ENVIRONMENTAL AND TEMPORAL DETERMINANTS OF COMMUNITY VARIABILITY USING NATURAL AQUATIC MICROCOSMS

By

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A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

ABIOTIC DETERMINANTS OF COMMUNITY PATTERNS

DOCTOR OF PHILOSOPHY (2000)
(Biology)

McMaster University
Hamilton, Ontario

TITLE: Environmental and Temporal Determinants of Community Variability using Natural Aquatic Microcosms

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NUMBER OF PAGES: xx, 218

Abstract

Histories, biotic factors, and abiotic factors interact to determine biodiversity. These factors also influence community composition, community structure, and community constancy (persistence) over time. By examining multiple communities from a common species pool in a system that spans a range of physical conditions, it may be possible to determine the role environmental variables play in forming and maintaining community composition and structure, especially over time. Species richness and diversity were determined by abiotic pool conditions such that the observed community consisted of tolerant species that accumulated over time. These abiotic variables also can be used to represent habitat heterogeneity. I showed that increased habitat heterogeneity promoted increased biodiversity, which, in turn, further increased biodiversity by self-generation of heterogeneity. Frequency of pool desiccation was another abiotic variable considered and it was found that diversity, richness, and abundance all decreased with increased frequency of desiccation while compositional stability decreased. Temporary pools were shown to have a similar "type" of community structure; one dominated by a few species with good dispersal and colonization abilities.

One abiotic variable, pool salinity, was found to most strongly influence community composition and structure. For example, freshwater pools were dominated by ostracods and insects while brackish water pools were dominated by copepods. As salinity increased, ostracod abundances decreased while copepod abundances increased.

As expected, community constancy was greatest over short temporal intervals. Environmental variability reduced community constancy. Pool temperature was shown to affect species abundances but pool salinity determined the community composition. Increased environmental variability (based on temporal changes in physicochemical variables) also resulted in increased community and population variability with community structure being more variable in unstable habitats.

In conclusion, much of the results indicate that communities respond independently and asynchronously to environmental variables.

Preface

This thesis contains six papers that either have been published in the primary literature or have been submitted to journals to be considered for publication. Five of these papers were co-authored with my supervisor, Dr. Jurek Kolasa. Although he contributed ideas and comments to improve these manuscripts, a majority of each paper consists of my own original research. The general procedure we used was that I would develop each paper into a coherent document first, and then Jurek would make suggestions on how the manuscript might be improved, much in the way peers comment on the work of a colleague.

Acknowledgements

All of the data used in this thesis was collected at the Discovery Bay Marine Laboratory, University of the West Indies, Jamaica. I would like to thank the staff and the director, Dr. Michael Haley, for making the fieldwork possible.

The processing of the field samples involved numerous undergraduate students at McMaster University without whose help much of the data would not be in a useable form.

Much of the fieldwork was completed thanks to the support of an NSERC operating grant to Dr. Jurek Kolasa. My salary came from two primary sources, an NSERC PGS B during the first two years of study, and OGS Scholarships during the last two years. This financial support was greatly appreciated and provided me the opportunity to focus entirely on data analyses and publications.

I would like to thank Drs. Susan Dudley and Peter Yodzis who served on my supervisory committee and provided me with extremely helpful suggestions that kept my research focused while conveying the greater importance of the results. Their insights contributed to the publications contained within this thesis.

Dr. Jurek Kolasa, my thesis supervisor, provided invaluable insight into many issues contained in this thesis. Without his theoretical insights, some of the results of this thesis would not have had the general applicability they have now. He acted as a colleague to bounce ideas off and to debate issues I thought were perfectly clear (not always the case). Thanks Jurek.

Last, but not least, I would like to thank my wife, Jennifer Therriault, who not only provided numerous editorial suggestions on the six manuscripts contained in this thesis but provided much needed support over the four years I was doing this research. Her encouragement kept me focused while providing me “a life” away from the university.

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Introduction to Causes of Community Patterns in Jamaican Rock Pools

Introduction

Biological communities are shaped by a number of processes including historical events, biotic variables and abiotic variables. Communities vary in the number of species and the number of individuals both over time and between habitats (Connell and Sousa, 1983; Horne and Schneider, 1995). Understanding the processes that shape communities, both in space or in time, is important for understanding ecology and has implications for species conservation (Quintana-Ascencio and Morales-Hernández, 1997), metapopulation dynamics (Hanski and Gilpin, 1997), and other applied issues in ecology (Bengtsson et al., 1997).

Recently, biodiversity has received much attention from both conservationists and ecologists (McGrady-Steed et al., 1997; McGrady-Steed and Morin, 2000). Ecologists have long been examining questions about the promotion or maintenance of diversity (Forbes, 1887; Cowles, 1899; Grinnell, 1917; Gleason, 1926; Clements, 1936). More recently, ecologists have been attempting to determine both natural and anthropogenic causes for the global decline of biodiversity (Botsford et al., 1997; Chapin et al., 1997; Dobson et al., 1997; Matson et al., 1997; Noble and Dirzo, 1997; Vitousek et al., 1997). Furthermore, there has been considerable effort to reverse the reduction of biodiversity through the restoration of populations (Montalvo et al., 1997), communities (Palmer et al., 1997), and ecosystems (Ehrenfeld and Toth, 1997) while understanding that each varies spatially and temporally (White and Walker, 1997). In order to understand completely what maintains diversity, we must understand the forces that shape and maintain communities, including the contribution of environmental variables.

Community structure (species composition and relative abundances) likely is controlled by a combination of biotic and abiotic factors. Biotic factors such as predation, competition, mutualism and interference can influence species diversity, which, in turn, can cause changes in community structure, especially over time (Pianka, 1994). Also, it is possible that biotic factors such as predation or competition are mediated by abiotic conditions. Abiotic variables also might reflect biotic processes. Abiotic variables are often invoked to explain observed community patterns because they are usually measured more easily.

The System

It is preferable to minimize the confounding effects of geographical variation and pool history by examining communities from a single geographical area that has a shared species pool (Therriault and Kolasa, 1999a, 1999b; Spencer et al., 1999). To determine the impact of environmental variables on community structure, it is necessary to examine habitats that span a range of different physicochemical conditions. This system consists of pools that span a range of physicochemical properties, represent habitats of differing patterns of drying (frequency and duration) and are home to numerous invertebrate species and communities resulting from a common species pool (Kolasa et al., 1996; Therriault & Kolasa, 1999a).

The pools used in the following studies are formed on up-lifted fossil reef along the north coast of Jamaica. These supra-tidal pools are small (~ 20 to 60 cm across), shallow (> 50 cm deep), and primarily rain-fed which makes them prone to desiccation.

However, these pools are in close proximity to each other (usually ~ 10 to 20 cm between pools) with a maximum distance of less than 50 meters across the entire habitat used here. The precise mechanisms of dispersal remain largely unknown for many of the invertebrates found in these unique pools, but metapopulation dynamics must be critical to the maintenance of overall biodiversity patterns. Kolasa and Drake (1998), using a sub-set of the rock pool data, suggested that ecological specialization was more important than metapopulation dynamics to the determination of species abundances. However, it is important to note that they were able to detect the impact of metapopulation dynamics, which might be more important in determining species presence rather than their relative abundance.

Environmental (Abiotic) Factors

Abiotic factors have been among some of the most studied variables that influence species diversity. Previous studies have found relationships between diversity and latitude (Wallace, 1878; Fischer, 1960; 1961; Pianka, 1966), climate (Terborgh, 1973), habitat heterogeneity (Simpson, 1964b; Cook, 1969), habitat complexity (MacArthur and MacArthur, 1961), habitat structure (McCoy and Bell, 1991; Downes et al., 1995), disturbance (Connell, 1975; Keough, 1984; Collins et al., 1995), habitat area and isolation (Hamilton et al., 1963; MacArthur and Wilson, 1967; Abbott, 1980; Tonn and Magnuson, 1982; Brönmark, 1985; Matuszek and Beggs, 1988), in addition to an array of physical and physicochemical variables (Simpson, 1964; Larson et al., 1989; Kohn and Walsh, 1994; Lapin and Barnes, 1995). Huston (1994) and Rosenzweig (1995) discuss other relationships between abiotic or biotic variables and biodiversity. In general, diversity is reduced with increased physical stress such as the stress gradient that exists with increased latitude or elevation. Conversely, diversity is promoted by increased habitat heterogeneity or complexity, increased habitat size and increased permanence or connectedness, and, in general, lower physical stress.

It has been suggested that geographical or physicochemical variables are important in determining community structure in aquatic systems (Townsend et al., 1983; Corkum, 1989). Geographical variables represent historic or evolutionary events while physicochemical variables represent local and regional processes that control species tolerances and distributions. Abiotic factors also have been shown to influence community persistence. According to Townsend et al. (1987), sites with lower variability in abiotic factors support communities that are more persistent. Differences in community structure have been attributed to both the physical and chemical conditions of the habitat for ephemeral pools (King et al., 1996) and freshwater springs (Williams, 1997) specifically, in addition to aquatic habitats in general (Harrel and Dorris, 1968; Hodda and Nicholas, 1986; Steneck and Dethier, 1994; Gouvis et al., 1997). The level of salinity has been suggested as a major determinate of community structure in coastal marine systems (Jorcin, 1999) and has been shown to influence the distribution and abundance of organisms in saline lakes (Timms, 1983) and in freshwater springs (Williams et al., 1997). It is important to determine the relative contribution of abiotic and biotic affects (or their interactions) to the determination of community structure and to determine the extent of the impact of environmental variables on community structure.

Habitat Heterogeneity

Habitat heterogeneity has been cited as one mechanism through which high diversity is maintained (Huston, 1994), especially in the tropics (Connell, 1978). Both spatial and temporal habitat heterogeneity affect the structure and dynamics of ecological communities (Kolasa and Pickett, 1991; Tilman, 1994) by increasing species diversity in terrestrial and aquatic systems (MacArthur and MacArthur, 1961; Downing, 1991; Huston, 1994). Increased species diversity can be maintained by the rescue effect (Gotelli, 1991) or the mass effect (Shmida and Wilson, 1985), which arises through various mechanisms such as differential use of microhabitats in space and time and inter-habitat migration (Jobbagy et al., 1996). Thus, habitat heterogeneity is important for the maintenance of these effects. However, habitat heterogeneity has often proven problematic to measure since organisms perceive the landscape differently (Harmon et al., 1986; Knaapen et al., 1996; Wiens, 1994). If habitat heterogeneity is not measured at a scale relevant to the organisms being studied, then a habitat might be defined as homogenous when it is not or, conversely, be considered heterogeneous when an organism or community perceive it as homogenous. Previous studies have shown that heterogeneity promotes diversity at different scales (Arita, 1997, Vivian-Smith, 1997). Increases in small-scale heterogeneity can increase local diversity while inter-habitat heterogeneity promotes diversity at continental or global scales. Rare species appear to benefit more from increased habitat heterogeneity than common species (Vivian-Smith, 1997), suggesting that habitat-generalists and habitat-specialists differ in their response to changes in habitat characteristics, including heterogeneity.

Habitat Duration

Pool duration can be influenced by a number of factors including precipitation, evaporation, surface area, wind, temperature, and permeability of the substrate (Marcus and Weeks, 1997). Pool desiccation causes cascading effects on other physical pool conditions including increased water temperature, increased salinity or increased concentration of dissolved ions, decreased pH, and changes in sulfur and nitrogen cycles (Van Dam, 1988). Pool desiccation also can influence biotic interactions by increasing the density of animals, resulting in greater competition and other density dependent effects (e.g. Aspbury and Juliano, 1998) or by influencing colonization, survival, and developmental rates and strategies (Blaustein et al., 1999). These factors contribute either directly or indirectly to the formation, maintenance, and existence of aquatic communities.

It was argued initially that temporary ponds were species-poor because of difficulties adapting to a desiccating environment (Wiggins et al., 1980). However, more recently, Mahoney et al. (1990), Taylor and Mahoney (1990), and Bazzanti et al. (1996) have shown that natural temporary ponds can support rich zooplankton communities and phytoplankton communities (often 40 or more taxa are identified). In addition, other temporary aquatic habitats, including temporary streams (Moreno et al., 1997) and floodplain ponds (Corti et al., 1997), have been shown to support rich communities.

Several factors including habitat area (Ward and Blaustein, 1994; March and Bass, 1995) and hydroperiod (Schneider and Frost, 1996) influence the biodiversity of temporary pools. Generally, species richness increases with pool duration (Schneider, 1997; Schneider and Frost, 1996) and community structure in temporary pools depends on life history strategies (Wiggins et al., 1980). For example, some organisms produce drought-resistant propagules that will emerge when water conditions are once again favorable while others rely on dispersal from nearby permanent water bodies. Therefore, pool permanence can strongly influence the formation and maintenance of community structure.

Despite a growing number of studies on species adaptations to temporary environments (e.g. Hamer and Appleton, 1991a; 1991b; Maier, 1993; López and Theis, 1997; Marcus and Weeks, 1997), there have been relatively few studies on these systems at the community level (e.g. Lake et al., 1989; Wyngaard et al., 1991; Bonner et al., 1997; Peterson and Boulton, 1999). Pools with a high frequency of desiccation should support fewer species and hence simpler communities because these pools should only support a subset of the regional species pool. Harsh environmental conditions will limit the ability of some species to colonize and survive in variable habitats. Community persistence (constancy in composition over time) should be high in temporary pools because they should be dominated by species with good dispersal abilities (Scarsbrook and Townsend, 1993). Furthermore, these species should show typical *r*-selection characteristics including early reproduction and rapid individual and population growth (Pianka, 1970). It is also possible that rare species with good dispersal abilities might lower community persistence (by changing composition from time to time) and result in varied community assemblages. In order to determine the effect of desiccation frequency on communities, it is necessary to examine changes in several community metrics over time. Desiccation frequency can restrict species distributions, but it is unclear how community composition or structure will be affected by repeated drying events.

Habitat Variability (Stability)

Habitat variability is another abiotic variable that influences aquatic communities (Pickett and White, 1985; Death and Winterbourn, 1994). Habitat variability affects the absolute and relative abundance of species in a community, thereby, representing a strong structuring force for communities (Death, 1995). Deterministic processes that impact community structure, such as competition and predation, are mediated by habitat variability (McAuliffe, 1984; Meffe, 1984). Several studies show that, with an increase in habitat variability, population variability increases and community persistence declines. This applies to stream invertebrates (Death and Winterbourn, 1994), fish (Ross et al., 1985), and non-aquatic insects (Wolda et al., 1992).

Despite attempts to determine the influence of habitat variability (stability) on community structure, its role remains unclear. Site-specific differences or differences in the definition of habitat stability or variability may confound these inferences. Specifically, defining and measuring habitat stability has proven problematic (Rykiel, 1985) and the impact of habitat variability changes depending on the spatial, temporal, and taxonomic scales used in the study (Rahel, 1990; Sale and Guy, 1992).

Sometimes, geographical or physicochemical variables are more important than habitat variability (stability) in determining community structure (e.g. Townsend et al., 1983; Corkum, 1989). In aquatic systems, it is important to consider the impact of individual physicochemical variables relative to a combination of these variables (often used to quantify habitat stability) (Death, 1995).

Measuring community variability has also proven problematic (Micheli et al., 1999) and depends on the measure used (Gaston and McArdle, 1994). Since community variability involves changes in species composition and changes in species' relative abundances over time (Magurran, 1988), it is hypothesized that community and population variability should be greater in pools with higher overall habitat variability (increased variability in environmental variables over time) due to impacts on community and population dynamics. Consequently, communities in variable pools should show greater temporal changes in species composition and structure. In the most variable pools, those that dry up from time to time or experience more disturbance events, colonization events increase the probability for changes in the community composition and the relative abundance of different species through differential dispersal, increased biotic interactions and metapopulation dynamics. Therefore, it is important to determine the effect of habitat variability on various components of community variability.

Scale

Community composition often varies over time (Wiens, 1989) and temporal processes can lead to alternate forms of community organization or structure (Morris, 1990). Temporal scales can range from small (seconds, minutes, hours) to long (evolutionary, millennia), but the most practical ecological time scales are intermediate (a few weeks to several years). Along this continuum, further categorization is possible and time scales can represent intra-annual variation (i.e. seasonal) or inter-annual (i.e. "long-term") variation. Seasonal time scales are among some of the most studied, especially with respect to seasonal succession of planktonic (e.g. Lewis, 1978; Mengestou et al., 1991) and benthic (e.g. Meintjes, 1996) communities. Seasonal changes in invertebrate community composition have been documented for fauna from several aquatic environments including intermittent and permanent streams (Smith and Pearson, 1987; Rosillon, 1989; Boulton and Lake, 1992), ponds (Mahoney et al., 1990; Oertli, 1995; Bazzanti et al., 1996), and marine habitats (Jorcin, 1999). Seasonal patterns are not limited to aquatic systems. Mammal (Brown and Heske, 1990) and bird (Loiselle and Blake, 1991) assemblages also have been shown to exhibit seasonal changes in community structure.

Temperate systems might be expected to show stronger seasonal effects, but this is not the only case. Seasonal differences have been noted for sub-tropical (Mahoney et al., 1990; García et al., 1997; Gasith and Resh, 1999), tropical (Nacorda and Yap, 1997; Podrabsky et al., 1998; Colombini et al., 1998), and temperate systems (Kevrekidis, 1997; Tockner et al., 1997). However, there are considerably fewer studies that have documented changes in community structure over longer time periods (i.e. greater than a few years), especially in aquatic systems (but see Bengtsson et al., 1997; for birds). To understand large-scale processes, long-term studies of temporal patterns of community structure are needed, especially in poorly studied systems (Oertli, 1995). It is expected that long-term studies reduce some of the variability that results from unusually severe or unpredictable events.

Community constancy (persistence) and stability should be greater at shorter temporal intervals and should decrease at longer temporal intervals because of the cumulative effects of habitat change and species turnover. However, how such effects add up to shape the community is unknown (i.e. linear vs. asymptotic function). Thus, a simple assessment of community change between two points in time would be entirely arbitrary without any useful reference framework. The ability to determine unambiguously the amount of change in a community is important to both monitoring protocols for diversity and testing theories of community dynamics. Furthermore, community constancy should be greater in environmentally stable pools (those with low variability in physicochemical conditions) because environmental stability favors lower local extinction rates among component species. It is possible to argue that, as pool variability increases, community constancy decreases because more niches open to invading species or habitat specialists (Leigh, 1990). Field data are needed to verify this claim.

Summary

Here, I examine the impact of environmental variables on the determination and maintenance of community structure using invertebrate communities inhabiting a unique system of Jamaican rock pools. Data were collected over several years, allowing an examination of the temporal dynamics of community structure. The ecological characteristics of the fauna (taxa) inhabiting these erosional rock pools have not been extensively documented (but see Therriault & Kolasa, 1999a; 1999b). The relative taxonomic composition of these unique invertebrate communities is needed and will provide a baseline for future studies on this system.

The role of abiotic variables in the determination and maintenance of diversity, community composition, and community structure have not been fully examined in the ecological literature to date. Furthermore, most studies have been unable to remove the confounding effects of historical or biogeographical processes. Most studies have only sought correlations between easily measured variables in the field and measures of diversity, primarily species richness. Thus, using a rigorous approach, I hope to further the understanding of how abiotic variables affect community composition and the time-scales over which they act. It is also possible that the variability in the habitat or specific physicochemical variables are more important than single date measures or their means (over time) for the determination of community composition or structure or its variability over time.

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Chapter 2:

Physical determinants of richness, diversity, evenness, and abundance in natural aquatic microcosms

This chapter was published in Hydrobiologia (complete citation follows) and is published here with the permission of Kluwer Academic Publishers (Appendix 1). This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W., and J. Kolasa. 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. Hydrobiologia 412: 123-130.

Abstract

Histories, biotic factors, and abiotic factors interact to determine biodiversity. A comparison of systems formed over a range of physical conditions may help to evaluate the role of physical factors in determining community structure. We investigated abiotic determinants of species richness, abundance, biomass, diversity, and evenness using a series of erosional rock pools on the northern coast of Jamaica. Aquatic invertebrate community data were collected from 1989 to 1997, along with repeated measurements of physical variables, including descriptors of pool conditions, morphometric characteristics and other derived measures to a total of 17 variables. These variables were used to evaluate a range of regression models, from simple to complex, which explained the observed biodiversity. Simple regression models were occasionally significant but explained little variance. Multiple regression models (using a forward stepwise approach) significantly increased the explained variance of these biodiversity models. Diversity models that emphasized species richness (rather than dominance or evenness) of the community, were preferred. These results suggest that much of the observed species richness/diversity is determined by abiotic pool conditions and represents an accumulation of tolerant species, either directly or indirectly (i.e. modulated by biotic interactions). However, regression models attempting to predict abundance/biomass based on abiotic variables explained less variance than did those predicting richness/diversity. This may indicate that biotic factors within pools at population or community levels are controlling species densities.

Introduction

Species richness is controlled by a combination of history and biotic and abiotic factors. As a historical phenomenon, species richness may represent an equilibrium between accumulation and loss of species over time (Fischer, 1960). Biotic factors influence species diversity through a variety of factors such as predation, competition, mutualism, and interference (Pianka, 1994). Abiotic factors have been some of the most studied variables that influence biodiversity. Previous studies have found relationships between diversity and latitude, climate, habitat heterogeneity, and habitat size, among others, and have been reviewed previously (see Huston, 1994; Rosenzweig, 1995).

Endogenous and exogenous processes may interact and contribute in varying degrees to the determination of species richness for a single community (Kolasa and Biesiadka, 1984). Studying plant communities, Partel et al., (1996) found that the available species pool (determined by evolutionary and historical processes) largely determines local species richness. Theoretical studies suggest that considerable variability arises due to endogenous processes alone, particularly in metacommunities with strong deterministic interactions (e.g. Drake et al., 1992; Wilson, 1992). Palmer and van der Maarel (1995) demonstrated that low variance in species richness might be a result of physical limits to the number of individuals in a sample and spatial dependence. Using ephemeral pools in northern California, King et al. (1996) found differences in species composition among pools that corresponded with the physical and chemical aspects of the habitat.

It is important to determine the degree to which abiotic conditions of the habitat control or limit richness. There is a need to examine habitats representing different ranges of conditions and variability. We examine the impact of physical variables on species richness, abundance, biomass, diversity and evenness using a data set from invertebrate communities inhabiting a system of rock pools in Jamaica. The system is tropical and therefore exhibits lower seasonal variability and it allows an examination and comparison of multiple communities potentially composed of the same species (e.g. Schuh and Diesel, 1995; Kolasa et al., 1996). Each species could potentially inhabit any pool, but this is not seen. Thus, we assume that differences in richness, abundance, biomass, diversity, and evenness among pools represent differences due to abiotic pool conditions or biotic interactions mediated by abiotic pool conditions. In either case, the joint contribution of abiotic conditions can be evaluated by regressing environmental variables on community descriptors.

Methods and Materials

This study was conducted at the Discovery Bay Marine Laboratory, Jamaica, West Indies. The erosional pools studied were formed on coastal limestone rocks from an uplifted fossil reef on the northern coast of Jamaica. Forty-nine pools were selected within a 50 m radius (Figure 1). These pools are small (most are 20 - 60 cm across) and relatively shallow (less than 50 cm deep). Most are rain-fed and are located above the high tide level but many pools receive sea mist under storm conditions.

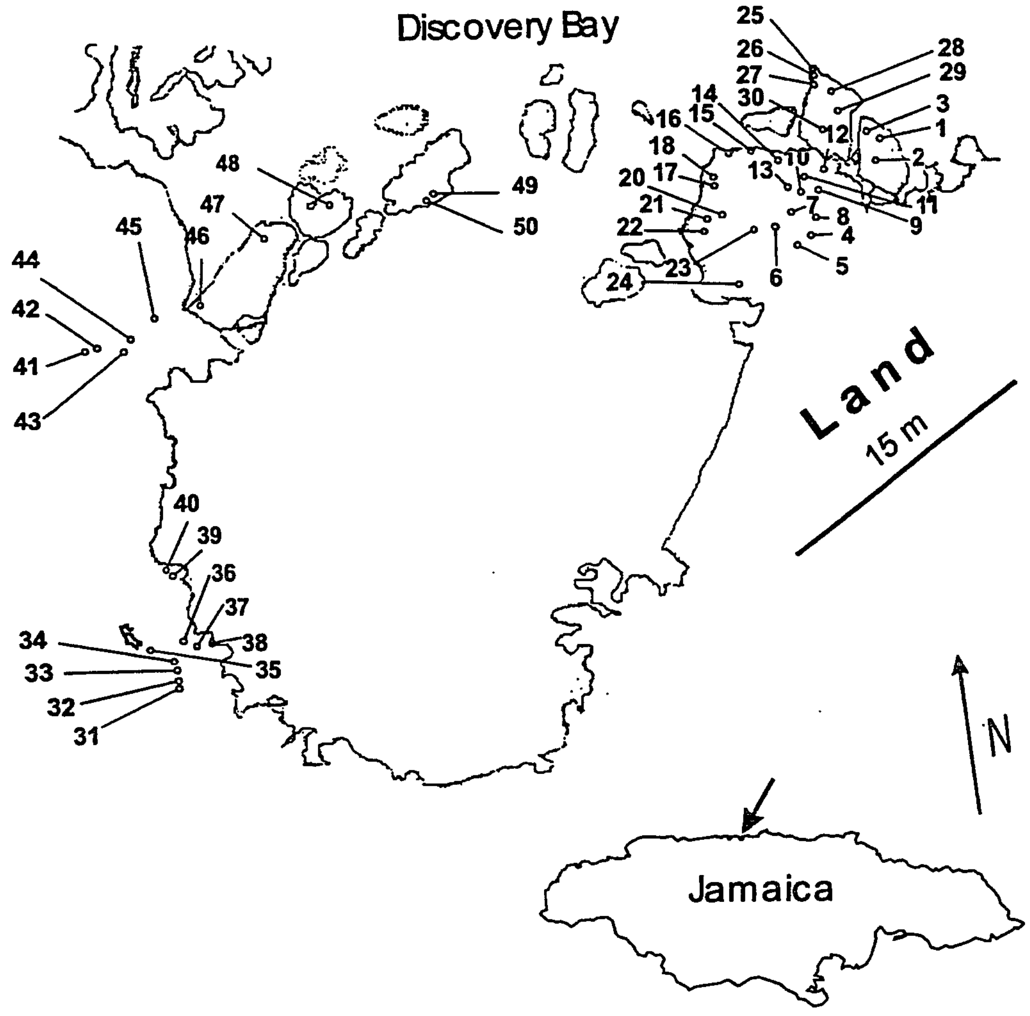

Figure 1: Location of the rock pool communities used in this study. The outline differentiates the backreef area of Discovery Bay and the coastal rocks upon which the pools are found. An arrow on the map of Jamaica indicates the location of Discovery Bay.

Faunal samples used in this study were collected on seven different occasions: Dec. 1989, Jan. 1990, Jan. 1991, Jan. 1992, Jan. 1993, Jan. 1997, and June 1997. Samples were generally collected in one day. To obtain the sample, 0.5 L of water and sediments was taken from the pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution) and passed through a 63 µm net. Organisms were caught in a collecting container and immediately preserved in 50 - 60% ethanol. In the laboratory, animals were identified and counted. Seventy species have been identified in this system and belong to several higher taxa including ostracods, crustaceans, worms, and aquatic insect larvae and pupae.

Physical variables describing pool conditions including temperature, dissolved oxygen, salinity, and pH were measured. These measurements were completed within an hour for the entire set of 49 pools. Morphometric variables including pool depth (from the lip), length, width, volume, surface area, and elevation were also measured.

We used the physical and morphological variables to generate a range of regression models, from simple to complex. Our goal was to evaluate how these variables account for mean species richness, abundance (total number of individuals of all species), biomass (log (abundance)), diversity (Shannon-Wiener and Simpson's), and evenness (based on the Shannon-Wiener index). Diversity indices were calculated using the formulae in Magurran (1988). Mean indices were calculated by averaging the dependent variable (i.e. richness, abundance, etc.) for each pool over the seven sampling periods. Independent variables used in these analyses were either morphometric measures or measures representing maximum, minimum, or mean values for physical conditions (i.e. temperature, salinity, dissolved oxygen, and pH).

Models were evaluated based on their explained variance (R^2) and the number of significant variables in the model. All statistical analyses were performed using the multiple regression module (STATISTICA software from StatSoft). For the stepwise regressions, the F-value had to be at least 1.00 to enter the model. The level of significance was set at $\alpha=0.05$ for all analyses. Residuals were examined for normality and independence from the model.

Results

Independent Dates

Initially, we examined simple regressions to determine the effects of physical and morphometric variables on species richness, abundance, biomass, diversity, and evenness. Among the physical variables, temperature ($p=0.0004$), dissolved oxygen ($p=0.0350$), and pH ($p=0.0016$) were negatively related to species richness. The Shannon-Wiener diversity index was negatively related to temperature ($p<0.0001$) and pH ($p=0.0280$). Evenness was negatively related to temperature ($p=0.0004$) and salinity ($p=0.0244$). Simpson's diversity index showed a negative relationship with temperature ($p=0.0018$). Species abundance was the only variable to show a significant positive relationship, and that was with temperature ($p=0.0258$). The explained variance (R^2) of these models was low and ranged from about 2 to 7%.

We also considered the impact of morphometric variables using simple regressions and found significant positive relationships between pool depth from the lip (the upper edge of the pool cavity) and species richness ($p<0.0001$), Shannon-Wiener index ($p<0.0001$), Simpson's diversity index ($p=0.0008$), evenness ($p=0.0339$), and biomass ($p=0.0408$). Biomass also showed a positive relationship with pool length ($p=0.0352$). Again, the explained variance of the models based on morphometric variables was low, ranging from about 1 to 12%.

