding regularities in this complex picture would be of considerable help to conceptualization and measurement of community stability. While the concept of stability itself is rich and many different measures of stability have been developed (e.g., 13), we use one of these measures as example only. We measure stability as constancy in the numbers of individuals (e.g., 14).

HT postulates one important regularity in the form of prediction. The prediction states that components of an ecological entity existing at lower hierarchical levels operate at higher frequencies or change at higher rates than components at hierarchical levels above them (15-16, Waltho, N. & Kolasa, J. 1992 - presented at the 77th Annual Meeting of the Ecological Society of America). Our goal is to test this prediction. We conduct the test by applying the Habitat-Based Model of community structure, HBM (2), to the fish assemblages associated with coral reef patches. This model is based on the following assumptions reflecting the habitat structure and species properties: (a) habitat is a nested hierarchy of multidimensional patches, (b) patches become smaller and more fragmented with increased resolution of habitat grain, i.e., when one moves down the hierarchy, (c) regionally available species display a broad range of specializations relative to this habitat structure, and (d) species from that pool are sorted to various patches of the habitat according to their abiotic requirements, competitiveness, predation pressure, available

resources, and facilitating interactions. All these variables are dimensions of the model. In practice the model appears as a nested mosaic of microhabitats, primarily because most variables, even such as patterns of variation in time, can be represented in space. Distribution of species in the mosaic provides indirect means of assessing their performance in the multidimensional space without actually analyzing individual dimensions of that space. Like any general model, HBM is weaker at addressing specific mechanisms but should be more useful for analyzing aggregated patterns. Expected abundance of species is calculated as the function of ecological range and the size of habitat occupied. The general formula used in an earlier paper has the form (modified from (2)):

$$N_i = F \left(\frac{ER_i}{ER_{max}} \right)^2 \qquad \text{(Equation 1)}$$

where N_i is the abundance of species i, F is a site or taxon specific coefficient or function (if known and necessary), ER_i is the range of species i, and ER_{max} is the maximum range available to species in the community in question.

Thus a species occupying large and less isolated patches should have higher mean density than a species occupying small and more isolated microhabitats. This approach has been taken by Hanski (17) to one level of habitat mosaic and it predicts a bimodal distribution of abundances (18). HBM addresses several levels of habitat mosaic and predicts polymodal distribution of abundances. The ecological range can be estimated in a variety of ways depending on the available data. Ideally, all relevant ecological dimensions should be quantified to obtain the niche volume which could then be used in the model as

a measure of ecological range, either in its entirety (e.g., 19) or by choosing the most limiting dimension only. More likely, because of the data limitations, the range will be estimated as a portion of a gradient over which a species is present. We take this latter approach on the basis that a species found on a greater number of patches and/or a larger mean patch size is exposed to a broader gradient of microhabitat conditions and biotic interactions (e.g., larger patches tend to have more fish, coral, algal and invertebrate species; 20). We accept this approach because it captures well the general relationship of species to their habitat (see below). Earlier tests show that the model correctly and uniquely predicts existence of several discontinuities in the ecological ranges of species (2, 18, 21). These discontinuities lead to an emergence of clusters of species with similarly scaled ecological ranges. In consistency with HT such scaled clusters of ranges are indicative of and interpreted as hierarchical levels of organization. They have been experimentally shown in a stream setting to reflect the nested structure of habitat mosaic (2). While the identification of levels is indirect and relies on distributional patterns (2,3) and there are logical limits to their independent specification (22), such identification makes the test possible. As quantitative data on frequency or rate of change may be difficult to obtain, we use a measure of variability instead. We first established that hypothetical populations changing at lower rates (or with longer periods), when sampled at relatively small temporal scales, reveal less variation than populations changing more quickly (see Appendix 3.1 for details). Furthermore, the simulation indicates that the relationship between frequency of change and estimates of variation is linear (in preparation). The test is specifically defined then as demonstrating that, on average,

species assigneable to lower hierarchical levels (=smaller scale of habitat use), i.e., species with narrow ecological ranges, show greater variability than ecologically broad species that 'use' hierarchical levels (see Fig. 3.1 for more explanation). The null model (Fig. 3.1B) states that the mean relative variability of species descriptors, abundance and ecological range in this test, does not differ among species classified at different hierarchical levels.

3.6 DATA AND ANALYSIS

We used data on the composition and abundance of 52 fish species associated with coral back reef patches in Discovery Bay, Jamaica, at depths of 3 to 10 m. Data were collected over two winter seasons (1990: 35 patches, 876 individuals; 1991: 40 patches, 1380 individuals) from the same area. Different numbers of fish in each year are due to the model standardization. The standardization requires that the sampled ecological range is greater than that of the most broadly distributed species. Annual changes in regional density may thus result in different sample sizes. Each patch has been censused and its diversity and abundance recorded. We report details of the field work elsewhere (23). For the purpose of this study, we equate the ecological range of species with the size of the habitat used by a species. The habitat size includes two components: the number of separate patches and the size of these patches.

First, we established that the community structure is hierarchical (multi-scaled) with respect to habitat use and reveals discontinuities in the pattern of ecological ranges (Fig.

3.2) as predicted by HBM (2). Individual ecological ranges used in the cluster identification (Fig. 3.2) were obtained by including the number of patches and the sizes of patches, and modified by fitting constants. The constants were fitted to improve the power of ecological range in predicting species abundances. Second, we found that the community conforms with other expectations of HBM, i.e., it shows a strong positive correlation between species ecological range and abundance (Fig. 3.3) and that ecological ranges are nested (Cochran's $Q = 288$, communiqué Collins). For this test we used an equation without the fitted constants (Fig. 3.3). While this last finding is not new (24), it affirms the adequacy of the data set and of the model for the test. Finally, we examined the variation within clusters by grouping fish species of similar ecological ranges. The abundance and range values of the clusters are represented on 0-1 scales in Fig. 3.4. For each fish species we calculated the absolute change of abundance and range values from one year to another. Subsequently, we made the within cluster means of these differences relative to the mean cluster abundance and range, respectively, by dividing them by the respective cluster mean. We plotted this relative variation against the mean ecological range of fish comprised in the cluster. This procedure provided an indirect means for depicting variability of four individual hierarchical levels detected through the cluster analysis (Fig. 3.4).

We also created a second null model to assess the effect of stochastic variation on the results. Such variation alone might produce the observed patterns because the same observational error will result in greater relative variation among rare than common species. The model assumed random variation of fish abundance with 50% turnover rate

and 70% increase in total abundance in year 2 (=actual change from year 1 to 2). The curves representing the simulated and observed cluster variability (Fig. 3.3A) differ in slopes and intersects, when log transformed, ($p<0.001$). This indicates that stochasticity of considerable magnitude cannot explain the observed differences in variability between habitat generalists and specialists. The shape of the simulated curve indicates further that declining variation in clusters containing ecologically broad species is not an artifact of the division by increasingly larger means. Variation in ecological range behaved similarly to that of abundance (Fig. 3.4B) suggesting that actual ecological range is not fixed by individual species requirements but is co-defined by the community condition. Turnover rates of 0% and 100% show no significant difference to the 50% rate plotted. Rates higher than 100% are unrealistic for the species censused because such rates would imply that individuals older then 1 year are all replaced by similar individuals within 12 months.

3.7 DISCUSSION

Possible sources of error include statistical artifacts and the effects of heterogeneity. Small standard errors reduce the possibility that the link between the mean and variance (power law) caused the pattern (cf. 25). Indeed, the mean abundance of narrow species was much smaller than that of broad habitat users but the number of habitat specialists was much greater than the number of generalists (2 in cluster representing the highest level of hierarchy). Furthermore, as largely the same patches were sampled in both years, we rule out the effect of spatial heterogeneity as an alternative explanation.

Our results are not isolated. Moths, aphids, and bracken insects reveal the same general pattern (data in Gaston and Lawton (26)). These authors analyzed absolute variation and concluded that habitat specialists vary less than generalists. Comparing the variation among absolute abundances of habitat generalists and specialists cannot address the question of stability for two reasons. It ignores limits imposed by the habitat grain: A habitat specialist that uses a fraction of the habitat cannot change its ecological range as much as a generalist that uses most of it. Second, different initial densities and density means define how much species operating at different levels of hierarchy may change in abundance.

Our results also suggest that the question of community persistence cannot be resolved by simple field tests or adjustments of scale, whether spatial, temporal, or taxonomic, as recently attempted (27) because communities are organized hierarchically. Different levels in this hierarchy may display different degrees of stability, as measured by the variation in abundance and spatial distribution in this case. We believe that similar regularities will be discovered at the population and ecosystem levels as well.

3.8 REFERENCES CITED

1. Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: perspectives for ecological complexity* (The University of Chicago Press, Chicago), p. 1-310.

2. Kolasa, J. (1989) *Ecology* 70, 36-47.

3. Patterson, B.D. & Brown, J.H. (1991) *J. Biogeogr.* 18, 395-402.

4. Steele, J.H. (1989) in *Perspectives in ecological theory*, eds. Roughgarden, J., May, R.M. & Levin, S.A. (Princeton University Press, Princeton, New Jersey), p. 177-180.

5. Wiens, J.A. (1989) *Funct. Ecol.* 3, 385-397.

6. O'Neill, R.V. (1989) in *Perspectives in ecological theory*, eds. Roughgarden, J., May, R.M. & Levin, S.A. (Princeton University Press, Princeton, New Jersey), p. 140-156.

7. O'Neill, R.V., Johnson, A.R. & King, A.W. (1989) *Landsc. Ecol.* 3, 193-205.

8. Ricklefs, R.E. (1987) *Science* 236, 206-207.

9. May, R.M. (1973) *Stability and complexity in model ecosystems* (Princeton University Press, Princeton, N.J.), p. 1-235.

10. Allen, T.F.H. & Wileyto, E.P. (1983) *J. theor. Biol.* 101, 529-540.

11. Rahel, F.J. (1990) *Am. Nat.* 136, 328-344.

12. Maurer, B.A. (1985) *Ecol. Monogr.* 55, 295-312.

13. Law, R. and Morton, R.D. (1993) *Ecology* 74, 1347-1361.

14. Connell, J.H. and Sousa, W.P. (1989) *Am. Nat.* 121, 789-824, .

15. Simon, H.A. (1962) *Proc. Am. Phil. Soc.* 106, 467-482.

16. Kolasa, J. & Pickett, S.T.A. (1989) *Proc. Nat. Acad. Sci. USA* 86, 8837-8841.

17. Hanski, I. (1982) *Oikos* 38, 210-221.

18. Collins, S.L. & Glenn, S.M. (1990) *Am. Nat.* 135, 633-648.

19. Burgman, M.A. (1989) *Am. Nat.* 133, 228-239.

20. Risk, M. (1972) *Atoll Res. Bull.* 153, 1-6.

21. Ardisson, P.-L., Bourget, E. & Legendre, P. (1990) *Can. J. Fish. Aquat. Sci.* 47, 1364-1377.

22. Allen, T.F.H. & Hoekstra, T.W. 1992. *Toward a unified ecology* (Columbia University Press, New York), p. 1-384.

23. Waltho, N. & Kolasa, J. (1996) *Coral Reefs* (submitted).

24. Brown, J.H. and Maurer, B.A. (1989) *Science* 243, 1145-1150,

25. Levin, S.A. (1991) in *Ecosystem experiments*, eds. Mooney, H.A. Medina, E. Schindler, D.W. Schultze, E.-D. & Walker, B.H. (J. Wiley, Chichester), p. 215-226.

26. Gaston, K.J. & Lawton, J.H. (1988) *Nature* 331, 709-712.

27. Sale, P.F. & J.A. Guy (1992) *Coral Reefs* 11, 147-154.

FIGURE 3.1. THE MODEL AND THE TEST

The three graphs show how the postulate of HT about level frequencies translates into variation of parameters measurable in the field. A - representation of a simple habitat with two levels of resolution and three units; one occupied by a generalist species (g) and two by specialists (s). B - null model: the relative variability expressed as some measure of variation, e.g., σ, over the mean (x) is the same for specialists and generalists. C - the prediction of hierarchy theory: the relative variability of generalists is less than that of specialists. Y - axis in (B) and (C) stands for some observed community or species parameter, e.g. abundance, ecological range, richness. Note that the qualitative result will not change irrespective of the temporal scale of observation (shaded areas indicate two different time intervals for comparison).

A — Habitat generalist level (g)

Habitat specialist level (s)

$a_g = a_s$

$a_g = 1/2\, a_s$

B

$\sigma_g / \bar{x} = a_g$

1.25
1.00
0.75
0.50
0.25
0.00

$\sigma_g / \bar{x} = a_s$

Time

C

$\sigma_g / \bar{x} = a_g$

1.25
1.00
0.75
0.50
0.25
0.00

$\sigma_g / \bar{x} = a_s$

Time
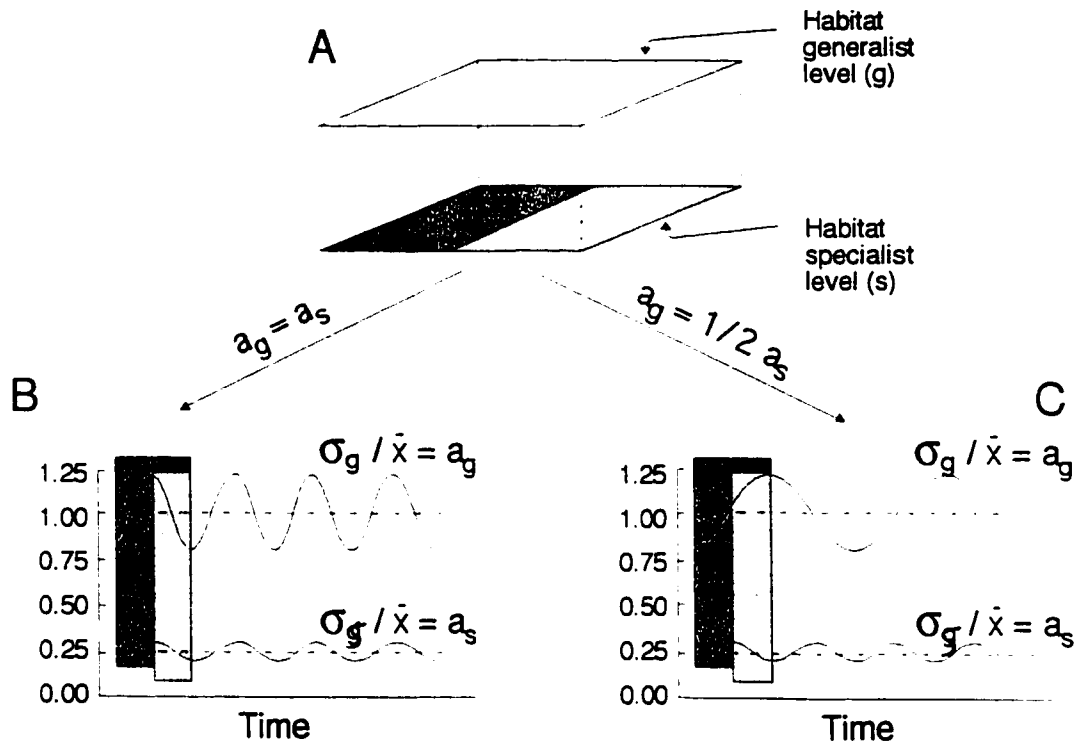
FIGURE 3.2. SPECIES ECOLOGICAL RANGES

Box-plots (showing median, quartiles, and confidence limits) of species ecological ranges grouped into four clusters (Cluster analysis, average linkage, SYSTAT). Group differences are significant in log-transformed data (Bartlet test for homogeneity =8.452, DF =3, P =0.061; Tukey HSD multiple comparisons - all P <0.001, SYSTAT). Ecological ranges are calculated using the equation that gives the best prediction of abundance (see Equation 1):

$$ER = a(n_i / n_{total}) + b(SA_i / SA_{total}) \qquad \text{(Equation 2)}$$

where a and b are constants fitted by linear regression to minimize the residuals; n_i and SA_i are the number of patches and cumulative surface area of all patches occupied by species i, and n_{total} and SA_{total} are the total number of patches and surface area available.
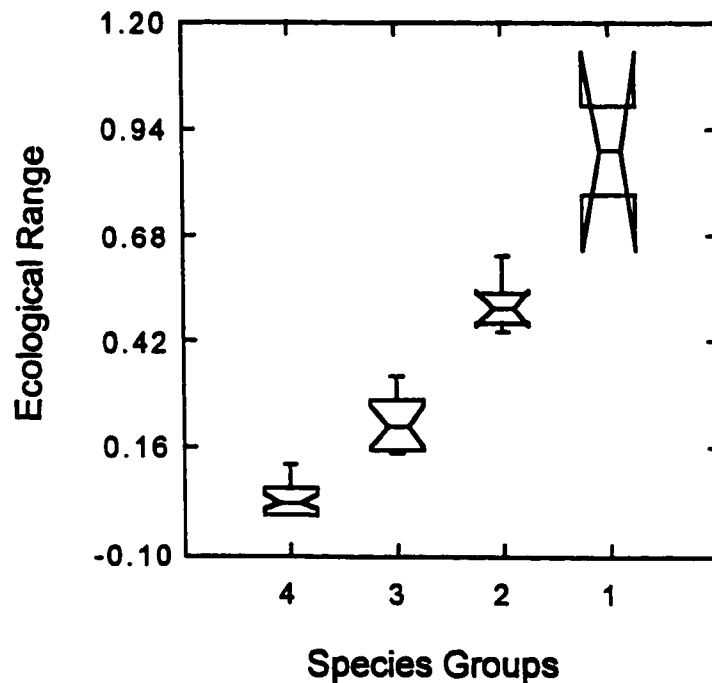
FIGURE 3.3.   SPECIES RELATIVE ABUNDANCES

Predicted (horizontal axis, see Equation 1) and observed (vertical axis) relative

abundances of 52 species of fishes in 1990 (□) and 1991 (●) (loglinear regression; r^2 =

0.745, 0.503, respectively, P<001, SYSTAT). To test the relation between predicted and

observed, ecological range has been calculated from habitat attributes alone:

$$ER_i = \sqrt{(n_i * SA_i)} / \sqrt{(n_{total} * SA_{total})} \qquad \text{(Equation 3)}$$

Observed fish abundances were corrected for the unequal times they were present on or

near patches (17).
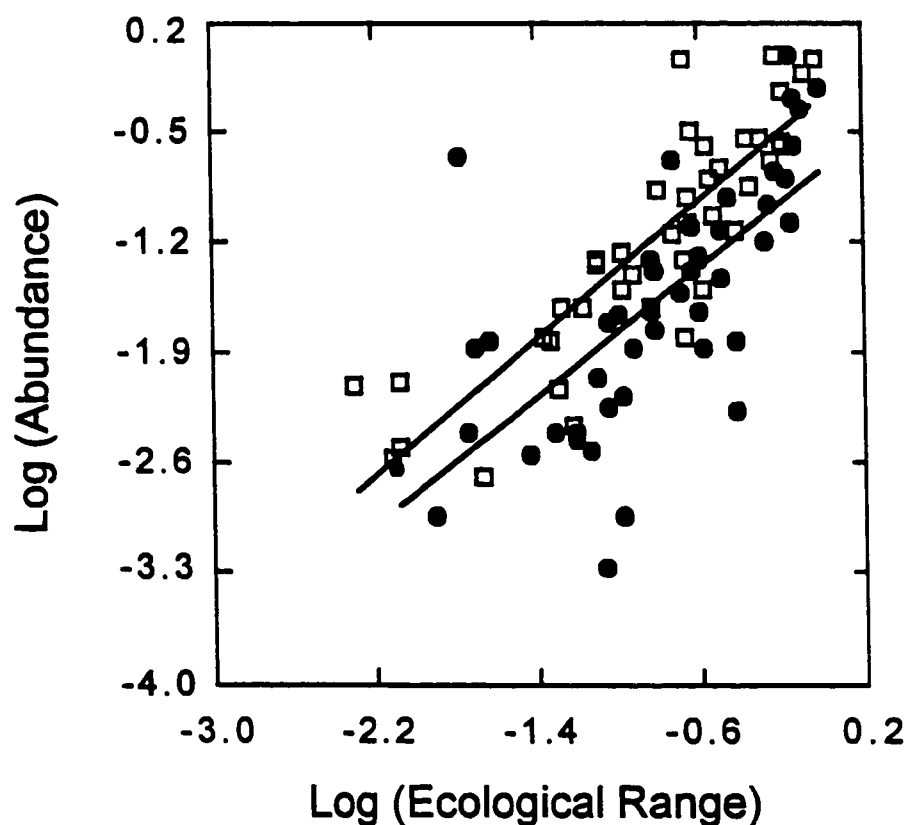
FIGURE 3.4. GROUP VARIATION

