THE RELATIONSHIP BETWEEN DIVERSITY AND STABILITY IN TROPICAL ROCK POOLS

By

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ABSTRACT

This dissertation examines the relationship between diversity and stability in aquatic rock pool invertebrate communities. Previous tests of the relationship between diversity and stability have suggested that diversity stabilizes communities properties but either destabilizes or is unrelated to population properties; however, a comprehensive test of the relationship between diversity and stability has not previously been conducted in aquatic ecosystems. I used two approaches to examine diversity-stability relationships in rock pools. First, I used time series data of population and community densities collected on 49 rock pool communities over 8 years, and second, I experimentally manipulated diversity and nutrient conditions in rock pool container habitats.

I found that diversity was negatively related to community variability in both natural unmanipulated rock pools and experimental rock pools consistent with the diversity-stability hypothesis. However, the stabilizing effect of diversity was modulated by environmental conditions. In natural unmanipulated rock pools strong correlations between diversity and community variability were identified in abiotically stable rock pools and temporary rock pools that were subject to frequent desiccation events. In contrast, there was no relationship between diversity and community stability in rock pools with variable abiotic conditions or permanent rock pools which were not subject to desiccation events.

That environmental conditions might modulate the relationship between diversity and stability was further confirmed experimentally. In experimental rock pools the responses of community and population stability to different diversities depended on nutrient conditions. Diversity stabilized both community and population densities in oligotrophic rock pools but not in mesotrophic or eutrophic rock pools. The stabilizing effect of diversity on community density supports previous studies in other ecosystems, however, this is the first study to show a stabilizing effect of diversity on population densities.

The results of this study suggest that under some conditions stability is dependent on diversity, however there is no necessary relationship between diversity and stability in rock pool communities. Furthermore, contrary to the general conclusions drawn from mathematical models and experimental studies in plant communities, populations may be stabilized rather than destabilized by diversity depending on the system under consideration.

PREFACE

This thesis contains five papers that either have been published in the primary literature or have been submitted to journals for publication. All of these papers were co-authored with my supervisor, Dr. Jurek Kolasa. While Dr. Kolasa contributed ideas and comments to improve these manuscripts the majority of each paper consists of my own original research. In addition to the papers reproduced herein, two additional papers have been published in the course of my thesis research that are not included in this thesis. These are:

Romanuk, T.N. and J. Kolasa. 2001. Simplifying the complexity of temporal diversity dynamics: a differentiation approach. Ecoscience 8: 259-263.

Romanuk, T.N. and J. Kolasa. 2002. Abundance and diversity in natural aquatic microcosms: a test and a refinement of the niche-limitation hypothesis. Community Ecology 3: 87-94.

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I would like to thank my supervisor Jurek Kolasa for his confidence in this research and his approach to guidance. Dave Rollo provided inspiration and expanded my scientific and personal horizons. Susan Dudley and Jim Quinn sat on various committees and provided opportunities for learning and growth. Susan Marsh and Roger Thompson helped with the field work, and either edited various manuscripts or this dissertation. Special thanks go to a raft of unnamed people who read my papers and assisted in the process of publication. Thanks to Cam Ortis, Gloria and David Roberts, Rene Lange, and especially to my parents Fred and Jan Romanuk for continued support.

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Chapter 1:

The relationship between diversity and stability

INTRODUCTION

> "Biodiversity is the key to the maintenance of the world as we know it. Life in a local site struck down by a passing storm springs back quickly; opportunistic species rush in to fill the spaces. They entrain the succession that circles back to something resembling the original state of the environment"
>
> \- E. O. Wilson (1992)

Background and Rationale

Three billion years ago the entirety of biological diversity was represented by microscopic organisms similar to cyanobacteria (blue-green algae) and bacteria-like species. The first eukaryotic organisms evolved 1.8 million years ago. At first they were single celled, reminiscent of modern protozoans, but before long they evolved into more complex organisms composed of cells organized into tissues and organs. Macroscopic organisms, large enough to be seen with the naked eye, evolved 540 to 500 million years ago. The rapid diversification of life during this epoch, the Cambrian explosion, established the major adaptive types of organisms that exist today. Throughout geological time, biological diversity has slowly increased, punctuated by five major extinction events and numerous smaller collapses. After each of these extinction events, the Ordovician, Devonian, Permian, Triassic, and Cretaceous, biodiversity has generally recovered to pre-extinction levels, however after each mass extinction it took between 20 and 100 million years for a complete recovery of biodiversity.

The earth is presently undergoing the sixth mass extinction event (Wilson, 1992). Species are presently going extinct at a rate that far exceeds the five mass extinction events whose collapses punctuate the fossil record (McCann, 2000). Wilson (1992) predicts that over a fifth of all species on the planet will be extinct by the year 2020, and the Nature Conservancy predicts that one third of the world's species are currently at risk of extinction (McCann, 2000). Wilson (1992) calculated the natural background extinction rate to be one extant species per million per year. The number of documented extinctions in the last 400 years is 611 species, which exceeds the natural background extinction rates. However, using the most conservative estimates of extinction rates, and only taking into consideration forest loss from land-use changes in tropical forests, Wilson (1992) estimates that each year 27,000 species are going extinct. This is at least 26,970 more extinctions each year than predicted by natural background extinction rates.

These widespread reductions in global biodiversity have raised numerous questions about the consequences of species loss (Elton, 1958; Odum, 1959; McNaughton, 1977, 1993; Schultze and Mooney, 1993; Vitousek and Hooper, 1993; Tilman and Downing, 1994; Tilman, 1996). Biodiversity is generally considered to be a resource (Myers, 1996), and many valid reasons have been documented for "saving" biodiversity from purely economic reasons to the moral and ethical responsibility of people to care for life on earth (Wilson, 1992). However, the most important reason to conserve biodiversity is that biodiversity is a life support system. Directly and indirectly, biodiversity influences the structure and functioning of ecosystems, providing essential "ecosystem services" upon which people depend (Wilson, 1992).

Diversity and stability

Ecologists have long hypothesized that the number of different species in an ecosystem might influence the stability and sustainability of various ecosystem properties. Darwin (1872) stated that:

> "The more diversified in habits and structures the descendents … become, the more places they will be enabled to occupy…It has been experimentally proved, if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can be raised in the latter than in the former case."

The idea behind this hypothesis, that biodiversity is an important driver of ecological processes, has received considerable support (e.g. Tilman, 1999; Loreau et al., 2001; Cardinale et al., 2002). Species loss has been shown to affect resistance to invasion by novel species (Darwin, 1872; Elton, 1958; Tilman, 1997; Dukes, 2001), rates of decomposition (Naeem and Li, 1997), productivity (Trenbath, 1974; Harper, 1977; Naeem et al. 1994; Tilman et al. 1997a, 2001), and predictability (McGrady-Steed et al. 1997), to name just a few processes and attributes of ecological systems that have been shown to be affected by changes in diversity.

Diversity has also been shown to affect community and population stability (i.e. *temporal invariability*; McNaughton, 1977; Tilman, 1996; McGrady-Steed and Morin, 2000; Chapter 3-6), and it is this "ecosystem function" of diversity that is my focus in this dissertation. Despite considerable effort to answer the question "does diversity beget stability", whether and how diversity affects the stability of communities and populations is still heavily debated (see Naeem, 2002).

Definitions of stability and diversity

Stability can refer to resistance to disturbance, resilience (rate of recovery following a disturbance), or temporal invariability (i.e. how constant a property is over time; Pimm, 1984). Throughout this dissertation I focus solely on temporal variability in the numbers of individuals in a community or in populations. Temporal variability is measured using the variance in a time series of abundances. Variance must be rescaled relative to the mean as abundances may differ between species. The traditional method to rescale variance to the mean has been to use coefficients of variation where CV=standard deviation/mean (see Tilman, 1999). Smaller values of CV indicate greater stability, and larger values indicate less stability. Throughout this dissertation, 'biodiversity' or 'diversity' refers primarily to species richness, the number of species in a habitat, and where diversity refers instead to a composite measure such as a diversity index (i.e. Shannon-Weiner Index), this will be made clear.

The diversity-stability debate

The relationship between the diversity of ecological communities and their stability has been hotly debated for the past three decades. The first debate has focused on the inconsistency between how diversity affects aggregate community properties such as the total biomass of a community as opposed to biomasses of individual populations (King and Pimm, 1983). Elton (1958) observed that depauperate communities were more easily upset than diverse communities. In contrast, May (1973) showed mathematically that populations were less stable in more diverse communities. Tilman (1996) suggested a resolution for this paradox for grassland communities by showing that at the aggregate level (total community biomass) increases in diversity were stabilizing, while for individual populations increases in diversity were destabilizing. Tilman (1996) hypothesized that interspecific competition was the mechanism that unified his seemingly dichotomous results. In a competitive community, a perturbation which changes the abundance of one species will affect the abundances of many other species in the competitive network, resulting in more variable populations as diversity increases. However, competition should also stabilize the total community biomass because disturbance-resistant species will compensate for decreasing abundance of disturbance-prone species. May (1973) predicted this dichotomy as well,

> "if we concentrate on any one particular species our impression will be one of flux and hazard, but if we concentrate on total community properties (such as biomass in a given trophic level) our impression will be of pattern and steadiness".

This debate continued primarily because of the lack of empirical evidence (McNaughton, 1977) and still continues today. Despite substantial research effort, the only study to show that diversity stabilizes communities and destabilizes populations is Tilman (1996, 1999), and his results for population stability were ambiguous.

The second area of debate has centered on the possible mechanisms by which diversity promotes stability. A number of mechanisms have been proposed, both biological and statistical, however there is little consensus for a single underlying biological mechanism. In plant communities, both species composition, i.e. the positive effects of particular species (Tilman et al., 1997b; Hooper and Vitousek, 1997) and the positive additive effects of diversity and diversity within functional groups have been shown to contribute to community stability (Tilman et al., 1997b). Furthermore, a number of population and community properties have been isolated that affect the relationship between diversity and stability, including evenness of abundance, mean-variance relationships, degree and direction of interspecific species responses, and positive diversity-productivity relationships, i.e. overyielding (Tilman, 1999; see Table 1).

The third area of debate is concerned with the limited number of community types in which relationships between diversity and stability have been considered. With only a few exceptions (see Schlapfer and Schmid, 2000 for a review; Naeem and Li, 1997; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002; Chapter 3-6), the relationship between diversity and stability has only been experimentally examined in terrestrial plant communities (McNaughton, 1977, 1985, 1993; Frank and McNaughton, 1991; Dodd et al. 1994; Tilman and Downing, 1994; Silvertown et al., 1996; Tilman, 1996, 1999; Wardle, 1999; Pfisterer and Schmid, 2002). This emphasis on one ecosystem and group of organisms has both facilitated and inhibited our understanding of the importance of biodiversity to ecosystem functioning and stability. In grasslands, there is evidence that biodiversity increases community stability (Tilman and Downing, 1994; Tilman, 1996), facilitates higher productivity (Tilman, 1999), and increases resistance to invasion (Tilman, 1997), or at the very least, covaries with other elements of the environment that do (Sankaran and McNaughton, 1999).

However, the intensity and types of ecological interactions vary in different ecosystems (Steele, 1985, 1991). While grassland are structured largely by competitive interactions (Tilman, 1999), aquatic systems are often strongly structured by both predation and competition (Zaret, 1980). Moreover, in grasslands, the relationship between diversity and productivity is generally positive, whereas in aquatic systems, unimodal relationships are more predominant (Dodson et al., 2000; Waide et al., 1999). As competitive interactions and positive diversity-productivity relationships are two of the mechanisms hypothesized to affect diversity-stability relationships, it is unlikely that diversity-stability theory derived from terrestrial plant communities will apply directly to aquatic systems (see Johnson et al., 1999), or that ecosystem stability should be universally dependent on species diversity (Johnson et al., 1999).

Furthermore, the majority of biodiversity studies have been conducted on species-rich ecosystems. There is concern among some ecologists that the experiments of Tilman (1996), Naeem and Li (1997), and McGrady-Steed and Morin (2000) among others, may have little applicability to species-poor communities, and other community types (D. Schindler, personal communication). The need for a broader consideration of the role of biodiversity in a wider range of ecosystems is the next step in biodiversity research (Loreau et al., 2001). A broader range of ecosystems will facilitate the development of more general models for biodiversity effects, if there are any, and a more mechanistic approach to the role of biodiversity will expand our understanding of how biodiversity interacts with particular environment conditions.

To improve our understanding of the relationship between diversity and stability new data, new methodologies, and evaluation of diversity-stability relationships in a wide range of communities are required. The purpose of this dissertation, therefore, is to derive a better understanding of the relationship between diversity and stability by focusing on aquatic invertebrate communities. Ecological theory predicts that environmental conditions may modulate diversity-stability relationships, and this is the second focus of this dissertation, to determine whether and how environmental conditions affect the resulting correlations between diversity and stability.

The general hypotheses that I attempt to disprove in this thesis are (i) that there is a relationship between diversity and stability (i.e. the inverse of temporal variability) for aggregate community abundance, i.e. total density of all populations in a community, and ii) that there is a relationship between diversity and the stability of individual population densities. These two hypotheses, the diversity-community variability hypothesis and the diversity-population variability hypothesis, are often combined as the diversity-stability hypothesis. Here, I will discuss them separately because there is no widely accepted theory that links the relationships between diversity and both community and population stability.

The diversity-community variability hypothesis

MacArthur (1955), Elton (1958), and Odum (1959) suggested that diverse communities would be more resistant to disturbance than depauperate communities because diverse communities contained more alternative pathways for energy-flow and nutrient cycling. Increasing diversity was hypothesized to provide a form of biological insurance, ensuring that if some species failed, there would be other species than could increase in abundance and maintain the overall stability of the community (Yachi and Loreau, 1999). McNaughton (1977) showed that diverse grassland communities were more resistant to disturbance by grazers than species-poor grasslands. Tilman and Downing (1994) and Tilman (1996, 1999) showed that diverse grassland plots were more stable than species-poor grassland plots in terms of biomass. Naeem and Li (1997) and McGrady-Steed and Morin (2000) expanded the applicability of this pattern to aquatic microcosms containing algae and protozoans, and Romanuk and Kolasa (2002; Chapter 3) demonstrated a similar relationship between diversity and stability in natural aquatic microcosms inhabited by zooplankton and benthic invertebrates. While the results of some of these studies have been debated, the evidence to date suggests that diverse communities are generally more stable than species-poor communities.

Table 1. Guide to the statistical and biological mechanisms that may influence the relationship between diversity and the variability of aggregate community metrics such as biomass, abundance, and density.

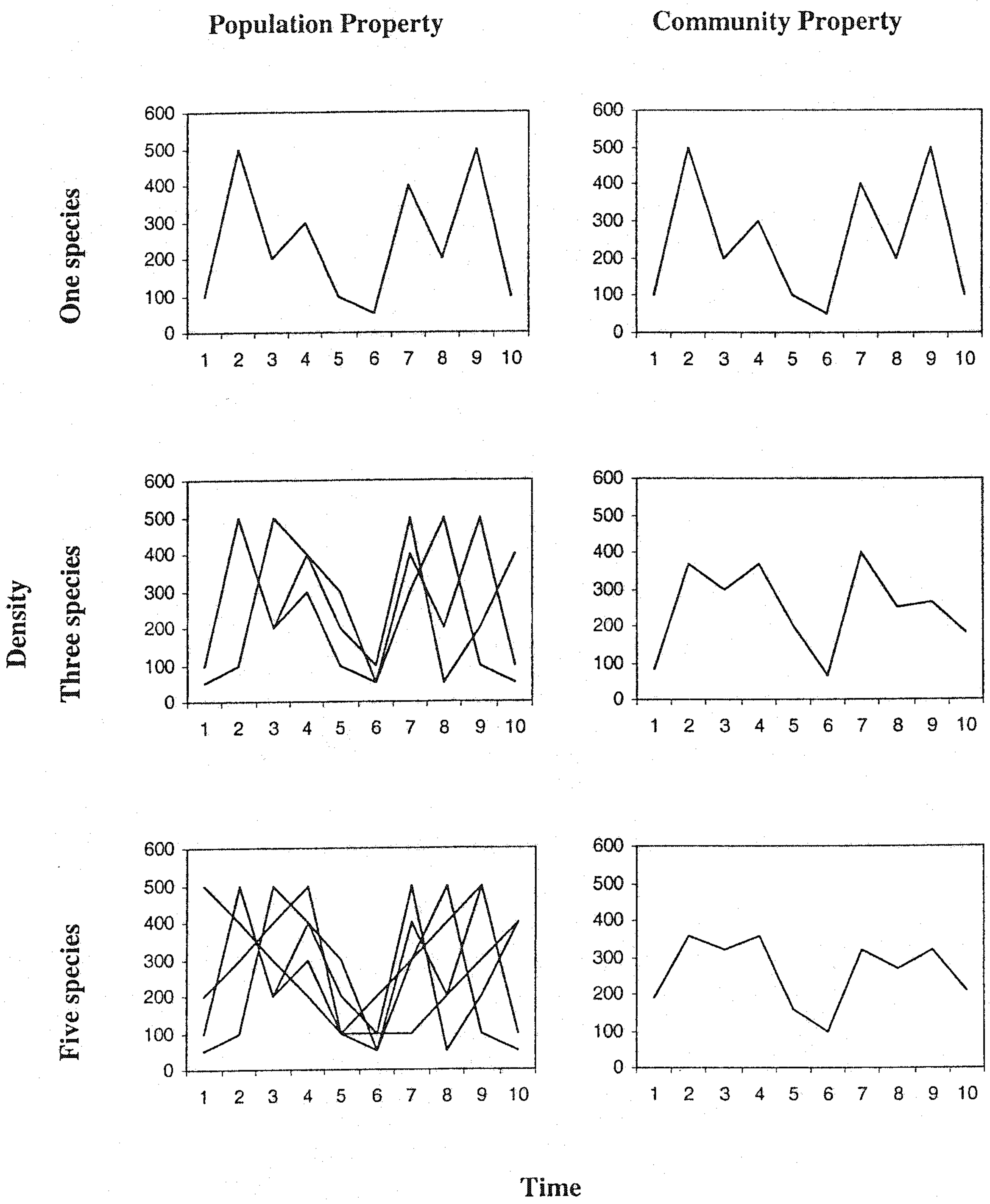
Statistical	
Statistical averaging (portfolio effect)	If the temporal fluctuations of species in a community are not perfectly correlated, the variability of an aggregate community metric will be lower than the variability of the individual species due to averaging across species. See Figure 1.
Mean-variance rescaling	If the variance of a population property increases with the mean, as is generally expected, variability of the associated aggregate community metric should decline with increasing species richness.
Biological	
Evenness	The greater the evenness, the greater the role of each species in decreasing aggregate variability due to statistical averaging. There is little statistical averaging if a few species dominate.
Overyielding	Occurs when an aggregate community property increases with increasing richness, i.e. when mixtures are more productive than monocultures. Broadens the range of scaling coefficients z for which community variability decreases with increasing richness.
Competition	Should encourage negative covariance and therefore decrease community variability.
Insurance effect	Applies when increased richness leads to larger differences in species responses to environmental fluctuations. May facilitate more negative covariance between species and result in greater statistical averaging.
Population variability	Occurs when populations are less variable in richer environments leading directly to less variable aggregate community properties.
Environmental	
Disturbance	Should increase positive covariances in the fluctuations between species as the strength of the disturbance increases thereby decreasing the effect of richness on community variability.
Fluctuations in abiotic conditions	Should increase positive covariances between species as the abiotic conditions became more variable decreasing the effect of richness on community variability.
Resources	Should decrease competition intensity, thereby increasing positive covariances and decreasing the effect of richness on community variability.

Mechanisms of community stability

The majority of theoretical models have also supported the proposition that a more diverse community will be more stable due to a statistical property known as statistical averaging (Doak et al., 1998; see Table 1, Fig. 1). Statistical averaging or 'the portfolio effect' is the notion that the sums of several randomly and independently varying items are less variable than the average item. Statistical averaging has been proposed to decrease variability in more diverse communities independently of biological processes (Fig. 1). Averaging or portfolio effects are commonly compared to holding stocks in the stock market. The more stocks one has in a portfolio, the less sensitive the portfolio as a whole will be to fluctuations in market conditions (Tilman, 1999). The identification of portfolio effects in diversity-community variability studies by Doak et al. (1998) provided a general mechanism for increased stability with increasing diversity, and has also been proposed as a null model: if the effect of statistical averaging is less than the empirical reduction in variability seen with increases in biodiversity, then the portion of variation unexplained by averaging effects may be due to diversity *per se*.

A number of other mechanisms have also been suggested to explain reductions in variability with increasing diversity including: (i) complementarity, which refers generally to the additive effects of adding species on the biomass or density of the remaining species (Hooper, 1998; Tilman, 1999; McGrady-Steed and Morin, 2000; Cardinale et al., 2002), (iii) insurance effects, the probability that a more diverse community will include species with a wider range of traits (e.g. degree of resistance to

Figure 1. Graphical depiction of statistical averaging (the portfolio effect). Simulated fluctuations in a species property such as density ('Population Property'; left column) and the aggregate community property created by summing density ("Community Property'; right column), through time for communities with one species, three species, and five species. Note the apparent dampening of variability as the number of species increases (figure based on Cottingham et al., 2001).


Population Property
Community Property
One species
Three species
Five species
Density
Time
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desiccation) and that this wider range of traits ‘insures’ that some species will survive when others fail (Yachi and Loreau, 1999), (iiii) weak interaction effects, the stabilizing effect of lowering the strength of species interactions (Hughes and Roughgarden, 1998; McCann et al., 1998), (iv), or sampling effects, the increased probability of the most productive species being included in high diversity treatments (Huston, 1997).

The diversity-population variability hypothesis

For populations, the effect of diversity on temporal variability in density or biomass is less clear than for communities (see review in Cottingham et al., 2001). Theoretical predictions are diverse and contradictory, with models predicting that diversity can increase (May, 1973; Tilman et al., 1998), decrease (Ives et al., 1999, 2000; Li and Charnov, 2001) or have no effect on population variability (Tilman, 1999) depending on model construction. May (1973) showed that increasing the strength and number of species interactions results in increasing population variability. Extending May’s model of logistic growth, Tilman (1999) showed that for a single population that experiences random variation in its environment, its variance scales linearly with mean abundance, i.e., the scaling coefficient $z = 1$ (Tilman et al., 1998; Tilman, 1999). Populations in natural communities are expected to have scaling coefficients between 1 and 2 (Murdoch and Stewart-Oaten, 1989), suggesting that if all else remains equal, populations should become more variable as richness increases (Table 2). Diversity has also been predicted to decrease population variability. Ives et al. (1999) show that population variance in biomass may either increase or decrease with the strength of competition among species leading to decreasing population variability as diversity increases. In contrast to these theoretical predictions, the majority of empirical studies show non-existent or only very weak effects of diversity on population variability (Tilman, 1996; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002). In grasslands, the only experiment detecting a significant relationship between diversity and population variability was Tilman's (1996) who found that increases in diversity destabilized population biomasses. McGrady-Steed and Morin (2000) found no relationship between diversity and protist population variability in laboratory microcosms, and Romanuk and Kolasa (2002; Chapter 3) showed that when calculated according to the definition of Tilman (1996) and McGrady-Steed and Morin (2000), there was no relationship between population variability and diversity in natural rock pool communities. However, Romanuk and Kolasa also showed that when the variance arising from local processes was removed, diversity was negatively related to population variability (Chapter 5).

Environmental modulation of diversity-stability relationships

Doak et al. (1998) suggested that environmental fluctuations may modulate the relationship between diversity and community variability. When species respond similarly to environmental conditions, the resulting positive covariances should weaken

Table 2. Guide to the statistical and biological mechanisms that may influence the relationship between species richness and the variability of individual population metrics such as biomass, abundance, and density.

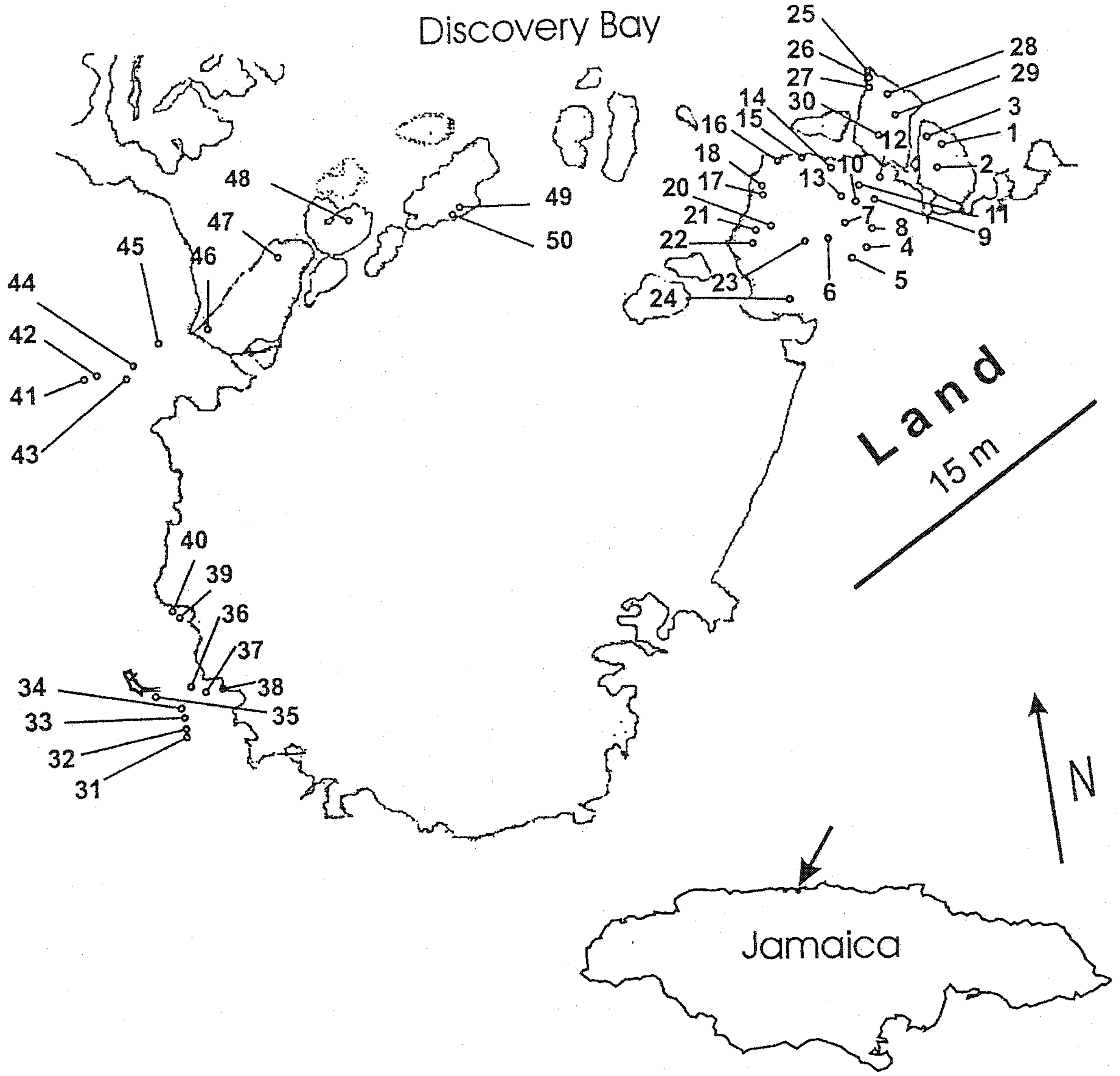
Statistical	
Mean-variance relationships	The relationship between population variability and species richness depends on the scaling coefficient z. Specifically, population variability is predicted to be independent of richness when $z = 2$, increase with richness when $z > 2$, and decrease with richness when $z < 2$.
Biological	
Interspecific competition	Population variance in biomass may either increase or decrease with strength of competition among species, α, and the number of species, S. Eigenvalues, λ_k, which measure partial correlation among species, increase with α and decrease with S. Therefore, when $\lambda_k > 0$, increasing α or decreasing S increases λ_k^2, increasing population variances. When $\lambda_k < 0$, increasing α or decreasing S initially decreases λ_k^2 but then increases λ_k^2 if λ_k becomes positive. Thus, decreasing S may initially stabilize population variances, but will eventually lead to increasing population variability.
Environmental	
Disturbance	Should increase variability in abundance. May alter competitive interactions, mean-variance relationships.
Fluctuations in abiotic conditions	Should increase variability in abundance. May alter competitive interactions, mean-variance relationships.
Resources	May increase or decrease fluctuations in abundance. Increases in species richness may dampen the effects of increased resources. Increases in species richness may facilitate more competition if resources are decreased.

but not entirely cancel the degree to which community variability declines with increasing richness. Romanuk and Kolasa (2002; Chapter 3) showed that in rock pools with greater variability in abiotic conditions there is no relationship between diversity and community variability, but that in pools with more stable abiotic conditions diversity is negatively related to community variability. This modulation of the diversity-stability relationship also arises between temporary pools, i.e. pools which are subject to frequent desiccation events, and permanent pools. In temporary pools, diversity is negatively related to community variability, however in permanent pools there is no relationship (Chapter 4). A similar pattern arises between oligotrophic microcosms in which community variability is stabilized by increasing diversity, and eutrophic microcosms where community variability is unrelated to diversity (Chapter 6). The role of environmental conditions in modulating the relationship between diversity and variability is also seen for populations. In oligotrophic microcosms population abundances are stabilized by diversity, whereas in eutrophic microcosms there is no relationship between diversity and population variability (Chapter 6).

The Rock Pool System

All of the research for this dissertation was conducted using zooplankton and benthic invertebrate communities inhabiting tropical coastal rock pools located near the grounds of the Discovery Bay Marine Laboratory in a small cay called the Blue Maze (Therriault and Kolasa 1999, 2000; Romanuk and Kolasa, 2001). The long-term data sets are compiled from annual and in some cases seasonal sampling of 49 rock pools. The experimental manipulations include assemblages from three homogeneous freshwater rock pools. The rock pools are all located within a 25 m radius and the long-term data set samples 21% of the rock pools (49/230) within an area of about 60x50 m. The rock pools are located around the cay on up-lifted fossil reef, and are formed by dissolution. The pools are primarily filled with rain water, although some pools (n=7) experience tidal flooding. During storms the pools are also affected by sea spray. The pools range from true freshwater pools through to brackish and hypersaline. A complete characterization of the environmental conditions and the rock pool invertebrate assemblages is presented in Chapter 2.

Figure 2. Map of the rock pool system near the grounds of the Discovery Bay Marine Laboratory (DBML) in Jamaica. Shown are the locations of the 49 rock pools discussed in Chapters 2-5.


Discovery Bay
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THESIS OUTLINE

This dissertation is divided into eight sections. In Chapter 1, the general introduction, I review the rationale for biodiversity studies, the general patterns that have been shown both empirically and theoretically, and the mechanisms proposed by which diversity affects community and population variability. Chapter 2-6 are presented as journal articles. Each of these sections begins with a set of objectives and a rationale for the journal article.