Stepwise regressions were conducted using both the physical and morphometric variables used in the simple regressions. However, the explained variance (R^2) was low for species richness (18.37%), total abundance (4.48%), species biomass (10.16%), Shannon-Wiener diversity index (13.44%), evenness (5.62%), and Simpson's diversity index (2.95%). In addition, of the 10 variables included in the stepwise regression (temperature, salinity, dissolved oxygen, pH, pool length, width, depth, surface area, volume, and elevation), no more than 2 were significant in any one model despite the fact that all of the models were significant ($p<0.05$).

Combined Dates

It was believed that the relationships between species diversity and abiotic variables might be clearer if inter-annual variability was reduced. Therefore, we calculated the mean value of each diversity measure for each pool. Similarly, we calculated the mean, minimum, and maximum values for physical pool conditions including temperature, salinity, dissolved oxygen, and pH. The morphometric measures, when added by stepwise regression, indicated that pool depth from the lip and elevation tended to be important variables for determining diversity. However, the explained variance of these models was low (Table 1). When considering the mean, minimum, or maximum measures of the physical pool conditions alone, the explained variance was substantially higher (Table 1). In fact, the highest explained variance was noted when the minimum values of physical measures were used with respect to the diversity measures (species richness, Shannon-Wiener index, evenness, and Simpson's diversity index). Maximum values of physical measures explained more variance in mean pool abundance and mean pool biomass.

Not surprisingly, the compound models resulting from stepwise regression explained the most variance for all of the dependent variables (Table 1), ranging from 41% for mean abundance and biomass to 63% for mean species richness. It is important to determine the correlation between the variables and to ensure that the observed relationships are not biased due to statistical properties of the data (i.e. environmental variables that are highly correlated). As expected, some variables were highly correlated with others (Table 2). Thus, we were able to exclude mean pool temperature and mean pool salinity from the model by retaining minimum and maximum measures of these variables. Similarly, pool volume can be excluded if both pool length and surface area are included. The high correlation coefficients between the measures of pool dissolved oxygen and pool pH indicate that maximum dissolved oxygen and minimum pH will suffice as measures of pool productivity in the optimized model.

Table 1: Explained variance (R^2) for the stepwise regression models for various measures of pool diversity. Numbers in parentheses indicate the number of variables added to the regression models. P-values are also given.

Response Variable	Morphometric Variables	Mean Physical Measures	Minimum Physical Measures	Maximum Physical Measures	All Measures Combined
Mean Species Richness	0.2829 (2) p=0.00048	0.4616 (4) p=0.00001	0.5021 (4) p<0.000001	0.3060 (3) p=0.00085	0.6303 (9) p<0.000001
Mean Abundance	No terms (0)	0.0799 (2) p=0.14737	0.1407 (2) p=0.03058	0.1762 (1) p=0.00268	0.4058 (5) p=0.00032
Mean Biomass	0.0706 (1) p=0.06501	0.1249 (3) p=0.10819	0.0715 (2) p=0.18174	0.2026 (4) p=0.03747	0.4086 (9) p=0.00826
Shannon-Wiener Index	0.2860 (2) p=0.00043	0.3493 (2) p=0.00005	0.4364 (3) p=0.00001	0.1975 (1) p=0.00138	0.5929 (8) p=0.00001
Evenness	0.0438 (1) p=0.14877	0.1915 (2) p=0.00752	0.2363 (1) p=0.00040	0.1799 (3) p=0.02904	0.4863 (9) p=0.00091
Simpson's Diversity Index	0.1481 (2) p=0.02502	0.2263 (2) p=0.00273	0.2943 (3) p=0.00121	0.1320 (2) p=0.03856	0.4925 (8) p=0.00032

Table 2: Pearson correlation matrix for variables with greater than 70 % correlations.

	Mean Temperature	Mean Salinity	Mean Oxygen	Mean pH	Minimum pH	Maximum pH	Volume
Minimum Temperature	0.8849						
Maximum Temperature	0.7291						
Minimum Salinity		0.8399					
Maximum Salinity		0.8465					
Minimum Oxygen			0.8101	0.7226	0.7799		
Maximum Oxygen			0.9104	0.7411		0.8138	
Mean pH			0.8378				
Minimum pH				0.9171		0.7513	
Maximum pH			0.8460	0.9285			
Length							0.7376
Surface Area							0.9042

When the correlated variables were removed, the resulting model for mean species richness did not sacrifice any explained variance ($R^2 = 0.6301$; $p<0.0001$). A similar observation was made for the model explaining the mean Shannon-Wiener diversity index ($R^2 = 0.5894$; $p<0.0001$) and the model explaining mean species abundance ($R^2 = 0.3847$; p=0.0006). The variables included in the species richness and the Shannon-Wiener models were the same and included minimum pH and temperature, minimum and maximum salinity, maximum dissolved oxygen, elevation, length, and pool depth from the lip. Differences were noted in the models for biomass ($R^2 = 0.1845$; 3 terms; p=0.0258); evenness ($R^2 = 0.2627$; 2 terms; p=0.0009); and Simpson's diversity index ($R^2 = 0.3710$; 5 terms; p=0.0010). A closer examination of the variables that were added to the biomass model indicated that initially 9 variables (including several that were correlated with each other) were added but once the correlated variables were eliminated from the analyses, only 3 variables contributed to the final model. A similar observation was made for the evenness model with 9 variables included initially (again, several were correlated with each other) and 2 remaining in the final model. The model for Simpson's diversity index was intermediate and initially contained 3 additional terms (2 were highly correlated with other variables), which is why the explained variance dropped by only 10%. For each of the above models, residuals were examined and were normally distributed. There was no evidence of trends, thereby confirming model linearity.

When the impact of specific variables on the diversity/abundance models is considered, five variables were significant for one or more of the models. These variables represent physical and chemical properties (with the exception of depth) of the pools (Figure 2). Depth from the pool lip was only significant for one model, total abundance, and the relationship was positive. It is interesting to note that minimum temperature and maximum salinity showed negative relationships with the diversity models (species richness, the Shannon-Wiener index, evenness, and Simpson's diversity index) but showed positive relationships with the abundance models (total species abundance and biomass). Similarly, minimum salinity showed a positive relationship in the species richness model but a negative one in the total abundance model.

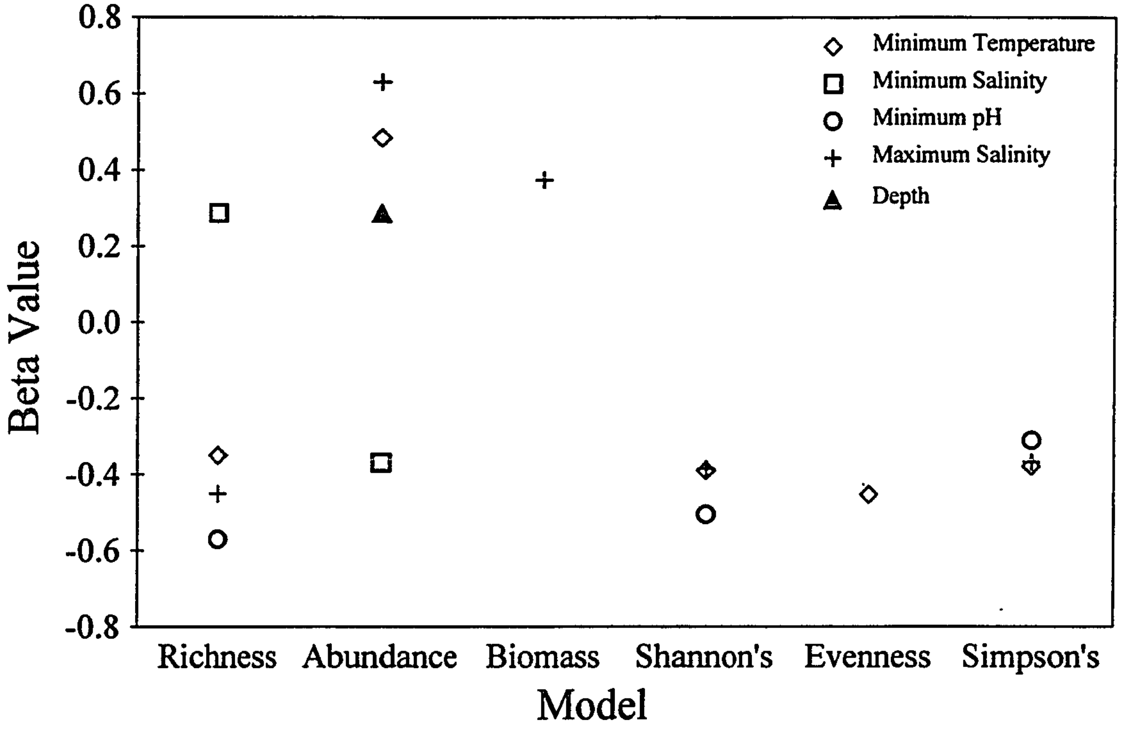

Figure 2: Beta values for the significant variables retained in the stepwise regression approach for the mean diversity/abundance models. Variables retained in at least one model include minimum temperature, minimum salinity, minimum pH, maximum salinity, and pool depth.

The models (regardless of the dependent variable) are influenced predominately by physical measurements rather than morphometric measurements. Measures of pool temperature, salinity, dissolved oxygen, and pH were more correlated (higher R^2) than morphometric measures and were always added first using the stepwise approach.

It is of interest to know how much explained variance results from the interaction of multiple independent variables versus variables that represent correlated terms. In order to examine this relationship, the physical and morphometric variables were reduced using PCA analyses and the resulting factors (in this case 4) were regressed against the dependent variables (i.e. richness, abundance, etc.). Once again, forward stepwise regressions were used to add variables to the models. This approach showed that using PCA factor scores produced significant models (5 of 6 cases $p<0.05$), but did not improve the models' explained variance (R^2). The explained variance for these models is given: species richness ($R^2 = 0.3369$; $p=0.0003$); abundance (not significant); biomass ($R^2 = 0.0973$; $p=0.0292$); Shannon-Wiener index ($R^2 = 0.3360$; $p= 0.0003$); evenness ($R^2 = 0.2248$; $p=0.0029$); and Simpson's diversity index ($R^2 = 0.2437$; $p=0.0053$).

Discussion

The 49 pools are located within close proximity, and most are no further than 50 cm from a neighbor. A total of 70 species was identified from all the samples, but a maximum of 16 species was found in any one pool during any one sampling event. There is much variation in species richness, both between pools and between years. By calculating the mean over seven sampling events, this variability is reduced and patterns become more apparent. King et al. (1996) found that species assemblages varied among pools within the same site, and not all species occurring at a site were found within a single pool.

Using aquatic plants in the Adirondack region of New York state, Weiher and Boylen (1994) found that the regression models explaining the most variance in species richness (R^2=0.74) included pH, a connectedness predictor, and an area measure (either lake surface area or littoral zone area). Thus, multiple regression models were preferred. The multiple regression models developed in this study explained much more variance when compared to the simple regression models. In addition, there was a significant increase in explained variance by increasing the number of terms in the models through addition of independent variables rather than the addition of independent PCA factor scores. This implies the existence of multiple independent determinants of richness, especially interaction effects, that are not seen when data is reduced using PCA techniques.

The stepwise regression models that accounted for correlation between variables developed for mean species richness and mean Shannon-Wiener index had similar levels of explained variance (around 60%) and included the same variables. This is not surprising considering that both of these measures of diversity are strongly affected by richness (Magurran, 1988). This also means that dominant and rare species contribute equally to these measures of diversity. The model for the Simpson's diversity index included fewer terms and explained less of the variance (about 37%) than the species richness or Shannon-Wiener models. Magurran (1988) indicates that this measure of diversity is strongly influenced by dominance and, thus, dominant species contribute more to the calculation of this index than rare ones. These findings indicate that physical and morphometric variables have a greater impact determining the number of species present in aquatic communities but have less impact in determining community abundance structure. Furthermore, the abundance models developed in this study had considerably lower explained variance (R^2) than richness or diversity models (Table 1). These results suggest that, while the physical conditions set the limits to distribution (i.e. presence and absence of species), it may be the biotic factors, acting at population and community levels, that have a greater impact on species abundances.

There was a negative relationship between the diversity measures and minimum pool temperature (Figure 2). As the pool temperature increases, the number of species able to survive at warmer water temperatures should decrease because of deteriorating pool conditions as well as the direct effects of higher temperatures on many organisms (Hutchinson, 1967). The positive relationship observed between the total abundance model and minimum temperature indicates a few species are able to exploit warmer water conditions and their abundances increase accordingly.

As maximum salinity increased, species diversity decreased (Figure 2). This is an expected phenomenon since many of the species inhabiting these rock pools are freshwater organisms. Many are able to tolerate low levels of salinity, but very few are able to tolerate hypersaline environments (Hutchinson, 1967; Therriault and Kolasa, 1999; Therriault and Kolasa, unpubl. data). However, as maximum salinity increased, total abundance (and biomass) also increased (Figure 2). This indicates that a few species are able to flourish under saline conditions. This may represent a shift in community structure from a primarily freshwater community to a primarily marine community.

Previous studies have shown that, for macroinvertebrate communities, species diversity declined at lower pH (Simpson et al., 1985; Wade et al., 1989). This was also true in three of the diversity models (species richness, the Shannon-Wiener index, and Simpson's diversity index; Figure 2).

Pool depth from the lip showed a significant positive relationship in the total abundance model. This was expected because the greater the water volume (effectively a larger "island") and thus habitat available to aquatic organisms, the greater the probability of the pool supporting more individuals and the lower the probability of extinction (Hanski and Gyllenberg, 1993; Tonn et al., 1995). In addition, the depth of the pool from the lip further reduces the probability of extinction by reducing variability in desiccation frequency, temperature, and salinity. Some studies have shown that species richness is correlated with hydroperiod, pool size (King et al., 1996) and depth (Sheldon and Meffe, 1995).

In conclusion, these results imply that much of the observed species richness is due to an accumulation of species able to tolerate pool conditions, whether directly or indirectly via modulated biotic interactions. The relevance of this finding lies in its potential usefulness in biodiversity estimations based on a limited number of easily measured parameters. Indeed, this potential depends on further developments and accumulation of similar empirical models and how well they perform with respect to a species pool and habitat in question. Admittedly, the usefulness of empirical models based on physical attributes of the environment declines in benign habitats with weak gradients.

Acknowledgements

We would like to thank the staff of the Discovery Bay Marine Laboratory, University of the West Indies, for helping make the fieldwork possible and all the students at McMaster University that helped with data collection and sample processing. This work benefited from comments from D. Currie and two anonymous referees, and editing suggestions from J. Therriault. This research has been supported by an NSERC operating grant (JK) and NSERC and OGS Scholarships (TT). This is contribution Number 616 from the DBML.

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Chapter 3:

Explicit links among physical stress, habitat heterogeneity and biodiversity

This chapter was published in Oikos (complete citation follows) and is reprinted here with permission from Oikos (Appendix 1). This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W., and J. Kolasa. 2000. Explicit links among physical stress, habitat heterogeneity and biodiversity. Oikos 89: 387-391.

Abstract

We tested the links among biodiversity, habitat heterogeneity and physical stress in a system of artificial rock pools on the north coast of Jamaica that mimic natural aquatic invertebrate communities. The experimental design consisted of three tiers of small plastic pools arranged at increasing distances from the shore. As a result of community development over six months (January to June 1997), we observed considerable differentiation of physical conditions among replicate habitats at the benign end of the physical gradient, with a concurrent increase in biodiversity (species richness per habitat unit). The most probable explanation for this observed gradient is self-generated habitat heterogeneity that, in turn, promotes biodiversity, likely through species interactions. Using additional analyses, including randomization techniques, we excluded the effects of sample size and external factors as sources for the observed increase in biodiversity in the third tier (furthest from the sea). We interpret this result as evidence for the complex causal relationship among physical stress, habitat heterogeneity and biodiversity.

Introduction

Stressful environments often have low species diversity. Stress has negative effects on biodiversity by reducing productivity, individual survival and colonization (slow and difficult for species without special adaptations) (Colinvaux, 1986). Specific causes of stress differ among habitats and taxa, but the impacts of stress tend to interfere with species performance and may result from nutrient deficiency, excessive or inadequate physical conditions, and intensive grazing or predation. Stress has been correlated with both the decline of diversity with elevation (Whittaker, 1977; Yoda, 1967) and the latitudinal gradient from the tropics to the poles (Fischer, 1960; Wallace, 1878). Various explanations, including different levels of heterogeneity, have been cited in ecology textbooks to account for diversity gradients.

Both spatial and temporal habitat heterogeneity affect the structure and dynamics of ecological communities (Kolasa and Pickett, 1991; Tilman, 1994) by increasing species diversity in terrestrial and aquatic systems (Downing, 1991; Huston, 1994; MacArthur and MacArthur, 1961). This increase, known as the rescue effect (Gotelli, 1991) or the mass effect (Shmida and Wilson, 1985), arises through various mechanisms such as differential use of microhabitats in space and time and inter-habitat migration (Jobbagy et al., 1996). The scale and degree of heterogeneity within a landscape are perceived differently by different organisms (Harmon et al., 1986; Knaapen et al., 1996; Wiens, 1994). Heterogeneity promotes diversity at different scales (Arita, 1997; Vivian-Smith, 1997) and rare species appear to benefit more than common species (Vivian-Smith, 1997). How local diversity is related to biogeographic gradients remains unanswered (Davidovitz and Rosenzweig, 1998).

Recently, biodiversity has received much attention from both conservationists and ecologists and has been addressed by microcosm studies (McGrady-Steed et al., 1997). Globally, habitat heterogeneity decreases as physical stress increases due to human impacts (Botsford et al., 1997; Chapin et al., 1997; Dobson et al., 1997; Matson et al., 1997; Noble and Dirzo, 1997; Vitousek et al., 1997). Both habitat heterogeneity and physical stress are implicated in species biodiversity and we need to gain a better understanding of how diversity is promoted, how habitat heterogeneity and physical stress are related, and how biodiversity will be affected if their direction and/or intensity change. Interactions between the two may help assess the effects of habitat change on biodiversity.

Methods and Materials

We evaluated links among biodiversity (as species richness, S), habitat heterogeneity and physical stress using 48 experimental, artificial rock pools arranged in three tiers (or blocks) located near the Discovery Bay Marine Laboratory on the north coast of Jamaica. This microcosm system accumulated species via natural colonization over a period of six months (January 1997 to June 1997) and produced a habitat heterogeneity gradient that negatively correlated with the initial physical stress gradient. The most stressful environment was near the ocean and the least stressful environment was in the coastal scrub forest.

Faunal samples were collected in one day by obtaining 250 ml of water and sediments from the pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution) and passed through a 63 μm net. Organisms were caught in a collecting container and immediately preserved in 60% ethanol. Invertebrates sampled included worms, crustaceans, and aquatic insect larvae and pupae. A total of 13 species were identified in the 48 pools. Physical variables describing pool conditions including temperature, salinity, dissolved oxygen, and pH were measured at the time of biotic sampling. Measurements for all pools were completed within one hour.

The experimental design consisted of 3 tiers (3 m, 11 m and 21 m from the ocean respectively) and each tier consisted of 2 rows with 8 pools (3 L volume) per row, totaling 48 identical artificial plastic pools embedded in concrete. Pool biodiversity represented the end point of community development from January to June of 1997.

We adopted a proxy measure of stress that was the inverse of the mean combined species abundance in each pool pair (see below) on the assumption that such a combined abundance realistically reflects the overall quality of conditions within each pool. Given that aquatic organisms generally respond positively (i.e. increasing abundance) when physical stress is low, species abundances allow for a quantification of the level of stress in this system. This measure coincided with the gradient of physical conditions from the ocean's edge inland.

Habitat heterogeneity was quantified as the variability in Principal Component Analysis (PCA) scores obtained from data on pool temperature, salinity, pH, and dissolved oxygen. Again, this variability was calculated pairwise for adjacent pools in both directions, within each tier. Therefore, an extreme measurement for any single pool would not bias the results.

Since the communities were allowed to develop naturally (pools were dry at the start of the experiment), the initial habitat heterogeneity data were collected during an earlier study where communities of different invertebrates (from the same species pool) were randomly distributed over the 48 artificial rock pools. Half of the introduced communities were an identical mixture of species and half were transplants from natural pools. The habitat data collected at the conclusion of this study illustrates the degree to which the biological communities modify their habitat and increase pool heterogeneity.

Statistical analyses were completed using Statistica and SAS at a significance level of $\alpha=0.05$.

Results

The tiers differed significantly in levels of physical stress ($df=2,43$; $F=5.93$; $p=0.0053$) and species richness or biodiversity ($df=2,43$; $F=17.45$; $p<0.0001$). As expected, species diversity was affected by both physical stress and habitat heterogeneity (Figure1). Species diversity increased ($df=2,43$; $F=17.45$; $p<0.0001$) with decreasing levels of stress and with increasing habitat heterogeneity. Furthermore, no gradient existed within a tier for species abundance or for species richness indicating that the only significant cline of conditions was perpendicular to the shore.

The negative relationship between physical stress and biodiversity may be explained by a positive relationship commonly observed between the number of

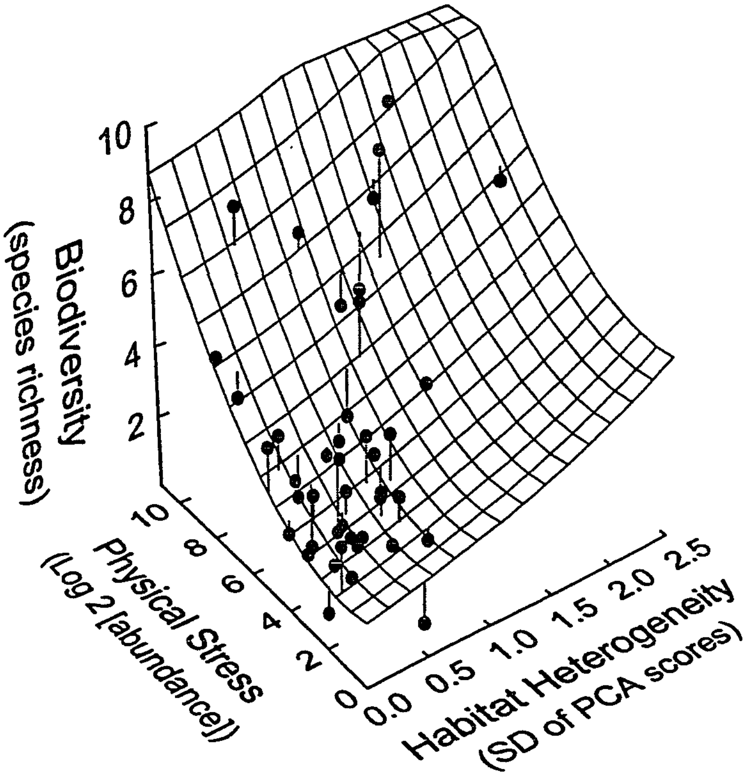

Figure 1. Biodiversity as a function of physical stress and habitat heterogeneity in a system of artificial rock pools. Biodiversity was measured as species richness, physical stress was represented by the logarithm of abundance and habitat heterogeneity as the variability in PCA scores of pool conditions.

individuals in a sample and species richness, the rarefaction curve. In order to control for the sample size effect, we created a rarefaction curve by randomizing the biotic community data independently of pool location. This was done by randomizing the biotic data among pools and among species, which allowed us to determine "new" species abundances and species richness values for each pool. We also randomized the data within each tier (block randomization) to retain a dependence on location: the same randomization procedure (i.e. among pools and among species) was followed except biotic data were randomized among the 16 pools located within each tier independently. Thus pool location was critical in determining this rarefaction curve. Randomizations were carried out 30 times for both independent and dependent pool communities. By comparing the two curves, we were able to determine if the higher observed biodiversity in the third tier was a function of greater total abundance per pool within this tier. If the higher diversity in the third tier were simply a function of the sampling design, the two curves would be the same. However, we found that the rarefaction curve for data randomized within a tier (different habitat zones) produced more species given the same abundance than the curve for the entire habitat gradient (homogeneity of slopes, transformed as ln [abundance]; df=1,2758; F=337.10; p<0.0001; Figure 2). This indicated that the observed increase in biodiversity in the third tier was due to differences in factors other than abundance. Differences in habitat heterogeneity is the only factor, of which we are aware, that increase biodiversity.

It is important to note that habitat heterogeneity may be generated by both external factors and by the resident biological community, or their interactions. Data obtained

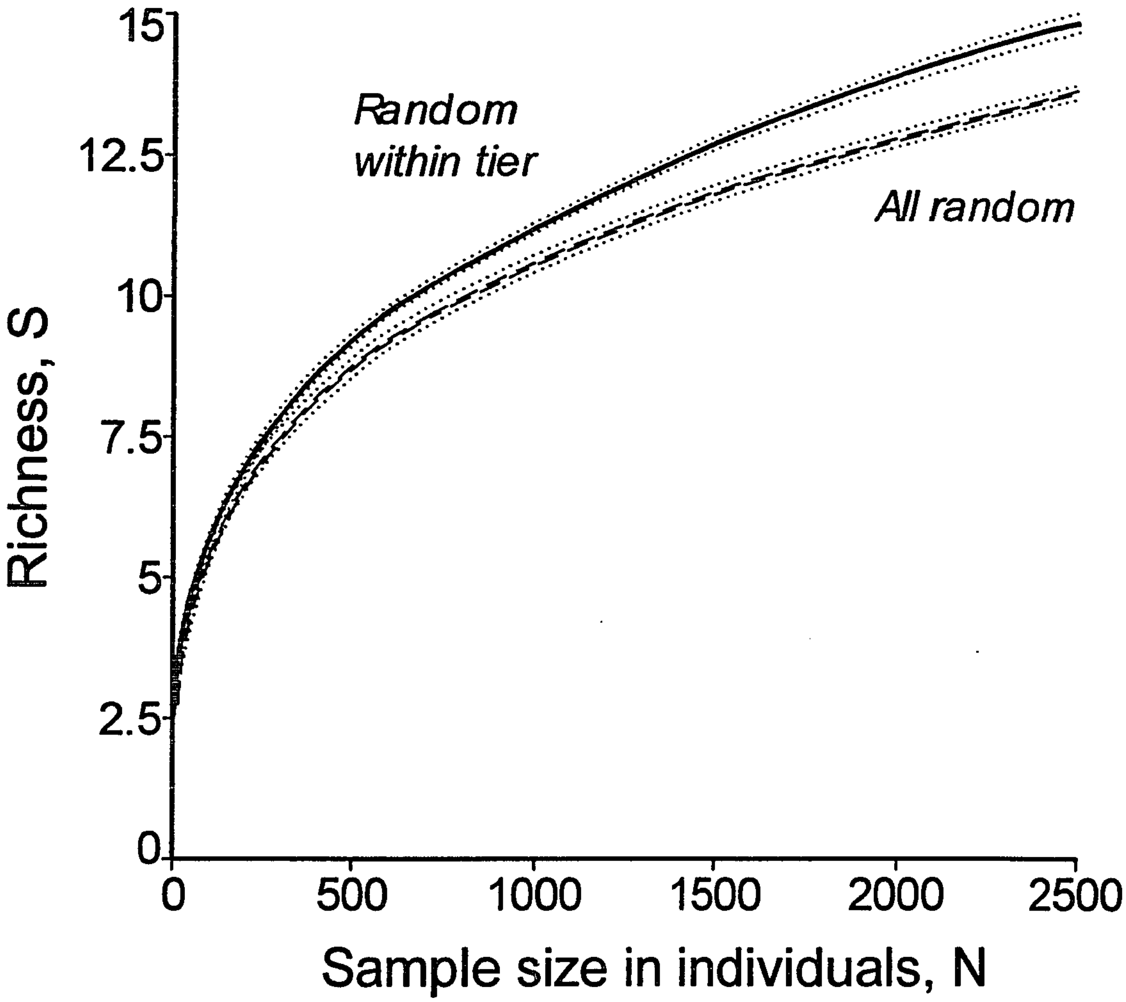

Figure 2. The rarefaction curves for randomized pool communities across the entire habitat gradient (broken line) and randomized within a tier (continuous line). Data were randomized 30 times for each case (total N=1380 for each curve). Fine dotted lines show the 95% confidence limits around the rarefaction lines.