Group variation as a function of habitat level associated with a group. High mean values of the ecological range correspond to high habitat levels. The trend is highly significant for abundance whether plotted against the group abundance or ecological range means (Fig. 3.4A, log transformed linear regression r^2 = 0.960, P=0.006; Fig. 3.4B, log transformed linear regression r^2 = 0.981, P=0.013, SYSTAT) but not significant for simulated variation (P=0.071). Variation of the ecological ranges behaves similarly to that of abundance (Fig. 3.4B, log transformed linear regression r^2 = 0.879, P=0.041). Bars represent Standard Errors.
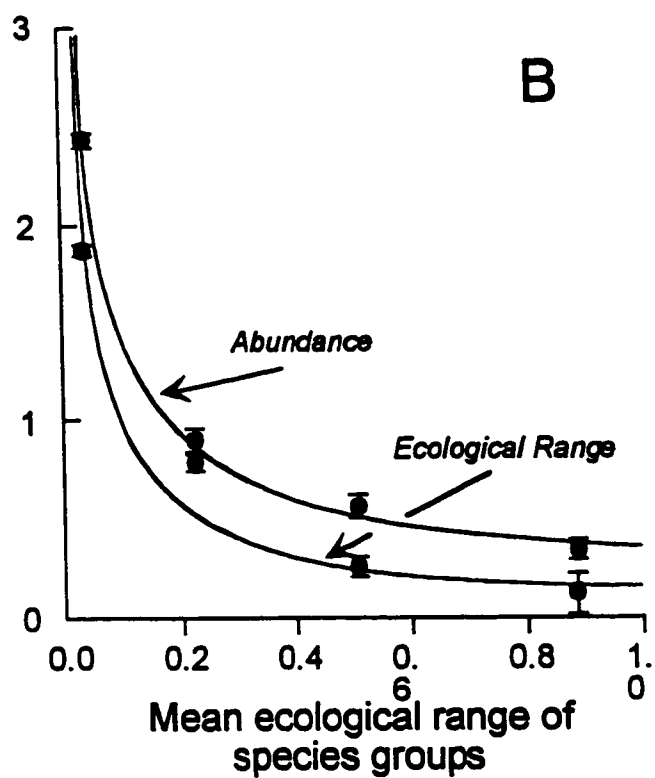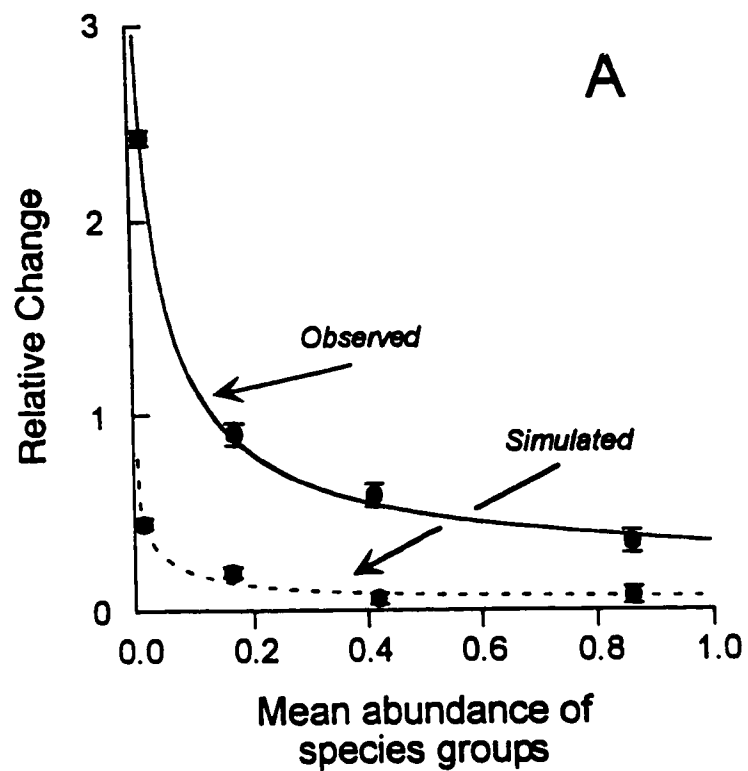
FIGURE 3.5. POPULATION VARIATION AS A FUNCTION OF SAMPLING PERIOD

Illustration of the link between the frequency of variation in population size and the measured variance at time scales less than one full period, with 1 representing the fastest behavior and 1/5 the slowest. A - One of the three data sets used to calculate standard deviations and the size of the sampling window for data in B. Fractions describe the portion of the period of each curve shown in the figure. B - Trend in standard deviations as a function of the frequency or period length.
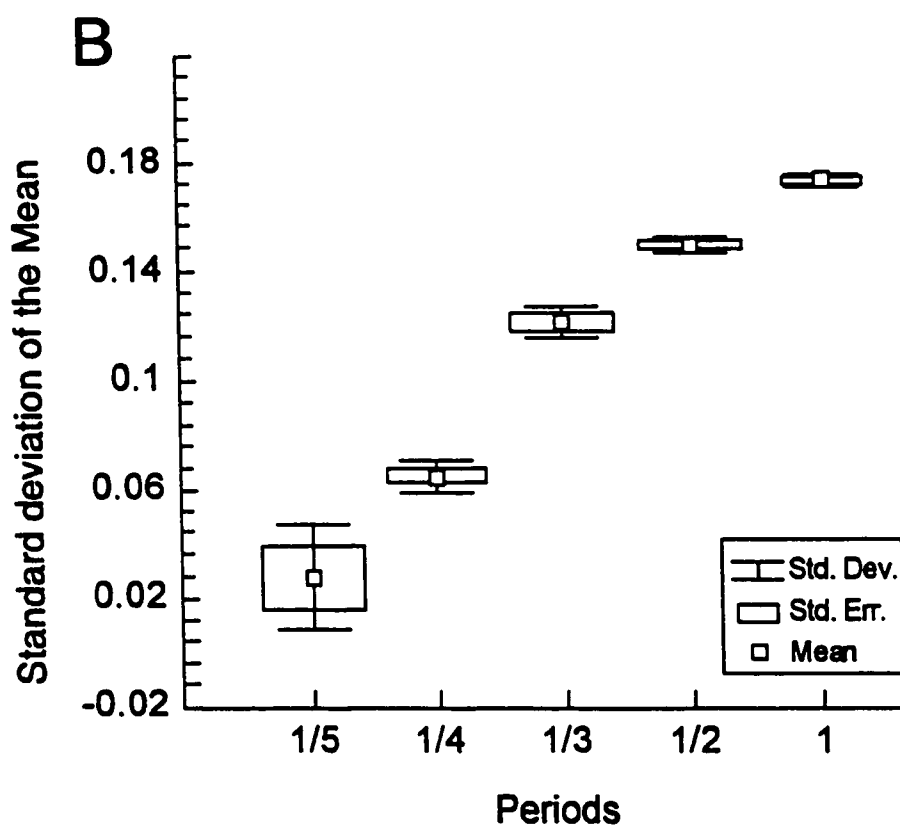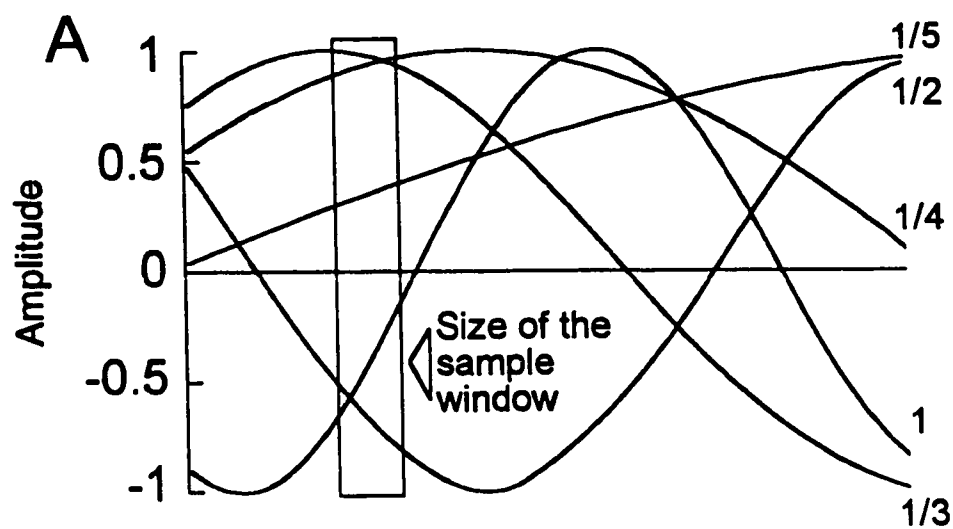
APPENDIX 3.1. POPULATION CHANGE

The link between frequency of population change and estimate of variation at short time scales.

1. We represented changes in population size as a sin function of time. This simplified model illustrates steps needed to establish the link between the frequency (or period after which the function returns to the original state) and a measure of variation. A natural population may not undergo cyclic changes and it may show other periodicities and stochastic variation. These factors have little bearing on the nature of the relationship we need to demonstrate.

2. We created five functions of increasingly shorter period: $y_1 = x\sin\pi$, $y_2 = x\sin2\pi$, $y_3 = x\sin3\pi$, $y_4 = x\sin4\pi$, $y_5 = x\sin5\pi$. Values of each function were calculated for 1000 time units for the interval x (0,2) such that the slowest behaved function $y = x\sin\pi$ contained values covering one complete period.

3. The five functions were randomized as to when they began their course on the x-axis. Three randomized sets of data were created. A random length of the x-axis corresponding to the length of the shortest period ($y = x\sin5\pi$, 200 values for each y_i) was used to estimate variation of each 'population' (Fig. 3.5A).

4. The five populations were sampled using a moving window of twenty adjacent values (Fig. 3.5A) to calculate standard deviations for each curve. These standard deviations vary in response to the portion of the curve and the sampling window size. Details of these patterns of variation are described separately (in preparation).

5. We obtained means of standard deviations for three sets of data and then plotted between-set means and respective errors (Fig. 3.5B). Thus, the figure shows variation between replicated simulations and the overall trend in means.

SECTION IV

STOCHASTIC DETERMINANTS OF ASSEMBLAGE PATTERNS IN CORAL REEF
FISHES:
A QUANTIFICATION BY MEANS OF TWO MODELS

4

Stochastic determinants of assemblage patterns in coral reef fishes: a quantification

by means of two models

4.1 RATIONALE AND OBJECTIVES

Recall that the central theme of this thesis is to derive a more accurate understanding of the processes involved that determine the structure of fish communities on coral reefs. A question that has drawn considerable attention from reef fish ecologists is of special interest in this context: species accumulate in larger numbers on larger patches reefs but the cause of this accumulation is unclear. Two views have been proposed. The first view is that larger patches are simply bigger traps for passing recruits. This implies that fish recruit to reefs 'passively', under stochastic principles as a function of encounter probability. The second view holds that relative to smaller patches, larger patches contain more habitat types and therefore can contain greater species richness and diversity. This second view implies that species "choose" or are "restricted" to their patches according to some habitat attribute. The extent to which either view is correct needs to be determined. The purpose of this Section, therefore, is to identify the extent to which patch size contributes towards species membership and population distributions across the landscape of patch reefs.

The analytical methods I use involve correlating observed distributions of fish species to two theoretical distributions. The first theoretical distribution assumes fish to be randomly distributed over patch reefs according to stochastic expectations (i.e., the larger the patch the greater the effective trap). The second theoretical distribution assumes fish to be distributed over patch reefs in conformity with a gradient of restrictions imposed by the habitat template (i.e., species choose or are restricted to specific patches). The methods and distributions are developed and described in detail throughout the Section.

4.2 LETTER OF CONSENT

Letter of consent from Kluwer Academic Publishers, the Netherlands, granting permission to include the published journal article (Waltho and Kolasa 1996) as part of the present thesis. It should be made clear though, that several areas have been slightly modified to reflect the standards set by the Ph.D. requirements.

**Kluwer
academic
publishers**

Spuiboulevard 50
P.O. Box 17
3300 AA Dordrecht
The Netherlands

Telephone (central) +31(0)78-6392000
Telefax +31(0)78-6392254
Bankers: ABN-AMRO, Dordrecht
Account Number 51.94.52.205
Postal Cheque Account Number 447884
Chamber of Commerce Dordrecht
Commercial Register Number 28051057
VAT number NL.08.31.19.532.B48

Telephone (direct) 6392 130

Date 16 July 1997

McMaster University
Dr. Nigel Waltho
Dept. of Biology
1280 Main Street West
Hamilton, Ontario L8S 4K1
Canada

Re: *Environmental Biology of Fishes* 47:225-267, 1996, Waltho

Dear Dr. Nigel Waltho,

With reference to your request (copy herewith) to reprint material on which Kluwer Academic Publishers control the copyright, our permission is granted, free of charge, for the use indicated in your enquiry.

This permission
* allows you non-exclusive reproduction rights throughout the World.
* excludes use in an electronic form. Should you have a specific project in mind, please reapply for permission.

Full credit (Kluwer Academic Publishers book/journal title, volume, year of publication, page, chapter/article title, name(s) of author(s), figure number(s), original copyright notice) is given to the publication in which the material was originally published, by adding: with kind permission from Kluwer Academic Publishers.

Permission free of charge on this occasion does not prejudice any rights we might have to charge for reproduction of our copyrighted material in the future.

With kind regards,

Ms. Lanette Setkoski
KLUWER ACADEMIC PUBLISHERS
Rights and Permissions

PS. Permission also granted to McMaster University and the National Library of Canada to register in database.

4.3 TITLE PAGE

STOCHASTIC DETERMINANTS OF ASSEMBLAGE PATTERNS IN CORAL REEF FISHES: A QUANTIFICATION BY MEANS OF TWO MODELS. Env. Biol. Fishes 47:255-267 (1996)

NIGEL D. WALTHO & JUREK KOLASA

Department of Biology, McMaster University, 1280 Main Street West, Hamilton, Ontario, L8S 4K1, Canada

4.4 ABSTRACT

One perspective emphasizing the importance of stochastic processes in determining coral reef fish assemblages implies that there is little organization in species richness, abundance structure, and spatial distribution. We examine the degree to which this perspective is correct by analyzing distribution of fishes on a collection of patch reefs (Discovery Bay, Jamaica). We ask the question whether these patches accumulate species and individuals in a manner consistent with stochastic expectations. To address this question we use two conceptual models, each permitting a different insight. One model assumes that fish are distributed stochastically on patches while the other assumes presence of restrictions on fish distribution due to habitat structure. For each conceptual model we use two types of benchmark: we compare observed patterns to those predicted by theoretical models, and we also compare observed patterns to those obtained from a random reallocation of fish individuals to patches. We found that the conceptual model assuming stochastic processes appeared to provide weaker explanation of patterns than the conceptual model that includes restrictions due to habitat structure. Further, and more importantly, we found that (i) the community is shaped by a mixture of stochastic and non-stochastic mechanisms, and (ii) the stochastic assembly processes decrease in importance for species restricted to fewer microhabitat types and sites. Our study therefore indicates that patches do accumulate individuals and species in a manner consistent with stochastic expectations, however, this applies primarily to the habitat generalists (unrestricted species). By the same token, increased habitat specialization by

some species imposes constraints on the stochastic model such that the stochastic model eventually fails.

4.5 INTRODUCTION

Assemblages of coral reef fish are systems exceptionally rich and highly variable in time and space. This has challenged ecologists to provide an explanation that has resulted in a number of models and perspectives (e.g., Anderson et al. 1981, Sale 1980). Of these, the stochastic perspective has gained considerable momentum and available evidence appears to support it. Specifically, fish composition and its variability on patch reefs is explained as a function of random events including (a) fish arrival, (b) creation of vacant sites via mortality and migration, and (c) establishment on or colonization of patches (Sale & Dybdahl 1978, Williams 1982, Victor 1983, Sale & Douglas 1984, Sale & Steel 1986, Doherty & Williams 1988, Bohnsack 1989, Robertson & Duke 1990). Some argue that any organization in reef fish assemblage reported by others may therefore be a function of biologically trivial factors such as sampling biases (e.g., Sale & Guy, 1992).

This stochastic explanation, however, leads to the counter-intuitive conclusion that there is little organization in the coral reef fish assemblages. It does so despite a high number of interacting species and the general expectation that complex systems are organized (e.g., Drake et al. 1995, Kauffman 1993). We suggest, therefore, that these assemblages may be more organized than the stochastic view implies. We also suggest that the failure to detect their organization is due, in part, to insufficient attention paid to proper

scaling of observations and analyses. For example, if species within an assemblage perceive and therefore respond to the environmental template at more than one spatial and temporal scale (e.g., Hanski 1982, Kolasa 1989, Wiens 1989, Kotliar & Wiens 1990, Kareiva 1990, Milne 1991), then the distribution pattern may appear deterministic (ordered or clumped) or stochastic (variable) depending on the scale of observation (Allen & Starr 1982, Maurer 1985, Collins & Glenn 1990). Such dependence on the method and approach is bound to produce alternative and sometimes conflicting explanations.

We therefore pose a question: given a landscape of different size patches and an available species pool represented by n individuals, **does each patch accumulate individuals and species in a manner consistent with expectations of stochasticity?** Stated differently, is the presence of a species on a patch a probability function of patch size and number of individuals participating in the lottery, or is the presence of a species dependent on non-stochastic alternatives—the simplest involving restrictions on which patch a species may colonize and survive on? To answer this question we use data from a natural fish community to test two different conceptual models that emphasize different ecological mechanisms.

The first model borrows a combination of assumptions underlying both the 'island biogeography theory' (IBT, MacArthur & Wilson 1967) and variable recruitment in space and time (Sale 1980). Indeed, patches are not islands in the sense of MacArthur & Wilson (1967) because patch assemblages are not self maintaining populations, but aspects of IBT do apply to fragmented environments such as coral reef patches (Putman 1994). Thus, we use IBT only partially by borrowing one of its assumptions that the number of species on a

patch is a function of the species immigration and emigration rates (or recruitment and subsequent removal of individuals). The assumption that these rates are influenced by patch size is not unreasonable (Sale 1980, Anderson et al. 1981, Ogden & Ebersole 1981, Bohnsack 1983, Rahel et al. 1984, Clarke 1988, Sale & Steel 1989, Winemiller & Pianka 1990). In fact, similar assumptions are made in patch dynamic models in general.

The combined 'IBT-variable recruitment' conceptual model neither expects nor requires species to aggregate within the patch reefs system according to species specific criteria such as patch quality or presence of other species. The model thus evaluates assemblage patterns as a function of patch size and chance recruitment alone (Fig. 4.1A). Consequently, this model is insensitive to any habitat structure that might be perceived by species if other attributes of patches were relevant. For example, there might be two groups of patches, one with good hiding crevasses and the other without. Next, within each group of patches fish might discern those with predators to those without predators, and so on. The perception of such habitat subdivision by fish might result in their structured distributions. This aspect is best analyzed by the second model—the 'habitat-based model' (HBM; Kolasa & Strayer 1988, Kolasa 1989).

The 'habitat-based model' assumes nested patchiness (i.e., patches within patches) of habitat space as a major force shaping species distribution and abundance. This means that species differ in their ability to use the habitat. For example, according to HBM, there will be species with broad ecological ranges (or habitat tolerances) which span the diverse and complete set of microhabitats (habitat generalists), and there will also be species restricted to a subset of microhabitats only (habitat specialists). Since ecological

ranges and site distributions of specialists are largely nested within those of generalists (i.e., habitat specialists may be considered as operating at subdivisions or lower levels of habitat structure - Fig. 4.1B), we view the habitat and the associated community as being hierarchical. In such a hierarchy, specialists face a more fragmented environment than generalists that permits, given some additional assumptions, to calculate their expected relative abundances. This means that the colonization and extinction lottery is limited to varying degrees depending on the number and kind of patches the species are permitted to use under the 'habitat-based model'. For example, species with special habitat requirements will be able to engage in the stochastic lottery on some patches only while species with few restrictions have the potential to colonize any patch.

The two alternative models, one with no restrictions on patch colonization and the other with species-specific restrictions, result in different expectations of community patterns. Such expected community patterns can be compared to those observed in a natural system. Differences in the relative fit of the expected (= theoretical) versus observed values indicate and contrast the relative importance of stochastic effects alone vis-à-vis habitat structure effects.

We wish to emphasize here that we are not interested in the merits of the models themselves but only in their ability to discriminate whether other mechanisms are involved that may, incidentally, produce an appearance of stochastic pattern. Unfortunately, patterns predicted by each model are not directly comparable (i.e., the first predicts richness, and the second predicts abundance). Thus, to gain and document insights into the mechanisms structuring fish community we take the additional steps:

(i) divide the species pool into groups according to whether a species is a habitat

specialist or generalist (cf. HBM Kolasa 1989), and

(ii) apply the 'IBT-variable recruitment' model to each of the species groups.

This strategy permits mutual verification of results produced by the two conceptual models.

Specifically, we hypothesize that if the HBM indicates strong effects of habitat structure,

then IBT will apply well to broad range species only and fail with narrow range species.

The reason for this prediction is simple: As the restrictions as to which patch reefs can be

effectively colonized increase in importance, a corresponding decline in importance of

individual numbers and patch size is expected.