The first of these journal articles (Chapter 2) is a manuscript titled: "The roles of physical forcing and disturbance on temporal variability in natural rock pool communities". In this manuscript I examine whether environmental conditions affect temporal variability in species richness and community abundance. Physical forcing explained over 90% of the variance in variability in species richness, but only 34% of the variance in variability of community abundance. This suggests that variability in community abundance may be affected by biotic structure, such as the number of species, or possibly, unmeasured environmental conditions.

Chapter 3 contains an article "Environmental variability modulates the relationship between species richness and community variability in abundance in natural rock pool microcosms", published in Ecoscience (Romanuk and Kolasa, 2002). In this manuscript I show that species richness and community variability are negatively related across both environmentally variable and environmentally stable pools, however within these two subsets of pools, a relationship between species richness and temporal variability in community abundance is only present in environmentally stable pools. I also show that species richness and population variability are unrelated when calculated according to previous conventions (Tilman, 1996).

Chapter 4 contains an article "Diversity, disturbance, and stability: a test of the insurance hypothesis in natural rock pool microcosms." In this manuscript I show that species richness and community variability are negatively related in temporary rock pools, which are subject to desiccation events, but not in permanent rock pools.

Chapter 5 contains an article "Lower-level noise masks a global relationship between species richness and population variability". In this manuscript I show that by reducing the noise arising from local processes such as environmental conditions and species interactions, a strong negative relationship between species richness and population variability is seen. This result represents the first empirical demonstration that species richness is negatively related to population variability.

Chapter 6 contains an article "Effects of species richness and nutrients on the stability of an aquatic invertebrate community". In this manuscript I report on an experiment where I manipulated both diversity and nutrient conditions. Diversity stabilized both community and population abundances in oligotrophic microcosms but not in eutrophic microcosms.

Chapter 7 is the general discussion of the results presented in this dissertation. In this section I summarize the results presented in this dissertation.

The eighth section, Appendix A, discusses five mechanisms: statistical averaging, evenness, overyielding, competition, and insurance effects, that have been hypothesized to affect, or account for, the relationship between diversity and stability. For each mechanism I discuss whether the diversity-stability patterns seen in rock pool communities can be attributed to that particular mechanism.

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Chapter 2:

The roles of physical forcing and fluctuating conditions on the dynamics of tropical rock pool communities

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

Romanuk, T.N. and J. Kolasa. The roles of physical forcing and fluctuating conditions on the dynamics of tropical rock pool communities. Hydrobiologia.

RATIONALE AND OBJECTIVES

The thesis of this dissertation is that there is a relationship between the number of species in a rock pool community and the temporal variability of both total community density and the density of individual populations. The first four chapters in this dissertation use long-term data from 49 rock pools to determine whether there is a correlation between species richness and temporal variability. Using observational rather than experimental approaches necessitates a consideration of whether environmental conditions, such as desiccation, rock pool morphometry, and abiotic factors can be used to model temporal variability in density. In this article, I model temporal variability in both total community density and species richness using a suite of environmental variables. I found that:

1. Environmental variability was strongly related to temporal variability in species richness, explaining 94% of the variability in species richness (CV).
2. Temporal variability (CV) of community density was not well explained by environmental variability, with only 34% of the variability explained.

These results suggest that temporal variability in community density may be regulated, in part, by biotic factors.

ABSTRACT

Physical processes are a primary structuring force in aquatic habitats. However, the relative impact of physical forcing may vary among measures of community structure. We determined the relationship between physical forcing and variability in the number of species, the number of individuals, and community similarity of invertebrate assemblages in 49 coastal rock pools censused 8 times over 9 years. Rock pools, which ranged in size from 10-248 cm in length, supported an average of 1606 individuals per litre of 6 species at any one time. These were drawn from a total pool of 71 species. Structure of the assemblage in each pool, in terms of species richness, density, and community similarity, varied through time. Mean similarity of assemblages in the same pool was 0.518, ~ 28% greater than between assemblages in different rock pools. Morphometric attributes of the pools, other than pool cavity depth, were of little value in predicting the variability of the invertebrate assemblages formed. In contrast, attributes related to environmental variability explained 94% of the variance in relative variability of species richness and 34% of the variance in relative variability of community density.

Keywords: abundance, community composition, disturbance, species richness, temporal variability

INTRODUCTION

Communities are established and change through a variety of regional and local processes. In aquatic habitats, physical processes appear to exert a major influence on community structure (Wellborn et al., 1996), likely due to the close coupling between the physical environment and the biota (Steele, 1985). The combination of environmental factors and their variability, termed here physical forcing, has been shown to affect the dynamics and characteristics of a wide range of aquatic communities from fish (Kushlan, 1976; Horwitz, 1978; Closs and Lake, 1994; Poff and Allan, 1995), to benthic marine invertebrates (Peterson, 1975), temperate tide-pool communities (Dethier, 1984), kelp forests (Dayton et al., 1992), diatom communities (Peterson, 1987), meiobenthic copepods (Coull and Fleeger, 1977) and stream insects (Gurtz and Wallace, 1984; Schlosser and Ebel, 1989). Physical forcing is also thought to be more important in variable than in stable environments (Capone and Kushlan, 1991).

The variability components of physical forcing are of particular interest because they appear to have specific general impacts on community structure in terms of the number of species and the number of individuals. By contrast, gradients of physical conditions can be expected to influence composition by defining tolerance ranges of species and thus community composition, but may have a more limited direct impact on general patterns of community structure. For example, in tropical supralittoral rock pools, the salinity of a pool affects the number of species, the number of individuals (Therriault and Kolasa, 1999), and the identity of species present in that rock pool (see results). Despite the importance of salinity in determining some aspects of community structure, knowing the concentration of salt provides no information about the effect of increasing salinity in aquatic systems, as its specific effects are limited to the system under consideration. In contrast, variability in an important physical control may provide more generalized information. For example, desiccation frequency has similar effects across a wide range of small water bodies (Williams, 1987; Wellborn et al., 1996), resulting in reductions in the number of species and often more predictable community composition (Williams, 1987). In addition to determining the number of components in a system, physical forcing can also drive the dynamical nature of communities (Romanuk and Kolasa, 2001; Romanuk and Kolasa, 2002). The effects of variability in physical conditions on temporal variability in the numbers of species, numbers of individuals, and community similarity may provide even more generalized information concerning the effects of physical forcing on the dynamical nature of communities.

The importance of physical forcing and in particular its variability component has received considerable attention (Schlosser, 1982, 1985; Poff and Allan, 1995; Dunham and Reiman, 1999; Lenihan, 1999; Marchetti and Moyle, 2001; Taylor and Warren, 2001). However, in spite of the substantial body of knowledge (e.g., Powell, 1989), many questions are difficult to answer because the information is either fragmentary or is derived from systems that cannot be directly compared. It is important to know, for example, whether and how variability at one scale simultaneously affects variation in the number of species, the number of individuals, and community similarity among different time periods. Furthermore, knowing the magnitude of impact that physical forcing has on each of these components is crucial to an understanding of how biotic interactions affect community dynamics, a question of great importance to ecology. Such an evaluation will only be possible if a system is examined comprehensively from a variety of angles and at more than one spatial and temporal scale.

To obtain a comprehensive picture of how physical forcing affects community dynamics, we examine the relative role of physical forcing in tropical rock pool communities inhabited by a diverse assemblage of zooplankton and benthic invertebrates. We use a suite of variables to gauge physical forcing that includes three major attributes of rock pools: pool morphometry, environmental conditions and their variability, and disturbance regime. We then assess the relative strength of physical forcing in determining variability in the number of species, the number of individuals, and community similarity among locations and dates. We also examine the role of physical forcing in determining community composition (species identity). As physical forcing includes both local and regional components, we also consider whether differences exist in how the number of species and the number of individuals respond to physical forcing at different spatial and temporal scales.

METHODS

Study Site

Data were obtained on the invertebrates assembled in each of 49 rock pools present around Blue Maze, an inlet approximately 50 m across located near the Discovery

Bay Marine Laboratory, Jamaica (18°28' N/ 77° 25' W). Thirty of the rock pools were on the south side of the inlet and 19 were on the north side of the inlet. The pool bottoms were covered with fine sediments, pieces of coral rubble, dead macroalgae, detritus, and leaf litter (Schuh and Diesel, 1995; personal observations). In some pools high algal densities resulted in yellow-brown, green, and opaque water. Apart from the 71 species that were identified as permanent pool fauna, some other animals were found living or temporarily visiting the rock pools: gastropods (Littorinidae and Neritidae), isopods, hermit crabs, and the brachyuran crabs *Pachygrapsus* sp., *Grapsus grapsus, Cyclograpsus integer, Geograpsus lividus, Armases ricordi* and *Aratus pisonii* (Schuh and Diesel, 1995; personal observations).

The pools range from 14 to 248 cm in length and 10 to 188 cm in width (mean length = 56 cm ± 35.0 SD and mean width = 32.9 cm ± SD 26.8), and in depth from 1-37 cm (mean = 12.8 cm ± 8.3 SD). All pools were located within 5 m of the nearest-neighbour. Elevation above sea level ranged from 1-235 cm (mean = 76.6 cm ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Seven pools were tidal (16, 17, 19, 22, 24, 49, 50; although tidal flooding was not daily). The remaining 42 pools were maintained by rainwater and, very occasionally, wave splash water.

Sampling

We monitored 21% of the rock pools (49/230) with a volume greater than 250 ml for 9 years. The procedure used to census the invertebrates has been described in Kolasa et al. (1996, 1998), Therriault and Kolasa (1999, 2000, 2002) and in Romanuk and Kolasa (2001, 2002). Briefly, 500 ml of pool water was taken from a pool thoroughly stirred to dislodge organisms from its sides and bottom and to homogenize their distribution. A 100 ml dip container was used to obtain animals from a variety of locations in each pool (water surface, pool bottom, pool sides, water column); number of dips depended on pool area, shape, and depth. Samples were filtered with a 60 μm net and organisms not passing through the net were immediately preserved in 50-70% ethanol. A total of 392 samples were taken over 9 years and those with individuals (365/392) were included in the analysis. A total of 289,975 individuals were counted from all samples. Eight censuses were made of each pool over a 9-yr period: Dec. 1989, Jan. 1990, Jan. 1991, Jan. 1992, Jan. 1993, Jan. 1994, Jan. 1996, Jan 1997, and June 1997. Censuses were all made in one day.

Measured rock pool attributes

Ten attributes of the rock pools were measured in order to relate them to the dynamics of their invertebrate fauna. These can be separated into categories related to 1) pool morphometry or location, 2) abiotic conditions, and 3) physical variability. We measured the following morphometric/locational attributes: (a) surface area, (b) volume, (c) length (longest axis), (d) width (at widest point, perpendicular to length), (e) pool cavity depth (depth from the deepest point in the rock pool to the lip of the cavity), and (f) elevation above sea level. The attributes related to abiotic conditions were (a) pH, (b) temperature, (c) dissolved oxygen concentration, and (d) salinity. Temperature and pH were measured with a Hanna meter, HI-9025. Dissolved oxygen was measured using a YSI meter. Salinity was measured with a hand refractometer. Attributes related to physical variability included (a) desiccation frequency, (b) annual variability in abiotic conditions, (b) seasonal (winter-summer) variability in abiotic conditions, and (c) diurnal variability in abiotic conditions. Desiccation frequency was obtained by counting the number of times a pool dried after a wet phase (these records were taken each year over a period of two-three weeks). Annual variability in abiotic conditions was calculated as the standard deviation of the variable over winter censuses (n=8). Seasonal variability in abiotic conditions was calculated as the standard deviation of the variable from summer to winter censuses (n=4). Diurnal variability was calculated as the standard deviation of a variable measured at 2hr intervals over a 24hr period (n=24). Thus, calculations for annual, seasonal, and diurnal variability result in 3 scores (standard deviations) for each of the abiotic variables. Pools that were dry at the time of sampling were not used in the analyses.

Data analysis

The Morisita-Horn Index (MH) was used to assess 1) temporal changes in the fauna of each rock pool across censuses, and 2) similarity of assemblages in different rock pools for each census.

$$MH = 2\sum_{i=1}^{S}(an_i x bn_i)/(daxdb)(aNxbN)$$

Where S is the total number of species in both sites, aN is are the total number of individuals at site A, an_i is the number of individuals of the i^{th} species at site A, and:

$$da = \sum_{i=1}^{S} an_i^2 / aN^2 \qquad db = \sum_{i=1}^{S} bn_i^2 / bN^2$$

The Morisita-Horn Index calculates the probability that two randomly drawn individuals from two samples will belong to the same species, relative to the probability of randomly drawing two individuals of the same species from either of the two samples (pools in this case) alone (Horn, 1966). The index ranges from 0.0 when two samples have no species in common to 1.0 when the distribution of individuals among species is identical between samples. The Morisita-Horn Index was chosen over other similarity indices as 1) it is based on abundance data rather than binary data (Magurran, 1988), and 2) the index has been shown to be less dependent on sample size and diversity than other quantitative indices (Morisita, 1959; Wolda, 1981). Similarity values between different censuses were grouped using k-means clustering to determine whether there were identifiable clusters of pools that differed significantly in similarity.

Linear regression was used to assess the degree to which attributes related to morphometric, abiotic, and physical forcing could be used to predict 1) species richness, S, 2) community density (all species combined, N), 3) temporal variability in both richness (CVs) and community density (CV_N) of each pool over the eight censuses, and differences between pools on the north and south sides of the inlet, between brackish and freshwater pools, and to assess seasonal differences. Temporal variability was calculated as the coefficient of variation (standard deviation/mean) of total number of species and total number of individuals in each pool over the eight censuses. Numerical data were log transformed where necessary to stabilize variances. Regression analysis used a step-up procedure in which successive independent variables were added to the regression in that sequence, which, at each step, maximized the variance accounted for. The procedure was halted when no remaining variables significantly improved the regression equation. These and all other statistical analyses in this study were carried out with STATISTICA 5.5 (Statsoft, 1995), except for the Morisita-Horn Index, which was calculated using Estimate S (Ver. 6.0b1; Colwell, 2001).

RESULTS

The fauna present

The invertebrate fauna consisted of 73 species. With the exception of two species that we classified as non-residents (isopod sp., amphipod sp.), the majority of invertebrate species in each pool belonged to fully aquatic taxa (exceptions are aquatic insect larvae). The 71 species classified as residents differed greatly in density, with five common species accounting for >80% of individuals. These were *Nitocra spinipes* (Boeck), a harpacticoid copepod (45%), *Orthocyclops modestus* (Herrick), a cyclopoid copepod (12%), the ostracods *Potamocypris* sp. (10%) and *Cypridopsis cf. mariae* Rome

Table 1. Abundance, occupancy, and frequency of the 25 most common species. Number of individuals refers to the total over 8 censuses.

Species	Individuals	Rock pools	Censuses
Nitocra spinipes	129385	47	8
Orthocyclops modestus	33845	46	8
Potamocypris sp.	29383	36	8
Cypridopsis cf. mariae Rome	28076	31	8
Ceriodaphnia rigaudi	23950	20	8
Leidigia sp., *Alona davidii*	11372	20	8
Nematode sp.	5505	36	8
Heterocypris sp.	5112	31	8
Cypricercus sp.	3322	13	8
Cytheromorpha sp.	3195	30	8
Oligochaete sp.	2508	26	7
Candona sp.	2290	10	8
Armases miersii	1872	39	8
Ceratopogonid sp.	1498	33	8
Gyratrix hermaphroditus	1404	21	8
Culex sp.	1248	33	8
Paracyclops fimbriatus	546	29	8
Metis sp.	521	11	7
Ostracod sp.13	403	13	6
Midge larvae	237	18	8
Polychaete sp.	181	8	6
Ostracod sp. 9	175	7	6
Polychaete T	132	15	7
Coleoptera sp.	85	10	8
Dolichopodid sp.	49	12	8

(10%), and *Ceriodaphnia sp.*, a cladoceran (8%). Twenty-five species accounted for > 95% of individuals. These 25 species belong to five major taxa: Crustacea, Nematoda, Platyhelminthes, Insecta, and Annelida, of which entomostracan crustaceans were the most abundant taxa accounting for >90% of total individuals. These 25 species varied in the total density, the number of rock pools they occupied (occupancy), and the number of censuses (frequency) in which they were recorded (Table 1). The rank-abundance structure of the rock pools exhibits substantial unevenness (Fig. 1; see Therriault and Kolasa, 1999). Of the 71 resident species, 14 were found only once during the study.

On average, individual pool samples (500ml) contained 803 ± 1482 (SD) individuals of 5.73 ± 2.69 (SD) species at any one census. These mean numbers varied among pools from zero to as many as 50,634 individuals per 1 litre (pool 27). Species richness ranged from pools with no species (pools 43 and 45 on some dates) to 16 species at any one time (pool 17). Cumulatively over the 8 censuses, each pool supported substantially more species than were present at any one census (Table 2).

The relationship between density (N) and richness (S) was used to assess if each pool was potentially able to support all 71 species (Fig. 2). On average, each pool only supported 7% of the regional species pool in any one census. Over all dates, each pool supported 13% of the regional species pool, ranging from 7% (pool 43) to 33% (pool 16).

Figure 1. Species abundance curve based on mean density ($\log_{10} + 1$).

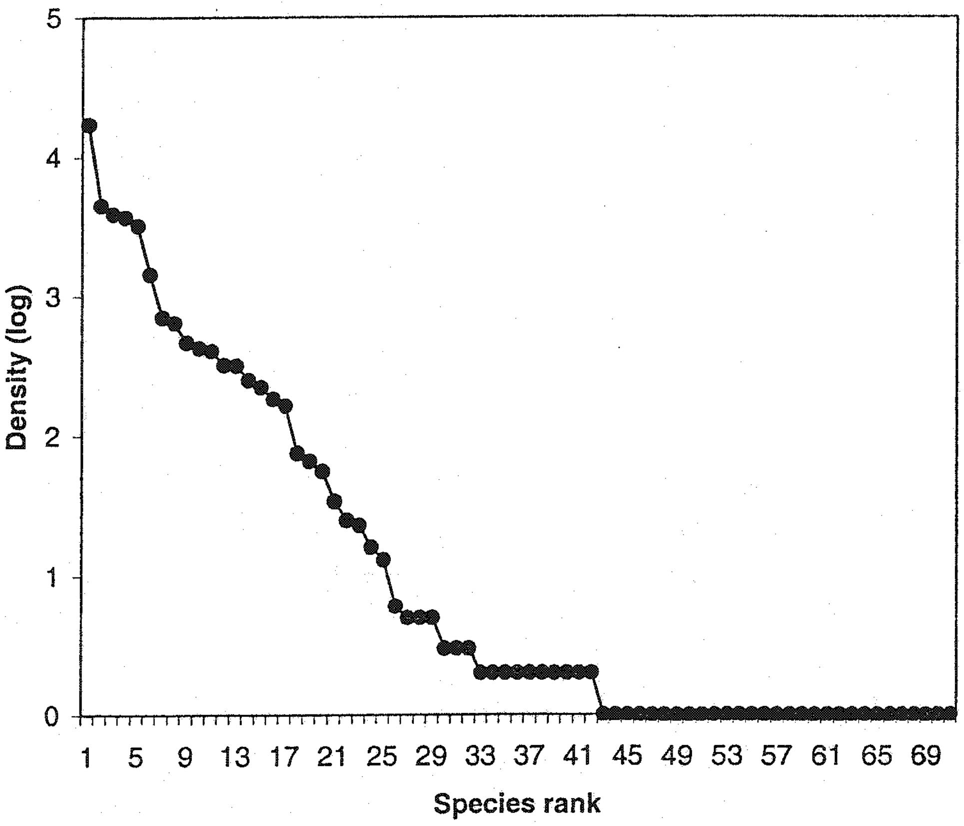
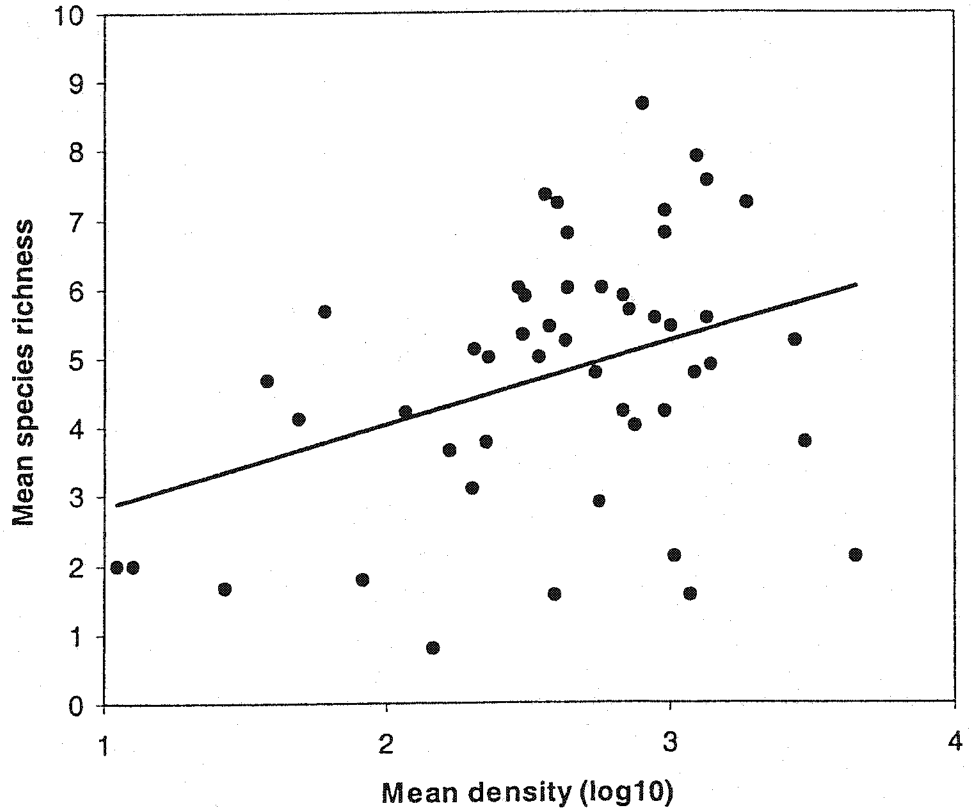

Density (log)
5
4
3
2
1
0
1
5
9
13
17
21
25
29
33
37
41
45
49
53
57
61
65
69
Species rank

Table 2. Species richness and total community density for each rock pool

Pool ID	Species richness		Density	
	Total	Per census	Total	Per census
1	13	6.0	4318	560
2	8	4.8	9123	1212
3	13	5.7	5700	712
4	18	6.0	3337	425
5	18	7.1	7467	944
6	13	4.9	10983	1390
7	18	6.0	2070	287
8	11	5.1	1544	201
9	13	5.4	2819	368
10	14	5.0	2660	339
11	16	7.2	2964	394
12	13	4.1	378	48
13	12	5.3	2207	300
14	11	4.0	5968	746
15	11	2.9	4027	557
16	24	8.7	6282	797
17	19	6.8	3363	427
18	17	5.7	419	59
20	14	4.2	5276	677
21	16	3.8	1543	224
22	20	7.6	10617	1334
23	13	4.2	7071	952
24	16	5.9	2231	304
25	10	1.7	188	26
26	5	1.6	8943	1185
27	7	2.1	33253	4460
28	9	2.1	7454	1040
29	14	5.0	1712	225
30	9	2.0	76	11
31	14	5.6	7608	1331
32	12	4.8	2923	539
33	15	5.6	4966	880
34	17	7.9	9156	1241
35	18	6.8	6281	956
36	12	4.2	867	116
37	16	4.7	266	37
38	15	7.2	13392	1846
39	17	5.4	7597	1007
40	10	3.7	1276	167
41	13	5.9	4438	673
42	9	2.0	84	12
43	5	0.8	1166	145
44	11	5.2	18507	2744
45	8	1.8	577	82
46	7	1.6	2696	385
47	11	5.2	2912	421
48	10	3.1	1400	199
49	14	3.8	23398	2963
50	21	7.3	2722	356

Figure 2. Richness as a function of individuals based on mean number of individuals and species for each rock pool.


10
9
8
7
6
5
4
3
2
1
0
Mean species richness
1
2
3
4
Mean density (log10)

Differences in fauna according to location

Despite significant differences between the north and south sets of rock pools in pool cavity depth ($F_{1,47} = 8.87$, $p = 0.0045$), elevation ($F_{1,47} = 47.33$, $p > 0.0001$), and salinity ($F_{1,47} = 23.9$, $p > 0.0001$), both sets of pools supported similar N (the south set of pools supported 57% of all individuals). There were differences however in the composition of the assemblages they supported. Nineteen of the 25 most abundant species in freshwater pools (i.e. primarily on the north side of the bay) were among the most abundant in the brackish pools (i.e. primarily south side of the bay). No significant association existed between the rank abundance of the 25 most abundant species in the brackish and the freshwater pools (Spearman's $r = 0.103$, $p = 0.969$). Only *N. spinipes*, the 1st ranked species in brackish pools and the 5th ranked species in freshwater pools, was among the top five numerically dominant species in both brackish and freshwater pools. There were wide variations between brackish and freshwater pools in the rank of other common species.

Differences in fauna according to census date

All but 6 of the 25 most common species were present in all 8 censuses, although their densities fluctuated widely. Analysis of variance was applied to the census data on richness and density. Rock pool identity and census date were the factors. Both richness and density showed significant variation among rock pools and among censuses. A

Student-Newman-Keuls test of the census effect showed that significantly more species were found in rock pools during January 1992 than in the other years. No other significant differences existed in species richness, but densities were higher in January 1993 than on any other date ($p < 0.05$). Despite the significant census differences, the census effect accounted for only 14.6% and 2.5% of the variation in richness and density, respectively. While there was no seasonal difference in richness ($p = 0.893$), Student-Newman-Keuls analysis of the seasonal effect showed that densities were higher in the summer than in the winter ($p = 0.048$). While significant, this difference accounted for only 2.2% of the variation in species density.

Variability in the compositional similarity (CV_{MH}) of rock pool fauna

Differences in fauna among individual pools were assessed by calculating the similarity (Morisita-Horn Index, MH) between all pairs of assemblages for a single census date. The mean similarity among rock pools over all censuses was 0.234, ranging from 0.172 (January 1997) to 0.301 (January 1992). The January 1991 census illustrates typical data: mean similarity in January 1991 was 0.233 and ranged from 0 (no species in common) to 1 (all species and their abundance in common). It shows that substantial differences in composition exist between assemblages in different pools.

We also determined the similarity (Morisita-Horn Index, MH) of the assemblages recorded at each census to that at each of the other censuses for each pool. The results of this comparison, for all 49 pools, lead to two main observations:

1) The fauna present in each rock pool at one census is more similar to that present in the same pool at the other seven census times than to other pools. The mean degree of similarity was 0.518 ± 0.178 (SD).
2) Rock pools vary in the average level of similarity among censuses, and the censuses differ in their levels of mean similarity. Similarity across pools ranged from 0.172 (pool 25) to 0.979 (pool 28) with a mean similarity of 0.234 ± 0.04 (SD). Mean census similarity ranged from 0.172 (date 7) to 0.301 (date 4).

Thus, spatial differences in community composition were 28.4% greater than temporal differences. On average, pools differed from each other by 76.6% on any one date. In contrast, successive censuses of a rock pool differed on average by 48.2%. We examine the possible causes of these patterns below.

Relation of rock pool attributes to faunal similarity (MH)

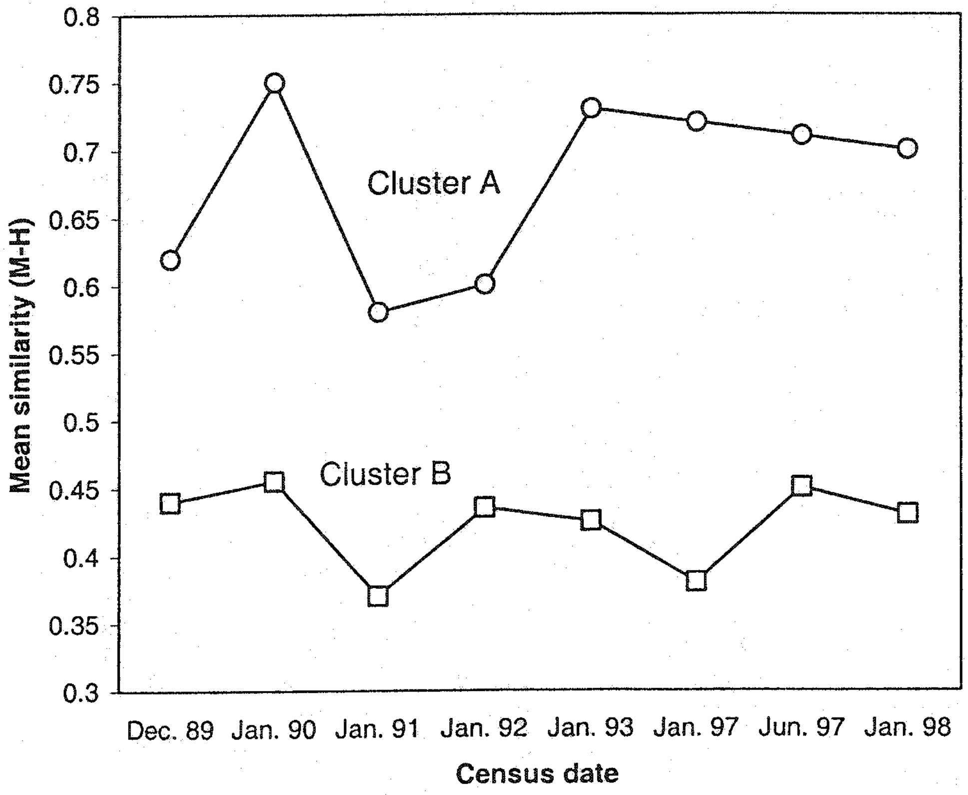
We searched for patterns within these similarity data in two ways. To determine the extent to which mean inter-census similarity was influenced by attributes related to pool morphometry and location, desiccation frequency, or other abiotic conditions, we ran a forward stepwise linear regression of mean inter-census similarity for each pool against these factors. Mean inter-census similarity was not related to any of the independent variables in separate regressions; however, average salinity was retained as significant in the stepwise regression ($r = 0.527$, $p = 0.0368$). Average salinity is negatively correlated with both elevation ($r = -0.74$, $p > 0.001$) and cavity depth ($r = -$

0.37, p = 0.009). Thus, in general, deeper pools at higher elevations, which also have lower average salinities, have more similar fauna between the censuses than the fauna of the shallow, low elevation, and more saline pools.

Cluster analysis of faunal similarity(MH)

Our second method to identify pattern in the similarity data was to use k-means clustering to identify groups of pools with (1) the minimum variability within clusters, and (2) the maximum variability between clusters. While theoretically, increasing the number of k random clusters will produce increasingly homogenous groups of pools, increasing the number of k clusters will also produce increasingly lower variability between clusters. We assumed *a priori* that pools could be classified into two groups that significantly differ in mean inter-census similarity: 1) pools with high inter-census similarity, and 2) pools with low inter-census similarity. Cluster A is composed of 12 pools in which mean inter-census similarity ranges from 58 to 75%. Cluster B is composed of 21 pools in which mean inter-census similarity ranges from 36 to 45%. In both clusters, mean similarity is lowest in January 1991 and highest in January 1990 (Fig. 3). We used ANOVA to determine relationships between cluster membership (independent variable) and rock pool attributes (dependent variables). No significant difference was found for any of the dependent variables as a function of cluster identity. Furthermore, there were no differences in mean inter-census similarity between the north and south pools.