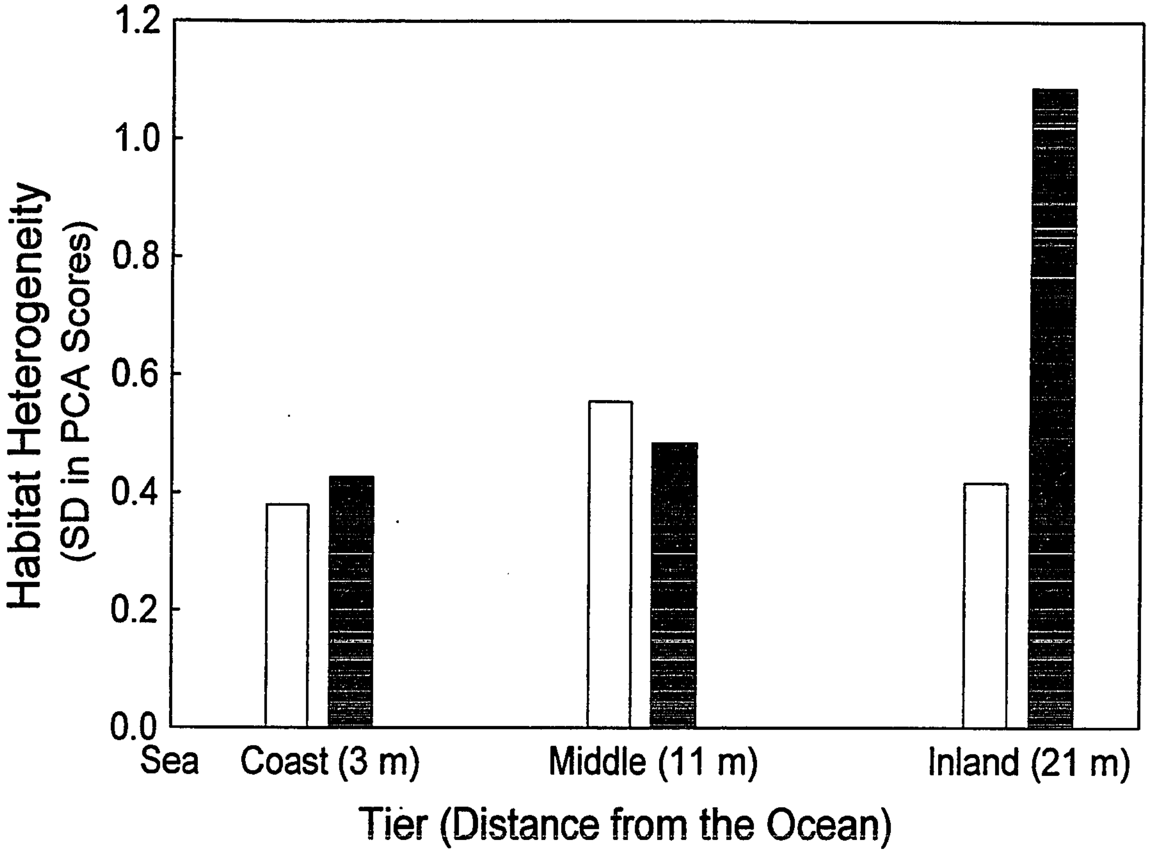

Figure 3. Spatial heterogeneity within groups of pools increased during the course of study (filled bars) and developed a gradient from the ocean's edge inland. Note that initial habitat heterogeneity was constant across tiers (open bars). Again, habitat heterogeneity was measured as the variability in PCA scores of pool conditions.

during a previous study using the same experimental set of pools indicated no difference in habitat heterogeneity among tiers at the beginning of an experiment (df=2,9; F=0.59; p=0.5756; Figure 3). However, the data collected during this study showed a significant difference in habitat heterogeneity among tiers (df=2,9; F=11.92; p=0.0030; Figure 3) with the greatest habitat heterogeneity observed in the third tier. Furthermore, we have replicated the experiment in 1998 and collected organic matter on a 1 mm mesh sieve to determine if allochthonous inputs could have produced the heterogeneity differences among pools. We found that the amount of organic matter, primarily leaves, was not significantly greater in Tier 3 compared to Tier 2 (Tier 1 had no leaves and was excluded). While the mean standard deviation among pairs of adjacent pools was larger in the third tier, the relative pool-to-pool differences were smaller (recall that the third tier had the greatest habitat heterogeneity). We conclude that exposure differences due to location alone, do not produce significant small-scale heterogeneity. Thus, such heterogeneity must have been generated by the biotic activity in adjacent pools. There were also significant differences in biodiversity between the first two tiers and the third tier (Tiers 1 and 3, p=0.0001; Tiers 2 and 3, p=0.0001). However, there were no significant differences between Tiers 1 and 2 for either habitat heterogeneity (p=0.9069) or biodiversity (p=0.9910).

Discussion

Biodiversity has a significant influence on the level of habitat heterogeneity. Tiers 2 and 3 are susceptible to similar exogenous factors (i.e. differential shade, wind, and plant debris inputs) and, if the increase in heterogeneity were due to those factors alone, one would expect to find similar levels of habitat heterogeneity between these two tiers. However, the only known difference between Tiers 2 and 3 is biodiversity (S), hence we suggest it had a significant influence on the level of habitat heterogeneity. If this is the case, the biological community contributes significantly to the development of habitat heterogeneity that, in turn, boosts biodiversity. We, therefore, postulate a link among biodiversity, habitat heterogeneity and physical stress as an important factor to consider in assessment of environmental processes promoting or demoting biodiversity.

One plausible interpretation of the experimental results is that communities at the benign end of the gradient developed over progressively divergent trajectories (cf. Samuels and Drake, 1997). This developmental divergence appears to have had a strong effect on physical conditions in individual pools and may have further enhanced differential settlement and persistence of new colonizers. Thus, a low variation, low stress environment led to self-generated biodiversity mediated by autogenic spatial heterogeneity. We tested this idea further by examining the individual and combined effects of physical stress and habitat heterogeneity on biodiversity. The interaction effect between stress and heterogeneity on biodiversity was not significant (SAS-GLM, df=1,40; F=1.83; $p=0.1840$) but individually, both low physical stress and high habitat heterogeneity contributed significantly to biodiversity ($p<0.0001$ and $p=0.0011$, respectively). It is possible that higher productivity at the benign end of the stress gradient (on average higher observed chlorophyll concentrations) also may have contributed to higher biodiversity by removing energetic constraints and permitting longer food chains (Pimm, 1982). However, it is not clear how higher productivity alone could explain higher spatial heterogeneity. Another mechanism likely to contribute to the differentiation of pools might be cascading trophic relationships. We have often observed, although not quantified, that pools with dragonfly larvae have few midges and high chlorophyll concentrations. However, pools without dragonfly larvae often support many midges and have low chlorophyll concentrations (clear water).

While we identify a probable direct link among low physical stress, self-generated heterogeneity, and biodiversity, we acknowledge that other factors also may be important. Their relative contributions should be evaluated further through field experimentation. It is probable that disturbance, stress, heterogeneity, productivity, and rescue effect all play roles in enhancing and maintaining high species richness, even in a single ecosystem.

Our study adds one more direct and potentially important mechanism through which human produced environmental stress may reduce biodiversity. If the reverse process is true, then stress related reduction of heterogeneity might be responsible for species extinctions. Species extinctions may additionally reduce heterogeneity and encourage a cascade of steps leading to further extinctions.

Acknowledgements

Funding for this project was provided by NSERC and OGS scholarships to T.W.T. and an NSERC operating grant to J.K.. We thank the staff of the D.B.M.L. for their assistance. This manuscript was improved by comments from R. Bailey and P.

Marquet and editorial suggestions from J. Therriault. This is contribution No. 617 from the DBML.

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Chapter 4:

Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools

This chapter has been accepted for publication in the Israel Journal of Zoology (partial citation follows). This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W., and J. Kolasa. 2000. Desiccation frequency reduces species diversity and predictability of community structure in coastal rock pools. Israel Journal of Zoology (in press).

Abstract

Success of aquatic organisms in temporary ponds depends on both survival through the dry period (i.e. resting eggs) and population dynamics through the wet period (i.e. recolonization, dispersal). We hypothesized that pools with high desiccation frequency would contain simpler communities (fewer species) and these communities would have greater compositional constancy (persistence) due to a restricted set of species. To test these hypotheses we examined diversity, species richness, abundance, evenness, community persistence, and community structure (species ranking) over time using 49 erosional rock pools located on the north coast of Jamaica. Diversity, species richness, and abundance decreased with increased frequency of pool desiccation. Pools were classified as temporary or permanent. In temporary pools, despite substantial inter-pool differences, diversity, species richness, evenness, and abundance did not change significantly over time. Contrary to our hypothesis, community persistence (compositional stability) decreased with increased frequency of pool desiccation. Species rank also changed significantly over time in pools that were classified as temporary. However, temporary pools had lower variability in community structure, suggesting the existence of a common type of community: one dominated by "weedy" species with good dispersal and colonization abilities. A somewhat unexpected conclusion is that high habitat variability (i.e. temporary pools) may lower the variability in some community descriptors. However, the reduction of community variability is achieved at the expense of its richness and diversity.

Introduction

Ephemeral or temporary ponds are an important aquatic habitat for many species. Some animals use these ponds for resources while others use them to complete a life history stage such as breeding (e.g. Peterson and Boulton, 1999; Bonner et al., 1997). Many invertebrates live permanently in these habitats (Spencer et al., 1999; Schneider, 1997) despite their variability, notably cladocerans (López and Theis, 1997; Maier, 1993), anostracans (Marcus and Weeks, 1997), and phyllopods (Hamer and Appleton, 1991). Temporary ponds or pools typically pass through three distinct phases (filling, aquatic, and drying), each of which may contain different faunal groups (Wiggins et al., 1980). Pool duration can be influenced by a number of factors including precipitation, evaporation, surface area, wind, temperature, and permeability of the substrate (Marcus and Weeks, 1997). Pool desiccation can cause cascading effects on other physical pool conditions including increased water temperature, increased salinity or increased concentration of dissolved ions, decreased pH, and changes in sulfur and nitrogen cycles (Van Dam, 1988). Pool desiccation also can influence biotic interactions by increasing the density of animals, resulting in greater competition and other density dependent effects (e.g. Aspbury and Juliano, 1998) or by influencing colonization, survival, and developmental rates and strategies (Blaustein et al., 1999).

Success of aquatic organisms in temporary ponds depends on survival through the dry season and dynamics through the wet season (Wyngaard et al., 1991). Invertebrates have adapted to survive in these extreme environments by producing resting stages and/or life cycles with terrestrial and aquatic stages (see Wiggins et al., 1980). In addition, other invertebrates have adapted to these variable habitats by evolving entirely aquatic life stages but are able to disperse by flying (e.g. Notonectids). It was argued initially that temporary ponds were species-poor due to the difficulties of adapting to a desiccating environment (Wiggins et al., 1980). However, more recently, Mahoney et al. (1990), Taylor and Mahoney (1990), and Bazzanti et al. (1996) have shown that natural temporary ponds can support rich zooplankton communities and phytoplankton communities (often 40 or more taxa are identified). In addition, other temporary aquatic habitats, including temporary streams (Moreno et al., 1997) and floodplain ponds (Corti et al., 1997), have been shown to support surprisingly rich communities.

Despite a growing number of studies on species adaptations to temporary environments, there have been relatively few studies on these systems at the community level (e.g. Lake et al., 1989). Several factors are believed to influence the species richness of temporary pools including habitat area (Ward and Blaustein, 1994; March and Bass, 1995) and hydroperiod (Schneider and Frost, 1996). Furthermore, species richness increases as pool duration increases (Schneider, 1997; Schneider and Frost, 1996) and community structure in temporary pools depends on life history strategies (Wiggins et al., 1980). We hypothesize that pools with a high frequency of desiccation should support fewer species and hence simpler communities because these pools should only support a subset of the regional species pool. Harsh environmental conditions will limit the ability of some species to colonize and survive in variable habitats. We expect community persistence (constancy in composition over time) to be high in temporary pools because they should be dominated by species with good dispersal abilities (Scarsbrook and

Townsend, 1993) and these species should show typical *r*-selection characteristics including early reproduction and rapid individual and population growth (Pianka, 1970). It is also possible that rare species with good dispersal abilities might lower community persistence (by changing composition from time to time) and result in varied community assemblages. To evaluate these hypotheses, it is preferable to minimize the confounding effects of geographical variation and pond history by examining communities from a single geographical area that has a shared species pool (Therriault and Kolasa, 1999; Spencer et al., 1999). In order to determine the effect of desiccation frequency on communities, we examined changes in several community metrics over time using a system of erosional rock pools on the north coast of Jamaica. This system consists of pools that span a range of physicochemical properties, represent habitats of differing patterns of drying (frequency and duration) and are home to numerous invertebrate species and communities resulting from a common species pool.

Methods

We examined species richness, diversity, abundance, evenness, community persistence and community structure over time using 49 erosional rock pools located on the north coast of Jamaica near the Discovery Bay Marine Laboratory (Figure 1). Some of the temporary rock pools used in this study are shown in Figure 2. Sampling dates were Dec. 89, Jan. 90, Jan. 91, Jan. 92, Jan. 93, Jan. 97, and June 97. Faunal samples were collected in one day by passing 500 ml of water and sediments from each pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution) through a 63 μm net. Organisms were caught in a collecting container and immediately were preserved in 50 – 60 % ethanol. Animals sampled included lower invertebrates (except rotifers and gastrotrichs), crustaceans, and aquatic insects (larvae and pupae). Seventy species have been identified from the 49 pools. Physical variables describing pool conditions including temperature, salinity, dissolved oxygen concentration, and pH were measured at the same time as the biotic samples were collected. Physical measurements for all pools were completed within one hour. Morphometric measures including pool length, width, depth, surface area, and volume also were made.

We employed several measures of habitat permanency in this study. The frequency of desiccation was measured directly as the number of times a pool dried out over the period of observations. We also quantified pool duration indirectly. In some studies, the ratio of surface area to volume has been used to represent the likelihood of desiccation and, consequently the length of dry period, such that when the ratio is high, the rate of evaporation should be greater (Marcus and Weeks, 1997). To represent the rate of pool evaporation we used the natural logarithm of the surface area to volume ratio. One additional measure used to quantify pool duration was the relative change in pool depth. In general, dry pools tend to be refilled synchronously during precipitation events; the duration of the dry period is primarily determined by how early a pool dries. Based on a series of 3 depth measurements taken over a 1-week period in January 1998, we quantified the likelihood of a pool drying out, with large reductions in pool depth indicating pools with a high probability of drying early.

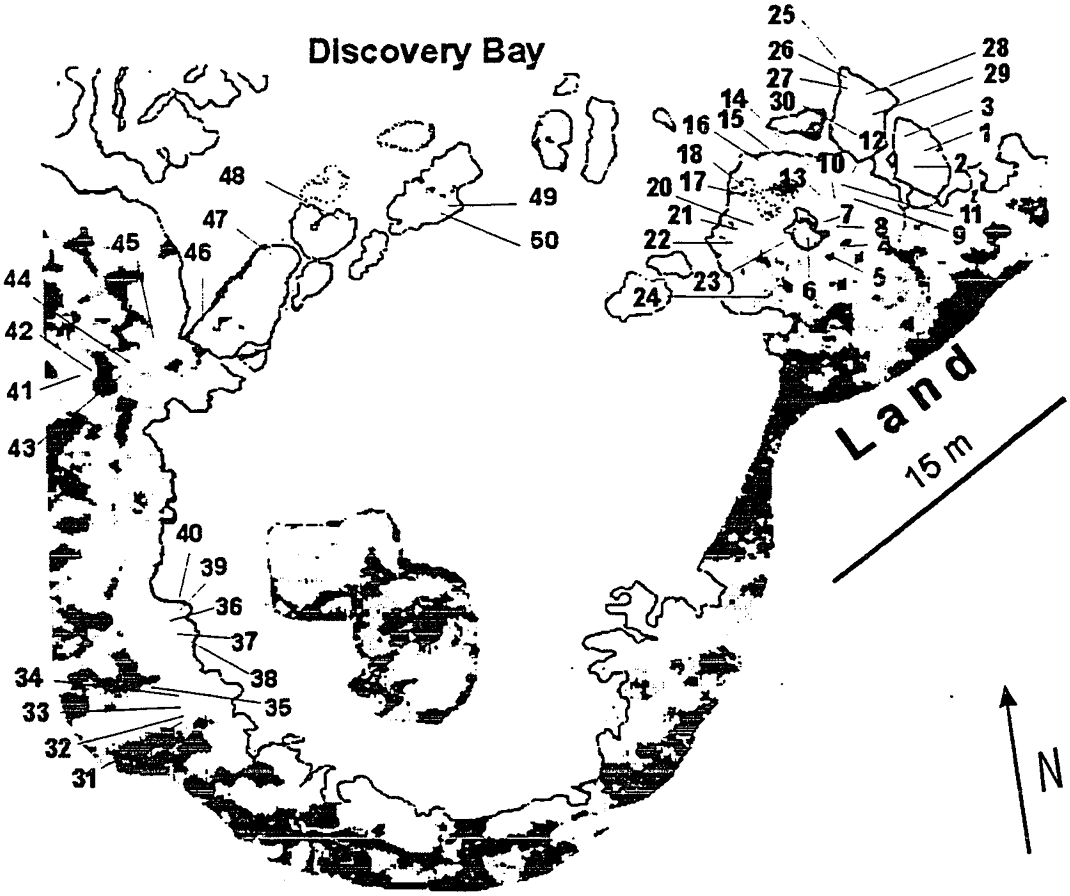

Figure 1: Map of the rock pools in the proximity of the Discovery Bay Marine Lab, Jamaica. All pools are shown (note there is no Pool 19) and range from temporary to permanent habitats. The numbers on the map correspond to the numbers in the text for temporary pools. Shading represents the rocky shore.

Pools also were classified as permanent or temporary. We define pools as temporary if they were found dry on at least three occasions out of a total of 12 surveys of physical parameters (11 pools; Pools 6, 12, 15, 24, 25, 30, 32, 37, 43, 45, 46; Figures 1 and 2). Additionally, we define pools as temporary if they were found dry on at least one of the seven biotic sampling dates (15 pools; Pools 12, 14, 15, 21, 25, 27, 28, 30, 31, 32, 33, 37, 43, 45, 46; Figures 1 and 2).

Five community metrics were calculated for each pool and sampling date, including Simpson's diversity index; Shannon-Wiener diversity index (H'); evenness (E; based on the Shannon-Wiener index) (Magurran, 1988); species richness (S'); and total abundance of all individuals in the community (N) where: N was transformed as $\log_{10}(x+1)$.

To evaluate the mean rate of change in community structure, we calculated three similarity measures (Jaccard's similarity index, Sorenson's similarity index (Magurran, 1988), and the number of species in common, i.e. the number of shared species between adjacent sampling dates) for each pool on consecutive sampling dates and then averaged these values among all dates. We also evaluated changes in community structure over time using both Cochran's Q test and Kendall's coefficient of concordance (W). Cochran's Q test was used to test for differences among sampling dates in the faunal assemblage composition (presence/absence) and Kendall's coefficient of concordance (W) was used to assess the constancy in ranked relative abundance of species among the sampling dates. For these analyses, dry pools were treated as if they contained zero individuals and zero species. Results were similar when dry pool records were treated as

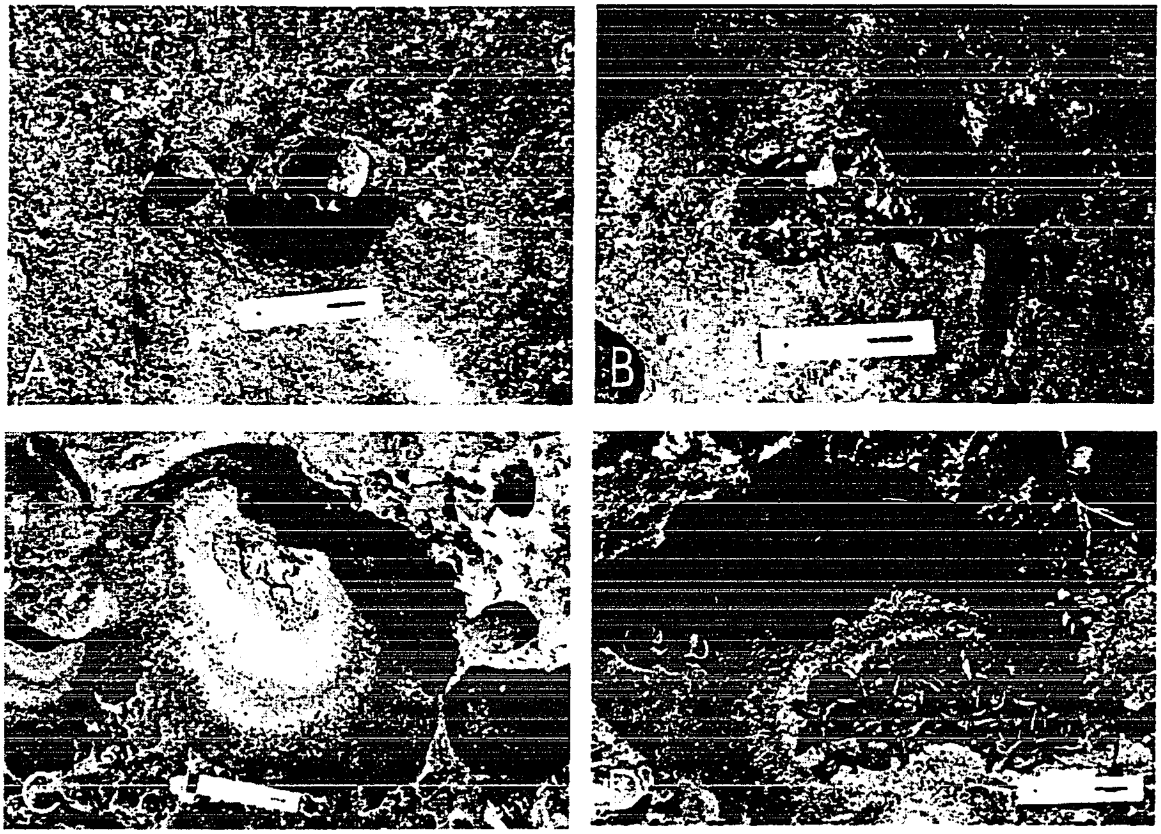

Figure 2: Photographs showing some of the temporary rock pools used in this study including: A) Pool 12; B) Pool 30; C) Pool 43; and D) Pool 45. Note that pool numbers correspond to those used in Figure 1. Each pool is shown when dry and the scale represents 15 cm.

missing data. We also considered the effects of rare species on the calculation of both Kendall's *W* and Cochran's *Q* and calculated both for each temporary pool using: a) all species, and b) the 17 most common species (defined by their abundance and occurrence).

We used General Linear Models, ANOVA's and regressions to evaluate the effects of pool desiccation frequency on community metrics. All statistical analyses were completed using Statistica at a significance level of α=0.05. Additionally, for all General Linear Models, residuals were checked for normality and correlation with model terms to validate model assumptions.

Results

Mean species richness, diversity (as Shannon-Wiener index), and abundance all decreased with increased number of times a pool dried (Table 1; Figure 3). Mean Simpson's diversity index and mean evenness did not show significant relationships with the number of times a pool was dry, implying that desiccation does not affect general dominance patterns, even though individual species rankings may have changed. Pools that dried less frequently (permanent) supported more species than pools that often dried (temporary). Minimum and maximum values for species richness, the Shannon-Wiener diversity index, and total abundance all decreased with increased number of times a pool dried (Table 1).

The mean for both diversity indices (Simpson's index and Shannon-Wiener index) decreased in pools more likely to dry often (higher evaporation rate; increased ratio of surface area to volume) (Table 1). Other measures of diversity, including minimum Simpson's index, minimum Shannon-Wiener index, minimum evenness, and maximum Shannon-Wiener index were also negatively related to evaporation rate (ratio of surface area to volume) (Table 1).

Species richness, diversity (Shannon-Wiener index), and total abundance all decreased with reductions in relative pool depth (i.e. reduced pool duration) (Table 1). Changes in relative depth also limit the minimum and maximum values of species richness and abundance. Minimum species richness and abundance were higher in pools of greater duration (i.e. small relative change in pool depth) (Table 1). In addition, maximum species richness, total abundance, and diversity decreased with reductions in relative pool depth (Table 1).

Community structure (composition and ranked relative abundance) changed at different rates among pools that dried more frequently (or had a high likelihood of drying) than pools that did not dry often (or had a low likelihood of drying). Community similarity and the number of shared species decreased as the number of times a pool dried increased (Sorenson's index, Jaccard's index, number of species in common; Table 2; Figure 4). Furthermore, the number of species in common also decreased as the number of times a pool dried increased when the dry dates were eliminated from the analyses while the similarity indices (Jaccard's and Sorenson's) showed no trend (Table 2). Community structure changed more in pools where depth decreased substantially (short duration pools) than in pools where depth remained relatively constant (long duration pools). Pools with large changes in relative depth retained fewer species in common among dates and lower community similarity (Table 2). Again, when dry pools were omitted from the analyses, the trends were similar (even if not significant) to the findings when dry pools were considered to have no species (Table 2). Interestingly, the ratio of surface area to volume (desiccation likelihood) appears to have no effect on community similarity (Table 2).

Table 1: Regression summary for different community metrics versus three measures of habitat permanency (desiccation frequency and habitat duration).

	Number of times a pool dried		Ratio of surface area to volume		Relative change in pool depth	
Community Metric	$F_{1,47}$	p	$F_{1,47}$	p	$F_{1,47}$	p
mean richness	11.56	0.0016	3.19	0.0805	17.89	0.0001
minimum richness	12.92	0.0008	3.36	0.0733	17.50	0.0001
maximum richness	7.75	0.0077	3.38	0.0564	10.16	0.0025
mean Simpson's index	1.46	0.2323	4.39	0.0415	1.53	0.2222
minimum Simpson's index	0.02	0.8838	6.46	0.0144	0.00	0.9694
maximum Simpson's index	0.90	0.3468	1.64	0.2061	1.74	0.1935
mean Shannon-Wiener index	11.18	0.0016	6.53	0.0139	8.72	0.0049
minimum Shannon-Wiener index	7.47	0.0088	4.73	0.0347	2.64	0.1107
maximum Shannon-Wiener index	6.68	0.0129	4.06	0.0496	6.81	0.0121
mean evenness	0.10	0.7500	2.43	0.1257	0.45	0.5063
minimum evenness	0.74	0.3927	5.76	0.0204	1.77	0.1904
maximum evenness	0.45	0.5066	0.04	0.8476	0.38	0.5416
mean abundance	17.11	0.0001	0.44	0.5099	17.65	0.0001
minimum abundance	14.37	0.0004	0.92	0.3435	10.61	0.0021
maximum abundance	6.58	0.0136	0.15	0.6981	7.97	0.0070

Table 2: Regression summary of measures of community similarity versus three measures of habitat permanency (desiccation frequency and habitat duration). Analyses were done including dry pools and omitting dry pools.

	Number of times a pool dried		Ratio of surface area to volume		Relative change in pool depth	
Similarity Measure	$F_{1,47}$	p	$F_{1,47}$	p	$F_{1,47}$	p
	Dry Pools Included (0 richness and 0 abundance)					
Sorrenson's index	9.44	0.0035	0.63	0.4316	5.21	0.0270
Jaccard's index	9.18	0.0040	0.16	0.6929	10.37	0.0023
number of species in common	13.04	0.0007	1.19	0.2814	12.83	0.0008
	Dry Pools Omitted					
Sorrenson's index	1.09	0.3025	1.05	0.3116	2.08	0.1560
Jaccard's index	1.91	0.1737	0.10	0.7551	5.22	0.0269
number of species in common	8.62	0.0051	1.69	0.1994	11.64	0.0013

Not surprisingly, responses of community descriptors are consistent with the previous results when pools are classified into two categories, temporary and permanent. Community composition changed significantly among sampling dates in temporary pools. Composition based on species presence or absence changed significantly among dates for nine of the 11 pools (Cochran's *Q*). In addition, species rank also changed significantly among sampling dates in eight of the pools (Kendall's *W*). In contrast, in the 38 permanent pools, composition changed significantly in 11 pools while species rank changed significantly in 15 pools. Temporary pools showed greater change in species composition than permanent pools (Cochran's *Q*: $G_{adj}=9.620$; $p<0.005$) but species rank was not significantly different between temporary and permanent pools (Kendall's *W*: $G_{adj}=3.692$; $p>0.05$). Using the group of temporary pools expanded by those dry during biotic sampling (see Methods), assemblage composition changed significantly among dates for 13 of these 15 pools (Cochran's *Q*). In addition, species rank also changed significantly among sampling dates for 12 of these 15 pools (Kendall's *W*). In contrast, in the 34 permanent pools, composition changed significantly in seven pools while species rank changed significantly in 11 pools. Temporary pools showed greater change in species composition and species rank compared to permanent pools (Cochran's *Q*: $G_{adj}=19.153$; $p<0.001$; Kendall's *W*: $G_{adj}=9.563$; $p<0.005$). Temporary pools (regardless of the definition) showed greater change in species composition (Cochran's *Q*: $G_{adj}=13.599$; $p<0.001$) and in species rank (Kendall's *W*: $G_{adj}=9.413$; $p<0.005$).

It is possible that temporary pools are dominated by a few species that are able to exploit these unpredictable habitats, at least in terms of desiccation timing. We tested this hypothesis by determining the relationship between the number of times a pool dried and the relative abundance of the dominant species. The minimum relative abundance for dominant species increased as pools dried more often ($F_{1,47}=5.54$, $p=0.0228$) and the range of relative abundances decreased with increased number of times a pool dried ($F_{1,47}=4.67$, $p=0.0358$). Consistently, the mean and maximum values of relative abundance of the dominant species increased as the ratio of surface area to volume (pool evaporation rate) increased ($F_{1,47}=6.89$, $p=0.0117$ and $F_{1,47}=6.24$, $p=0.0160$) and pools that showed little change in relative depth had higher minimum relative abundances for dominant species and lower relative abundance ranges for these species ($F_{1,47}$=5.20, p=0.0272 and $F_{1,47}$=4.60, p=0.0373).