4.6 METHODS

4.6.1 Field

Data on fish distributions were collected from patch reefs in Discovery Bay, Jamaica,

over three two-week periods (1990-12-27 to 1991-01-12, 1991-12-27 to 1992-01-12, and

1993-12-27 to 1994-01-12). All observations were conducted during daylight hours by

direct visual census using SCUBA. We minimized weaknesses normally associated with

this method (Diamond & May 1977, Rahel et al. 1984, Andrew & Mapstone 1987, Fowler

1987, Bellwood & Alcala 1988, Greene & Alevizon 1989) with the following procedures:

(i) two divers settle simultaneously on opposite sides of a patch-reef,

(ii) each diver records one half of the local species pool (S_{total} = 71); the division

determined by species daytime local migratory behaviour (e.g., Pomacentridae and

Holocentridae versus Scaridae and Labridae),

(iii) fish counting starts after a five minute habituation period,

(iv) for the subsequent twenty minute observation all individuals within 1 m distance

from the patch surface are recorded, such that,

(v) the two divers complete a 360° rotation around the patch-reef in four five-minute

90° shifts.

After completing each assemblage enumeration, we recorded physical parameters for

the patch (depth, X-Y-Z dimensions, and distance to surrounding patches). We measured

depth as the perpendicular distance from the water surface to the base of the coral patch.

Although other methods have been used to determine reef surface area (e.g., Risk 1972,

Molles 1978), we approximated it by integrating the patch X-Y-Z dimensions into the

equation for the surface area of a half ellipsoid. We chose this particular method because

(a) we followed the assumption that in the back reef of Discovery Bay, Jamaica, large

patches contain proportionately the same habitat complexity relative to smaller patches

(communiqué Risk), and (b) of its simplicity. Distances to nearby patches were measured

by the shortest distance between the two patches.

The minimal number of patches to sample was determined by a requirement of the

'habitat-based model' (Kolasa 1989) that the ecological range covered by sampling exceeds

that of the broadest species. This ensures that the scale of sampling is sufficient to

measure all species adequately. Operationally, we define the ecological range of species i

(ER$_i$) as a ratio of the number of patches a species is found on (n$_i$) and the cumulative area

of these patches (SA$_i$) to the total habitat available (n$_{total}$* SA$_{total}$). Ecological range is

thus:

$$ER_i = \sqrt{(n_i * SA_i / n_{total} * SA_{total})} \qquad (1)$$

The measure scales from zero to one. Species with ER values close to zero are those

species found on few and/or small patches. By contrast, species with ER values close to

one are found on the majority of the patches, especially the larger patches. Although this

measure of ecological range is arbitrary (other parameters such as consumable resource

range or microhabitat requirements could be used instead) we believe that, given the

nature of our tests, the above parameters are adequate. The biological interpretation of

this measure is that the number of sites reflects, to some degree, the exposure of a species

to different environmental conditions and, indeed, its ability to cope with them (cf. Brown

1984, Kolasa 1989). It also links the ecological range to the size of a patch by assuming

that larger patches, not unlike larger islands, expose fish to a more diverse habitat (e.g.,

Risk 1972, Tonn & Magnuson 1982). We sampled 114 patch reefs from a 10 000m^2 area

of back reef from Discovery Bay, Jamaica. No patch was more than 15 m deep, nor were

any patches closer than 2m to their next nearest patch. Patch surface area ranged from

0.24m^2 to 33 m^2 (with a higher frequency of smaller patches compared to larger patches:

mean patch size is 7.2 m^2 and the S.D. equal to 6.86 m^2, Table 4.1). Total patch surface

area is 820m^2 (8% of back reef habitat).

The first term in equation 1, n_i, is abundance of species i totaled for all patches. For

some species (e.g., species of greater local mobility—Scaridae and Acanthuridae), species abundance could be overestimated if some individuals are counted several times on different patches. We reduced this source of error by weighting each species abundance by the mean time species were observed in association with patches. This was estimated by timing randomly selected individuals for five minutes (daylight hours, N_{timed}= 580 fish). The number of individuals timed differed among species and may be a source of error.

We identified and included in the analysis 71 species of fish from 21 families (Table 4.3). Patch association ranged from 10% (*Inermia vittata*) to 100% (e.g., *Stegastes* sp.). Depending on the sampling season, single species abundance ranged from 0 (*Chromis cyanea*) to 387 (*Scarus coeruleus*). Species abundance totals are 813, 1554, and 991 for the three seasons respectively. The maximum patch richness observed was 25 species ($S_{minimum}$ = 1 species, mean = 10.0 species, and S.D. = 4.8 species).

4.6.2 Theoretically expected and null community patterns

Recall that we posed the question of whether each patch accumulated individuals and species in a manner consistent with expectations of stochasticity. Statistical evaluation of the observed patterns calls two types of benchmark. We need to know what would be the patterns if each of the models were correct. We also need to know what patterns would emerge if most processes were stochastic. The approach we take to answer the question involves two steps. First, we search for the best fitting theoretical equations and, second, we create a 'null assemblage' (random reallocation of fish to patches) to test observed

data for stochastic effects.

Step 1: Theoretical equations

The first step contrasts the relative fit between the expected (= theoretical) and observed patterns for both richness (IBT- variable recruitment) and abundance (HBM). Because we do not necessarily know what the expected patterns are, we evaluate a family of related equations to choose one that best describes the observed data (Table 4.2). Once an equation is selected, we interpret its coefficient of determination as an indirect measure of importance of processes reflected in the assumptions of each model.

As a direct comparison of the two models does not permit a definitive answer as to whether stochastic processes dominate the community structure (primarily because the models predict different parameters—richness and abundance), we attempt to combine insights from each of the two models by the following procedure.

Step 2: Null assemblage

We grouped species according to species-specific criteria and then compared patterns obtained within each species group to 'null patterns' produced by stochastic processes alone. We then chose the ratio of 'coefficient of determinations' between observed and null richness for each species group as an index of pattern consistency with stochastic expectations. Specifically,

(i) we created a null (=stochastic) assemblage by random allocation of individual fish species onto patch reefs with probability of colonizing a particular patch proportional to

the total abundance of that species and surface area of the patch. This simplification ignores other factors such as patch proximity to other patches, competitive and opportunistic adult and predator-prey interactions and others, but this appears to be an acceptable strategy to generate stochastic assemblages suitable for our tests (Sale 1980, Anderson et al. 1981, Ogen & Ebersole 1981, Bohnsack 1983, Rahel et al. 1984, Clarke 1988, Sale & Steel 1989, Winemiller & Pianka 1990). We verified this assumption, for patch richness only, by showing that the relationships in so generated assemblages approximate those in the observed assemblage. Specifically, we find that the regression model that maximizes the correlations (see Appendix 4.1) between patch richness and patch surface area is the same for both the observed and null (=stochastic) assemblages. This model assumes the form: $S = \beta_0 + \beta_1 (SA)^{0.5}$ where S is patch richness, and SA is patch surface area ($r^2_{observed} = 0.343$, and $r^2_{null\ assemblage} = 0.886$, $p_{null\ and\ observed} < 0.001$). The significant difference between the respective regression models lies in the values of the beta coefficients. This difference leads to a prediction of a higher patch richness for the null assemblage (paired t-test mean difference = 1.553, p = 0.005) (Fig. 4.2).

(ii) we allocate each species in the species pool to species groups based on the principles of the 'habitat-based model' (for both null and observed assemblages). We use the 'habitat-based model' specifically because it groups species by similarities in how they perceive and respond to a template of diverse microhabitats. The model clusters species according to similarities in their ecological range and abundance. The assumption made is that the fewer microhabitat types a species perceives to be suitable, the more restricted and, possibly, patchy its range becomes. This results in a cost (e.g., finding mates, shelter from

predation, foraging) which is measurable in terms of the species abundance and distribution. The two variables, ecological range and abundance, can then be used to group species on the premise that such grouping will reflect major differences in how species relate to their habitat. We use a cluster analysis with Euclidean distance and average linkage on species ecological range and abundance to identify three such groups.

(iii) the coefficients of determination for the area-richness relationship obtained for the entire observed and null (stochastic) assemblages differ in magnitude ($r^2_{observed}$ = 0.343, $r^2_{null\ assemblage}$ = 0.886). The coefficients of determination for the three species groups identified by the cluster analysis are obtained via an equation selection process that involves several decision steps (see Appendix for more details). In order to assess how different species groups contribute to the overall explanation of 34% and 89% of variance obtained for the entire assemblages, respectively, we express values obtained for the three species groups in relative terms (i.e., group coefficient / assemblage coefficient). These relative values are directly comparable between the observed and null data sets by generating a ratio, an 'index of stochasticity', of the observed to null coefficients of determination. A ratio value close to 1.0 means that the observed patterns are similar to the null one and, consequently, that a particular species group is distributed over the landscape of patches in a manner consistent with the stochastic mechanisms. A ratio value smaller than 1.0 means that members of the group respond to some other mechanisms.

4.7 RESULTS

4.7.1 Step 1: Theoretical equations

The equation $S = SA^{0.5} \ln SA$ (S = richness, and SA = patch surface area) optimized the fit between the expected (theoretical) and observed richness pattern (Table 4.2, $r^2_{IBT - variable\ recruitment} = 0.339$). Similarly, the equation, $N = ER (\ln ER)^{-1}$ (N = species abundance, ER = ecological range) optimized the fit between the expected (= theoretical) and observed abundance patterns ($r^2_{habitat-based\ model} = 0.852$). Of the two coefficients of determination, the one obtained for 'HBM' is significantly higher than that for 'IBT - variable recruitment'. This implies that significant constraints are in place on how the stochastic processes are allowed to operate. A quantitative evaluation of this aspect follows.

4.7.2 Step 2: Null assemblage

We identified three species groups using cluster analysis on ecological range and abundance of species. The three groups differ significantly in their mean ecological range and abundance (ANOVA Tukey HSD matrix of pair-wise comparison probabilities all p < 0.001). Group 1 (S_{Group1} = 9 species) is best characterized by species that are highly abundant and found throughout most of the habitat range for each of the three sampling seasons. Group 3 (S_{Group3} = 34 species) is comprises species having low abundance (possibly even zero for one or two sampling seasons) and found on few patch reefs only.

Group 2 (S_{Group2} = 28 species) shows intermediate characteristics between Group 1 and Group 3 (Table 4.3).

'IBT - variable recruitment' models for species Groups 1, 2, and 3 differ in the proportion of variance they explain between the observed and null data sets (Fig. 4.3, Table 4.4). Specifically, the 'index of stochasticity' decreases from habitat generalists (Group 1) to habitat specialists (Group 3). These results suggest that the stochastic assembly processes decrease in importance for species groups restricted to fewer microhabitat types and sites. They do so even despite the high richness found in species Group 3.

4.8 DISCUSSION

A preliminary comparison of the two models (as outlined in Step 1 of the Results section) leads to somewhat contradictory conclusions, and difficulties with a meaningful quantitative interpretation. On one hand, the 'IBT - variable recruitment' model points to significant stochastic processes as governing the distribution of fish species on patch reefs. On the other hand, the 'habitat-based model' clearly points to non-stochastic factors as governing fish distributions. To add to this apparent contradiction each model describes a different pattern (richness versus abundance), and therefore a direct quantitative comparison is not immediately informative (34% vs. 85% of variance explained, respectively).

The analysis performed in Step 2 removes this apparent contradiction and quantitative limitation as to whether stochastic or non-stochastic factors structure the fish assemblage. This analysis shows:

(i) that the community is shaped by a mixture of stochastic and non-stochastic mechanisms,

(ii) there is a shift in predominance from stochastic to non-stochastic processes along the generalist-to-specialist species gradient.

We thus conclude that the two models are in fact consistent; according to the 'IBT - variable recruitment' model habitat generalists are distributed according to stochastic expectations. According to the 'habitat-based model' constraints apply to the habitat specialists, and this is precisely where the 'IBT - variable recruitment' model should fail and does fail.

In summary, our analysis indicates that patches do accumulate individuals and species in a manner consistent with stochastic expectations ('IBT - variable recruitment' model). However, this applies to the habitat generalists only. The analysis further indicates that increasing habitat specialization by some species imposes constraints on the stochastic model such that, at the opposite extreme (that of the habitat specialists), the stochastic model fails. This is not surprising if we assume habitat specialists are restricted to a specific set of patches within the template of patch reefs. Thus, a lottery approach to their distribution is unlikely to show a pattern of species accumulation that parallels the distribution pattern of habitat generalists.

By contrast, the 'habitat-based model' performs well because it predicts species abundances as a function of landscape fragmentation. The model requires that habitat specialists be restricted to some patches only and be not permitted to use other patches. The model has a good fit to the data because some, but not all, species are subject to such spatial restrictions.

If we are correct, one can view the assemblage structure as hierarchical, with groups of species characterized by different habitat resolutions and different densities. In such a hierarchical structure stochastic factors may be important at any single level (species group), but in different proportions and with different implications for generic models such as 'IBT - variable recruitment' and habitat partitioning models such as the 'habitat-based model'.

4.9 ACKNOWLEDGMENTS

4.10 REFERENCES CITED

Allen, T.F.H. & T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, 293 pp.

Anderson, G.R.V., A.H. Ehrlich, P.R. Ehrlich, J.D. Roughgarden, B.C. Russell & F.H. Talbot. 1981. The community structure of coral reef fishes. Amer. Nat. 117:476-495.

Andrew, N.L. & B.D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. Oceanogr. Mar. Biol. Ann. Rev. 25: 39-90.

Bellwood, D.R. & A.C. Alcala. 1988. The effect of minimal length specification on visual estimates of density and biomass of coral reef fishes. Coral Reefs 7: 23-28.

Bohnsack, J.A. 1983. Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs 1:223-228.

Bohnsack, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. 44:631-645.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. Amer. Nat. 124:255-279.

Clarke, R.D. 1988. Chance and order in determining fish species composition on small coral patches. J. Exp. Mar. Biol. Ecol. 115:197-212.

Collins, S.L. & S.M. Glenn. 1990. A hierarchical analysis of species abundance patterns in grassland vegetation. Amer. Nat. 135:633-648.

Diamond, J.M. & R.M. May. 1977. Species turnover rates on islands: dependence on census interval. Science 197:266-270.

Doherty P.J. & D.McB. Williams. 1988. Are local populations of coral reef fishes equilibrial assemblages? The empirical database. Proc. Int. Coral Reef Symp., 6th 1:131-139

Drake, J.A., C.L. Hewitt, G.R. Huxel & J. Kolasa. 1995. Diversity and higher levels of organization. In: Gaston K. (ed.) Biodiversity: A Biology of Numbers and Differences. Cambridge University Press (in press).

Fowler, A.J. 1987. The development of sampling strategies for population studies of coral reef fishes: a case study. Coral Reefs 6: 49-58.

Greene, L.E. & W.S. Alevizon. 1989. Comparative accuracies of visual assessment methods for coral reef fishes. Bull. Mar. Sci. 44: 899-912.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite hypothesis. Oikos 38: 210-221.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Phil. Tran. Royal Soc. London, Ser. B 330:175-190.

Kauffman, S.A. 1993. The origins of order. Oxford University Press, Oxford. 709 pp.

Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology 70:36-47.

Kolasa, J. & D. Strayer. 1988. Species abundance patterns: a comparison of two hierarchical models. Oikos 53: 235-241.

Kotliar, N.B. & J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

MacArthur, R.H. & E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

Maurer, B.A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecol. Monogr. 55:295-312.

Milne, B. 1991. Heterogeneity as a multiscale characteristic of landscapes. pp. 69-84 In: J. Kolasa & S.T.A. Pickett (ed.) Ecological Heterogeneity. Ecological Studies 86, Springer-Verlag, New York.

Molles, M.C. 1978. Fish species diversity on model and natural reef patches: Experimental insular biogeography. Ecol. Monogr. 48:289-305

Ogden, J.C. & J.P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long term study of a large artificial reef. Mar. Ecol. Prog. Ser. 4:97-104.

Pickett, S.T.A., W.T. Parker & P.L. Fiedler. 1992. The new paradigm in ecology: implications for conservation biology above the species level. pp. 65-88 In: P. Fiedler & S. Jain (ed.) Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management, Chapman and Hall, New York.

Putman, R.J. 1994. Community ecology. Chapman and Hall, London, pp. 178.

Rahel F.J. 1990. The hierarchical nature of community persistence: a problem of scale. Amer. Nat. 136:328-344

Rahel, F.J., J.D, Lyons & P.A. Cochran. 1984. Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. Amer. Nat. 124:583-589.

Risk, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull. 153:1-6

Robertson A.I. & N.C. Duke. 1990. Mangrove fish communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass, and community structure. Mar. Biol. 104:369-379

Sale P.F. & R. Dybdahl. 1978. Determinants of community structure on coral reef fishes in isolated coral heads at lagoonal and reef slope sites. Oecologia 34:57-74

Sale P.F. & W.A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecol. 6:409-422

Sale P.F. & W.J. Steel. 1986. Random placement and the distribution of fishes among coral patch reefs. Mar. Ecol. Prog. Ser. 28:165-174

Sale, P.F. 1980. Assemblages of fish on patch reefs - predictable or unpredictable? Env. Biol. Fish. 5:243-249.

Sale, P.F. & J.A. Guy. 1992. Persistence of community structure: what happens when you change taxonomic scale? Coral Reefs 11:147-154.

Sale, P.F. & W.J. Steel. 1986. Random placement and the structure of reef fish communities. Mar. Ecol. Prog. Ser. 28:165-174.

Sale, P.F. & W.J. Steel. 1989. Temporal variability in patterns of association among fish species on coral patch reefs. Mar. Ecol. Prog. Ser. 51:35-47.

Tonn, W. M. & J.J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149-1166.

Victor, B.C. 1983. Recruitment and Population Dynamics of a Coral Reef Fish. Science 219:419-420

Wiens, J.A. 1989. Spatial scaling in ecology. Funct. Ecol. 3: 385-397.

Williams, D.McB. 1982. Patterns in Distribution of Fish Communities across the central Great Barrier Reef. Coral Reefs 1:35-43

Winemiller, K.O. & E.R. Pianka. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Monogr. 60:27-55.

TABLE 4.1. PATCH DESCRIPTORS

Summary of patch reef descriptors. Frequency distribution of surface areas is skewed towards the smaller patches (p < 0.05).

Parameters	Sampling Weeks		
	Season 1	Season 2	Season 3
Number of patches	35	40	39
Minimum surface area (m^2)	0.20	0.30	1.10
Maximum surface area (m^2)	19.5	33.1	30.9
Mean surface area (m^2)	5.43	8.00	7.97
Standard deviation (m^2)	4.55	8.42	6.70
Skewness	1.098	1.464	1.479
Total surface area (m^2)	190.3	312.0	318.8

TABLE 4.2. REGRESSION MODELS

Fits (coefficients of determination, r^2) among the predicted patch richness (S) and species abundance (N) and the observed data. The predicted values were obtained using the family of equations listed. We find that the equations that create the best correlations are equation no. 9 and no. 11 for the two models respectively (shown by an asterisk).

Equation	IBT- Variable recruitment	r^2	Habitat based model	r^2
1	$S = SA$	0.335	$N = ER$	0.727
2	$S = SA \ln SA$	0.316	$N = ER \ln ER$	0.157
3	$S = SA^{1.5}$	0.307	$N = ER^{1.5}$	0.790
4	$S = SA^2$	0.276	$N = ER^2$	0.816
5	$S = SA^2 \ln SA$	0.257	$N = ER^2 \ln ER$	0.562
6	$S = SA^{2.5}$	0.248	$N = ER^{2.5}$	0.825
7	$S = SA^3$	0.226	$N = ER^3$	0.827
8	$S = e^{SA}$	0.064	$N = e^{ER}$	0.774
9	$S = SA^{0.5} \ln SA$	0.339*	$N = ER^{0.5} \ln ER$	0.150
10	$S = (\ln SA)^2$	0.314	$N = (\ln ER)^2$	0.212
11	$S = SA (\ln SA)^{-1}$	0.002	$N = ER (\ln ER)^{-1}$	0.852*
12	$S = \ln SA (SA)^{-1}$	0.005	$N = \ln ER (ER)^{-1}$	0.071
13	$S = \ln SA (SA)^{-2}$	0.038	$N = \ln ER (ER)^{-2}$	0.037

TABLE 4.3. SPECIES DATA

Fish community from the back reef of Discovery Bay, Jamaica. 'Time' refers to the species

percent time associated with patch reefs; 'Abundance' shows species abundances for each

of the three sampling seasons; 'Patches' is the number of patch reefs the species was

observed during a corresponding season (maximum possible: season 1 - 35 patches,

season 2 - 39 patches, and season 3 - 40 patches); 'Total surface area' is the area of patch

habitat a species was observed (maximum possible: season 1 - 190 m^2, season 2 - 312 m^2,

and season 3 - 319 m^2); 'Gp' is the 'habitat-based model' group designation number.