Figure 3. Cluster analysis of community similarity across censuses for rock pools. Only rock pools that contained individuals on all eight census dates were used in the analysis.


0.8
0.75
0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
Mean similarity (M-H)
Cluster A
Cluster B
Dec. 89
Jan. 90
Jan. 91
Jan. 92
Jan. 93
Jan. 97
Jun. 97
Jan. 98
Census date

Relation of faunal variability to rock pool morphometry

The relationships between temporal variability in species richness (CV_S) and density (CV_N) and the five measured morphometric and locational attributes of rock pools were examined by a forward stepwise linear regression. Among the five independent variables, there were 16 cases of significant correlation with $r^2 > 0.123$.

Variability in richness (CV_S) was negatively related to pool cavity depth ($r = -0.39$, $p = 0.033$) and elevation ($r = -0.313$, $p = 0.045$) when tested separately. Including volume resulted in a combined model that explained 19% of the variance in variability of richness ($p = 0.004$). Additional variables gave no further improvement. Variability in density (CV_N) was lower in pools with greater cavity depth ($r = -0.33$, $p = 0.015$) but was not related to any other measured variable.

Relation of faunal variability to other abiotic variables

The relationships between variability of richness (CV_S) and of density (CV_N) and the four measured abiotic variables (average pH, oxygen, temperature, and salinity) were also examined by forward stepwise linear regression. Among the independent variables there was a significant correlation between temperature and oxygen ($r = 0.41$). The variability of richness (CV_S) was positively related to temperature ($r = 0.326$, $p = 0.028$) but to no other variable. Variability of density (CV_N) was positively related to temperature ($r = 0.305$, $p = 0.042$). Thus, variability in both richness and density was greatest when temperature was high.

Relation of faunal variability to physical forcing

Four measures of physical forcing were calculated: annual variability, seasonal variability, diurnal variability, and number of times a pool was found dry (desiccation frequency). Variability for each abiotic variable in a pool was calculated as the standard deviations across census dates. Variability in richness (CV_S) positively correlated with desiccation frequency ($r = 0.846$, $p < 0.0001$), annual variability in salinity ($r = 0.547$, $p < 0.0001$), and diurnal variability in temperature ($r = - 0.367$, $p < 0.0001$). The combined model explained 94% (adjusted R^2) of the variance and left no unexplained variance after adding any other variable. None of the predictive variables retained in the model were significantly correlated.

Variation in density (CV_N) positively correlated only with desiccation frequency ($r = 0.475$, $p = 0.005$) when all independent variables were tested separately. The explained variance increased to 34% when seasonal variability in pH was included ($p > 0.0001$). Thus, variability in richness is higher in pools that dry more frequently, vary more in salinities at the seasonal time scale, and undergo larger diurnal changes in temperature. Variability in density is higher in pools that dry more frequently and have higher seasonal variability in pH. Overall, our regression models for variability in richness and density show that:

1) Variability in both richness and density is lower in deeper pools, in pools with higher average temperatures, and in pools with lower desiccation frequencies.
2) Variability of richness and density is lower in less abiotically variable pools. Variability in richness is lowest in pools that do not vary substantially in salinity between winter and summer censuses and that have smaller diurnal changes in temperature.
3) Variability in richness is almost completely explained by physical forcing. Desiccation frequency, seasonal variation in salinity, and diurnal variation in temperature cumulatively explained 94% of the variance in richness variability (CV_S). In contrast, variability in density (CV_N) is poorly explained (34% of variance) by the independent variables. Only desiccation frequency was reliably, positively related to variability in density.

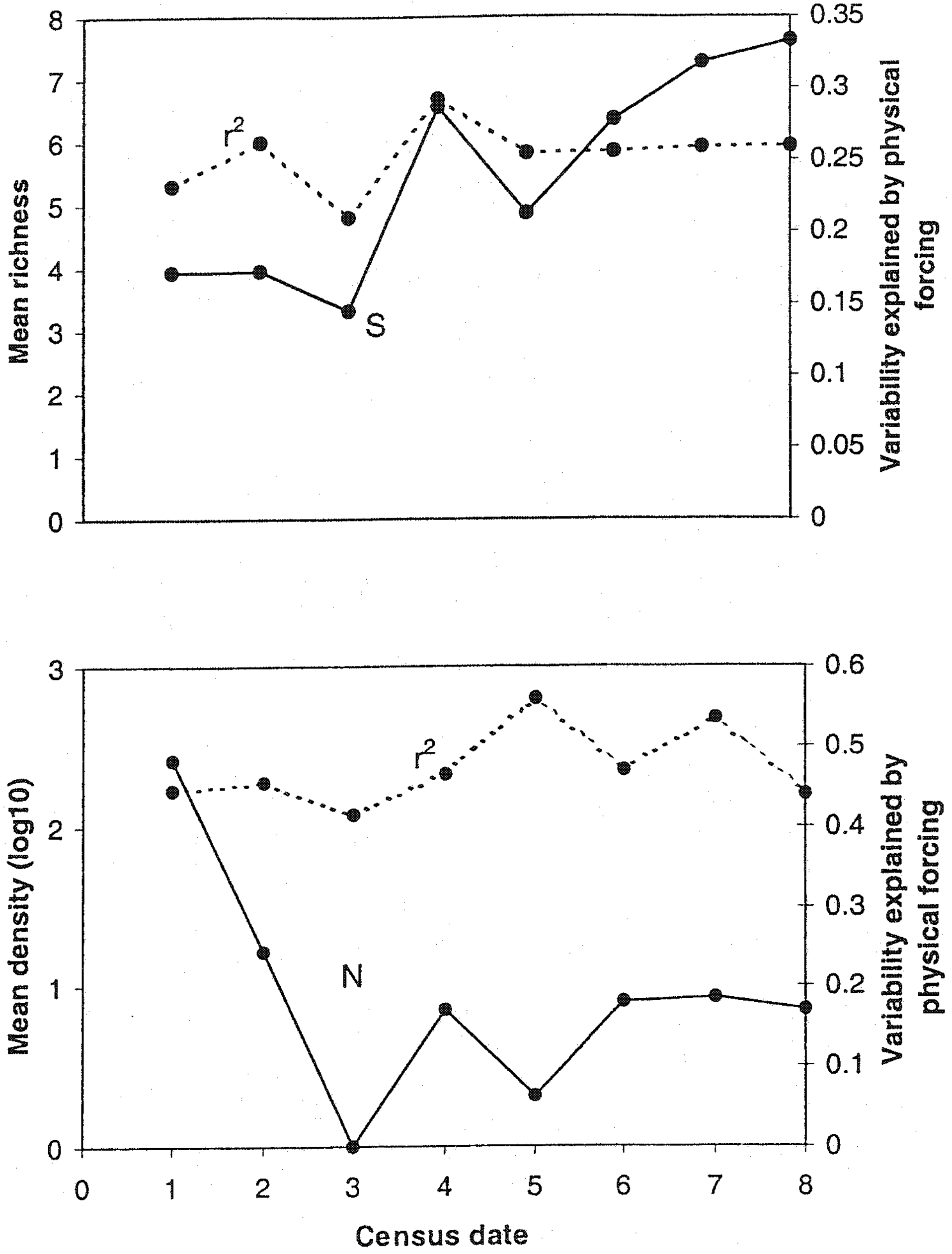
Changes in the relationship between rock pool attributes and community structure

To assess the temporal variability of the relationships between rock pool attributes and faunal structure (i.e. richness and density), we regressed pool richness and community density at each census against these attributes. We only used the attributes that were shown to have significant effects on temporal variability of richness and density: desiccation frequency, cavity depth, volume, seasonal variability in salinity and pH, and diurnal variability in temperature. The explained variance and regression slopes varied from census to census for both richness and density (Fig. 4). Richness and density were significantly related to rock pool attributes in 6 of the 8 censuses.

To determine if the magnitude of richness or density influenced the resulting correlation coefficients, we performed separate regressions for minimum, maximum, mean, and standard deviations of both richness and density at each date as independent variables, and the correlation coefficients for richness and density models at each date. Model performance, as reflected by r^2 values, for richness at each date was not significantly affected by any of the independent variables; however, a positive trend emerged between mean richness and model performance ($r^2 = 0.413$, $p = 0.085$, $n = 8$) indicating that low richness may decouple variation in richness from variation in pool attributes. Similarly, model performance for density was not significantly affected by any of the independent variables, however model performance showed a decreasing trend with maximum abundances ($r^2 = 0.441$, $p = 0.072$, $n = 8$) indicating that high density may decouple variation in density from variation in physical pool attributes.

Overall, this suggests that 1) attributes of the pools explain more variance in richness across separate censuses when the pool richness is higher, and 2) attributes of the pools explain more variance in density across separate censuses when the population densities are lower.

Figure 4. Variability in richness and density across censuses. a) Left axis: variability in mean richness and mean density at each census date – solid lines. b) Right axis: variance explained (r^2) by rock pool attributes in richness and density values for each census – dotted lines.


Mean richness
0
1
2
3
4
5
6
7
8
Variability explained by physical forcing
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
r2
S
Mean density (log10)
0
1
2
3
Variability explained by physical forcing
0
0.1
0.2
0.3
0.4
0.5
0.6
r2
N
0
1
2
3
4
5
6
7
8
Census date

Effect of rock pool attributes on the 10 most abundant species

Because the most abundant species dominate community dynamics (Therriault and Kolasa, 2000) we also examined the relationship between the density of individual species and rock pool attributes (morphometric, abiotic and physical variability). This was done for the 10 most common species. Distributions and abundance of 1 of these 10 species, a nematode, was not related to any of the rock pool attributes. Of the remaining 9 species, distributions of 6 were related most strongly to mean salinity (*Heterocypris* sp., *Cytheromorpha* sp., *Cypridopsis cf. mariae Rome*, *Potamocypris* sp., *Nitocra spinipes*, *Leydigia* sp.). The distributions of the remaining 3 species were most significantly related to elevation (*Cypricercus* sp. and *Ceriodaphnia rigaudi*), and desiccation frequency (*Orthocyclops modestus*). Worth noting are the facts that a) in 5 cases the relationship failed to improve significantly after including more than one independent variable, b) salinity was retained by the analysis in 8 of the 10 relationships, c) temperature was included in 4 of the 10 relationships, d) elevation was included in 2 of the 10 relationships, and e) desiccation frequency was only included in 1 of the 10 relationships.

DISCUSSION

This study has shown that variability in the natural occurring assemblages of micro- and meio - invertebrates in small, erosional rock pools is (a) affected weakly by morphometric attributes of the rock pools, (b) affected strongly by physical forcing with respect to richness (CV_S) but not density (CV_N) or compositional similarity (CV_{MH}), and that (c) relationships between richness, density and rock pool attributes vary among censuses.

None of the rock pool attributes used in the model, including desiccation frequency, significantly explained variation in assemblage similarity (MH) in separate regressions, suggesting that assemblage formation may be affected by other factors (for example, biotic interactions, productivity, asynchronous cycles of reproduction and dispersal) or by chance. At successive censuses, rare species appeared and disappeared, while densities of common species fluctuated and their abundance relative to one another changed. For example, the abundance of *N. spinipes*, the most abundant species in the rock pools, ranged over 4 orders of magnitude (0-50,634 individuals per litre) in pool 27 over the eight census dates. While *N. spinipes* was the numerical dominant for seven census dates in pool 27, local extinction of *N. spinipes* during January 1993 resulted in its replacement by the second most abundant *Orthocyclops modestus* as the dominant species in the pool.

Effect of physical forcing on variability in richness and density

Physical forcing reliably accounted for variability in richness (CV_S) but not variability in density (CV_N). Separate analyses of each census, however, showed that relationships between rock pool attributes and both richness and density were variable

(Fig. 4). Possible causes of this may include recent history (i.e. time to the last desiccation event), which could result in communities being sampled at different stages of recovery at different censuses, or factors related to the population dynamics of dominant species which have been shown to affect community variability (Therriault and Kolasa, 2000). Another possibility is that differences in regional conditions such as climate could dissociate or weaken relationships between physical forcing and richness and density. Regional conditions could also result in shifts in species composition as different from the richness values considered in this paper, thereby affecting community responses to physical forcing.

A model of assemblage formation

Physical attributes of pools appear to impose some restrictions on even the most common habitat generalists; however, in spite of this clearly detectable effect, the invertebrate assemblages possess a structure largely undetermined by physical attributes of the rock pools, and one that changes through time. In other words, while there may be a strong interaction between the physical environment and species performance, this interaction does not result in a specific and identifiable community structure. On this basis, we suggest the following reconstruction of assemblage formation.

Not unlike in most other habitats, individuals of each species colonize rock pools from time to time, and whether or not a particular species colonizes a particular rock pool will depend to a large extent on chance events (resulting from passive dispersal) and the tolerance of that species to salinity and fluctuations in salinity. Colonization will depend to only a small extent on the characteristics of that rock pool, with elevation being the most important factor. The variability of both richness and density in a rock pool is determined in part by the frequency of desiccation events. Desiccation is more likely to determine variability in richness as opposed to density, possibly because only a few desiccation tolerant species are able to survive through the dry phase. Individuals are lost from rock pool populations through mortality and, in some species, by movement to other habitats following the juvenile life stage (crabs, insects). The strong aseasonal variation in density arises partly from mortality due to desiccation or variable abiotic conditions. However, the low explained variance of the regression models for variability in density (CV_N) suggests that other processes such as variation in colonization rates or primary productivity may have a much stronger effect.

The generality of our results cannot be assessed without a comparison. The question arises then how similar with respect to their variability and susceptibility to physical forcing are the rock pool assemblages in Blue Maze to other rock pools? While a substantial literature on tide pools has accumulated (Metaxas and Scheibling, 1993), much less in known about rock pools. The few studies on freshwater and brackish rock pools conducted so far are in temperate habitats in Europe (Ganning, 1971; Pajunen, 1977, 1990; Ranta, 1982; Ranta and Nuutinen, 1984; Ranta et al., 1987; Preston and Moore, 1988; Pajunen and Salmi, 1991), and/or contain fish (Ranta and Nuutinen, 1984). Below we identify some of the salient differences and similarities between rock pools in Jamaica and other rock pool and tidal pools systems.

Rock pools and tide pools are often highly variable in both space and time (Metaxas and Scheibling, 1993; Therriault and Kolasa, 1999). Much of this temporal variability in temperate zone tide pools is related to seasonal differences (Metaxas and Scheibling, 1993). This contrasts strongly with the tropical rock pools in Blue Maze, where there is no seasonal variability in richness, and less than 3% of variability in density can be attributed to seasonal factors. This difference between rock pools and tide pools can partially be attributed to seasonal recruitment of micro- and macroalgae in tide pools (Aleem, 1950; Dethier, 1984; Underwood and Jernakoff, 1984).

Disturbance is a major structuring force in both tide pools and rock pools. Changes in fish abundance have been associated with boulder disturbances (Rinkus, 1978), and Thompson and Lehner (1976) showed that fish species composition in tide pools is affected by short-term changes in temperature. In the Blue Maze rock pools, desiccation appears to be the most important measured variable determining variability in both richness and density.

In temperate rock pools both richness and density are often correlated with depth (Pajunen, 1977; Ranta, 1982). Similarly, deeper rock pools in Blue Maze have higher species richness and density than shallow rock pools (Therriault and Kolasa, 1999), as well as lower variability in richness and density. The variance explained by depth however is very low. Overall, morphometric variables explain less then 29% of the spatial variation in richness, and none of the spatial variability in density (Therriault and Kolasa, 1999).

In summary, the tropical rock pools at Blue Maze are highly variable in space and in time. Attributes relating to salinity are the primary determinants of local composition. Attributes related to morphometry of the pools other than pool cavity depth are of little value in predicting variability in richness or density. Instead, variability in richness and density is predominantly related to the variability components of physical forcing, which explains 94% of the variance in richness and 34% in density. Our initial interest in the effect of physical properties on variability in richness, density, and compositional similarity arose from a previous study (Romanuk and Kolasa, 2002), which suggested that richness might play a role in determining variability in density. The models presented here show that attributes related to morphometry, abiotic conditions, and disturbance play only a minor role in density fluctuations. This raises the possibility that biotic or possibly unmeasured physical parameters may play a major role in determining community density fluctuations.

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Chapter 3:

Environmental variability alters the relationship between species richness and community variability in natural rock pool microcosms

This chapter was published in Ecoscience (complete citation follows) and is published here with the permission of Ecoscience (Appendix B). This chapter has been re-formatted to maintain consistency throughout the thesis.

Romanuk, T.N. and J. Kolasa. 2002. Environmental variability alters the relationship between species richness and community variability in natural rock pool microcosms. Ecoscience 9:55-62.

RATIONALE AND OBJECTIVES

In Chapter 2, I showed that temporal variability in total community density was not well explained by environmental conditions. This suggests that biotic factors may have an impact on temporal variability. In this Chapter I determine whether there is a relationship between the species richness of a rock pool and the temporal variability (CV) of both total community density and the densities of individual populations. I additionally consider whether environmental variability, which has previously been shown to impact the variability of aquatic communities, modulates the relationship between species richness and temporal variability. I found that:

1. Species richness explained 18% of the variability in total community density across all 49 rock pools, but was unrelated to the variability of individual population densities.
2. Diurnal abiotic variability in pH, salinity, dissolved oxygen, and temperature appeared to modulate this relationship. In pools with higher variability in abiotic conditions there was no relationship between species richness and temporal variability in community density, whereas in pools with lower variability in abiotic conditions there was a negative relationship between species richness and temporal variability in community density.

These results suggest that species richness may impact the temporal variability of total community density and that environmental conditions may modulate the impact of species richness on variability.

ABSTRACT

The effect of species richness on the temporal variability of communities and populations continues to inspire investigations and debates; however, few empirical studies have addressed the crucial question of how richness-variability relationships change along a gradient of environmental variability. We determined the relationship between species richness (S) and variability (coefficient of variation, CV) of both community and population abundances in 49 tropical coastal rock pools inhabited by aquatic invertebrates that differ in environmental variability. When all pools are considered, results support the hypothesis that variability in community abundance decreases with increases in species richness. In contrast, abundances of individual populations in more speciose communities vary no more than in species-poor communities. Richness-variability relationships were detected in i) low variability rock pools (as measured by a multivariate index of environmental variability) and in ii) rock pools with low diurnal variability in pH, oxygen, temperature and salinity. The presence of richness-variability relationships in the less environmentally variable rock pools as opposed to their absence in the more variable rock pools suggests that environmental variability may play an important role in modulating richness-variability relationships.

Keywords: diversity-stability hypothesis, environmental variability, invertebrates, microcosms, rock pools, temporal variation

INTRODUCTION

Communities and populations fluctuate through time, and the causes and consequences of this variation hold a fundamental place in ecological thought. That species richness (S) *per se* may regulate variability has fascinated ecologists for almost half a century (MacArthur, 1955; Elton, 1958; Odum, 1959), and has emerged as a topic of considerable scientific and public interest (see McCann, 2000 and Cottingham et al., 2001 for recent reviews; Mellinger and McNaughton, 1975; McNaughton, 1977, 1985; Berish and Ewel, 1988; Tilman and Downing, 1994; Tilman, 1996, 1999; Naeem and Li, 1997; Collins, 2000; Lehman and Tilman, 2000; McGrady-Steed and Morin, 2000). Recently, theoretical studies have suggested that environmental variability may strongly influence the relationship between richness and variability of species abundances (Doak et al., 1998; Hughes and Roughgarden, 1998; Ives et al., 1999; Yachi and Loreau, 1999).

Environmental fluctuations are a primary structuring force in many aquatic communities and have been shown to affect community composition (Death, 1995; Romanuk and Kolasa, Chapter 1), mediate the effects of competition and predation (McAuliffe, 1984; Meffe, 1984), increase population variability, and lower community persistence and constancy (Ross et al., 1985; Wolda et al., 1992; Death and Winterbourne, 1994). When species respond similarly to environmental fluctuations, the resulting positive covariances should weaken, but not entirely cancel, the degree to which community variability declines due to increased species richness (Doak et al., 1998). This suggests that environmental fluctuations should modulate the effect of species richness on community and population variability.

Environmental variability can alter richness-variability relationships in three ways. First, environmental variability can force variability of population abundances and thus community variability. For example, Peterson (1975) found that temporal variability of species abundances was greater in sites that experienced frequent heavy rains than at sites that experienced less severe rainstorms. Second, environmental variability can determine species richness, which in turn may regulate or covary with community variability (Sankaran and McNaughton, 1999). Kushlan (1976) found that a prolonged period of stable water conditions in Everglades marshes increased fish species richness but favored alterations in the composition of the community, shifting it from a community previously regulated by fluctuating abiotic conditions to one regulated by predation. Conversely, communities in harsh environments (high environmental variability) often have lower species richness (Connell, 1978), increasing the probability that proportionately higher numbers of community members will fail to function as the environment fluctuates (Petchey et al., 1999; Yachi and Loreau, 1999). Third, environmental variability is thought to influence richness-variability relationships by altering the variance-covariance structure of populations (Tilman, 1999). When species respond differently to environmental conditions, the resulting negative covariances should buffer aggregate properties against change (Ives et al., 1999; Yachi and Loreau, 1999).

Aquatic invertebrate communities inhabiting rock pool microcosms are particularly suitable for analyzing richness-variability relationships. On the north coast of Jamaica, coastal rock pools are a common feature on uplifted fossil reefs. The rock pools span a gradient from freshwater to hypersaline conditions, and contain communities of micro- and meio-invertebrates (insects, crustaceans, and worms). Many species are euryhaline, e.g. *Nitocra spinipes* (Boeck), and able to tolerate a wide range of salinity. Rock pool communities are also highly variable in space (Therriault and Kolasa, 1999) and time (Schuh and Diesel, 1995; Therriault and Kolasa, 2000; Romanuk and Kolasa, 2001) with a complex disturbance regime consisting of frequent high intensity disturbances (desiccation events) that interact with diurnal and annual abiotic variability to affect spatial and temporal dynamics (Therriault and Kolasa, 2001; Romanuk and Kolasa, 2001). Further, these small aquatic communities represent a natural analogue to many experimental systems (Tilman, 1996; Naeem and Li, 1997; McGrady-Steed and Morin, 2000).

We use long-term data from a series of 49 rock pools to test the general hypothesis that community abundance is less variable in rock pools with greater species richness (MacArthur, 1955; Elton, 1958; Odum, 1959; McNaughton, 1977; Tilman, 1996), while variability in the population abundances of individual species increases with richness (Gardner and Ashby, 1970; May, 1973; DeAngelis, 1975; Gilpin, 1975; Pimm, 1979). We further hypothesized that environmental variability (see Therriault and Kolasa, 2000) would alter the relationship between richness and community variability (Yachi and Loreau, 1999). It was expected that increasing environmental variability would increase the positive covariances between species (i.e. species will respond more similarly to environmental fluctuations as those fluctuations increase in magnitude). Therefore, richness-variability relationships should be stronger (i.e. show higher correlation) in less variable rock pools and weaker (i.e. show no or low correlation) in the more variable rock pools. Finally, if some populations are able to compensate for the decreasing abundance of disturbance prone populations, the relationship between richness and population variability should be stronger in the less variable rock pools.

METHODS

Study site

Two hundred and thirty dissolution rock pools with a maximum volume greater then 250 ml are present on the fossil reef within a radius of 25 m of mixed land and sea environment on the northern coast of Jamaica, West Indies, at the Discovery Bay Marine Laboratory (Kolasa et al., 1996, 1998). A few mangrove trees (*Rhizophora mangle*) grow between the rocks, and along with *Croton*, *Jacquinia*, and *Strumfia* bushes, are a major source of detritus in some rock pools. Forty-nine rock pools were randomly chosen (Kolasa et al., 1996) and monitored yearly in late December or early January for 8 years. The rock pools are small in size, ranging from 13-235 cm in width and length, and vary from 1-37 cm in depth (mean = 12.8 ± 8.3 SD). Volumes are highly diversified and range up to 115 liters with a mean of 12 ± 21 SD. On average the rock pools are located within 1 m of the nearest neighbor and none are separated by more than 5 m from the next nearest rock pool. Their elevation above sea level ranges from 1-235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Four rock pools are tidal (although tidal flooding is not daily) but most are maintained by atmospheric precipitation and, very occasionally, wave splash water.

Biotic Composition

Samples of fauna were collected on the same day as the physical measurements were taken (see below). Each sample consisted of 500 ml of water and sediments from a pool slightly stirred to dislodge organisms from its sides and bottom and to homogenize their distribution. Organisms were caught in a 63 μm net with a collecting container and immediately preserved in 50-70% ethanol. Overall, 392 samples have been analyzed from 49 rock pools over 8 dates. Additional information on pool dimensions, physical variables, overall variability, and their impact on species richness and composition have been reported previously (Therriault and Kolasa, 1999; Romanuk and Kolasa, 2001). The dominant species are a harpacticoid copepod, *Nitocra spinipes* (present in 70% of samples), a cyclopoid copepod, *Orthocyclops modestus* (70%), an ostracod *Candona* sp. (34%), a nematode species (31%), and a *Culex* mosquito (31%). Other common species include a daphnid, *Ceriodaphnia rigaudi*, and ostracods representing several fresh and brackish water families and genera. The majority of species are small benthic animals ranging from approximately 0.5-5 mm but some are plankton-like (*O. modestus, C. rigaudi*) and swim in the water column. The full list of the taxa (69 species) identified to date are: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1) and Insecta (18).

Environmental Variability

Physical measurements (dissolved oxygen, pH, salinity, temperature) for each pool were taken on numerous occasions between December 1989 and January 2000. Individual measurements of physical variables for all rock pools were completed in less than one hour. Environmental variability was evaluated in three ways. 1) We calculated a multivariate measure of diurnal variability using PCA factor scores. 2) We calculated diurnal variability in specific physicochemical properties separately. 3) We calculated annual variability in specific physicochemical properties separately over the eight sampling dates. Throughout all analyses, we used the mean SD to differentiate between low and high variability pools. While this division has the potential to introduce a level of subjectivity to the analyses, using the mean SD to separate low and high variability pools standardizes this decision rule across the analyses.

1) A multivariate score was calculated to represent several physical characteristics simultaneously (Therriault and Kolasa, 2000). We used scores of PCA 1 produced by a Principal Component Analysis performed on the variability in physicochemical variables (standard deviations SD, of pool temperature, salinity, dissolved oxygen, and pH) measured every two hours over a 24 h period. Therriault and Kolasa (2000) used a

similar index to investigate the effects of environmental variability on community evenness, population variability, and community structure. The index represents a gradient ranging from environmentally variable to environmentally constant rock pools (Therriault and Kolasa, 2000). The mean SD was used to differentiate between high and low variability pools, thus, rock pools scoring less than 3 (out of a possible 6) on the environmental variability index were considered low variability, while rock pools scoring more than 3 were considered high variability.

2) We calculated annual variability of specific physicochemical variables (pool temperature, salinity, dissolved oxygen, and pH) to determine whether any of the physicochemical variables was more important when considered independently than when combined into an index, such as the environmental variability index (see above). We used standard deviations of each physicochemical variable (over eight dates) to investigate the effects of specific variables in contributing to changes in richness-variability relationships. The mean SD was used to differentiate between low and high environmental variability pools.

3) We calculated diurnal variability of specific physicochemical variables (pool temperature, salinity, dissolved oxygen, and pH) measured every two hours over a 24 h period to determine whether there was a general trend between short-term measures of physicochemical variability and richness-variability relationships, and to compare the effects of diurnal as opposed to annual variability on richness-variability relationships. The mean SD was used to differentiate between low and high environmental variability pools.

Study design

Temporal variation, the variation in a time series of density (Tilman, 1999) was calculated for both communities (all species combined) and populations of individual species. Year-to-year variability in community abundance was calculated as the coefficient of variation, CV, (standard deviation/mean) of abundance (untransformed data) of all species combined that share a pool (total N per sample) across all years (8 sampling dates). Year-to-year variability in population variability was calculated on a species-by-species basis for each pool, using the abundance of a species in a pool over the 8 sampling dates. These calculations are analogous to Tilman's (1996) definitions of community and population stability. Smaller values of CV represent lower variability and higher values represent greater variability. Because CV standardizes for the mean, it provides an index of year-to-year variability in abundance independent of the mean (Tilman, 1996). While use of CV is burdened with its own bias as CV tends to increase at low N values in random data sets (Waltho and Kolasa, 1994) and thus requires somewhat different interpretations for species with low abundances, this should not affect our results because we restricted population analyses to the 36 most abundant species. Species richness (S) is the average richness of a rock pool across all sampling dates (N=8).

A homogeneity of slopes General Linear Model (GLM) was used to test for significant differences between pools with low and high variability. The independent variable was species richness, the dependent variable was community variability, and the categorical predictor was abiotic variability calculated using the Multivariate Index of Variability (low abiotic variability versus high abiotic variability pools). We also tested for differences between the group means after controlling for the covariate (abiotic variability).

Analyses were performed using linear regression (STATISTICA, ver. 5.5 or 6.0, from StatSoft). The level of significance was set at $\alpha=0.05$ for all analyses except for the homogeneity of slopes model where the level of significance was set at $\alpha=0.1$ as we assumed *a priori* a one-tailed distribution. Residuals were evaluated for normality and independence from the model. Despite the difficulties associated with showing unequivocal relationships in natural communities, our system is particularly suitable for analyzing richness-variability relationships because: 1) the pool communities are similar with respect to successional stage; 2) there are no significant richness-area effects (Therriault and Kolasa, 1999); 3) the small area of the study site implies that regional conditions and inputs are more homogenous than in other studies of natural systems; (4) species ranges extend far beyond the site boundaries thus there is no density decrease associated with range limits (see Brown, 1984); (5) organisms with short generation times allow us to avoid many of the confounding effects which plague studies on longer-lived species (e.g. Huston, 1997).

RESULTS

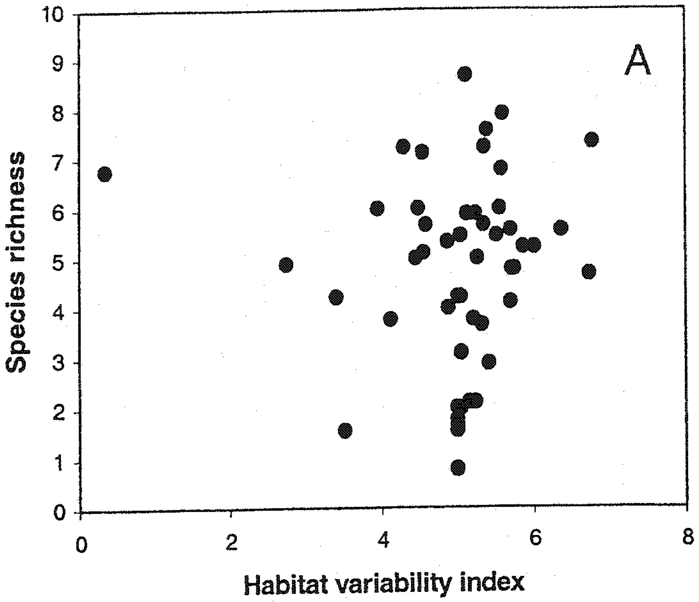
Environmental Variability

Mean species richness did not change along a gradient of environmental variability ($p = 0.849$; Fig. 1a). Diurnal environmental variability was unrelated to temporal variability of community abundance ($p = 0.132$; Fig. 1b). Variability in community abundance was not related to diurnal variability in temperature ($p = 0.292$), salinity ($p = 0.231$), oxygen ($p = 0.801$), or pH ($p = 0.924$). Similarly, mean species richness was not significantly related to variability in any specific physicochemical variables ($p>0.05$).

