THE ROLE OF ENVIRONMENTAL VARIABILITY ON DIVERSITY

A MULTISCALE STUDY OF THE ROLE OF ENVIRONMENTAL VARIABILITY ON THE DIVERSITY AND ABUNDANCE OF ROCK POOL COMMMUNITIES

By

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A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Masters of Science

McMaster University

September 2003

Master of Science (2003) McMaster University

(Biology) Hamilton, Ontario

Title: A Multiscale Study of the Role of Environmental Variability on the Diversity and Abundance of Rock Pool Communities

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Number of Pages: 155

ABSTRACT

One of the main goals of ecological research is to understand the factors that determine how communities are structured over both space and time. However, our understanding of any system is largely a function of the scale at which we make our observations. Thus, the mechanisms that determine patterns in community structure are likely to change depending on the scale of observation. This thesis explores how environmental variability affects community structure and species performance, and how the resulting patterns change as a function of scale. Specifically, I asses the role of variability in temperature, oxygen, pH, and chloride, on species richness, abundance, diversity, and species performance, at three observational scales: micro-spatial, local-temporal, and landscape-temporal scales, in 49 natural erosional rock pool microcosms, located on the northern coast of Jamaica. I found that while environmental variability was not a primary determinant of species richness or abundance, it did play a role in determining species compositions in the pools. I also show that community patterns are strongly affected by the scale of observation. Recognizing scale-dependent changes in community patterns is a prerequisite for predicting the consequences of changes in ecological systems induced by variability in abiotic factors.

ACKNOWLEDGEMENTS

All data used in this dissertation was collected at Discovery Bay Marine Laboratory, University of the West Indies, Jamaica. I would like to thank the entire staff of the research centre and especially Mrs. June Lawrence for her care and support. Thank you to Jurek Kolasa for his funding and research support.

I would like to thank my supervisor, Dr. Jurek Kolasa, for his guidance, expertise, and friendship. Dr. David Rollo has provided me with direction and inspiration and a kind and listening ear. Also, thank you to Dr. Nigel Waltho for providing me with helpful suggestions that have kept my research focused. My committee members have not only been excellent teachers of wisdom and knowledge, but also teachers about life lessons. They have supported me through many trials and errors and for that I thank them all.

Thank you to NSERC for awarding me the NSERC PGS B award. This financial support was greatly appreciated and provided me the opportunity to focus entirely on my research.

I would like to thank Dr. Tamara Romanuk for being my mentor. Your understanding and guidance have helped me immensely. Your passion for ecology inspired me and your friendship has enlightened me. Also, April Hayward has provided me with insight on the world of statistics. She has been my foundation of support for life in Hamilton. I will always treasure both their gifts of friendship.

Special thanks goes to Pat Hayward, Susan Marsh, Andy Biggers and the Biology department office staff, for their support and encouragement. Last but not least, thank you to my family; Lloyd, Helen and Janet Reid. They not only supported me emotionally during my higher education, but also financially. Thank you and I love you all.

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Introduction: The role of Environmental Variability on Biodiversity

Introduction

Biological diversity, the "...variety and variability among living organisms and the ecological complexes in which they occur" (Noss, 1990) is a fundamental descriptor of ecological communities (Yachi and Loreau, 1999). Why biodiversity changes within and across habitats through space and time is of great interest to community ecologists (Drake, 1990). To understand community structure, ecologists need to focus on the mechanisms that either develop, or maintain patterns of biodiversity (Waltho, 1997).

Abiotic factors interact with biotic factors in determining community structure (Whittaker *et al.*, 1973; Townsend *et al.*, 1983; Corkum, 1989; Dunson and Travis, 1991; Wellnitz and Poff, 2001). Biotic factors such as predation, competition, and mutualism affect species diversity (Pianka, 1994). Abiotic factors determine potential niches, affecting the survival of organisms in the environment and the identity of species in the community (Dunson and Travis, 1991).

Abiotic factors that have been shown to affect species diversity include climate, elevation, disturbance, habitat heterogeneity (structural complexity), and physicochemical environmental variability. For example, both increasing latitude and elevation have been associated with a decline in species diversity (Davidowitz and Rosenzweig, 1998; Pianka, 1966a). High levels of disturbance may also render the habitat temporarily unsuitable which disrupts species life cycles, thereby decreasing species diversity (White and Pickett, 1985; Aspbury and Juliano, 1998). Habitat heterogeneity increases species diversity because it can increase the number of microhabitats, thereby increasing the potential for various species to colonize the space

within the microhabitats (Wilkinson, 1999). Finally, physicochemical variables, such as depth, volume, surface area, temperature, pH, oxygen and salinity, can both positively and negatively affect species richness and abundance patterns (Ranta, 1982; Fairweather and Underwood, 1991; Grillet *et al.*, 2002a, 2002b; Kochsiek *et al.*, 1971; Norberg and DeAngelis, 1997; Wellnitz and Poff, 2001).

Hierarchy theory: A Matter of Scale

There are a variety of mechanisms that are implicated in determining community structure. However, the importance of these mechanisms differs among communities, making it difficult to generalize about the determinants of community structure (Drake, 1990). Understanding the hierarchical nature of a community and what mechanisms function at each hierarchical level may help to explain how communities are structured.

The central idea of hierarchy theory is that an entity such as a habitat can be divided into smaller units and subunits, thereby creating a hierarchy of subdivisions (Kolasa and Biesiadka, 1984; Kotlier and Wiens, 1990). Within each hierarchical subdivision certain community patterns dominate, and within that level, there is generally a predominant mechanism that determines the community pattern (Allen and Starr, 1982; Kolasa, 1989; Kotliar and Wiens, 1990). Processes such as competition, habitat preference, predation, and abiotic influences can be viewed as mechanisms that sort species into various microhabitats and levels, thereby creating these subdivisions of habitats (Kolasa, 1989). Thus, knowledge about the hierarchical structure of the habitat is an important element of describing the responses of organisms, diversity, and abundance

at different hierarchical levels (Kotliar and Wiens, 1990). For example, Kolasa (1989) used species relative and actual abundances for eight different biotic communities (e.g. rodent, bird, turbellarian etc.) to show that species cluster by range and abundance. His model demonstrates that the nested hierarchy of habitats (environmental structure) contributes to the structure of biotic communities. Overall, by using empirical data, Kolasa (1989) argued that both biotic and abiotic controlling factors, sort species into various microhabitats and levels.

Organisms respond to hierarchical levels of habitat along a gradient from generalists to specialists (Wiggens *et al.*, 1980; Kolasa, 1989; Bell *et al.*, 1999). Generalists are able to exist at high levels within the habitat hierarchy, or low levels of resolution within the habitat. Essentially, habitat generalists are those species that have large geographical ranges and high abundances (Therriault and Kolasa, 2000). Conversely, specialists can survive only at low levels within the habitat hierarchy, or at high levels of resolution within the habitat (Kolasa, 1989). Organisms being categorized as a generalist or specialist are the result of both biotic and abiotic mechanisms; specifically, abiotic controlling factors, such as the physical characteristics (niche) of the habitat that sorts species into their respective level and habitats (Kolasa, 1989). In short, determining the type of species (generalist or specialist) that persist in a habitat can provide information on the environmental controls and vice versa (Kolasa *et al.*, 1996).

The mechanisms which shape the patterns of species in each hierarchical level change with observational scale (Legendre *et al.*, 1986). For example, at the community scale, processes such as habitat heterogeneity may sort species into different

microhabitats and levels, while at the population scale, processes such as predation, and competition may shape the organization of species in their environment. A change in observational scale often results in different interactions and relationships between both species and species and their environment being observed (O'Neill and King, 1998). For example, Anderson et al. (1981) concluded that differences in patterns of diversity of coral-reef fish reflected analysis done at different scales of observations.

Using a single, often inadequate, observational scale can result in drawing incorrect conclusions about species patterns (Allen and Hoekstra, 1991). With this in mind, a multi-scale comparison (looking at more than one scale) implies different levels of resolution, thereby allowing a more complete picture of biological organization (Allen and Wyleto, 1983; Rahel, 1990). Community metrics, such as species richness and abundance, are sensitive to differences in scale; therefore, the most effective studies on species richness and abundance should look at patterns and processes over multiple scales (Wiens, 1989). For example, Hammer and Hill (2000) found that the effects of forest disturbance on species diversity differed at large and small spatial scales. As the scale decreased, a positive effect on diversity occurred. Research with an emphasis on community patterns at an arbitrary scale, without consideration of other scales, or the hierarchical nature of the ecosystem, is likely to be incomplete (Wiens, 1989; Kotliar and Wiens, 1990; Rahel, 1990).

Community structure and composition varies over time (Wiens, 1989) and within space (Menge and Olson, 1990; Pickett *et al.*, 1997). Temporal scales can range from seconds, minutes, and hours to long periods of time such as years, decades, and

millenniums. Furthermore, diversity fluctuates within a region (landscape or global scale), among sites in a region (intermediate scale), within a site (local scale), or in a location within the site (micro scale) (Menge and Olson, 1990).

To date, many ecological studies have only been executed across small areas over short time periods. Surprisingly, 50% of experiments published in the journal of Ecology, over a 7 year period (1980-1987), were carried out on portions of land less than 1 meter in diameter (Kareiva and Anderson, 1986). Likewise, Tilman (1989) reported that a mere 7% of experiments were carried out on a time scale greater than 5 years. Large spatial and temporal scale patterns and processes of natural systems were therefore, incompletely understood. Fortunately, there has been a recent increase in studies looking at processes at different grains and extents of scale and over various time scales. (Wiens, 1989; Wu, 1999).

Physicochemical Factors

Temperature, oxygen, chloride, and pH in aquatic ecosystems function as constraints which limit which species will occupy which habitats. As a result of these constraints, some aquatic habitats will be more suitable for species to exist than other aquatic habitats (Poff, 1997; Wellnitz and Poff, 2001). For example, species richness and abundance of aquatic zooplankton and insect communities are significantly higher in less saline aquatic conditions (Kochsiek *et al.*, 1971; Grillet *et al.*, 2002). Also, varying pH and variations in temperature have a negative relationship with both species richness and abundance of zooplankton (Townsend *et al.*, 1983; Norberg and DeAngelis, 1997). High

water temperature results in reduced dissolved oxygen in the water column. Since species need oxygen to respire and function efficiently, an increase in temperature which reduces dissolved oxygen results in species being unable to tolerate such conditions and therefore decreases diversity (Truchot and Duhamel-jouve, 1980). Indeed, the chemical aspect of the niche is an important influence on community structure.

Environmental Variability within Rock Pools

Rock pools are a particularly appropriate ecosystem in which to study the effects of environmental variability on community structure because the pools are numerous, small, and have natural aquatic abiotic fluctuations within them (Pajunen, 1982). Studies in coastal Jamaican rock pools show that temperatures within the pools range from 21 to 36.6 °C and pH values range between pH 5.12 to 11.12. Salinity varies depending upon the weather and evaporation rates. Dissolved oxygen values fluctuate between 0 and 19.6 mg/L (Romanuk and Kolasa, 2002). Indeed, rock pool environments have a high degree of variability in environmental conditions which makes them a suitable ecosystem to study how physicochemical conditions affect biota (Schuh and Diesel, 1995; Diesel *et al.*, 2000).

Therriault and Kolasa (1999) show that as temperature, salinity, pH and dissolved oxgyen in rock pools increases, species richness decreases, which means that as the physical conditions become more variable they reduce that ability for species in the system to persist (Kolasa *et al.*, 1998). Similarly, Romanuk and Kolasa (2002) found, using the same rock pool communities, that variability in pH and oxygen, had a negative

relationship with species richness. While it is expected that abiotic conditions exert control on the persistence and presence of species, little is known about how much the variability in physicochemical environmental variables affects species richness and abundance.

Previous work on the rock pool community

Past investigations by Kolasa and associates focused on the role of abiotic environmental factors on the local scale community patterns in both spatial and temporal dimensions. However, the role of abiotic environmental factors on community patterns has not been studied at multiple spatial scales. In past studies, measurements of environmental variables (salinity, oxygen, pH and temperature) and samples of biota were conducted in the middle of each pool (local scale). These local measurements were probably not sufficient to resolve microhabitat effects on biodiversity because they fail to provide measurements for each location within each pool. In this study, finer scale sampling with more attention to microhabitat conditions was done to determine the role of microhabitat environmental variability on species richness and abundance of invertebrate species. In this thesis I will compare these results on micro-scale variability to the role of environmental variability on diversity and abundance at other spatial and temporal scales. Specifically, I will examine the role of environmental variability on invertebrate species richness and abundance at three observational scales of study (micro-spatial, local-temporal and landscape-temporal scales). Micro-spatial scale is a within-pool scale for each rock pool at one time (on one sampling date). Local-temporal scale is

a pool by pool scale for each of the 49 rock pools over time. Landscape-temporal scale is an aggregate scale for all 49 rock pools over time.

At the micro-spatial scale, physical measurements such as pH, salinity, oxygen and chloride, of individual microcosms focus on the internal differentiation of pools, in particular, three dimensional picture of that differentiation. This work hypothesizes that at the micro-spatial scale and the local scale over time, greater internal spatial differentiation of pool conditions decreases diversity and abundance. Increased variation of abiotic conditions within a pool may exceed species tolerances and therefore decrease the number and abundance of species. However, I hypothesize that at the landscape scale, greater internal spatial differentiation of pool abiotic conditions will increase diversity and abundance. Increased variation in abiotic conditions across all pools will increase the potential for species to find a suitable environment to exist (Romanuk and Kolasa, 2002; Therriault, 2000).

The System

I investigated a system of Jamaican coastal rock pools inhabited by invertebrate communities. This system is suitable to assess the role of environmental variability on diversity and abundance at different scales of study because the rock pools have natural fluctuations of physicochemical properties and environmental conditions, have no confounding affects of geographical variation (pool communities from a single geographical area), have well defined boundaries, and also span several spatial scales. Furthermore, the numerous invertebrate species and communities within each rock pool

are a part of a common species pool. In short, the coastal Jamaican rock pool system has the potential to provide a complete picture of community processes working at multiple scales (Kolasa *et al.*, 1998; Romanuk and Kolasa, 2001, 2002; Schuh and Diesel, 1995).

The 49 small aquatic rock pools are formed on an exposed fossil reef located at Discovery Bay Marine Laboratory, in a small bay called the Blue Maze (18°28'N/77°25'W). The Blue Maze inlet is approximately 50 m across and all pools were located within 5 m of the nearest neighbor. The rook pools are located between terrestrial and inter-tidal habitats. These supra-tidal rock pools are shallow (less than 50 cm deep), small (~ 20 to 60 cm width) and are predominantly rain-fed, and are therefore susceptible to desiccation. During the day time the high solar radiation results in water evaporating from the rock pools. This can cause dramatic variation in abiotic conditions and can even lead to drought (Kolasa *et al.*, 1996; Schuh and Diesel, 1995). Sea water is sometimes added to the pools because of spray from waves. Also, unusually high tides and surges of spray that come through fissures within the rocks can cause the aquatic pools to have a range of salinities. These conditions result in pools with a wide range of salinity from true freshwater pools through to brackish water and hyper saline pools (Kolasa *et al.*, 1996; Schuh and Diesel, 1995; Therriault and Kolasa, 1999a).

The pools contain at least 70 different types of zooplankton and benthic invertebrate species (Therriault and Kolasa, 1999, 2000; Romanuk and Kolasa, 2001). Because of Jamaica's tropical weather, there is less seasonal variation, thereby giving invertebrate communities the potential to inhabit the rock pool system year round. A

complete characterization of the physicochemical conditions and the rock pool invertebrate assemblages are presented in the Methods section.

Materials and Methods

Materials and Methods

Study Site

This study was conducted using data on 49 natural rock pools located around the Blue Maze (Fig. 2.1) inlet located near the Discovery Bay Marine Laboratory on the North coast of Jamaica. The rock pools form by rainwater erosion on fossil reefs. The pools contain various amounts of fine sediments, detritus, leaf litter, and coal rubble (Fig. 2.2) (Schuh and Diesel, 1995; personal observation, 2002).

The pools length ranged from 14 to 248 cm (mean length = 56 cm +/- 35 standard deviation, SD),10 to 188 cm in width (mean width = 32.9 cm +/-26.8 SD), 1-37 cm in depth (mean depth = 12.8 cm +/- 8.3 SD). Elevation of the pools above sea level ranged from 1-235 cm (mean = 76.6 cm +/- 80.1 SD) at high tide, with the tide usually not exceeding 30 cm. The only pools that were tidal were pool numbers 16, 17, 22, 49 and 50 (tidal flooding did not occur daily for all these pools). The other 45 pools received primarily rainwater and the occasional sea spray under storm or wave conditions.

Figure 2.1. View of the study site, the Blue Maze, at the landscape scale (all 49 pools shown). Circled rock formations contain the rock pools used in this study. The distance from one side of the bay to the opposite side is 50m.