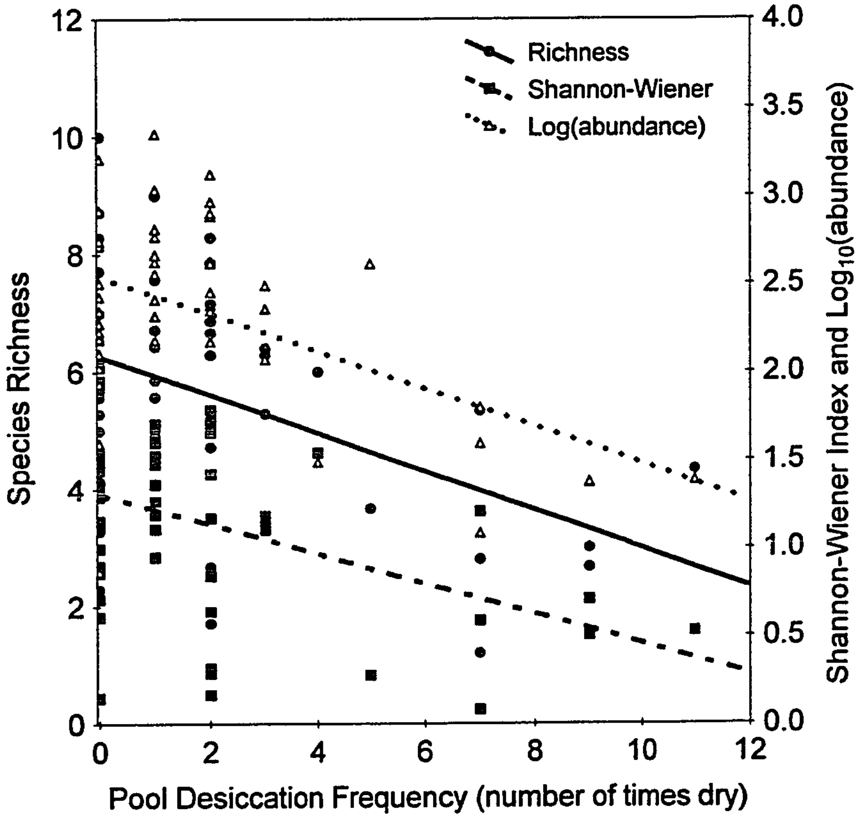

Figure 3: Mean species richness, diversity (Shannon-Wiener index), and total abundance change in response to desiccation frequency measured as the number of times a pool was recorded dry. The regression equations are y = a(SE) + b(SE)* times dry + ε : mean richness = 6.263(0.322) – 0.444(0.131) * times dry + ε, R^2=19.74; mean Shannon-Wiener index = 1.303(0.085) – 0.438(0.131) * times dry + ε, R^2=19.22; mean total abundance = 2.539(0.086) – 0.517(0.125) * times dry + ε, R^2=26.69.

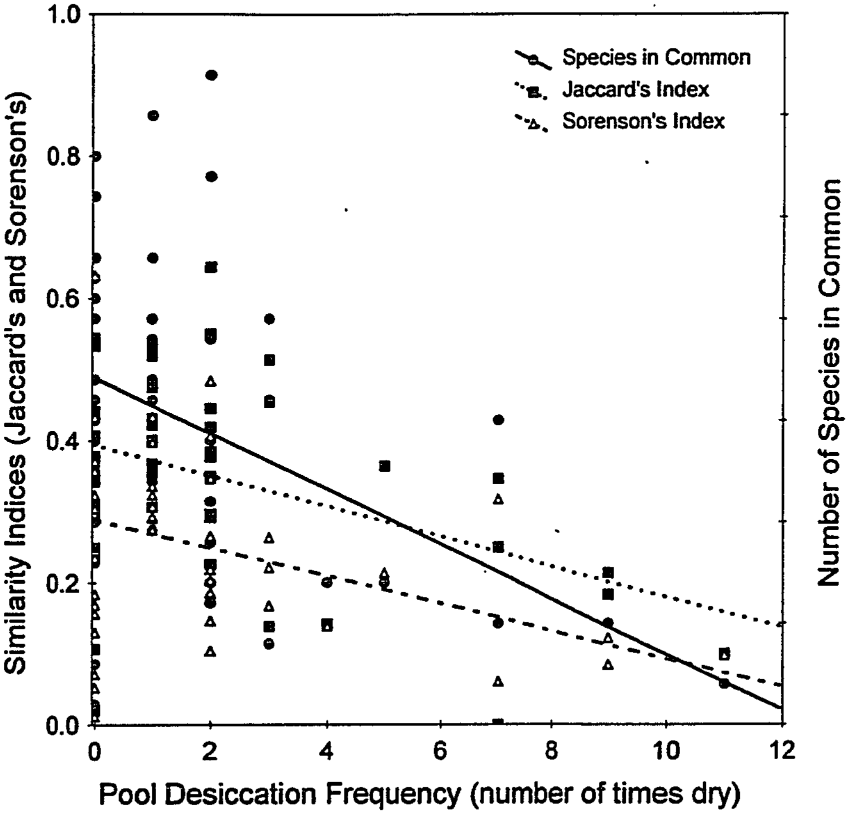

Figure 4: Community similarity over time measured as Jaccard's similarity index, Sorenson's similarity index, and the number of species in common on consecutive dates, as a function of pool desiccation frequency (number of times dry). The regression equations are y = a(SE) + b(SE)* times dry + ε : Jaccard's index = 0.394(0.024) – 0.404(0.133) * times dry + ε, R^2=16.34; Sorenson's index = 0.288(0.021) – 0.409(0.133) * times dry + ε, R^2=16.73; number of species in common = 3.417(0.253) – 0.466(0.129) * times dry + ε, R^2=21.72.

Discussion

Species diversity decreased with the indicators of short and discontinuous pool existence (greater reductions in pool depth and increased evaporation rate). Species richness and total abundance also decreased with greater reductions in pool depth. These findings are consistent with Spencer et al. (1999), Schneider (1997), and Schneider and Frost (1996) who showed that species richness increased as pool duration increased. In addition, the range of dominant species was lower for temporary pools and the minimum level of dominance (relative abundance) was greater in temporary pools, suggesting that variable habitats are dominated by fewer species that are able to exploit these conditions. Furthermore, Schneider and Frost (1996) found that increased pond duration resulted in more biotic interactions, which may be consistent with lower levels of dominance in permanent ponds, and is in agreement with this study. However, these findings are in disagreement with Corti et al. (1997) who showed that both invertebrate abundance and richness decreased as pond duration increased. We attribute this difference to the seasonal nature of the floodplain ponds they studied.

Community similarity decreased as desiccation frequency increased. Bradshaw and Holzapfel (1988) found that, in tree-hole communities, habitat duration negatively affected species survivorship, which, along with re-colonization, may contribute to decreasing values of similarity between dates. We further found that pools that are susceptible to desiccation (those with high evaporation rates or large decreases in relative depth) have fewer species and a more unpredictable community structure than pools that are not susceptible to desiccation through better water retention, lower evaporation, and seawater inputs. Similarly, García et al. (1997) showed that, in saline lakes, the annual hydrological budget affected both physical variation and biological changes between years with differing budgets. Although we did not directly measure the hydrological budget for any of the pools, our data show that the pools in this study span a gradient of habitat duration, and, therefore, a gradient of hydrological budgets.

In addition to the effects of pool duration, desiccation frequency also affected community metrics. Mean diversity, richness, and total abundance decreased with increased frequency of pool desiccation. Pool desiccation represents a severe perturbation event for aquatic communities. As the frequency of pool desiccation increases, it is likely to result in higher individual mortality in many populations, some of which will go extinct locally. However, pools may refill with rain or seawater before drying completely. This radical change in environment may result in indirect mortality in some species, thereby lowering the species richness. The contrasts between direct and indirect mortality has been discussed elsewhere (see Aspbury and Juliano, 1998), especially as it pertains to disturbance events (see Pickett and White, 1985; Connell and Sousa, 1983). However, it is interesting to note that some of our measures of pool permanency might account for the indirect effects of pool desiccation. For example, species diversity decreased with increased evaporation rate (as estimated by the ratio of surface area to volume). The relationship between diversity and the relative change in pool depth shows a similar trend - also an indication of the indirect effects of pool desiccation on aquatic communities.

Community structure in this system of erosional rock pools is not static. Both temporary and permanent pools changed in community composition and species rankings over time, with changes being greater in temporary pools. This might indicate that the community composition of temporary pools is determined primarily by abiotic factors (frequency or severity of pool desiccation). Despite adaptations to living in these harsh environments (see Wiggins et al., 1980), the invertebrate communities will be determined largely by the wet period of the pool. If the pool dries too quickly, some species might not be able to complete their aquatic life stages before the pool dries (i.e. mosquitoes). It is also possible that the community composition is determined largely by colonization events (Death, 1995) or through metapopulation dynamics (Hanski and Gilpin, 1997), both of which are likely more variable in variable habitats than in stable ones. Similarly, Bonner et al. (1997) found that abiotic factors were primarily responsible for determining community structure in other temporary habitats.

It is possible that the relationship between desiccation frequency (number of times pool dried) and community similarity (Figure 4) is an artifact. Since similarity indices are partially a function of the number of species present, the lower similarity in pools that dried often could be a result of lower species richness in these pools (see Wolda, 1981). If species richness and abundance are included as covariates in the regression between similarity index and number of times dry (full factorial design), the desiccation frequency is not statistically significant ($p>0.05$). However, all the rock pools in this system are relatively species poor (maximum richness was 16 species in one pool) making it difficult to determine if the observed relationship is simply an artifact. Furthermore, despite the variability observed in pools that often do not dry, the similarity indices were clearly lower for pools that dry frequently. This provides some indication that regardless of the reason (i.e. lower richness in these pools or degree of habitat permanency), pools that dry more often have a more variable community structure. Species diversity and relative abundances may change, but the type of community will likely be similar: one dominated by a few species with good dispersal and colonization abilities.

Temporary habitats, at least in this system, appear to be dominated by a few, well-adapted species. These findings agree with other studies of temporary habitat fauna including cladocerans (López and Theis, 1997; Maier, 1993), anostracans (Marcus and Weeks, 1997), and phyllopods (Hamer and Appleton, 1991). Furthermore, in this system, almost all of the pools that were classified as temporary contained cyclopoid copepods on at least one sampling date. Of the 17 pools that could be classified as temporary, 14 contained cyclopoid copepods and they were present in 56.3% of the samples collected from these pools. Pools 25, 45 and 46 were the only temporary pools that did not contain cyclopoid copepods on any date. In addition, cyclopoid copepods were among the first colonists to pools that were cleaned, dried, and allowed to colonize naturally (pers. obs.). Clearly, copepods were able to exploit these variable habitats successfully. These findings are in agreement with other studies that have found that cyclopoid copepods thrive in unpredictable habitats. Studying temporary ponds in South Carolina, Wyngaard et al. (1991) found that cyclopoid copepods were good at exploiting these ephemeral habitats. Copepods might do well in unpredictable environments because of their number of *r*-selected traits. In this rock pool system, copepods appear to have good dispersal abilities and high reproductive rates. This agrees with the suggestion that species in unpredictable habitats should demonstrate a greater number of *r*-selected traits (Pianka, 1970).

In conclusion, low pool permanency affects species richness, diversity, evenness, and total abundance. Temporary pools were more variable over time with respect to species composition and ranked abundances. These findings imply that temporary habitats are dominated by a few weedy species with good dispersal and colonization abilities. It is also important to distinguish between desiccation frequency and pool duration, as they need not be the same thing. Desiccation frequency has direct impacts on species diversity while pool duration (quantified by relative change in pool depth and evaporation rate) indirectly affects diversity and community structure. However, pool permanency, whether frequency or duration, show that temporary habitats contain fewer species in a more simplified community structure.

Acknowledgments

We would like to thank the staff of the Discovery Bay Marine Laboratory, Jamaica, for helping make the fieldwork possible and all the students at McMaster University who helped with sample processing. We would also like to thank J. Therriault for editorial suggestions and two anonymous reviewers for helpful comments on a previous version of this manuscript. This research has been supported by an NSERC operating grant (JK) and NSERC and OGS Scholarships (TT). This is contribution number 620 from the DBML.

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Chapter 5:

Patterns of community variability depend on habitat variability and habitat generalists in natural aquatic microcosms

This chapter has been submitted to Community Ecology (partial citation follows) to be considered for publication. This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W., and J. Kolasa. Patterns of community variability depend on habitat variability and habitat generalists in natural aquatic microcosms. Community Ecology (in review).

Abstract

Habitat variability is largely an external mechanism influencing community variability by affecting abundances and precipitating other community changes but the nature of this influence is poorly understood. The absence of systematic quantitative studies appears to be a major reason for this deficiency. To address the problem, we have evaluated community and population variability in invertebrate communities collected from 49 coastal Jamaican rock pools with contrasting levels of habitat variability.

We calculated a multivariate index of habitat variability based on temporal changes in physicochemical variables. Variability in diversity indices (Simpson's and Shannon-Wiener), evenness (2 measures), and species richness represented community variability and species rank correlations and community constancy represented changes in community structure. Additionally, we analyzed the impact of three habitat generalists (harpacticoid copepod, cyclopoid copepod, and an ostracod) on overall community variability. As habitat variability increased, both community and population variability increased. Community structure (ranked abundances) was also more variable in unstable habitats compared to stable habitats but communities in these unstable habitats retained greater constancy of composition suggesting that highly variable habitats are dominated by a few species with good dispersal abilities. Rare species may come and go, but the dominant species persist in these habitats.

Habitat generalists influenced temporal community variability differently, especially evenness (based on the Shannon-Wiener index). Positive relationships were found between the population variability of an ostracod and cyclopoid copepod and the variability in evenness while a negative relationship was found between the variability in evenness and the variability of harpacticoids.

Our study suggests that individual communities respond independently and asynchronously to environmental factors. We conclude that the form of community structure in variable habitats remains constant. The species composition and relative abundances can change over time but the relative abundance of the dominant species stays high and the remaining species, regardless of their numbers, make relatively small contributions to the overall community variability pattern.

Key-words: invertebrates, population, rock pools, stability

Introduction

The nature and meaning of community variability has been discussed frequently over the past 25 years (May, 1973; McNaughton, 1977; Connell and Sousa, 1983; Pimm, 1991; Micheli et al., 1999). This variability (in space and time) has implications for examining species conservation (Quintana-Ascencio and Morales-Hernández, 1997), metapopulation dynamics (Hanski and Gilpin, 1997), and assemblage structure (Pimm, 1991; Brown et al., 1985). Understanding of community variability demands understanding of its internal and external causes.

Habitat variability is one external mechanism identified as influencing community variability (Pickett and White, 1985; Death and Winterbourn, 1994). Habitat variability influences the relative abundance of species in a community and represents a strong structuring force for communities (Death, 1995). Deterministic processes that impact community structure, such as competition and predation, are mediated by habitat variability (McAuliffe, 1984; Meffe, 1984). Several studies show that with an increase in habitat variability, population variability increases and community persistence declines. This applies to stream invertebrates (Death and Winterbourn, 1994), fish (Ross et al., 1985; but see Grossman et al., 1982), and non-aquatic insects (Wolda et al., 1992; but see Van Dijk, 1986).

Despite attempts to determine the influence of habitat stability (variability) on community structure, its role remains unclear. Site-specific differences or differences in how habitat stability or variability is defined may confound these inferences. Specifically, defining and measuring habitat stability has proven problematic (Rykiel, 1985). A consensus on what habitat stability means and how to properly measure stability in different ecosystems is lacking. One additional confounding issue is that the impact of habitat variability changes depending on the spatial, temporal, and taxonomic scales used in the study (Rahel, 1990; Sale and Guy, 1992). One common method to measure habitat stability is to determine the variability in habitat parameters over time. Habitats are considered stable if the variability is low and considered unstable if the variability is high. A single multivariate variability score representing "overall" habitat variability has been used successfully for streams (Death and Winterbourn, 1994).

Measuring community variability has also proven problematic (Micheli et al., 1999). Community variability involves changes in species composition and changes in species' relative abundances over time (Magurran, 1988). Detecting this variability depends on the measure used (Gaston and McArdle, 1994). In this paper, we recognize three components of variability: (a) variability in composition; (b) variability in species rankings (relative abundance); and (c) variability in individual species abundances (as opposed to variability of all species taken jointly). There are four primary relationships possible between species composition and rank correlations in species relative abundances (Figure 1). Communities might show small changes in community composition and strong rank correlations over time (Figure 1; region A) or large changes in community composition and weak rank correlations over time (Figure 1; region D). However, it is also possible that communities will show small changes in community composition but have low rank correlations over time (Figure 1; region C) or large changes in community composition but strong rank correlations over time (Figure 1;

region B). These relationships will depend on a variety of factors including species identity (Sankaran and McNaughton, 1999), habitat variability, and spatial and temporal scales used in the analyses (Pickett and White, 1985; Rahel, 1990; Sale and Guy, 1992; Death and Winterbourn, 1994).

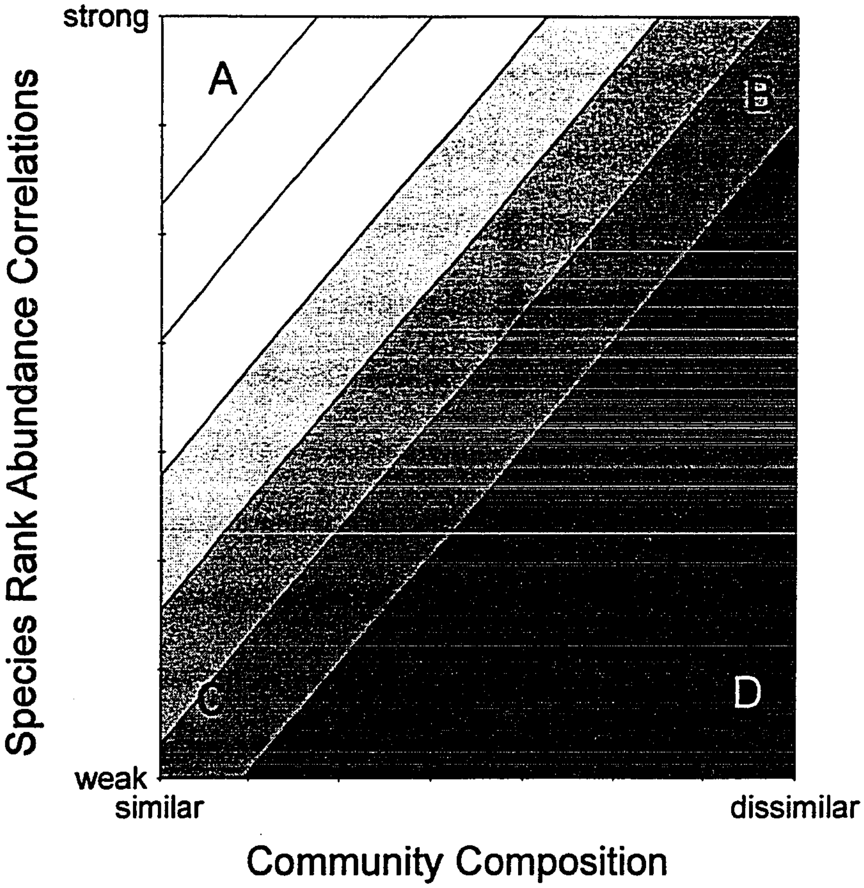

Figure 1: Possible relationships between species rank abundances and changes in community composition over time: (A) communities with small changes in community composition and strong rank correlations; (B) large changes in community composition and strong rank correlations; (C) communities with small changes in community composition and have low rank correlations; (D) large changes in community composition and weak rank correlations.

Sometimes geographical or physicochemical variables are more important than habitat variability (stability) in determining community structure (e.g. Townsend et al., 1983; Corkum, 1989). In aquatic systems, it is important not to ignore the impact of individual physicochemical variables relative to a combination of these variables, which is often used to quantify habitat stability (Death, 1995). To fully determine the role of habitat stability, it is useful to use a system from a small geographical area. This minimizes differences due to large-scale patterns such as weather, biogeography or historical colonization patterns. In this study, we use a system of rock pools to study the effects of habitat variability on community variability, including variability of individual populations and temporal changes in community structure. The system includes 49 pools that span a range of physicochemical properties and are home to communities assembled from a shared and diverse species pool (Therriault and Kolasa, 1999a).

It is possible that for aquatic communities, community and population variability would be greater in pools with higher overall habitat variability. Consequently, communities in variable pools should show greater temporal changes in species composition and structure. In the most variable pools, those that dry up from time to time or experience more disturbance events, colonization events increase the probability for changes in the community composition and the relative abundance of different species through differential dispersal, increased biotic interactions and metapopulation dynamics.

It is possible that population variability might influence strongly community variability, especially aggregated measures of it (Micheli et al., 1999). This influence might be further enhanced by greater habitat variability. Since different populations could impact communities differently (via biotic interactions, trophic cascades, etc.), the strongest effect on community variability should be observed for habitat generalists (species that have large geographical ranges and high abundances). While we adopt a convention that physical habitat variability is of extraneous origin, this is not entirely true. Some variation (e.g. in dissolved oxygen or pH) can be strongly influenced by biotic processes. However, these processes do not directly impact invertebrate community structure such that we feel justified in categorizing them as external (along with pool salinity and temperature. Thus, the purpose of this paper is to determine the effect of habitat variability on various components of community variability. The possible alternative outcomes mentioned above serve as specific hypotheses to be tested.

Materials and Methods

Study Site

Community and environmental data were collected from 49 natural rock pools located near the Discovery Bay Marine Laboratory on the north coast of Jamaica. Pool locations have been reported elsewhere (Therriault and Kolasa, 1999a; 1999b). The rock pools are small (most are less than 50 cm deep and 20 to 60 cm wide), erosional in nature, and are located above the high tide level. Therefore, most are filled by rainfall but a few pools receive seawater by periodic inflows or occasional wave splash. Physical pool conditions were measured when biotic samples were collected (details below). We measured pool temperature, salinity, dissolved oxygen concentration, and pH. Measurements were completed for all pools within one hour during the morning (starting at ~ 9 a.m.) to eliminate diel differences that may arise due to changing pool conditions over the course of the day. Data on physical conditions in the pools have been presented elsewhere (Therriault and Kolasa, 1999a; 1999b), including morphological characteristics (surface area, volume, elevation, etc.).

Sampling dates were December 89, January 90, January 91, January 92, January 93, January 97, June 97, and January 1998. Due to the small nature of these pools, faunal samples were collected in one day by passing 500 ml of water and sediments from each pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution) through a 63 μm net. Organisms were caught in a collecting container and immediately preserved in 50 – 60 % ethanol. Seventy species were collected including lower invertebrates (with the exception of rotifers and gastrotrichs), crustaceans, and aquatic insects (larvae and pupae).

Community and Population Variability

For each pool and sampling date, we calculated five community metrics, including Simpson's diversity index (1/D; where $D = \Sigma ([n_i\{n_i - 1\}]/[N\{N - 1\}])$; Shannon-Wiener diversity index (H′; where $H' = - \Sigma p_i \log_2 p_i$); evenness (E; based on the Shannon-Wiener index where $E = H'/ \log_2 S'$); Hill's evenness (Hill's = $[\Sigma\{p_I\}^2]^2/\Sigma\{p_I\}^3$); and species richness (S′). Total abundance of all individuals in the community was also determined (transformed as: $\log_{10} [x + 1]$). In the above equations, p_i is the proportion of the i^{th} species; n_i is the number of individuals of the i^{th} species, and N is the total number of individuals in the sample. Community variability was assessed by calculating the coefficient of variation (CV; where CV = standard deviation/mean) of each community metric based on the eight sampling periods. In addition, we calculated population variability (CV) over time for three habitat generalists (two copepod species and one ostracod species), in each pool in the same manner as for other metrics.

Community Structure

Temporal changes in community structure were evaluated using both Kendall's coefficient of concordance (W) and Cochran's Q test. We used Cochran's Q test to evaluate differences in the faunal assemblage composition (presence/absence) among sampling dates and Kendall's coefficient of concordance (W) to assess the constancy in relative abundance of species among the sampling dates. We also considered the effects of rare species on the calculation of both Kendall's W and Cochran's Q. Therefore, we calculated both for each pool using all species, the 17 most common species (based on abundance and occurrence; Top 17).

Habitat Variability

One way to effectively represent several physical characteristics at a site is by using a multivariate score (Death and Winterbourn, 1994). We used scores of Factor 1 produced by Principal Component Analysis performed on the variability in physicochemical variables (SD of pool temperature, salinity, dissolved oxygen, and pH) over the eight sampling dates. This variability index (PCA Factor 1 + 3; a constant used to eliminate negative numbers in the index), accounted for 52.13 % of the variance in SD of physical variables. In order to eliminate any possible seasonal effects (recall there was one sampling date in June) the June sampling date was eliminated and the analysis re-done (resulting in an explained variance of 48.97 % for Factor 1). Similarly, an argument could be made that the December 1989 sampling date might not be independent of the January 1990 sampling date and it too should be eliminated from the analyses to remove any possible bias (resulting in an explained variance of 49.52 % for Factor 1). Additionally, we examined the effects that variability of individual physical variables (e.g. temperature, salinity, dissolved oxygen, and pH) had on community variability. Analyses were done using all data (i.e. June included); all data except June; and all data except June 1997 and December 1989. Results from all analyses were similar and the correlation among the resulting community metrics, population data, and habitat data (habitat stability score and SD in physical pool conditions) determined by the three criteria listed above was high (> 88% for community metrics; > 93 % for population measures; and > 70 % for habitat measures). Therefore, for clarity and brevity, only the results from the analyses that excluded both June 1997 and December 1989 sampling dates are shown.

Statistical analyses were completed using Statistica at a significance level of $\alpha=0.05$. For all General Linear Models, residuals were checked for normality and correlation with model terms to validate model assumptions.

Results

Habitat Variability Effects

The multivariate measure of habitat variability (PCA Factor 1) represents a gradient ranging from stable to unstable habitats. As habitat variability increased, the variability in evenness (based on the Shannon-Wiener index) decreased ($F_{1,46}$=4.08; p=0.0493) while the population variability of harpacticoid copepods increased ($F_{1,44}$=13.49; p=0.0006).

It is possible that the variability of specific physicochemical variables (i.e. SD for pool temperature, salinity, dissolved oxygen, and pH) are more important when considered independently rather than when combined into an index, such as the habitat variability index. Community variability was not significantly affected by the variability in either pool temperature or pool pH (p>0.05). However, the variability in species richness was negatively related to the variability in pool dissolved oxygen concentration ($F_{1,47}$=12.82; p=0.0008) and the variability in Simpson's index was negatively related to the variability in pool salinity ($F_{1,47}$=4.73; p=0.0348). The variability in pool salinity was also positively related to the variability in the Shannon-Wiener index ($F_{1,47}$=5.65; p=0.0216) and the variability in evenness based on the Shannon-Wiener index ($F_{1,46}$=17.91; p=0.0001).

Population variability was also related to the variability in physical pool conditions. As variability in pool salinity increased, the variability in the ostracod species increased ($F_{1,33}$=6.87; p=0.0132) but the variability in the harpacticoid copepods decreased ($F_{1,44}$=23.39; p<0.0001). Similarly, as the variability in pool pH increased, the variability in harpacticoid copepods decreased ($F_{1,44}$=9.64; p=0.0033). The variability in cyclopoid copepods was negatively related to the variability in pool dissolved oxygen concentration ($F_{1,44}$=4.96; p=0.0311). Again, the variability in pool temperature did not have any significant impact on population variability (p>0.05).

Changes in community structure depended on habitat variability (Figure 2). Species ranks among dates tended to be more strongly correlated as habitat variability increased (Figure 2A: Kendall's W; $F_{1,47}$=7.96; p=0.0070) and community structure tended to diverge with increased habitat variability, although not significantly (Figure 2B: Cochran's Q; $F_{1,47}$=2.32; p=0.1345). This pattern was clearer when we excluded all rare species from the analysis and reanalyzed only the 17 most common species (Figure 2A: Kendall's W; $F_{1,47}$=7.19; p=0.0101; Figure 2B: Cochran's Q; $F_{1,47}$=5.10; p=0.0286).

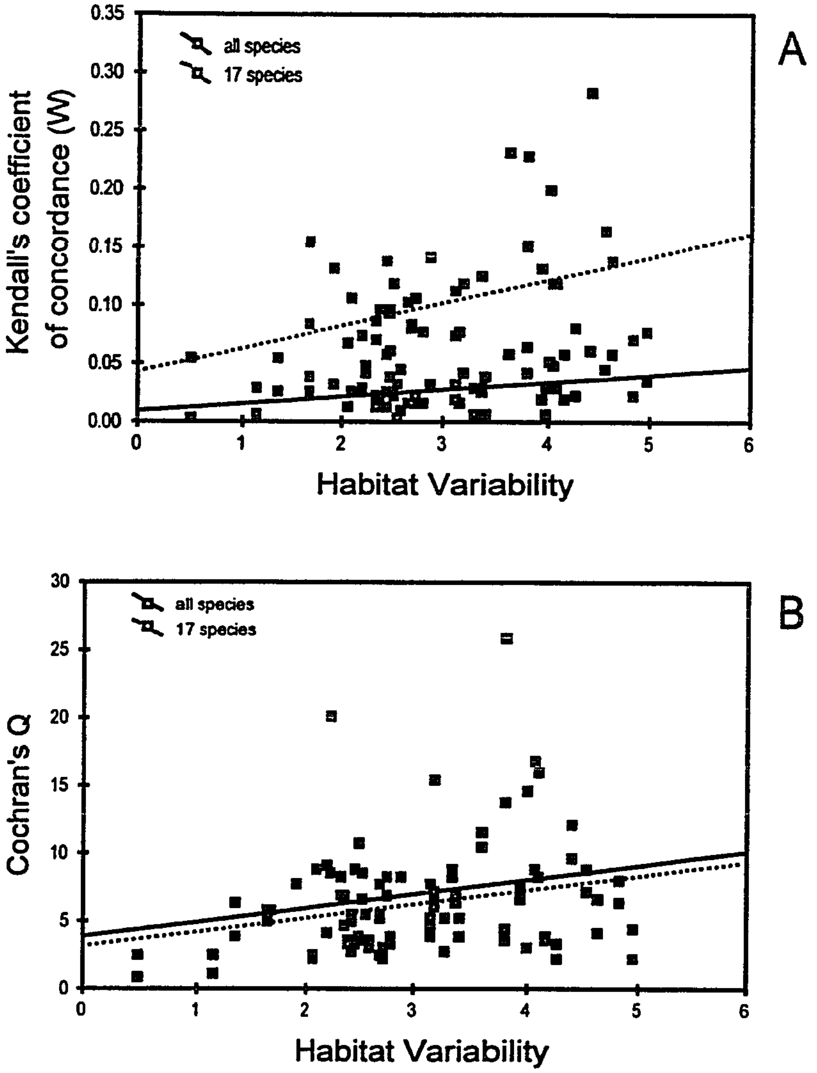

Figure 2: Relationship between habitat variability and variability in community structure among sampling dates for: (A) Kendall's coefficient of concordance (W); and (B) Cochran's Q. Solid lines indicate the relationships when all species were included and dashed lines indicate the relationships when only the 17 most common species were used.