Richness and variability - general observations

When all rock pools were considered, our data supported the hypothesis that total community abundance would be less variable in rock pools with more species ($r = 0.428$, $p = 0.002$, $n = 49$; Fig. 2a) and that population variability in abundance would be unrelated to species richness ($p>0.5$; Fig. 2b).

Figure 1a-b. Relationship between the Multivariate Environmental Variability Index (see text) and a) average species richness, and b) variability of total community abundance (CV). There is no relationship between environmental variability and species richness or variability in total communal abundance.


A
Species richness
0
1
2
3
4
5
6
7
8
9
10
Habitat variability index
0
2
4
6
8

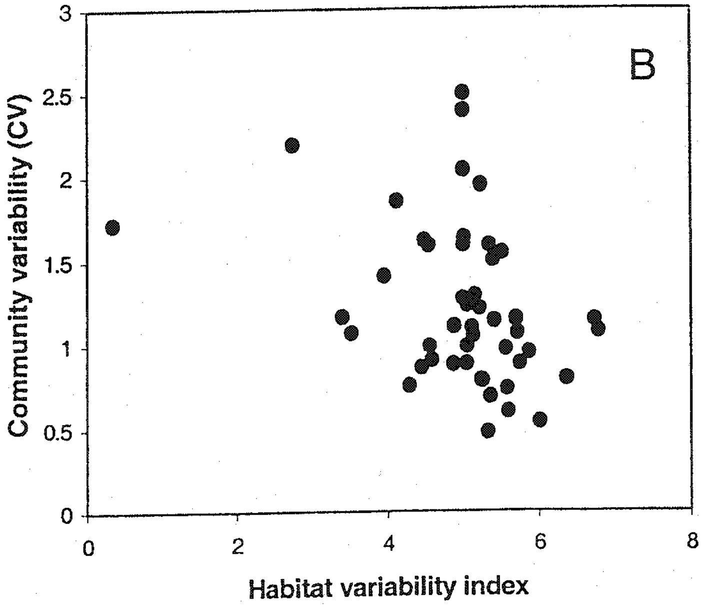
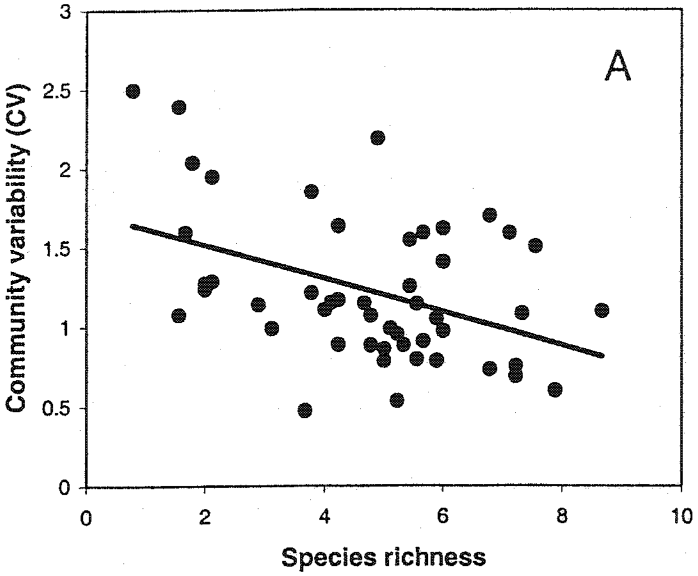
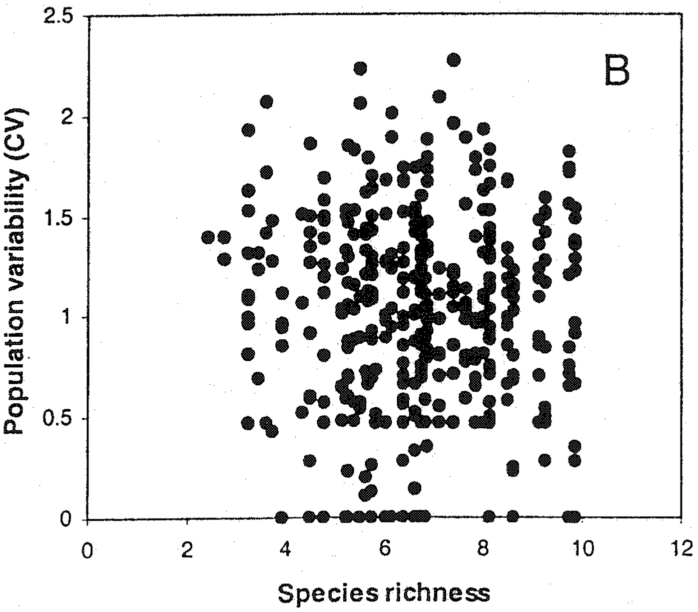

B
Community variability (CV)
0
0.5
1
1.5
2
2.5
3
Habitat variability index
0
2
4
6
8

Figure 2a-b. Relationship between richness and (a) variability of combined community abundance and (b) variability of individual populations in each pool. Variability is expressed as coefficients of variation (CV). Each point represents (a) one rock pool community or (b) one individual species in a rock pool.


A
Community variability (CV)
0
0.5
1
1.5
2
2.5
3
0
2
4
6
8
10
Species richness


B
Population variability (CV)
0
0.5
1
1.5
2
2.5
0
2
4
6
8
10
12
Species richness

Richness-variability relationships under different environmental regimes

Environmental variability, as measured by the multivariate index of diurnal variability (Therriault and Kolasa, 2000), altered the relationship between richness and communal variability in abundance (Table 1; Fig. 3a-b). In low variability rock pools, richness and variability in community abundance were related ($r = 0.455$, $p = 0.0501$, $n = 19$; Fig. 3a). There was no relationship between richness and community variability in the high environmental variability pools ($r = 0.311$, $p = 0.169$, $n = 20$; Fig. 3b). In contrast, population variability was unrelated to species richness in rock pools with either low or high environmental variability ($p = 0.863$ and 0.631, respectively; Fig. 4a-b).

A homogeneity of slopes General Linear Model (GLM) tested for significant differences in the relationship between species richness and community variability between high and low abiotic variability pools. There were no significant differences in slope between pools with low and high abiotic variability (Table 1); however, significant differences were identified in group means after abiotic variability had been controlled for using a one-tailed test for significance ($F_{1,45} = 3.53$, $p = 0.066$). The full model was highly significant (Adj $R^2 = 0.26$, $F_{3,45} = 6.622$, $p = 0.008$).

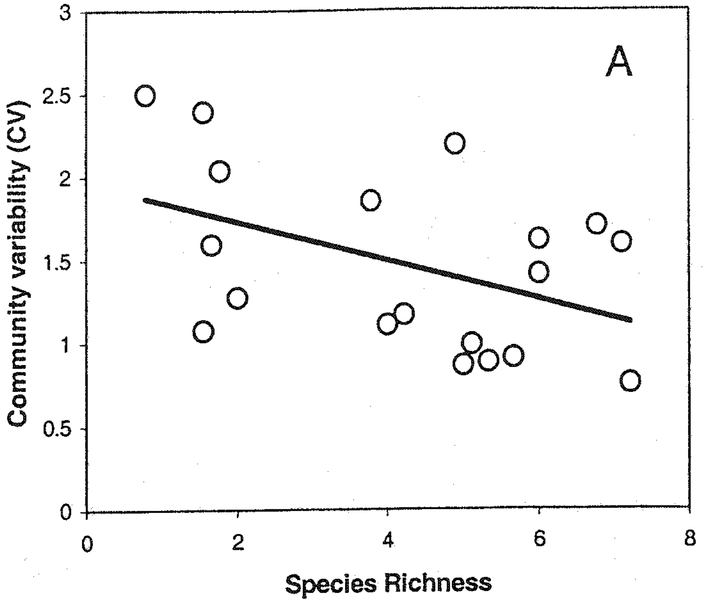
Variability in specific physicochemical variables altered the relationship between richness and community abundance (CV). Rock pools with low variability in temperature ($r = 0.543$, $p = 0.013$, $n = 20$; Fig. 5a), salinity ($r = 0.443$, $p = 0.0097$; Fig. 5c), pH ($r = 0.506$, $p = 0.009$, $n = 25$), and oxygen ($r = 0.458$, $p = 0.0083$, $n = 32$) exhibited a significant relationship between richness and variability in community abundance,

Table 1. Statistics of General Linear Model ANCOVA for the effect of abiotic variability (high versus low) on the relationship between species richness and community variability.

Effect	df	SS	MS	F	b
Intercept	1	17.950	17.950	***111.824	
Abiotic variability	1	0.567	0.567	*3.534	0.625
Species richness (S)	1	1.257	1.257	**7.830	-0.356
Abiotic variability*S	1	0.138	0.138	0.865	-0.309
Error	45	7.223	0.160		

Note: b represents the slope of the equation. * significant at $p < 0.1$, ** significant at $p < 0.01$, *** significant at $p < 0.001$.

Figure 3a-b. Multivariate Environmental Variability Index. Relationship between richness and variability of total communal abundance in (a) low variability rock pools, and (b) high variability rock pools. The regression line is shown for the statistically significant trend only.


A
Community variability (CV)
Species Richness
0
0.5
1
1.5
2
2.5
3
0
2
4
6
8

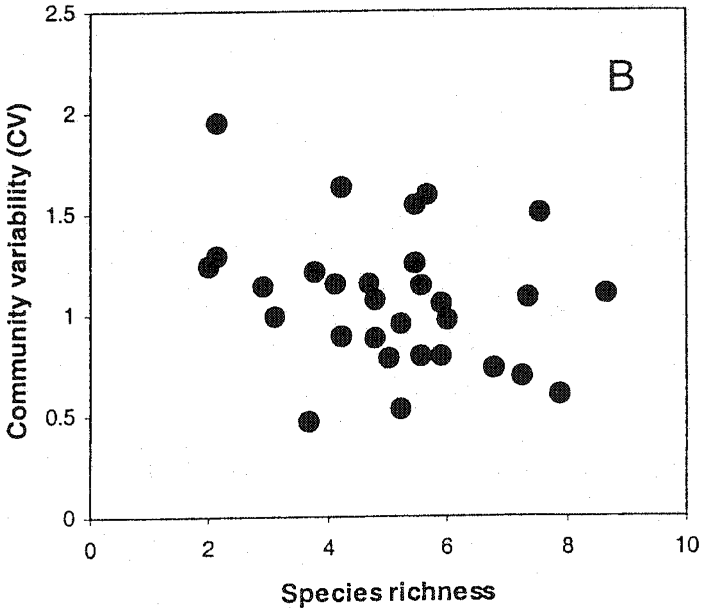
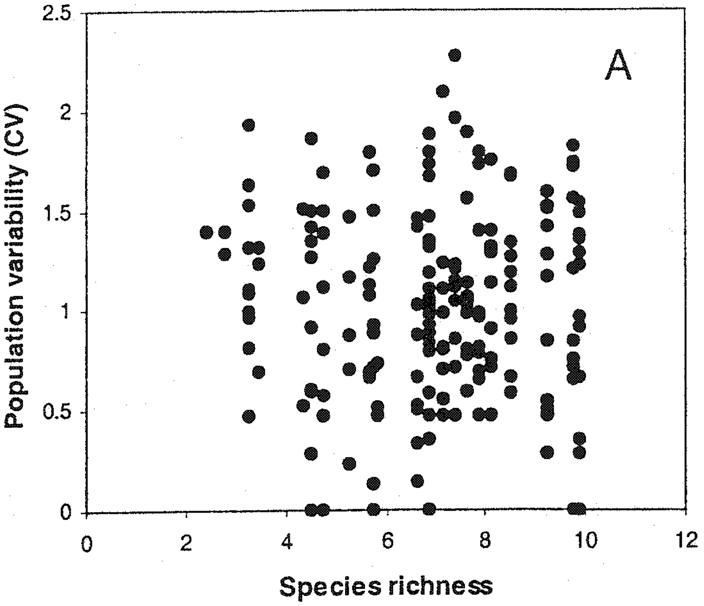

B
Community variability (CV)
Species richness
0
0.5
1
1.5
2
2.5
0
2
4
6
8
10

Figure 4a-b. Multivariate Environmental Variability Index. Relationship between richness and population variability in (a) low variability rock pools, and (b) high variability rock pools. Each point represents one individual species in a rock pool.


A
Population variability (CV)
0
0.5
1
1.5
2
2.5
0
2
4
6
8
10
12
Species richness

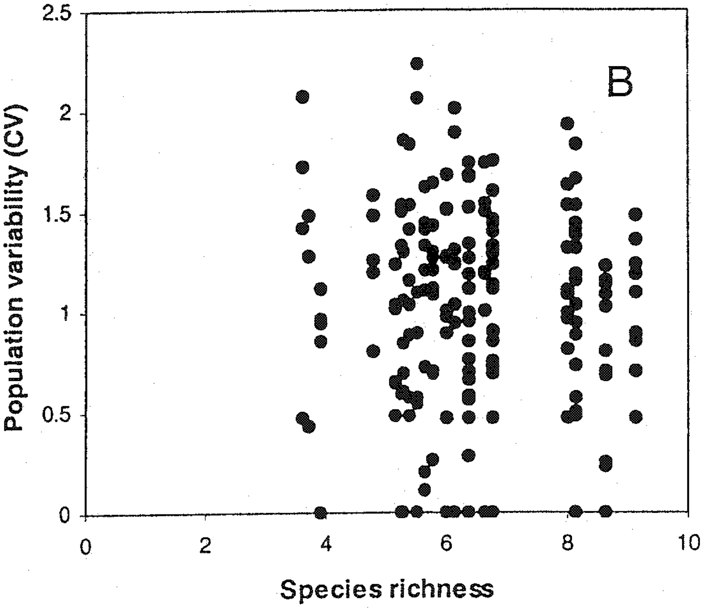
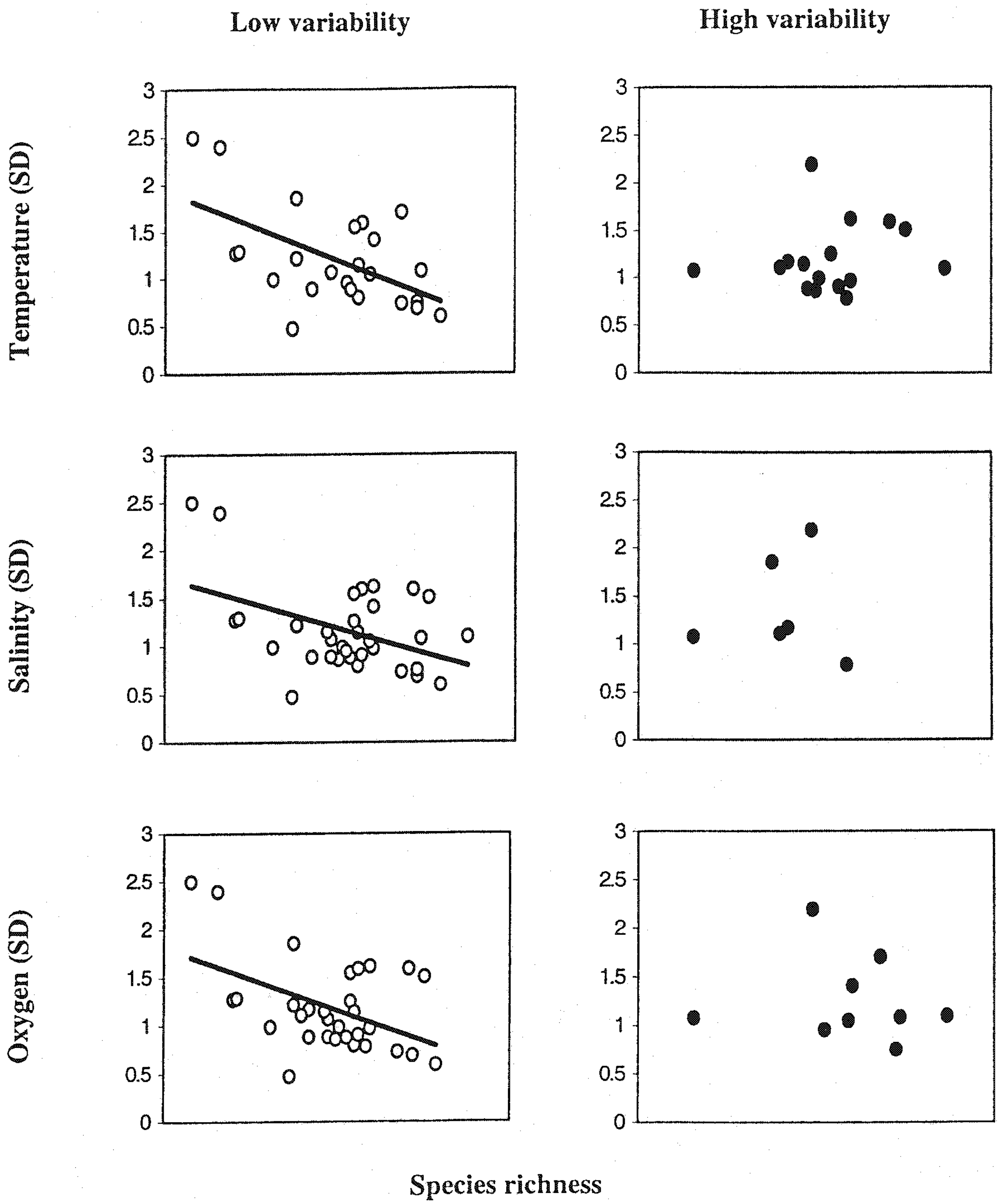

B
Population variability (CV)
0
0.5
1
1.5
2
2.5
0
2
4
6
8
10
Species richness

Figure 5a-d. Relationship between richness and variability of total community abundance in (a) rock pools with low variability in temperature, (b) rock pools with high variability in temperature, (c) low variability in salinity, and (d) high variability in salinity, (e) rock pools with low oxygen variability, (f) rock pools with high oxygen variability, (g) low pH variability, and (h) high pH variability. The regression line is shown for the statistically significant trend only.


Low variability
High variability
Temperature (SD)
Salinity (SD)
Oxygen (SD)
0
0.5
1
1.5
2
2.5
3
Species richness

while rock pools with high variability in temperature, salinity, pH, and oxygen did not (temperature $r = 0.263$, $p = 0.236$, $n = 22$, Fig. 5b; salinity $r = 0.288$, $p = 0.218$, $n = 20$, Fig. 5d; oxygen $r = 0.295$, $p = 0.127$, $n = 28$, Fig. 6b; pH $r = 0.284$, $p = 0.134$, $n = 29$, Fig. 6d).

DISCUSSION

When all rock pools are considered, the results support the hypothesis that community variability is negatively related to species richness. In contrast, population variability appears to be unrelated to species richness. This concurs with the majority of empirical and theoretical evidence that has shown community biomass to be stabilized by species richness (McNaughton, 1977; Tilman and Downing, 1994; Tilman, 1996; Naeem and Li, 1997; Yachi and Loreau, 1999; Lehman and Tilman, 2000; McGrady-Steed and Morin, 2000).

Evidence for the destabilizing effect of species richness on population variability (May, 1973; Pimm, 1979; Lehman and Tilman 2000) is less clear. McGrady-Steed and Morin (2000) found no difference in variability of the majority of populations along an experimental richness gradient. In contrast, Peterson (1975) found that species variability of benthic invertebrates was lower in more diverse (and less disturbed) sites. In contrast yet again, Tilman (1996) showed a decrease in population stability with increasing species richness. Thus, there exists a range of empirical results for the effects of richness on population variability, many of which are not consistent with theoretical predictions

(King and Pimm, 1983; Lehman and Tilman, 2000). Furthermore, environmental variability did not alter richness-population variability relationships. In all cases, population variability was unrelated to species richness. This suggests that either negative covariances between populations did not change as a result of environmental variability, or that richness-variability relationships are not a function of species richness *per se*, but of factors that determine or covary with species richness (Sankaran and McNaughton, 1999).

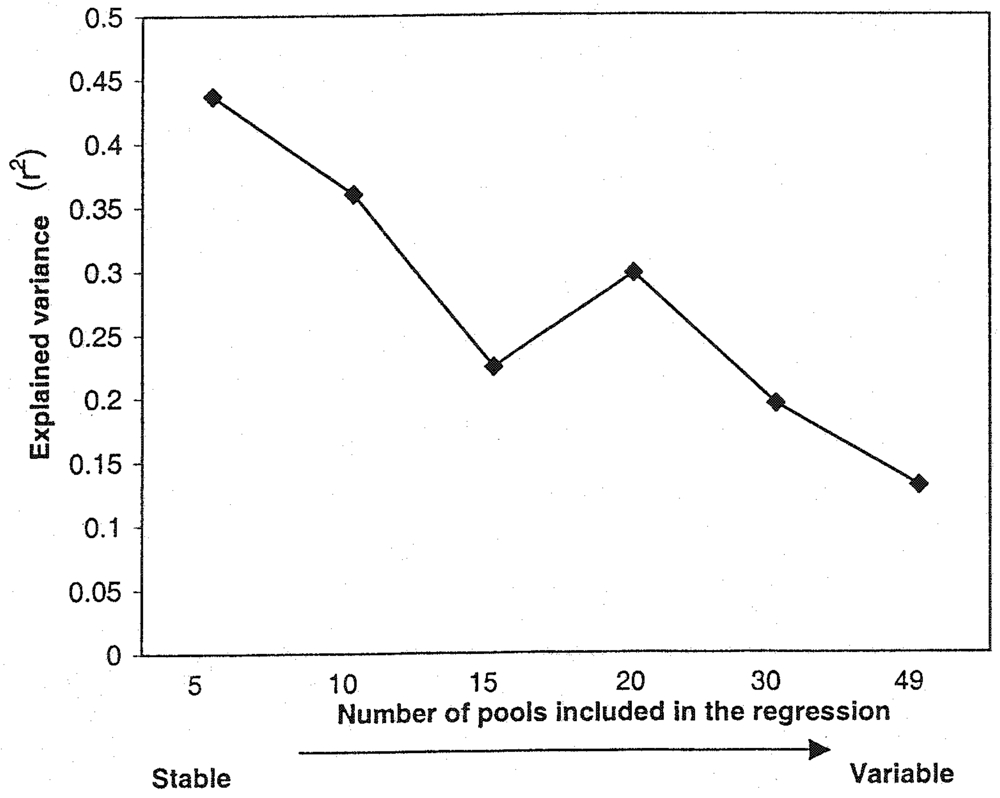
Community variability declined with increasing species richness when all rock pools were considered without a distinction between physically variable and stable ones. However, the relationship between community variability and species richness was not the same across rock pools along the gradient of environmental variability. Temporal variability of total community abundance was significantly related to species richness only in the low environmental variability rock pools. Whether the trend of variability decreasing with species richness in low environmental variability rock pools is due to species richness *per se* or other determinants (Sankaran and McNaughton, 1999) cannot be conclusively resolved using a simple correlation approach. However, the presence of a trend in the low environmental variability pools, when compared to the lack of a significant relationship in the high environmental variability pools, is intriguing. Ross et al. (1985) found that community variability was lower in rock pools with lower relative environmental variability. Peterson (1975) found that community variability was similar in both disturbed and undisturbed sites, but that species variability was lower in the more diverse, low disturbance sites. Tilman (1996) found strong richness-variability relationships in both drought and non-drought years. The range of results, while not entirely consistent, seems to give some support to the destabilizing effect of environmental variability, at least on the communal, aggregated measure of abundance.

Richness-variability relationships were also affected by variability in specific physicochemical variables. Variability in communal abundance is not related to richness in rock pools with high variability in temperature, salinity, pH, or oxygen. Temperature and salinity are both external variables that may force richness-variability relationships through decreasing the number of species in a pool. Species richness decreases with both increasing temperature and salinity in the rock pools (Therriault and Kolasa, 1999). Variability in temperature is also a sign of poorer conditions (higher frequency of desiccation) and has adverse direct effects on many organisms (Hutchinson, 1967). Species richness also declines with increasing salinity in the rock pools (Therriault and Kolasa, 1999). While many freshwater species are able to tolerate low levels of salinity, few are able to tolerate hypersaline conditions (Hutchinson, 1967). Variability in salinity has also been shown to increase year-to-year variability in species richness (Romanuk and Kolasa, personal observations).

In contrast to forcing by temperature and salinity, variability in oxygen and pH are largely due to biotic factors. Dissolved oxygen and pH are strongly correlated, i.e., >80%, and can be used as a surrogate measure of pool productivity (Therriault and Kolasa, 1999). Rock pools with low variability in oxygen and pH showed strong richness-variability relationships, while richness was unrelated to community variability in pools with high variability in oxygen and pH. High variability in pH and oxygen may act similarly to temperature and salinity, forcing species richness to decline due to harsher conditions.

It is important to note however, that variability in total communal abundance and species richness were unrelated to diurnal physicochemical variability in any of the specific variables we measured. This was confirmed by both the regressions presented earlier, and in additional multivariate analyses where we used temporal variability in community abundance as the dependent variable, and both 1) mean species richness and 2) variability in each physicochemical variable separately (temperature, salinity, pH, and oxygen) as independent variables. In all four regressions, mean species richness was the only variable significantly related to temporal variability in community abundance. This indicates that physicochemical variability may be affecting the relationships between species richness and community variability independent of the effects of physicochemical variability on species richness or community variability *per se*. When we added pools into the regression analysis according to their variability in specific physicochemical measures, we see that very stable pools show strong relationships between richness and variability. As we continue to add pools that are increasingly more variable, the explained variance decreases from an average of 44% explained variance in very stable pools, to 13% for all pools (Fig. 6). This analysis confirms that environmental variability modulates the relationship between richness and community variability in a systematic

Figure 6. Relationship between the mean explained variance (y-axis) in the relationships between species richness and community variability (CV) for all physicochemical variables and the number of pools included in the analysis (x-axis). Pools were added to the regression analysis in order of their variability for each physicochemical property, such that for $n = 5$, the r^2 shown refers to the average explained variance of the temperature, salinity, oxygen, and pH for the 5 most stable pools in each of these variables. As n increases, more variable pools are included in the analysis.


0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Explained variance (r^2)
5
10
15
20
30
49
Number of pools included in the regression
Stable
Variable

way, and is not overly sensitive to the cut-off used to separate low vs. high variability pools (in all cases the mean variability was used). It is important to note that neither variability in total communal abundance nor species richness are related to diurnal physicochemical variability.

Our results are consistent with the hypothesis that species richness begets stability at the community abundance level. This hypothesis however was not supported for environmentally variable pools (as measured by the multivariate index), for pools with high variability in temperature and salinity, or for rock pools with low yearly variability in productivity. In contrast, population variability of individual species was unrelated to richness across the range of situations. Whether these patterns are directly caused by environmental variability remains an open question. However the presence of richness-variability relationships in the less variable rock pools as opposed to its absence in the more variable rock pools suggests that environmental variability may play an important role in modulating richness-variability relationships.

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Chapter 4:

Diversity, stability, and disturbance: a test of the insurance hypothesis in natural aquatic rock pools

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Romanuk, T.N. and J. Kolasa. Diversity, stability, and disturbance: a test of the insurance hypothesis in natural aquatic rock pools. Acta Oceologica.

RATIONALE AND OBJECTIVES

In the preceding chapter I showed that while temporal variability in community density was negatively related to species richness, environmental variability modulated this relationship. To further explore the role of environmental conditions in modulating the relationship between species richness and community variability, I grouped the rock pools into either temporary or permanent pools according to their susceptibility to desiccation. I found that:

1. There was a strong negative relationship between species richness and temporal variability in temporary rock pools.
2. There was no relationship between species richness and temporal variability in permanent rock pools.
3. Species richness did not affect temporal variability through an overyielding effect (i.e. total community density was not higher in pools with more species).

These results provide support for the insurance hypothesis, which predicts that in fluctuating environments an increase in the number of species may buffer the community against changes in density by increasing the probability that some species will be disturbance-resistant and can compensate for declining abundance of disturbance-prone species.

ABSTRACT

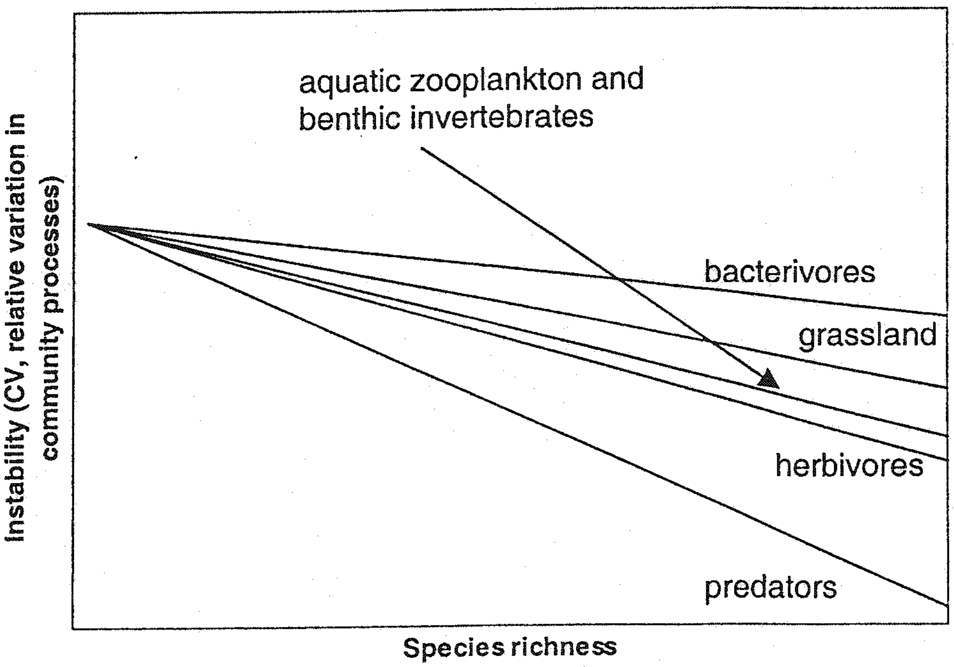
We tested the predictions of the insurance hypothesis in temporary and permanent aquatic invertebrate communities inhabiting supralittoral rock pools. The hypothesis posits that species richness decreases temporal variability (the buffer effect) and increases the temporal mean (the performance effect) of total community biomass. In permanent rock pools there was no buffer or performance enhancing effect of richness on abundance – refuting both predictions of the insurance hypothesis. The data from temporary pools were consistent with the buffer effect but not the performance enhancing effect. Our results provide empirical support for the insurance hypothesis, possibly due to a buffering effect of richness on community processes. However, data only support the insurance hypothesis in temporary rock pools.