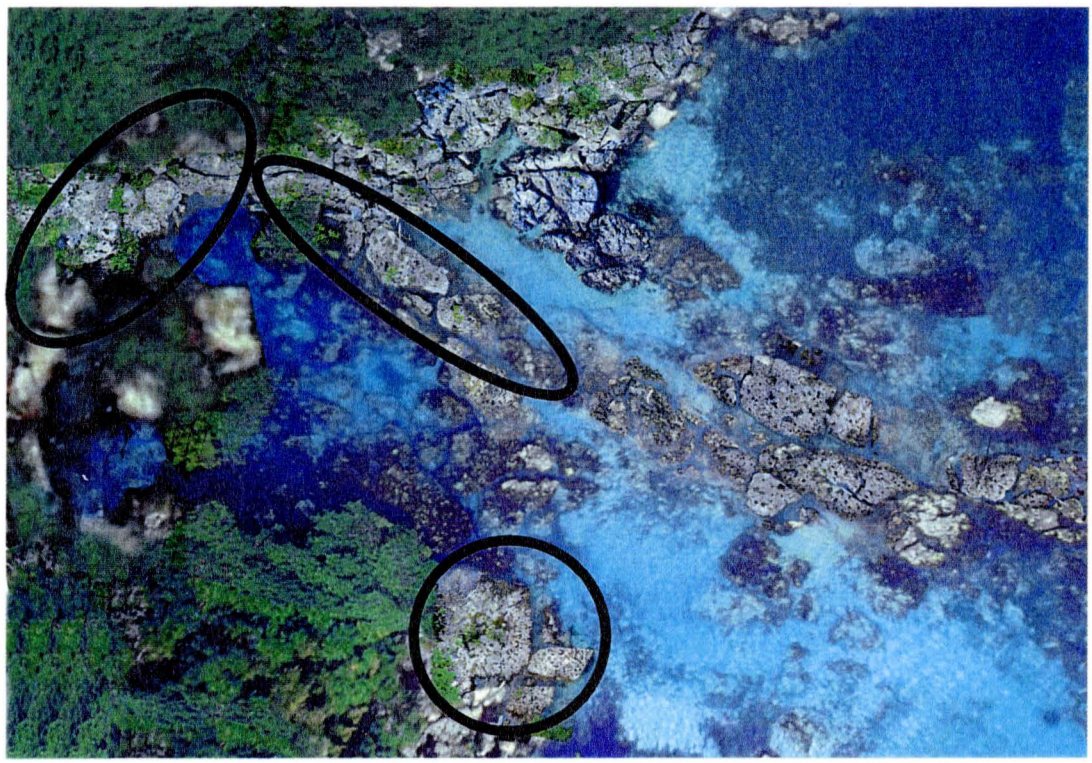
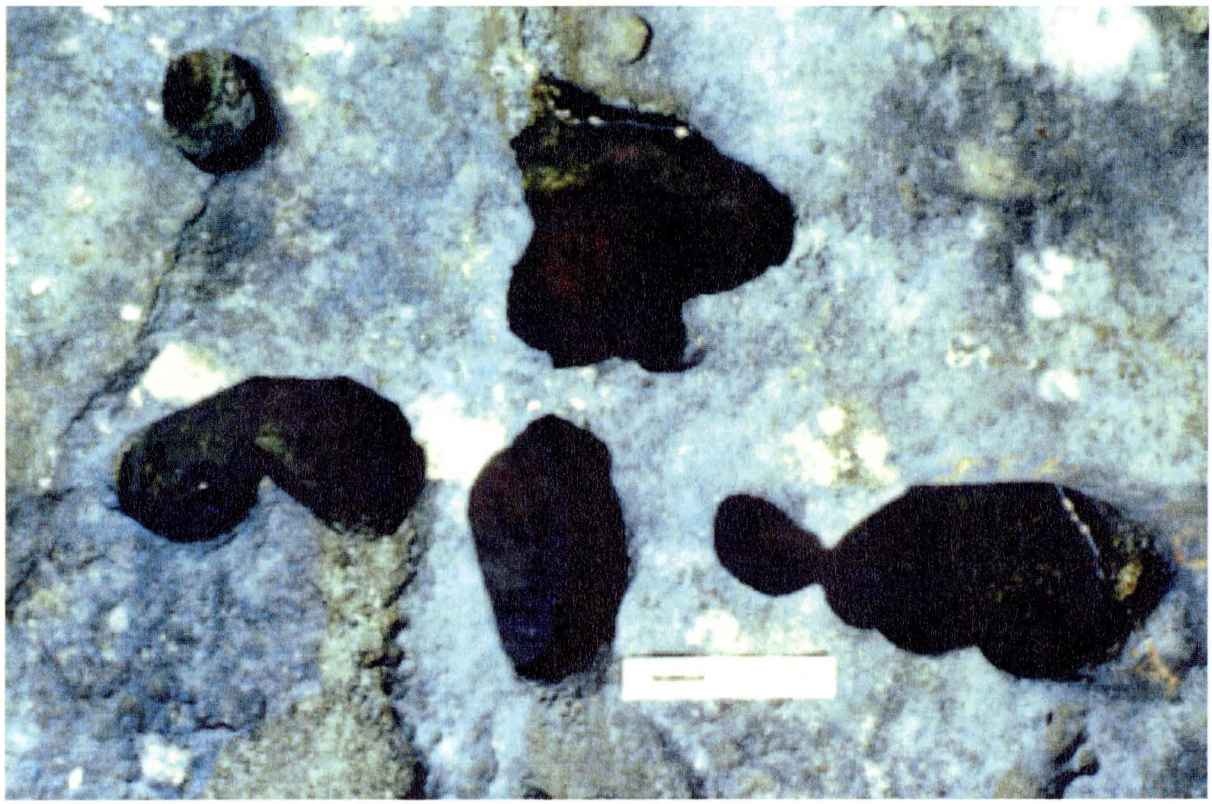


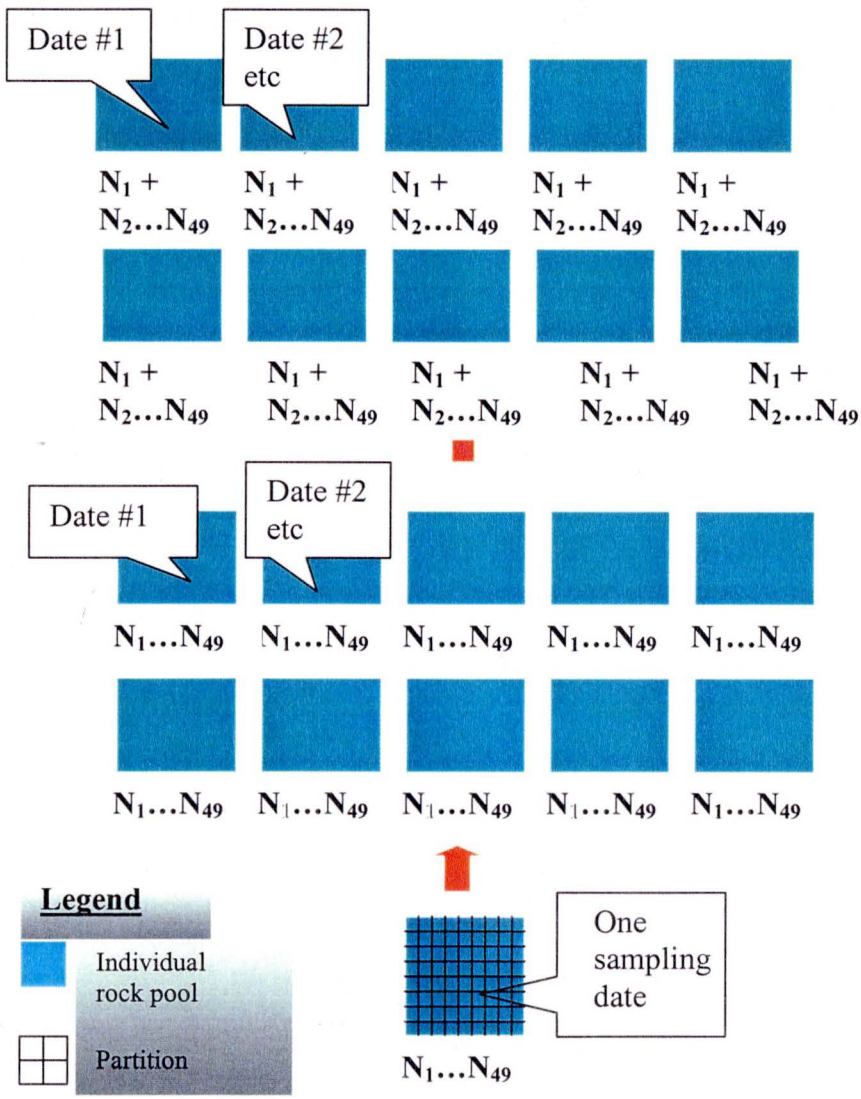
Figure 2.2. This photo was taken from above the surface of rock pool 9. It shows various forms of detritus and rubble on the pool bottom.



Study Scales

This study was conducted at three scales of observation: an aggregate scale for all 49 rock pools over ten years (landscape-temporal scale), a pool by pool scale for each of the 49 pools over time (local-temporal scale), and a within-pool scale for each pool at one time (micro-spatial scale) (Fig. 2.3). The landscape-temporal scale is the highest scale of the study. At this scale, focus is on the effects of abiotic factors on community patterns (species richness and abundance) occurring across all rock pools, for ten different sampling dates. The local-temporal scale focuses on the role of abiotic factors on community patterns in both spatial and temporal dimensions (i.e. sampling occurs once, within each rock pool for each of ten sampling dates). Finally, the micro-spatial scale focuses on internal abiotic differentiation of pools. Specifically, this scale looks at the effects of three dimensional abiotic differentiations on community patterns (abiotic environmental measurements were collected from multiple locations and depths within each rock pool at only one sampling date). Table

Figure 2.3. Scales used in this study. Micro-spatial partitions the pool into microhabitats. Local-temporal is at the level of an entire pool, on ten sampling dates. Landscape-temporal is an aggregate of all 49 pools together for each of ten sampling dates.



Landscape-temporal scale

is an aggregate of all 49 pools together for each of ten sampling dates

Local-temporal scale

is at the level of an entire pool, on ten sampling dates

Micro-spatial scale

partitions each of the 49 pools into microhabitats

Biotic Sampling and Community Composition

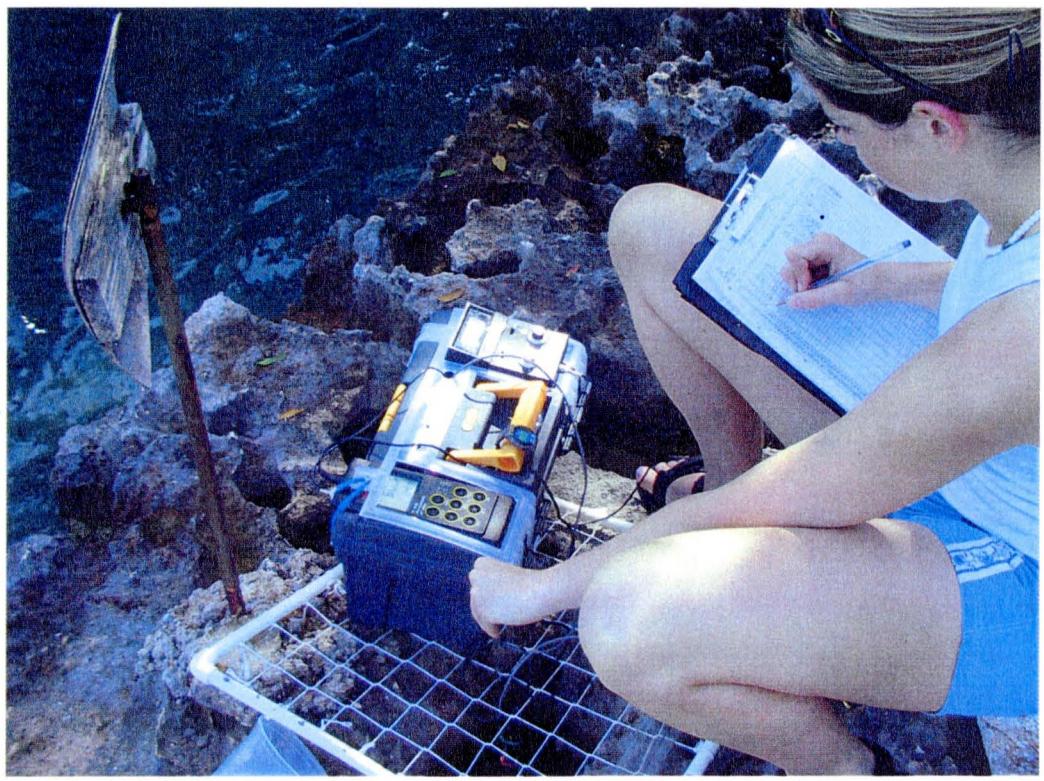
Samples used in the landscape-temporal and local-temporal analyses spanned ten sampling dates: December of 1989, January of 1990, 1992, 1993, 1994, 1996, 1997, 1998, 2001, and 2002. Samples collected for the analyses at local-temporal and landscape-temporal scales were collected from the rock pools once annually on the above mentioned sampling dates, within the time frame of one hour. Samples used in the micro-spatial analysis were collected once for each pool within a two week period, in January of 2002. The local-temporal and landscape-temporal samples were collected within one day after abiotic samples had been collected. For all biotic collections, the pool was stirred to dislodge organisms from pool walls and to homogenize their distribution. Next, 500 mL of water and sediments were taken from each of the stirred pools. The water and sediment were then passed through a 63 μm net into a collecting container and then immediately preserved in a 50-70% ethanol. Organisms were then counted and identified in the laboratory. Over 70 different invertebrate species have been identified in the rock pool system. The full list of taxa identified to date include: Turbellaria (7), Polychaeta (5), Oligochaeta (2), Nematoda (1), Ostracoda (20), Copepoda (6), Decapoda larvae (crab) (1), Cladocera (4), Decapoda (shrimp) (3), Isopoda (1), Amphipoda (1) and Insecta (18) (Appendix 1).

Abiotic Sampling and Variables

Micro-spatial Scale

I measured four abiotic attributes during January of 2002 in order to determine the spatial abiotic differentiation within each rock pool. Oxygen, temperature, pH, and chloride ion were measured within each of the 49 pools (see Appendix 2 for chloride measurement information). Measurements were taken at locations that were separated by 5 cm, and at a maximum of 4 different depths within each location (1 cm, 6 cm, and 11 cm below the surface, and at the bottom of the pool). Temperature and pH were measured using a Hanna meter, HI-9025. Dissolved oxygen and chloride were taken using Lazar labs micro probes for chloride and oxygen. In order to ensure that each measurement was taken 5 cm apart within the pools, a 50 by 50 cm grid was constructed and placed over the top of each rock pool. Each square within the grid system was 5 cm by 5 cm. The micro probes were then gently dropped through the grid system, at the bottom right hand corner of each grid location, into the pool below (Fig. 2.4).

Figure 2.4. A 50 cm by 50 cm grid was placed over top of the rock pool to maintain a 5 cm separation of each set of abiotic measurements taken by the micro probes.



Local-temporal and Landscape-temporal Scales

Four abiotic attributes of the rock pools, temperature, dissolved oxygen, pH, and chloride, were measured in order to determine their effects on the invertebrate fauna. These abiotic factors were measured on the same sampling dates for which the biotic samples were collected. Measurements for each variable were taken in each of the 49 pools, within one hour. Temperature and pH were measured with a Hanna meter, HI-9025. Dissolved oxygen was measured using an oxygen meter and Data Sonde. Salinity was measured using a refractometer.

Data Analysis

Three community metrics, species richness, abundance, and diversity, Shannon-Weiner index (H'), were calculated for each pool for a) one sampling date (the micro-spatial scale), or b) as the mean of ten sampling dates (local-temporal scale). Species richness is defined as the total number of species observed in a defined sampling unit measured at one observational scale (Magurran, 1988) (Table 2.1). Abundance is defined as the total number of individuals in a sampling unit, also measured at one observational scale. Abundance was log transformed in order to satisfy the assumption of normality for the statistical analyses performed. The Shannon-Weiner index was used to calculate diversity, H'. Diversity index, H', incorporates both the number of species and the number of individuals. The Shannon-Weiner index was used because both dominant and rare species contribute equally to this measure of diversity (Magurran, 1988). H', was

calculated as the $H' = -\sum p_i \ln p_i$ where p_i is the proportion of individuals found in the *i*th species (Magurran, 1988).

At the micro-spatial scale, the environmental variability measure of each pool was expressed as a geometric mean of the standard deviations (SD) of the four abiotic variables (temperature, oxygen, pH, and chloride), on one sampling date. Micro-spatial environmental variability values were not normally distributed and were therefore log transformed. At the local-temporal scale, environmental variability was expressed as a geometric mean of the standard deviations (SD) of oxygen, temperature, pH, and salinity for each pool, over all ten sampling dates (including January 2002 spatial data, where pool data were averaged in order to obtain an overall standard deviation for each pool). At the landscape-temporal scale, environmental variability was expressed as a geometric mean of the standard deviations (SD) of oxygen, temperature, pH, and salinity for all pools together during one sampling date. Thus, there were ten landscape environmental variability values in total for ten different sampling dates (Table 2.1).

Five pools were not included in the statistical analyses because the data for these pools were either incomplete, or the pools dried up during the course of the study. Thus, pool number 6, 24, 25, and 45 were excluded.

Univariate regressions were used to determine the effects of both independent abiotic variables and environmental variability on species richness, abundance and H' in all rock pools and at three scales of study (micro-spatial, local-temporal and landscape-temporal scale) (Fig. 2.5).