Family	Species	Common name	Time	Abundance			Patches			Total surface area			Gp
				1	2	3	1	2	3	1	2	3	
Acanthuridae	Acanthurus bahianus	Surgeon	0.3	0	0	17	0	0	10	0.0	0.0	121.1	3
	A. chirurgus	Doctorfish	0.3	17	26	42	7	11	18	46.0	126.9	148.5	1
	A. coeruleus	Blue Tang	0.3	10	9	1	5	8	1	38.9	123.4	5.9	2
Apogonidae	Apogon binotatus	Barred Cardinal	1.0	6	31	19	4	14	12	15.2	100.6	83.9	2
	A. townsendi	Belted Cardinal	1.0	0	8	1	0	5	1	0.0	72.4	10.6	3
	Phaeoptyx pigmentaria	Dusky Cardinal	1.0	0	0	8	0	0	5	0.0	0.0	55.3	3
Aulostomidae	Aulostomus maculatus	Trumpet	1.0	0	2	0	0	2	0	0.0	40.7	0.0	3
Callionymidae	Paradiplogrammus bairdi	Lancer Dragonet	1.0	0	1	0	0	1	0	0.0	1.6	0.0	3
Chaetodontidae	Chaetodon capistratus	Foureye Butterfly	0.4	8	17	2	6	8	2	51.1	110.8	22.0	2
Cirrhitidae	Amblycirrhitus pinos	Red Spotted Hawkfish	1.0	0	0	1	0	0	1	0.0	0.0	2.0	3
Diodontidae	Diodon holocanthus	Balloon	1.0	0	3	0	0	3	0	0.0	16.7	0.0	3
Gerreidae	Gerres cinereus	Yellowfin	0.2	0	0	15	0	0	9	0.0	0.0	60.8	3

Family	Species	Mojarra / Common name											
Holocentridae	Holocentrus adscensionis	Squirrel	1.0	26	40	0	14	17	0	80.3	204.4	0.0	2
	H. rufus	Longspine Squirrel	1.0	1	8	22	1	7	15	8.5	67.5	186.6	2
	Myripristis jacobus	Black Squirrel	1.0	1	1	0	1	1	0	1.0	4.5	0.0	2
	Neoniphon marianus	Longjaw Squirrel	1.0	3	6	4	3	5	4	22.5	57.1	44.3	2
	Sargocentron coruscus	Reef Squirrel	1.0	11	20	5	4	12	5	34.4	120.6	57.4	2
	S. vexillarius	Dusky Squirrel	1.0	2	0	1	2	0	1	20.5	0.0	5.3	2
Inermiidae	Inermia vittata	Boga	0.1	0	0	1	0	0	1	0.0	0.0	7.2	3
Labridae	Bodianus rufus	Spanish Hogfish	0.7	0	2	0	0	2	0	0.0	40.7	0.0	3
	Halichoeres bivittatus	Slippery Wrasse	0.7	21	3	5	5	1	4	40.5	2.8	35.3	2
	H. garnoti	Yellowhead Wrasse	0.7	18	0	1	9	0	1	55.3	0.0	12.6	3
	H. maculopinna	Clown Wrasse	0.7	44	0	0	11	0	0	75.1	0.0	0.0	3
	Thalassoma bifasciatum	Bluehead Wrasse	0.7	10	36	12	4	11	10	22.0	122.8	85.9	2
	Xynchtys martinicensis	Rosy Razor Wrasse	0.7	0	0	1	0	0	1	0.0	0.0	4.0	3
Lutjanidae	Ocyurus chrysurus	Yellowtail Snapper	0.3	0	1	3	0	1	3	0.0	1.6	35.0	3
Monacanthidae	Cantherhines pullus	Orange Spotted Filefish	0.4	1	0	0	1	0	0	2.3	0.0	0.0	3
	Monacanthus tuckeri	Slender Filefish	0.3	2	0	0	1	0	0	2.3	0.0	0.0	3
Mullidae	Mulloidichthys martinicus	Yellowtail Goatfish	0.3	1	0	0	1	0	0	7.4	0.0	0.0	3
	Pseudupeneus maculatus	Spotted Goatfish	0.3	3	0	7	3	0	6	19.9	0.0	57.4	2
Pomacanthidae	Holacanthus bermudensis	Blue Angel	0.7	2	3	11	2	3	2	12.3	34.3	7.9	2
Pomadasyidae	Haemulon aurolineatum	Tomtate Grunt	1.0	0	61	18	0	2	12	0.0	1.8	92.3	3
	H. flavolineatum	French Grunt	1.0	12	15	11	4	8	7	34.8	111.2	74.5	2
	H. macrostomum	Spanish Grunt	1.0	0	0	1	0	0	1	0.0	0.0	10.0	3
	H. striatum	Striped Grunt	1.0	0	4	14	0	3	7	0.0	57.7	85.0	2
Pomacentridae	Abudefduf saxatilis	Sergeant Major	1.0	2	0	5	2	0	2	21.2	0.0	20.9	2

Family	Species	Common name											
	Microspathodon chrysurus	Yellowtail Damselfish	1.0	0	0	3	0	0	3	0.0	0.0	21.7	3
	Stegastes diencaeus	Longfin Damselfish	1.0	29	11	12	15	6	9	87.8	76.3	137.7	1
	S. fuscus	Dusky Damselfish	1.0	18	102	4	8	29	4	45.0	248.1	31.1	2
	S. leucostictus	Beaugregory Damselfish	1.0	115	151	10	29	37	10	161.7	300.9	107.4	1
	S. partitus	Bicolor Damselfish	1.0	4	17	21	4	11	16	22.1	77.6	129.7	2
	S. planifrons	Threespot Damselfish	1.0	89	120	151	22	22	34	134.5	259.0	300.7	1
	S. variabilis	Cocoa Damselfish	1.0	16	60	17	6	23	9	23.6	246.6	112.6	2
	Chromis cyanea	Blue Chromis	1.0	0	7	10	0	4	2	0.0	33.2	24.5	2
Scaridae	Scarus coeruleus	Blue Parrot	0.4	0	1	0	0	1	0	0.0	1.1	0.0	3
	S. iserti	Striped Parrot	0.4	103	387	93	13	22	26	91.5	241.8	249.4	1
	S. taeniopterus	Princess Parrot	0.4	140	203	138	18	24	34	98.3	249.6	292.1	1
	Sparisoma atomarium	Greenbloch Parrot	0.4	1	1	3	1	1	3	1.5	33.1	34.5	2
	S. aurofrenatum	Redband Parrot	0.4	10	35	73	6	15	28	29.8	177.2	265.1	2
	S. chrysopterum	Redtail Parrot	0.4	2	2	23	2	2	15	12.1	43.7	121.6	2
	S. radians	Bucktooth Parrot	0.4	0	1	0	0	1	0	0.0	1.1	0.0	3
	S. rubripinne	Yellowtail Parrot	0.4	0	0	2	0	0	1	0.0	0.0	1.1	3
	S. viride	Stoplight Parrot	0.4	19	40	31	7	22	17	49.5	228.1	202.7	1
Serranidae	Cephalopholis cruentata	Graysby	1.0	0	0	1	0	0	1	0.0	0.0	7.2	3
	C. fulvus	Coney	1.0	0	0	4	0	0	3	0.0	0.0	19.6	3
	Epinephelus guttatus	Red Hind Bass	1.0	0	0	1	0	0	1	0.0	0.0	17.3	3
	Hypoplectrus aberrans	Yellowbelly Hamlet	1.0	4	1	1	3	1	1	19.8	22.7	4.7	2
	H. chlorurus	Yellowtail Hamlet	1.0	0	0	8	0	0	8	0.0	0.0	69.5	3

|	Species	Common Name											
	H. guttavarius	Shy Hamlet	0.8	0	0	2	0	0	2	0.0	0.0	30.4	3
	H. indigo	Indigo Hamlet	1.0	13	13	2	9	11	1	67.6	137.6	2.0	2
	H. nigricans	Black Hamlet	1.0	0	8	8	0	8	8	0.0	117.7	77.7	2
	H. puella	Barred Hamlet	0.9	24	29	58	14	18	33	78.0	172.0	273.0	1
	H. unicolor	Butter Hamlet	0.5	3	8	2	3	5	2	23.1	62.8	5.5	2
	Hypoplectrus sp.	Masked Hamlet	1.0	0	3	0	0	2	0	0.0	41.9	0.0	3
	Liopropoma rubre	Peppermint Bass	1.0	0	1	0	0	1	0	0.0	29.9	0.0	3
	Mycteroperca tigris	Tiger Grouper	1.0	0	0	1	0	0	1	0.0	0.0	17.3	3
	Serranus tabacarius	Tobaccofish	1.0	0	0	1	0	0	1	0.0	0.0	5.8	3
	S. tigrinus	Harlequin Bass	1.0	0	5	0	0	4	0	0.0	37.1	0.0	3
Synodontidae	Synodus saurus	Bluestriped Lizardfish	0.5	0	0	7	0	0	7	0.0	0.0	44.8	3
Tetraodontidae	Canthigaster rostrata	Sharpnose Puffer	0.7	22	47	74	11	22	31	54.0	226.7	288.4	1
	Sphoeroides spengleri	Bandtail Puffer	0.7	0	4	2	0	2	2	0.0	2.8	26.4	2

TABLE 4.4. INDEX OF STOCHASTICITY

Proportion of variance explained by correlation between the observed and null (= stochastic) data sets. We show for each species group (a) the regression model that maximizes the fit between patch richness and patch surface, (b) the respective coefficients of determination (r^2_i), (c) r^2 relative to one obtained for the whole assemblage (i.e., observed $r^2 = 0.343$, and null $r^2 = 0.886$), and (d) 'index of stochasticity' (this is the ratio between the r^2 obtained from the observed data and those for the null [stochastic] models).

|	(a) Regression Model	p	(b) r^2_i	(c) Relative r^2_i	(d) 'Index of stochasticity'
Observed data					
Group 1 $_{obs.}$	$S = b_0 SA^{b1}$	<0.001	0.300	0.874	1.113
Group 2 $_{obs.}$	$S = b_0 + b_1 SA$	<0.001	0.269	0.784	0.871
Group 3 $_{obs.}$	$S = b_0 + b_1 SA^{0.5}$	<0.05	0.059	0.172	0.415
Null assemblage					
Group 1 $_{null}$	$S = b_0 + b_1 SA^{0.5}$	<0.001	0.696	0.785	N/A
Group 2 $_{null}$	$S = b_0 + b_1 SA^{0.5}$	<0.001	0.797	0.900	N/A
Group 3 $_{null}$	$S = b_0 + b_1 SA^{0.5}$	<0.001	0.367	0.414	N/A

FIGURE 4.1. THEORETICAL MODEL

Contrast between spatial patterns produced by unrestricted (A) and micro-habitat restricted fish distributions (B). For simplicity we use two species only and do not show individual patches. Both species (Species 1 "□", N_1 = 80; Species 2 "●", N_2 = 20) are placed randomly such that in Figure 4.1B Species 2 "●" is restricted to a micro-habitat (darker shading). This case would occur if the two species respond to two different levels of habitat structure with Species 1 utilizing all micro-habitats (habitat generalist) and Species 2, restricted to one micro-habitat only (habitat specialist).
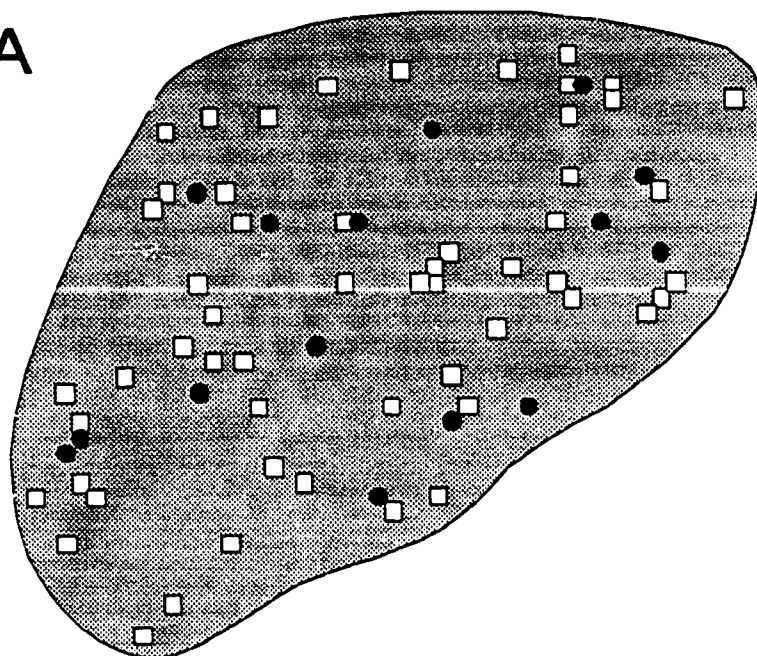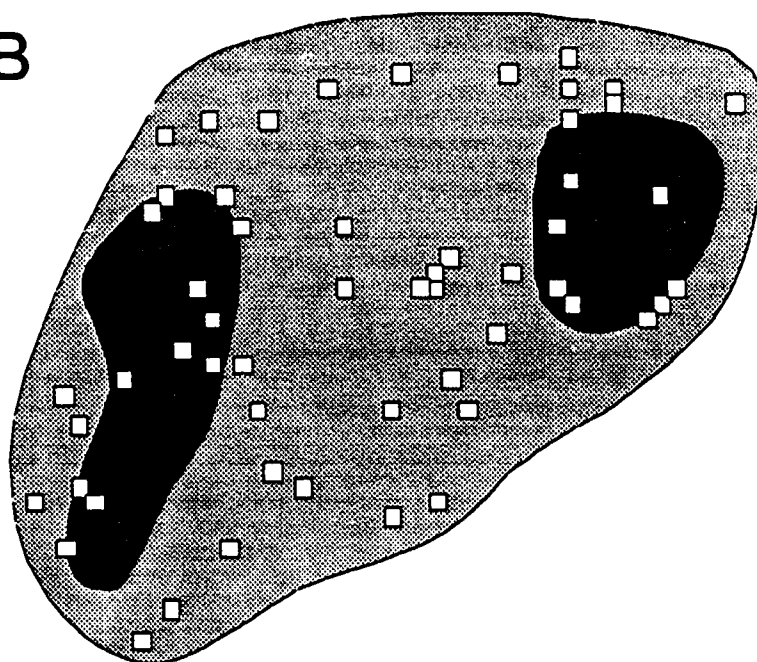
FIGURE 4.2.   PATCH RICHNESS - COMMUNITY LEVEL

A test of the null (=stochastic) distribution where patch richness is a function of patch size.   Specifically, we contrast the observed distribution (closed circles, continuous line) to the null distribution (open circles, dashed line).   Both distributions are best described by the nonlinear equation: $S = \beta_0 + \beta_1 (SA)^{0.5}$ (Appendix 4.1; $r^2_{null} = 0.886$, p < 0.001, $r^2_{observed} = 0.343$, p < 0.001, TableCurve 2D).
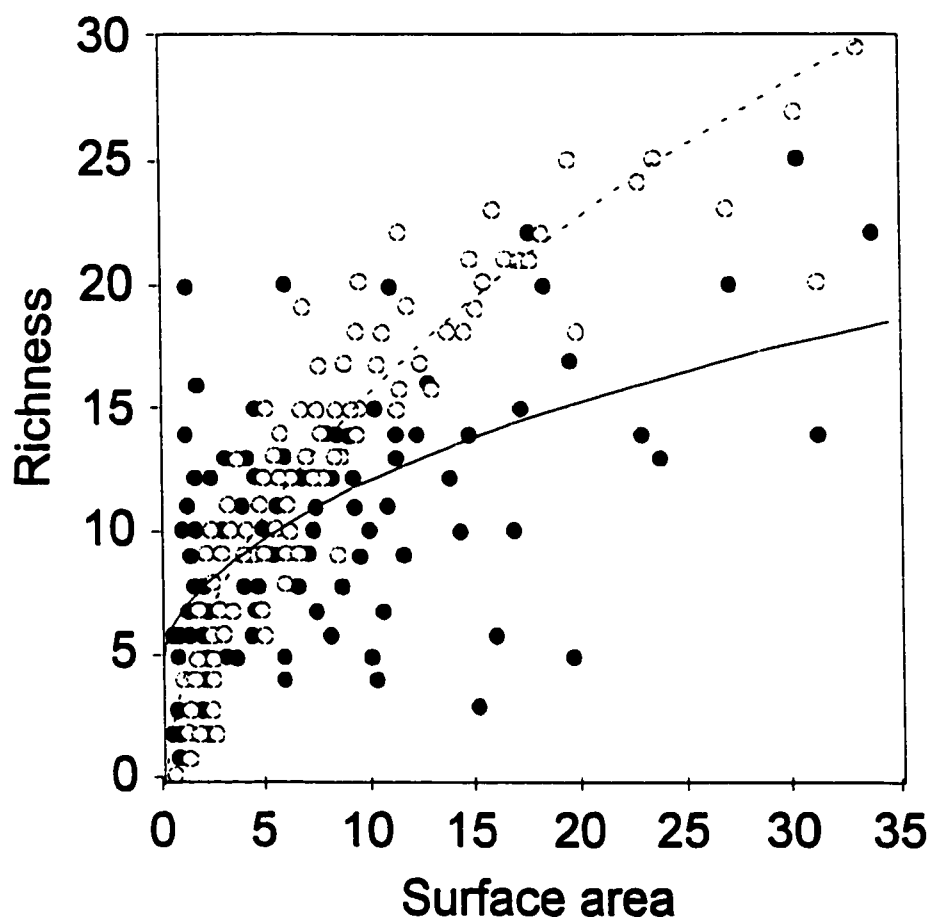
FIGURE 4.3. PATCH RICHNESS - SPECIES GROUPS

Patch richness explained as a function of patch size for three groups of species: Group 1 - habitat generalists, Group 2 - intermediate species, and Group 3 - habitat specialists. The null assemblage (A) exhibits substantially stronger relationships than the observed assemblage (B) but the trends associated within the groups are similar. The uppermost line (dotted) is the fit line for the whole assemblage (as in Figure 4.2).
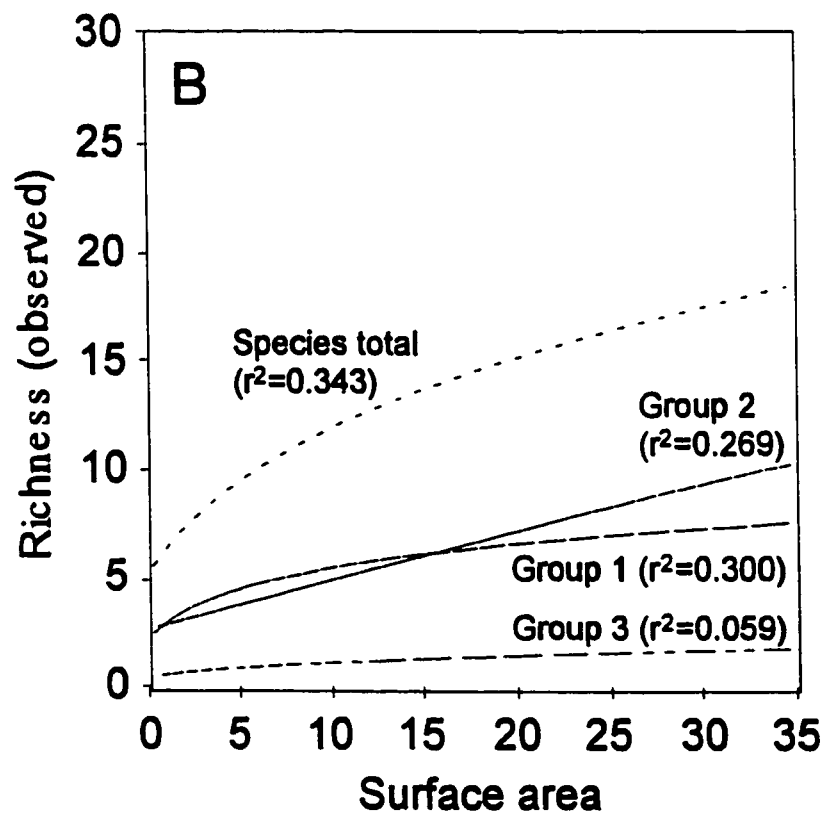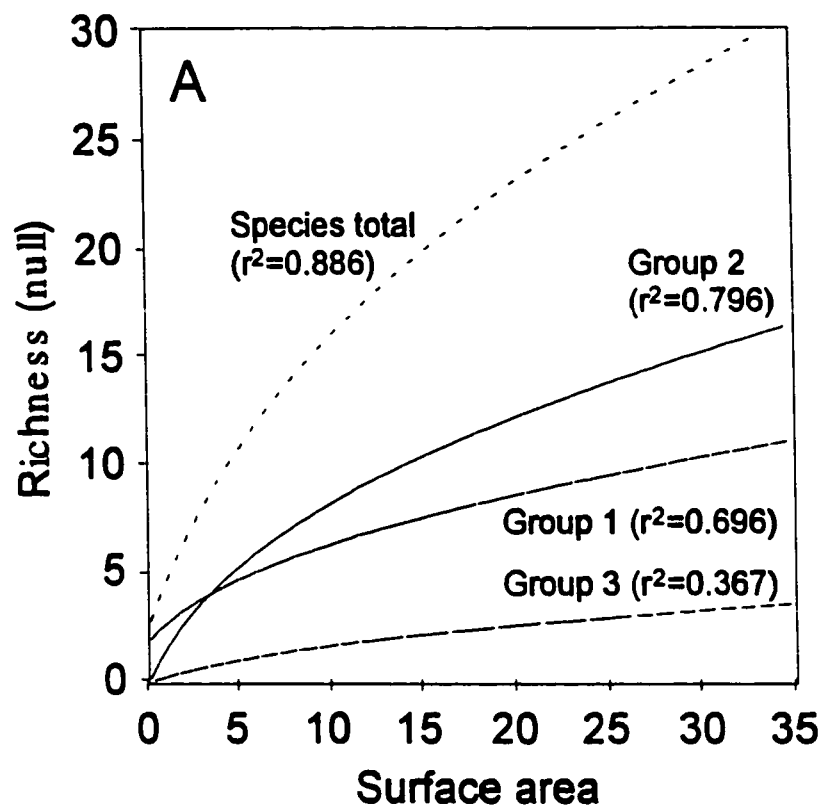
APPENDIX 4.1. OPTIMAL REGRESSION MODELS

We use a family of simple curvilinear and polynomial regression models to optimize the fit between patch richness and patch surface area for (a) entire null and observed assemblages, and (b) null and observed species groups (TableCurve 2D - Jandel 1994). We use the following steps and criteria to choose the most optimal equation:

(i) the regression model is statistically significant,

(ii) the beta coefficient for the highest ordered term must be statistically significant,

(iii) once an equation meets the above criteria we compare its F statistic with the F statistic for the next equation that also meets these criteria but has one less ordered term. We choose the model with the higher F statistic,

(iv) iterate the above process (steps i to iii) for equations with consecutively fewer terms,

(v) if no curvilinear or polynomial equation is accepted, we chose the simple linear regression model (equation no. 41) to describe the relationship (assuming it has not already been chosen through the iterative process).