Keywords: buffer effect, desiccation, invertebrates, rock pools, temporal variability

INTRODUCTION

The insurance hypothesis predicts that the presence of more species should increase the probability that some species will continue to function and expand their contribution when others fail as a result of the environmental changes (McNaughton, 1977; Petchey et al., 1999; Yachi and Loreau, 1999). A compensatory response of such species would result in greater stability of diverse communities in comparison to simpler communities with a restricted suite of functional roles. It has been suggested that the greater stability of diverse communities is a result of two insurance effects: (i) a buffering effect - which reduces temporal variation in ecosystem functioning, and (ii) a performance enhancing effect - which increases the temporal mean of ecosystem functioning (Yachi and Loreau, 1999), with functioning referring here to biomass production. The basic mechanism behind both the buffer and the performance effect is asynchronicity in the ways species respond to environmental fluctuations (Doak et al., 1998; Ives et al., 1999, 2000; Yachi and Loreau, 1999). In a system with many species, transient low productivity or abundance of some species does not necessarily affect total community abundance, as other species will increase in abundance in response to environmental fluctuations, resulting in a low temporal variability in total production and abundance (Ives et al., 1999, 2000; Yachi and Loreau, 1999). In order for the performance effect to express itself, in addition to asynchronicity, some species must perform better in each environmental condition. Such an adaptive mechanism would thus increase mean biomass. Yachi and Loreau (1999) suggest that any mechanism, even weak, that favors some species under certain environmental conditions by increasing their productivity would be sufficient to result in a performance enhancing effect as the community diversity increases (see Cottingham et al., 2001 for a recent review). Previously we have demonstrated that in rock pool communities richness appears to have a buffering effect on total communal abundance (aquatic microinvertebrates in Fig. 1; Romanuk and Kolasa, 2002). This concurs with the majority of experimental evidence to date from grasslands (Mellinger and McNaughton, 1975; McNaughton, 1977; Tilman and Downing, 1994; Tilman, 1996, 1999) and from laboratory microcosms (McGrady-Steed et al., 1997; Naeem and Li ,1997; McGrady-Steed and Morin, 2000). However, our previous results also support the Sankaran and McNaughton (1999) hypothesis that, in habitats subjected to disturbances characteristic of their natural environment, it may not be species richness *per se* that determines the relationship between diversity and stability but underlying determinants of diversity such as community type, disturbance type, and susceptibility to disturbance (Romanuk and Kolasa, 2002). Thus, while the general trend reported in the literature (Fig. 1) appears to conform to the expectation that greater richness reduces relative variation of combined community metrics such as biomass or abundance (i.e. a buffer effect), the range of the effect, the mode (buffering or performance enhancement), and habitat type (stable or disturbed) by which and where the reduction occurs have not been investigated under natural conditions. Here we test this relationship in an array of communities that share the same species pool but differ in the magnitude of disturbance, i.e., in permanent and temporary pool communities.

Figure 1. The effect of richness on variation of community metrics in various systems. Compiled from Tilman 1996 (grasslands), McGrady-Steed and Morin 2000 (bacterivores, herbivores, predators), Romanuk and Kolasa 2002 (aquatic microinvertebrates). High variation of community metrics or processes, labeled as INSTABILITY and measured by coefficients of variation, CV, declines with increases in species richness, S. As the original graphs represented data in different units and at different scales, in order to facilitate the comparison we have arbitrarily shifted their origins to the same point on the y-axis but retained their slopes thus the slopes represent a trend rather than a quantitative comparison of magnitude.


aquatic zooplankton and benthic invertebrates
bacterivores
grassland
herbivores
predators
Instability (CV, relative variation in community processes)
Species richness

METHODS

Study site

We tested the predictions of the insurance effect model in aquatic invertebrate rock pool communities that experience different disturbance (desiccation) frequencies in Blue Maze, a small cove near the grounds of the Discovery Bay Marine Laboratory, along the northern coast of Jamaica. The study site consists of a set of 49 coastal rock pools that are formed primarily by rain erosion of fossil reef (Kolasa et al., 1996, 1998; Schuh and Diesel, 1995). The pools range from 14 to 248 cm in length and 10 to 188 cm in width (mean length = 56 cm ± 35.0 SD and mean width = 32.9 cm ± SD 26.8), and vary from 1-37 cm in depth (mean = 12.8 cm ± 8.3 SD). On average the rock pools are located within 1m of the nearest neighbor and none is separated by more than 5m from the next nearest rock pool. Their elevation above sea level ranges from 1-235 cm (mean = 76.6 cm ± 80.1) at high tide, with the tide rarely exceeding 30 cm. Seven rock pools are tidal (although tidal flooding is not daily) but most are maintained by atmospheric precipitation and, very occasionally, wave splash water.

Biotic Composition

Samples of fauna were collected on the same day as the physical measurements. Each sample consisted of 500 ml of water and sediments from a pool slightly stirred to dislodge organisms from its sides and bottom and to homogenize their distribution.

Organisms were caught in a 63 μm net with a collecting container and immediately preserved in 50-70% ethanol. Overall, 343 samples have been analyzed from 49 pools over 8 dates. Additional information on pool dimensions, physical variables, overall variability, and their impact on species richness and composition have been reported previously (Kolasa et al., 1998; Therriault and Kolasa, 1999, 2000, 2002; Romanuk and Kolasa, 2001). Sixty-nine species have been identified and counted totaling 226,224 individuals from all samples. The majority of species are small benthic animals ranging from 60 μm -0.5 mm but some are plankton-like (*O. modestus, Ceriodaphnia sp.*) and swim in the water column. The full list of the taxa identified to date includes: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1) and Insecta (18). The pool communities experience high desiccation, especially through the summer months when most of the shallow pools may become completely dry (Therriault and Kolasa, 2002). Coupled with the short generation times of the organisms (between less than a week and three months) the annual samples constitute relatively independent events (i.e. the current community structure is only partially determined by the community state a year prior to the sampling due to partial reassembly from a species-pool of short-lived organisms and cumulative stochastic effects of environmental and biotic variability; Romanuk and Kolasa, unpublished manuscript).

Study design

Data on abiotic and biotic conditions in the rock pools were used to obtain the following metrics:

(a) Relative temporal variation in community abundance, that is, the variation in a time series of community abundances (Tilman, 1999). Temporal variability was calculated over 8 sampling dates (over 9 years) as the coefficient of variation, CV, (standard deviation/mean) of summed abundances (untransformed data). Smaller values of CV represent greater stability and higher values represent lower stability (sometimes referred to as instability).

(b) Mean values of physical parameters for each pool over the multiple measurements taken over eight two-week periods.

(c) Variation in observed values of physical parameters measured as standard deviations.

(d) Species richness evaluated as the mean number of species observed in a pool over the eight dates.

(e) Disturbance level – total number of times a pool dried after being filled, counted over a 10 year period. Because most visits were two weeks long, and there were some shorter, summer visits, the number of desiccation events actually refers to a cumulative period of about 25 weeks punctuated by 6-11.5 months of no-observation periods. Thus, this measure should be viewed as an index of susceptibility to desiccation rather than a direct record of disturbance.

The buffer effect was assessed by strength and direction of the relationship between average species richness over eight dates and the coefficient of variation of total community abundance for both permanent and temporary pool communities. The performance enhancing effect was investigated by regressing average abundance (log transformed) on average species richness.

A homogeneity of slopes General Linear Model (GLM) was used to test for significant differences between temporary and permanent pools. The independent variable was species richness, the dependent variable was community variability, and the categorical predictor was desiccation (temporary versus permanent pools). We also tested for differences between the group means after controlling for the covariate (desiccation).

It is possible that underlying determinants of diversity rather then diversity *per se* may cause diversity-stability relationships. Sankaran and McNaughton (1999) suggest that diversity will covary with factors that regulate the distribution and abundance of species, not an unreasonable proposition given that zero abundance is equivalent to absence of a species. In rock pools, environmental variables are related to varying degrees with both spatial and temporal variability in species richness and abundance (Therriault and Kolasa, 2000). Furthermore, these environmental factors influence the potential member species in a rock pool. For example, the best single predictor of average diversity in a rock pool is the total numbers of species that were found in that rock pool over all sampling dates (Romanuk and Kolasa, unpublished data).

To determine how much of the observed community stability in temporary pools was attributable to environmental characteristics rather than diversity itself, we used a backwards multiple stepwise regression analysis on community stability to separate effects of species richness from 1) morphometric features of the rock pools (pool length, pool width, pool volume, pool surface area, elevation, pool cavity depth), 2) abiotic variables (pH, temperature, salinity, oxygen, desiccation frequency), and 3) annual and diurnal variability in pH, salinity, oxygen. Analyses were performed using Statistica Version 5.5 (StatSoft Incorporated). Significance level was $\alpha = 0.05$.

RESULTS

Of the 49 pools, 31 were found dry on one or more dates and 18 were never found dry. These are called respectively, temporary and permanent pools. Species richness declined with desiccation frequency ($r^2 = 0.326$, $p > 0.0001$; Fig. 2a). Similarly, community stability was lower in pools with frequent disturbances ($r^2 = 0.225$, $p = 0.0005$; Fig. 2b). A buffering effect of diversity on variability in abundance was seen in the temporary pools ($r = -0.615$, $r^2 = 0.3785$, $p = 0.0002$; Fig. 3b) but not the permanent pools ($r = 0.115$, $r^2 = 0.013$, $p = 0.647$; Fig. 3a). There was no performance enhancing effect of diversity on density in either temporary or permanent pools ($p > 0.05$, Fig. 4a-b).

ANCOVA showed that there were significant differences between temporary and permanent pools (Table 1). The full model explained 26% of the variability in community variability (Adj $R^2 = 0.555$, $F_{3,45} = 6.664$, $p = 0.0008$). There were significant differences between the group means after covarying the effects of desiccation (F1,45 = 7.828, $p = 0.007$).

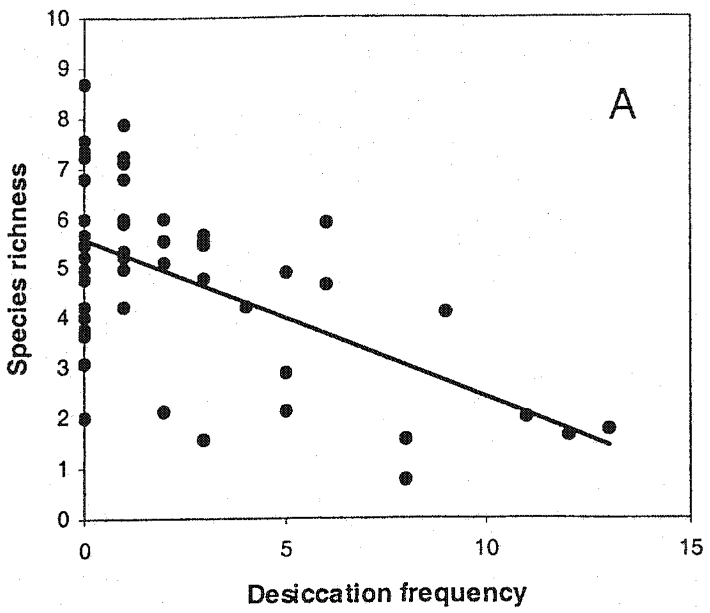
Species richness and morphometric variables (pool length, pool width, pool volume, pool surface area, elevation, pool cavity depth) cumulatively explained 38% of the observed variation in community stability in temporary pools (Adj $R^2 = 0.379$, $F_{1,29} = 17.695$, $p = 0.002$), but only species richness was retained as significant (beta = -0.62, $p = 0.0002$). Other determinants of diversity that may influence stability are abiotic features of the environment. To examine this we used mean values of pH, temperature, salinity, oxygen, desiccation frequency, and species richness as independent variables. The variables cumulatively explained 38% of the observed variation in community stability (Adj $R^2 = 0.357$, $F_{1,29} = 17.695$, $p = 0.0002$); however, once again only species richness was retained in the model (beta = -0.62, $p = 0.0002$). As a further check, instead of mean values we used both annual and diurnal variability in abiotic variables (derived variables) along with species richness as independent variables. Species richness and measures of yearly variability and diurnal variability explained 39% of the observed variation (Adj $R^2 = 0.394$, $F_{1,19} = 14.042$, $p = 0.001$), but only species richness was significant (beta = -0.651, $p = 0.001$). In all cases, species richness was the only variable that was retained in the regression models developed for temporary pools).

Table 1. Statistics of General Linear Model ANCOVA for the effect of desiccation (temporary versus permanent) on the relationship between species richness and community variability.

Effect	df	SS	MS	F	b
Intercept	1	11.615	11.615	***72.501	
Desiccation	1	1.254	1.254	**7.828	-1.034
Species richness (S)	1	0.683	0.683	*4.263	-0.279
Desiccation * S	1	1.256	1.256	**7.843	1.017
Error	45	7.209	0.160		

Note: b represents the slope of the equation. * significant at $p < 0.05$, ** significant at $p < 0.01$, *** significant at $p < 0.001$.

Figure 2a-b. Desiccation a) decreases average species richness and, b) increases variability in community abundance (CV).


A
Species richness
10
9
8
7
6
5
4
3
2
1
0
0
5
10
15
Desiccation frequency

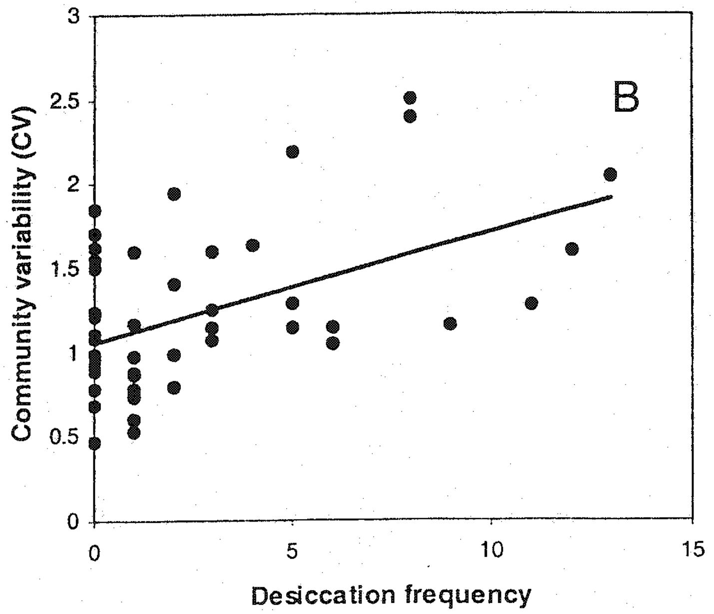
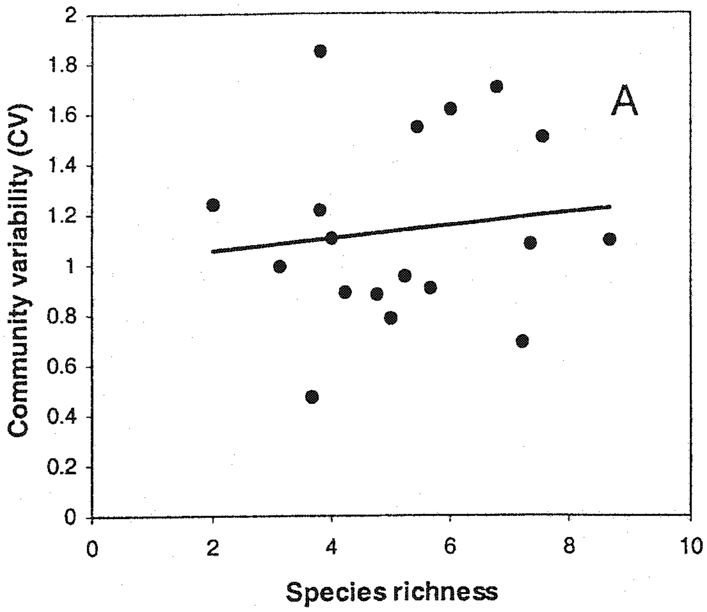

B
Community variability (CV)
3
2.5
2
1.5
1
0.5
0
0
5
10
15
Desiccation frequency

Figure 3a-b. Buffer effect. Variability in community abundance (CV) is a) unrelated to species richness in permanent pools, and b) negatively related to species richness in temporary pools.


A
Community variability (CV)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Species richness
0
2
4
6
8
10

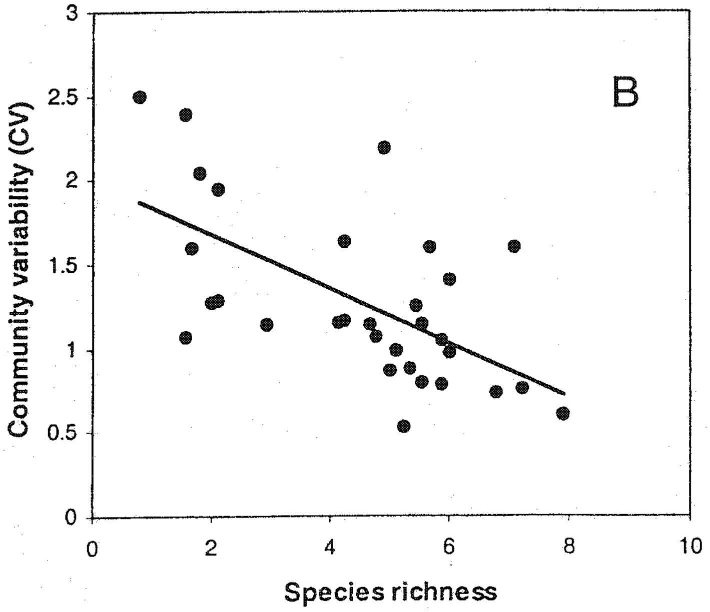
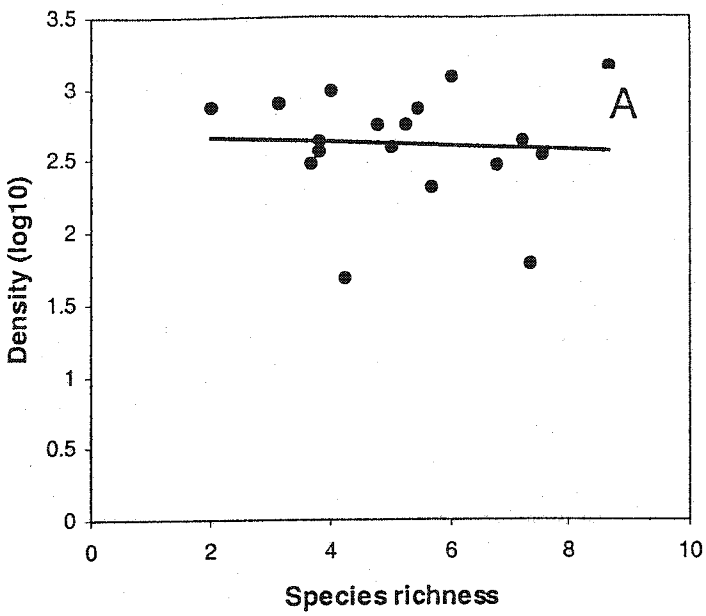
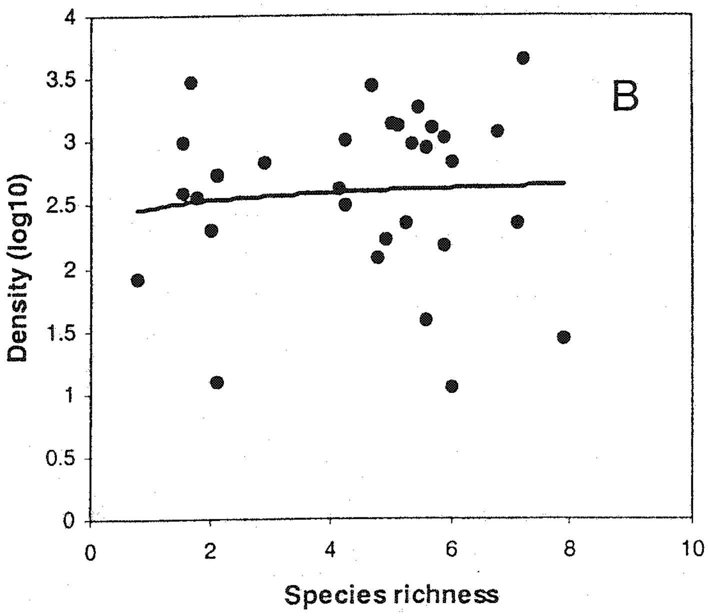

B
Community variability (CV)
0
0.5
1
1.5
2
2.5
3
Species richness
0
2
4
6
8
10

Figure 4a-b. Performance effect. Abundance and species richness are unrelated in both a) permanent, and b) temporary rock pools.


A
Density (log10)
3.5
3
2.5
2
1.5
1
0.5
0
0
2
4
6
8
10
Species richness


B
Density (log10)
4
3.5
3
2.5
2
1.5
1
0.5
0
0
2
4
6
8
10
Species richness

DISCUSSION

Support of Insurance Hypothesis

The insurance hypothesis predicts that in diverse communities total abundance will have a lower temporal variance (buffer effect) and a higher temporal mean (performance effect) than in species-poor communities. Neither of these predictions was supported for permanent, physically less variable pools (Fig. 3a, Fig. 4a). Data from the temporary, physically more variable pools support the buffering effect (Fig. 3b) but not the performance effect (Fig. 4b; as expressed by no change in the mean abundance of the whole community with increasing richness). The failure to identify a strong performance enhancing effect of diversity in rock pools was unexpected. However, Yachi and Loreau (1999) suggest that the performance enhancing effect is more likely to be found in communities governed by strong competition (i.e. resource competition in grasslands), which allows other communities not to conform to this expectation.

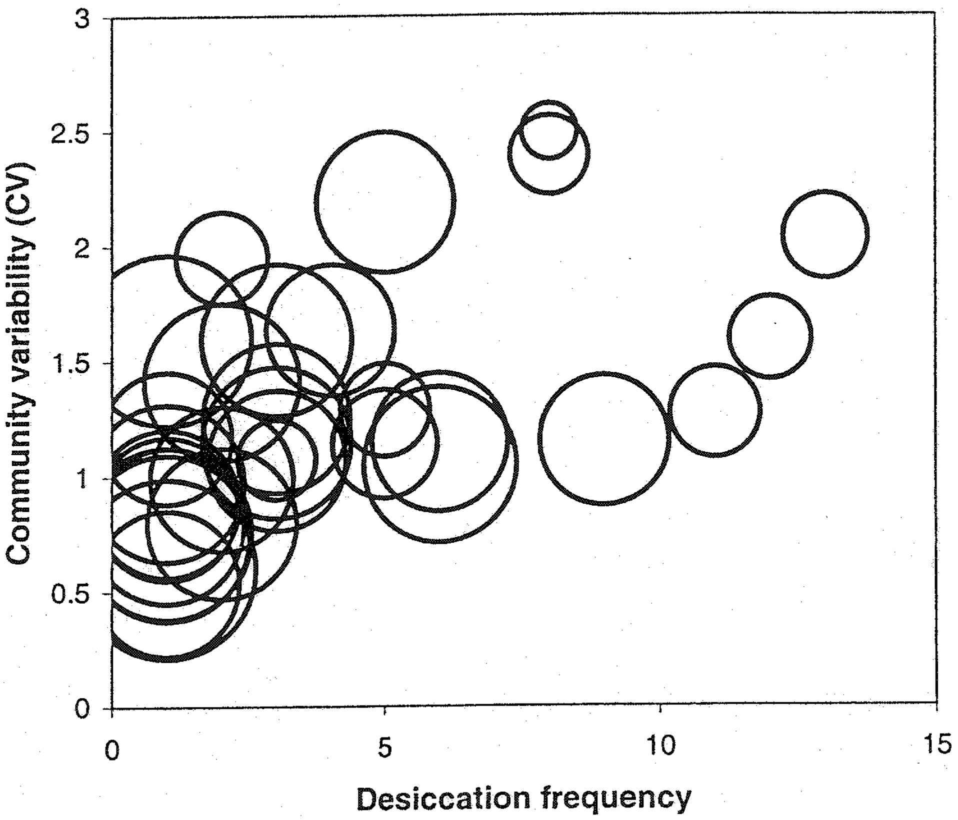
The relationship between diversity and temporal variability in abundance in the frequently disturbed temporary pools was unexpected. Desiccation in supralittoral pools is a major disturbance removing all living faunal biomass and/or forcing some species into diapause (Williams, 1987). Menge and Sutherland (1976) have argued that in communities where distribution and abundance patterns are directly related to catastrophic environmental episodes, biological interactions between species are likely to be of lower intensities and thus these habitats can be considered physically controlled. Furthermore, Li and Charnov (2001) proposed that in communities close to equilibrium, i.e. undisturbed communities, S determines the reduction of CV. Previously, Romanuk and Kolasa (2002) showed that richness-variability relationships were stronger in rock pools with lower variability in salinity and temperature. Based on these suggestions, we predicted that temporary pool communities should be regulated primarily by physical variables (and show either no buffering effect of diversity on stability or one that was explained by underlying determinants of species richness). By contrast, the permanent pool communities should allow more biotic controls of their structure and thus show a link between diversity and stability. Thus, in the context of the stability question, it might be expected that variability in community abundance in temporary pools would be regulated by abiotic variability or disturbance frequency, while permanent pools may show evidence of relationship between diversity and community stability. Our counterintuitive result may tentatively be explained by both the general community dynamics and specific adaptations of community members.

First, in permanent pools, communities and their component species are more stable and thus the relative absence of change makes the expression and importance of compensatory effects less relevant. By contrast, communities in temporary pools are more variable. Here, the differential performance of species is more likely to contribute to smoothing out of the communal variability whenever one or more species (higher S) share similar functional attributes. This effect is more clearly illustrated when all three variables, CV, desiccation frequency, and richness, are plotted jointly (Fig. 5). Species richness is greater in pools with a lower frequency of disturbance (the larger circles), and variability in community abundance is lower in pools with less frequent desiccation events.

Alternatively, special adaptations to temporary habitats may contribute to reduced variability of communal density. Desiccation in tropical rock pools may be analogous to fire disturbances in forest and grassland ecosystems. Fires play an important role in the persistence of these ecosystems by, for example, breaking seed dormancy. Similarly, the species that inhabit temporary tropical rock pools are well adapted to desiccation and exhibit physiological (diapause, anhydrobiosis) or behavioral strategies (active dispersal) that enable rapid faunal emergence when water fills the pool (Williams, 1987).

To summarize, the predictions of the insurance hypothesis (Yachi and Loreau, 1999), that diversity provides both a buffering and a performance enhancing effect are partially supported from empirical data from rock pool communities that experience natural disturbance events. While the data from temporary pools are consistent with the buffering effect, they are not consistent with the performance enhancing effect. Data from

Figure 5. Desiccation frequency is positively related to variability in community abundance. Circle size is proportional to species richness. As desiccation frequency increases, variability increases and species richness decreases.


3
2.5
2
1.5
1
0.5
0
0
5
10
15
Community variability (CV)
Desiccation frequency

the permanent pools do not support either predictions of the insurance hypothesis. Disturbance appears to be the key in the expression of the buffering effect in rock pools. Temporal variability of communal abundances in stable environments, i.e. permanent pools, is regulated primarily by factors other than diversity. In temporary pools, the retention of species richness as the only significant variable in backward multiple regressions using abiotic conditions, morphometric variables, and variability in abiotic conditions, suggests that diversity alone is the most likely candidate for contributing to constancy of communal abundance in time.

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Chapter 5:

Lower-level noise masks a global relationship between species richness and population variability

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Romanuk, T.N. and J. Kolasa. Lower-level noise masks a global relationship between species richness and population variability. Roy. Acad. Sci. Proc B.

RATIONALE AND OBJECTIVES

In Chapter 2 I showed that there is no relationship between species richness and population variability. However, if the relationship between species richness and community variability arises from a biological mechanism, then species richness must affect population densities. I hypothesized that the lack of a relationship between species richness and population variability may have resulted from the presence of extensive noise in local processes due to environmental conditions and local interactions, and that by removing this noise it may be possible to detect a relationship between species richness and population variability. I found that:

1. When noise arising from local processes was removed, species richness explained 16% of the variability in temporal variability of population densities.

This suggests that populations do respond to species richness. That populations may be stabilized be increasing richness had been predicted theoretically, but prior to this study has not been demonstrated empirically. It also suggests an alternative mechanism for why species richness reduces the variability of total community densities. If populations are less variable in richer environments, then this may reduce total community variability.

ABSTRACT

Ecological theory predicts that species richness should impact population variability. In contrast, empirical evidence suggests no or only a weak positive relationship between richness and population variability. We investigated the hypothesis that the obscuring noise of local processes, such as differences in local environmental conditions and biotic interactions, may mask the effects of richness on population variability. Using long-term data on invertebrate populations in rock pools, we considered richness-population variability relationships using three analytic resolutions in which data for the two key variables, richness and population variability, were progressively averaged for each population. The resolution most useful in making predictions about the effect of richness on population variability removed the most noise in population responses arising from local processes. Our results show that populations are less variable in species-rich environments, a finding that reiterates the importance of species richness not only for aggregate properties such as biomass stability, but also for individual species abundances. Comparing results at different resolutions also provides a methodology to identify relevant detail in richness-population variability relationships.

Keywords: environmental noise, population variability, stability, rock pools

INTRODUCTION

Species richness appears to affect variability in community abundance or biomass differently than population variability (May, 1973; Peterson, 1975; Tilman, 1996; Hughes and Roughgarden, 1998; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002). For communities, greater richness reduces temporal variability (reviews, McCann, 2000; Cottingham et al., 2001; Loreau et al., 2001) through biological and statistical processes including overyielding (Tilman, 1999), complementarity (Hooper, 1998; Tilman, 1999; Norberg, 2000; Cardinale et al., 2002), insurance effects (Yachi and Loreau, 1999; Petchey et al., 1999), weak interaction effects (McCann et al., 1998), statistical averaging (Doak et al., 1998), mean-variance relationships (Cottingham et al., 2001), or sampling effects (Huston, 1997). For populations, the effect of richness on variability in abundance or biomass is unclear (McCann, 2000; Cottingham et al., 2001). Theoretical predictions are idiosyncratic, with some models predicting that richness can increase (May, 1973; Lehman and Tilman, 2000), decrease (Ives et al., 1999, 2000; Li and Charnov, 2001) or have no effect on population variability (Tilman, 1999) depending on model construction.

May (1973) showed that increasing the strength and number of species interactions results in increasing population variability. Extending May's model of logistic growth, Tilman (1999) showed that for a single population that experiences random variation in its environment, its variance scales linearly with mean abundance, i.e., the scaling coefficient $z = 1$ (Tilman, 1999). When the average scaling coefficient for all populations in a community is $z < 2$, population variability should increase with increasing species richness. If $z = 2$, species richness will have no impact on population variability. If $z > 2$ population variability should decrease as species richness increases. Populations in natural communities are expected to have scaling coefficients between 1 and 2 (Murdoch and Stewart-Oaten, 1989), suggesting that if all else remains equal, populations should become more variable as richness increases.

Species richness has also been predicted to decrease population variability. Ives et al. (1999) show that population variance in biomass may either increase or decrease with strength of competition among species, α, and the number of species, S. Eigenvalues of the Jacobian matrix, λ_k, which measure partial correlation among species, increase with α and decrease with S. Therefore, when $\lambda_k > 0$, increasing α or decreasing S increases λ_k^2, increasing population variances. When $\lambda_k < 0$, increasing α or decreasing S initially decreases λ_k^2 but then increases λ_k^2 if λ_k becomes positive. Thus, decreasing S may initially stabilize population variances, but will eventually lead to increasing population variability (Ives et al., 1999).