Multiple regression analyses were used in order to determine whether species richness, abundance and H' were affected by the environmental variability (Fig 2.6).

Because absolute salinity has been suggested as a major determinate of community structure in coastal marine systems (Jorcin, 1999), pools were grouped according to their average salinities into freshwater, brackish, and marine pools. Grouping pools based on salinity could expose community patterns at different scales of observation. The pools that had an average salinity between 0 and 5.9 ppm were categorized as freshwater pools. Brackish pools had an average salinity between 6 and 15.9 ppm and marine pools were greater than, or equal to, 16 ppm. Within each salinity grouping and at the three observational scales of study, the role of environmental variability on community metrics was analyzed. All regression analyses were completed using STATISTICA, version 6.0, (StatSoft Inc., 2001). The level of significance was set at alpha = 0.05 (Fig. 2.7).

Canonical Correspondence Analyses (CCA) was used to determine whether environmental variability affected rock pool species differently at the three spatial scales and in three different types of pools (freshwater, brackish and marine pools) (Fig. 2.8, Fig. 2.9). CCA is a combination of ordination and multiple regression statistical techniques. Ordination (by itself) is the construction of ordination axes (theoretical variables) that best fit a set of data, thereby explaining as much of the variance in the data as possible. In a CCA, the sample scores are regressed (multiple regression) against the environmental variables. Overall, a CCA is an analysis which produces an ordination

with an environmental basis; therefore, the environmental variability data (at different scales of study) will help explain the patterns in the species data (Biometris, 2002).

Environmental data used in these analyses included variability in chloride, oxygen, temperature, and pH. The biotic data included 71 taxa of invertebrates. Data were log transformed when necessary.

In order to use the CCA (using Canoco), the species data must have a unimodal responses to the environmental gradients. In order to check for this type of species response, a Detrended Correspondence Analysis (DCA) was performed on the species data. A gradient length > 4 standard deviations indicated unimodal species responses.

A Monte-Carlo permutation test was used to determine the significance of the relationship between the species and the environmental variables in the CCA. The null hypothesis of this test is that there is no relationship between the species and the set of environmental variables. This test was performed on all analyses and all analyses were significant at an alpha level of 0.05; thus, the null hypothesis was rejected. I concluded that there was a significant relationship between the species and the set of environmental variability variables existed.

Ordination diagrams graphically display the relationships between the samples, species, environmental variables, and the ordination axes. In ordination diagrams, the environmental variables are represented as vectors. The direction of the arrow indicates the nature of the relationship between that variable and the ordination axes and the length of the arrow indicates the strength of the relationship. Eigenvalues indicate the

importance of each axis and range between 0 and 1. The eigenvalue indicates the amount of variance in the species data that is explained by the environment variables. To determine the strength of the relationship between the vector and a species, a perpendicular line can be drawn from the vector to the species, resulting in a right angle between the species and the vector. The location of the right angle on the vector denotes the strength of the relationship. An angle that is located closer to the origin of a vector indicates that a species is associated with less variability for an environmental factor. Canoco DRAW created the bi-plots of species data and environmental data (Biometris, 2002).

Table 2.1 Summary of data analyses for each of the three scales of observation (micro-spatial, local-temporal, and landscape-temporal scales)

	Micro-spatial scale	Local-temporal Scale	Landscape-temporal Scale
Dates	2002	Ten sampling dates throughout 1989-2002	Ten sampling dates throughout 1989-2002
Pools	Single	Single	Aggregate of all 49 pools
Calculation of Species Richness	Observed species richness	Average of dates	Average of dates and pools
Calculation of Abundance	Observed abundance in each pool	Average of dates for each pool	Average of pools for each date
Calculation of Individual Abiotic factors	Standard deviation for each pool	Standard deviation of recorded temperature, O2, pH or chloride values for 10 sampling dates	Standard deviation of absolute (temperature, O2, pH or chloride) values for all pools on one sampling date
Calculation of Environmental Variability	Geometric mean of the four abiotic factors	Geometric mean of the four abiotic factors	Geometric mean of the four abiotic factors

Figure 2.5. Flow chart of regression analyses for three scales of observation

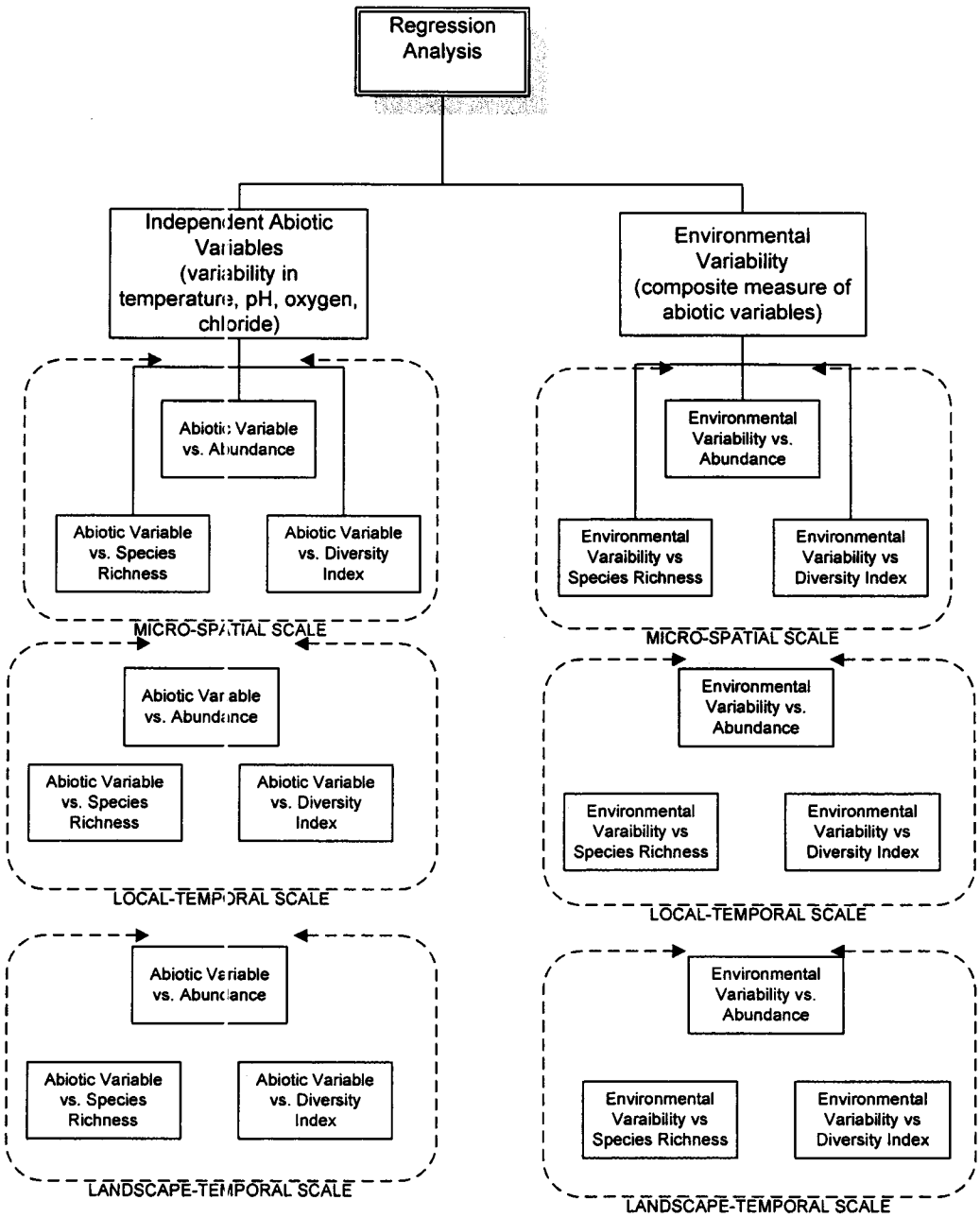

Regression Analysis
Independent Abiotic Variables (variability in temperature, pH, oxygen, chloride)
Environmental Variability (composite measure of abiotic variables)
Abiotic Variable vs. Abundance
Abiotic Variable vs. Species Richness
Abiotic Variable vs. Diversity Index
MICRO-SPATIAL SCALE
Abiotic Variable vs. Abundance
Abiotic Variable vs. Species Richness
Abiotic Variable vs. Diversity Index
LOCAL-TEMPORAL SCALE
Abiotic Variable vs. Abundance
Abiotic Variable vs. Species Richness
Abiotic Variable vs. Diversity Index
LANDSCAPE-TEMPORAL SCALE
Environmental Variability vs. Abundance
Environmental Varaibility vs Species Richness
Environmental Variability vs Diversity Index
MICRO-SPATIAL SCALE
Environmental Variability vs. Abundance
Environmental Varaibility vs Species Richness
Environmental Variability vs Diversity Index
LOCAL-TEMPORAL SCALE
Environmental Variability vs. Abundance
Environmental Varaibility vs Species Richness
Environmental Variability vs Diversity Index
LANDSCAPE-TEMPORAL SCALE

Figure 2.6 Flow chart of multiple regression analyses for three scales of observation

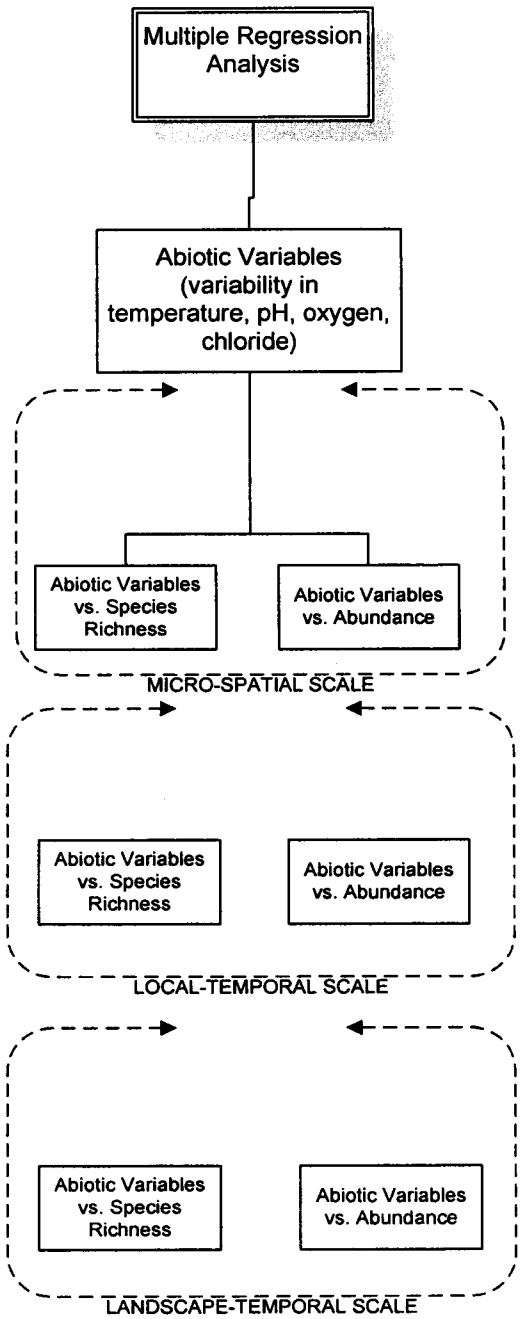

Multiple Regression Analysis
Abiotic Variables (variability in temperature, pH, oxygen, chloride)
Abiotic Variables vs. Species Richness
Abiotic Variables vs. Abundance
MICRO-SPATIAL SCALE
Abiotic Variables vs. Species Richness
Abiotic Variables vs. Abundance
LOCAL-TEMPORAL SCALE
Abiotic Variables vs. Species Richness
Abiotic Variables vs. Abundance
LANDSCAPE-TEMPORAL SCALE

Figure 2.7 Flow chart of Regression analyses for three different scales of observation and for pools grouped according to absolute salinity.

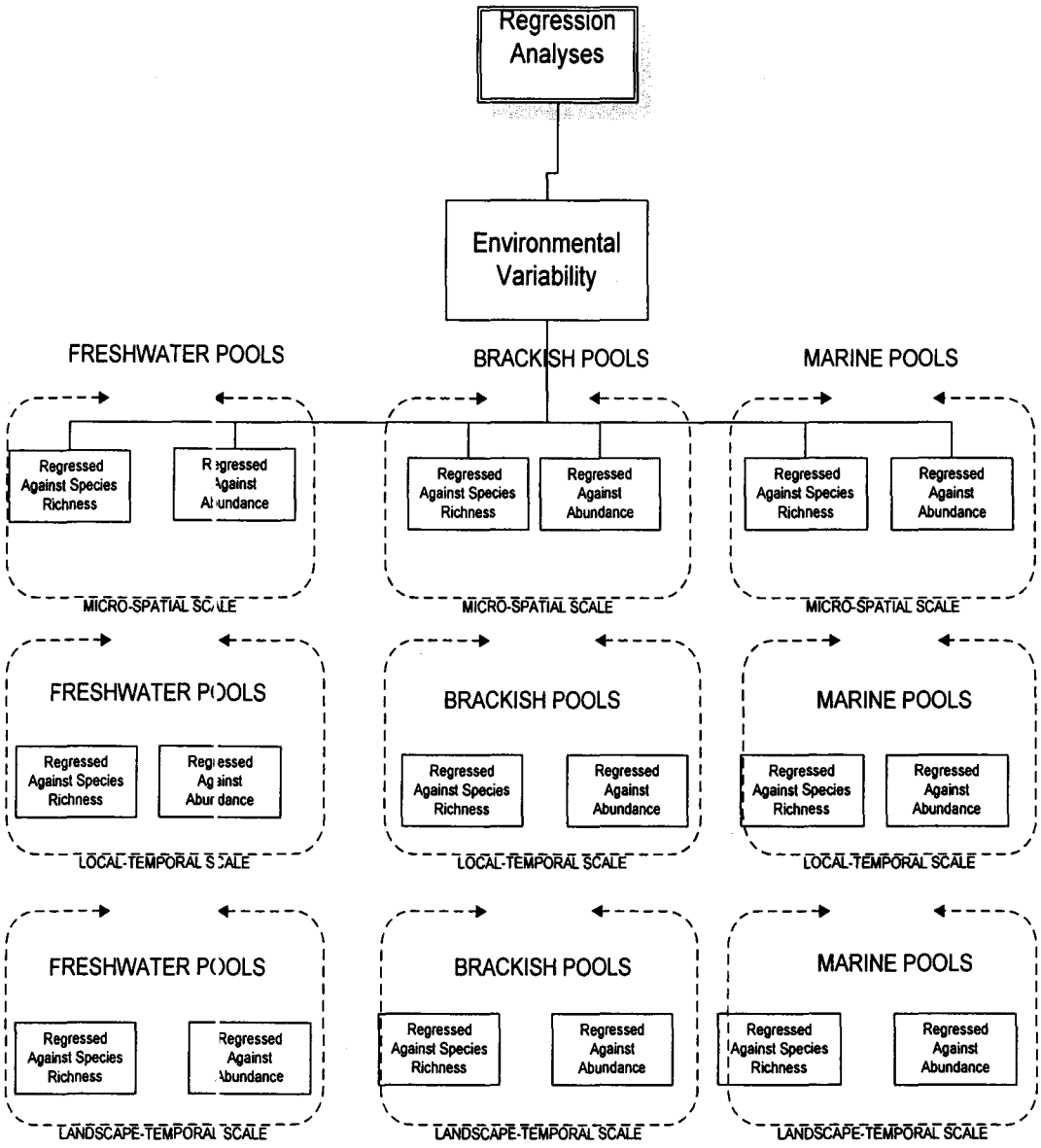

Regression Analyses
Environmental Variability
FRESHWATER POOLS
BRACKISH POOLS
MARINE POOLS
Regressed Against Species Richness
Regressed Against Abundance
MICRO-SPATIAL SCALE
LOCAL-TEMPORAL SCALE
LANDSCAPE-TEMPORAL SCALE