Community, Population, and Habitat Variability

When we considered community variability with respect to population variability of the three habitat generalists (harpacticoid copepod, cyclopoid copepod, and an ostracod species) and habitat variability, we found several patterns. The variability in the ostracod species did not significantly affect the variability of any of the community metrics used in this study. The variability in evenness (based on the Shannon-Wiener index) was negatively related to the variability in harpacticoid copepod populations ($F_{1,43}=9.31$; $p=0.0039$). The cyclopoid copepods had the greatest effect on community variability. The variability in species richness, the variability in the Shannon-Wiener index, and the variability in evenness (based on the Shannon-Wiener index) were all positively related to the variability in cyclopoid populations ($F_{1,44}=29.25$; $p<0.0001$; $F_{1,44}=29.36$; $p<0.0001$; and $F_{1,43}=13.31$; $p=0.0007$, respectively) while the variability in evenness (based on Hill's index) was negatively related to the variability in cyclopoid populations ($F_{1,44}=5.98$; $p=0.0185$).

The variability in evenness (based on the Shannon-Wiener index) showed several interesting patterns that require further explanation. This measure of community variability was significantly related to each of the three habitat generalists (i.e. the ostracod, harpacticoid copepod, and cyclopoid copepod; Table 1; Figure 3). The variability in evenness was negatively related to harpacticoid variability but positively related to both ostracod and cyclopoid copepod variability (Figure 3), implying that population variability strongly affects species ranking. Habitat variability was also negatively related to the variability in evenness (Figure 3B).

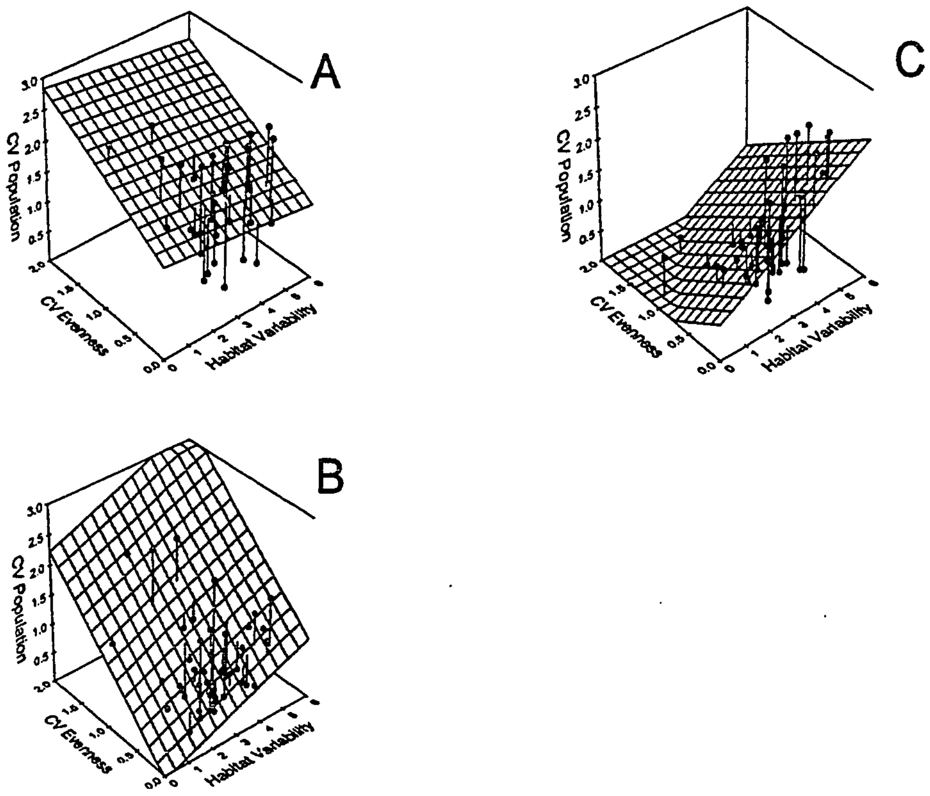

Figure 3: Relationships among variability in evenness (based on the Shannon-Wiener index), habitat variability and the three habitat generalists: (A) the ostracod; (B) harpacticoid copepod; and (C) cyclopoid copepod.

Table 1: ANOVA table showing the relationships among the variability in evenness (based on the Shannon-Wiener index), habitat variability, and population variability of the three habitat generalists.

	Ostracod			Harpacticoid Copepod			Cyclopoid Copepod		
	df	F	p	df	F	p	df	F	p
Population Variability (P)	1	4.57	0.0407	1	6.22	0.0167	1	12.42	0.0011
Habitat Variability (H)	1	1.33	0.2579	1	4.83	0.0337	1	0.64	0.4272
P * H	1	3.46	0.0727	1	3.84	0.0570	1	5.64	0.0223
Error	30			41			41		

Discussion

Habitat Variability

The current results identify the variability in the physicochemical variables as being particularly important, perhaps more so than their mean values in affecting communities. This is true of both the multivariate index that characterizes overall variability and of specific variables that had strong effects on community variability. In a previous study, models based on multiple variables resulted in better predictions of the observed diversity patterns compared to simple models (Therriault and Kolasa, 1999a).

A number of variables could be added to this study but, due to biotic and abiotic interrelationships among them, the variability index would be unlikely to change radically. For example, desiccation frequency, productivity, or DOC are all, in principle, related to the variables we have already included in the analysis. Similarly, Death and Winterbourn (1994) used a multivariate index to characterize "overall" habitat variability and included several, but not an exhaustive set, of variables.

Two consistent patterns emerged that differ from other studies and thus require an explanation: (a) species abundance ranks changed less over time in high variability (unstable) pools than in low variability (unstable) ones (Figure 2A); and (b) stable pools had more persistent community structure than unstable pools (Figure 2B). It is possible that high habitat variability is responsible for the reduced temporal variation in population size by restricting the population growth. Communities in harsh environments (high habitat variability, high levels of disturbance) have lower species richness (Connell, 1978) and tend to be dominated by a few "weedy" species (Scarsbrook and Townsend, 1993). Invertebrate and fish studies have suggested that stability and persistence of communities is greater in benign (low habitat variability, low levels of disturbance) than in harsh environments (Ross et al., 1985) and that abiotic factors can affect community persistence over time (Townsend et al., 1987). Furthermore, Death and Winterbourn (1994) showed that, for invertebrate communities in lotic ecosystems, communities tended to diverge compositionally as habitat variability increased (stability decreased). This may indicate that, in this system, unstable pools are dominated by a few taxa that have good dispersal and colonization abilities thereby maintaining high community similarity over time. Given that unstable pools tend to dry out more frequently than stable pools, recolonization abilities are likely to determine the observed community composition (but not structure). Provided recolonization of these empty patches is somewhat variable, community structure will change slightly over time, resulting in different assemblages in unstable pools, especially when compared to stable pools that are less likely to be affected by colonization. Interestingly, there was no significant relationship between mean species richness (among dates) and habitat variability ($p=0.3943$; $R^2=1.55\%$), indicating that unstable pools could support as many species as stable ones. However, the community assemblage changed more in unstable pools (Fig. 2B). Additionally, one possible explanation for the differing trends in community constancy (Kendall's W) between stream and rock pool systems is the number of taxa. Death and Winterbourn (1994) report finding 42 – 92 taxa present at each stream site. The number of taxa present in the rock pool system ranges from 0 – 16 species per pool (Therriault and Kolasa, pers. obs.), although the system contains 70 species or more. Greater species richness has been suggested as one possible mechanism that can stabilize community structure and thus potentially lower community variability (Tilman, 1996).

Community variability differed between stable and unstable pools but depended on the measure of community variability considered: one based on species presence or one based on relative abundance. Simpson's index gives more weight to dominant species than to rare ones while species richness and the Shannon-Wiener index give equal weighting to rare and dominant species (Magurran, 1988). Generally, community variability increased with increased population variability. This indicates that rare species are important in determining overall community variability and community structure. A negative relationship between habitat variability and population variability on one side and variability in evenness on the other indicates that, as habitats become more variable and as population variability increases, community structure tends to become fixed. Higher variability in diversity with decreased habitat variability suggests that communities in unstable environments are more persistent. It is possible that communities in these highly variable habitats are structured more by stochastic processes than deterministic processes (sensu Townsend et al., 1987). Given the harsh, and often unpredictable nature of variable habitats, species surviving in such habitats should show high extinction rates and low dispersal and colonization rates, in spite of their adaptations to disperse. If the species composition of variable pools is restricted, the variability in diversity will be low simply because the same few species return to the available habitat via repeated colonization events (Connell, 1978), possibly in proportion to their occupancy of landscape patches (Hanski and Gilpin, 1997). These results suggest that the form of community structure in variable habitats remains constant. The species composition and relative abundances can change over time (i.e. be variable) but the relative abundance of the dominant species will be high and the remaining species, regardless of their numbers, will remain relatively unimportant in the overall community makeup. Although the exact mechanisms remain unclear, variable habitats are dominated by a few species, likely those well adapted to take advantage of variable habitats.

Community Variability

An important finding was the relationships among population variability and community variability. It is possible that at larger spatial scales, the variability in the meta-community is relatively low compared to the variability of individual communities.

Such an effect would be produced if the individual communities responded independently and asynchronously to environmental factors or if environmental factors were independent and asynchronous in individual pools (cf. Micheli et al., 1999). In addition, metapopulation dynamics of the three habitat generalists (harpacticoid copepod, cyclopoid copepod and an ostracod) may contribute to the observed community variability. Although the exact mechanisms of dispersal for these animals are poorly understood, these organisms are typically the first to colonize and establish populations in open patches (Therriault, unpubl.).

In conclusion, there is a clear link between community variability and habitat variability (stability). This study shows that analysis of community variability may lead to a range of apparently disparate results if it is considered independently of confounding variables such as habitat variability and the variability in populations of habitat generalists. Increased community variability is promoted by decreased habitat stability. Furthermore, habitat generalists influenced the interpretation of community variability. Habitat generalists are expected to contribute substantially to community variability given their likely contributions to inter- and intra-pool dynamics, either through influences on colonization or through biotic interactions such as trophic dynamics.

Acknowledgements

This manuscript has benefited from suggestions by S. Dudley and J. Therriault. I also would like to thank the staff of the Discovery Bay Marine Lab and the students who helped with the sample sorting at McMaster University. Funding for this project was provided through an NSERC operating grant to Jurek Kolasa and NSERC and OGS scholarships to TT. This is contribution No. 000 from the DBML.

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Chapter 6:

Variability in invertebrate community structure from natural aquatic microcosms: time and salinity effects

This chapter has been submitted to the journal Hydrobiologia to be considered for publication (partial citation follows). This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W. Variability in invertebrate community structure from natural aquatic microcosms: time and salinity effects. Hydrobiologia (submitted April, 2000).

Abstract

Aquatic invertebrate data were collected from 1989 to 1998 in order to describe the community structure and temporal patterns of species distributions from a unique series of erosional rock pools on the north coast of Jamaica. Forty-nine pools, classified as brackish (31) or freshwater (18), were used to determine the stability of community structure over time, and to determine the degree to which salinity impacted community structure. There were significant differences in community structure between freshwater and brackish pools. Freshwater pools were dominated by ostracod species and insects contributed substantially to overall community structure while brackish pools were dominated by copepod species. Pool salinity also contributed to understanding temporal changes in community structure. When all pools were considered together, there were no significant differences in community structure over time. However, when pools were classified, freshwater pools showed significant temporal variability due to changes in the worm taxa while brackish pools showed significant temporal variability due to changes in both the insect and copepod taxa. Physicochemical variables were shown to impact taxon relative abundance with the strongest relationships observed for pool salinity. As salinity increased, the relative abundance of ostracods decreased and the relative abundance of copepods increased. These findings suggest that specific abiotic variables, namely pool salinity, can largely determine overall invertebrate community structure but the possibility exists that other abiotic variables have a similar impact in other aquatic systems.

Introduction

Communities vary in the number of species and the number of individuals both over time and between habitats (Connell and Sousa, 1983; Horne and Schneider, 1995). Understanding the causes of this variability is important for ecology (Wiens, 1989; Levin, 1992) and has implications for species conservation (Quintana-Ascencio and Morales-Hernández, 1997), metapopulation dynamics (Hanski and Gilpin, 1997), assemblage structure (Pimm, 1991; Brown et al., 1995), and applied ecological questions (Bengtsson et al., 1997). Community structure is likely controlled by a combination of biotic and abiotic factors. Biotic factors such as predation, competition, mutualism and interference can influence species diversity, which, in turn, can cause changes to community structure, especially over time (Pianka, 1994). Similarly, abiotic or environmental variables can influence population and community dynamics. Abiotic variables, usually easily measured, are often invoked to explain observed community patterns. It has been suggested that geographical or physicochemical variables are important in determining community structure in aquatic systems (Townsend et al., 1983; Corkum, 1989). Geographical variables represent historical or evolutionary events while physicochemical variables represent local and regional processes that control species tolerances and distributions.

Differences in community structure have been attributed to both the physical and chemical conditions of the habitat for ephemeral pools (King et al., 1996) and freshwater springs (Williams, 1997). Furthermore, the level of salinity has been suggested as a major determinate of community structure in coastal marine systems, such as lagoons

(Jorcin, 1999), but this finding need not be limited to marine systems. Salinity has been shown to influence the distribution and abundance of organisms in saline lakes (Timms, 1983) and in freshwater springs that receive salt via runoff from roads (Williams et al., 1997).

Abiotic factors are not the only causes of community structure changes. Community composition is often variable over time (Wiens, 1989) and temporal processes can lead to alternate forms of community organization or structure (Morris, 1990). Seasonal changes in community composition have been documented for fauna of intermittent and permanent streams (Smith and Pearson, 1987; Rosillon, 1989; Boulton and Lake, 1992) and ponds (Mahoney et al., 1990; Oertli, 1995; Bazzanti et al., 1996), in addition to some marine habitats (Jorcin, 1999). Seasonal patterns are not limited to aquatic systems. Mammal (Brown and Heske, 1990) and bird (Loiselle and Blake, 1991) assemblages also have been shown to exhibit seasonal changes in community structure. It might be expected that temperate systems show stronger seasonal effects, but this need not be the case. Seasonal differences have been noted for sub-tropical (Mahoney et al., 1990; García et al., 1997; Gasith and Resh, 1999) and tropical systems (Nacorda and Yap, 1997; Podrabsky et al., 1998; Colombini et al., 1998), in addition to temperate ones (Kevrekidis, 1997; Tockner et al., 1997). However, there are considerably fewer studies that have documented changes in community structure over longer time periods (i.e. greater than a few years), especially in aquatic systems (but see Bengtsson et al., 1997; for birds). To understand large-scale processes, long-term studies of temporal patterns of community structure are needed, especially in poorly studied systems (Oertli, 1995). It is expected that long-term studies reduce some of the variability that results from unusually severe or unpredictable events.

It is important to determine the relative contribution of abiotic and biotic affects (or their interactions) in determining community structure. It is also important to know the degree to which environmental variables influence changes in community structure and if there is a limit to the impact of abiotic factors. To determine the impact of environmental variables on community structure, it is necessary to examine habitats that span a range of different physicochemical conditions. Here, I examine the impact of environmental variables on the determination of community structure using invertebrate communities inhabiting a unique system of Jamaican rock pools. This system includes multiple communities composed from the same species pool (Kolasa et al., 1996; Therriault and Kolasa, 1999a). In addition, data were collected over several years, allowing an examination of the temporal patterns of community structure. The ecological characteristics of the fauna (taxa) inhabiting these erosional rock pools have not been extensively documented (but see Therriault and Kolasa, 1999a; 1999b). This study will provide a baseline for future studies on this system and will provide the relative taxonomic composition of these unique invertebrate communities.

Methods and Materials

This study was conducted at the Discovery Bay Marine Laboratory, Jamaica, West Indies. The 49 erosional rock pools used were described previously (Therriault and Kolasa, 1999a) and are shown in Figure 1. Most pools are small (~ 20 to 60 cm), shallow

(> 50 cm), located above the high-tide level and rain-fed. Saltwater enters these pools through sea spray or under severe storm conditions. These pools support phytoplankton and algal colonies but lack other aquatic vegetation.

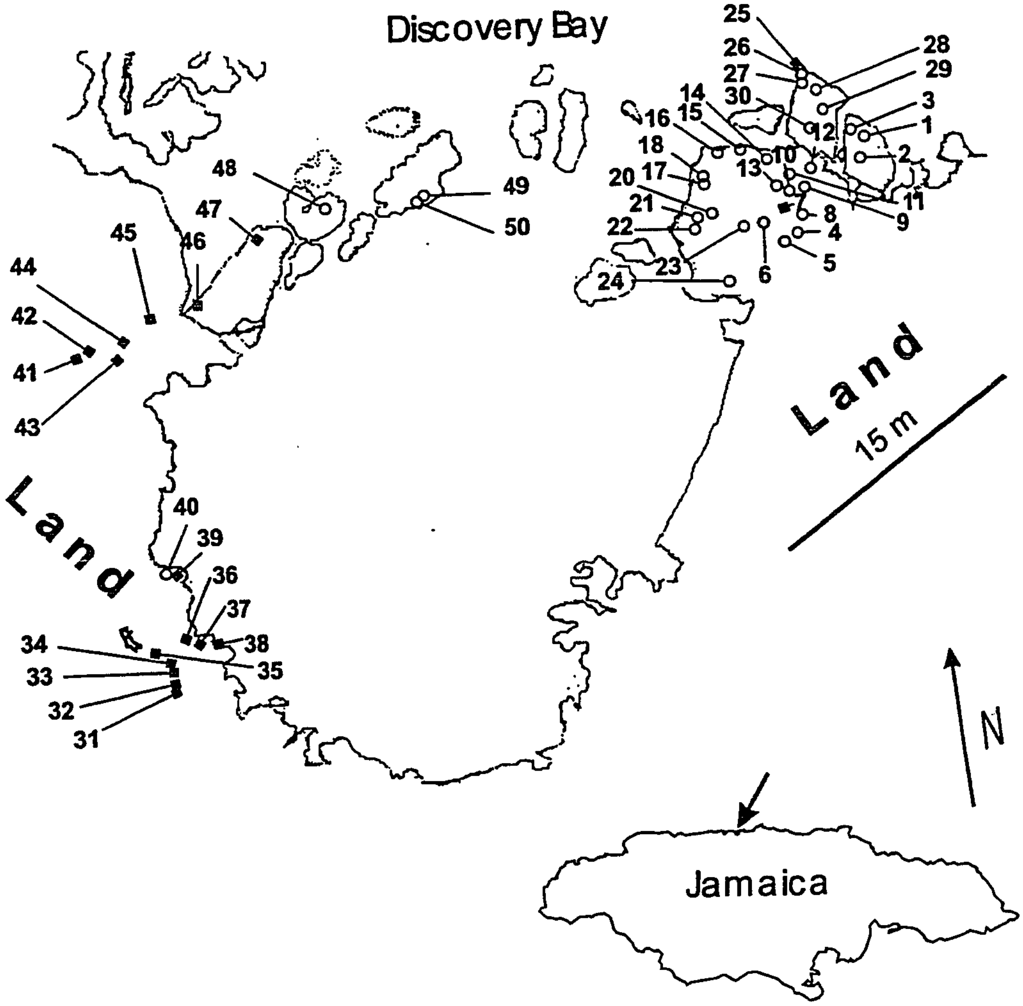

Figure 1: Location of the rock pool communities used in this study. The outline differentiates between the coastal rocks upon which the pools are found and the backreef area of Discovery Bay. The arrow indicates the location of Discovery Bay on the map of Jamaica (insert). Pools that were defined as freshwater are represented by the closed squares and the open circles represent pools defined as brackish. Note there is no pool 19.

Faunal samples were collected on eight occasions: December 1989; January 1990; January 1991; January 1992; January 1993; January 1997; June 1997; and January 1998. Each pool was gently stirred to dislodge organisms from the pool walls and to homogenize their distribution. Then 500 ml of water and sediment was randomly collected from different parts of the pool and passed through a 63 µm net. Samples were preserved in 50 – 60 % ethanol. In the laboratory, organisms were separated from the sediment following an established visual detection method and species were identified and counted. For this study, species were divided into five taxonomic groups including ostracods (20 species); copepods (including harpacticoids, cyclopoids, and cladocerans, 10 species); insects (larvae and pupae, 18 species); worms (including oligochaetes, polychaetes, and turbellarians, 15 species); and other crustaceans (6 species).

Temperature, salinity, dissolved oxygen concentration, and pH were measured for each pool when faunal samples were collected. These measurements were completed within an hour for all pools.

It was anticipated that pool salinity would have the greatest impact on community structure due to the response of individual species to different salinity concentrations. Because the rock pools in this system span a range of salinity concentrations, from freshwater to marine, colonists could potentially originate from either source. Therefore, depending on tolerances, a change in salinity (if any) and its magnitude (small vs. large) should affect each species differently. The other physicochemical variables measured were expected to have a less pronounced effect on community structure. For this study, freshwater pools were defined as having a mean salinity of less than 5 ppt over the eight sampling dates. Brackish pools were defined as having a mean salinity greater than 5 ppt and less than 27 ppt. One pool (Pool 26) did not fit the above definition because it became hyper-saline on two occasions, thereby raising the mean salinity of the pool beyond typical conditions. Rather than omitting this pool from the analyses, it has been included in the brackish pool group based on the range of conditions observed on other dates.

Community structure was determined for each pool on each date by calculating the relative abundance of each of the taxonomic groups (taxon abundance/total abundance of all taxa). To compare pools of different salt concentrations, I calculated the mean relative abundance for all freshwater pools and all brackish pools separately using the data from each of the eight sampling dates. Similarly, to determine the community structure over time, I calculated the mean taxon relative abundance for all pools together, only the freshwater pools, or only the brackish pools (definitions above).

General Linear Models were used to evaluate differences in terms of community structure and physicochemical variables (between freshwater and brackish pools) and to determine if there were differences over time among the eight sampling dates for either community structure or physicochemical variables. Regression analyses were used to examine relationships between taxon relative abundance and physicochemical variables. All statistical analyses were conducted using the STATISTICA software (from StatSoft) and the significance level was set at $\alpha=0.05$.

Results

Environmental Conditions

Over time, there was variability in physical pool conditions, but more importantly, there were noticeable differences between freshwater and brackish pools (Table 1). There was a significant difference among dates in pool temperature for both freshwater pools ($F_{7,120}$=4.69; p=0.0001) and brackish pools ($F_{7,230}$=17.99; p<0.0001) with June 1997 showing the warmest pool temperatures for both groups of pools. Freshwater pools also showed significant differences among dates in pool salinity ($F_{7,118}$=2.41; p=0.0240), and dissolved oxygen concentration ($F_{5,86}$=2.89; p=0.0184). Brackish pools showed significant differences among dates in pool salinity ($F_{7,229}$=33.62; p<0.0001), dissolved oxygen concentration ($F_{5,168}$=8.29; p<0.0001), and pH ($F_{4,143}$=25.60; p<0.0001). By definition, freshwater pools should have had significantly lower salinity concentrations relative to brackish water pools and this was the case. It is important to note that the three other physicochemical variables measured in this study, temperature, dissolved oxygen concentration, and pH, were not significantly different between freshwater and brackish water pools (ANOVA, p>0.05).

Table 1: Mean values for physicochemical pool conditions on the eight sampling dates. Pools were classified as brackish or freshwater. Minimum and maximum values are also shown.

	Temperature °C	Salinity ppt	Dissolved Oxygen (mg/L)	pH
Freshwater Pools				
December 1989	25.42	2.32		
	23.0 – 31.0	1.0 – 5.0		
January 1990	25.58	1.61		
	23.9 – 29.5	1.0 – 4.5		
January 1991	26.18	1.29	8.44	8.65
	23.9 – 29.9	0.3 – 4.8	1.4 – 13.9	7.67 – 10.60
January 1992	25.85	3.45	7.29	
	24.0 – 30.0	0.0 – 12.5	1.5 – 13.1	
January 1993	25.83	0.68	5.78	8.96
	24.5 – 29.5	0.0 – 2.5	0.8 – 11.4	7.46 – 10.33
January 1997	25.42	0.92	7.59	8.43
	24.4 – 28.0	0.0 – 4.0	2.9 – 14.5	7.65 – 10.83
June 1997	28.82	3.14	4.65	8.17
	27.2 – 29.4	0.0 – 19.0	1.1 – 8.8	7.71 – 9.05
January 1998	27.15	1.33	5.44	8.43
	25.4 – 32.9	0.0 – 8.0	0.0 – 15.0	7.70 – 9.28
Brackish Pools				
December 1989	25.25	14.42		
	23.8 – 29.3	1.5 – 24.5		
January 1990	26.20	9.32		
	24.8 – 27.8	1.0 – 21.0		
January 1991	26.67	9.54	9.46	8.79
	24.4 – 29.6	1.0 – 19.8	5.4 – 14.9	8.03 – 9.82

Table 1: Continued

January 1992	26.00	33.37	7.98	
	23.5 – 33.0	11.0 – 86.0	2.4 – 15.5	
January 1993	25.11	4.79	6.46	9.47
	24.0 – 28.0	1.0 – 12.0	1.8 – 13.0	8.46 – 10.50
January 1997	25.57	15.06	9.17	8.62
	23.5 – 27.7	0.0 – 34.0	4.5 – 13.8	7.80 – 9.73
June 1997	28.02	22.58	5.17	8.26
	27.0 – 30.5	0.0 – 61.0	0.0 – 11.7	7.39 – 9.72
January 1998	26.08	28.90	6.17	8.42
	25.1 – 29.8	19.0 – 40.0	0.0 – 15.0	7.51 – 9.44

Community Structure

There were significant differences in community structure between freshwater and brackish pools (Figure 2). Ostracod species were more dominant in freshwater pools compared to brackish ones ($F_{1,47}=19.60$; $p<0.0001$) while copepod species were more dominant in the brackish water pools ($F_{1,47}=25.37$; $p<0.0001$). Similarly, insects were more prevalent in the structure of freshwater pool communities ($F_{1,47}=5.55$; $p<0.0227$) while worms were more prevalent in brackish water pool communities ($F_{1,47}=4.94$; $p<0.0311$). The other crustacean species (primarily crab larvae) were not significantly different between freshwater and brackish pools.

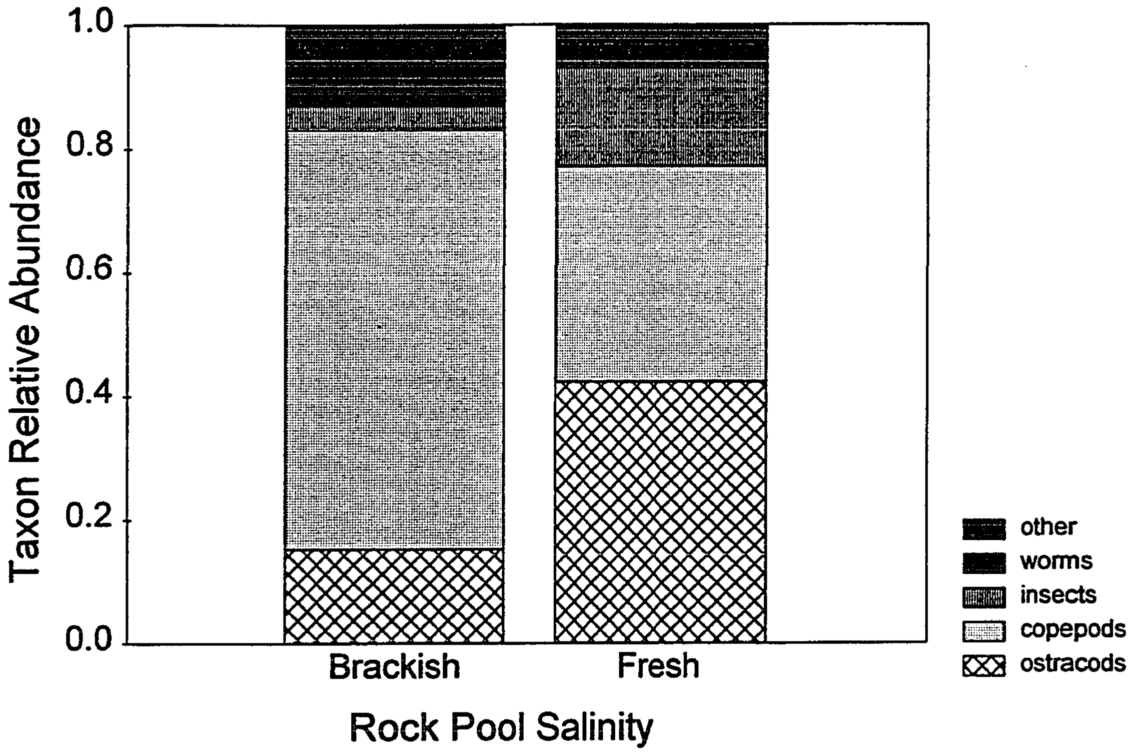

Figure 2: Differences in community structure as a function of pool salinity. Pools were defined as freshwater or brackish and the relative abundance of each taxonomic group for both salinity classifications is shown.