In contrast to these theoretical predictions, empirical studies show non-existent or only very weak effects of richness on population variability (Tilman 1996, McGrady-Steed and Morin, 2000; Wardle et al., 1999). The only experiment detecting a significant relationship between richness and population variability was Tilman's who found that richness destabilized population abundances (Tilman, 1996). However, only 2% of the variance in population variability was explained by richness. McGrady-Steed and Morin (2000) found no relationship between richness and protist population variability in laboratory microcosms, and Romanuk and Kolasa (2002) showed that population variability was unaffected by richness in natural rock pool communities.

Despite this lack of empirical support, ecologists expect populations to respond to species richness. This arises from a number of assumptions. First, if communities are less variable in richer environments due to biological reasons, this must involve responses (either positive or negative) of populations (see Tilman, 1996; Ives et al., 1999). That communities are less variable in richer environments has received considerable support (Tilman, 1996; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002), suggesting that community richness may be linked to variability at the population level. For example, Ives et al. (1999) showed that the variance in total community biomass depends only on how species respond to environmental fluctuations. Interspecific competition and species number have little influence on community-level variances directly (Ives et al., 1999). Second, evidence is accumulating for species complementarity (Hooper, 1998; Tilman, 1999; Norberg, 2000; Cardinale et al., 2002). Complementarity, an increase in abundance resulting from increases in richness, is composed of two distinct mechanisms: niche differentiation, the increasingly specialized use of resources as richness increases, and facilitation, the direct or indirect positive effects of adding one species on the productivity of others (McGrady-Steed and Morin, 2000; Loreau and Hector, 2001; Cardinale et al., 2002). If adding species facilitates higher population densities, either through niche differentiation or facilitation, populations are less likely to become locally extinct due to fluctuations at low densities (Lande, 1993).

Four possible population responses to increasing richness are: i) richness could increase population variability (Tilman, 1996, 1999), ii) richness could decrease population variability, a response which has yet to be shown empirically, but which has been predicted theoretically (Ives et al., 1999, 2000; Li and Charnov, 2001), iii) richness could have idiosyncratic effects, altering population variability differently depending on specific community attributes (Lawton, 1994), iv) richness could have no effect on population variability (McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002).

The paucity of data detecting population responses to richness suggests either the latter possibility or a methodological failure to detect a relationship. Population variability largely reflects interspecific and intraspecific interactions (Tilman et al., 1997) and variation in the physical environment including resources (Loreau, 1998). These "local" processes strongly vary among sites, resulting in extensive scatter (noise) in population variability values for any given S value (Tilman, 1996; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002; see also Tilman et al., 1997; Loreau, 1998). This noise might mask a relationship between richness and population variability. We examined whether noise could account for an insignificant impact of richness on population variability (Romanuk and Kolasa, 2002) using data from a system of tropical rock pools inhabited by zooplankton and benthic invertebrates. To accomplish this we tested the relationship between richness and population variability using three alternative resolutions of data. This method removed increasingly more noise in population responses to increasing richness and allowed us to determine the level of resolution most useful in making predictions about the effect of richness on population variability.

We conducted our study in the supratidal zone near the Discovery Bay Marine Laboratory (18°28′ N/ 77° 25′ W) on the north coast of Jamaica (Schuh and Diesel, 1995; Kolasa et al., 1996, 1998; Therriault and Kolasa, 1999, 2000, 2002; Romanuk and Kolasa, 2001, 2002). The study site covered an area 50m in diameter of mixed land and sea habitat. A few scattered mangrove trees (*Rhizophora mangle*) grew between the rocks and were a major source of detritus in some rock pools. Forty-nine pools were randomly chosen (Kolasa et al., 1996) and sampled in late December or early January in 1989, 1990, 1991, 1992, 1993, 1997, 1998, and in June 1997. Pools ranged from 14 to 248 cm in length (mean = 56 cm ± 35.0 SD), 10 to 188 cm in width (mean = 32.9 cm ± 26.8 SD), and in depth from 1-37 cm (mean = 12.8 cm ± 8.3 SD). Elevation above sea level ranged from 1-235 cm (mean = 76.6 cm ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Seven pools were tidal (although tidal flooding was not daily). The remaining 42 pools were maintained by rainwater and, very occasionally, wave splash or storm water.

Ecology and biota of tropical rock pools

The pool communities consisted of aquatic meio- and micro-invertebrates. The dominant species were a harpacticoid copepod *Nitocra spinipes* Boeck (present in 70% of samples), a cyclopoid copepod *Orthocyclops modestus* Herrick (70%), an ostracod *Candona* sp. (34%), a nematode species (31%), and a *Culex* mosquito (31%). Other common species included a cladoceran, *Ceriodaphnia sp.*, and several fresh and brackish water ostracods. Most species were benthic animals ranging from 0.6mm - 5 mm but some were plankton-like (i.e. *O. modestus*). The full list of taxa included: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda larvae and various shrimps (4), Amphipoda (1), Isopoda (1), and Insecta (18). Apart from the 69 species that were included in our primary data set, some other animals were found as transient visitors, including gastropods (Littorinidae and Neritidae), hermit crabs, and the brachyuran crabs *Pachygrapsus* sp. (Schuh and Diesel, 1995).

There are no pronounced species-area effects on abundance or species richness. Pool volume was unrelated to both mean richness ($r^2 = 0.001$, $p = 0.819$, $n = 365$) and mean community density ($r^2 = 0.037$, $p = 0.194$, $n = 365$). Seasonal differences in richness and abundance were low due to the relatively constant annual temperature (Romanuk and Kolasa, Chapter 2) and accounted for < 2% of the variability in density and none of the variability in species richness (Romanuk and Kolasa, Chapter 2).

Pool communities experienced high colonization and desiccation. Following desiccation and refilling, fauna was rapidly re-established. A range of 0.4-17.6 copepods ml^{-1} was counted in the detritus layer 24h after rain, although their source was not determined (Schuh and Diesel, 1995). The system-wide mean species richness was 5.73 ± 2.69 SD per pool, with an abundance of 1606 ± 2964 SD; ranging from zero to > 50,000 individuals per liter. In colonization experiments involving 20 natural pools with no initial *in situ* sources of individuals, comparable mean species richness was attained within 6 months or earlier. Furthermore, 27 artificial pools exposed only to colonization accumulated 13 species after only 17 days (unpublished data), indicating that dispersal could completely reconstitute the fauna within 12-month long sampling intervals. The pool communities dry out frequently (Therriault and Kolasa, 2002). Of the 49 pools, 31 were found dry on one or more dates and 18 have never been found dry. On any one sampling date 7% of pools are without water.

METHODS

Sampling

Each pool sample consisted of 500 ml of water and sediments. Water was thoroughly stirred to dislodge organisms from pool sides and bottom to ensure a homogenous sample. Next, a variety of locations (water surface, pool bottom, pool sides, water column) were sampled using a 100 ml dip container. Organisms were caught in a 63 μm net with a collecting container and immediately preserved in 50% ethanol. This collection technique did not retain protozoans or smaller micrometazoans (e.g. copepod nauplii). Overall, 392 samples were collected from 49 pools over 8 censuses, with 365 containing organisms. Sixty-nine species were identified and counted totaling > 300,000 individuals from all samples.

Data Analysis

We applied three alternative analyses that successively removed more noise arising from local processes. The "high noise" analysis preserved variance arising from local process and is analogous to the calculation of species or population variability presented in Tilman (1996), McGrady-Steed and Morin (2000), and Romanuk and Kolasa (2002). The "intermediate noise" analysis reduced variance in richness for each population while preserving the range of population variability responses at each richness value. The "low noise" analysis reduced both richness and population variance.

Two values of species richness were used to relate species richness to population variability. For individual pools, species richness was calculated as the mean number of species over all census dates for each pool in which a species occurred (S_{local}).

$$Slocal = \sum S / D \qquad (1)$$

where, S_{local} is the local richness of a pool, S is richness observed on a single date, and D is the number of census dates. For example, the harpacticoid copepod *Nitocra spinipes* occurred in 46 out of 49 rock pools. Species richness was then averaged for each rock pool over the eight census dates to obtain 46 S_{local} values of S for *N. spinipes*. S_{local} values were obtained for each species included in the analysis (n = 28).

In contrast, regional richness for a species was calculated as the mean number of species found in each pool across all dates where a species of interest occurred (S_{region}).

$$Sregion = \sum S_i / k \qquad (2)$$

where S_{region} is the mean of richness values experienced by local populations of a species, S_i is the richness of a pool when the population was present in that pool, and k is the number of pools a populations of a given species occurred in. For example, *N. spinipes* occurred in 223 of 365 samples, cumulatively over the eight dates. Species richness was then averaged for the 223 instances to obtain the regional richness, S_{region} for *N. spinipes.* S_{region} values were obtained for each species included in the analysis (n = 28). A species was excluded from the analysis if it was present on less than two sampling dates, i.e. coefficient of variation could not be obtained.

Population variability of a species was calculated as the coefficient of variation (CV, standard deviation/mean) of a population density in each pool (CV_{local}), or of a population density summed over all pools (CV_{region}). Smaller values of CV indicate a population whose density varies less among sampling dates. Local population variability was determined for each species in each pool as:

$$CVlocal = Stdv(n_k)/[(\sum_{k=1}^{D} n_k)/D] \qquad (3)$$

where CV_{local} is the coefficient of variation in population abundance of species, n_k is a population size on date k, D is the number of sampling dates ($D = 8$). Regional population variability was determined for each species across all pools as:

$$CVregion = stdv(\sum N_k)/[\sum N_k)/D] \qquad (4)$$

where CV_{region} is the coefficient of variation in population abundances summed over all pools, N_k is abundance of that species across all pools on one date, D is the number of sampling dates (D=8). Preliminary data exploration suggested that all three analyses conformed to a 1st order linear model allowing regression analysis where: i) High noise $S_{local} = aCV_{local} + b$, ii) Intermediate noise, $S_{region} = aCV_{local} + b$, and iii) Low noise, $S_{region} = aCV_{region} + b$.

RESULTS

The regression analysis yielding the best resolution removed the most noise arising from local processes. S_{region} was negatively related to CV_{region}, with 16% of the variance explained ($p = 0.032$, $n = 28$; Fig 1, (e) solid line). Although S_{region} was also negatively related to CV_{local}, it explained only 5% of the variance ($p = 0.00001$, $n = 390$, Fig 2a). In contrast, no relationship was detected between S_{local} and CV_{local} ($p = 0.715$, $n = 390$, Fig 2b) in spite of the high power of the test. Because abundant species vary less in relative terms (Waltho and Kolasa, 1994), we considered that such species might respond differently to S_{region} than rare species. When populations were added into the regression in groups of high to low density, variability of populations with the highest density (1-5) was strongly negatively related to S_{region} ($r^2 = 0.953$, $p = 0.004$, $n = 5$; Fig 1, (a) dotted line). As groups of populations with lower density were added into the regression (Fig 1, lines b-e), the explained variance decreased from 58% (rank 1-10) to 16% (rank 1-28). Interestingly, when populations were added into the analysis individually, species

Figure 1. Low noise model. Population variability (*CV_{region}*) is negatively correlated with average richness, *S_{region}*. Each dot represents one population. Regression lines are for populations according to rank order in density. a) 1-5 ($r^2 = 0.953$, $p = 0.004$, $n = 5$), b) 1-10 ($r^2 = 0.58$, $p = 0.01$, $n = 10$), c) 1-15 ($r^2 = 0.219$, $p = 0.078$, $n = 15$), d) 1-20 ($r^2 = 0.157$, $p = 0.083$, $n = 20$), e) 1-28 ($r^2 = 0.164$, $p = 0.032$, $n = 28$).

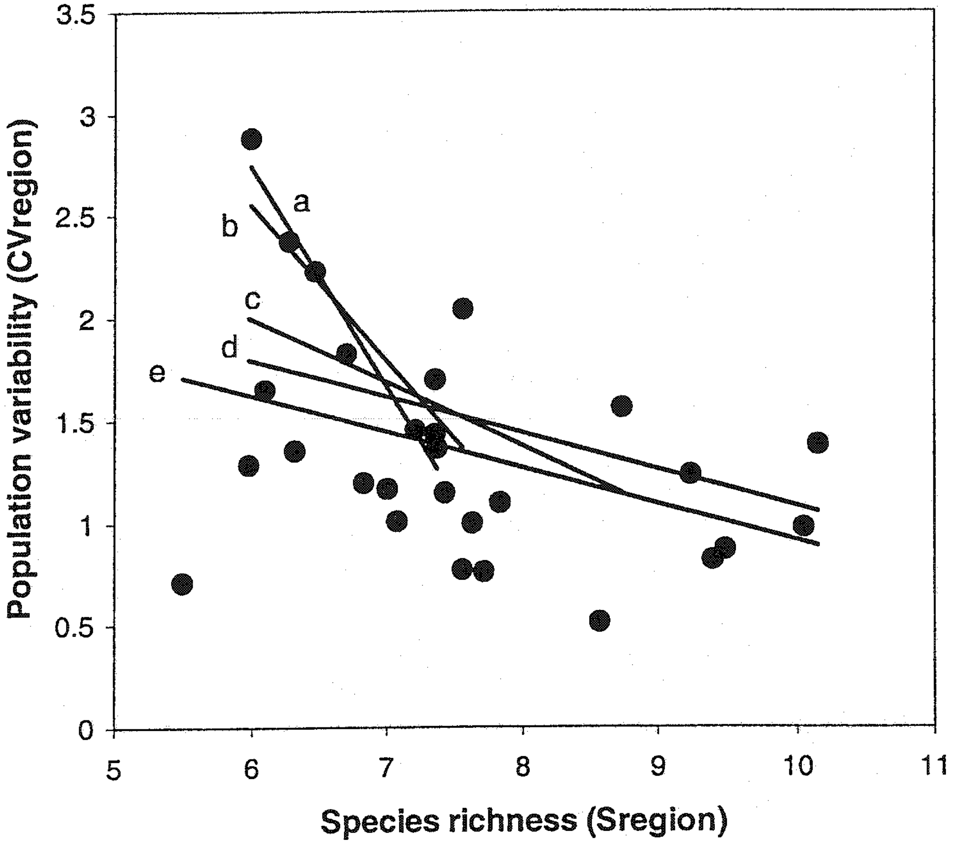
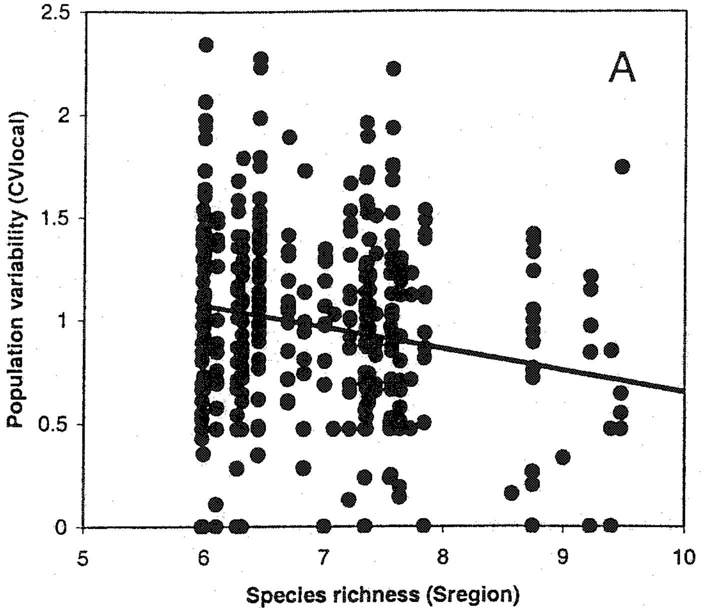
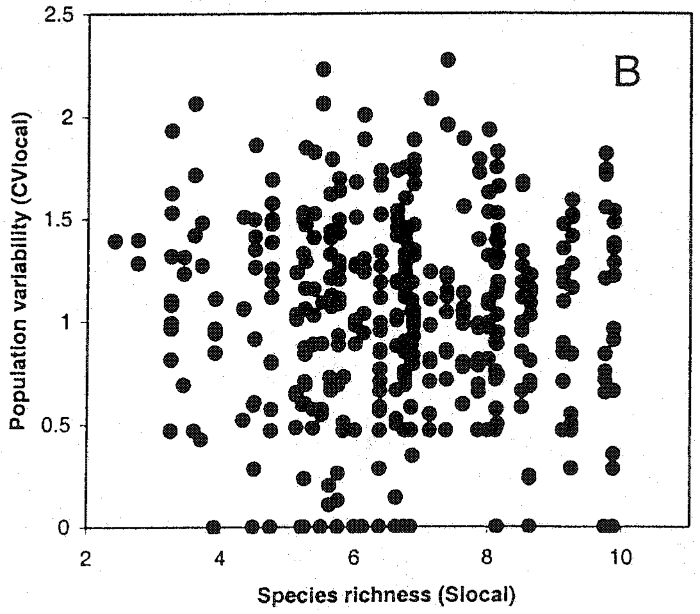

3.5
3
2.5
2
1.5
1
0.5
0
5
6
7
8
9
10
11
a
b
c
d
e
Population variability (CVregion)
Species richness (Sregion)

Figure 2a-b. Temporal variability of populations in each rock pool as a function of richness. a) Intermediate noise model. Population variability (CV_{local}) of each population in each rock pool as a function of average richness, S_{region}. All the populations of one species have by definition the same S_{region}, thus each vertical set of points represents a range of values observed within a population of a single species (except when two species happen to have the same S_{region}). B) High noise model. Population variability (CV_{local}) of each population in each rock pools as a function of local richness, S_{local}.


A
Population variability (CVlocal)
2.5
2
1.5
1
0.5
0
5
6
7
8
9
10
Species richness (Sregion)

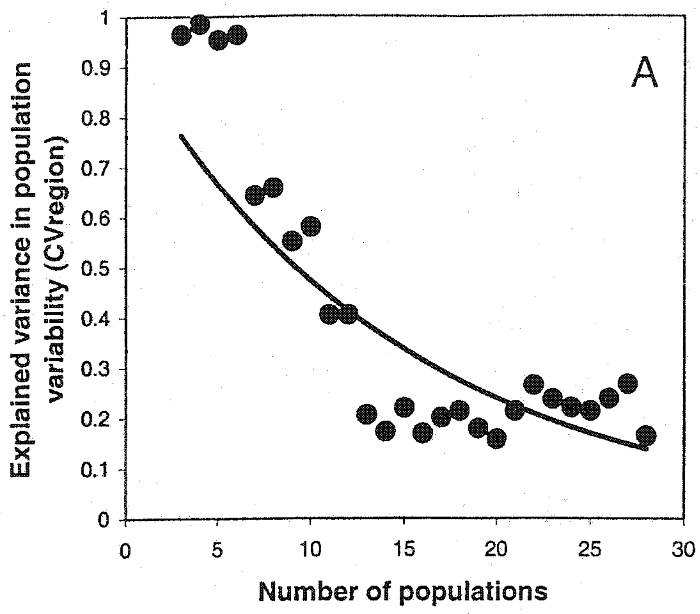

B
Population variability (CVlocal)
2.5
2
1.5
1
0.5
0
2
4
6
8
10
Species richness (Slocal)

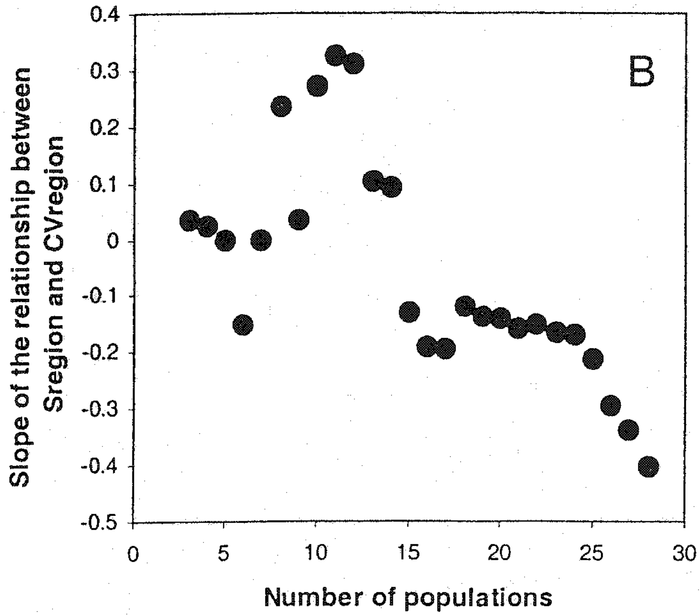
additions beyond the 11 top-ranking populations became asymptotic (i.e. they had no further effect on the global relationship, Fig 3a).Thus, richness may affect the variability of high-density populations differently than low-density populations. This hypothesis is supported by an alternative analysis where populations were iteratively added into the regression analyses in reverse order (Fig 3b). Populations with low-density ranks were more variable in pools with higher S_{region} (Fig 3b). Thus, richness appears to strongly affect the variability of high-ranking populations, but low-ranking populations were less affected. There is even some suggestion that low-ranking populations became more variable as richness increased.

DISCUSSION

Our results show that changing the resolution at which variability is analyzed allows detection of the effects of species richness (Tilman et al., 1997; Loreau, 1998). There was no relationship between S_{local} and CV_{local} (the high noise analysis). In contrast, S_{region} was significantly correlated with both CV_{local} and CV_{region}. The scale which removed the most variance arising from local processes, CV_{region} (the low noise analysis), resulted in the most sensitive test, and allowed discrimination of ecological patterns which otherwise were statistically invisible (high noise analysis; Fig 2b) or underestimated (intermediate noise analysis; Fig 2a). Thus, as local differences are removed from the calculations of both richness and population variability, the explained variance between richness and population variability dramatically increased.

Figure 3a-b. Contributions of each population into the model for population variability (CV_{region}) according to rank in density. a) Explained variance at each step with populations added into the model from the highest to the lowest rank. b) Explained variance at each step with populations added into the model from the lowest to the highest rank.


A
Explained variance in population variability (CVregion)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
Number of populations

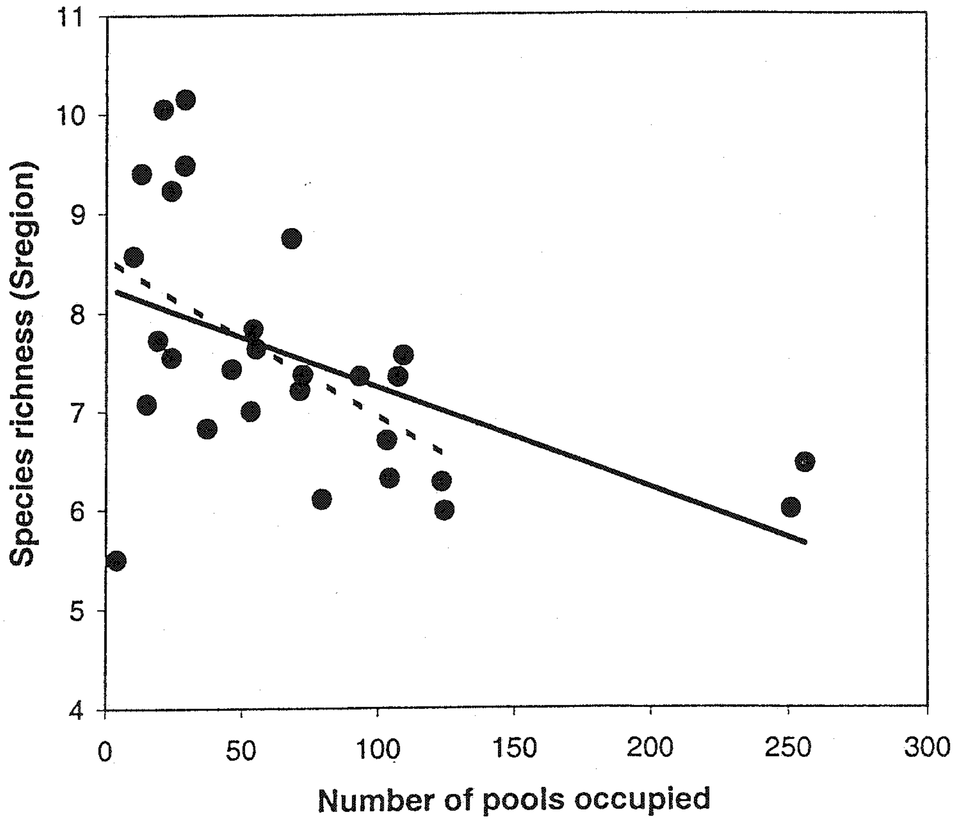

B
Slope of the relationship between Sregion and CVregion
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
0
5
10
15
20
25
30
Number of populations

The obscuring effects of local processes may be especially pronounced in populations with high variability such as these rock pools, where population CVs exceed 50% of the mean (range = 0.51 to 2.89, mean = 1.35 ± 0.545 SD). In these cases, sample error and environmental noise are likely to obscure many biological patterns. Thus, the rationale for using different levels of aggregation is primarily to remove this noise. However, aggregation also removes the statistical error of non-independence of points that exists in traditional population variability-species richness analyses, where each population in each plot is considered the unit of analysis (e.g. Tilman, 1996; McGrady-Steed and Morin, 2000; Romanuk and Kolasa, 2002).

Population variability significantly declined in pools with greater species richness supporting the hypothesis that populations are stabilized by richness. It is of interest, however, whether this pattern of decreasing variability in richer environments is a result of statistical averaging (Doak et al., 1998) or is biologically generated. The role of statistical as opposed to biological mechanisms in generating richness-variability relationships has been the subject of considerable debate (see Cottingham et al., 2001). In particular, statistical averaging or portfolio effects, i.e. that the sum of several randomly and independently varying items are less variable than the average item, have been proposed to decrease variability in richer communities independently of direct compensation between species (Doak et al., 1998). The question then is whether averaging effects could be invoked to explain reductions in population variability in richer environments as the effects of statistical averaging are incorporated in our calculation of regional population variability. Averaging effects could be invoked if more pools were averaged together for populations with higher exposure richness. However, occupancy is negatively correlated with the exposure richness of populations ($r^2 = 0.262$, $p < 0.005$, $n = 28$; Fig 4). Thus, unlike richness-community variability relationships where reductions in variability can be explained in part by the results of statistical averaging (Doak et al., 1998), our analyses suggest that in these rock pools, the observed reduction of population variability with increasing richness probably reflects biological factors. Although successive collapse of variance might be expected to improve resolution, this is overpowered by large reductions in N (from 390 to 28 data points), which should have an opposite contribution in regression analysis. The fact that a clear pattern (Fig. 1) was obtained by the method of collapsing variance (where no pattern was visible otherwise; Fig. 2b) suggests a biological reality regardless of the statistical method for achieving resolution.

One biological mechanism highly relevant to richness and variability is competition (Tilman et al., 1997 and references therein). Differences in the response of individual species to environmental fluctuations are hypothesized to result in increasing population variability and decreasing community variability in richer environments (Tilman et al., 1997). In rock pools we see a different pattern of responses, with both population variability (this paper) and community variability (Romanuk and Kolasa, 2002) decreasing as richness increases. This pattern has been predicted theoretically. Ives et al. (1999) have shown that species number may have diverse effects on variability measured at the population level, but there are no direct effects of species number at the aggregate community level.

Figure 4. Average richness, S_{region} as a function of pool occupancy. Pool occupancy is significantly correlated with S_{region} (total pools over 8 sampling dates, n = 365). The relationship remained strong when the most broadly distributed populations (occupancy >200) were removed from the analysis ($r^2 = 0.245$, $p < 0.01$, $n = 26$; dotted line).


Species richness (Sregion)
11
10
9
8
7
6
5
4
0
50
100
150
200
250
300
Number of pools occupied

Instead, biodiversity may decrease community variability by increasing the diversity of species responses to environmental fluctuations (Ives et al., 1999). In this way, a decrease in population variability with increasing richness may translate into lower variability of communities. Our results support this hypothesis. If we consider the community as a hierarchical system where lower levels in the hierarchy affect the properties of higher levels, stabilizing effects of richness on populations of component species could yield more stable communities in richer environments.

There are two key differences between this and previous studies. Firstly, this study involves a consumer community spanning several trophic levels. Previous studies have focused primarily on terrestrial plant communities (McNaughton, 1985; Tilman, 1996; Naeem and Li, 1997; Wardle et al., 1999). The possible implications of multiple trophic levels should not be discounted (Cottingham et al., 2001). However, Ives et al. (1999) suggest that there should be no qualitative difference in richness-variability relationships for multi-trophic communities. Secondly, species richness was not artificially manipulated (Romanuk and Kolasa, 2002). Instead, we used a natural richness gradient to test the relationship between richness and population variability. Such unmanipulated communities have much greater variation than experimental systems, which could preclude detecting any clear richness-variability relationships. Remarkably, results obtained utilizing the procedures developed here appear to be quite unambiguous compared to those reported in any previous studies (cf. Tilman, 1996; McGrady-Steed and Morin, 2000).

We previously showed that, in natural aquatic rock pools, communities with more species are less variable than species-poor communities (Romanuk and Kolasa, 2002). Furthermore, when the full range of variance arising from local processes is preserved in the model, population variability is unrelated to richness (*sensu* McGrady-Steed and Morin, 2000, Romanuk and Kolasa, 2002; Fig. 2b). Our previous work (5) supported the majority of studies that species-rich communities are less variable in their aggregated density than species-poor communities, and that there is no or only a weak relationship between richness and population variability (Tilman, 1996; McGrady-Steed and Morin, 2000). However, removing noise from local processes exposes strong effects of richness on population variability and its dependence on density. That richness could stabilize populations has been hypothesized theoretically (Ives et al., 1999), but this important hypothesis has had no prior empirical support.

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Chapter 6:

Effects of diversity and nutrients on the stability of an aquatic invertebrate community

This chapter has been prepared for publication in Proc. Natl. Acad. Sci (partial citation follows). This chapter has been re-formatted to maintain consistency throughout the thesis.

Romanuk, T.N. and J. Kolasa. Effects of diversity and nutrients on the stability of an aquatic invertebrate community. Proc. Natl. Acad. Sci.

RATIONALE AND OBJECTIVES

I previously showed that the relationship between species richness and community variability was modulated by environmental conditions using long-term data from a series of rock pools. In this Chapter I present the results of an experiment where I manipulated diversity and nutrient conditions in outdoor experimental microcosms. I found that:

1. Increasing diversity stabilized both community and population densities in nutrient-poor but not nutrient-rich microcosms.
2. That community variability was strongly and positively related to population variability.

These results provide experimental evidence that diversity affects the variability of both communities and populations. Moreover, they provide experimental evidence that environmental conditions can modulate the relationship between diversity and variability. This study also suggests that in rock pool communities diversity affects community stability, in part, through the effect of diversity on population stability.