Figure 2.8 Flow chart of CCA analyses for three scales of observation

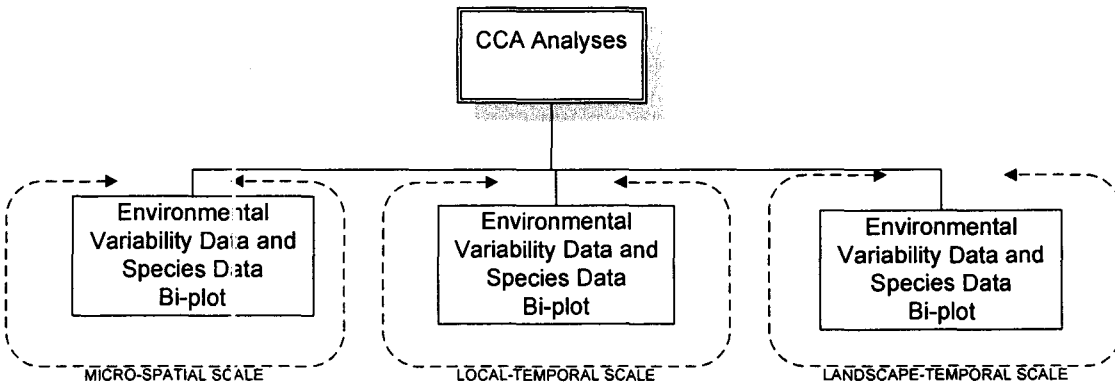
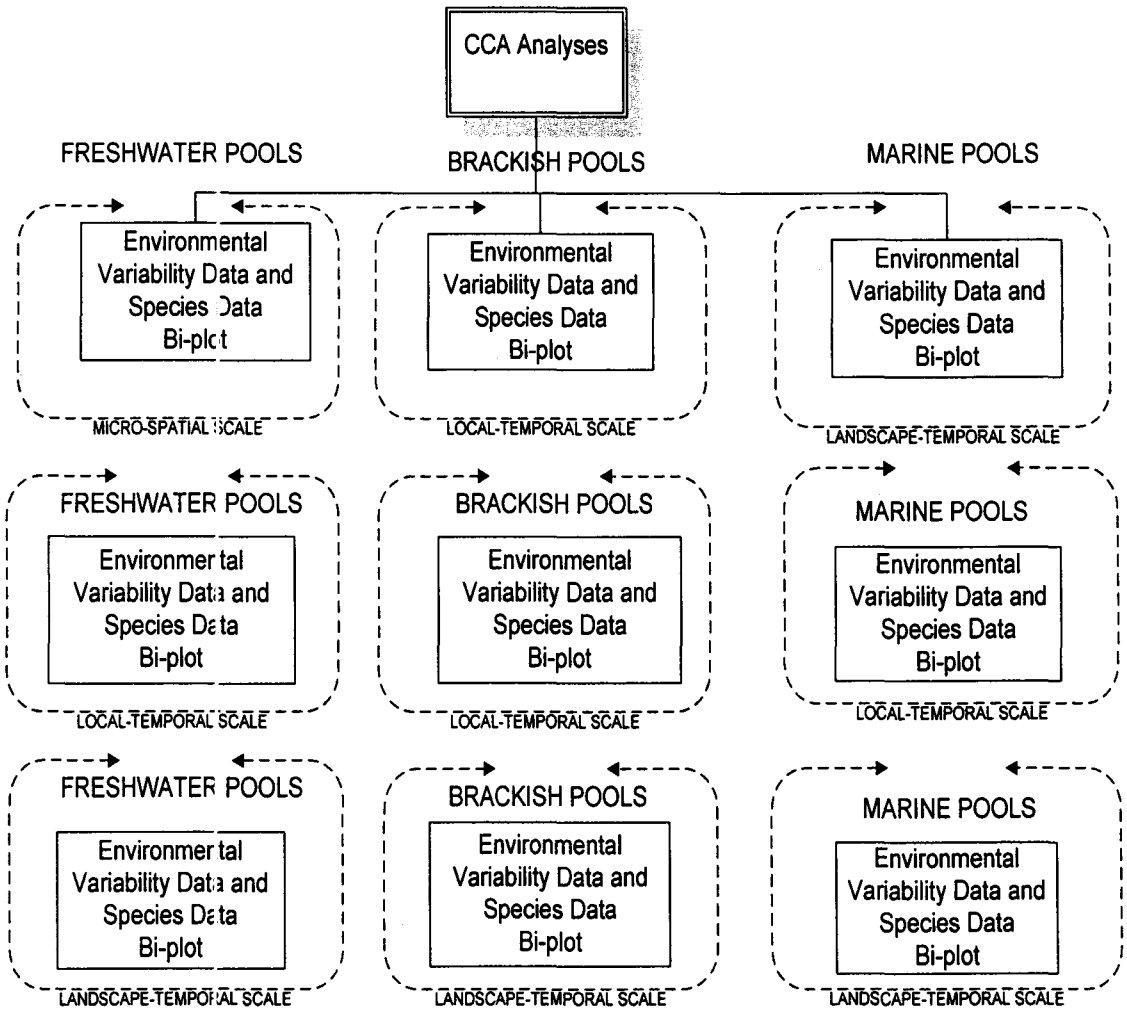

CCA Analyses
Environmental Variability Data and Species Data Bi-plot
Environmental Variability Data and Species Data Bi-plot
Environmental Variability Data and Species Data Bi-plot
MICRO-SPATIAL SCALE
LOCAL-TEMPORAL SCALE
LANDSCAPE-TEMPORAL SCALE

Figure 2.9 Flow chart of CCA analyses for three scales of observation and for pools grouped according to absolute salinity.


CCA Analyses
FRESHWATER POOLS
BRACKISH POOLS
MARINE POOLS
Environmental Variability Data and Species Data Bi-plot
MICRO-SPATIAL SCALE
LOCAL-TEMPORAL SCALE
LANDSCAPE-TEMPORAL SCALE
FRESHWATER POOLS
BRACKISH POOLS
MARINE POOLS
Environmental Variability Data and Species Data Bi-plot
LOCAL-TEMPORAL SCALE
LOCAL-TEMPORAL SCALE
LOCAL-TEMPORAL SCALE
FRESHWATER POOLS
BRACKISH POOLS
MARINE POOLS
Environmental Variability Data and Species Data Bi-plot
LANDSCAPE-TEMPORAL SCALE
LANDSCAPE-TEMPORAL SCALE
LANDSCAPE-TEMPORAL SCALE

Chapter 3:

Results

Results

Independent Abiotic Factors

At all spatial scales, linear regression analyses showed that there were no significant (alpha level= 0.05) relationships for each of the three dependent variables, species richness, abundance and H' regressed against individual independent variables, (variability of temperature, oxygen, pH and chloride) (Table 3.1).

Table 3.1. Community metrics regressed against variability of individual abiotic variables, at all three scales of study.

	Independant Variable	Variability of Temperature		Variability of Oxygen	
Scale	Dependent Variable	p- value	r^2value	p-value	r^2value
Micro-spatial	Species richness	0.69	0.003	0.23	0.03
	Abundance	0.50	0.010	0.28	0.03
	H'	0.56	0.009	0.25	0.03
Local-temporal	Species richness	0.97	0.000	0.11	0.06
	Abundance	0.46	0.010	0.94	0.00
	H'	0.55	0.010	0.85	0.00
Landscape -temporal	Species richness	0.59	0.003	0.19	0.12
	Abundance	0.38	0.020	0.60	0.00
	H'	0.40	0.020	0.55	0.00

	Independent Variable	Variability of pH		Variability of Chloride	
Scale	Dependent Variable	p-value	r^2value	p-value	r^2value
Micro-spatial	Species richness	0.54	0.009	0.76	0.002
	Abundance	0.82	0.001	0.54	0.009
	H'	0.67	0.008	0.75	0.002
Local-temporal	Species richness	0.17	0.250	0.09	0.070
	Abundance	0.22	0.040	0.81	0.001
	H'	0.20	0.040	0.10	0.060
Landscape -temporal	Species richness	0.56	0.010	0.35	0.010
	Abundance	0.28	0.040	0.90	0.007
	H'	0.50	0.015	0.60	0.004

Multiple Regression Analyses

Six multiple regressions were performed using variability in temperature, oxygen, pH and chloride as the independent variables (Table 3.2). At all three scales of observation, there were no significant relationships between abundance and the variability of temperature, oxygen, pH, or chloride. Likewise, there was no relationship between species richness and the four environmental variability factors at both the micro-spatial and the landscape-temporal scales. However, at the local-temporal scale of study, there was a significant relationship between species richness and the variability of oxygen, temperature, pH and chloride (r^2=0.25, p=0.02). The significant beta values included the variability in temperature and pH (variability in temperature b=0.39, variability in pH b=-0.50).

Table 3.2. Multiple regression analyses with variability of temperature, oxygen, pH and chloride as the independent variables. The dependent variables are species richness or abundance.

	Independent Variable	Variability of Temperature, Oxygen, pH, chloride	
Scale	Dependant Variable	p- value	R^2value
Micro-spatial	Species richness	0.74	0.05
Micro-spatial	Abundance	0.73	0.05
Local-temporal	Species richness	0.02	0.25
Local-temporal	Abundance	0.55	0.07
Landscape-temporal	Species richness	0.62	0.06
Landscape-temporal	Abundance	0.65	0.06

Variability of Combined Abiotic Factors

The variability of individual abiotic factors was combined into one independent environmental variability term for all three scales of study (micro-spatial, local-temporal and landscape-temporal scales). At the micro-scale, this was accomplished by taking the geometric mean of the standard deviation of each individual abiotic factor, on one sampling date. At the local-temporal scale, environmental variability was calculated for each pool by taking the standard deviation of each abiotic factor over all sampling dates and then finding the geometric mean of those four standard deviations. At the landscape-temporal scale, environmental variability was calculated for each sampling date by taking the total standard deviation of individual abiotic factors in all pools, and then taking the geometric mean of those four standard deviations. The Lazar lab micro-probe which measured chloride malfunctioned during the sampling procedures. As a result, the chloride values were analyzed to confirm their accuracy (see Appendix 2). Thus, two sets of regression analyses were performed. The first set includes an independent environmental variability term which consists of the variability of only three abiotic environmental factors; temperature, oxygen, and pH. The second set of analyses included an independent environmental variability term which consists of the variability of four abiotic environmental factors: temperature, oxygen, pH, and chloride.

At the three scales of observation (micro-spatial, local-temporal and landscape-temporal) there were no significant linear regression relationships between the independent variables, environmental variability (both with and without chloride values), and the dependent variables, species richness, abundance and H' (Table 3.3).

Table 3.3. Results of regression analysis for environmental variability, species richness, abundance, and diversity, H', at three scales of study. The first set of analyses had an environmental variability term which did not include values for the variability of chloride, whereas the second set did include values for the variability of chloride.

	Independent Variable	Micro-spatial Environmental Variability		Local-temporal Environmental Variability	
	Dependent Variable	p-value	r^2value	p-value	r^2value
Set 1	Species richness	0.37	0.02	0.27	0.03
	Abundance	0.34	0.02	0.43	0.01
	H'	0.40	0.01	0.33	0.02
Set 2	Species richness	0.60	0.00	0.27	0.03
	Abundance	0.97	0.00	0.64	0.00
	H'	0.42	0.01	0.48	0.01

	Independent Variable	Landscape-temporal Environmental Variability	
	Dependent Variable	p-value	r^2value
Set 1	Species richness	0.58	0.04
	Abundance	0.49	0.06
	H'	0.61	0.00
Set 2	Species richness	0.42	0.08
	Abundance	0.45	0.07
	H'	0.80	0.00

Canonical Correspondence Analysis: CCA

At the micro-spatial scale (variability of chloride included) species were positioned around the first axis (eigenvalue = 0.64) and most species were negatively associated with the environmental variability vectors (variability of oxygen, pH, and temperature from all pools) (Fig. 3.1). Although some species were associated with low variability in oxygen and pH, overall, species were positively associated with the variability of chloride therefore making it the most important vector in the bi-plot. There were two major groupings of species on this bi-plot (Fig. 3.1). One group of marine species was positively associated with the variability in chloride vector. The other grouping of freshwater species preferred stability in environmental conditions and therefore was negatively associated with the environmental variability vectors. The CCA bi-plot that did not include the variability of chloride vector, indicated that temperature was the most important factor and loaded onto axis 1 (eigenvalue = 0.49; Fig. 3.2). Many of the species were associated with low variability in temperature, oxygen and pH. However, there were still a number of species that were positively associated with stability in environmental factors. Overall, at the micro-spatial scale, the variability of oxygen, pH, and temperature across all 49 pools, was only weakly associated with the species data. Variability of chloride was more strongly associated with species data than the other factors.

At the local-temporal scale (variability of chloride included) species were fairly evenly distributed around the environmental variability vectors (Fig. 3.3). The most

important vector in this plot was pH, which loaded onto axis 1 (eigenvalue = 0.39). However, heterogeneity of chloride also had a strong association with the species data which can be seen in the number of species positioned around this vector, as well as the length of the vector. The CCA bi plot that did not include variability of chloride also had an even distribution of species positioned around the origin of the axes. Without the chloride vector, variability of temperature was the most important factor and loaded onto axis 2 (Fig. 3.4) (eigenvalue= 0.39). Overall, at the local-temporal scale, the species data were associated most with the variability of pH and chloride.

At the landscape-temporal scale (variability of chloride included) species were again positioned fairly evenly around the origin of the axes, suggesting that certain environmental variability factors were associated with certain species (Fig. 3.5). The most important factor in this plot was the variability of pH, which loaded onto axis 1 (eigenvalue = 0.3). Both the variability of oxygen and chloride were also strongly associated with the species data. Many species were positioned around the top of the chloride vector. This suggests that those species were associated with high variability in chloride. When the chloride vector was removed, the most important vector became the variability of temperature, which loaded onto axis 2 (Fig. 3.6) (eigenvalue = 0.2). The ordination of the species data changed and most of the species became associated with either low heterogeneity of temperature, oxygen, or pH, or were associated with stability of those factors. Overall, the CCA analyses for the landscape-temporal scale suggested that environmental variability was related to the species data, but that the relationship was complex.

Figure 3.1. CCA of species and environmental data from the 49 rock pools, at the micro-spatial scale of observation ($p = 0.002$)

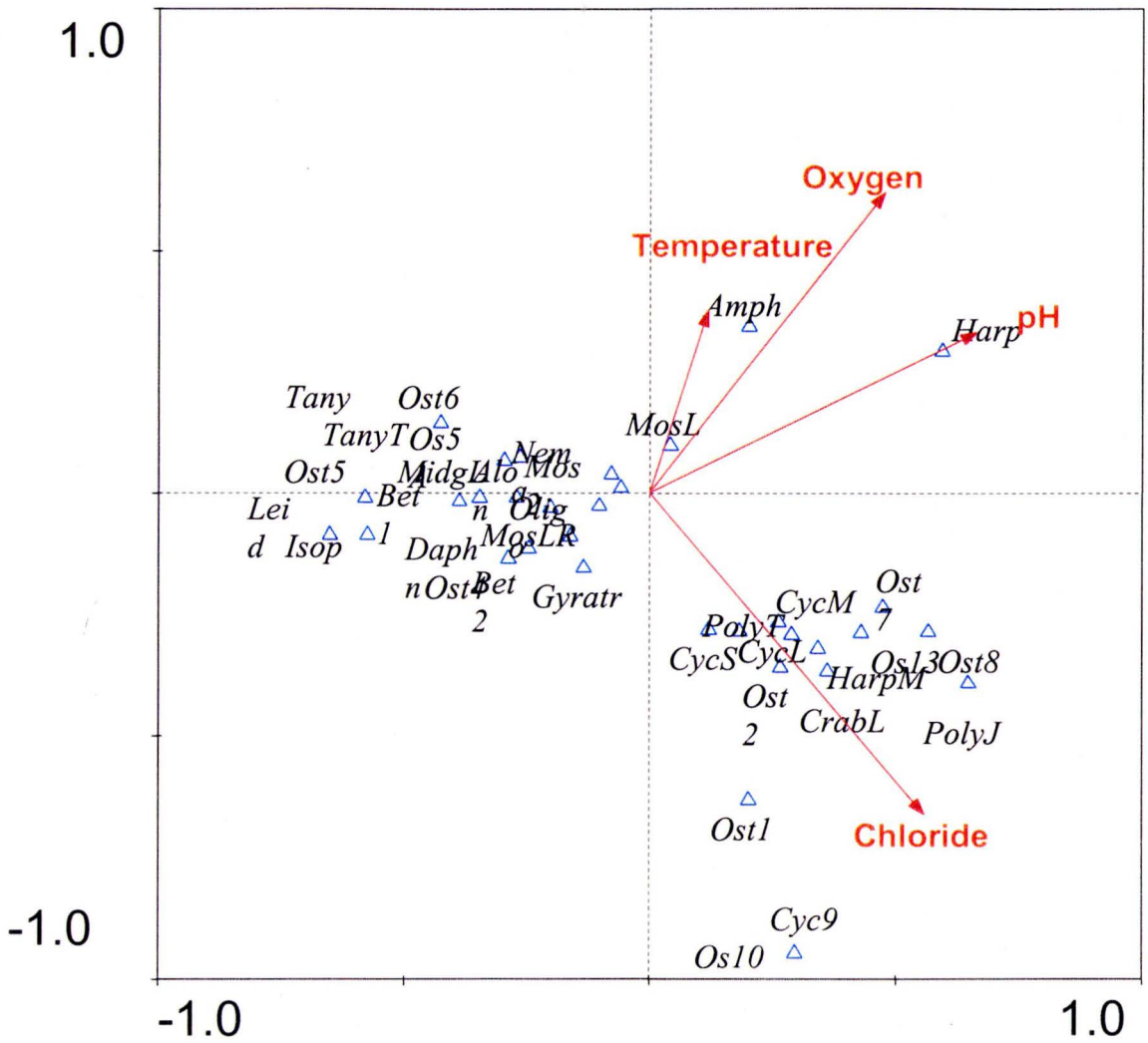

1.0
-1.0
-1.0
1.0
Oxygen
Temperature
pH
Chloride
Amph
Harp
MosL
Tany
Ost6
TanyT
Os5
Ost5
Nem
Mos
Lei
d
Isop
Bet
1
Daph
nOst
4
Bet
2
Gyratr
CycM
Ost
7
PolyT
CycS
CycL
Os13
Ost8
HarpM
Ost
2
CrabL
PolyJ
Ost1
Cyc9
Os10

Figure 3.2. CCA of species and environmental data from the 49 rock pools, at the micro-spatial scale of observation (variability of chloride values not included) ($p = 0.002$).