Community structure also changed over time (Figure 3) but the specific changes in community structure depended on the salinity of the pool. When all the pools were considered together (Figure 3A) there were no significant changes over time for the five taxonomic groups (ANOVA, $p>0.05$ for each group). However, there were significant differences when pool salinity was considered. In freshwater pools (Figure 3B), there was a significant difference among dates for the worm taxa ($F_{7,355}=2.12$; $p=0.0412$).

Worm species were more prevalent in the freshwater communities from January 1992 and January 1997. There were no significant differences among dates for the other four taxonomic groups in freshwater pools. Significant differences in community structure were also noted for the brackish water pools (Figure 3C). The copepod taxa were less prevalent in the January 1997 communities ($F_{7,229}$=2.33; p=0.0257) while the insect taxa were almost non-existent in the samples from January 1992, 1993, 1998, and June 1997 ($F_{7,229}$=3.50; p=0.0014).

Salinity had the greatest effect on taxon relative abundance. As mean pool salinity increased, mean relative abundance of ostracod species decreased ($F_{1,47}$=19.53; p<0.0001; R^2=29.36) but mean relative abundance of copepod species increased ($F_{1,47}$=21.25; p<0.0001; R^2=31.14). This provides evidence that the ostracods are better adapted to freshwater habitats while copepods are better able to exploit brackish habitats (see Figure 1), at least in this unique system of erosional rock pools. Additional negative relationships were found between the mean relative abundance of ostracods and mean dissolved oxygen concentration ($F_{1,47}$=5.95; p=0.0185; R^2=11.24) and mean pH ($F_{1,47}$=6.56; p=0.0137; R^2=12.24). This might indicate that the relative abundance of ostracod species decline in pools that are more productive (i.e. lower pH and greater oxygen concentration). A positive relationship was found between mean pool temperature and the mean relative abundance of insects ($F_{1,47}$=24.86; p<0.0001; R^2=34.60), possibly indicating that insects are better adapted to warmer water temperatures. A positive relationship was also found between mean pH and the mean relative abundance of other crustaceans ($F_{1,47}$=9.45; p=0.0035; R^2=16.73), indicating that in more productive pools, diversity increases as other species contribute more to the overall community structure.

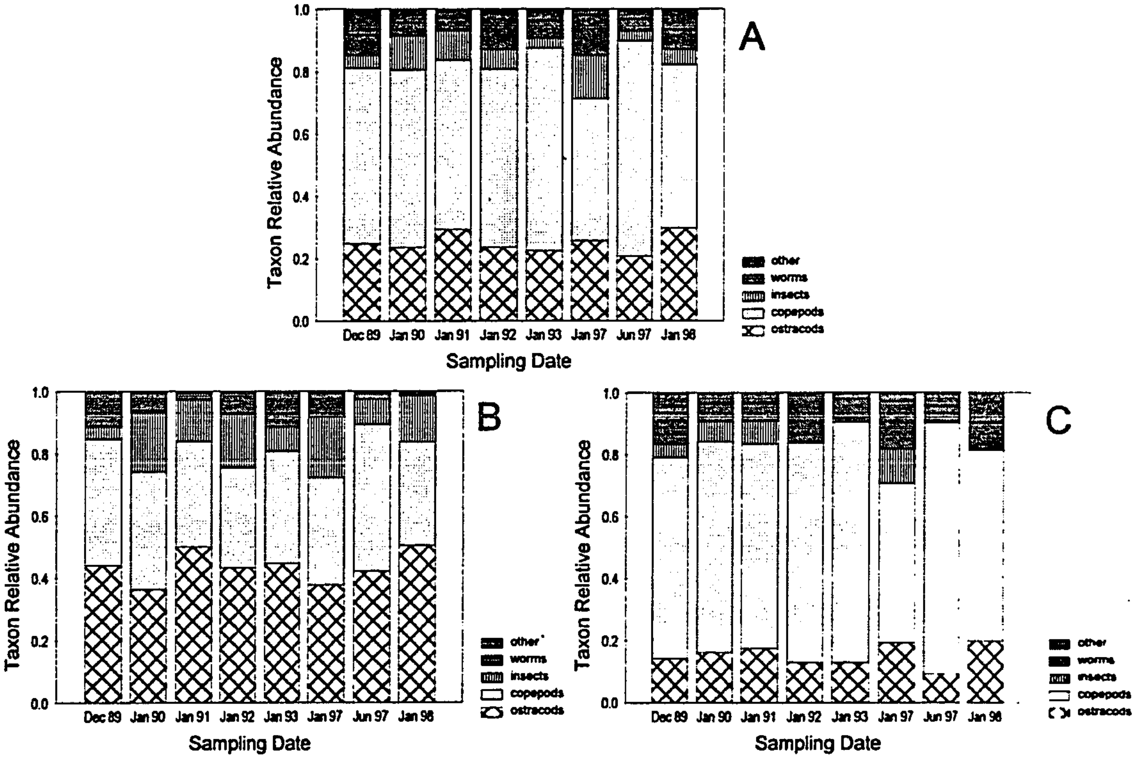

Figure 3: Differences in community structure over time. Relative abundance of each taxonomic group is shown for each of the eight sampling dates included in the analyses. Data is shown for: A) the mean of all pools used in this study (49); B) the mean of all the freshwater pools (18); and C) the mean of all brackish water pools (31).

Discussion

Invertebrate community structure varied significantly in both space and time and was strongly influenced by pool salinity. There were significant differences in community structure between freshwater and brackish pools. Also, there were significant differences in community structure over time for both freshwater and brackish pools. Patterns of change in community composition over time were both dependent and independent of pool classification. Some temporal changes in community structure were observed in both freshwater and brackish pools while others were observed for only one classification or the other.

Pool salinity had the greatest impact on invertebrate community structure in this rock pool system. Differences in taxon relative abundance were observed for four of the five groups studied between freshwater and brackish pools (Figure 2). This finding agrees with others. Williams et al. (1997) identified a strong relationship between groundwater spring taxon occurrence and chloride concentrations. Green and Mengestou (1991) showed the Rotifera communities in Ethiopian inland waters were strongly influenced by salinity with salty waters (> 2 ppt) showing a marked reduction in species richness. And Timms (1983) showed that benthic communities in shallow saline lakes were determined primarily by salt concentration. In addition, there was a significant negative relationship between pool salinity and the relative abundance of ostracods and a significant positive relationship between pool salinity and the relative abundance of copepods. Previous studies have shown that species relative abundance's are sometimes influenced by salinity (e.g. Timms, 1983), as found in this study, while others have found no significant relationship with salinity (e.g. Jorcin, 1999). These differences indicate that site-specific or species-specific differences might be more important than salinity in the determination of species abundance at any particular site. Furthermore, there was a significant positive relationship between pool temperature and the relative abundance of insect taxa, possibly indicating that, as pool temperatures increase, only a few species (insects) are able to exploit these conditions. In a previous study, Therriault and Kolasa (1999a) found that species diversity declined with increasing pool temperatures and suggested the explanation that few species are able to exploit these less than ideal conditions.

Time had a significant impact on community structure in both freshwater and brackish water pools. In general, for freshwater pools, community structure remained relatively consistent from year to year (Figure 3B). The only significant change among dates was in the worm taxa. Worms contributed more to the overall community structure in January of 1992 and 1997 but the reasons for these differences are not clear. The physicochemical variables (i.e. temperature, salinity, dissolved oxygen, and pH) do not show significant differences on these dates relative to the other dates used in this study (Table 1). Furthermore, there was no consistent change in the contribution of the other taxa to overall community structure on these dates. It is possible that inter-pool differences or the interaction between physical pool conditions and the biotic communities resulted in the observed difference. Menconi et al. (1999) make a similar argument to account for inconsistent temporal fluctuations for invertebrate communities on rocky shores and Threlkeld (1983) invoked it to explain the variation in zooplankton communities in a riverine reservoir.

Temporal changes in community structure also were observed for brackish pools (Figure 3C). Inconsistent temporal fluctuations in relative abundance were observed for some taxa, including copepods and insects. As suggested for freshwater pools, inter-pool differences likely account for much of the observed variation. However, there is an important difference between freshwater and brackish pools. Freshwater pools most likely contain taxa arising only from freshwater whereas brackish pools likely contain a combination of taxa, some originating from freshwater and others originating from the marine environment. For example, many insects may be limited by the salinity of the pool at the time of oviposition. If the salt concentration is too high (or too low), some species may find the pool unsuitable for breeding. Timms (1983), studying Australian saline lakes, reported that two species of chironomid dominated at lower salinities while another dominated at higher ones. It is interesting to note that the relative contribution of the copepod species is lowest in January 1997. One possible explanation for this pattern is the greater contribution of both worm and insect taxa to the overall community structure. This may have reduced the copepod relative abundance via biotic interactions including competition and predation. Both mosquitoes and midges (the two most common insects in this system) feed primarily on algae and organic debris, although predation can occur (Bland and Jaques, 1978) suggesting that competition for resources may be responsible for determining the overall community structure under these conditions.

A closer examination of the changes in community taxa shows some interesting and consistent patterns between freshwater and brackish pools. For example, copepods contributed the least to overall community structure in January 1997 and contributed the most in June 1997. This pattern was apparent for both freshwater (Figure 3B) and brackish (Figure 3C) pools and suggests that seasonal changes favor copepods that are able to better exploit unpredictable environments. This finding agrees with others that have found seasonality can result in the invertebrate fauna becoming dominated by a few taxa (usually copepods), able to tolerate more stressful environments (Bunn et al., 1986; Wyngaard et al., 1991; López and Theis, 1997); Therriault and Kolasa, 2000). Not only do copepod species appear better suited to survive the warmer summer pool conditions, but ostracod species appear less suited to these conditions. They contributed less to the overall community structure during the summer compared to the winter either before or after. It is possible that, under these harsher conditions, the copepod species are competitively superior, resulting in a suppression of ostracod species. Seasonal patterns for the other taxa considered in this study were difficult to detect and no clear pattern was obvious. This agrees with Menconi et al. (1999) who suggested that detecting seasonal changes in community composition and structure could be difficult and interpreting changes complicated.

In addition to the observed seasonal patterns, there were inter-annual differences in the community structure of both freshwater and brackish pools. Inter-annual variability is common in ecological studies as communities change with respect to species composition and abundance over time. Inter-annual variability in invertebrate communities has been reported for many systems including meiobenthic communities (Coull and Fleeger, 1977), pond communities (Oertli, 1995), and stream communities (Bunn et al., 1986; Boulton and Lake, 1992). Patterns of inter-annual variability in this system were difficult to detect when all data were considered together, and were only clarified when pool salinity was considered. When all pools were considered together, there was no significant change in community structure (Figure 3A), however, when pool salinity was considered, small temporal changes were discovered (Figures 3B and 3C). One possible explanation for this finding is that, although there could be considerable turnover at the species level, at the higher level of taxonomic classification used here, smaller-scale trends are obscured. Previous studies have found that changing taxonomic scale can result in a range of disparate results (see Sale and Guy, 1992; Rahel, 1990). It is also possible that community structure is determined primarily by functional groups. This system might only support a certain density of filter feeders (i.e. ostracods or copepods) and this will impact the determination of overall community structure. This finding is consistent with the river continuum concept that shows a change in community structure from the headwaters to the mouth based on functional feeding groups in relation to stream characteristics (see Vannote et al., 1980).

In conclusion, the results of this study suggest that much of the observed community structure is determined by the salinity concentration of the pool. Salinity, at least in this system, likely determines the species that are able to colonize and survive under these conditions either directly (i.e. physiological response to salinity) or indirectly (i.e. modulated biotic interactions). It is also possible that, in other aquatic systems where salinity does not impact community structure, another abiotic variable (i.e. nitrogen, phosphorus, etc.) does. Additional empirical studies are needed to verify this hypothesis and determine the impact of abiotic variables on community structure. However, this study shows the need to consider community structure at different time intervals in order to reduce the noise caused by seasonal and inter-annual variability. Investigations at single time periods may be misleading due to this variability.

Acknowledgements

I would like to thank the staff of the Discovery Bay Marine Laboratory, University of the West Indies, Jamaica, for helping make the fieldwork possible. There are numerous students from McMaster University who contributed to the processing of the field samples, for which I am grateful. This manuscript has benefited from editorial suggestions by J. Therriault. Funding for this work came from a variety of sources including NSERC and OGS Scholarships and an NSERC operating grant to J. Kolasa. This is contribution number 000 from the DBML.

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Chapter 7:

Community constancy at different temporal scales in natural microcosms of differing environmental variability

This chapter has been re-submitted to the journal Ecology to be considered for publication (partial citation follows). This chapter has been re-formatted in order to maintain consistency throughout this thesis.

Therriault, T.W., and J. Kolasa. Community constancy at different temporal scales in natural microcosms of differing environmental variability. Ecology (re-submitted September, 2000).

Abstract

The magnitude and rate of change in community composition, species relative abundance, and importance of species are crucial ingredients for understanding community dynamics. We investigated community variability over several different temporal intervals and examined how it is affected by environmental variability. We used invertebrate communities collected from 49 rock pools on the north coast of Jamaica sampled at time intervals of 2 weeks, 6 months, and 1 to 8 years. We assessed community constancy (an inverse measure of variability) for both species composition and ranking using Jaccard's Similarity Index (JSI), Sørensen's Similarity Index (SSI), the number of common species between dates, and Spearman correlation coefficients for species abundances. The number of species in common did not change among time intervals of different duration (range: 0 to 10; mean: 3.09). However, both measures of constancy in species composition showed differences among intervals: JSI and SSI ranged from 0 to 1 with means of 0.39 and the highest values noted at the two shortest time intervals (2 weeks or 6 months). Constancy in species ranking changed significantly over time and was greatest at shorter time intervals. Environmental variability reduced community constancy. Constancy, when measured using SSI, decreased with increasing variability in pool temperatures. Similarly, both the number of species in common and JSI decreased with increasing variability in pool salinity. Constancy was greatest in pools with stable temperatures and salinity indicating that abiotic factors might be more important for determining the predictability of communities and affecting the overall

outcome of internal biotic interactions. Generally, increasing temporal scale and environmental variability reduce community constancy.

Introduction

Understanding what causes communities and populations to vary over time or space is essential for ecology (Wiens, 1989; Levin, 1992) and has implications for species conservation (Quintana-Ascencio and Morales-Hernández, 1997), metapopulation dynamics (Hanski and Gilpin, 1997), and assemblage structure (Pimm, 1991; Brown et al., 1995). Ecological communities are established and change through colonization and survival in a habitat, both of which are mediated by a variety of abiotic and biotic factors. Communities may comprise either tolerant, locally available species added by stochastic processes or species added via biological interactions (Townsend et al., 1987). Tracking community changes at different time scales may help to increase understanding of the importance of biotic interactions or environmental variation in the maintenance of community structure (i.e. deterministic vs. stochastic processes). Communities undergoing a directional succession have received a lot of attention but little is known and understood about communities oscillating around climax-like states, particularly with respect to temporal scales of such variability. Whenever this intrinsic variability was investigated (e.g., Collins and Glenn, 1991; Sankaran and McNaughton, 1999; Micheli et al., 1999), no direct effort was made to assess it at different temporal scales. However, scale of variability may provide information on the nature of assembly and disassembly processes, information currently lacking in ecological studies. For example, a gradual decay of community states (i.e. similarity) may imply a different mechanism of community change than one where the dynamic of community change is described by curvilinear pattern or creates plateaus with contrasting values of community similarity.

The former could be interpreted as allowing stochastic effects to dominate over the alternative equilibrium states described by the latter.

In this paper, we use a unique system of erosional rock pools on the north coast of Jamaica to examine temporal patterns of community constancy. This system includes 49 pools formed by limestone dissolution that span a range of physicochemical properties. The pools are home to a variety of organisms assembled in a range of different associations. By examining community constancy in a system of pools that share history, weather patterns, and a common species pool, we aim at determining the relative importance of abiotic effects on community constancy. To fully characterize the constancy and to avoid the potential pitfalls of interpretation when dealing with data restricted to only one scale, we consider the effects of several temporal scales on community constancy.

The ecological literature contains several definitions of community constancy. Sometimes, persistence is the continued existence of species while stability is the constancy of relative species abundances as long as the temporal interval between sampling is long enough for populations to undergo at least one turnover (Connell and Sousa, 1983; Huston and Law, 1985). Community constancy is commonly evaluated for either species composition or species ranking. Either of these measures of community constancy can offer an aggregated account of environmental (e.g. disturbance) and biotic (e.g. competitive interactions) influences on the species in a community. Further information is needed to separate the environmental and biotic influences on community constancy.

Both biotic and abiotic factors can influence community constancy. Initially, May (1973) proposed that greater species richness would result in lower community constancy. However, empirical studies have found that species richness increases community constancy (Tilman, 1996; McGrady-Steed et al., 1997, McGrady-Steed and Morin, 2000) and stability (Doak et al., 1998). Theoretical studies also suggest that a decline in species richness results in reduced community constancy (see Pimm, 1984). Some postulate that species diversity may contribute to community stability as resistance and resilience of ecosystem functional processes increase with diversity (Frank and McNaughton, 1991). This does not necessarily imply that individual species would benefit. Rodríquez and Gómez-Sal (1994) found that resistance of communities to change in species composition decreased as diversity increased. By contrast, De Grandpré and Bergeron (1997) found that species composition changed less at more species rich sites. Among communities with relatively low evenness, resistance to disturbance-induced species composition change decreases as richness increases, but the opposite is true when evenness is higher (Rodríquez and Gómez-Sal, 1994).

Abiotic factors also have been shown to influence community constancy. According to Townsend et al. (1987), sites with lower variability in abiotic factors support communities that are more persistent. However, it is possible that this may be a system- and scale-dependent result. There is an obvious lack of clarity as to the patterns and causes of community constancy. Using multiple temporal scales, we examined community constancy (species persistence) and stability (population changes) over time. We hypothesized that community constancy would be greater at shorter temporal intervals and would decrease at longer temporal intervals due to the cumulative effects of habitat change and species turnover. Furthermore, community constancy should be greater in environmentally stable pools (those with low variability in physicochemical conditions) because environmental stability should favor lower local extinction rates among component species. It is possible to argue that as physical pool variability increases, community constancy decreases as more niches open to invading species or habitat specialists (Leigh, 1990). However, field data are needed to verify this claim as such habitats might offer competitive advantage to variability-adapted species that, in turn, could dominate and persist in them.

Some studies have found that geographical or physicochemical variables are important in determining community structure (i.e. Townsend et al., 1983; Corkum, 1989). These studies often involve a broad range of habitats and environmental conditions, or a single habitat sampled several years apart, making inferences about constancy patterns difficult. It is preferable to examine community dynamics or patterns using a system from a single geographical area that is assembled from a shared species pool (Therriault and Kolasa, 1999a). Many ecological patterns and processes require analysis within a hierarchical framework (Rahel, 1990). Spatial, temporal and taxonomic scales can influence the determination of whether assemblages are stable or not. Therefore, in this paper we examine community constancy at multiple temporal scales.

Methods

Study Site

Community and environmental data were collected from 49 natural rock pools of similar size located near the Discovery Bay Marine Laboratory on the north coast of Jamaica. Pool locations have been reported elsewhere (Therriault and Kolasa, 1999a; 1999b). The rock pools are small (less than 46 cm deep, except one that is 55 cm, and 20 to 60 cm wide), often with steep walls, and are located above the high tide level (i.e., this is not a tide pool system). Therefore, most are filled by rainfall but a few pools receive seawater by periodic inflows or occasional wave splash. Physical pool conditions were measured when biotic samples were collected (details below). We measured pool temperature, salinity, dissolved oxygen concentration, and pH. Measurements were completed for all pools within one hour. Data on physical conditions in the pools have been presented elsewhere (Therriault and Kolasa, 1999a; 1999b), including morphological characteristics (surface area, volume, elevation, etc.).

Sampling dates were December 89, January 90, January 91, January 92, January 93, January 97, June 97, and January 1998. Faunal samples were collected in one day by passing 500 ml of water and sediments from each pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution while, at the time, collecting several water volumes using a 125 ml beaker) through a 63 μm net. This volume represents a substantial proportion of the water in these pools and was determined to be an adequate sampling volume. Also, the processes of water column homogenization and taking several smaller volumes adding up to 500 ml, was intended to insure unusually high sampling accuracy of the pool community. We verified sampling efficiency by sampling a double-basin freshwater pool of comparable size to the other freshwater pools used in this study. Comparing Jaccard's Similarity Index (see below) for both basins to all the other freshwater pools (hence expected similar species composition), the two basins were significantly more similar to each other in taxonomic composition than with any other pool used in the analysis. Organisms were caught in a collecting container and immediately preserved in 60% ethanol. Animals sampled included lower invertebrates, crustaceans, and aquatic insect larvae and pupae. Seventy species have been identified in the 49 pools and were used in the following analyses. We have identified 20 species of ostracods, 10 species of copepods and cladocerans, 15 species of worms (polychaetes, oligochaetes, turbellarians, and nematodes), 18 species of insects (chironomid, other dipteran, coleopteran, heteropteran, and odonate), and 6 species representing other crustaceans (decapods, isopods, and amphipods). Rotifers were also found but were not included in the analyses because the net used in sampling retained only some individuals thus these data were considered not to be representative. Unfortunately, while we cannot comment on the specific life histories of all the species as some have only recently been identified (Therriault and Kolasa, 1999b) and others are likely new species, some generalizations are true for a majority of these species. Most species in this system are short-lived and have generation times of a few days to a week. Some (odonates, heteropterans, beetles, decapods) may have longer generation periods, but generally not exceeding more than a few months.

Temporal Windows

Sampling dates allowed the creation of 18 temporal intervals, representing the time elapsed between paired sets of records. The intervals were arranged into temporal windows of 2 weeks, 6 months, 1 year, 2 years, 3 years, 4 years, 5 years, 6 years, 7 years, and 8 years. For example, the 8-year window represents comparisons made between data collected on the two dates, January 1990 and January 1998, but does not include other data collected during this interval. In addition to evaluating the degree of community change among dates, we compared differences in physical conditions of the pools. To accomplish this, we calculated the standard deviation and the coefficient of variation (standard deviation/mean) for both pool temperature and salinity. Dissolved oxygen concentration and pH also were measured, but on fewer occasions than temperature and salinity. Dissolved oxygen and pH were measured on dates that allowed evaluation over seven temporal intervals (6 months, 1 year, 2 years, and 4 to 7 years).

For each interval we calculated several measures of community constancy, including two measures of similarity, Jaccard's Similarity Index (JSI) where:

$$\mathrm{JSI} = j / (a + b - j)$$

and j is the number of species in common between the two dates defining a temporal window for a given pool, a is the number of species at time A, and b is the number of species at time B; and Sørensen's Similarity Index (SSI) where:

$$\mathrm{SSI} = 2_{jN} / (aN + bN)$$

and aN is the number of individuals at time A, bN is the number of individuals at time B, and jN is the sum of the lower of the two abundances of species which occur at both times. Both JSI and SSI range between 0 (no constancy) and 1 (maximum constancy). Additionally, we used the number of species in common between two sampling dates and calculated Spearman Rank Pair Correlation Coefficients for all species and for the five most common species. Spearman Rank Pair Correlation Coefficients (r_s) represent the constancy of species' rank abundances between dates. Spearman Rank Pair Correlation Coefficients range between –1 (no constancy) and +1 (maximum constancy).

Since pool communities form on a gradient of environmental conditions so they may respond differently depending on environmental conditions and biotic interactions. Thus, we used Detrended Correspondence Analysis (DCA) to additionally quantify their constancy. DCA is an ordination method that orders species and samples (based on the similarity and differences of species and their abundances) at the same time and is capable if incorporating non-linear responses. This procedure sorts pool communities along an ordination axis based on both the species identity and species abundances. Plotting communities (pools) based on their DCA score at one time versus that at another provides information on changes in community structure. We used bivariate plots of the first DCA axes to determine if communities had changed between two dates. Weak correlations between axes indicate change in community structure while strong correlations indicate no change in the community structure.

Statistical analyses including general linear models (GLM's), ANOVA's and regressions were completed using Statistica and SAS at a significance level of α=0.05. Multivariate analyses including Detrended Correspondence Analyses (DCA) were completed using PC-ORD (McCune and Mefford, 1995).

Results

There was considerable variability in physical pool conditions at different time scales (Figure 1; Table 1). The measures of temperature and salinity differed among temporal windows. Variability in temperature peaked at the 6-month interval while the variability in salinity changed significantly over time but no clear pattern was apparent. Recalling that there were fewer measurements for dissolved oxygen and pH, absolute and relative variability in dissolved oxygen (SD Oxygen and CV Oxygen) differed significantly among temporal windows, with variability peaking at the 5-year window. Similarly, both the relative and absolute variability in pool pH (SD pH and CV pH) differed significantly among temporal windows with increased variability at intermediate length temporal intervals.

Community constancy was highly variable (Table 2), often ranging from complete similarity to complete dissimilarity. Each measure of constancy shows that regardless of the time interval (data summarize all measures) there were times when communities did not change at all (similarity indices = 1, rank correlations = +1) but there were also times when the community changed completely from one time period to the next (similarity indices = 0, no shared species, rank correlations = -1). Therefore, there are significant inter-pool differences that are contributing to the overall level of community constancy.

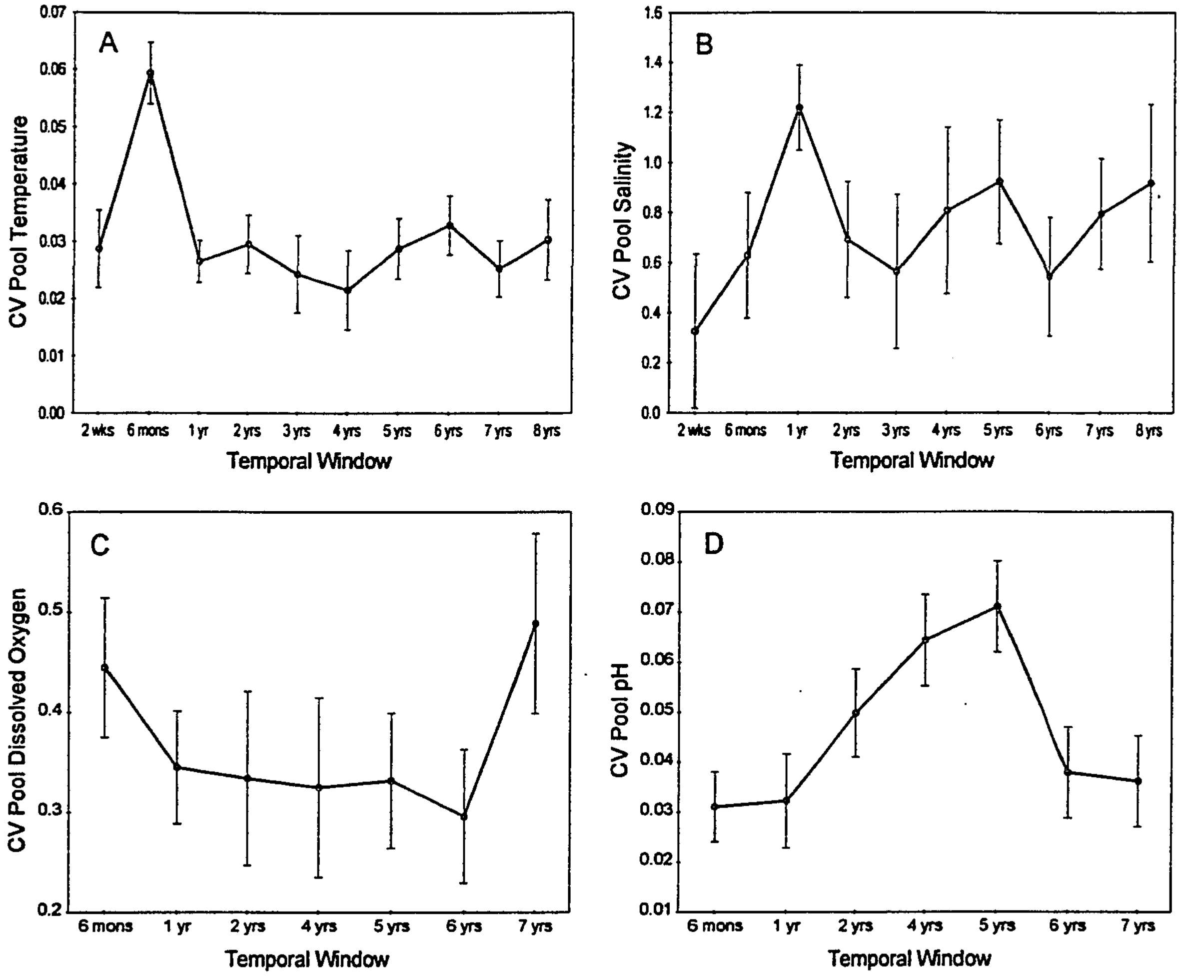

Figure 1: Variability (shown as the coefficient of variation) in physical pool conditions at different temporal scales (time elapsed between sampling events) for: A) water temperature; B) salinity; C) dissolved oxygen concentration; and D) pH. Error bars represent standard errors of the mean among temporal windows.

Table 1: Differences in physical measurements among temporal windows including mean; standard deviation (SD), and coefficient of variation (CV). Note there were fewer measures available for dissolved oxygen and pH.