ABSTRACT

We experimentally manipulated nutrient input to rock pool invertebrate communities that differed in diversity to determine (i) whether nutrients affected community and population variability, (ii) whether diversity affected community and population variability, (iii) how the relationship between diversity and variability might change under different nutrient conditions, and (iv) the mechanism by which community variability is stabilized by increasing diversity. Nutrients increased community density but had no effect on community variability. Diversity strongly affected variability, with lower community and population variability in microcosms with higher diversity. Nutrient additions modulated the effect of diversity on community and population variability. As nutrients increased, the stabilizing effect of diversity on community and population variability weakened.

Keywords: biodiversity, community variability, diversity-stability, population variability, rock pool invertebrates

INTRODUCTION

To understand and predict the consequences of species loss, it is becoming increasingly apparent that ecologists must learn how to link population level dynamics to both community and ecosystem level processes. Recent models predicts that reductions in the numbers of species in a community will increases the variability of its component populations (Ives et al. 1999, 2000; Ives and Hughes, 2002). These model provides a means to link ecosystem, community, and population processes by incorporating the consequences of environmental fluctuations to species interactions. In these models, increasing the strength of competition or decreasing species richness has no effect on community variability directly. Instead, the variability in community biomass depends only on how species respond to environmental fluctuations (Ives et al. 1999, 2000; Ives and Hughes, 2002). This contrasts with arguments that interspecific competition may decrease community-level variances by driving negative covariances between species abundances (Tilman et al. 1998, Tilman, 1999).

Whether the number of species in an ecosystem might affects the stability of that system has been the subject of considerable debate. McArthur (1955), Elton (1958), and Odum (1959) proposed that diverse communities would be less variable than species-poor communities. May (1973) suggested that while aggregate community properties such as variability in biomass would be more stable in diverse communities, populations would be destabilized by increasing diversity. Tilman (1996) provide a potential resolution to this paradox by showing that in plant communities total community biomass was more stable in diverse plots, while population biomasses were destabilized by increasing diversity. Recent models however have suggested however than diversity might also stabilize population properties (Ives et al., 1999, 2000; Li and Charnov, 2001; Ives and Hughes, 2002). For example, Ives et al. (1999) showed that the variance in total community biomass depends only on how species respond to environmental fluctuations. Interspecific competition and species number have little influence on community-level variances directly (Ives and Hughes, 2002). Furthermore, in natural unmanipulated rock pool communities, Romanuk and Kolasa (Chapter 5) demonstrated a negative relationship between species richness and population variability as long as the "noise" resulting from local conditions such as environmental differences and interspecific interactions was statistically removed.

Determining the mechanism by which stability of an ecological community is achieved, and which model is more applicable to natural communities, requires field experiments where an environmental signal is manipulated along with diversity. Rock pool communities of micro- and meio- invertebrates have proven highly tractable for experimental and observational investigations (Romanuk and Kolasa, 2002; Chapter 2-5. Previous observational studies have shown a strong correlation between the species richness of rock pool fauna and both community and population variability (Romanuk and Kolasa, 2002; Chapter 3). Furthermore, ecosystem level processes have been shown to modulate the correlations between species richness and community variability (Romanuk and Kolasa, 2002; Chapter 3-4).

In this paper I report the results of experimental manipulations of nutrients and diversity using a consumer community of rock pool invertebrates to determine (i) whether nutrients affected populations of rock pool invertebrates, (ii) whether diversity affected community and population variability, (iii) if nutrient conditions would alter the relationships between diversity and variability in a consistent fashion, and (iv) the relationship between population variability and community variability.

METHODS

I conducted this experiment on the grounds of the Discovery Bay Marine Laboratory (DBML) on the north coast of Jamaica (18°28‘ N/ 77° 25‘ W) from September to October 2001. I used a 5 x 3 factorial design with five levels of diversity and three levels of nutrient additions. Artificial ‘rock pools’ were plastic cups, 8 cm in diameter and 15 cm deep. The rock pools were filled to a depth of 10 cm (volume 500 ml) with water and were set up outdoors approximately 25 m from the natural rock pools. The size of the experimental rock pools used in this experiment were representative of smaller natural rock pools from which the invertebrates were collected (Kolasa et al., 1996, 1998). The rock pools were placed on a 3 x 1 m table that was 1 m in height and were covered loosely with a 5mm mesh fiberglass screening to partially prevent oviposition by aquatic insects. The experimental rock pools were sampled at the beginning of the experiment to provide baseline data. After 7 days each rock pool was sampled by gently stirring the water of the rock pool with a glass stirrer and using a 50 ml dip container to collect 30 ml of water. This water was sieved through a 63μm mesh sieve and then stored in a centrifuge tube in 50%-70% ethanol. Sampling was repeated weekly for 4 weeks. Overall, five samples were taken including the baseline samples, however only the last 4 weeks of samples were used in the analysis. This was done because population growth in the first week was very high. Using 5 sample dates would have artificially inflated community and population variability with initial population growth. Samples were enumerated using a dissecting microscope and individuals were identified to species or genus. Where a taxa is only identified to genus, the taxa represents one species only and not a number of different species in the same genus.

Nutrient additions

The rock pools were fertilized on September 25 with soluble phosphorous (KH_2PO_4) and nitrogen (NH_4NO_3) with an N:P ratio of 20:1. Nutrient level I was obtained adding nutrients once at the start of the experiment (n=15). Nutrient level II was obtained by adding nutrients at the start of the experiment and again after the first week (n=15). The other 15 microcosms had no nutrients added and served as controls for the nutrient manipulations. The control treatment (no nutrients) averaged 0.105 μg P (SD 0.015) and 1.61 μg N (SD 0.426). Nutrient level I averaged 3.35 μg P (SD 0.225) and 11.83 μg N (SD 0.752). Nutrient level II averaged 5.483 μg P (SD 0.923) and 26.5 μg N (SD 1.87).

Diversity manipulation

To experimentally manipulate diversity, I collected 30 liters of rock pool water with a standard salinity of 0 ppt and filtered half of the rock pool water through a 63μm mesh filter. This procedure removed all of the target species (i.e. zooplankton and benthic invertebrates) but did not remove smaller metazoans (i.e. rotifers) or protozoans. This manipulation resulted in 15 liters of "filtered" rock pool water from which all organisms larger than the mesh size had been removed, and 15 liters of "natural" rock pool water. The diversity levels were created by mixing the "filtered" water and the "natural" water together to create five diversity levels (0%, 25%, 50%, 75%, and 100%). The percent given represents the amount of natural 'unfiltered' water in each diversity level (i.e. percent of unmanipulated diversity present in the diversity level). For example, the 0% level was composed of only filtered water (i.e. control), and the 25% level contained ¼ "natural" water and ¾ "filtered" water. Likewise, the 50% level contained ½ "filtered" water and ½ "natural" water.

Rock pool fauna

The natural rock pool communities used in this experiment contained 11 species of zooplankton, benthic invertebrates, insect larvae, and worms, including three species of ostracods (*Candona* sp., *Cypridopsis* sp., *Potamocypris* sp.), a chydorid (*Alona sp.),* a daphnid (*Ceriodaphnia sp.),* a copepod (*Orthocyclops modestus* Herrick), a larval decapod (*Armases miersii* Rathbun), two worms (*Nematode* sp., *Oligochaete* sp.) and two insect larvae (*Culicoides* sp. and *Culex* sp.).

Data analysis

The diversity manipulation protocol affected both the number of species and the number of individuals, thus instead of using species richness as our measure of biodiversity, we use diversity, H', calculated using the Shannon-Weiner index (Magurran, 1988). Diversity, H' was calculated as the $H' = \Sigma\, p_i \ln(p_i)$ where p_i represents the proportional contribution of the *i*th species to the community.

Temporal variation in community density (densities of all species combined in each rock pool, CV_C) was calculated as the coefficient of variation, CV, (standard deviation/mean) of density (untransformed data) over 4 sampling dates (weeks). Temporal variation in population density was calculated two ways. First, in order to directly compare our results with previous work on diversity-stability relationships in rock pools (Romanuk and Kolasa, 2002), as well with studies on other systems (Tilman, 1996; McGrady-Steed and Morin, 2000) we calculated population variability for each population in each rock pool (CV*local*) as

$$CV_{local} = StDev(N_k)/\left[(\sum_{k=1}^{D} N_k)/D\right] \qquad (1)$$

where CV*local* is the coefficient of variation in population abundance of species, N_k is a population size on date k, D is the number of samples ($D = 4$).

This calculation is analogous to the calculations of population variability presented in Tilman (1996), McGrady-Steed and Morin (2000), and Romanuk and Kolasa (2002; Chapter 3, Chapter 5 eq. 3). The second way we calculated population variability was by taking the mean variability of all the populations in a rock pool (CV_{POP}). This was done in order to compare community variability and population variability directly. CV_{POP} was calculated as

$$CV_{POP} = \Sigma\, cvi/s \qquad (2)$$

where cv*i* is the average variability of all populations in a sample, and s is the number of species in the sample.

We used ANOVA and a homogeneity of slopes General Linear Model (GLM) to test for effects of diversity and nutrient condition on community variability. Linear regression tested for correlation between diversity and CV. The Gamma statistic was used to test for differences in rank-abundance structure. Covariances among species were calculated using pearson correlation coefficients.

RESULTS

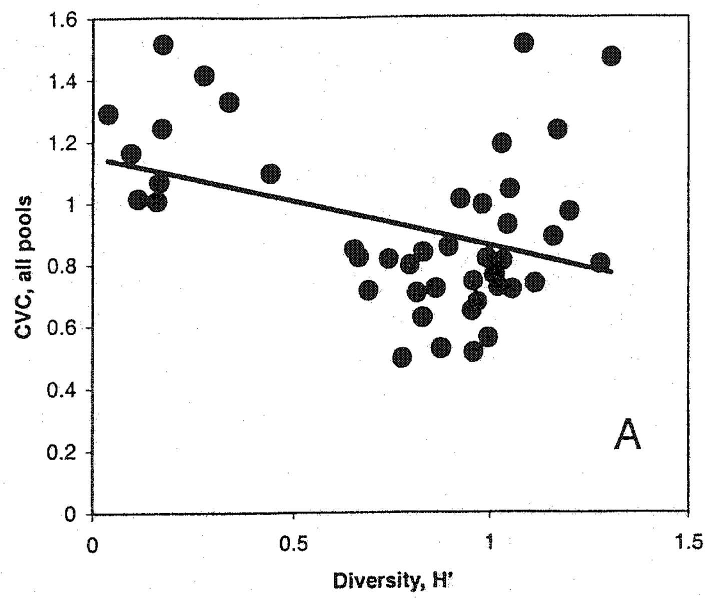
Community variability (CV_C)

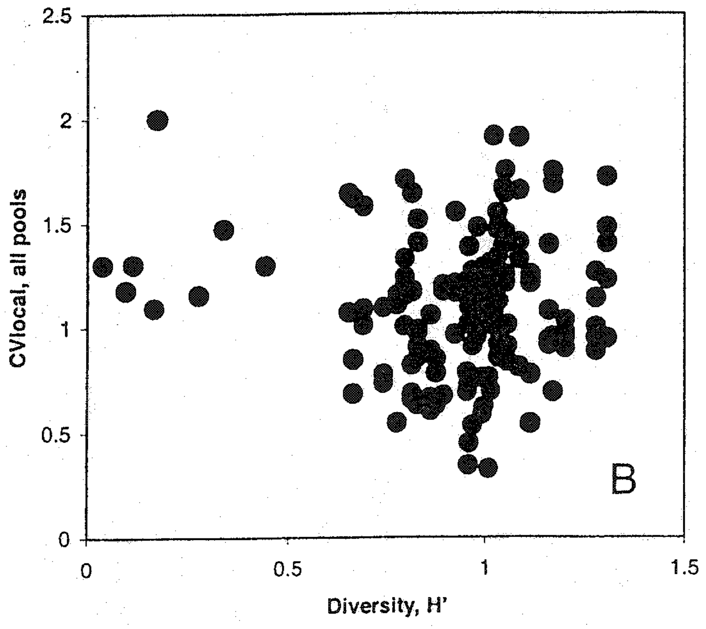
Community variability (CV_C) significantly decreased with diversity across all nutrient levels (CV_C, $r^2 = 0.145$, $p = 0.01$, $n = 45$, Fig. 1). This global pattern, however, did not extend to each of the three nutrient levels. Under oligotrophic conditions diversity significantly decreased variability, explaining 47% of the variance in CV_C (oligotrophic CV_C, $p = 0.0028$, $n = 15$, Fig. 2a). Under mesotrophic and eutrophic conditions, however, there was no impact of diversity on CV_C (mesotrophic CV_C, $r^2 = 0.12$, $p = 0.111$, $n = 15$, Fig. 2b; eutrophic CV_C, $r^2 = 0.05$, $p = 0.584$, $n = 15$, Fig. 2c).

Individual population variability (CVlocal)

Variability in the density of individual species (CV*local*) showed similar results. While there was no relationship between diversity and population variability (CV*local*) across all nutrient conditions (all nutrient conditions CV*local*, $r^2 = 0.01$, $p = 0.198$, $n = 150$), in oligotrophic conditions CV*local* decreased with diversity (CV*local*, $r^2 = 0.111$, $p = 0.016$, $n = 43$, Fig. 2d). In mesotrophic and eutrophic conditions diversity did not affect CV*local* (mesotrophic CV*local*, $r^2 = 0.0009$, $p = 0.839$, $n = 50$, Fig. 2e; eutrophic CV*local* $r^2 = 0.002$, $p = 0.907$, $n = 57$, Fig. 2f).

Figure 1. Relationship between diversity H' and a) community variability (CV_C) and b) population variability (CV*local*) across all nutrient conditions. Community variability (CVc) declines with increasing diversity in the experimental rock pools while population variability (CV*local*) is unrelated to diversity.


1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
CVC, all pools
0
0.5
1
1.5
Diversity, H'
A


2.5
2
1.5
1
0.5
0
CVlocal, all pools
0
0.5
1
1.5
Diversity, H'
B

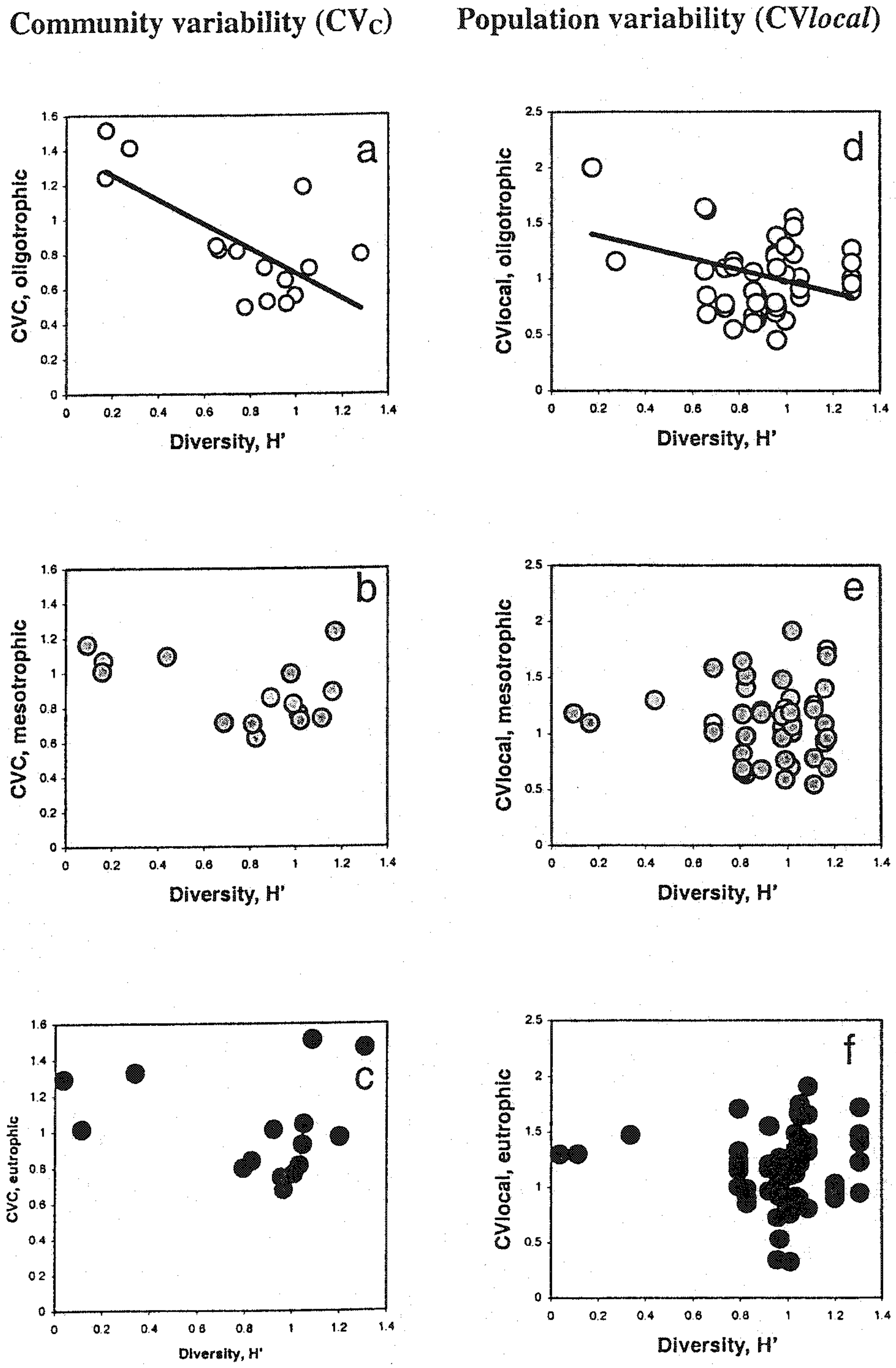
Average population variability in each rock pool (CV_{POP})

In order to directly compare the effects of population variability on community variability, we also calculated population variability as the mean variability of all populations in each rock pool (eq. 2; CV_{POP}). Diversity explained 27% of the variance in average population variability across all nutrient conditions (all nutrient conditions CV_{POP}, $r^2 = 0.271$, $p = 0.0002$, $n = 45$; Fig. 3). In oligotrophic conditions CV_{POP} decreased with diversity (CV_{POP}, $r^2 = 0.613$, $p = 0.0005$, $n = 15$, Fig. 4a). In mesotrophic and eutrophic conditions diversity did not affect CV_{POP} (mesotrophic CV_{POP}, $r^2 = 0.16$, $p = 0.139$, $n = 15$, Fig. 4b; eutrophic CV_{POP} $r^2 = 0.138$, $p = 0.171$, $n = 15$, Fig. 4c).

Relationship between population and community variability

Population variability (CV_{POP}) explained 32% of the variance in community variability (CV_C) across all nutrient conditions ($p = 0.00002$, $n = 45$; Fig. 5). CV_{POP} explained more variability in community density (CV_C) in the eutrophic rock pools ($r^2 = 0.482$, $p = 0.004$, $n = 15$; Fig. 6c) than in either the oligotrophic (CV_{POP} $r^2 = 0.396$, $p = 0.012$, $n = 15$; Fig. 6a) or mesotrophic rock pools (CV_{POP} $r^2 = 0.323$, $p = 0.027$, $n = 15$; Fig. 6b).

Figure 2a-f. Dampening effect of richness on community (CV_C, a-c) and population variability (CV_{local}, d-e) attenuates across a gradient of nutrient conditions from oligotrophic (a, d; open circles), through to mesotrophic (b, e; grey circles), and eutrophic (c, f; black circles) in experimental rock pools.



Community variability (CVc)

Population variability (CV*local*)

Figure 3. Relationship between diversity and average population variability in each experimental rock pool (CV_{POP}) across all nutrient conditions. Population variability is stabilized by diversity.

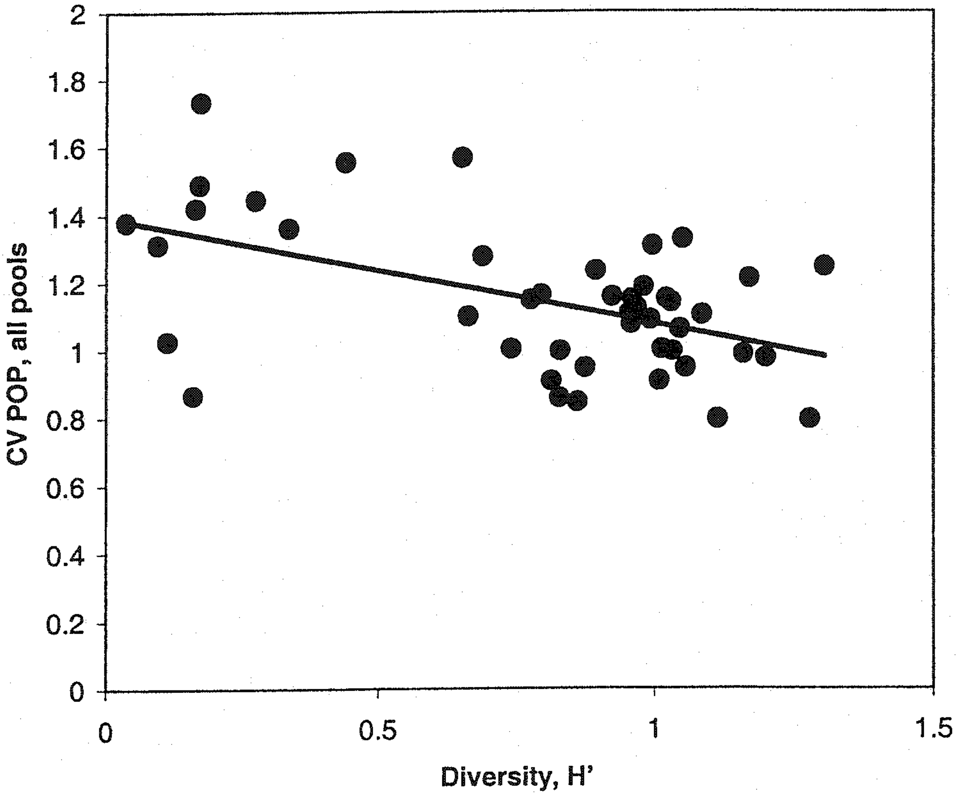
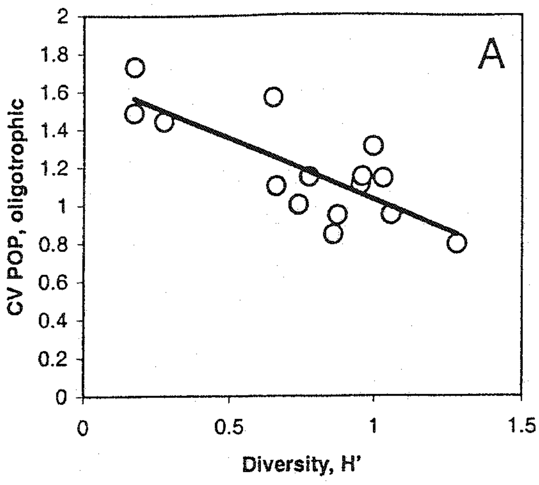
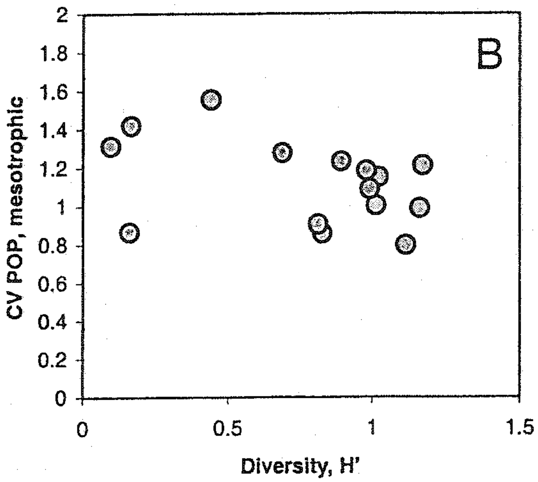
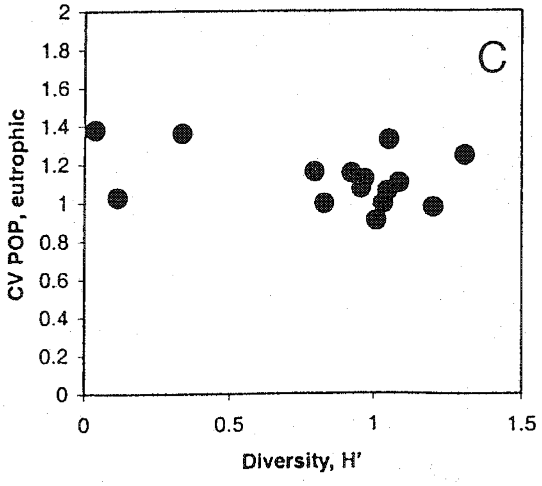

2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
CV POP, all pools
0
0.5
1
1.5
Diversity, H'

Figure 4a-c. Relationship between diversity and average population variability in each experimental rock pool (CV_{POP}) for a) oligotrophic, b) mesotrophic, and c) eutrophic rock pools. Population variability is stabilized by diversity in the oligotrophic rock pools.


A
CV POP, oligotrophic
Diversity, H'
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0
0.5
1
1.5


B
CV POP, mesotrophic
Diversity, H'
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0
0.5
1
1.5


C
CV POP, eutrophic
Diversity, H'
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0
0.5
1
1.5

In a multiple regression with CV_{POP} and diversity H' as the independent variables and CV_C as the dependent variable, CV_{POP} was the only variable retained in the regression equation for community variability across all nutrient conditions ($R^2 = 0.341$, $p = 0.0002$, $n = 45$). In contrast, in oligotrophic rock pools, only diversity, H' was retained in the regression equation ($R^2 = 0.518$, $p = 0.002$). In the mesotrophic pools neither CV_{POP} nor diversity was retained as significant ($R^2 = 0.378$, $p = 0.057$). In the eutrophic rock pools only CV_{POP} was retained as significant ($R^2 = 0.484$, $p = 0.018$).

Effect of diversity on the variability of each species

Adding nutrients also affected whether individual populations were stabilized by diversity. In oligotrophic rock pools, densities of *Potamocypris* sp., *Cypridopsis* sp., and *Alona* sp. were less variable in more diverse rock pools ($p>0.05$). In contrast, only *Potamocypris* sp was stabilized by diversity in mesotrophic rock pools ($p = 0.019$). In eutrophic rock pools there was no relationship between the variability of any single species variability and diversity.

Effects of nutrient additions

Nutrient additions had no significant affect on either community (CV_C, $F_{2,42} = 0.732$, $p = 0.487$) or population variability (CV_{POP}, $F_{2,42} = 0.328$, $p = 0.722$) directly. Likewise, adding nutrients did not affect diversity (H', $F_{2,42} = 0.241$, $p = 0.787$),

Figure 5. The relationship between population variability (CV_{POP}) and community variability (CV_C) across all nutrient conditions.

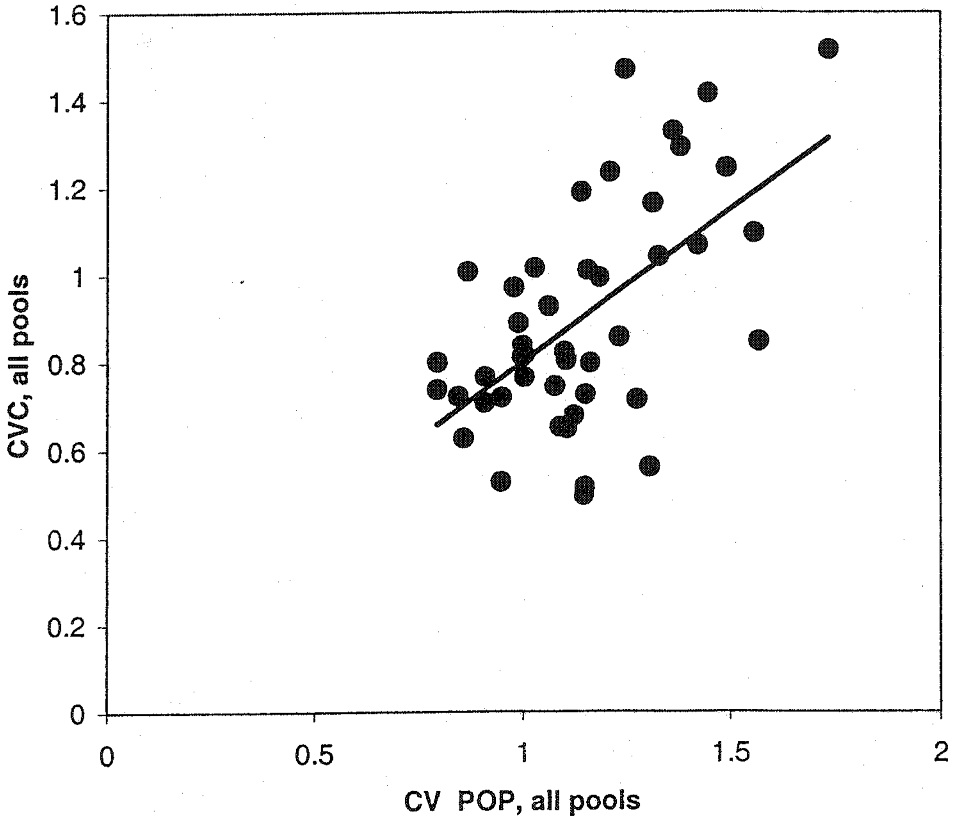
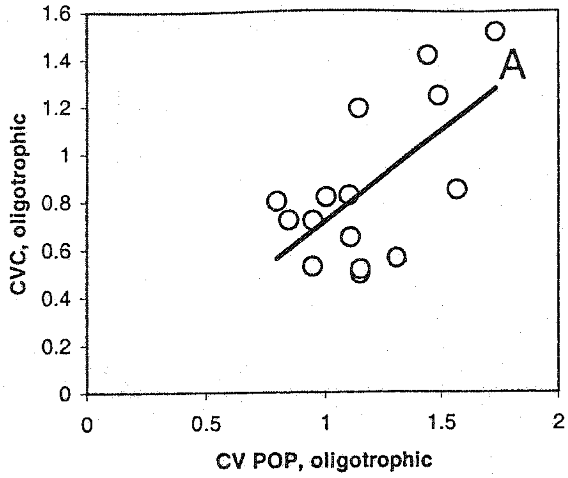
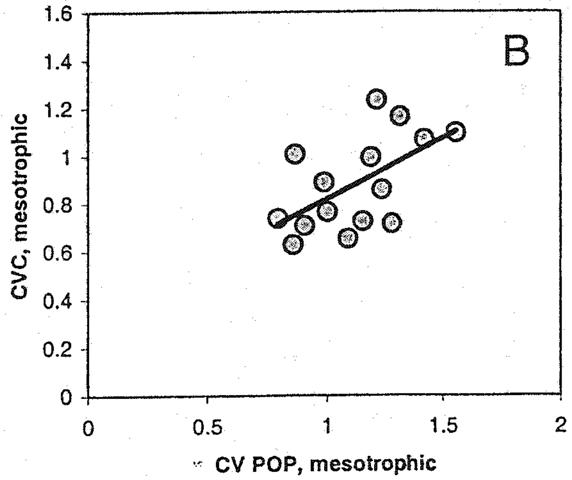

1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
CVC, all pools
0
0.5
1
1.5
2
CV POP, all pools

Figure 6a-c. The relationship between population variability (CV_{POP}) and community variability (CV_C) in a) oligotrophic, b) mesotrophic, and c) eutrophic rock pools. Population and community variability are positively related within each nutrient condition.