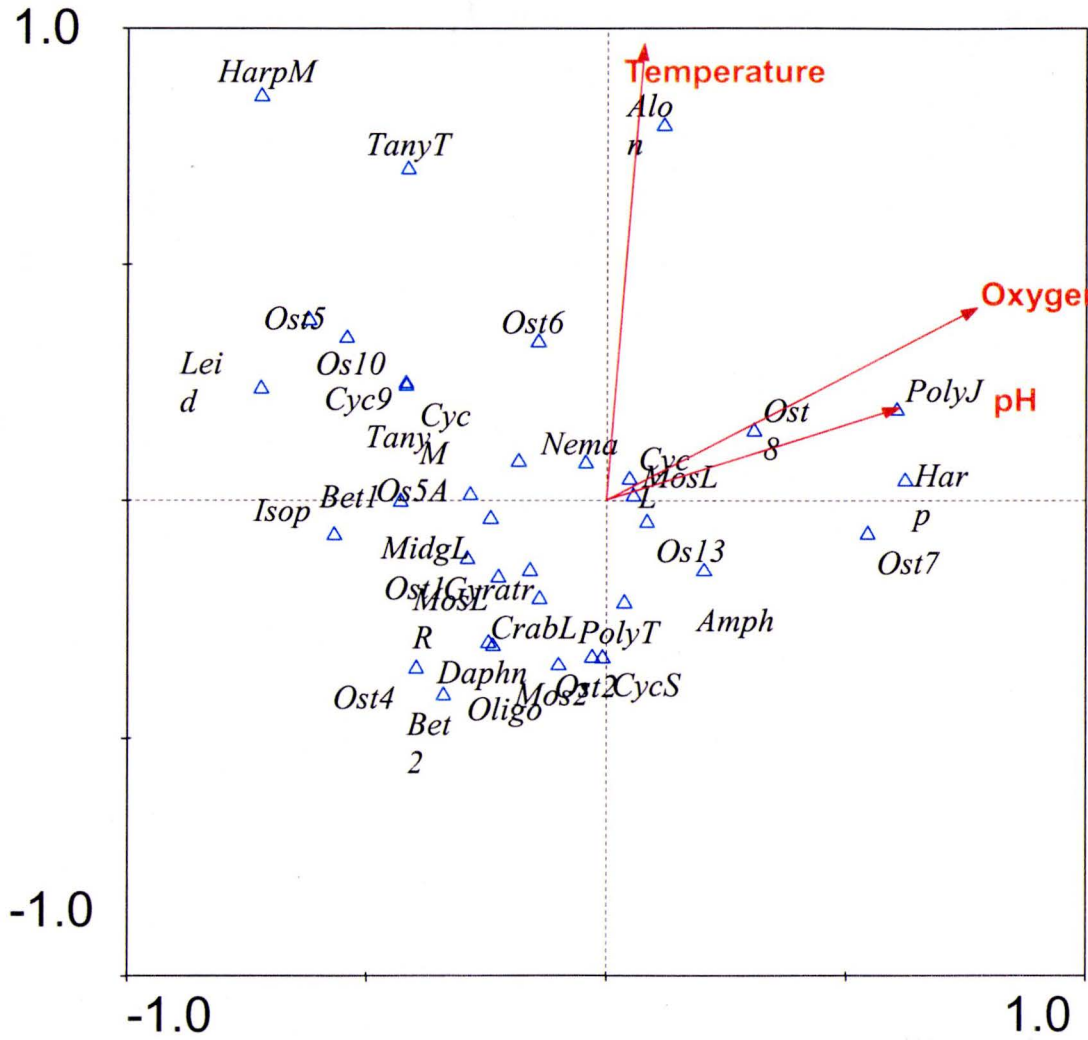

1.0
-1.0
-1.0
1.0
Temperature
Oxygen
pH
HarpM
TanyT
Alon
Ost5
Ost6
Lei
d
Os10
Cyc9
Cyc
M
Tany
Nema
Cyc
L
MosL
Ost
8
PolyJ
Har
p
Isop
Bet1
Os5A
MidgL
Os13
Ost7
Ost1
Cyratr
MosL
R
CrabL
PolyT
Amph
Daphn
Ost4
Oligo
Mos2
Ost2
CycS
Bet
2

Figure 3.3. CCA of species and environmental data from the 49 rock pools, at the local-temporal scale of observation (p=0.008).

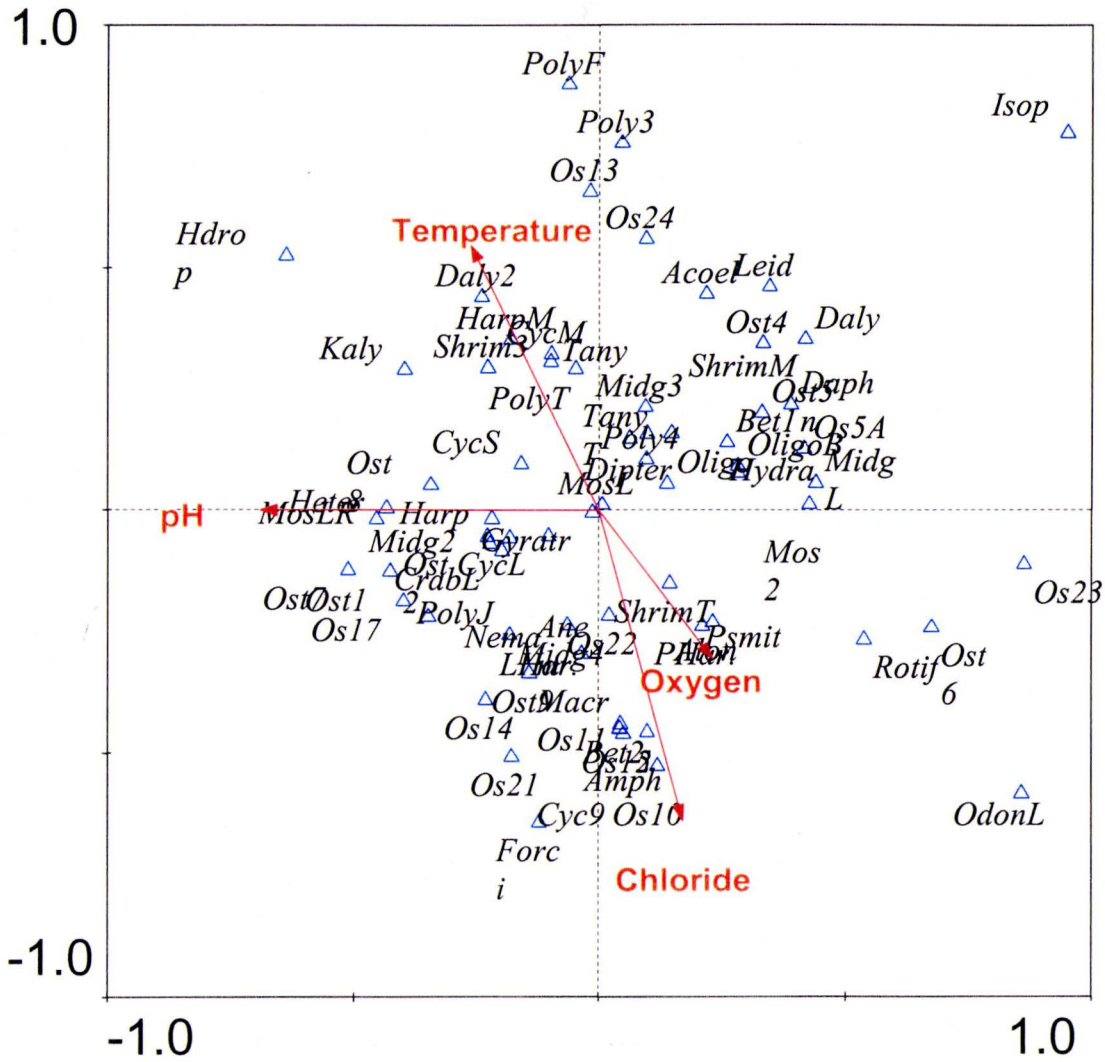

1.0
-1.0
-1.0
1.0
Temperature
pH
Oxygen
Chloride
PolyF
Poly3
Os13
Os24
Isop
Hdro
p
Daly2
Acoel
Leid
Ost4
Daly
HarpM
CycM
Kaly
Shrim3
Tany
ShrimM
Midg3
PolyT
Ost5
Daph
Tany
Bet1n
Os5A
Poly4
OligoB
CycS
Ost
Midg
Hydra
MosL
L
Harp
Midg2
Cyrdtr
Mos
2
Os23
CycL
CrdbL
Ost1
Os17
PolyJ
ShrimT
Psmit
Os22
Rotif
Ost
6
Macr
Os14
Os21
Amph
Cyc9
Os10
OdonL
Forc
i

Figure 3.4. CCA of species and environmental data from the 49 rock pools at the local-temporal scale of observation (variability of chloride values not included) ($p=0.01$).

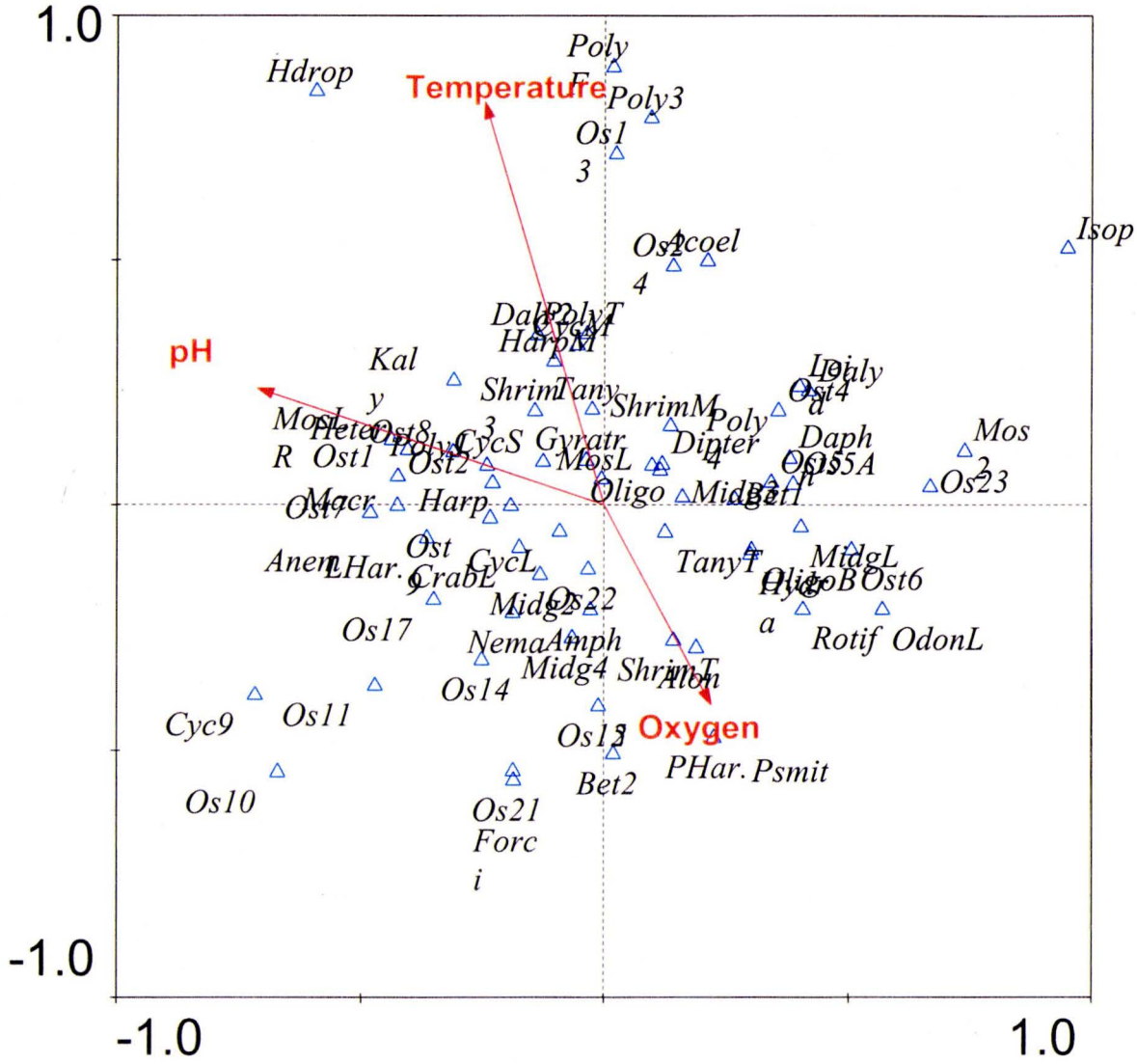

1.0
-1.0
-1.0
1.0
Temperature
pH
Oxygen
Hdrop
Poly
Poly3
Os13
Os24
Isop
Kaly
ShrimT
ShrimM
Dipter
Daph
Mos2
Os23
Oligo
Harp
Ost
CycL
CrabL
Os22
Midg2
Os17
NemaA
Amph
Midg4
ShrimT
Os14
Os11
Cyc9
Os10
Os13
Bet2
PHar.
Psmit
Os21
Forci
TanyT
MidgL
Rotif
OdonL
Ost6

Figure 3.5. CCA of species and environmental data from the 49 rock pools, at the landscape-temporal scale of observation ($p = 0.048$).

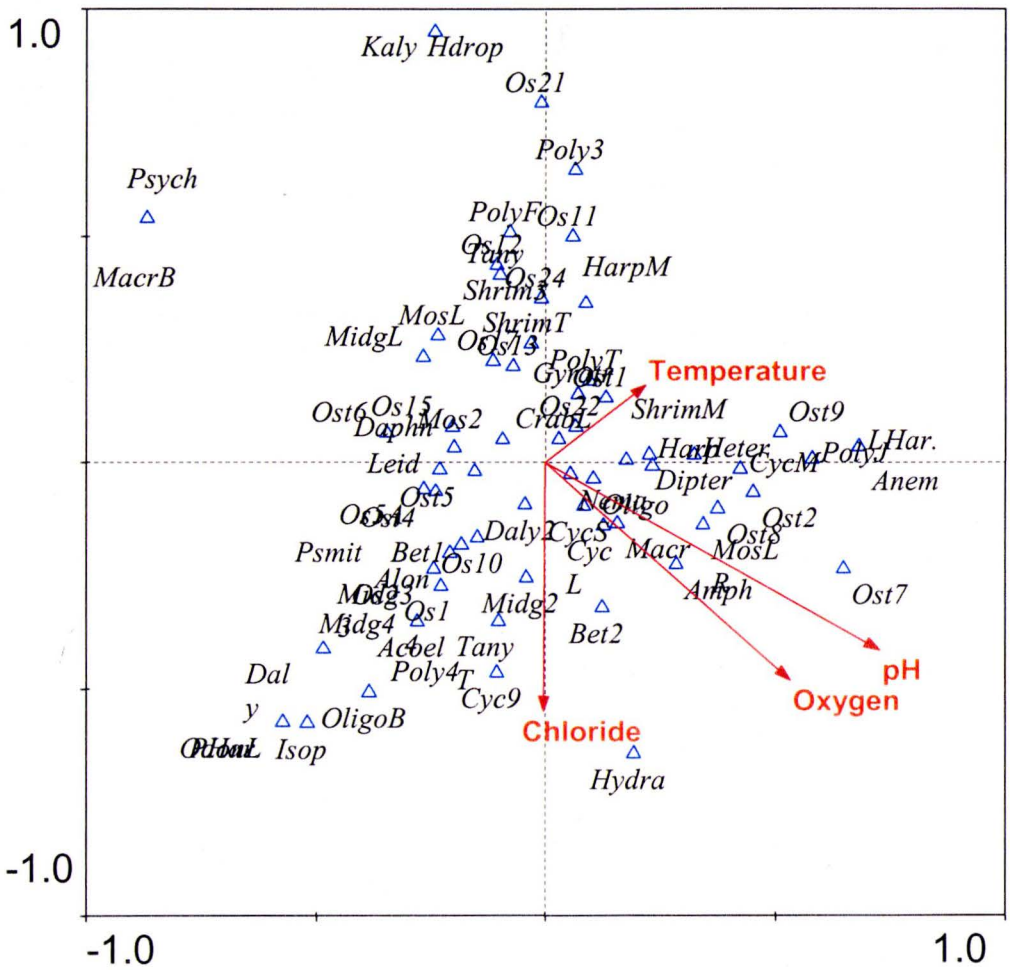
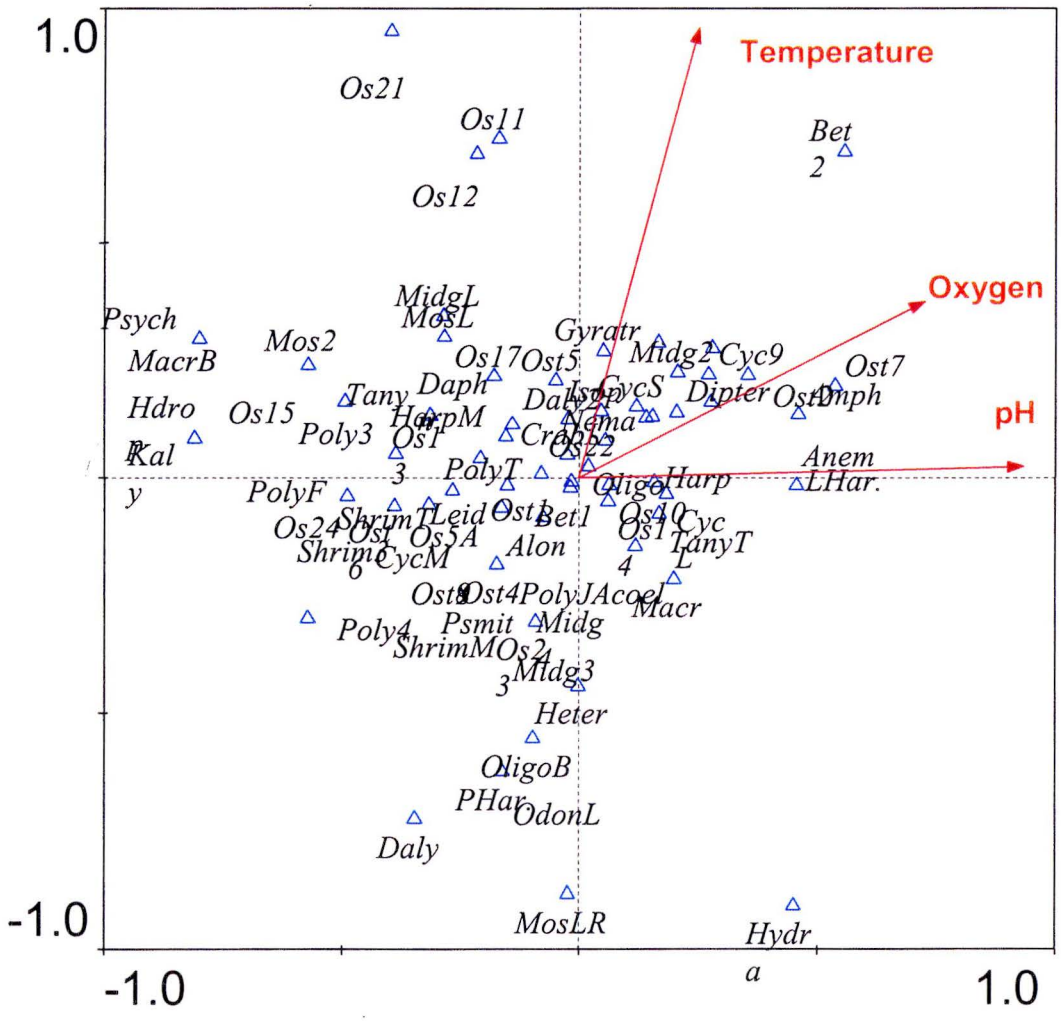