Simple curvilinear and polynomial equations (maximum 4th order polynomial) used:-

1	$\ln y = a+bx+cx^2+dx^3$		22	$y = a+b(x)^{-2}$
2	$y^2 = a+bx+cx^2+dx^3$		23	$y = a+b\ln x(x)^{-2}$
3	$y^{0.5} = a+bx+cx^2+dx^3$		24	$y = a+b(x)^{-1.5}$
4	$y^{-1} = a+bx+cx^2+dx^3$		25	$y = a+b(x)^{-1}$

5    $y = a+b(\ln x)^{-1}+c(\ln x)^{-2}+d(\ln x)^{-3}$

6    $y = a+b(x)^{-1}+c(x)^{-2}+d(x)^{-3}$

7    $y = a+b\ln x+c(\ln x)^{2}+d(\ln x)^{3}$

8    $y = a+b(\ln x)^{2}+c\ln x+d(\ln x)^{-1}$

9    $y = a+bx+cx^{2}+d(x)^{-1}$

10    $y = a+bx+cx^{2}+dx^{3}$

11    $\ln y = a+bx+cx^{2}$

12    $y^{2} = a+bx+cx^{2}$

13    $y^{0.5} = a+bx+cx^{2}$

14    $y = a+b(\ln x)^{-1}+c(\ln x)^{-2}$

15    $y = a+b(x)^{-1}+c(x)^{-2}$

16    $y = a+b\ln x+c(\ln x)^{-1}$

17    $y = a+b(\ln x)^{2}+c\ln x$

18    $y = a+bx+c(x)^{-1}$

19    $y = a+bx+cx^{2}$

20    $\ln y = a+bx$

21    $y = a+be^{-x}$

26    $y = a+b\ln x(x)^{-1}$

27    $y = a+b(x)^{-0.5}$

28    $y = a+b(\ln x)^{-1}$

29    $y = a+b\ln x$

30    $y = a+bx^{0.5}$

31    $y = a+bx(\ln x)^{-1}$

32    $y = a+b(\ln x)^{2}$

33    $y = a+bx^{0.5}\ln x$

34    $y = a+be^{x}$

35    $y = a+bx^{3}$

36    $y = a+bx^{2.5}$

37    $y = a+bx^{2}\ln x$

38    $y = a+bx^{2}$

39    $y = a+bx^{1.5}$

40    $y = a+bx\ln x$

41    $y = a+bx$

SECTION V

CORAL REEF FISH AND HIERARCHICAL COMMUNITY ORGANIZATION - THE HABITAT DIMENSION MODEL

5

Coral reef fish and hierarchical community organization - the habitat dimension model

5.1 RATIONALE AND OBJECTIVES

The results from Section 3 suggest that the structure of fish communities on coral reefs conforms to the ideas of multi-level systems. This means that species that occur on most patch reefs (habitat generalists) have relatively low changes in population densities, and species that occur on few patch reefs (habitat specialists) have relatively high changes in population densities.

The results from Section 4 provide a hint of one possible mechanism that may contribute to this observed regularity. Specifically, the results described in Section 4 suggest a trend of *decreasing* correlation (and significance) between patch size and species distributions from habitat generalists (species found on many different patches) to habitat specialists (species found on few patches). This suggests that the habitat template (patch size in this case) is involved, to at least some extent, in controlling habitat generalists, but does not provide insight for why habitat specialists occur where *they* do. It is reasonable to assume, therefore, that there must be a second habitat attribute (or another process altogether) that is effective in controlling habitat specialists, but not

necessarily so for the habitat generalists. This interpretation agrees with the general model of multi-level community organization in that different assembly processes are dominant at different levels of the community structure. The purpose of Section 5, therefore, is to further illuminate the nature and significance of differences between habitat generalists and specialists, and thereby gain further insight into the overall organization of fish on coral reefs.

5.2 TITLE PAGE

CORAL REEF FISH AND HIERARCHICAL COMMUNITY ORGANIZATION - THE HABITAT DIMENSION MODEL (Submitted to Ecology)

by: Nigel Waltho

Jurek Kolasa

Department of Biology, McMaster University, 1280 Main St. W., Hamilton, Ontario, Canada, L8S 4K1

Tel (905) 525-9140   Waltho: Ext. 23041   Kolasa: Ext. 23100

e-mail: Waltho: walthond@mcmaster.ca   Kolasa: kolasa@mcmaster.ca

Fax (905) 522-6066

5.3 ABSTRACT

Species composition and richness in coral reef fish vary in space and time. This variability is thought to be due to stochastic processes, predominantly those originating *off-reef*. However, the evidence that the off-reef stochastic control is responsible for community structure is circumstantial. As an alternative, we suggest community structure is shaped by several *on-reef* non-stochastic processes that together, produce an appearance of stochastic patterns.

To test this hypothesis we use a hierarchical model to evaluate patterns at several scales. The hierarchical model we use differs from the more traditional spatial hierarchical models by being inspired by the Cartesian dimensions—points, lines, and planes—instead of spatial windows. Specifically, for each dimension we test for differences between the observed community patterns and those expected from simulated stochastic processes (random models). We found for the equivalent of the habitat point dimension that patch richness does not differ from the random model. Further, for the same dimension, patch abundance does differ from the random model. For the second dimension, the line (=habitat gradient), we found that smaller patches are more similar and large patches are less similar than expected by the random model. For the third dimension, the plane (=habitat landscape), we found that patch location relative to other patches significantly affects assemblage structure. We synthesize these results and those from prior studies into a new model of assemblage organization on patch reefs. This model emphasizes a gradient of constraints in perception of the habitat template from habitat specialists to

habitat generalists. The resulting range of responses translates into a complex pattern of richness and abundance. This pattern may, unless properly decomposed, appear as stochastic and thus give a false impression of underlying mechanisms.

5.4 INTRODUCTION

Fish assemblages on coral patch vary in space and time producing patterns of remarkable diversity. One explanation of such variability invokes off-reef stochastic processes that limit numbers of successful recruits and thus reduce the importance of on-reef mechanisms (e.g., such as competition; Victor 1983, Richards and Lindeman 1987, Doherty and Williams 1988, Sale and Steel 1986, Roberts 1991). However, the evidence for off-reef stochastic control of community organization alone is circumstantial. Further, the increasing awareness that measures of ecological effects are rate and scale dependent (Ebersole 1985, Pickett et al. 1989, Collins 1990, Levin 1992, Pickett et al. 1992) suggests that the evidence for stochastic control alone needs to be re-assessed. One approach to this problem is to assume that the appearance of off-reef stochastic control is instead a composite effect of several non-stochastic processes prevalent throughout recruitment and the following adult sedentary life stages (e.g., predation and preemptive behaviour; Shulman 1984, Jones 1991, Shapiro 1991). It is possible that these non-stochastic processes operate at different spatial and temporal scales and therefore we should view fish communities as complex systems, with the attendant analytic consequences. Hierarchy theory provides a framework for separating these composite

patterns into testable layers by drawing attention to on-reef processes expressed at different scales.

We use a hierarchical model, therefore, as a tool to re-examine the issue of variability in patch reef fish communities that appears central to our understanding of their organization (Williams 1982, Victor 1983, Doherty and Williams 1988, Bohnsack 1989, Robertson and Duke 1990, Sale and Guy 1992, Sale et al. 1994). Currently available hierarchical models (e.g., Allen 1987, O'Neill et al. 1988, Collins and Glenn 1991, Allen and Hoekstra 1992) are not suitable because they are space-dependent, that is, interpretation of fish assemblage structure is thought to depend to some degree on sampling frequency and patch or quadrat size (e.g., Gladfelter et al. 1980, Bohnsack 1983, Sale and Sharp 1983, Sale and Douglas 1984). We therefore introduce and use a new hierarchical model based on the ecological equivalents of Cartesian dimensions: points, lines, and planes, 'habitat-dimension model' or HDM. In the 'habitat-dimension model' each Cartesian dimension corresponds to one resolution (dimension) at which the physical habitat template can be perceived by fish. The model comprises three dimension: (a) a habitat point where only habitat presence or absence is of interest, (b) a habitat gradient formed by differences in habitat qualities, and (c) a habitat landscape where each patch has a unique spatial position relative to all other patches (Fig. 5.1).

Depending on the species perception of the habitat landscape, fish can respond to any or all of these dimensions in a detectable manner that can then be compared to corresponding stochastic expectations. In this context the null hypothesis states: observed patterns are no different from those obtained by simulating stochastic processes.

A rejection of the null hypothesis implies that processes other than stochastic mechanisms may be responsible for the appearance of stochasticity currently found in reef fish assemblages. Furthermore, comparison of assemblage patterns associated with each dimension may suggest which mechanisms are involved. Our analysis and interpretation proceeds via several steps:

(i) we introduce the hierarchical 'habitat-dimension model', HDM,

(ii) we use the HDM as a framework to test for differences between observed assemblage patterns and expected (=stochastic) patterns, and

(iii) we develop an organizational model consistent with our results and those from prior studies.

5.5 METHODS

We obtained data on patch reef fish (i.e., species composition, richness, and species abundances - see Appendix 5.1) from 40 patch reefs in Discovery Bay, Jamaica (for a description of field techniques refer to Waltho and Kolasa 1996). Distances to nearby patches were measured by the shortest distance between patch surfaces (as compared to patch centers). We used compass readings to determine the vector angles between patch pairs, from which with the help of triangulation procedures we created a map of patch reef locations (Fig. 5.2).

5.5.1 Habitat-dimension model (HDM)

The 'habitat-dimension model' comprises three dimensions. Different conceptual limitations are associated with each of these dimensions and therefore, assumptions and statistical procedures are necessarily dimension-specific. We outline these assumptions, null hypotheses, and statistical procedures for each dimension accordingly.

5.5.2 Habitat-point dimension (HPD)

This dimension is conceptually analogous to the Cartesian zero dimension—the point. Points in space are defined by their presence only, that is, points have no length, surface area, or volume that can be distinguished amongst. Our equivalent of the Cartesian point is the patch reef stripped of all measurable attributes (Fig. 5.1C). The 'habitat-point dimension', therefore, is the view in which patch reefs appear to fish as habitat points indistinguishable in both habitat properties and accessibility.

Within the confines of this dimension each patch is treated as a statistical replicate. At this level the allowable patterns one can analyze are those of patch richness and patch abundance distributions. We develop two null models accordingly: $H_{0-HPD(a)}$ observed patch richness, and $H_{0-HPD(b)}$ observed patch abundance distributions do not differ significantly from expected random test distributions (e.g., normal, lognormal, chi-square, and Poisson). Significant deviations (chi-square test, Rohlf and Sokal 1981) between the observed and random distributions are interpreted to suggest that fish respond to some patch attributes other than its mere presence.

5.5.3 Habitat-gradient dimension (HGD)

The 'habitat-gradient dimension' (HGD) is the second level in our hierarchical framework. It is analogous to the Cartesian one dimension where each point of a line is defined by its position along that line. Our ecological equivalent of the Cartesian line is the positioning of patches along some ecological gradient (Fig. 5.1C). Many different gradients may exist, each corresponding to a different ordering of patches (e.g., depth, percentage of live coral, habitat heterogeneity, availability of shelter sites). Further it is possible to construe a composite gradient consisting of several concurrent gradients. Thus, the 'habitat-gradient dimension' differs from the 'habitat-point dimension' in that patch reefs now appear to fish as points with some ecological properties that can be qualitatively assessed. Patch reefs, however, remain equally accessible (i.e., spatial relation among patches remains undefined).

For this second dimension we assume patches of similar size are comparable in habitat complexity, shelter, and resource availability (Tonn and Magnuson 1982, Risk communiqué), and therefore, should contain species assemblages more similar to one another than two patches that differ in size. We therefore develop the habitat gradient from a matrix of all possible combinations of inter patch similarities in surface area. However, these similarities must be weighted according to the surface area of all patches. For example, two small patches of equal size would have the same similarity value as two large patches of equal size unless the absolute size of the patches is accounted for. Thus,

the habitat gradient incorporates both the size ratio of the two patches, and their combined surface area. Specifically, we define the habitat gradient as:

$$SAI_{ij} = \log\left[\left(\frac{SA_i}{SA_j}\right) * e^{(SA_i + SA_j)}\right]$$

where SAI_{ij} is the 'surface area index' for patches i and j, SA_i is the surface area of the larger patch, and SA_j is the surface area of the smaller patch. This index gives a higher value to: (a) reef pairs whose surface area ratio is similar to another reef pair but whose combined surface area is greater, and (b) to reef pairs whose ratio is greater than another reef pair but whose combined surface areas are similar (Table 5.1). The index values for all pair combinations form the habitat gradient of patch similarities. We then correlate this gradient against the observed and expected assemblage similarities.

We simulate the expected stochastic fish assemblage patterns by distributing individuals according to the probability of settling on a particular patch as a function of the total abundance of the recruiting species and the surface area of that patch. We use this strategy because larger patches are expected to 'passively' sample the regional species pool more completely than small patches, and thus to form and retain more similar assemblages (Sale and Douglas 1984, Clarke 1988).

We can now formulate the null hypothesis for this dimension, H_{0-HGD}. Specifically, if observed assemblages are generated by stochastic processes, then the regression model that best describes the relation between observed assemblage similarities and the habitat gradient 'surface area index' (see Appendix 5.2) should not differ significantly from the regression model that best describes the relation between expected (=stochastic)

assemblage similarities and the same gradient 'surface area index'. However, since we do not know a priori which numerical resolution such as species presence and absence, species ranking, and species abundance to analyze the data at, we conduct the test using three similarity coefficients (Jaccard, Spearman, and Pearson) appropriate for each of the respective resolutions. This accounts for any potential differences, and hence interpretations, among the three numerical resolutions (e.g., Rahel et al. 1984, Frost et al. 1988, Rahel 1990).

We suggest that if the regression coefficients for the observed model lie within the 95% confidence limits of the stochastic model's, then the observed assemblage similarities do not differ from expected assemblage similarities (Sokal and Rohlf 1995). However, if the regression coefficients for the observed model lie outside 95% confidence limits of the stochastic model, then we interpret this to suggest that patch size plays a greater or lesser role in structuring fish assemblage than stochastic processes (e.g., passive recruitment) alone can account for.

5.5.4 Habitat-landscape dimension (HLD).

In Cartesian two dimensions every point on a plane has a specific spatial relation to every other point. Our ecological equivalent of the Cartesian plane is the landscape of patch reefs. This landscape is described by the spatial location or proximity (coordinates, vector distances) of each reef relative to other reefs. For fish, proximity to other patches could be important for (a) biotic interactions such as foraging, frequency of competitive

encounters, shelter from predation, finding mates, and (b) an indication of habitat quality such as light, siltation stress, water currents and temperature. It is possible that this proximity influences patch composition and abundance and thus assemblage similarity to other patches. For example, a patch spatially equidistant to two other similar sized patches may show different similarity values to each depending on <u>their</u> position relative to <u>their</u> neighbours. The 'habitat-landscape dimension' is the view in which fish perceive patches as qualitatively distinct (similar to that of the HGD) and spatially distinct (unique feature of this level).

To test the proximity effect we determine if observed assemblage similarities (Pearson correlation) depart significantly from stochastic expectations. The specific null hypothesis, H_{0-HLD}, is: If observed assemblages are generated by stochastic processes then the regression model that best describes the relation between assemblage similarities (calculated for observed locations) and 'inter patch distance' should not be significantly different from the regression model that best describes the relation between assemblage similarities (calculated from randomized locations) and 'inter patch distance'. Randomized location is produced by the re-allocation of each observed assemblage to a randomly selected patch within the patch reef template. For both regression models we include 'surface-area index' as a covariate (Sokal and Rohlf 1995).

If the regression coefficient for 'inter patch distance' is similar for observed and random location regression models, then we conclude that patch position does not influence assemblage structure. However, if the value of this coefficient is significantly

different between the two regression models then this is an indication that patch location has an effect on assemblage structure.

5.6 RESULTS

5.6.1 Habitat-point dimension (HPD)

Patch richness does not differ from any of the tested random distributions, whereas patch abundances differ significantly from all but the lognormal distribution (Fig. 5.3, and Table 5.2). The conformity of patch abundances to the lognormal distribution is similar to species abundance distributions in rich communities (e.g., Gaston 1994). Patch abundance distribution may thus be an artifact of species abundances because fish abundances also agree with the lognormal (p = 0.259). Thus, while the lognormal distribution of species abundances may be a product of multiple random factors (May 1975, Magurran 1988), it does not represent adequate evidence that random processes are the only ones determining the community structure. To the contrary, some interpret it as evidence of some organization (Ugland and Gray 1982). We therefore accept the null hypothesis for patch richness and reject it for patch abundance, that is, we accept that the distribution of patch richness agrees with stochastic expectations whereas patch abundance does not.

5.6.2 Habitat-gradient dimension (HGD)

The regression models (based on Pearson, Spearman, and Jaccard similarities) that best describe the relation between observed 'assemblage similarity' and 'surface area index' differ significantly from their corresponding stochastic regression models (Table 5.3). The differences are consistent in that observed similarities are greater than expected for assemblage pairs on small patches, and lower than expected for assemblage pairs on large patches (Fig. 5.4).

5.6.3 Habitat-landscape dimension (HLD)

Assemblage similarities (observed locations, Pearson correlation) are dependent on both the spatial distance between patches and the covariate 'surface-area index' ($F = 56$, $r^2 = 0.126$, $p_{patch\ distance} < 0.01$, and $p_{surface-area\ index} < 0.001$; Fig. 5.5A). Assemblage similarities produced by the random re-allocation of complete assemblages throughout the patch landscape are dependent on the covariate 'surface-area index' only ($F = 3.5$, $r^2 = 0.009$, $p_{patch\ distance} = 0.865$, and $p_{surface-area\ index} < 0.01$) (Fig. 5.5B). Furthermore, from the MANCOVA the value of the regression coefficient for 'patch distance' differs significantly between observed and random assemblage location models ($beta_{observed} = 0.00369$, $beta_{random} = -0.000106$, $p_{chi-square} < 0.01$).

5.7 DISCUSSION

The picture emerging from this study is potentially confusing. Some patterns are clearly different from randomly generated ones suggesting a role for non-stochastic organization processes. Some conform to random models and thus support the stochastic interpretation of community assembly, and some escape unequivocal interpretation (e.g., lognormal fit to patch abundances). To accommodate this apparently confusing mixture we develop an organizational model consistent with our results and those from prior studies. A graphical representation of this model permits examination of its behaviour and heuristic value (Fig. 5.6). Specifically, we suggest that species abundance distributions across the landscape of patch reefs are an inverse function of habitat fragmentation perceived by each species. Consider the following:

If a species perceives the habitat at low resolution (such that the landscape of patch reefs is perceived to be a single continuous entity), then a single density center develops peaking over a cluster of neighboring patch reefs. The further away a patch reef is from this density center the lower the species abundance is expected. This distribution develops because individuals of such habitat generalists move through landscape template without being penalized (Kolasa 1989) and subsequently recruit or migrate to that landscape region where conspecifics already occur (Shapiro 1987, Shapiro 1991, cf. Sale 1991). A density center of one species reduces chances for density centers other species to form at the same location. We provide supporting evidence for this by finding that assemblage similarity is higher than expected for patches in close proximity, and lower than expected for distant patches (habitat landscape dimension - HDL).

However, we suspect that species do differ in their perception of discontinuities in preferred habitat regions (cf. Kolasa 1989, Kareiva 1990, Waltho and Kolasa 1996). Therefore, a species perceiving the landscape of patches at a higher resolution (relative to that of the habitat generalist) sees the habitat template as discontinuous (i.e., as fragments consisting of groups of patches). 'Local density centers' form within each habitat fragment. Over the whole reef system such local density centers appear as random clumping. At a finer resolution, a habitat specialist is so constrained by habitat fragmentation that it cannot develop local density centers, and thus its individuals are spatially independent from each other.