Physical Measure	Mean	SD	CV
temperature	$F_{9,866}=7.15$ $p<0.0001$	$F_{9,770}=14.30$ $p<0.0001$	$F_{9,770}=14.64$ $p<0.0001$
salinity	$F_{9,862}=8.18$ $p<0.0001$	$F_{9,767}=9.21$ $p<0.0001$	$F_{9,736}=4.82$ $p<0.0001$
dissolved oxygen	$F_{6,573}=2.06$ $p=0.0563$	$F_{6,491}=31.94$ $p<0.0001$	$F_{6,491}=3.17$ $p=0.0046$
pH	$F_{6,381}=9.10$ $p<0.0001$	$F_{6,347}=14.87$ $p<0.0001$	$F_{6,347}=13.16$ $p<0.0001$

Table 2: Community constancy measured among the 18 temporal intervals. Data include the mean ± standard deviation, and ranges (minimum to maximum values) for each measure of constancy.

Measure of Constancy	Mean	SD	Range
Number of species in common	3.09	± 1.95	0 – 10
Jaccard's Similarity Index (JSI)	0.39	± 0.19	0 – 1
Sørensen's Similarity Index (SSI)	0.39	± 0.28	0 – 1
Spearman Rank Pair Correlations – Total	0.15	± 0.43	-1 – +1
Spearman Rank Pair Correlations – 5	0.30	± 0.50	-0.97 – +1

Community constancy depended on temporal scale. Three of the five measures of constancy were significantly different among temporal windows including JSI ($F_{9,772}$=4.27; p<0.0001); SSI ($F_{9,772}$=5.29; p<0.0001); and Spearman Rank Pair Correlation Coefficients (all species, $F_{9,740}$=2.51; p=0.0079)(Figure 2). Fisher LSD post-hoc tests were used to further explain the differences among temporal windows. The 2-week window for JSI was significantly different from all other temporal windows except 6-months while the 6-month window was significantly different from 1-year, 2-years, 5-years, 6-years, and 7-years. The most important difference among temporal windows for SSI was that the 2-week window as significantly different from all other windows. The 2-week and 6-month windows for Spearman Rank Pair Correlations (all species) were significantly different from the other temporal windows except each other, 3-years, and 8-years. Furthermore, an interesting pattern emerged. Initially, community constancy and similarity were high, and then decreased between 6 months and 1 year. After this decline, the values of community constancy leveled-off, possibly representing a "baseline" constancy level. Interestingly, the number of species in common did not change significantly among temporal windows ($F_{9,813}$=1.23; p=0.2735) suggesting the number of shared species remained relatively constant over time.

It is possible that since some temporal windows lacked replication (e.g. 2 weeks, 3 years, 4 years, and 8 years) the results might be considered an artifact due to an incomplete statistical design. Therefore, we considered community constancy over those temporal windows that were replicated. Community constancy still depended on temporal scale. Jaccard's Similarity Index (JSI) differed significantly among temporal intervals ($F_{5,606}$=3.99; p=0.0014) with the 6-month interval having greater similarity compared to the longer length windows. Spearman Rank Pair Correlation Coefficients (all species) also differed significantly among temporal intervals ($F_{5,584}$=2.23; p=0.0498), again with the greatest constancy noted for the shortest temporal window (6-months). The number of species in common did not change significantly among temporal intervals ($F_{5,642}$=1.13; p=0.3441) again suggesting the number of shared species remained relatively constant over time. Interestingly, Sørensen's Similarity Index was not significantly different among temporal windows ($F_{5,606}$=1.07; p=0.3734) which contrasted the results when all temporal windows were used. However, this measure of community constancy had the highest values at the shortest temporal interval (2 weeks) (Figure 2), for which no replication existed.

It has been suggested that species richness affects constancy via biotic interactions (Tilman, 1996; McGrady-Steed et al., 1997). Community constancy was positively related to initial species richness. All measures of community constancy and stability increased with increased species richness (species in common, p<0.0001; JSI, p<0.0001; SSI, p=0.0185; Spearman Ranks-all, p<0.0001; and Spearman Ranks-5, p=0.0021).

The influence of environmental variability on community constancy depended to some degree on the measure of community constancy (Table 3). Relationships between community constancy and mean pool conditions are also shown (Table 3). Community constancy decreased with increased environmental variability. It is important to note that

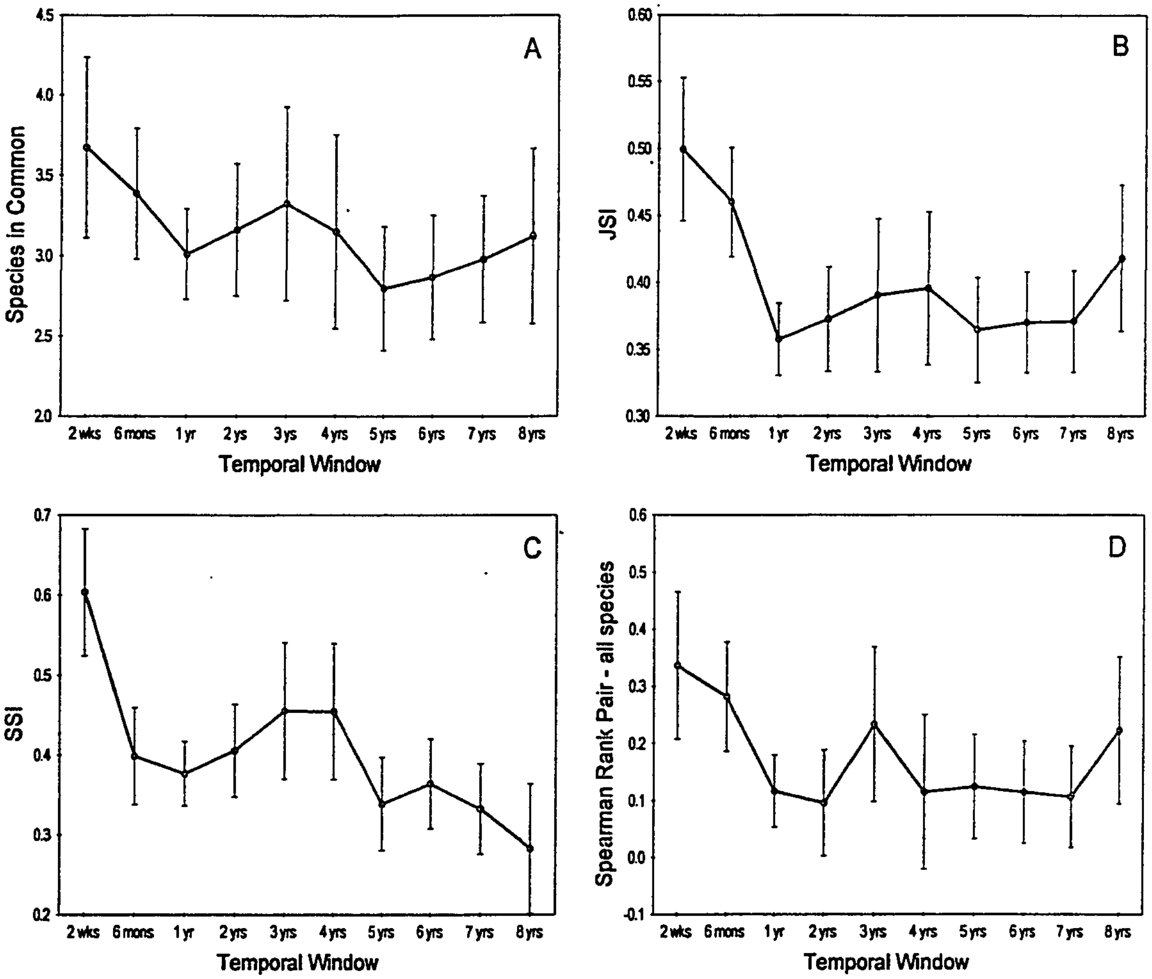

Figure 2: Community constancy measured at different temporal scales (time elapsed between sampling events) for: A) number of species in common; B) Jaccard's Similarity Index (JSI); C) Sørensen's Similarity Index (SSI); and D) Spearman Rank Pair Correlations – all species. Error bars represent standard errors of the mean among temporal windows.

several relationships between community constancy and environmental variability were not statistically significant thereby reducing the likelihood that environmental variability alone determines community constancy. Furthermore, for the relationships that were significant, the explained variance was often low ($R^2 < 0.1$), indicating that some other factors, possibly biotic processes, are likely to contribute to overall community constancy.

As indicated by the product moment correlations among the first DCA axis scores, community structure did not change significantly over the shortest temporal windows (2 weeks and 6 months; Figures 3 A-C). The 1-year and 2-year windows showed considerable variability. Community structure did not change (Figures 3 F,G,J) for half of these intervals, while community structure did change for the other half (Figures 3 D,E,I). Over longer temporal scales (3 years to 8 years) community structure stabilized with only two exceptions (Figures 3 N,Q). For these two intervals, community structure changed significantly, possibly due to changes between these dates in abiotic pool conditions.

Table 3: Regression relationships between community constancy and physical pool conditions. Nature of the relationship (+) positive or (-) negative and p-values are shown for significant relationships, NS = not significant (p>0.05).

Measure of Constancy	species in common	JSI	SSI	Spearman Rank – T	Spearman Rank – 5
Standard Deviation					
temperature	NS	NS	(-) p=0.0234	NS	(-) p=0.0337
salinity	(-) p<0.0001	(-) p=0.0098	NS	NS	NS
dissolved oxygen	NS	NS	NS	NS	(-) p=0.0076
pH	(-) p=0.0431	NS	NS	NS	NS
Coefficient of Variation					
temperature	NS	NS	(-) p=0.0242	NS	(-) p=0.0266
salinity	NS	NS	(-) p=0.0496	NS	NS
dissolved oxygen	(+) p=0.0342	NS	NS	NS	NS
pH	NS	NS	NS	NS	NS

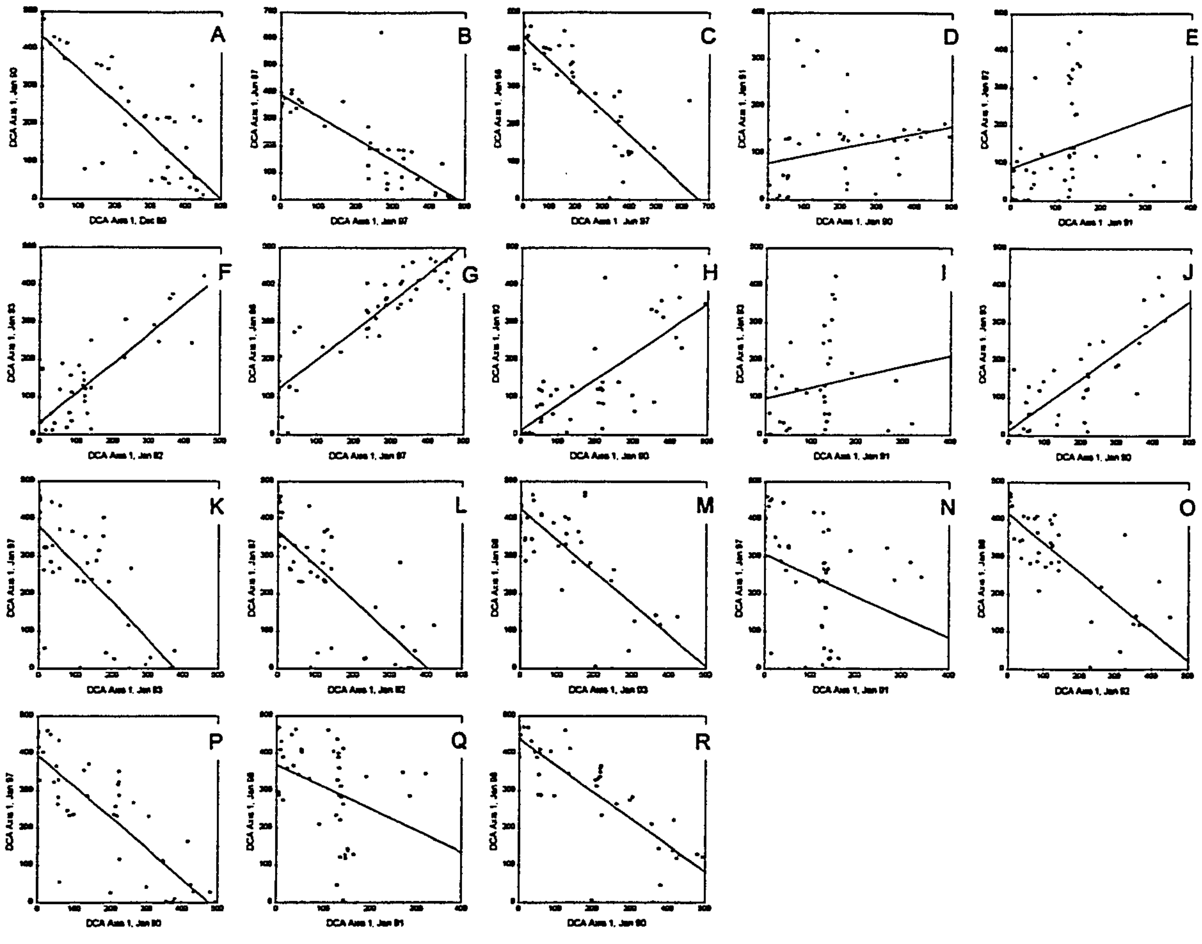

Figure 3: Bivariate plots of the first Detrended Correspondence Analyses (DCA) Axes between the initial date of the time interval and the final date of the time interval. A) 2 week window: Dec. 89 – Jan. 90 (r = -0.8024); B) 6 month windows: Jan. 97 – Jun. 97 (r = -0.7994); and C) Jun. 97 – Jan. 98 (r = -0.7992); D) 1 year windows: Jan. 90 – Jan. 91 (r = 0.2857); E) Jan. 91 – Jan. 92 (r = 0.2770); F) Jan. 92 – Jan. 93 (r = 0.8433); and G) Jan 97 – Jan 98 (r = 0.9072); H) 2 year windows: Jan. 90 – Jan. 92 (r = 0.7867); and I) Jan. 91 – Jan. 93 (r = 0.1918); J) 3 year widow: Jan. 90 – Jan. 93 (r = 0.8224); K) 4 year window: Jan. 93 – Jan.97 (r = -0.7096); L) 5 year windows: Jan. 92 – Jan. 97 (r = -0.7524); and M) Jan. 93 – Jan 98 (r = -0.7543); N) 6 year windows: Jan. 91 – Jan. 97 (r = -0.3028); and O) Jan. 92 – Jan 98 (r = -0.7875); P) 7 year windows: Jan. 90 – Jan. 97 (r = -0.8171); and Q) Jan 91 – Jan. 98 (r = -0.3470); and R) 8 year window: Jan. 90 – Jan. 98 (r = -0.8288).

Discussion

This study suggests that community constancy declines non-linearly with increasing temporal scale. Constancy is initially high, but declines rather abruptly to a "baseline" level at longer time scales (Figure 2). Community structure changed little at short time intervals even though the 6-month interval represents seasonal changes between January and June (or June and January) and the turnover of at least several generations. The community structure changed more at intermediate temporal windows (1 to 2 years). One possible interpretation of this finding, depending on the abruptness of the transition, indicates either a 'structural drift' (a slow modification of composition and abundances) or switching between alternative states. However, not all intermediate length intervals showed the same pattern (decrease in constancy), which indicates the year-to-year variability is sometimes high. At longer temporal windows (3 to 8 years) the community structure appeared to stabilize. This was contrary to our original hypothesis that increasing the time interval among samples would result in a progressive reduction of community constancy values.

The most probable explanation for high constancy at short time intervals is a lack of change in the species composition (i.e., species are not replaced or lost to any significant degree; Figure 2A). The number of species in common between dates was independent of the length of the time interval, possibly indicating that, at longer time intervals, different species were shared while composition changed. Although some species are widely distributed and may have good dispersal abilities (habitat generalists), it is possible that community constancy (i.e. JSI or SSI) is maintained primarily by species found in restricted habitats (rare species or habitat specialists), as suggested by the lack of change in the number of shared species among different time intervals.

If the number of shared species does not determine the pattern of change in community similarity, then either similarity in abundances or changes in species number must account for the observed pattern. The abundances may be constant due to the nature of biotic interactions or the absence of environmental variability. Previous studies have shown that environmental variability has some impact on community constancy (Townsend et al., 1987). As we noted earlier, variability in pool temperature was negatively correlated with differences in species abundances while variability in pool salinity negatively affected similarity in species presence. Pools that showed low environmental variability (i.e. stable temperature and salinity) had the highest level of community constancy. This might indicate that abiotic factors are more important than biotic factors in determining the constancy of communities in variable habitats while the physical environment, when it does affect community structure, only has small effects on community constancy. Variability in pool salinity had a greater impact on measures of community constancy that ignore species abundances (i.e. JSI and the number of species in common). This might indicate that pool salinity determines which species are able to colonize, survive, and persist in a particular habitat. Conversely, variability in pool temperature had a greater impact on measures of community constancy or stability that consider species abundances (i.e. SSI and the Spearman Rank Pair Correlation Coefficients). This might indicate that variability in pool temperature can cause the relative abundance of species to fluctuate but has relatively little impact on colonization or persistence. It is likely that most of the species identified in this rock pool system would be able to survive in any of the pools if only pool temperature is considered. Pool temperatures vary more over time than they do among pools within the system on any given sampling date (Therriault and Kolasa, unpubl.). In addition, the variability in dissolved oxygen and the variability in pH appear to influence measures of community constancy but without a clear pattern or regularity. The variability in these habitat characteristics affected similarly the measures that involve species abundances and those that do not. This might indicate that these components of environmental variability (dissolved oxygen and pH) have relatively little impact on community composition or species abundances and have negligible effects on community constancy. Alternatively, it is possible that the impact of these variables is highly diversified among pools such that, when many pools are considered together, the overall impact appears random. Most of these findings were expected. Organisms of freshwater origin were largely restricted to freshwater pools and organisms of marine origin to marine pools, but brackish pools showed the greatest variability in composition because of their ability to host species of broader origins. At the same time, brackish pools are most variable with respect to salinity, which may periodically cause species losses at either end of the adaptive spectrum.

Given the close proximity of the pools to each other, patch dynamics must be considered, especially at longer time intervals. If there were a continuous supply of colonists from the regional species pool, constancy would remain high. However, if there were no substantial contribution of new colonists to the existing community structure, communities should exhibit high variability. In fact, the level of variability in community constancy suggests this might be the case (Figure 2). This result is consistent with the conclusions drawn from the study of range-abundance relationships in the same system (Kolasa and Drake, 1998) which suggested that metapopulation dynamics were too weak to explain the pattern of abundances but who found occupancy patterns strongly correlated to ecological range of species. Furthermore, some studies on stream communities have shown that constancy might be a result of rapid recolonization of a site rather than continued existence of a population at a site (Grossman, 1982). This could be the case in this system as well.

In conclusion, while the mean value of constancy was low, individual pools spanned a gradient ranging from no change through to complete species change (i.e. all species are replaced). This indicates a considerable asynchrony and independence of processes among individual pools (cf. Micheli et al., 1999). It appears that three scales of community constancy can be distinguished, each with its own mechanisms and patterns. These scales differ in length among individual pools but share some attributes. At the shortest time scales, communities retain their structure through the continuation of their populations and likely are affected by a high level of similarity in environmental conditions. A decline in community constancy generally occurs at the longer but finite time scales. This may be caused by an accumulation of both stochastic (climatic vagaries) and deterministic (competition, predation, completion of life cycles) community changes, although we cannot be sure exactly how this happens. At the longest time scales, community constancy is low, but its level is constant. The most obvious explanation is, that in a landscape of discrete habitats, there is a background level of recolonization associated with a mean 'returning time'. It is possible to assume that spatial scale exerts similar effects on community constancy as temporal scale does. Extreme values of community constancy might be expected in studies conducted at either large temporal scales and small spatial scales or large spatial scales and small temporal scales (Figures 4 A and D). Specifically, at large spatial scales and small temporal scales, constancy would be high (Figure 4 D), but at large temporal scales and small spatial scales the constancy would be low (Figure 4 A). In addition, as spatial and temporal scales converge at any level, community constancy should be intermediate (Figures 4 B and C) as neither the temporal nor spatial scale can override the influence of the other. It is possible that this proposed overlap was the cause of some of the observed variability in community constancy.

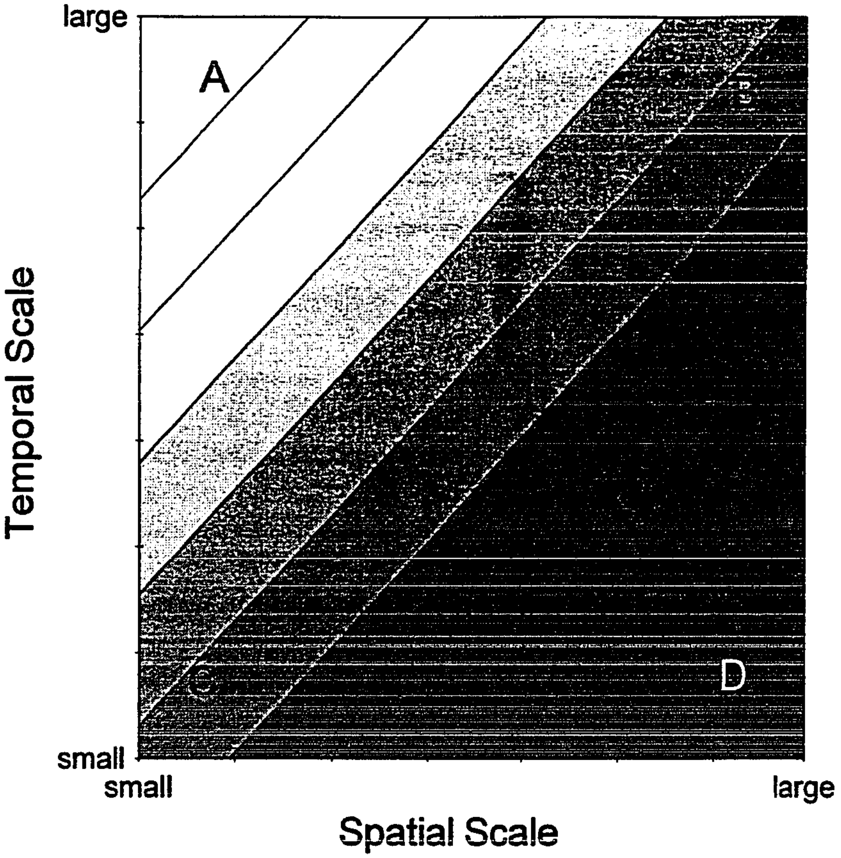

Figure 4: Hypothetical representation of how studies conducted at different spatial and temporal scales might result in different values of community constancy. The light-to-dark gradient (i.e. A to D) indicates how extreme combinations of spatial and temporal scales may result in extreme values of constancy (A [low constancy] and D [high constancy]) where as combinations of spatial and temporal scales that are similar (i.e. transition zone; gray area) may result in intermediate values of community constancy (B and C).

Acknowledgements

We would like to thank the staff of the Discovery Bay Marine Laboratory, University of the West Indies, for helping make the fieldwork possible and all the students at McMaster University that helped with data collection and sample processing. This work benefited from comments by two anonymous reviews of an earlier version of this manuscript and editing suggestions from J. Therriault. This research has been supported by an NSERC operating grant (JK) and NSERC and OGS Scholarships (TT). This is contribution number 000 from the DBML.

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Chapter 8:

Points of Discussion and Conclusions

General Points of Discussion

Environmental (Abiotic) Factors

The 49 pools are within close proximity to each other and most are no further than 50 cm from a neighbor. A total of 70 species was identified from all the samples, but a maximum of 16 species occurred in any one pool during any one sampling event. There is much variation in species richness, community structure and constancy, both among pools and years. King et al. (1996) found that species assemblages varied among pools within the same site, and not all species occurring at a site were found within a single pool.

There is evidence that implies the existence of multiple independent determinants of richness, especially interaction effects that escape detection when data are reduced using PCA techniques. The multiple regression models developed in Chapter 2 explained much more variance in species richness, diversity, evenness, and total abundance than the simple regression models. In addition, there was a significant increase in explained variance by increasing the number of terms in the models through addition of independent variables rather than the addition of independent PCA factor scores.

Physical and morphometric variables have a greater impact determining the number of species present in aquatic communities but have less impact in determining community abundance structure. Furthermore, while physical conditions set the limits to distribution (i.e. presence and absence of species) it may be the biotic factors, acting at population and community levels, that have a greater impact on species abundance. Dominant and rare species contribute equally to the calculation of species richness and the Shannon-Wiener index while dominant species contribute more than rare species to the calculation of Simpson's diversity index (Magurran, 1988). The stepwise regression models that accounted for correlation between variables developed for mean species richness and mean Shannon-Wiener index had similar levels of explained variance (around 60%) and included the same variables. In contrast, the model for Simpson's diversity index included fewer terms and explained less variance (about 37%) than the other two models.

Salinity has been shown previously to affect species diversity in non-marine systems (e.g. Timms, 1983; Green and Mengestou, 1991) and was hypothesized to be the primary measured abiotic variable influencing patterns of community structure. It is important to note that as maximum salinity increased, species diversity decreased (Chapter 2; Figure 2). This was expected because many of the species inhabiting these rock pools are freshwater organisms and as maximum pool salinity increased, there was a marked reduction in species richness. Many are able to tolerate low levels of salinity, but very few are able to tolerate hypersaline environments (Hutchinson, 1967; Therriault & Kolasa, 1999; Therriault & Kolasa, unpubl. data). However, as maximum salinity increased, total abundance and biomass also increased (Chapter 2; Figure 2). This indicates that a few species are able to flourish under saline conditions and may represent a shift in community structure from a primarily freshwater community to a primarily marine or brackish water community.

Pool salinity also had the greatest impact on invertebrate community structure. Differences in relative abundance of taxa were observed in four of the five taxonomic groups (i.e. ostracods, copepods, insects, worms, and other crustaceans) studied between freshwater and brackish pools (Chapter 6; Figure 2). This finding agrees with others. For example, Williams et al. (1997) identified a strong relationship between groundwater spring taxon occurrence and chloride concentrations. Green and Mengestou (1991) showed the rotiferan communities in Ethiopian inland waters were strongly influenced by salinity, which varies greatly among Ethiopian inland waters, with salty waters (> 2 ppt) showing a marked reduction in species richness. Timms (1983) showed that benthic communities in shallow saline lakes were determined primarily by salt concentration. In addition, there was a significant negative relationship between pool salinity and the relative abundance of ostracods and a significant positive relationship between pool salinity and the relative abundance of copepods. Previous studies have shown that species relative abundances are sometimes influenced by salinity (e.g. Timms, 1983), as found in this study, but this is not always the case (e.g. Jorcin, 1999), as site-specific or species-specific differences might be more important than salinity in the determination of species abundance at any particular site.

Habitat heterogeneity is another abiotic variable that can strongly influence species diversity. Examining the individual and combined effects of physical stress and habitat heterogeneity on biodiversity, I found that the interaction effect between stress and heterogeneity on biodiversity was not significant (SAS-GLM, df=1,40; F=1.83; p=0.1840). However, individually, both low physical stress and high habitat heterogeneity contributed significantly to biodiversity (p<0.0001 and p=0.0011, respectively; Chapter 3).

In general, abiotic variables affect species diversity via limitations on species tolerances. For each species in the system, each abiotic variable (measured or not) contributes to the determination of a species presence in any given pool on any given date by setting a threshold value above (or below) which the species will fail to survive. Thus, intermediate pool conditions represent a maximum for species occurrences. When pool conditions become less favorable, species richness declines as species encounter pool conditions beyond their tolerances.

The relationship between species richness and abiotic variables should show the "hump-shaped" pattern characteristic of the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978; Figure 1). Further evidence to support a "hump-shaped" pattern can be found by considering the origins of the species in this system. Some are believed to originate from the freshwater environment while others are believed to originate from the marine environment. Thus, any abiotic variable might represent the minimum tolerance for a freshwater organism but also represent the maximum tolerance for a marine organism. There were four abiotic variables measured repeatedly over the duration of this study; pool temperature, salinity, dissolved oxygen, and pH. For this system, pool temperature will likely only affect the upper tolerances of most organisms since the system is tropical and there is no indication that the minimum temperature required to support any organism has been reached. Conversely, dissolved oxygen concentrations will likely only affect the lower tolerances of most organisms since there is no indication that well oxygenated pools support fewer species. There is evidence to support the hypothesis that species richness declines in pools that become too acidic (Simpson et al., 1985; Wade et al., 1989; Therriault and Kolasa, 1999) but there is little data available to test the hypothesis that species richness also will decline in pools that become too basic (e.g. pH > 11).