1.0
-1.0
-1.0
1.0
Kaly
Hdrop
Os21
Poly3
Psych
PolyF
Os11
MacrB
HarpM
Os24
Shrim3
MosL
ShrimT
MidgL
Os13
PolyT
Temperature
Os15
Os22
ShrimM
Ost9
Daphn
Mos2
Leid
Dipter
Anem
Ost5
Oligo
Ost2
Daly1
Cyc5
Ost8
Psmit
Bet1
Cyc
Macr
MosL
Os10
Amph
Ost7
Midg2
Os1
Bet2
Tany
pH
Oxygen
Dal
y
Poly4
Cyc9
OligoB
Chloride
Isop
Hydra

Figure 3.6. CCA of species and environmental data from the 49 rock pools, at the landscape-temporal scale of observation (variability of chloride values not included) ($p = 0.05$)


1.0
-1.0
-1.0
1.0
Temperature
Oxygen
pH
Os21
Os11
Os12
Bet
2
MidgL
MosL
Psych
Mos2
MacrB
Os17
Ost5
Gyratr
Midg2
Cyc9
Ost7
Tany
Daph
Dipter
Hdro
Os15
HarpM
Poly3
Os1
Nema
Anem
LHar.
Kal
y
PolyF
PolyT
Oligo
Harp
Os24
Os5A
Alon
Os1Cyc
TanyT
CycM
Ost4
PolyJ
Acoel
Macr
Poly4
Psmit
Midg
ShrimM
Os2
Midg3
Heter
OligoB
PHar
OdonL
Daly
MosLR
Hydr
a

Overall, the CCA analyses showed that environmental variability was related to the species data. However, due to the spread of the biotic data on the local-temporal and landscape-temporal bi-plots the relationships were complex and difficult to interpret. Also, the micro-scale bi-plot shows that there are two groupings of species: those that can tolerate variable salinity (marine) and those species that favor stable salinity and other stable environmental conditions (freshwater). As a result of the patterns found at the micro-spatial scale and the complexity in patterns found at the intermediate and large scales , the rock pools were divided up into three different categories, freshwater, brackish, and marine, based on the average salinities of the pools over 10 sampling dates (see methods). It is hypothesized that grouping the pools based on absolute salinity would help patterns to emerge more clearly at the different scales of observation. Sixteen pools were placed in the freshwater category (0 - 5.9 ppm), 13 pools in the brackish category (6 – 15.9 ppm), and 16 pools in the marine category (16 ppm +) (Table 3.4).

Table 3.4. Categorization of pools into freshwater, brackish and marine, and their average salinities over ten sampling dates.

Freshwater Pool ID	Mean Salinity *	Brackish Pool ID	Mean Salinity *	Marine Pool ID	Mean Salinity *
3	4.3	1	6.7	5	19.4
7	3.2	2	7.4	11	18.5
31	0.8	4	12.9	15	23.8
32	0.4	8	7.0	17	20.5
33	0.3	9	15.7	18	21.3
34	0.3	10	13.1	20	18.1
35	0.3	12	13.1	21	17.1
36	0.7	13	8.3	22	23.6
37	0.4	14	15.9	23	25.0
38	0.2	30	9.4	26	24.2
39	1.4	40	8.7	27	19.0
41	1.9	43		28	16.6
42	4.6			29	17.4
44	1.3			48	21.8
46	1.6			49	26.4
47	1.0			50	25.5

* Mean Salinity- average of pools over ten sampling dates.

Environmental Variability: Chloride Values Not Included (See Appendix 1)

For freshwater pools at the local-temporal scale, environmental variability was negatively related to species richness ($p = 0.01$) (Fig. 3.7). At the other two scales of observation (micro-spatial and landscape-temporal scales) there were no significant relationships between environmental variability and species richness (Table 3.5). However, the consistent negative slopes of the regressions did suggest a possible trend of a negative association between environmental variability and species richness at all three scales of observation. There were no relationships between environmental variability and abundance at any of the three scales of observation (Table 3.5).

For brackish pools, there was a significant increase in species richness and abundance with environmental variability at the micro-spatial scale of study (species richness $p = 0.05$; abundance $p = 0.02$; Fig. 3.8, 3.9). A similar positive trend was seen at the local-temporal scale. However, at both the local-temporal and landscape-temporal scales there were no significant relationships between environmental variability and species richness or abundance.

For marine pools, there were no significant relationships between environmental variability and species richness or abundance at any of the three observational scales. However, there was a negative association between species richness and environmental variability (Table 3.5) and abundance was positively associated with environmental variability at all three observational scales of study (albeit insignificantly).

Figure 3.7. Local-temporal scale: environmental variability regressed against species richness in fresh water pools ($p = 0.01$). Variability of chloride values was not included. As environmental variability increases there is a decrease in species richness. Each sample point represents the species richness that exists at a given variable environmental condition.

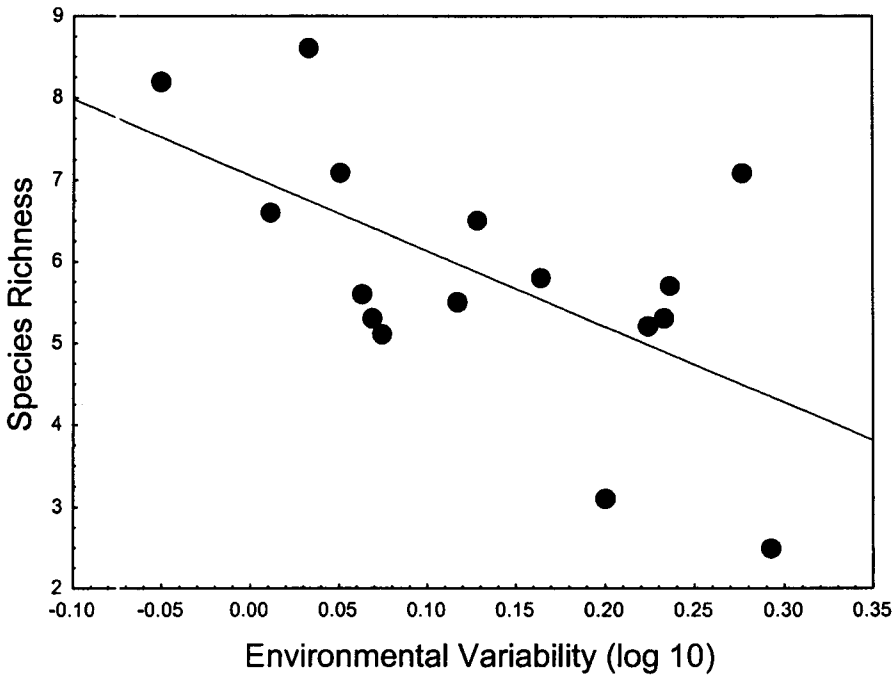

Species Richness
9
8
7
6
5
4
3
2
-0.10
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Environmental Variability (log 10)

Table 3.5. Regression analyses of environmental variability (variability of chloride values not included) against both species richness and abundance, at all three scales of observation.

Scale	Freshwater		Brackish		Marine	
	Species Richness	Abundance	Species Richness	Abundance	Species Richness	Abundance
Micro-spatial						
P=	0.19	0.77	0.05	0.02	0.22	0.79
r^2=	0.13	0.01	0.30	0.39	0.11	0.01
Local-temporal						
P=	0.01	0.78	0.89	0.53	0.99	0.09
r^2=	0.40	0.01	0.002	0.04	0.00	0.20
Landscape-temporal						
P=	0.12	0.45	0.79	0.74	0.3	0.89
r^2=	0.28	0.07	0.01	0.01	0.13	0.003

Figure 3.8. Micro-spatial scale: environmental variability regressed against species richness in brackish water pools ($p = 0.05$). Variability of chloride values was not included. As environmental variability increases there is an increase in species richness. Each sample point represents the species richness that exist at a given variable environmental condition.

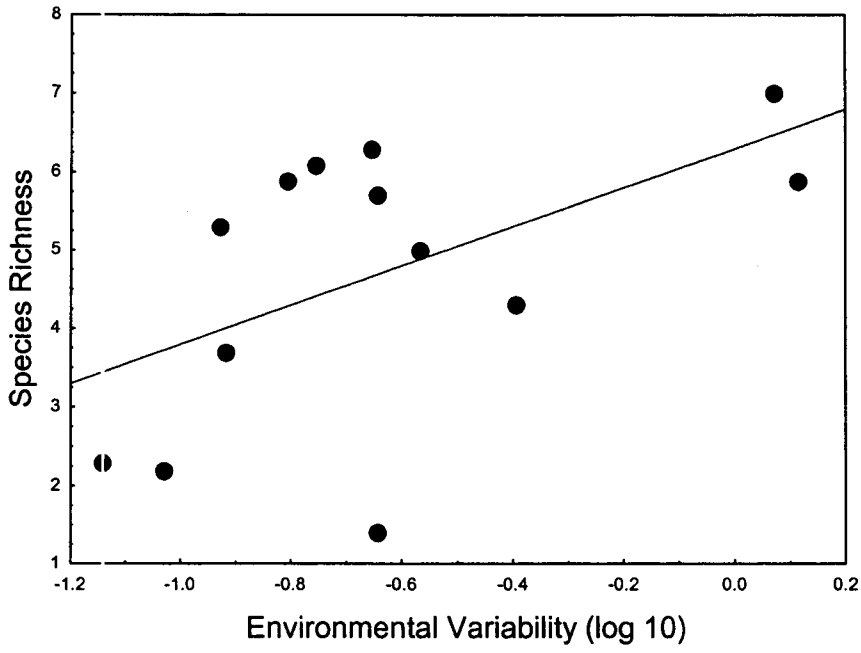
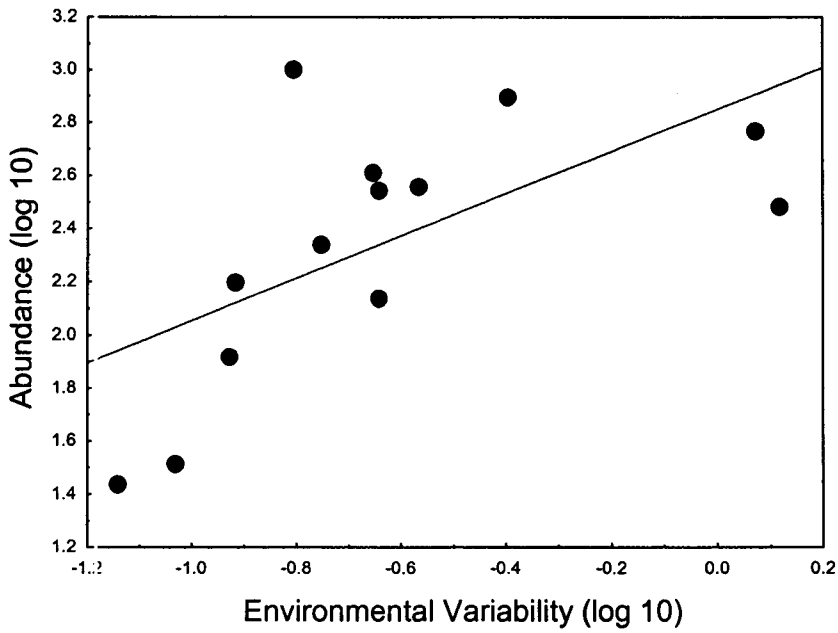

Species Richness
8
7
6
5
4
3
2
1
-1.2
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
Environmental Variability (log 10)

Figure 3.9. Micro-spatial scale: environmental variability regressed against abundance in brackish water pools ($p = 0.02$). Variability of chloride values was not included. As environmental variability increases, there is an increase in the abundances of species. Each sample point represents the number of individuals within a community at a given environmental condition.


Abundance (log 10)
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
Environmental Variability (log 10)

Environmental Variability: Including Chloride Values

At all three observational scales of study, there were no significant relationships between environmental variability and both species richness or abundance in freshwater pools. The association between environmental variability (variability of chloride values included) and species richness was negative at all scales of observation. The association of environmental variability and abundance at the micro-spatial and local-temporal scales was positive, but negative at the landscape-temporal scale (Table 3.6).

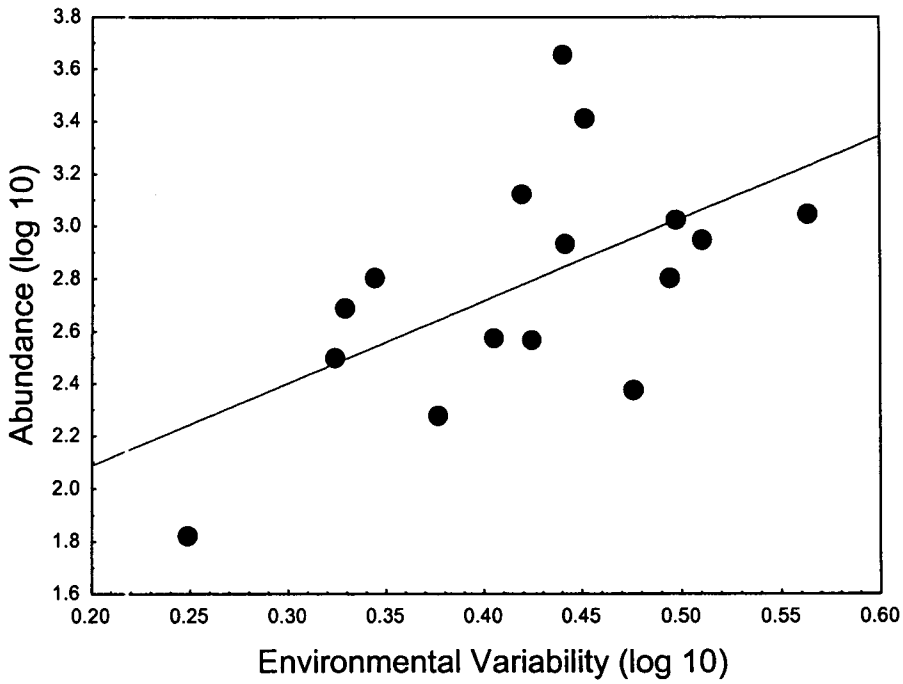
Species richness and abundance were unrelated to environmental variability in brackish pools at all observational scales. Both the micro-spatial and local-temporal scale the associations between environmental variability and species richness and abundance were positive; conversely, the association was negative at the landscape-temporal scale (Table 3.6).

In marine pools, abundance was positively correlated with environmental variability at the local-temporal scale ($p = 0.02$) (Fig. 3.10). However, at the micro-spatial and landscape-temporal scale, there was no relationship between environmental variability and abundance. There was also no relationship between species richness and environmental variability at all scales of observation (Table 3.6).

Table 3.6. Regression analyses of environmental variability (variability of chloride values included) against both species richness and abundance, at all three scales of observation.