Although this conceptual model remains untested, it is the most complete proposition accounting for the available observations - both in this and previous studies. We found or know that:

(i) species index of dispersion (Krebs 1989) increases linearly as a function of species abundance from 0.1 (over-dispersed]) to 1.5 (clumped), $r^2 = 0.463$, p < 0.001. This suggests that species low in abundance are over-dispersed, and species of high abundance are clumped;

(ii) patch richness does not differ from stochastic expectations (see HPD). About 80 percent of the available taxa have abundance and distribution indicative of habitat specialists. These species tend to spread randomly over the landscape (see above) and dominate the observed patch richness pattern;

(iii) patch abundance differs significantly from stochastic expectations (see HPD). About 20 percent of the available taxa have abundance and distribution indicative of habitat

generalists. These species tend to form density centers and, because they contain more than 80 percent of patch abundance, they dominate the observed abundance patterns;

(iv) small patches share assemblages that are more similar than expected, and large patches share less similar assemblages than expected (see HGD). We attribute this to two observations: first, there exists a positive relation in our habitat template between the 'surface area index' and inter-patch distances, that is, patches in close proximity tend to be smaller than distant patches ($p < 0.01$). Therefore, the non-overlapping 'density centers' of abundant species are more likely to span several small patches than large patches and increase small patch similarity. Second, it is possible that smaller patches have insufficient resources for habitat specialists to reside and therefore their similarity arises almost exclusively from the presence of habitat generalists.

(v) assemblage similarity is greater among close patches and lower than expected for distant patches (see HLD). Again, non-overlapping 'density centers' imply density gradients in which closer patches have more similar assemblages, both in terms of composition and abundance.

(vi) assemblage structure on individual patches appears to change stochastically through time (e.g., Bohnsack 1983, Winemiller and Pianka 1990, cf. Sale 1991). Indeed, the drift of 'density peaks' through the landscape of patches could alone be responsible for this. The drift could occur as a direct result of fish translocations (e.g., Scaridae and Acanthuridae), or paradoxically, as an indirect result of a species immobility (e.g., Promacentridae). The following scenario may apply. Juveniles recruit to and saturate individual patches in waves determined by stochastic extraneous factors and,

subsequently, associate with these patches for a long period of time. During this time colonizers either slowly emigrate or mature and die. Meantime, a new wave of recruits might begin to accrue in a different region of the patch landscape. While the first density peak dissolves through deaths and emigration, the new one builds up resulting in an effective shift of a density center. If many species go through a similar process, then any single patch will appear highly variable through time.

We conclude by suggesting that the assemblages on coral reef patches are partly determined by factors other than stochastic. These factors could include differential perception of elements of habitat mosaic and thus habitat fragmentation. We further suggest that the model we proposed requires further testing which could, for example, include searching and testing for 'density centers' and their movement.

5.8 ACKNOWLEDGMENTS

5.9 REFERENCES CITED

1. Allen T.F.H. (1987) Hierarchical complexity in ecology: a non-Euclidean conception of the data space. Vegetatio 69: 17-25

2. Allen T.F.H., and T.W. Hoekstra (1992) Toward a Unified Ecology. Columbia Univ. Press. N.Y., N.Y. 384 pp.

3. Bohnsack J.A. (1983) Species turnover and the order versus chaos controversy concerning reef fish community structure. Coral Reefs 1:223-228

4. Bohnsack J.A. (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. 44(2):631-645

5. Clarke R.D. (1988) Chance and order in determining fish species composition on small coral patches. J. Exp. Mar. Biol. Ecol. 115:197-212

6. Collins S.L. (1990) Patterns of community structure during succession in tallgrass prairie. Bull. Torrey Bot. Club 117(4):397-408

7. Collins, S.L. and S.M. Glenn (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72:654-664

8. Doherty P.J., and D.McB. Williams (1988) The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26:487-551

9. Doherty P.J., and D.McB. Williams (1988) Are local populations of coral reef fishes equilibrial assemblages? The empirical database. Proc. Int. Coral Reef Symp., 6th 1:131-139

10. Ebersole J. P. (1985) Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66:14-20

11. Frost, T.M., D.L. DeAngelis, S.M. Bartell, D.J. Hall, and S.H. Hurlbert (1988) Scale in the design and interpretation of aquatic community research. In: S.R. Carpenter (eds.) Complex interactions in lake communities Springer, New York. pp. 229-258.

12. Gaston, K.J. (1994) Rarity. Chapman and Hall, New York, 205 pp.

13. Gladfelter W.B., J.C. Ogden, and E.H. Gladfelter (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61:1156-1168

14. Jones G.P. (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: The Ecology of Fishes on Coral reefs (eds) P.F. Sale. Academic Press, San Diego pp. 294-328

15. Kareiva P. (1990) Population dynamics in spatially complex environments: Theory and data. Phil. Trans. R. Soc. Lond. B 330:175-190

16. Kolasa J. (1989) Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology 70(1):36-47

17. Krebs, C.J. (1989) Ecological Methodology. Eds. C.J. Krebs. Harper and Row, Publishers, New York. 654 pp.

18. Levin, S.A (1992) The problem of pattern and scale in ecology. Ecology 73:1943-1967

19. Magurran, A.E. (1988) Ecological diversity and its measurements. Chapman and Hall, London

20. May, R.M. (1975) Patterns of species abundance and diversity, In: Ecology and Evolution of Communities (eds. W.H. van Dobben and R.H. Lowe-McConnell). W. Junk, The Hague, pp. 81-120

21. O'Neill, R.V., B.T. Milne, M.G. Turner, and R.H. Gardner (1988) Resource Utilization Scales and Landscape Pattern. Landscape Ecol. 2:63-69

22. Pickett S.T.A., J. Kolasa, J.J. Armesto, and S.L. Collins (1989) The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129-136

23. Pickett, S.T.A., T.V. Parker, and P.L. Fiedler (1992) The new paradigm in ecology: Implications for conservation biology above the species level. In: Conservation biology: The theory and practice of nature conservation, preservation, and management, edited by Fiedler, P. and S. Jain. New York, Chapman and Hall, 1992, p. 65-88.

24. Rahel F.J. (1990) The hierarchical nature of community persistence: a problem of scale. Am. Nat. 136:328-344

25. Rahel F.J., J.D, Lyons, and P.A. Cochran (1984) Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. Am. Nat. 124:583-589

26. Richards W.J., and K.C. Lindeman (1987) Recruitment dynamics of reef fishes: Planktonic processes, settlement and demersal ecologies, and fishery analysis. Bull. Mar. Sci. 41:392-410

27. Roberts C.M. (1991) Larval mortality and the composition of coral reef fish communities. TREE 6(3):83-87

28. Robertson A.I., and N.C. Duke (1990) Mangrove fish communities in tropical Queensland, Australia; spatial and temporal patterns in densities, biomass, and community structure. Mar. Biol. 104(3): 369-379

29. Rohlf F.J., and R.R. Sokal (1981). Statistical Tables. Eds. F.J. Rohlf and R.R. Sokal. W.H. Freeman and Company, New York. 219 pp.

30. Sale P.F. (1980) Assemblages of fish on patch reefs - predictable or unpredictable? Env. Biol. Fish 5:243-249

31. Sale P.F. (1980) The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18:367-421

32. Sale P.F. (1991) Reef fish communities: open nonequilibrium systems. In: The Ecology of Fishes on Coral reefs (eds) P.F. Sale. Academic Press, San Diego pp. 564-598

33. Sale P.F., and B.J. Sharp (1983) Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2: 37-42

34. Sale P.F., and J.A. Guy (1992) Persistence of community structure: what happens when you change taxonomic scale? Coral Reefs (1992) 11:147-154

35. Sale P.F., and W.A. Douglas (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. Ecol. 65(2):409-422

36. Sale P.F., and W.J. Steel (1986) Random placement and the structure of reef fish communities. Mar. Ecol. Prog. Ser. 28:165-174.

37. Sale P.F., J.A. Guy, and W.J. Steel (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. Oecologia 98:83-99

38. Shapiro D.Y. (1987) Patterns of space use common to widely different types of social groupings of a coral reef fish. Environ. Biol. Fishes 18:183-194

39. Shapiro D.Y. (1991) Intraspecific variability in social systems of coral reef fishes. pp. 331-355 In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, N.Y., N.Y.

40. Shulman M.J. (1984) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecol. 66(3): 1056-1066

41. Sokal R.R., and F.J. Rohlf (1995) Biometry. Eds. R.R. Sokal and F.J. Rohlf. W.H. Freeman and Company, New York. 850 pp.

42. Ugland, K.I., and J.S. Gray (1982) Log normal distributions and the concept of community equilibrium. Oikos 39:171-178

43. Victor, B.C. (1983) Recruitment and Population Dynamics of a Coral Reef Fish. Science 219:419-420

44. Waltho, N. and J. Kolasa 1994. Organization of instabilities in multispecies systems, a test of hierarchy theory. Proc. Natl. Acad. Sci. 91:1682-1685

45. Waltho, N. and J. Kolasa (1996) Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models. Env. Biol. Fishes (in press)

46. Williams, D.McB. (1982) Patterns in Distribution of Fish Communities across the central Great Barrier Reef. Coral Reefs 1:35-43

47. Winemiller K.O., and E.R. Pianka (1990) Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Mono. 60(1): 27-55

TABLE 5.1. SURFACE AREA INDEX

We show two examples of the 'surface area index', SAI. In (a) both pairs of patch reefs have similar surface area ratios, although the second pair has a greater total surface area. We award the second pair the higher SAI. In (b) both pairs have the same total surface area, but the second pair has a greater surface area ratio. We award the second pair the higher SAI.

	Patch reef surface area (units)	Surface area ratio	Surface area total	Surface area index
(a)	①← →①	1	2	0.869
	②← →②	1	4	1.737
(b)	③← →③	1	6	2.606
	②← →④	2	6	2.907

TABLE 5.2. HABITAT-POINT DIMENSION

'Habitat-point dimension' patch richness and abundance test distributions. The null model is that observed patch richness and patch abundance distributions do not differ significantly from expected test distributions (e.g., Normal, Lognormal, Chi-square, and Poisson; in the Poisson distribution we divided the data range into 25 categories). We test each observed distribution against the expected test distributions using the Chi-square test statistic (STATISTICA). Asterisk identify significant differences.

Patch Resolution	Test Distribution	Observed Mean	Degrees of Freedom	Chi-square Test Statistic	p
(a) Richness	• normal	11.35	3	5.629	0.131
	• log-normal	2.37	3	1.940	0.585
	• chi-square	11.35	4	3.454	0.485
	• Poisson	lambda 11.35	3	0.800	0.849
(b) Abundance	• normal	24.78	3	15.855	<0.005*
	• log-normal	3.05	3	2.451	0.484
	• chi-square	24.78	4	25.994	<0.001*
	• Poisson	lambda 24.78	3	29.385	<0.001*

## TABLE 5.3. HABITAT GRADIENT DIMENSION

'Habitat-gradient dimension' assemblage similarities evaluated as a function of the 'surface-area index'. We report the equation that best describes the empirical relation (where 'y' equals the assemblage correlation, 'a' and 'b' are regression coefficients, and 'x' equals the 'surface-area index'). In all cases the observed regression coefficients lie outside the confidence limits for the expected regressions. Furthermore, all intercepts are higher than expected, and all slopes are lower than expected.

		Pearson	Spearman	Jaccard
	Equation	$y = a + bx^{0.5}$	$y = a + bx^{0.5}$	$y = a + bx^{0.5}$
Observed	r^2	0.115	0.104	0.104
	a	0.187	0.168	0.159
	b	0.102	0.075	0.051
Expected	r^2	0.311	0.257	0.206
	$a_{lower\ 95\%}, a_{upper\ 95\%}$	-0.106, -0.002	-0.032, 0.046	0.004, 0.067
	$b_{lower\ 95\%}, b_{upper\ 95\%}$	0.164, 0.203	0.106, 0.135	0.070, 0.093

FIGURE 5.1. HABITAT DIMENSION MODEL

Scale, dimensions, and the 'habitat-dimension model'. (A) A common hierarchical decomposition of pattern is the vary spatial (and temporal) scale; (B) a conceptually new approach uses the Cartesian dimensionality model of points, lines. and planes; (C) 'habitat-dimension model' requires that the habitat attributes be represented as Cartesian dimensions. Thus, the habitat template is viewed as a collection of patches each ecologically similar (habitat-point dimension); a linear ordering of habitat qualities (habitat-gradient dimension); and as a landscape of spatially distributed patches (habitat-landscape dimension).

A

Y

X
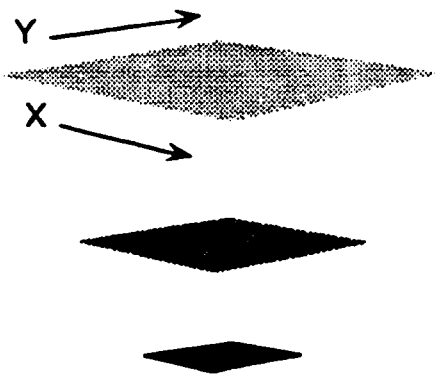
B

2-D, Plane

1-D, Line
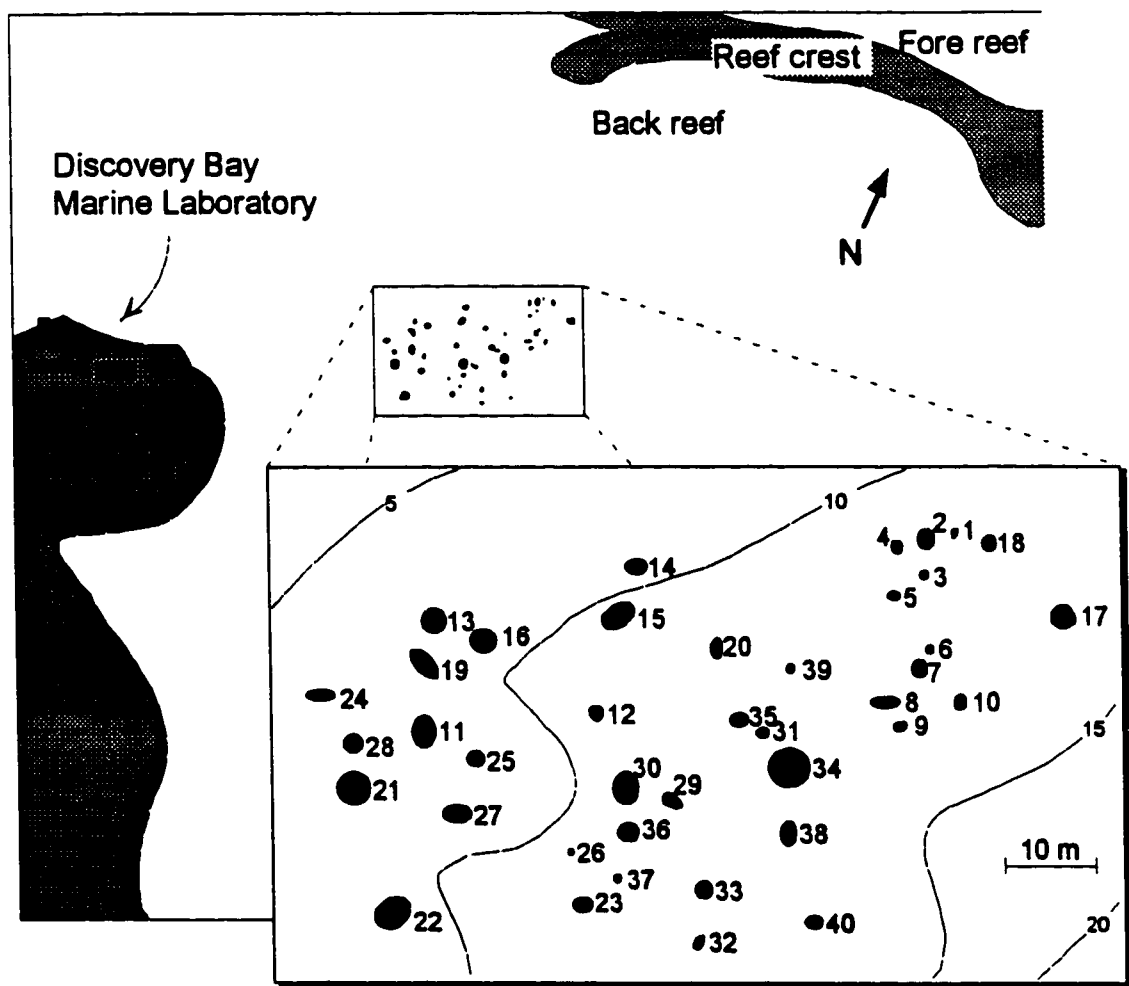
0-D, Point

**C**

Habitat-landscape

Habitat-gradient

Habitat-point

FIGURE 5.2. DISCOVERY BAY, JAMAICA

West coast of Discovery Bay, Jamaica showing back reef bathymetrics (m) and spatial

location of each reef patch.

FIGURE 5.3. HABITAT POINT DIMENSION

Habitat-point dimension (HPD): (A) Frequency distribution of patch richness does not differ from random distributions (i.e., null models); (B) frequency distribution of patch abundance differs from all random but the lognormal distribution.
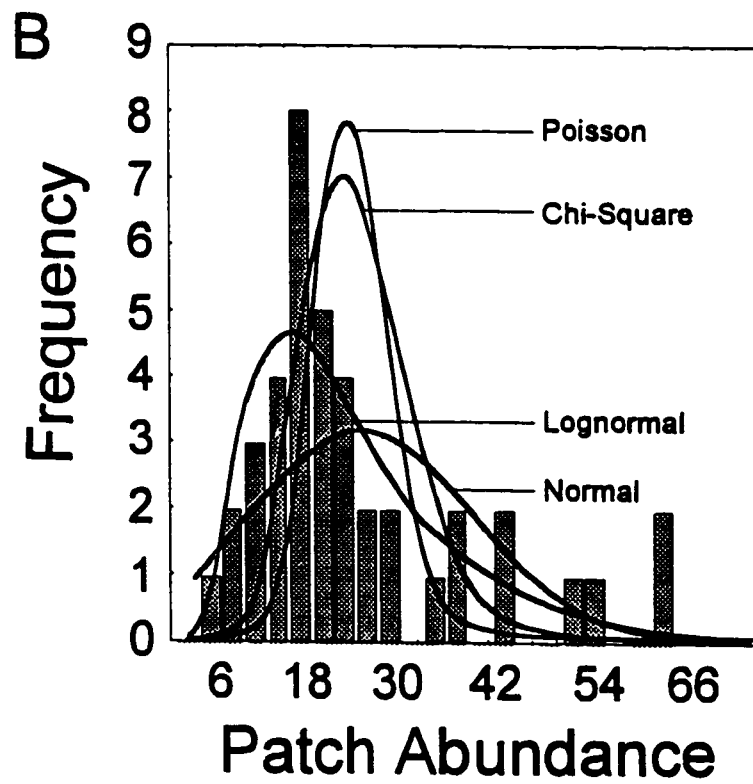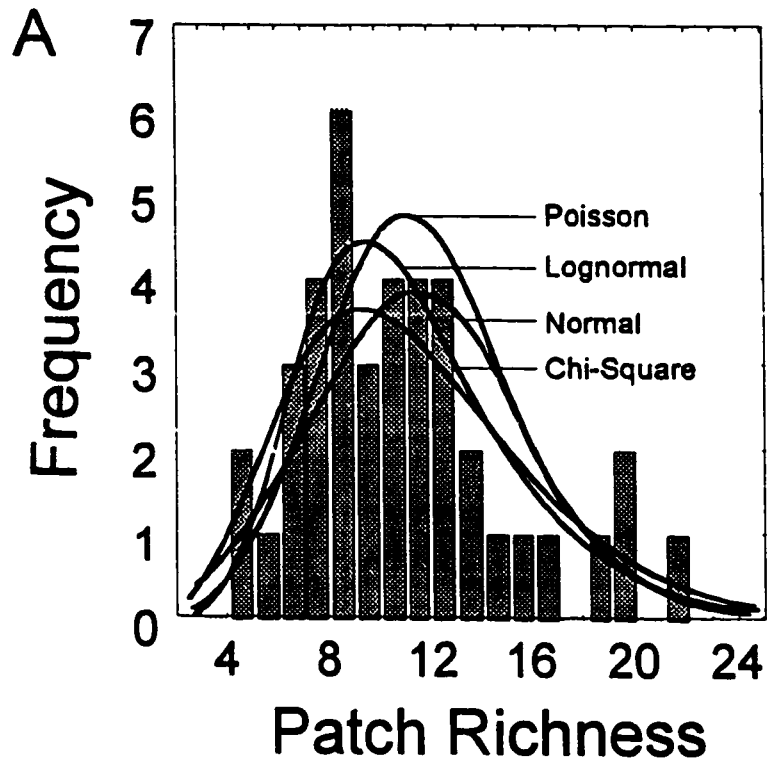
FIGURE 5.4. HABITAT GRADIENT DIMENSION