A
CVC, oligotrophic
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
0
0.5
1
1.5
2
CV POP, oligotrophic


B
CVC, mesotrophic
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
0
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1
1.5
2
CV POP, mesotrophic

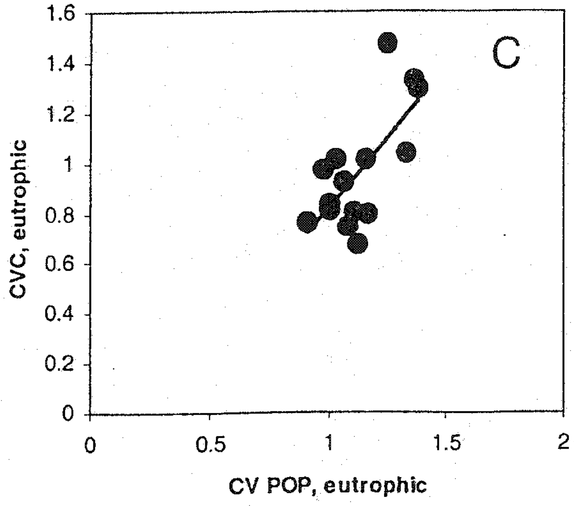
C
CVC, eutrophic
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
0
0.5
1
1.5
2
CV POP, eutrophic

Table 1. Statistics of General Linear Model ANCOVA for the effect of nutrient additions (oligotrophic, mesotrophic, eutrophic) on the relationship between species richness and community variability.

Effect	df	SS	MS	F
Intercept	1	10.306	10.306	***187.483
Nutrient	2	0.162	0.081	1.480
Average Diversity	1	0.650	0.650	***11.837
Nutrient*Average Diversity	2	0.350	0.175	*3.183
Error	39	2.143	0.054	

Note: b represents the slope of the equation. * significant at $p < 0.05$,

*** significant at $p < 0.001$.

or mean species richness (S, $F_{2,42}$= 0.804, p = 0.454). In contrast, adding nutrients had strong effects on mean community density (log N, $F_{2,42}$= 5.169, p = 0.0098) and the cumulative densities of *Culicoides* sp. larvae (p = 0.008) and *Alona davidii* (p = 0.013). Nutrient additions has no effect on the cumulative densities any of the other species.

A homogeneity of slopes GLM tested for effects of nutrient additions and diversity, H' on community variability. There was a significant interaction effect between nutrients and average diversity and the intercept of the relationship between diversity, H' and community variability was significantly different among the three nutrient conditions (Table 1).

DISCUSSION

In a previous study of the diversity-stability relationships in natural rock pool invertebrate communities, we showed that increasing species richness leads to a decrease in variability for both communities (Romanuk and Kolasa, 2002) and individual populations as long as noise arising from local processes is filtered out (Romanuk and Kolasa, 2002; Chapter 5). The former result is consistent with experimental evidence to date that variability in aggregate properties is lower in richer environments (Tilman, 1996; McGrady-Steed and Morin, 2000). The latter result that populations could also be stabilized by richness has been shown theoretically (Ives et al.. 1999; Li and Charnov, 2001) but until this study there has been no experimental evidence to suggest that populations densities may be stabilized by diversity. Moreover, results of studies in other ecosystems have suggested that there is either no or only a weak positive impact of diversity on population variability (May, 1973; Tilman, 1996; McGrady-Steed and Morin, 2000; Wardle, 1999). Our results demonstrate that under some conditions populations are stabilized by diversity. However, enrichment disrupted this clearly detectable effect.

The dichotomous impact of richness on community and population variability raises the question of why diversity only decreased CV_C and CV_{POP} under oligotrophy. Oligotrophy has been hypothesized to promote strong direct and indirect interactions, at least for lower trophic levels such as grazers (Neill, 1988). In the absence of fish, zooplankton community structure and dynamics are largely controlled by exploitative interactions within and among micrograzers and macrograzers (Neill, 1988); however under eutrophy, competition may have little impact on zooplankton (McQueen et al., 1986). In oligotrophic systems, competitive interactions may be stronger (McQueen et al., 1986).

We found that the covariance structure of rock pool populations was variable across nutrient levels consistent with this hypothesis. Under oligotrophy, 57% of covariances were negative, as opposed to only 36% under eutrophy. Moreover, mean per capita interaction intensity (i.e. strength of the negative covariations between populations) correlation was highest under oligotrophy, although this increase was only significantly greater than mesotrophic mean per capita interaction intensity (Wilcox matched pairs test, $p = 0.003$).

It is interesting to note that diversity itself did not significantly vary between nutrient levels. This suggests that statistical averaging, i.e. the sum of several randomly and independently varying items has lower variance than the average item (Doak et al., 1998), is not the cause of variability reductions. Instead, decreases in population variability contributed to the reductions in community variability. Population variability significantly affected community variability across all nutrient conditions. However, the effects of increased population variability on community variability were not the same for oligotrophic, mesotrophic, and eutrophic rock pools. Diversity was the only variable retained in a multiple regression which also included population variability in oligotrophic rock pools. In contrast, in eutrophic rock pools community variability was related only to population variability. In the mesotrophic rock pools neither diversity nor population variability affected community variability. The strong stabilizing effects of diversity on community variability observed under oligotrophy, disappeared under mesotrophy. Once eutrophic conditions had been achieved community variability was only related to population variability. Thus, nutrient enrichment appears to decouple diversity from community variability.

This study shows that increasing diversity of zooplankton and benthic invertebrates leads to decreases in community and population variability, but only under oligotrophic conditions. Nutrient additions had a detrimental effect on this relationship. This decoupling of richness from stability is likely to be widespread in aquatic systems where eutrophication has strong effects for both community structure and species interactions (Wetzel, 1985, Carpenter et al., 1988). Decreases in population variability are a potential stabilizing mechanism; however the positive effects of decreased population variability on community variability were only strong under eutrophic conditions.

An alternative explanation for different diversity-variability relationships under different nutrient conditions is that species composition changed in rock pools where nutrients had been added. Differences in rank abundance structure were found between oligotrophic and both mesotrophic (Gamma statistic, $z = 3.01$, $p = 0.002$, $n = 12$) and eutrophic microcosms ($z = 2.60$, $p = 0.009$), and between mesotrophic and eutrophic ($z =1.92$, $p = 0.054$) in support of this hypothesis. Thus, the effects of different species compositions cannot be excluded as potential mechanism for why diversity decreased stability only under oligotrophy. However, despite substantial differences in community structure, community variability and population variability did not differ between oligotrophic, mesotrophic, and eutrophic microcosms (t-test, $p> 0.05$). The two different response patterns arose instead through the differential impacts of diversity and population variability on variability under different nutrient conditions.

Other experimental modulations by nutrient enrichment have been documented, such as increased effects of *Chaoborus* on herbivorous zooplankton under eutrophy (Neill and Peacock, 1980) and increased reductions of phytoplankton biomass by *Daphnia* under eutrophic versus oligotrophic conditions (Vanni, 1986). The "paradox of the plankton" (Hutchinson, 1961) also predicts modulation of system behavior with enrichment, although we found no evidence for increasing variability for either communities or populations under different nutrient conditions.

Eutrophication has been variously shown to result in species loss especially at higher trophic levels (Wetzel, 1983), increased unpredictability and variability of phytoplankton (Cottingham et al. 2000), increases in producer biomass, shifts in community composition, simplification of food webs (Wetzel, 1983), and the development of alternate community states (Scheffer et al., 2001), among other effects. The results presented here add an additional impact to the list: decoupling of the impact biodiversity on stability.

In conclusion, responses of rock pool invertebrate communities to changes in diversity differed depending on nutrients. Nutrient additions had no effect on community or population variability directly, instead the different patterns arose because variability was strongly affected by diversity in the oligotrophic pools. In contrast, diversity did not effect community or population variability in mesotrophic or eutrophic pools. Population variability appeared to affect community variability; however, this response was strongest in eutrophic rock pools. In oligotrophic rock pools the variability of both community and population densities appeared to be affected primarily by changes in diversity.

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Chapter 7:

Conclusion

CONCLUSION

Main conclusions

The research presented in this dissertation represents the first comprehensive analysis of diversity-stability relationships in aquatic multi-trophic communities. Relative to the other community types in which relationships between diversity and both community and population stability have been documented, the relationship between diversity and stability in aquatic rock pool communities is at the same time less ambiguous and more complex.

Less ambiguous because the density of both communities and individual populations was found to be less variable in more diverse rock pools. This is the first empirical study to suggest that diversity stabilizes both community and population properties. Previous studies have shown that diversity either 1) stabilizes community properties and destabilizes population properties (Tilman, 1996), or alternately, that diversity 2) stabilizes community properties but is unrelated to population properties (McGrady-Steed and Morin, 2000). My results also suggest that diversity stabilizes community properties in rock pool communities, but that the appearance of a relationship between community stability and diversity results *at least in part* from the effect of diversity on one level below the community level, i.e. the population level. In rock pool communities, community stability appears to be a function of both diversity and population stability.

The relationship between diversity and stability in rock pool communities also appears to be more complex than in many previous studies. In rock pools, environmental conditions modulate the relationship between diversity and both community and population stability. Relationships between diversity and stability were observed in both unmanipulated abiotically stable rock pools and temporary rock pools, as well as in oligotrophic experimental rock pools (Table 1; Fig.1). These results suggest that environmental conditions can modulate the relationship between diversity and stability. That environmental fluctuations and conditions could modulate diversity-stability relationships had been previously suggested (Doak et al. 1998; Ives et al. 1999), however this is the first empirical study to document a change in the relationship between diversity and stability under different environmental conditions.

Why is the relationship between diversity and stability important?

The relationship between diversity and stability is of interest for a number of reasons. Stability is a fundamental property of ecological systems (Cottingham et al. 2001). Population and community properties such as density and biomass change over time and this variability can represent important information about the functioning of ecological systems. For example, increases in variability can be signals of ecosystem stress (Odum et al. 1979), lead to higher extinction rates (Pimm 1991), reduce reliability in ecosystem properties (Naeem and Li, 1997), and reduce our ability to detect and predict change (Cyr, 1997; Cottingham et al. 2000).

Figure 1. Summary of relationships between diversity and community variability in rock pool communities shown for the natural pools. Unstable and stable refer to the relationship between species richness and community variability according to high (abiotically variable pools) and low (abiotically stable pools) scores on the Multivariate Environmental Index (Chapter 3).

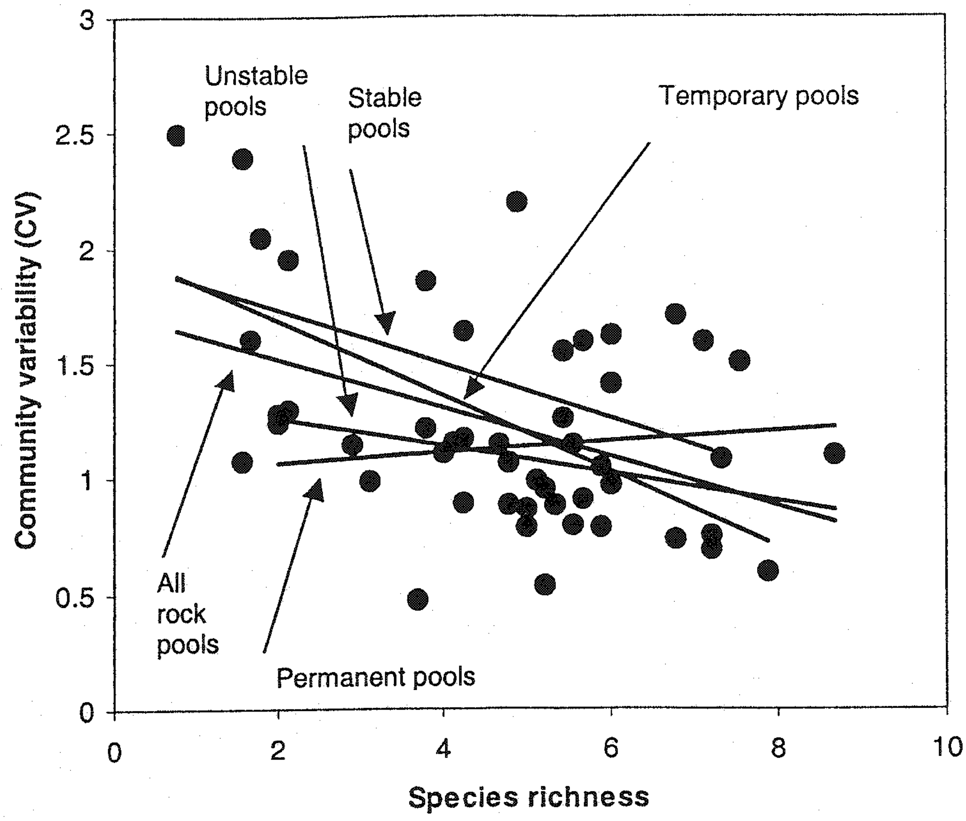
Unstable pools
Stable pools
Temporary pools
All rock pools
Permanent pools
Community variability (CV)
Species richness
0
0.5
1
1.5
2
2.5
3
0
2
4
6
8
10

Table 1. Summary of diversity-stability relationships in rock pool communities. Variable refers either to the experimental manipulation (Chapter 6) or to variable which was used to separate the rock pools into categories. Treatment refers to the sub-set of rock pools in which the relationship between diversity and stability was determined. Community corresponds to community variability. Population variability was calculated in a number of ways. Local population variability refers to the calculation of population variability presented in Chapter 3 and Chapter 5 (eq. 3). Average refers to either the calculation of population variability presented in Chapter 5 (eq. 4) or in Chapter 6 (eq. 2).

		Level		
Variable	**Treatment**	**Community**	**Population**	
			Local	*Average*
	All rock pools	Yes	Yes	Yes
Temperature	**High**	No	No	Not tested
	Low	Yes	No	Not tested
Salinity	**High**	No	No	Not tested
	Low	Yes	No	Not tested
Oxygen	**High**	No	No	Not tested
	Low	Yes	No	Not tested
pH	**High**	No	No	Not tested
	Low	Yes	No	Not tested
Disturbance regime	**Temporary pools**	Yes	No	Not tested
	Permanent pools	No	No	Not tested
Nutrient condition	**Oligotrophic**	Yes	Yes	Yes
	Mesotrophic	No	Yes	No
	Eutrophic	No	No	No

Resolving the relationship between diversity and stability is also important so that we can understand and predict the consequences of species loss. It is becoming increasingly apparent that ecologists must learn how to link population level dynamics to both community and ecosystem level processes. The roles that diversity plays in ecosystems are likely to impact all ecological levels and the consequences of this are important both theoretical and practically. If species loss results in more variable populations, it is likely that a "biodiversity feedback loop" will occur: species loss will lead to more variable populations, increased probability of local extinctions due to low population numbers (Lande, 1993), and further reductions in diversity.

Power of using both observational time-series data and experimental approaches

This is the first study to address the relationship between diversity and stability using both long-term data (Chapter 3-5) and experimental approaches (Chapter 6) and arrive at similar conclusions. While experimental studies are necessary to assign causality, laboratory and controlled field studies often suffer from a lack of relevance to natural unmanipulated systems. The identification of correlations between diversity and stability using long-term time series data (9-years) and the experimental confirmation that diversity is causally related to stability in rock pool communities represents strong evidence that diversity affects stability in these aquatic communities.

The mechanism of community stability

While a number of statistical and biological mechanisms likely affect the diversity-stability relationships in rock pools, my results suggests that diversity leads to greater community stability in part through the stabilizing effect of diversity on populations. In both the unmanipulated and the experimental rock pools, populations in more diverse rock pools were more stable than populations in species-poor rock pools. This stabilizing effect of diversity on populations has been predicted theoretically (Ives et al. 1999, Li and Charnov, 2001); however, this is the first empirical study to show that diversity may promote population stability.

Directions for future research

This was the first diversity-stability study to examine the effect on diversity on stability in the same ecosystem and with the same set of species using both long term time series data and experimental manipulations. It was also the first study to examine diversity-stability relationships under different environmental conditions.

Despite a large body of theoretical work on diversity-stability relationships (May 1973; King and Pimm 1983; Doak et al. 1998; Loreau, 1998; Hughes and Roughgarden, 1998; Tilman et al. 1998; Ives et al. 1999; Yachi and Loreau, 1999; Ives et al. 2000; Ives and Hughes, 2002) few empirical tests of the relationship between diversity and stability have been attempted (see Shlapfer and Schmid, 2000 for a review). Therefore many interesting questions remain to be answered.

First, it would be useful to test existing long-term time series data in a wide range of ecosystems. This has yet to be done, however existing data sets could be used to form a more comprehensive picture of diversity and stability patterns. Second, manipulative experiments that alter both diversity and environmental conditions are needed to assess how the relationship between diversity and stability changes under different disturbance regimes. Third, tests of the diversity-stability relationship have in most cases been limited to species-rich communities, and communities strongly structured by competition. Species loss may affect low diversity communities much more strongly than high diversity communities, thus tests in low diversity communities are imperative to assess the effects of species loss on these systems. While recent theoretical studies have suggested that competition should not affect the overall positive relationship between diversity and stability, empirical tests of this idea are needed. Fourth, it is important to know what long-term effects increasing variability might have on communities, and how feedback loops between species loss and increased variability might occur. Fifth, more studies are needed in multi-trophic communities. While theoretical work suggests that the patterns seen in communities of primary producers or consumers should also been seen in communities with multiple trophic levels, there have been no explicit manipulations of diversity at different trophic levels to determine if the general positive relationship between diversity and stability seen in simpler communities holds in more complex communities.

The effects of species-loss on ecosystem functioning and stability remains a rich area for ecological study, and determining the practical consequences of species-loss on ecosystems is imperative given that biodiversity is declining faster at the present time than at any time in geological history (McCann, 2000). However, the body of knowledge developed to date on the consequences of species-loss suggests that biodiversity is important to the continued functioning of ecosystems and unchecked will impair the ecosystem services on which people depend (Wilson, 1992).

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Appendix A:

Mechanisms of diversity-stability relationships

Is the diversity-stability relationship in rock pools a result of a statistical mechanism?

Statistical averaging and z –values

To assess whether statistical averaging contributed to the positive relationship between diversity and stability, I calculated z-values for each species in the community (Table 2). z – values represent the degree to which the variance in density of a population scales with its mean density, and this relationship (the mean-variance relationship; see Table 1.1) has been hypothesized to influence the relationship between diversity and stability. The positive relationship between the mean and the variance in density can be described using Taylor's power function (Taylor 1961) $s^2=cm^z$, where s^2 is the variance, c is a constant, m is the mean and z is the scaling coefficient, such that larger values of z indicate that the variance in density increases more rapidly than the mean. Tilman and colleagues (Tilman et al. 1998, Tilman 1999) have established that the value of the scaling coefficient z affects statistical averaging. Assuming that all species have identical density and variability (CV), statistical averaging will dampen community variability when $z > 1$. In grasslands, z is between 1.2 and 1.4 (Tilman et al. 1998; Tilman, 1999). For most species z values are between 1 and 2 (Murdoch and Steward-Oaten, 1989), suggesting that if all else remains equal, statistical averaging will operate in most communities.

For the rock pool invertebrate species, z values ranged from 0.5 to 0.99 (mean 0.79 ± 0.15; Table 2). These low z values suggest that statistical averaging is not a significant contributor to reductions in community variability with greater diversity.

However, low z values have also been predicted to result in increases in population variability when diversity increases (Tilman, 1999). This postulate was not supported in the rock pool communities, where populations appear to be stabilized by increasing diversity despite having low z values. This inconsistency with previous theoretical work may be due to the restrictive assumptions of equal abundance and identical CV's for each species used to model the consequences of changing z on population and community stability (see Tilman, 1999). Furthermore, it is unlikely that the densities of different populations would fluctuate with the same magnitude (i.e. identical CV's) especially in a diverse community. Thus, the relationship between diversity-stability in rock pool communities does not appear to be driven primarily by a statistical mechanism.

Biological mechanisms

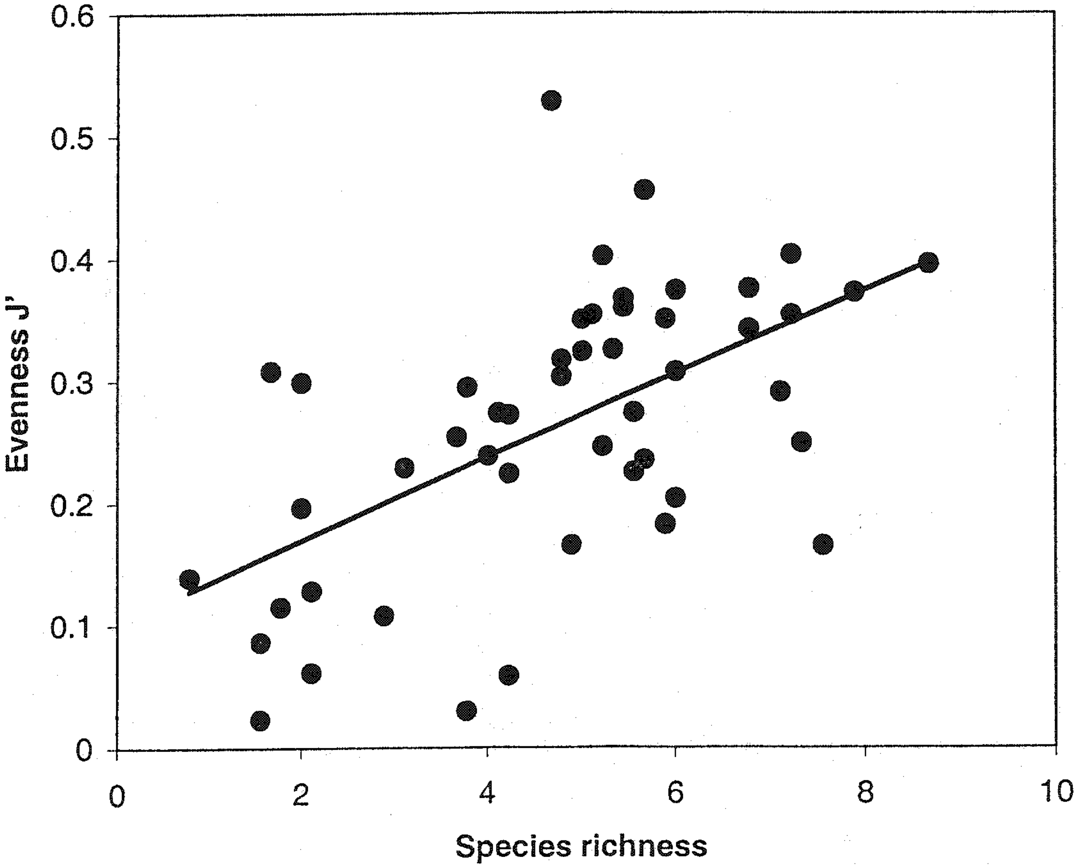
Evenness

In addition to statistical mechanisms, there are a number of biological mechanisms that have been proposed to account for positive relationships between diversity and stability: evenness, overyielding, and competition. Other than competition, these mechanisms have been hypothesized to contribute to the strength of statistical averaging (Cottingham et al. 2001). For example, the greater the evenness, the greater the contribution of each species is to decreasing variability due to statistical averaging. If only a few species dominate, there should be little statistical averaging. In rock pool communities, five species account for > 80% of individuals, with the rank-abundance

Table. 1. z-values showing the relationship between the standard deviation of density and mean density for each rock pool species. N refers to the number of rock pools a species was found in.

Species	z-value	n
Nitocra spinipes	0.801	47
Orthocyclops modestus	0.895	46
Armases miersii	0.775	39
Potamocypris sp.	0.969	36
Nematode sp.	0.824	36
Ceratopogonid sp.	0.661	33
Culex sp.	0.674	33
Cypridopsis cf. mariae Rome	0.913	31
Heterocypris sp.	0.893	31
Cytheromorpha sp	0.577	30
Paracyclops fimbriatus	0.494	29
Oligochaete sp.	0.529	26
Gyratrix hermaphroditus	0.669	21
Ceriodaphnia rigaudi	0.104	20
Leidigia sp., *Alona davidii*	0.787	20
Midge larvae	0.742	18
Polychaete T	0.982	15
Cypricercus sp.	0.237	13
Dolichopodid sp.	0.869	12
Metis sp.	0.987	11
Candona sp.	0.975	10
Coleoptera sp.	0.792	10
Polychaete J	0.962	8

Figure 1. The relationship between species richness and evenness.

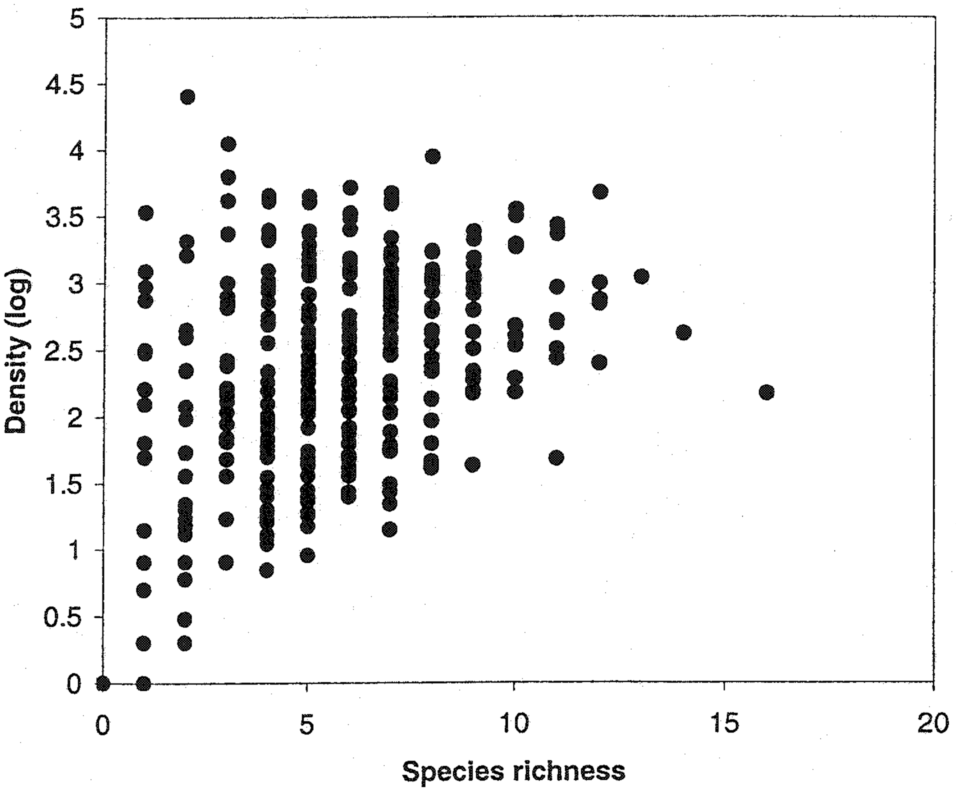

0.6
0.5
0.4
0.3
0.2
0.1
0
Evenness J'
0
2
4
6
8
10
Species richness

structure of the rock pool communities showing substantial unevenness (Chapter 2; Fig. 1). This suggests that reductions in variability are not simply a result of evenness. However, as evenness and the number of species are correlated in the natural rock pools (Fig. 2), evenness may contribute to the negative relationship between diversity and community variability.

Overyielding

Overyielding, an increase in the total community biomass or density above that predicted by the biomass or density of each species in monoculture, has been hypothesized to contribute to variability reductions by widening the range of scaling coefficients z that contribute to reduced variability. In rock pool invertebrate communities, there is no evidence of overyielding except in pools with very low community abundance > 200 individuals per litre (Romanuk and Kolasa, 2002). This is not surprising as in aquatic systems, the diversity-productivity relationship is generally unimodal and skewed towards low diversity (Waide et al., 1999; Dodson et al., 2000).

Figure 2. Overyielding. Abundance ($\log_{10}$) increases with species richness in rock pool microcosms (n = 365). Data are shown from 49 pools over 9 sampling dates. Pools with no individuals (that were dry at the time of sampling) are not plotted.



5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Density (log)
0
5
10
15
20
Species richness

Competition

Competition has been invoked as a mechanism for reductions in variability with increasing diversity (Tilman, 1999). In highly competitive communities, a change in the abundance of one species should result in changes in the abundance of the other species. As competition increases, this effect is expected to increase, such that in the most competitive communities there would be complete compensation and no changes in the total community property would be observed. In aquatic systems, competition is likely somewhat weaker than in grassland communities, however there is still some evidence that competition may explain part of the reduction in variability as richness increases. In the experimental rock pools (Chapter 6) 57% of covariances between species were negative in the oligotrophic microcosms, while only 34% and 36% respectively were negative under mesotrophy and eutrophy, suggesting a relaxation of competitive interactions as nutrients increased. It has been hypothesized that an increase in the positive covariances between species should dampen, but not entirely cancel, the relationship between diversity and community variability. We see some support for this hypothesis as under mesotrophy and eutrophy there was no relationship between diversity and community variability in eutrophic microcosms.

Insurance effects

I initially predicted that disturbance and environmental variability would promote increasing positive covariances among species leading to a reduction in the effect of species richness on community variability in more variable rock pools, i.e. there would be either no relationship or only a weak relationship between diversity and community stability in environmentally variable pools. This prediction was based on the insurance hypothesis (Yachi and Loreau, 1999) which predicts that increases in diversity lead to a greater diversity of species traits and larger differences in species responses to environmental fluctuations. When a habitat is disturbed, especially by a disturbance such as desiccation which removes all living biomass or forces species into diapause, positive covariances between species should increase (i.e. they will all be affected adversely by the disturbance) weakening the positive relationship between diversity and stability.

This hypothesis was supported by the results presented in Chapter 3, where the was no relationship between diversity and stability in the more environmentally variable pools. However, the consequences of the insurance hypothesis were not supported by the analysis presented in Chapter 4, where the correlation between diversity and stability was strong in temporary pools and absent in permanent pools.

These seemingly contradictory set of results can be explained by a number of factors. First, there was no relationship between abiotic variability (Chapter 3) and susceptibility to desiccation (Chapter 4). This was true for variability in pH, temperature, salinity, and oxygen, suggesting that susceptibility to desiccation and abiotic variability are unrelated and therefore are not analogous in terms of the their effects on diversity-stability relationships. Second, desiccation is a massive disturbance, removing all living biomass or forcing diapause in species able to survive through the dry phase. In temporary pools, diversity was strongly related to a decrease in community variability; however, community composition also changes systematically from temporary to permanent pools, with a decrease in desiccation-prone species such as insect larvae.

The negative diversity-community variability relationship in abiotically stable pools (and the absence of any relationship between diversity and community variability in abiotically variable pools) is likely due to the dampening effect of increasing positive covariances between species as environmental variability increases. In contrast, the negative diversity-community variability relationship in temporary pools is likely a statistical insurance effect. The higher the number of species present, the higher the probability will be that some of these species are resistant to desiccation. These species are able to increase in abundance rapidly following a desiccation event, which likely contributes to the maintenance of lower variability in more diverse communities. The presence of species highly adapted to desiccation ensures that some species will survive the dry phase.

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Appendix B:

Permission to include published material

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February 25th, 2002

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