Scale	Freshwater		Brackish		Marine	
	Species Richness	Abundance	Species Richness	Abundance	Species Richness	Abundance
Micro-spatial						
P=	0.16	0.79	0.37	0.46	0.83	0.69
r^2=	0.15	0.01	0.07	0.05	0.003	0.01
Local-temporal						
P=	0.46	0.67	0.34	0.63	0.18	0.02
r^2=	0.04	0.03	0.08	0.02	0.13	0.33
Landscape-temporal						
P=	0.06	0.26	0.50	0.73	0.35	0.71
r^2=	0.37	0.15	0.06	0.02	0.11	0.02

Figure 3.10. Local-temporal scale: environmental variability regressed against total abundance in marine water pools ($p = 0.02$). Variability of chloride values was included. As environmental variability increases, the abundance of species increases. Each dot represents the number of individuals within a community at a given environmental condition.


Abundance (log 10)
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
0.20
0.25
0.30
0.35
0.40
0.45
0.50
0.55
0.60
Environmental Variability (log 10)

Canonical Correspondence Analysis: CCA
Environmental data which includes chloride values

CCA: Freshwater Pools

At the micro-spatial scale, the most important factors affecting the ordination of species and their abundance were volume and variability in temperature (Table 3.7) (Fig 3.11). Variability in temperature and pH loaded onto the first axis (eigenvalue = 0.40). Volume, variability in oxygen, and variability in chloride loaded onto the second axis (eigenvalue = 0.30). The strength of the relationship between chloride and the second axis was not as strong as the other vectors and was therefore not a very important factor in explaining the relationship with the species data in fresh water pools. Approximately half of the species preferred moderate to high volume levels, and stability in temperature, oxygen, pH and chloride. Conversely, the other half of the species data was able to tolerate variability in environmental factors and could therefore withstand lower volume levels. Taxa, such as *Gyratrix* (kalyptorynchid) and oligochaetes, were associated with high volume, but preferred low environmental variability, suggesting that they prefer stable environmental conditions in freshwater ponds. Also the harpacticoids preferred variability in temperature, oxygen and pH and especially chloride.

At the local-temporal scale, the most important factors were variability in chloride and pH (Table 3.7) (Fig. 3.12). Volume and variability in oxygen, chloride, and temperature loaded onto the first axis (eigenvalue = 0.52), while the pH vector loaded onto the second axis (eigenvalue = 0.14). Most of the species were positioned fairly close

to the first axis and thereby were positively associated with volume and variability in chloride and oxygen. Overall, there was no distinct species pattern.

At the landscape-temporal scale of study, the most important factor was variability in temperature and oxygen (Table 3.7) (Fig. 13). Oxygen loaded onto the first axis (eigenvalue = 0.12) and pH, chloride, and temperature onto the second axis (eigenvalue = 0.08) Interestingly, at the landscape-temporal scale many of the species were associated with high variability in oxygen, temperature, pH, and chloride. Specifically, harpacticoids dominated in pools that had high variability of environmental conditions. However 12 species were associated with stable conditions of oxygen, temperature, chloride and pH. Of these 12 species, many were insects (i.e. mosquitoes) and have the ability to breathe air and therefore are not confined to certain pools (Pennak, 1989). Essentially, these insects have the option of leaving environmentally variable pools because they are not confined.

In freshwater pools, at all scales of observation, ostracod 6 *Potamocypris* sp, midge larvae, *Alona davidi,* and oligochaete B were associated with low variability in chloride, oxygen, and temperature. Conversely, ostracod 2 *Cytheromorpha sp.1*, nematode, mosquitc LR, and midge 4 at all scales were associated with high variability in chloride. Restricted to only freshwater pools are the forcipomyia, rotifera and pseudosmittia, which were associated with very low variability in chloride. Generally, ostracods and copepods were associated with tolerating both high and low variability in chloride, oxygen, pH, and temperature.

Table 3.7. Summary of freshwater CCA bi-plot results

Freshwater	p=	Most important factor on 1st axis	1st axis eigenvalue	Most important factor on 2nd axis	2nd axis eigenvalue
Micro-spatial scale	0.00	Variability in temperature	0.40	Volume	0.30
Local-temporal scale	0.02	Variability in chloride,	0.52	Variability in pH	0.14
Landscape-temporal scale	0.03	Variability in oxygen	0.12	Variability temperature	0.08

Figure 3.11. Micro-spatial scale: freshwater CCA bi-plot of species and environment data ($p = 0.004$)

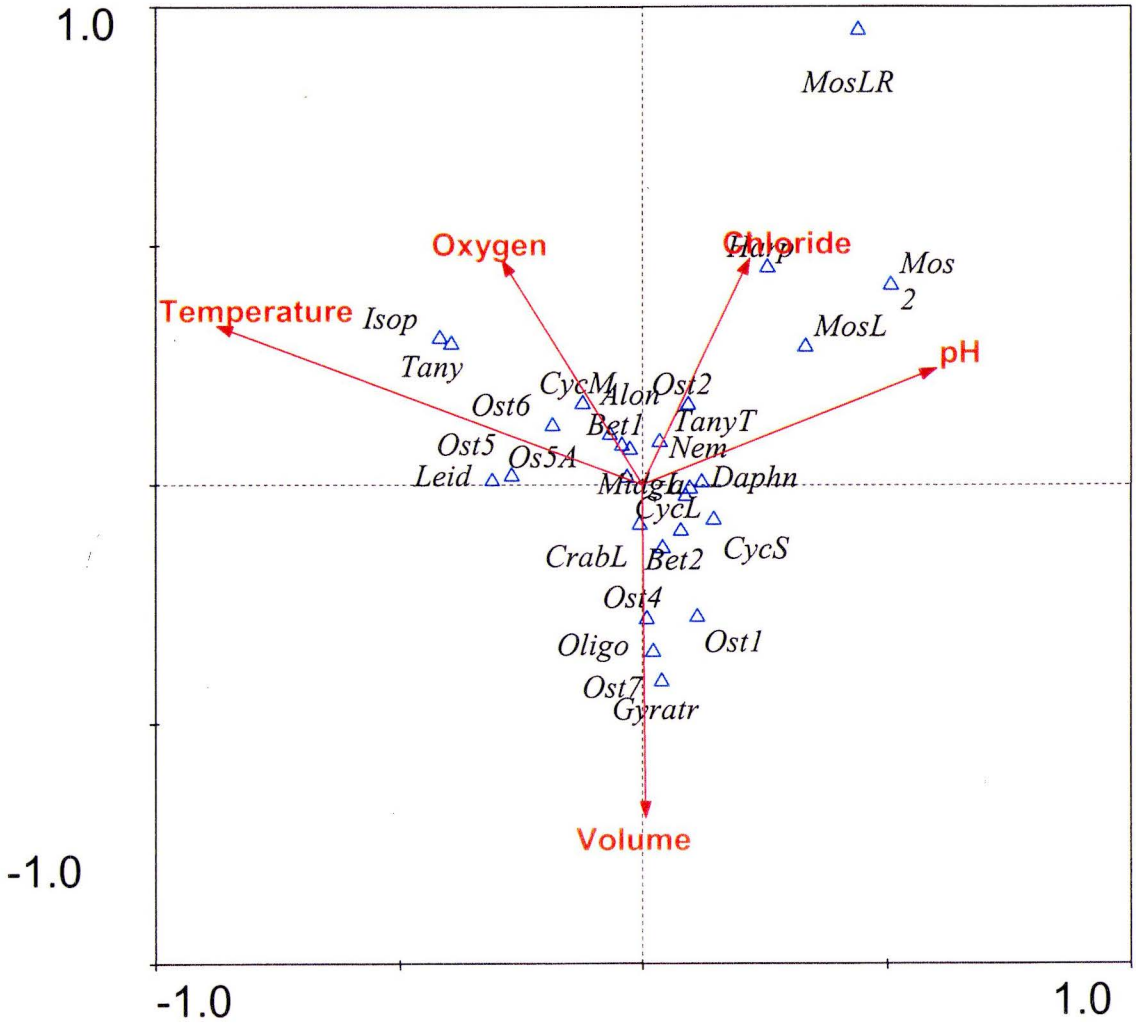

1.0
-1.0
-1.0
1.0
MosLR
Oxygen
Chloride
Harp
Mos
2
MosL
Temperature
Isop
Tany
pH
CycM
Alon
Ost2
Ost6
Bet1
TanyT
Nem
Ost5
Os5A
Leid
Daphn
CycL
CrabL
Bet2
CycS
Ost4
Oligo
Ost1
Ost7
Gyratr
Volume

Figure 3.12. Local-temporal scale: freshwater CCA bi-plot of species and environment data ($p = 0.02$).

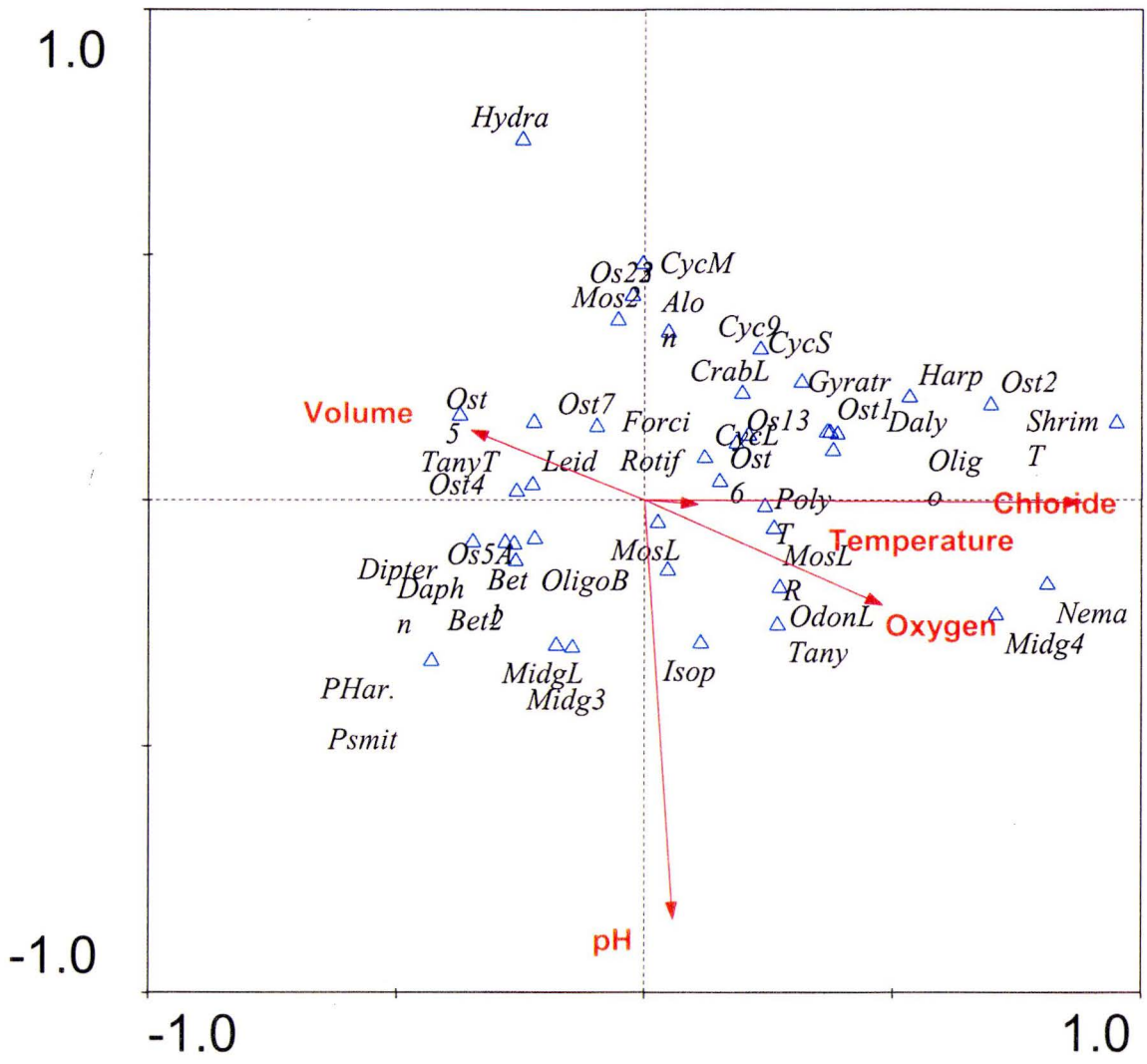
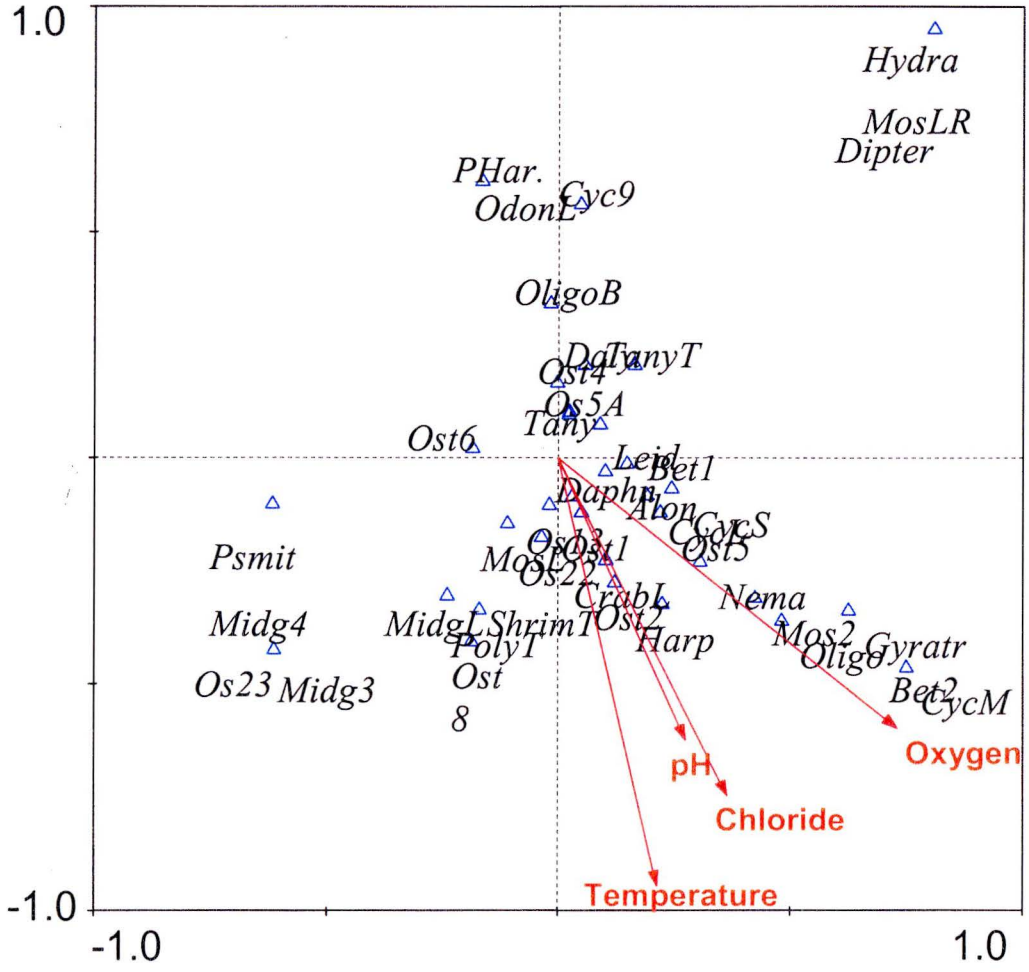

1.0
-1.0
-1.0
1.0
Hydra
CycM
Os23
Mos2
Alo
n
Cyc9
CycS
CrabL
Gyratr
Harp
Ost2
Volume
Ost
5
Ost7
Forci
Os13
Ost1
Daly
Shrim
TanyT
Leid
Rotif
Ost
6
Olig
o
T
Ost4
Poly
Chloride
T
Temperature
Os5A
MosL
MosL
Dipter
Daph
n
Bet
1
OligoB
Bet
2
R
OdonL
Oxygen
Nema
Midg4
Tany
Isop
MidgL
Midg3
PHar.
Psmit
pH

Figure 3.13. Landscape-temporal scale: freshwater CCA bi-plot of species and environment data ($p = 0.03$).


1.0
-1.0
-1.0
1.0
Hydra
MosLR
Dipter
PHar.
OdonL
Cyc9
OligoB
DaTanyT
Ost4
Os5A
Tany
Ost6
Leid
Bet1
Daphn
Chon
CycS
Ost5
Os03t1
MosL2
Os22
CrabL
Nema
Psmit
Midg4
MidgL
ShrimT
Ost2
Harp
Mos2
Gyratr
Oligo
PolyT
Ost
8
Os23
Midg3
Bet2
CycM
Oxygen
pH
Chloride
Temperature

CCA: Brackish Water pools

At the micro-spatial scale, the most important factor was variability in chloride (Table 3.8) (Fig 3.14). The first axis was described by volume and the variability of oxygen and temperature (eigenvalue = 0.67) and the second axis was described by chloride and pH (eigenvalue = 0.50). Most species were positioned close to the origin of the axis, and tended to be positively associated with the variability in oxygen, temperature, pH, and chloride. Approximately half of the species that were positively associated with the chloride vector are known to be able to tolerate a marine environment (i.e. cyclopoid) and the other half of the species were negatively associated with the chloride vector, which are known to be freshwater species (i.e. *Alona davidi*) (Pennak, 1989).