Habitat-gradient dimension (HGD): assemblage similarity as a composite function of patch size and size similarity within patch pairs (Surface Area Index, explained in text). Dashed lines represent 95% confidence limits around the null models for each of the three numerical resolutions. Thick continuous lines represent observed trends. Assemblages are more similar than expected on small patches (i.e., low Surface Area Index) and less similar than expected on large patches.
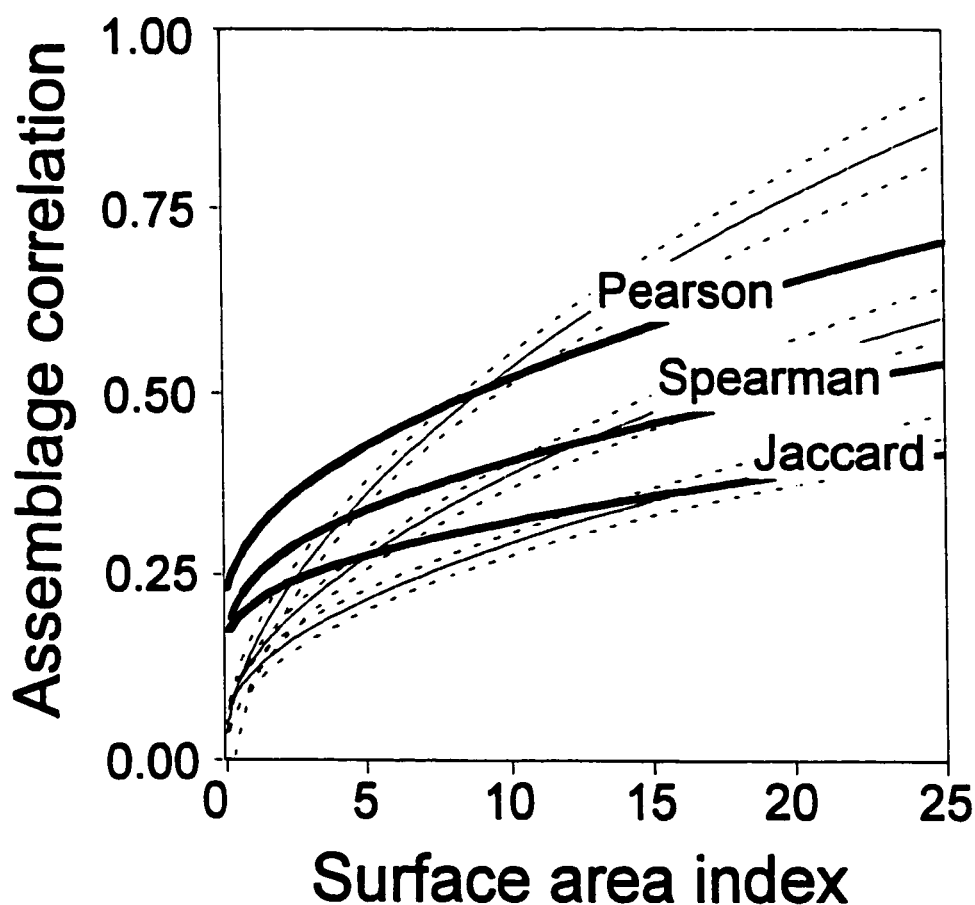
FIGURE 5.5. HABITAT LANDSCAPE DIMENSION

Habitat-landscape dimension: (A) Similarity among observed assemblages measured by Pearson correlation are significantly affected by both spatial distance between patches and their size relationship (Surface Area Index); (B) similarity among randomly dispersed assemblages show some dependence on Surface Area Index only.
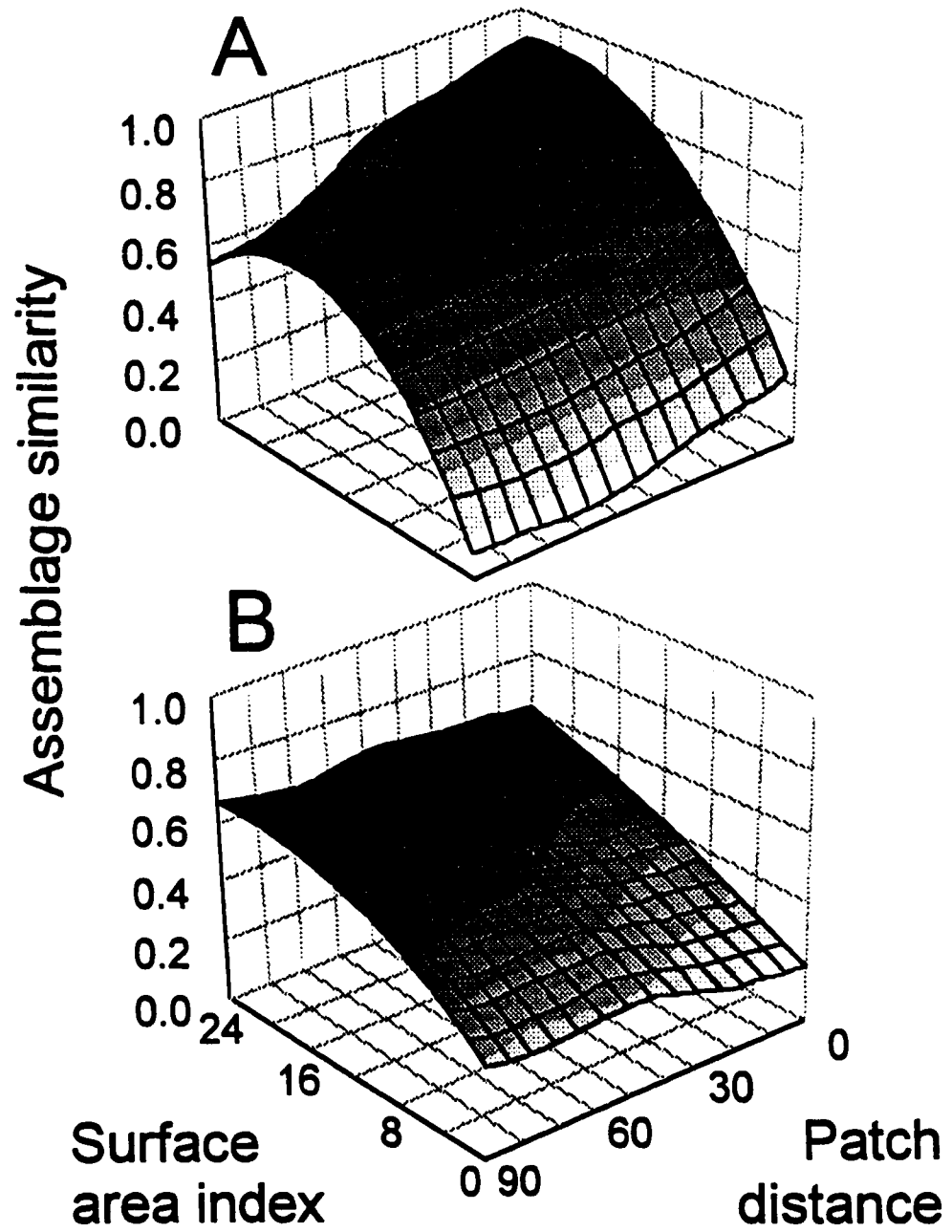
FIGURE 5.6. ASSEMBLAGE ORGANIZATION - A SYNTHESIS

Conceptual model of habitat structure, scale of perception, and their relationship to assemblage organization. (A) Actual landscape of patches in Discovery Bay (see Fig. 5.2); (B) possible scales at which various fishes perceive details of the landscape. For example, a habitat generalist perceives its habitat as unfragmented (top level) while a habitat specialist perceives a highly fragmented mosaic of patches (bottom level); (C) spatial, xy-plane, and numerical (abundance), z-axis, responses fishes exhibit depending on their perception of the landscape template: Species 1 and 2 (habitat generalists) are able to use the whole habitat and form mutually exclusive abundance peaks via intra-specific processes (see text); Species 3 uses some habitat sub-units only and forms regional abundance peaks; Species 4 (habitat specialist) is constrained to specific locations only.

.
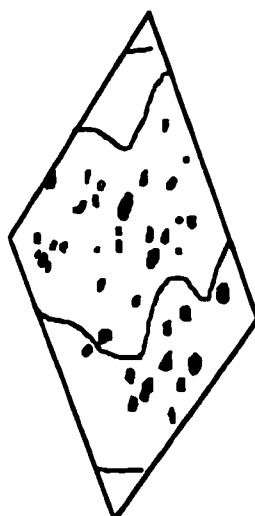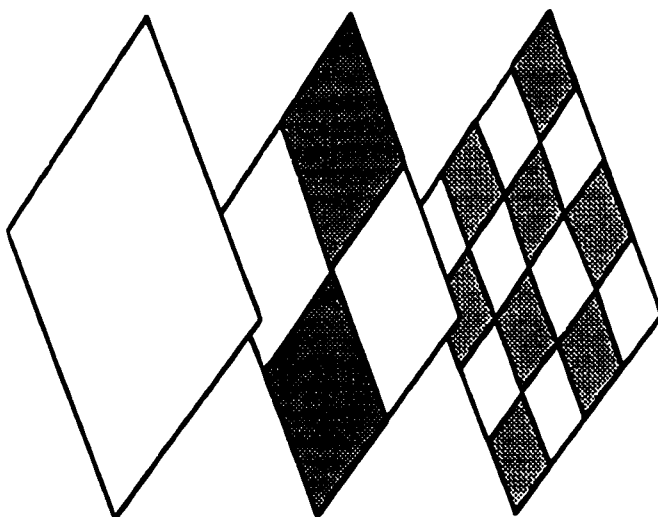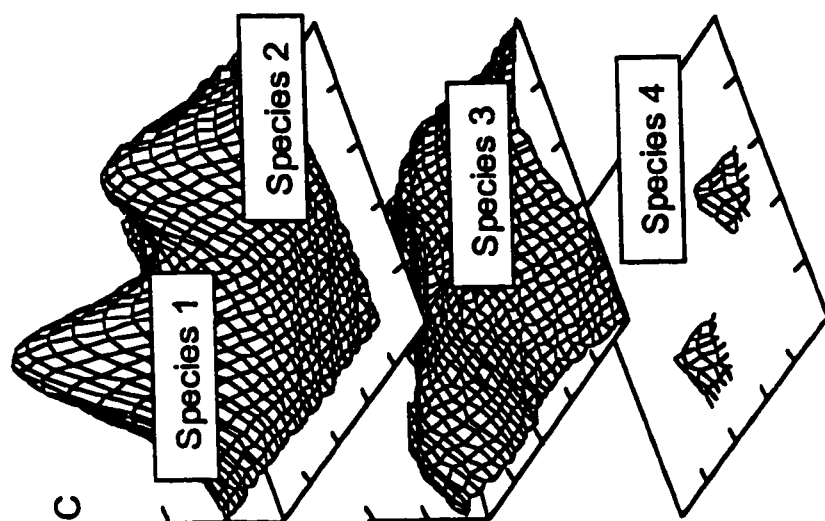
Appendix 5.1. Species data

Fish community from the back reef of Discovery Bay, Jamaica. 'Group' is the 'habitat-based model' group designation number for each species. 'N' refers to species abundance for all 40 patches. 'Patch' is the number of patch reefs the species was observed on. 'SA' is the area of patch habitat a species was observed (maximum possible 319 m^2). 'ER' is species ecological range. 'Dispersion' is species index of dispersion (Krebs 1989).

Group	Species	Common name	N	Patch	SA	ER	Dispersion
1	Stegastes partitus	Bicolor Damselfish	21	16	129.7	0.40	0.276
1	S. planifrons	Threespot Damselfish	151	34	300.7	0.90	2.118
1	Acanthurus chirurgus	Doctorfish	42	18	148.5	0.46	1.109
1	Hypoplectrus puella	Barred Hamlet	58	33	273.0	0.84	0.428
1	Scarus taeniopterus	Princess Parrot	138	34	292.1	0.88	1.164
1	S. viride	Stoplight Parrot	31	17	202.7	0.52	0.770
1	S. iserti	Striped Parrot	93	26	249.4	0.71	1.077
1	Sparisoma aurofrenatum	Redband Parrot	73	28	265.1	0.76	1.658
1	Canthigaster rostrata	Sharpnose Puffer	74	31	288.4	0.84	0.550
1	Holocentrus rufus	Longspine Squirrel	22	15	186.6	0.47	0.182
2	Apogon binotatus	Barred Cardinal	19	12	83.9	0.28	0.512
2	Phaeoptyx pigmentaria	Dusky Cardinal	8	5	55.3	0.15	0.500
2	Stegastes leucostictus	Beaugregory Damselfish	10	10	107.4	0.29	0.000
2	S. variabilis	Cocoa Damselfish	17	9	112.6	0.28	0.588
2	S. diencaeus	Longfin Damselfish	12	9	137.7	0.31	0.188

2	Pseudupeneus maculatus	Spotted Goatfish	7	6	57.4	0.16	0.143
2	Haemulon flavolineatum	French Grunt	11	7	74.5	0.20	0.182
2	H. striatum	Striped Grunt	14	7	85.0	0.22	1.667
2	H. aurolineatum	Tomtate Grunt	18	12	92.3	0.29	0.667
2	Hypoplectrus nigricans	Black Hamlet	8	8	77.7	0.22	0.000
2	H. chlorurus	Yellowtail Hamlet	8	8	69.5	0.21	0.000
2	Synodus saurus	Bluestriped Lizardfish	7	7	44.8	0.16	0.000
2	Gerres cinereus	Yellowfin Mojarra	15	9	60.8	0.21	0.450
2	Sparisoma chrysopterum	Redtail Parrot	23	15	121.6	0.38	0.267
2	Sargocentron coruscus	Reef Squirrel	5	5	57.4	0.15	0.000
2	Acanthurus bahianus	Surgeon	17	10	121.1	0.31	0.922
2	Thalassoma bifasciatum	Bluehead Wrasse	12	10	85.9	0.26	0.148
3	Holacanthus bermudensis	Blue Angel	11	2	7.9	0.04	.
3	Inermia vittata	Boga	1	1	7.2	0.02	.
3	Chaetodon capistratus	Foureye Butterfly	2	2	22.0	0.06	0.000
3	Apogon townsendi	Belted Cardinal	1	1	10.6	0.03	.
3	Chromis cyanea	Blue Chromis	10	2	24.5	0.06	0.000
3	Cephalopholis cruentata	Graysby	1	1	7.2	0.02	.
3	C. fulvus	Coney	4	3	19.6	0.07	0.250
3	Stegastes fuscus	Dusky Damselfish	4	4	31.1	0.10	0.000
3	Abudefduf saxatilis	Sergeant Major	5	2	20.9	0.06	0.200
3	Microspathodon chrysurus	Yellowtail Damselfish	3	3	21.7	0.07	0.000
3	Mycteroperca tigris	Tiger Grouper	1	1	17.3	0.04	.
3	Haemulon macrostomum	Spanish Grunt	1	1	10.0	0.03	.

3	Hypoplectrus unicolor	Butter Hamlet	2	2	5.5	0.03	0.000
3	H. indigo	Indigo Hamlet	2	1	2.0	0.01	.
3	H. guttavarius	Shy Hamlet	2	2	30.4	0.07	0.000
3	H. aberrans	Yellowbelly Hamlet	1	1	4.7	0.02	.
3	Amblycirrhitus pinos	Red Spotted Hawkfish	1	1	2.0	0.01	.
3	Sparisoma atomarium	Greenblotch Parrot	3	3	34.5	0.09	0.000
3	S. rubripinne	Yellowtail Parrot	2	1	1.1	0.01	.
3	Sphoeroides spengleri	Bandtail Puffer	2	2	26.4	0.06	0.000
3	Epinephelus guttatus	Red Hind Bass	1	1	17.3	0.04	.
3	Serranus tabacarius	Tobaccofish	1	1	5.8	0.02	.
3	Ocyurus chrysurus	Yellowtail Snapper	3	3	35.0	0.09	0.000
3	Sargocentron vexillarius	Dusky Squirrel	1	1	5.3	0.02	.
3	Neoniphon marianus	Longjaw Squirrel	4	4	44.3	0.12	0.000
3	Acanthurus coeruleus	Blue Tang	1	1	5.9	0.02	.
3	Xyrichtys martinicensis	Rosy Razor Wrasse	1	1	4.0	0.02	.
3	Halichoeres bivittatus	Slippery Wrasse	5	4	35.3	0.11	0.200
3	H. garnoti	Yellowhead Wrasse	1	1	12.6	0.03	.

Appendix 5.2. Optimal Regression Models

We use a family of simple curvilinear and polynomial regression models to optimize the fit for 'habitat-gradient dimension' and 'habitats-landscape dimension' empirical models (TableCurve 2D 1994). To choose the most optimal equation for each model we used the following steps and criteria.

(i) the regression model is statistically significant,

(ii) the beta coefficient for the highest ordered term must be statistically significant,

(iii) once an equation meets the above criteria we compare its F statistic with the F statistic for the next equation that also meets these criteria but has one less ordered term. We choose the model with the higher F statistic,

(iv) iterate the above process (steps i to iii) for equations with consecutively fewer terms,

(v) if no curvilinear or polynomial equation is accepted, we chose the simple linear regression model (equation no. 41) to describe the relationship (assuming it has not already been chosen through the iterative process).

1	$\ln y = a+bx+cx^2+dx^3$	22	$y = a+b(x)^{-2}$
2	$y^2 = a+bx+cx^2+dx^3$	23	$y = a+b\ln x(x)^{-2}$
3	$y^{0.5} = a+bx+cx^2+dx^3$	24	$y = a+b(x)^{-1.5}$
4	$y^{-1} = a+bx+cx^2+dx^3$	25	$y = a+b(x)^{-1}$
5	$y = a+b(\ln x)^{-1}+c(\ln x)^{-2}+d(\ln x)^{-3}$	26	$y = a+b\ln x(x)^{-1}$
6	$y = a+b(x)^{-1}+c(x)^{-2}+d(x)^{-3}$	27	$y = a+b(x)^{-0.5}$

7    $y = a + b\ln x + c(\ln x)^2 + d(\ln x)^3$

8    $y = a + b(\ln x)^2 + c\ln x + d(\ln x)^{-1}$

9    $y = a + bx + cx^2 + d(x)^{-1}$

10   $y = a + bx + cx^2 + dx^3$

11   $\ln y = a + bx + cx^2$

12   $y^2 = a + bx + cx^2$

13   $y^{0.5} = a + bx + cx^2$

14   $y = a + b(\ln x)^{-1} + c(\ln x)^{-2}$

15   $y = a + b(x)^{-1} + c(x)^{-2}$

16   $y = a + b\ln x + c(\ln x)^{-1}$

17   $y = a + b(\ln x)^2 + c\ln x$

18   $y = a + bx + c(x)^{-1}$

19   $y = a + bx + cx^2$

20   $\ln y = a + bx$

21   $y = a + be^{-x}$

28   $y = a + b(\ln x)^{-1}$

29   $y = a + b\ln x$

30   $y = a + bx^{0.5}$

31   $y = a + bx(\ln x)^{-1}$

32   $y = a + b(\ln x)^2$

33   $y = a + bx^{0.5}\ln x$

34   $y = a + be^x$

35   $y = a + bx^3$

36   $y = a + bx^{2.5}$

37   $y = a + bx^2\ln x$

38   $y = a + bx^2$

39   $y = a + bx^{1.5}$

40   $y = a + bx\ln x$

41   $y = a + bx$

SECTION VI

GENERAL DISCUSSION AND SUMMARY

6

GENERAL DISCUSSION AND SUMMARY

Fish on coral reefs form rich and highly diverse assemblages. An explanation of how these assemblages are organized (i.e., how species and individuals arrange themselves in space and time) provided much of the impetus for the initial reef studies. Since, four models of community organization have been developed. Each model stresses a different assembly process as dominant in controlling community organization. The first model, Interspecific Competition and Niche Specialization, suggests that species evolved specialized niche requirements to reduce competition for limited resources. Because of this and the assumed readily available supply of juvenile recruits, the community restores itself to its prior structure following any local disturbance.

The Lottery Hypothesis suggests instead that the combined probability of recruit and habitat availability control community organization. Specifically, if a recruit is not present at the time of habitat availability, then another recruit from a different species may move in to occupy the site. However, recruitment success is assumed independent of adult reproductive success, and therefore, any disturbance to the community structure is mitigated by the stochastic outcome of this lottery.

The third model, the Recruitment-Limitation Hypothesis, suggests that there are too few recruits available for the above lottery to occur. Therefore, the stochastic supply of recruits settling from the larval plankton stage dominates community organization.

Disturbances to the community structure are eventually obscured by the stochastic outcome of the recruit supply.

The Predation Hypothesis suggests that the high variability of species membership and population densities is not due to *pre-settlement* processes as in the above models, but is due to *post-settlement* processes such as opportunistic predation. Specifically, species density patterns developed at the time of recruitment are significantly altered by continuous, non-selective predation.

These four models of community organization emphasize different assembly processes as dominant in controlling the spatial and temporal distribution of fish on coral reefs. However, despite their differences the models are similar to each other in that each model requires only *one* assembly process to affect community organization, and furthermore, each model implies that all species respond to the assembly process within the *same* level of organization.