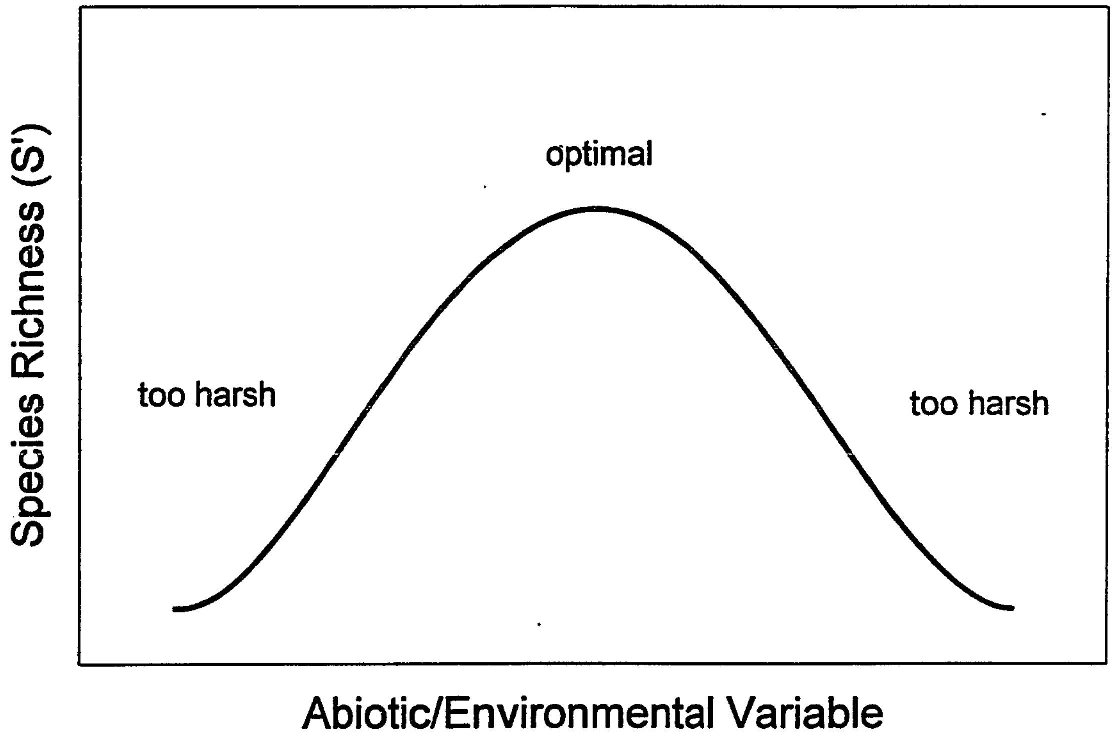

Figure 1: Hypothetical relationship expected between abiotic pool conditions and species richness (biodiversity). Richness is expected to peak at intermediate conditions that are "optimal" for supporting more species and decline as conditions become less favorable for supporting both freshwater and marine organisms.

Pool salinity, at least in this system, provides the strongest, single variable relationship to support an Intermediate Conditions Hypothesis (ICH). Species richness peaked in pools with intermediate levels of salinity. As salinity increased, species richness declined, because freshwater species were unable to tolerate pool conditions. Similarly, as salinity decreased, species richness declined, because marine species were unable to tolerate pool conditions. Thus species richness peaked at conditions that could support organisms arising from both freshwater and marine environments. Due to considerable variability in the data (i.e. background "noise"), fitting a polynomial equation to the data made the detection of a "hump-shaped" distribution difficult (Figure 2). However, species richness does peak at salinities around 20 ppt (Figure 2), providing qualitative support the ICH, despite the lack of a significant quantitative relationship between species richness and pool salinity. Admittedly, it is difficult to completely validate the ICH in this system because the gradients are weak and the pools typically do not reach severely unfavorable conditions with respect to variables other than salinity. However, experiments aimed at determining the exact tolerances of many species found in this system would greatly enhance the general applicability of an Intermediate Conditions Hypothesis. Also, a combination of abiotic variables, rather than a single variable, might explain a greater percentage of the variance in species richness as many environmental variables can interact to determine a species presence in a pool.

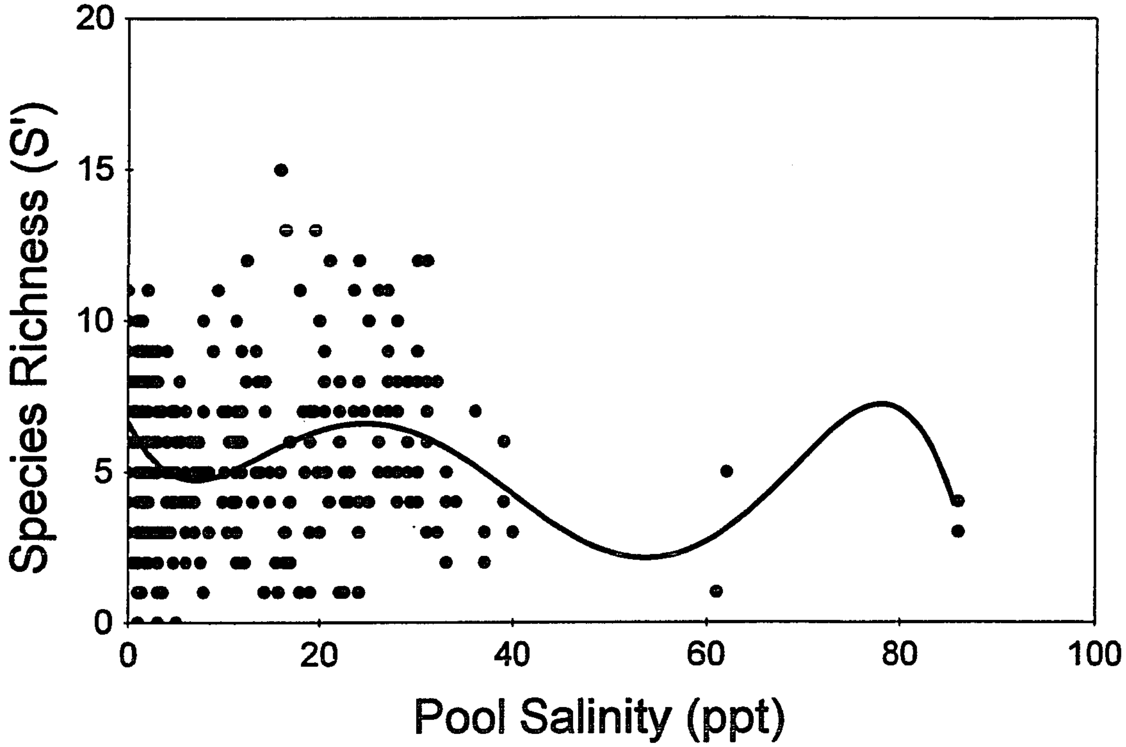

Figure 2: Observed relationship between pool salinity (believed to be the "key" abiotic variable) and species richness. A polynomial equation was fit to the data: $y = 6.644 - 0.643 * x + 0.069 * x^2 - 0.003 * x^3 + 3.604E^{-5} * x^4 - 1.763E^{-7} * x^5 + \varepsilon$.

Habitat Duration

Species diversity decreased with the indicators of short and discontinuous pool existence (greater reductions in pool depth and increased evaporation rate). Species richness and total abundance also decreased with greater reductions in pool depth. These findings are consistent with others who showed that species richness increased as pool duration increased (Schneider and Frost, 1996; Schneider, 1997; Spencer et al., 1999). This finding also is supported by the general hypothesis that species diversity (e.g. species richness) increases over time due to an accumulation of species (Rosenzweig, 1995). In addition, the range of the relative abundance of dominant species was lower for temporary pools and the minimum level of the relative abundance of dominant species was greater in temporary pools, suggesting that variable habitats are dominated by fewer species that are able to exploit these conditions. Furthermore, Schneider and Frost (1996) found that increased pond duration resulted in more biotic interactions (both per species and in number as more species were present), which may be consistent with lower levels of dominance in permanent ponds, and is in agreement with these findings.

Community similarity decreased as desiccation frequency increased. Bradshaw and Holzapfel (1988) found that, in tree-hole communities, habitat duration negatively affected species survivorship, which, along with recolonization, may contribute to decreasing values of similarity between dates. Furthermore, pools that are susceptible to desiccation (those with high evaporation rates or large decreases in relative depth) have fewer species and a more unpredictable community structure than pools that are not susceptible to desiccation through better water retention, lower evaporation, and seawater inputs. Similarly, García et al. (1997) showed that, in saline lakes, the annual hydrological budget affected both physical variation and biological changes between years with differing budgets. Although the hydrological budget was not directly measured for any of the pools, the data show that these pools span a gradient of habitat duration, and, therefore, a gradient of hydrological budgets.

Community similarity decreased as desiccation frequency increased. This may be due to sampling communities at different successional stages (sensu Bazzanti et al., 1996), such that the sampling scale did not adequately cover the temporal scale of community development. However, community similarity was assessed over several years and the number of times a pool was observed dry was recorded, based primarily on samples collected on the first day of January. Sampling at a fixed time each year, in the rainy season, most likely resulted in the communities being sampled at a similar successional stage. It is unlikely that differences in community similarity were solely a function of biased sampling. Instead, the observed differences in community similarity were likely a function of different temporary pools supporting communities of different compositions, probably at the end point of community development given that the sampling date coincided with the peak of the wet season. Each pool would have different physicochemical properties that would, in part, determine the species able to survive. Dispersal abilities and colonization order also might determine the community structure in these temporary habitats.

Pool desiccation represents a severe perturbation event for aquatic communities. As the frequency of pool desiccation increases, it is likely to result in higher individual mortality in many populations, some of which will go extinct locally. However, pools may refill with rain or seawater before drying completely. This radical change in environment may cause higher mortality in some species, thereby lowering the species richness. The contrasts between direct and indirect mortality have been discussed elsewhere (see Aspbury and Juliano, 1998), especially as they pertain to disturbance events (see Connell and Sousa, 1983; Pickett and White, 1985).

Community structure in this system of erosional rock pools is not static. Both temporary and permanent pools changed in community composition and species rankings over time, with changes being greater in temporary pools. This might indicate that the community composition of temporary pools is determined primarily by abiotic factors (frequency or severity of pool desiccation), either directly (response to drying habitat) or indirectly (increased biotic interactions due to changing conditions in a drying habitat). Despite adaptations to living in these harsh environments (see Wiggins et al., 1980), the invertebrate communities will be determined largely by the wet period of the pool. If the pool dries too quickly, some species might not be able to complete their aquatic life stages before the pool dries (i.e. mosquitoes). It is also possible that the community composition is determined largely by colonization events (Death, 1995) or through metapopulation dynamics (Hanski and Gilpin, 1997), both of which are likely to be more variable in variable habitats than in stable ones. Similarly, Bonner et al. (1997) found that abiotic factors were primarily responsible for determining community structure in other temporary habitats.

Temporary habitats, at least in this system, appear to be dominated by a few, well-adapted (i.e. good dispersal and colonization abilities) species resulting in a similar pattern of community structure (i.e. one or two species with large abundances). These findings agree with other studies of temporary habitat fauna including cladocerans (López and Theis, 1997; Maier, 1993), anostracans (Marcus and Weeks, 1997), and phyllopods (Hamer and Appleton, 1991). Furthermore, in this system, almost all of the pools that were classified as temporary contained cyclopoid copepods on at least one sampling date, indicating that this habitat generalist contributes to community structure and dynamics, especially over time. These findings are in agreement with other studies that have found that cyclopoid copepods thrive in unpredictable habitats (see Wyngaard et al., 1991). Experimental studies could be used to determine the specific influences this habitat generalist has on community structure and dynamics.

Communities in temporary habitats were dominated by a few species with good dispersal abilities. Pool accessibility, and possibly the order of colonization would account for differences in community structure between different temporary pools. Despite a similar "type" of composition (i.e. composed of good dispersers), the actual composition differs because of the spatial location of the pools. Some temporary pools are close to many other pools, hence a large potential source of colonists, while others are more isolated, hence fewer potential colonists. Abiotic pool conditions also can influence whether species are able to colonize or not. I suggested in Chapter 4 that pool salinity could limit the number of species able to inhabit certain pools, depending on their origins (i.e. freshwater vs. marine). If a temporary pool is initially filled by rainwater, then the colonists likely arise from freshwater adapted species. Conversely, if a temporary pool is initially filled by sea-splash or ocean spray, then the successful colonists likely will be of marine origins. It is important to note that over time, the environment will change depending on the environmental conditions a pool is exposed to, thereby altering physicochemical pool conditions and increasing the probability of additional colonizations. Unfortunately, I have no data that follow the development of temporary pool communities over shorter time scales (e.g. days to months), which would provide information on the specific mechanisms responsible for altering community composition and structure in temporary rock pool communities.

Habitat Variability (Stability)

The current results identify the variability in the physicochemical variables as particularly important, perhaps more so than their mean values in affecting communities. This is true of both the multivariate index that characterizes overall variability and of specific physicochemical variables that had strong effects on community variability. In an earlier study, models based on multiple variables resulted in better predictions of the observed diversity patterns compared to simple models (Therriault and Kolasa 1999; Chapter 2).

A number of additional variables could be considered but, due to biotic and abiotic interrelationships among them, the habitat variability index used here is unlikely to change radically. For example, desiccation frequency, productivity, and DOC are all, in principle, related to the variables already included in the analysis (e.g. temperature, salinity, dissolved oxygen, and pH).

Communities in harsh environments (high habitat variability, high levels of disturbance) have lower species richness (Connell, 1978) and tend to be dominated by a few "weedy" species (Scarsbrook and Townsend, 1993). Given that unstable pools tend to dry out more frequently than stable pools, recolonization abilities are likely to determine the observed community composition (but not structure). Provided recolonization of these empty patches is somewhat variable, community structure will change over time, resulting in different assemblages in unstable pools, especially when compared to physically stable pools that are less likely to be affected by colonization. Interestingly, there was no significant relationship between mean species richness (among dates) and habitat variability ($p=0.3943$; $R^2=0.0155$), indicating that unstable pools could support as many species as stable ones when considered over longer time periods. However, the community assemblage changed more in unstable pools (Chapter 5; Figure 2B).

Community constancy should be greater in stable environments (Ross et al., 1985; Townsend et al., 1987; Death and Winterbourn, 1994), possibly due to increased species richness in these habitats (Tilman, 1996). Thus biotic interactions could be considered intermediate and relatively constant (i.e. communities are stable such that species retain similar abundances over time). However, unstable environments should contain fewer species and have lower community constancy, such that biotic interactions are either greater or fewer (relative to stable pools) depending on the exact community composition and environmental variability. For example, if an unstable habitat is dominated by a few species with low abundances, biotic interactions are fewer (per species) if there are no limiting factors (space or resources). If an unstable habitat is dominated by a few species that flourish under variable conditions (high abundances), then biotic interactions might increase (per species) as space and resources become limiting factors. These hypotheses need testing under field conditions to verify their validity.

Scale

Invertebrate community structure varied significantly in both space and time. There were significant differences in community structure between freshwater and brackish pools. Also, there were significant differences in community structure over time for both freshwater and brackish pools. In general, the community structure of freshwater pools remained relatively constant with significant changes noted only for the worm taxa (Chapter 6; Figure 3B). Worms contributed more to the overall community structure (greater relative abundance and greater contribution of all taxa) in January of 1992 and 1997 but the reasons for these differences are not clear. They did not appear to result from differences in the physicochemical properties of the pools and there was no consistent change in the contribution of the other taxa to overall community structure on these dates. However, it is possible that the interaction between physical pool conditions and the biotic communities resulted in the observed difference. Menconi et al. (1999) make a similar argument to account for inconsistent temporal fluctuations in invertebrate communities on rocky shores and Threlkeld (1983) invoked it to explain the variation in zooplankton communities in a riverine reservoir. Also, it is possible that there were differences in an abiotic variable that was not measured (i.e. something other than temperature, salinity, dissolved oxygen, or pH).

Temporal changes in community structure also were observed for brackish pools (Chapter 6; Figure 3C). Irregular temporal fluctuations in relative abundance were observed for some taxa, including copepods and insects. As suggested for freshwater pools, inter-pool differences could account for much of the observed variation. However, there is an important difference between freshwater and brackish pools. Freshwater pools largely contain taxa arising only from freshwater whereas brackish pools likely contain a combination of taxa, some originating from freshwater and others originating from the marine environment. Timms (1983), studying Australian saline lakes, reported that two species of chironomid dominated at lower salinities while another dominated at higher levels. It is interesting to note that the relative contribution of the copepod species is lowest in January 1997. One possible explanation for this pattern is the greater contribution of both worm and insect taxa to the overall community structure. This may have reduced the copepod relative abundance via biotic interactions including competition and predation. Furthermore, there were negative relationships among the relative abundance of copepod taxa and the relative abundance of worm taxa ($r = -0.5439$) and the relative abundance of copepod taxa and the relative abundance of insect taxa ($r = -0.3248$). There was a very weak relationship between the relative abundance of worm taxa and the relative abundance of insect taxa ($r = 0.0514$). Considering observed abundances, the relationships were very weak between the copepod taxa and the worm taxa ($r = 0.10$) and the insect taxa ($r = -0.010$). It also is important to note that relationships among taxa are weaker in brackish water pools compared to freshwater ones.

Copepods contributed the least to overall community structure in January 1997 and contributed the most in June 1997 suggesting that seasonal changes favor copepods that are able to better exploit unpredictable environments. This finding agrees with others that have found seasonality can result in the invertebrate fauna becoming dominated by a few taxa (usually copepods), able to tolerate more stressful environments (Bunn et al., 1986; Wyngaard et al., 1991; López and Theis, 1997). Not only do copepod species appear better suited to survive the warmer summer pool conditions, but ostracod species appear less suited to these conditions. They contributed less to the overall community structure during the summer compared to the winter either before or after. It is possible that, under these harsher conditions, the copepod species are competitively superior, resulting in a suppression of ostracod species.

In addition to the observed seasonal patterns, there were inter-annual differences in the community structure of the pools (Chapter 6, Figure 3). Also, community constancy was similar over short-term or seasonal intervals but decreased over long-term or inter-annual intervals (Chapter 7, Figures 2 and 3). Inter-annual variability is common in ecological studies as communities change with respect to species composition and abundance over time and has been reported for invertebrate communities from many systems including meiobenthic communities (Coull and Fleeger, 1977), pond communities (Oertli, 1995), and stream communities (Bunn et al., 1986; Boulton and Lake, 1992).

However, patterns of inter-annual variability can be difficult to detect. Recall that patterns of inter-annual variability were difficult to detect when all pools were considered together, and were only clarified when pools were classified according to their salinity. When all pools were considered together, there was no significant change in community structure (Chapter 6; Figure 3A); however, when pool salinity was considered, small temporal changes were discovered (Chapter 6; Figures 3B and 3C). One possible explanation for this finding is that, although there could be considerable turnover at the species level, at the lower resolution of taxonomic classification used here, smaller-scale trends are obscured. Previous studies have found that changing taxonomic scale can result in a range of disparate results (see Sale and Guy, 1992; Rahel, 1990).

Previous studies have shown that environmental variability impacts community constancy (Townsend et al. 1987). As noted earlier, variability in pool temperature was negatively correlated with differences in species abundance while variability in pool salinity negatively affected similarity in species presence (Chapter 7). Pools that showed low environmental variability (i.e. stable temperature and salinity) had the highest level of community constancy. This might indicate that abiotic factors are more important than biotic factors in determining the constancy of communities in variable habitats while the physical environment, when it does affect community structure, only has small effects on community constancy. Variability in pool salinity had a greater impact on measures of community constancy that ignore species abundance (i.e. JSI and the number of species in common). This might indicate that pool salinity determines if species are able to colonize, survive, and persist in a particular habitat. Conversely, variability in pool temperature had a greater impact on measures of community constancy or stability that consider species abundance (i.e. SSI and the Spearman Rank Pair Correlation Coefficients). This might indicate that variability in pool temperature can cause the relative abundance of species to fluctuate but has relatively little impact on determining if species will be able to colonize or persist in certain pools. It is likely that any of the species identified in this rock pool system would be able to survive in any of the pools if only pool temperature is considered. Pool temperatures vary more over time than they do among pools within the system on any given sampling date (Therriault and Kolasa, unpubl.).

General Conclusions

The results of Chapter 2 imply that much of the observed species richness is due to an accumulation of species able to tolerate pool conditions, whether directly or indirectly via modulated biotic interactions. The relevance of this finding lies in its potential usefulness in biodiversity estimations based on a limited number of easily measured parameters. Indeed, this potential depends on further developments and accumulation of similar empirical models (e.g. Weiher and Boylen, 1994) and how well they perform with respect to a species pool and habitat in question. Admittedly, the usefulness of empirical models based on physical attributes of the environment declines in benign habitats with weak gradients.

While this research identifies a probable direct link among low physical stress, self-generated heterogeneity, and biodiversity, I acknowledge that other factors also may be important. Their relative contributions should be evaluated further through field experimentation. It is probable that disturbance, stress, heterogeneity, productivity, and rescue effect all play roles in enhancing and maintaining high species richness, even in a single ecosystem.

Chapter 3 adds one more direct and potentially important mechanism through which human produced environmental stress may reduce biodiversity. If the reverse process is true, stress related reduction of heterogeneity might be responsible for species extinctions. Species extinctions may additionally reduce heterogeneity and encourage a cascade of steps leading to further extinctions, exacerbating the 'extinction debt'.

Low pool permanency affects species richness, diversity, evenness, and total abundance (Chapter 4). Temporary pools were more variable over time with respect to species composition and ranked abundance. These findings imply that temporary habitats are dominated by a few weedy species with good dispersal and colonization abilities. It is also important to distinguish between desiccation frequency and pool duration, as they are not necessarily the same. Desiccation frequency has direct impacts on species diversity while pool duration (quantified by relative change in pool depth and evaporation rate) indirectly affects diversity and community structure. However, pool permanency, whether frequency or duration, shows that temporary habitats contain fewer species in a more simplified community structure.

Chapter 5 indicated a clear link between community variability and habitat variability (stability). Analysis of community variability may lead to a range of apparently disparate results if it is considered independently of confounding variables such as habitat variability and the variability in populations of habitat generalists. Increased community variability is promoted by decreased habitat stability. Furthermore, habitat generalists influenced the interpretation of community variability. Habitat generalists are expected to contribute substantially to community variability given their likely contributions to inter- and intra-pool dynamics, either through influences on colonization or through biotic interactions such as trophic dynamics.

The results presented in Chapter 6 suggest that much of the observed community structure is determined by one factor – in this case, the salinity concentration of the pool. However, it is possible that in other systems, community structure also is determined by one "key" variable. It is likely that such a "key" variable determines the species that are able to colonize and survive under different conditions either directly (i.e. physiological response) or indirectly (i.e. modulated biotic interactions). Thus, in other aquatic systems where salinity does not impact community structure such as observed for this rock pool system (i.e. pristine freshwater environments), another abiotic variable (i.e. nitrogen, phosphorus, etc.) does. Additional empirical studies are needed to verify this hypothesis and determine the impact of "key" abiotic variables on community structure.

Individual pools spanned a gradient ranging from no change through to complete species change (i.e. all species are replaced), depending on the length of the temporal interval considered (Chapter 7). This indicates considerable asynchrony and independence of processes among individual pools (cf. Micheli et al., 1999). It appears that three scales of community constancy can be distinguished, each with its own mechanisms and patterns. These scales differ in length among individual pools but share some attributes. At the shortest time scales, communities retain their structure through the continuation of their populations and likely are affected by a high level of similarity in environmental conditions. A decline in community constancy generally occurs at the longer but finite time scales. This may be caused by an accumulation of both stochastic (climatic vagaries) and deterministic (competition, predation, completion of life cycles) community changes, although I cannot be sure exactly how this happens. At the longest time scales, community constancy is low but constant. The most obvious explanation is that in a landscape of discrete habitats, there is a background level of recolonization associated with a mean ‘returning time’. Extreme values of community constancy might be expected from studies conducted at large temporal scales and small spatial scales or large spatial scales and small temporal scales (Chapter 7; Figures 4 A and D). Specifically, at large spatial scales and small temporal scales, constancy would be high (Chapter 7; Figure 4 D), but at small spatial scales and large temporal scales the constancy would be low (Chapter 7; Figure 4 A). In addition, as spatial and temporal scales converge at any level, community constancy should be intermediate (Chapter 7; Figures 4 B and C) as neither the temporal nor spatial scale can override the influence of the other. It is possible that this proposed overlap was the cause of some of the observed variability in community constancy.

General Summary

There are two important findings that are supported by this thesis. The first is that abiotic variables (i.e. physicochemical pool conditions, habitat heterogeneity, habitat stability, and habitat duration) contribute significantly to community composition, structure and constancy, especially over time. Furthermore, whether directly or indirectly, one abiotic variable had the most dramatic effect on community metrics. Pool salinity was identified as the “key” variable responsible, directly or via interactions with other variables, for the observed structure of these aquatic communities as well as for affecting pool diversity and taxon relative abundance.

It is important to note how community structure is maintained in this variable environment. Clearly, abiotic variables contribute significantly to this end; however, the component species within the community also contribute to the overall community make-up. Much of the data suggest that the component species are determined by the salinity of the pool. This agrees with others who have shown that species tolerances to salinity can limit their distributions (Timms, 1983; Williams et al., 1990; Williams et al., 1997). However, once a species is able to colonize a pool, other physicochemical variables appear to determine their abundance. I found that pool temperature and productivity (measured as dissolved oxygen concentration and pH) primarily determine species abundance patterns but contribute little to the determination of a species presence in a particular pool.

This thesis also demonstrates the importance of temporal scale and understanding how communities change in composition and structure over time, especially short-lived invertebrates in a highly variable environment. For this system, communities remained constant over time scales significantly longer than the turnover time expected of their invertebrate inhabitants. Thus, there was an underlying force that maintained community structure even when individuals within a population or community were lost. Given the close proximity of these pools to each other and to potential sources of colonists (inland or from the sea), it is possible that metapopulation dynamics contributed to much of the observed constancy in species over time scales less than one year. As long as some pools on the landscape remained water-filled (likely acting as refugia), overall community constancy should remain high. However, over longer time scales (several years), community constancy decreased, likely due to a number of severe disturbance events that created a patch mosaic that was unsuitable to the maintenance of communities under varying environmental conditions.

The data further suggest a community structure dominated by few species with good dispersal abilities. Also, it appears the remainder of the community is composed of species that are able to tolerate pool conditions at any given point in time such that when the environment becomes less suitable, they disappear. Similarly, these species appear when pool conditions are more favorable and colonists are able to survive and persist in a new habitat (pool). This implies that much of the observed community structure will depend primarily on the sequence of colonization or recolonization, rather than any single measure of habitat characteristics. This suggests asynchronous and unpredictable events are responsible for the maintenance of the invertebrate community structure, especially for communities inhabiting more variable environments.

It has been shown that both habitat duration (Chapter 4) and habitat variability (stability) (Chapter 5) each dramatically impact community structure. However, these two measures are not completely independent. If the habitat is short-lived such that each time the pool dries it must be re-established (either via rainfall or seawater inputs), then it is likely that the new physical properties will be different from those measured before the pool dried, even in the absence of a community. Biotic processes in the pool (community respiration, productivity, etc.) would only complicate the determination of the actual change in environmental conditions. This would introduce further variability that could make the detection of community patterns more difficult.

This study was unable to determine a single environmental variable as responsible for the determination and maintenance of communities over time. Pool salinity contributed significantly to the determination of species diversity, but failed to adequately account for changes in abundance patterns. However, at least for this system, this study identified four physicochemical variables, easily measured in the field (i.e. temperature, salinity, dissolved oxygen, and pH), which can be used successfully, either separately or in combination, to clarify and further our understanding of aquatic community dynamics. Also, it is possible that events that happen at intervals not covered by the sampling dates are extremely important for the determination and maintenance of aquatic communities in erosional rock pools. For example, events that occur during the spring and fall, when the hydroperiods of these pools might be more variable, could initiate a pattern of community formation or dynamics that might be observed or missed by the established sampling dates. Similarly, there could be mechanisms working at time scales of less than two weeks, the smallest time scale available here, which are important in the determination of the observed community patterns. Some of these questions will only be answered with further sampling, either in this system or another.

Future Considerations

One striking finding of Chapter 7 was the sudden change in community constancy at temporal intervals greater than six months but less than one year. This may indicate that there is considerable change in community structure in the fall between the drier, summer months and the wetter, winter months. Also, it is possible that at least once a year (either in the spring or in the fall) the environment forces changes in community structure or composition by exerting extreme pressure on abiotic pool conditions (i.e. severe weather patterns including drought or hurricanes). Such extreme disturbances could result in a "re-setting" of the pool communities as suggested by the Intermediate Disturbance Hypothesis (see Connell, 1978). In the future, data collected over shorter time intervals would provide better resolution to patterns of community constancy and structure, possibly at a time when environmental variability has the greatest impact on these communities.

Recently, studying a temporary pond in Italy, Bazzanti et al. (1996) provided data on the temporal succession of the macroinvertebrate fauna. Due to the size of this pond (length ~ 40 m; area ~ 1080 m^2) and the number of taxa (86) they were only able to document changes in this one pond. Given the smaller nature of the rock pools (length ~ 40 cm) and the fewer number of taxa that occur there (< 16 per pool per date), this system would be ideal to follow community development for many temporary pools. Studying many pools would allow a better understanding of the mechanisms that result in the observed community composition and structure. Recall that temporary pools were dominated by species with good dispersal abilities, which resulted in a pattern of community structure that was similar among temporary habitats (Chapter 4). However, there was no indication of how this structure was maintained, or the length of time the community could maintain its structure.

One important limitation of the data is a lack of trophic relationships among species and quantitative information on biotic interactions. Despite inferred relationships among species, there is no data on how component species within a community interact. This is not surprising given the little information published on this system. There is much in the general literature on food web dynamics, including some studies in predation rates in temporary ponds (see Schneider and Frost, 1996). However, there has been little published on extremely variable environments. Most studies on variable environments have focused on determining relationships with habitat variability or describing species found in these habitats (e.g. Death and Winterbourn, 1994; Williams et al., 1997; etc.). Information on specific biotic interactions would allow better separation of the effects of abiotic (environmental variables) and biotic factors, thereby providing a more detailed picture of the factors responsible for the formation and maintenance of community structure and composition over time in highly variable environments.

Future investigations might consider using an experimental approach to answering questions of how abiotic conditions shape or maintain community composition and structure. By establishing replicate communities, different abiotic variables could be manipulated in order to determine whether single, "key" variables are directly responsible for the observed community patterns or if environmental change indirectly alters communities by modulating biotic interactions. However, it is unlikely that these competing hypotheses are mutually exclusive and the interaction of the two might represent the strongest force responsible for the determination and maintenance of community composition and structure.

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