If these postulates are valid, then the organization of fish on coral reefs should be a relatively simple phenomenon. I test this in two steps. The first step I divide species into several groups. The second step I determine for each species group the correlation between species distributions and, for example, some attribute of the habitat template (e.g., patch size). If the spatial and temporal distribution of fish on coral reefs is dependent on stochastic processes as suggested, then no matter how I group the species, the correlations between species distribution and habitat attributes obtained for each species group should not differ. However, when I divide the species into groups based on similarities in ecological ranges, I find that correlations characteristic of one group differs

significantly from correlations found in other groups (Sections 3, 4, and 5). Specifically, these differences show trends of increasing correlation (or decreasing—depending on the habitat attribute) from habitat generalists to habitat specialists. For example, the correlation between species richness and *patch surface area decreases* from habitat generalists to habitat specialists (IBT/ Limited Recruitment Model; $r^2_{generalists} = 0.300$, $r^2_{intermediate} = 0.269$, $r^2_{specialists} = 0.059$; Section 4). A separate analysis shows that the correlation between species richness and *patch isolation increases* from habitat generalists to habitat specialists (Waltho & Kolasa 1997, Abstract in ESA Annual Meeting, Albuquerque, unpublished data; $r^2_{generalists} = 0.017$, $r^2_{intermediate} = 0.019$, $r^2_{specialists} = 0.412$).

These results indicate that the organization of fish on coral reefs is not a simple phenomenon (i.e., it can not be modeled successfully by a single-level model of organization). The question remains, therefore, how do the previously recognized assembly processes contribute to species spatial and temporal distributions.

One approach to this problem has been to view the community as an accumulation of individuals through time. As each wave of new recruits arrives the stochastic effects of recruitment limitation initially determine pre-settlement distribution patterns from which, competition for habitat space then filters. Once fish do successfully settle to the reef environment then opportunistic predation continues to modify species and population density patterns (Sale 1991, and references within). Each wave of recruits, therefore, contributes to an ever changing community mosaic of species patterns. The community structure, therefore, comprises of several layers of stochastic control whereby each layer comprises the individuals of a particular wave event. This approach to the community

organization of fish on coral reefs, however, is not a true multi-level model of organization

for two reasons:

- all individuals transcend from one layer of stochastic control to the next as

  individuals mature and develop,

- all species are expected to behave similarly to each other in their response to the

  various assembly processes.

In a true multi-level model of organization, species are expected to differ in their

response to various assembly processes. It is based of these differences that species can

be separated into groups (or levels), and the dominating assembly process identified for

each group. I therefore introduce a second approach to the problem of community

organization, based on the assumption that the effects of stochastic processes differs

between species. I develop the idea by considering the following hypothetical relations

and processes:

We can think of different species as perceiving and responding to the habitat template

at different resolutions (Fig. 6.1). This means that for species perceiving the habitat

template as continuous, there are no costs associated with emigrating or immigrating

throughout the landscape (habitat generalists, Fig. 6.1B). For these species localized

emigration and immigration offset the stochastic effects of opportunistic predation and

limited recruitment. If we accept the model of pre-emptive behaviour (e.g., Section 5),

then individuals should generally accumulate in areas where members of their species

already occur. Across the habitat template, therefore, population densities of these

generalists should develop with a single density center within an area comprising of several

or even many patches. If there is more than one habitat generalist, then interspecific competition should prevent the density centers from overlapping either spatially or temporally.

For other species, however, there are costs associated with moving throughout the habitat template. These costs, for example, could be loss of individuals from predation due to lack of shelter. This immediately creates areas of inadequate habitat surrounding areas of adequate habitat thus yielding a fragmented habitat landscape. Depending on the species, fragmentation could be perceived as mild (e.g., habitat intermediates, Fig. 6.1C) or severe (e.g., habitat specialists, Fig. 6.1D). I suggest, therefore, that the more severe a species perceives the extent of habitat fragmentation the greater stochastic effects of limited recruitment and opportunistic predation have in controlling the species distribution. Consider the following:

First, it is necessary to assume that because of the costs associated with moving through areas of inadequate habitat, there is little to no migration of fish between habitat fragments relative to the movement of fish within habitat fragments. If this assumption is valid, then the stochastic effects of limited recruitment will produce differences in species abundances between habitat fragments by chance alone. Second, for *each habitat fragment*, a ratio occurs between habitat size and the minimal area required for successful recruitment. As long as the ratio is significantly greater than one (i.e., in favour of habitat size), then a single density center should develop within the habitat fragment (for the same reasons as in habitat generalists). However, if the ratio between the two attributes approaches one then the stochastic effects of limited recruitment and opportunistic

predation appear more dominate in controlling the species distribution. This is because the localized stochastic effects of limited recruitment and opportunistic predation can no longer be offset by species behaviour. Therefore, as the habitat template appears more fragmented from a species perspective, the more significant the stochastic effects of limited recruitment and opportunistic predation are in controlling a species distribution relative to that of the habitat generalist. It is possible that for habitat specialists these stochastic assembly processes determine distributions most fully. This pattern of distribution of species densities is precisely what my results (Section 5) show and I found in additional analyses (Fig 6.2; unpublished).

In a multi-level model of community organization such as the one hypothesized, species membership and population densities can be expected to remain a composite property of stochastic and non-stochastic assembly processes because species perceive and respond to the habitat template at several levels of habitat resolution. In this model density distributions of low resolution species are controlled mostly by non-stochastic pre-emptive behaviour and interspecific competition: comparatively, density distributions of high resolution species are controlled mostly by stochastic limited recruitment and opportunistic predation. The effectiveness of each assembly process in organizing fish communities on coral reefs changes, therefore, along a gradient from significant to non-significant (or vice versa, depending on the assembly process) from habitat generalists to habitat specialists (Fig. 6.3).

I conclude by suggesting that the organization of fish communities on coral reefs is due to a mixture of stochastic and non-stochastic processes that occur (a) *simultaneously*

within the community, and (b) *differentially* between the species. Specifically, I suggest that attributes of the habitat template (e.g., patch size and patch location) and attributes of species behaviour (e.g., pre-emptive behaviour and interspecific competition) restrict the stochastic effects of limited recruitment and opportunistic predation in species-specific, non-stochastic ways.

## *FIGURE 6.1 An Assemblage of Fish on a Coral Patch*

An assemblage of fish on a coral patch as an external observer (e.g., like ourselves) may view it (A). (B) An example of how habitat generalists may view the reef, that is, there is little to no characterization of reef attributes. Fish migrate throughout the patch uninhibited therefore offsetting the stochastic effects of recruitment limitation and opportunistic predation. (C) Habitat intermediates view the reef as fragmented, that is, there are areas of adequate habitat surrounded by areas of inadequate habitat. Localized density centers may develop within each fragment. (D) Habitat specialists view the reef as severely fragmented. There is considerable characterization of reef attributes. Abundance patterns are restricted to the stochastic effects of limited recruitment because the effects of these processes are not offset through species behaviour.

158
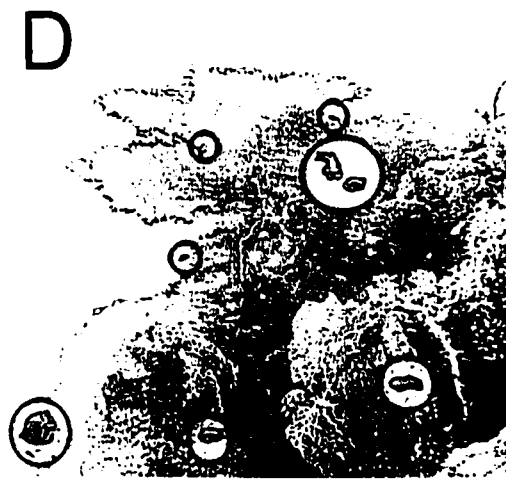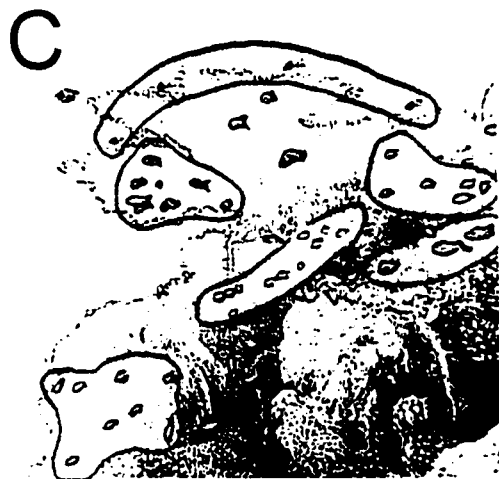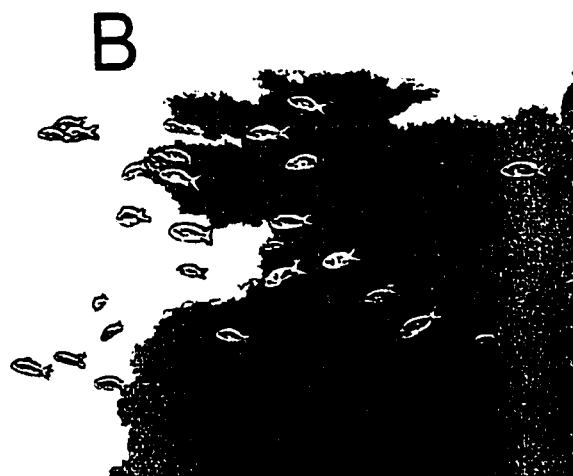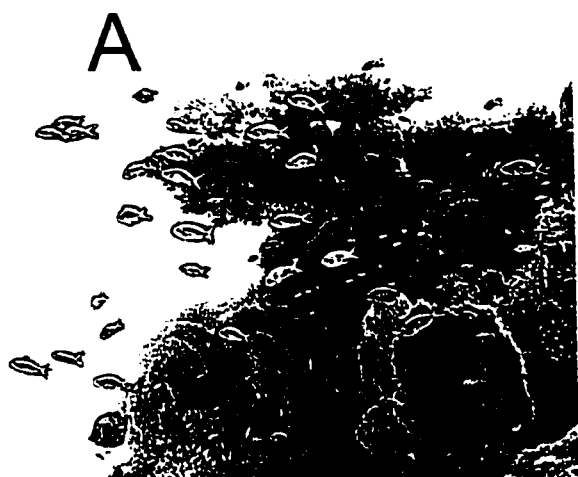
FIGURE 6.2 DENSITY DISTRIBUTIONS OF THREE SPECIES OF DAMSELFISH

The left column, Observed Distribution, is the density distribution of three species of Damselfish (A) Threespot, (B) Cocoa, and (C) Yellowtail. The three species represent the three species groups identified in Section 5 (Appendix 5.1). The x-y axis delineates the boundary of the 40 patch reefs in the back-reef of Discovery Bay, Jamaica (see Fig. 5.2). The density distributions of the Damselfish here closely approximate the patterns I hypothesized earlier in Fig. 5.6.

Species Group 1

Damsel Bicolour
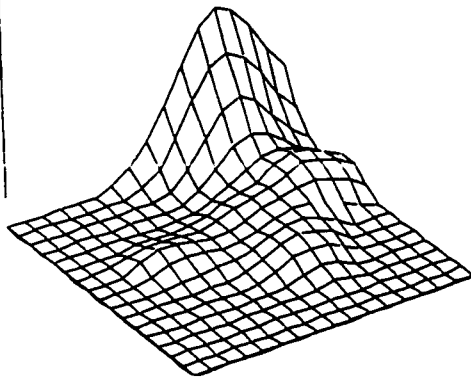
Damsel Threespot
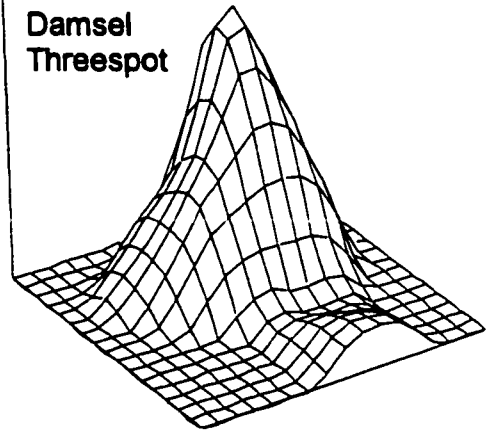
Species Group 2

Damsel Cocoa
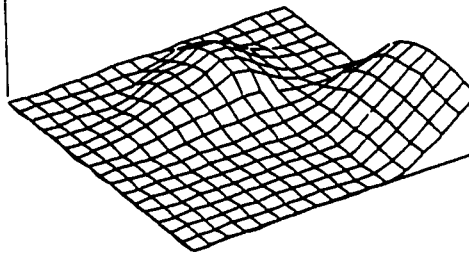
Species Group 3

Damsel Yellowtail
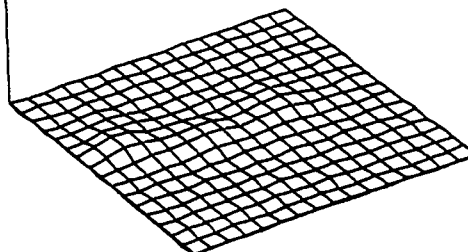
SECTION VII

GENERAL LITERATURE CITED

7

GENERAL LITERATURE CITED

Allen T.F.H. and E.P. Wyleto (1983) A hierarchical model for the complexity of plant

communities. J. Theor. Biol. 101:529-540.

Allen T.F.H., and T.B. Starr (1982) Hierarchy: perspectives for ecological complexity.

Univ. Chicago Press, Chicago. 310pp.

Allen, T.F.H. and T.W. Hoekstra (1992) Toward a unified ecology. Columbia University

Press, New York.

Bock C.E., and R.E. Ricklefs (1993) Range size and local abundance and distribution of

species. Am. Nat. 122:295-299.

Buchheim J.R., and M.A. Hixon (1992) Competition for Shelter Holes in the Coral Reef

Fish Acanthemblemaria spinosa Metzelarr. J. Exp. Mar. Biol. Ecol. 164:45-54.

Choat J.H., and D.R. Bellwood (1991) Reef fishes: their history and evolution. pp. 39-

66 In: Sale P.F. (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, New

York, New York.

Clements F.E. (1936) Nature and structure of the climax. J of Ecology 24:252-284.

Collins S.L., and S.M. Glenn (1991) Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72:654-664.

Connell J.H. (1980) Diversity and the coevolution of competition, or the Ghost of Competition Past. Oikos 35:131-138.

Connor, E.F. and D.S. Simberloff (1979) The Assembly of Species Communities: Chance or Competition? Ecology 60:1132-1140.

Doherty P.J., and D.McB. Williams (1988a) Are local populations of coral reef fishes equilibrial assemblages? The empirical database. Proc. Int. Coral Reef Symp., 6th 1:131-139.

Doherty P.J., and D.McB. Williams (1988b) The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Ann. Rev. 26:487-551.

Ehrlich P.R. (1975) The population biology of coral reef fishes. Annu. Rev. Ecol. Syst. 6:211-247.

Eldredge N., and S.N. Salthe (1984) Hierarchy and evolution. Oxford Survey of evolutionary Biology 1:184-208.

Getty T. (1981) Competitive collusion: the preemption of competition during the sequential establishment of territories Am. Nat. 118:426-431.

Getty T. (1987) Dear enemies and the prisoner's dilemma: why should territorial neighbours form defensive coalitions? Am. Zool. 27:327-336.

Gladfelter W.B., J.C. Ogden, and E.H. Gladfelter (1980) Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61:1156-1168.

Gleason A.H. (1922) On the relation between species and area. Ecology 3:158-162.

Gleason A.H. (1926) The individual concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

Goldman B., and F.H. Talbot (1976) Aspects of the ecology of coral reef fishes. pp. 125-154 in: Jones O.A., and R. Endean (eds.) Biology and Geology of Coral Reefs Vol. 3. Academic Press, New York.

Hanski I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210-221.

Hay M.E. (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. pp. 96-119 In: Sale P.F. (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, New York, New York.

Hiatt R.W., and D.W. Strasburg (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Mono. 30(1):65-127.

Hixon M.A. (1991) Predation as a process structuring coral reef fish communities pp. 475-508 In: Sale P.F (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, New York, New York.

Hixon M.A., and B.A. Menge (1991) Species diversity: Prey refuges modify the interactive effects of predation and competition. Theor. Pop. Biol. 39:178-200.

Hobson E.S. (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. pp. 69-95 In: Sale P.F. (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, New York, New York.

Jackson J.B.C. (1981) Interspecific competition and species distributions: the ghosts of theories and data past. Anim. Zool. 21:889-901.

Jones G.P. (1986) Food availability affects growth in a coral reef fish. Oecologia 70:136-139

Jones G.P. (1990) The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71:1691-1698.

Jones G.P. (1991) Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. pp. 294-328 In: Sale P.F. (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, New York, New York.

Kareiva P. (1990) Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B 330:175-190

Kaufman L.S. (1983) Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica Coral Reefs 2:43-47.

Kolasa J. (1989) Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology 70:36-47.

Kolasa J., and S.T.A. Pickett (1989) Ecological systems and the concept of biological organization. Proc. Natl. Acad. Sci. 86:8837-8841.

Kotliar N.B., and J.A. Wiens (1990) Multiple scales of patchiness and patch structure - a hierarchical framework for the study of he*srogeneity. Oikos 59:253-260.

Mauer B.A. (1985) Avian community dynamics in desert grasslands: observational scale and hierarchical structure. Ecol. Monogr. 55:295-312.

O'Neill R.V. (1989) Perspectives in hierarchy and scale. Pages 140-156 In: Roughgarden J., R.M. May, and S.A. Levin (eds.) Perspectives in Ecological Theory. Princeton University Press, Princeton, New Jersey.

O'Neill R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton. 253pp.

Pickett S.T.A., J. Kolasa, S. Collins, and J.J. Armesto (1989) The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129-136.

Robertson D.R., C.W. Peterson, and J.D. Brawn (1990) Lunar reproductive cycles of benthic-brooding reef fishes: reflections of larval-biology or adult-biology? Ecol. Monogr. 60:311-329.

Russell, B.C., F.H. Talbot, and S Domm (1974) Patterns of colonization of artificial reefs by coral reef fishes. Proc. Int. Coral Reef Symp., 2nd 1:207-215.

Sagova M., and M.S. Adams (1993) Aggregation of numbers, size and taxa of benthic animals at four levels of spatial scale. Archiv Hydrobiologie 128:329-352.

Sale P.F. (1974) Mechanisms of co-existence in a guild of territorial fishes at Heron Island. Proc. Int. Coral Reef Symp., 2nd 1:193-206.

Sale P.F. (1975) Patterns of use of space in a guild of territorial reef fishes. Mar. Biol. 29:89-97.

Sale P.F. (1977) Maintenance of high diversity in coral reef fish communities. Am. Nat. 111:337-359.

Sale P.F. (1978) Coexistence of coral reef fishes—A lottery for living space. Environ. Biol. Fishes 3:85-102.

Sale P.F. (1980a) Assemblages of fish on patch reefs - predictable or unpredictable? Env. Biol. Fish 5:243-249.

Sale P.F. (1980b) The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18:367-421.

Sale P.F., J.A. Guy, and W.J. Steel (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. Oecologia 98:83-99.

Sano M., M. Shimizu, and Y. Nose (1987) Long-term effects of destruction of hermatypic corals by Acanthaster planci infestation on reef fish communities at Iriomote Island, Japan. Mar. Ecol. Prog. Ser. 37:191-199.

Shapiro D.Y. (1991) Intraspecific variability in social systems of coral reef fishes. pp. 331-355 In: P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press, N.Y., N.Y.

Smith C.L., and J.C. Tyler (1972) Space resource sharing in a coral reef fish community. L.A. Co. Nat. Hist. Mus. Sci. Bull. 14:125-170.

Smith C.L., and J.C. Tyler (1975) Succession and stability in fish communities of the dome-shaped patch reefs in the West Indies. Am. Mus. Novit. 2572:1-18.

Stamps J.A., and V.V. Krishnan (1990) How to acquire a larger territory by settling next to a neighbour Am. Nat. 135:527-546.

Sweatman H.P.A. (1983) Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. Reticulatus*) on coral reefs. Mar. Biol. 75:225-229.

Sweatman H.P.A. (1985) The influence of adults of some coral reef fishes on larval recruitment. Ecol. Monogr. 55:469-485.

Talbot F.H., B.C. Russell, and G.R.V. Anderson (1978) Coral reef fish communities: unstable, high-diversity systems? Ecol. Monogr. 48:425-440.

Thorhallsdottir T.E. (1991) The dynamics of a grassland community - a simultaneous investigation of spatial and temporal heterogeneity at various scale. J. Ecol. 78:884-908.

Victor, B.C. (1983) Recruitment and Population Dynamics of a Coral Reef Fish. Science 219:419-420.

Victor, B.C. (1986) Coral Reef Fish Larvae: patch size estimation and mixing in the plankton. Limnol. Oceanogr. 29:1116-1119.

Wellington G.M., and B.C. Victor (1988) Variation in components of reproductive success in an undersaturated population of coral-reef damselfish population: a field perspective. Am. Nat. 131:588-601.

Williams D.McB. (1983) Daily, monthly, and yearly variability in recruitment of a guild of coral reef fishes. Mar. Ecol. Prog. Ser. 10:231-237.

Williams D.McB. (1985) Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short term effects of Acanthaster planci. Mar. Ecol. Prog. Ser. 28:157-164.

Williams D.McB. (1986) Spatial and temporal scales of processes determining inter-annual variation in recruitment of fishes of the Great Barrier Reef: some preliminary data. Int. Oceanogr. Comm. Workshop Rep., Suppl. 44:229-239.

Wu J., and O.L. Loucks (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quat. Rev. Biology 70:439-466.