At the local-temporal scale, the most important factor was volume because there was a positive association between volume and the majority of the species. Also, this vector was the longest in the bi-plot, thereby illustrating its strength of relationship with the species data (Table 3.8) (Fig. 3.15). The first axis was described by volume and all the environmental variability factors (eigenvalue = 0.34). There are distinct patterns in this bi-plot; for example, over half of the species were positively associated with volume and low variability in chloride. These species, such as daphnia, polycheates, and oligocheates, are unable to tolerate low volume and unstable environmental conditions. The other major grouping of species occurs around the environmental variability vectors. Species such as Dalelloid *Gieysztoria reggae*, Dalyelloid *Gieysztoria rastafari*,

cyclopoids and marine cyclopoids are tolerant to low volume levels (dessication) and variability in environmental conditions.

At the landscape-temporal scale, the most important factors were variability in temperature and pH (Table 3.8) (Fig. 3.16). The first axis was described by pH (eigenvalue = 0.4) and the second axis was described by the variability in temperature and to a lesser extent variability in oxygen (eigenvalue = 0.3). Most of the species at this scale were either positively associated with variation in oxygen and temperature, or were negatively associated with those vectors; thus, approximately half the species were associated with tolerating changes in temperature, oxygen, and chloride, but the other half were associated with the stability of those factors. Most of the species were associated with being able to tolerate variation in pH. Specifically, ostracod 5A is most abundant in brackish pools where there is varying pH and is therefore more abundant. In contrast, ostracod 6 prefers stability in pH and the other environmental conditions and therefore is less abundant at the landscape-temporal scale in brackish pools.

Overall, in brackish pools and at all scales of observation, *Sesarma miersi* associated with more stable chloride conditions and low variation in oxygen, pH and temperature. Over all scales of study, the harpacticoid *Nitocra spinipes* Boeck and *Gyratrix,* associated with stable conditions of oxygen, temperature and pH. Amphipod and *Leidigia leidigi* were associated with low variability in oxygen, temperature and pH. Harpacticoid *Nitocra spinipes Boeck* and *Gyratrix* associated with higher variation in chloride than did amphipod and *Leidigia leidigi*. Both *Alona davidii* and *Leidigia leidigi*

were exclusive to freshwater and brackish pools. In general, harpacticoids, copepods and ostracods preferred variability in chloride. In the CCA bi-plot the brackish water species were positioned close to the origin away from extreme variability in chloride. Thus, the bi-plot suggested that in brackish pools, species did not tolerate high variability of environmental factors because the pool conditions were already harsh in terms of variable chloride conditions.

Table 3.8. Summary of brackish CCA bi-plot results

Brackish	p=	Most important factor on 1st axis	1st axis eigenvalue	Most important factor on 2nd axis	2nd axis eigenvalue
Micro-spatial scale	0.01	Variability in chloride	0.67	Variability in pH	0.50
Local-temporal scale	0.04	Volume	0.34	No vectors on 2nd axis	
Landscape-temporal scale	0.05	Variability in pH	0.40	Variability in temperature	0.30

Figure 3.14. Micro-spatial scale: brackish CCA bi-plot of species and environment data ($p = 0.01$).

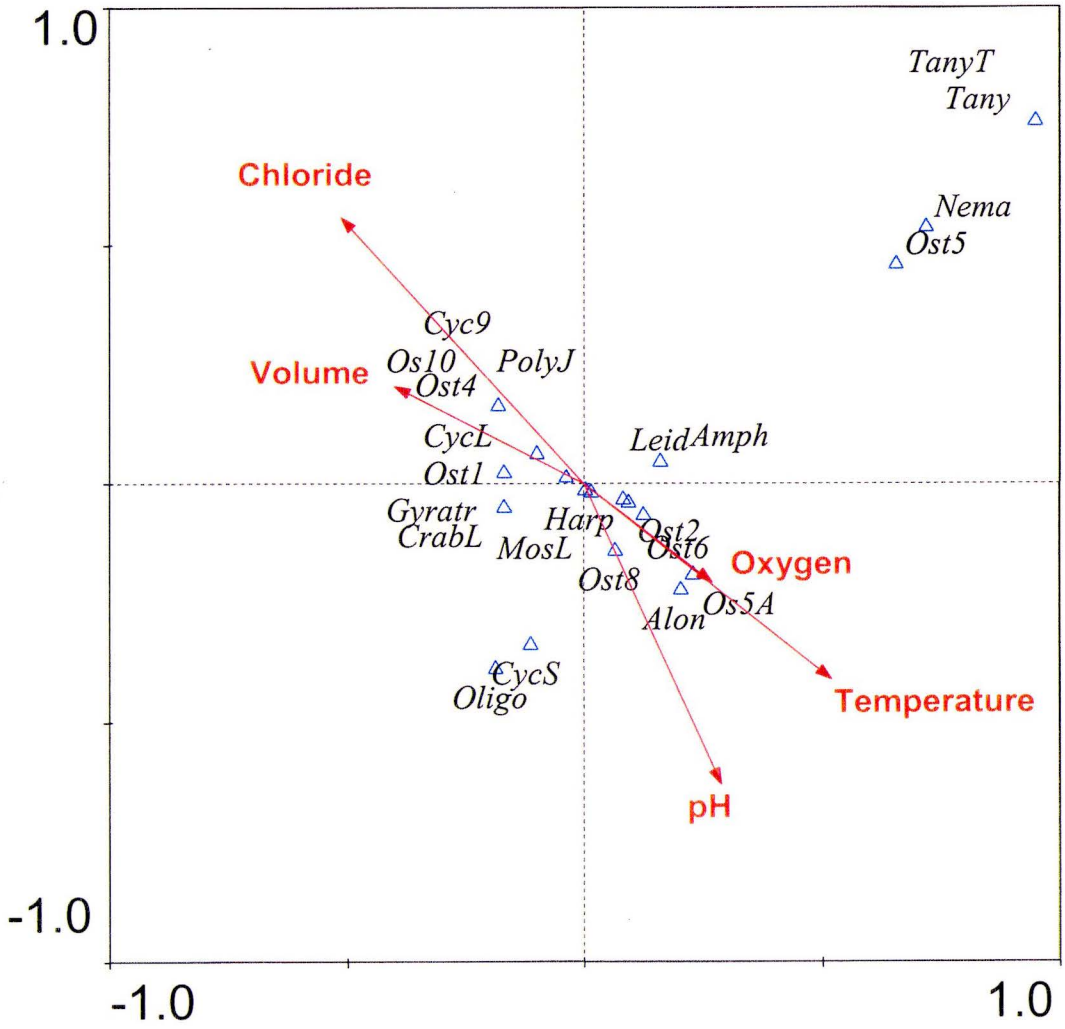

1.0
-1.0
-1.0
1.0
TanyT
Tany
Nema
Ost5
Chloride
Cyc9
Volume
Os10
PolyJ
Ost4
CycL
LeidAmph
Ost1
Gyratr
Harp
Ost2
CrabL
MosL
Ost6
Oxygen
Ost8
Os5A
Alon
CycS
Oligo
Temperature
pH

Figure 3.15. Local-temporal scale: brackish water CCA bi-plot of species and environment data ($p = 0.04$).

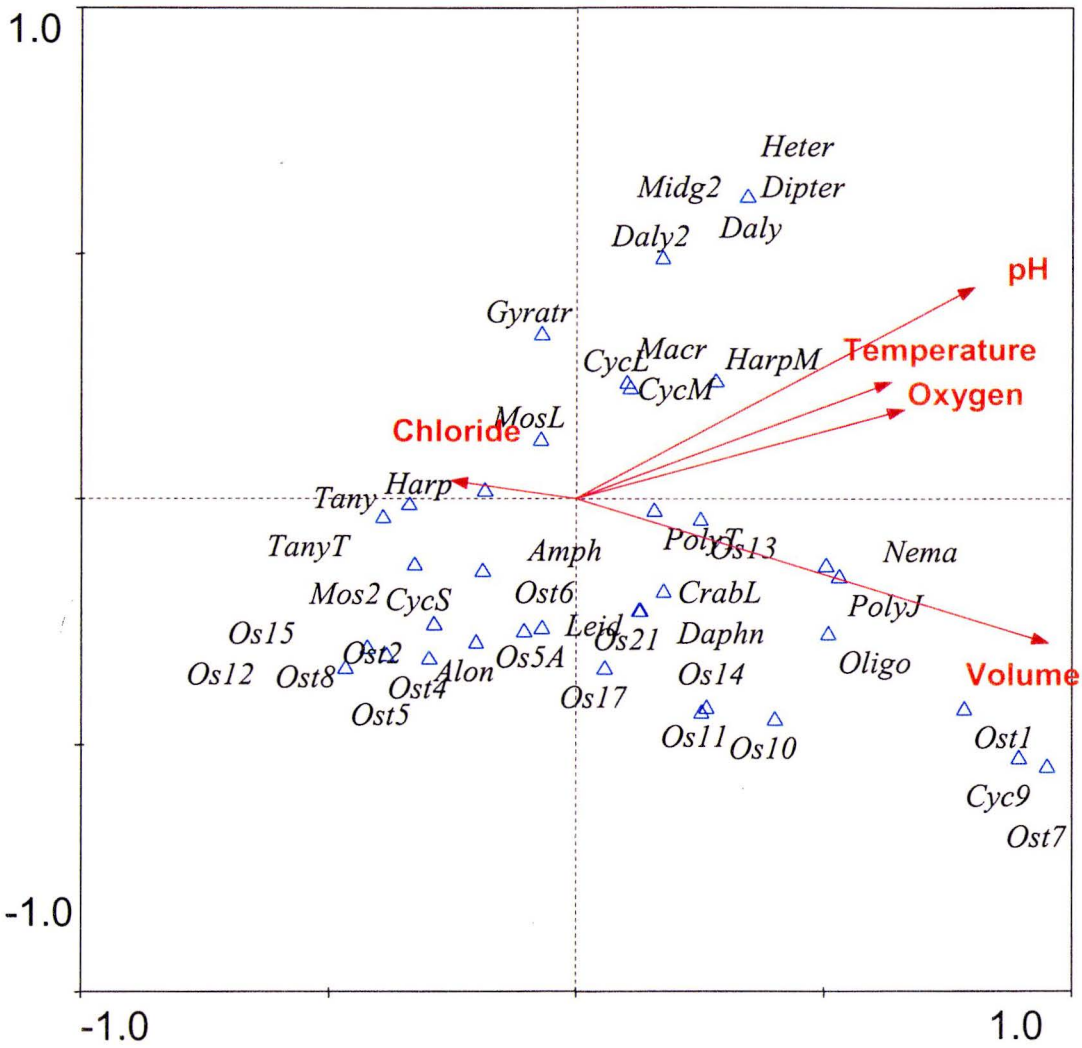
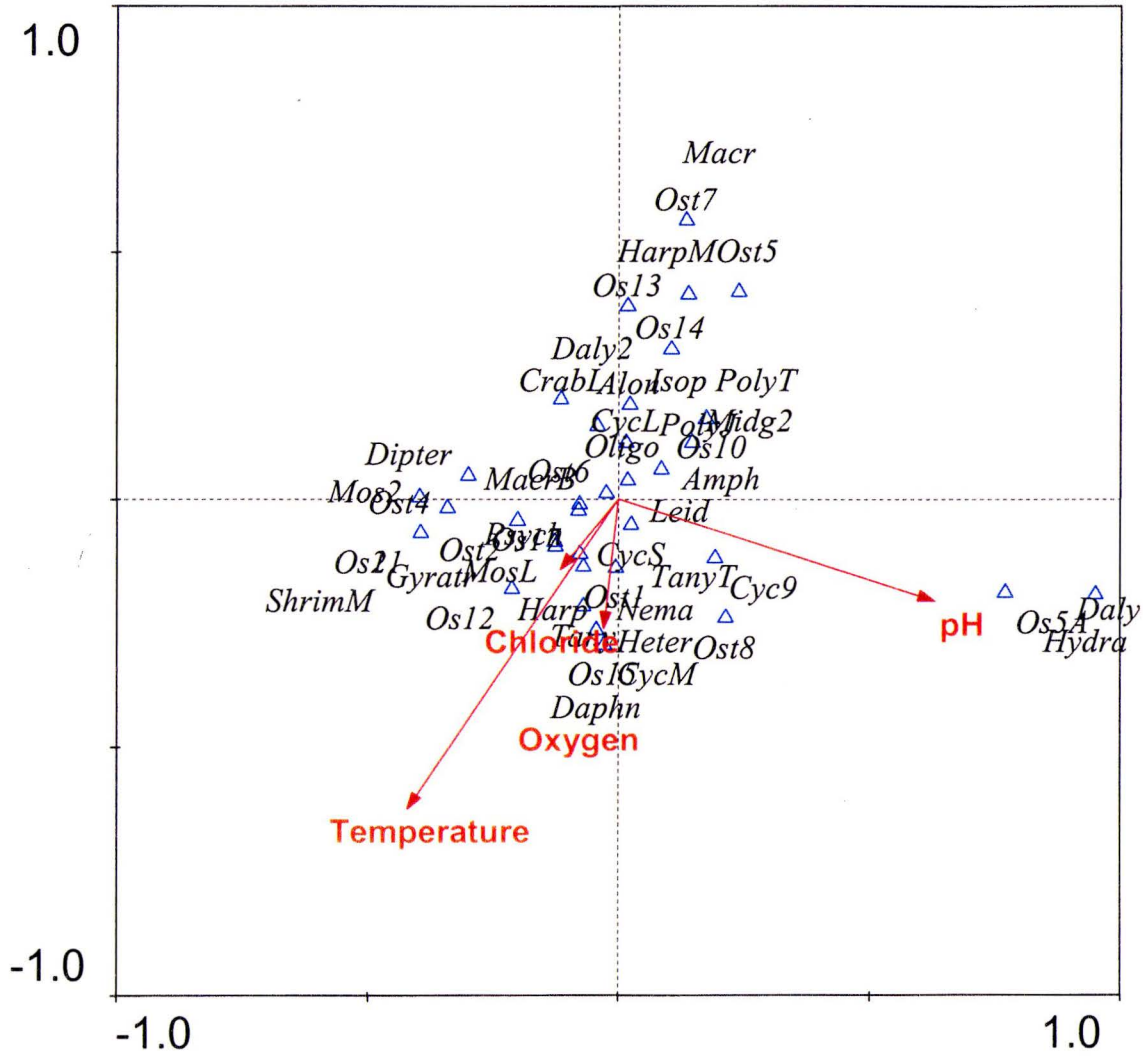

1.0
-1.0
-1.0
1.0
Heter
Midg2
Dipter
Daly2
Daly
pH
Gyratr
Macr
CycL
HarpM
Temperature
CycM
Oxygen
MosL
Chloride
Harp
Tany
TanyT
Amph
PolyT
Os13
Nema
Mos2
CycS
Ost6
CrabL
PolyJ
Os15
Leid
Os21
Daphn
Ost2
Os12
Ost8
Ost4
Alon
Os5A
Os14
Oligo
Volume
Os17
Ost5
Os11
Os10
Ost1
Cyc9
Ost7

Figure 3.16. Landscape-temporal scale: brackish water CCA bi-plot of species and environment data ($p = 0.05$).


1.0
-1.0
-1.0
1.0
Macr
Ost7
HarpM
Ost5
Os13
Os14
Daly2
CrabL
Alou
Isop
PolyT
CycLP
olyV
Midg2
Dipter
Oligo
Os10
Ost6
MaerB
Amph
Mos2
Ost4
Leid
Ryth1
Ryth2
Os11
Ost2
CycS
GyratM
MosL
TanyT
Cyc9
ShrimM
Ost1
Os12
Harp
Nema
pH
Os5A
Daly
Hydra
Chloride
TanyH
eter
Ost8
Os16
CycM
Daphn
Oxygen
Temperature

CCA: Marine Water Pools

At the micro-spatial scale, the most important factors were volume and variability in temperature (Table 3.9) (Fig. 3.17). The first axis was described by volume, oxygen, chloride, and pH (eigenvalue = 0.54) and the second axis was described by temperature (eigenvalue = 0.3). The species ordination pattern suggested that most species were positively associated with moderate to high volume levels, variability in chloride, and stability in oxygen and pH.

At the local-temporal scale, the most important factors were volume and variability in chloride (Fig. 3.18). The first axis was described by volume and variability in pH (eigenvalue = 0.34) and the second axis was described by variability in chloride and to a lesser extent, oxygen and temperature (eigenvalue = 0.17). Overall, there was no relationship between volume and any of the environmental variability vectors. Over half of the species Although there was no clear patterns of species in relation to the environmental variability vectors on the bi-plot, there were some species that did positively associate with high volume levels. The volume effects added rare species to the data set; for example, kalyptorhynchid *Polycystis felis*, and hydrophilid. These rare species are tolerant to variable salinity.

At the landscape-temporal scale, the most important factors were variability in temperature and oxygen (Fig. 3.19). The first axis was described by all the vectors (eigenvalue = 0.24). Essentially the plot can be divided into those species that were negatively associated with variation in temperature, oxygen, pH, and chloride (i.e. kalyptorhynchid *Polycystis felis*, and hydrophilid), and those that were positively

associated with environmental variability in these conditions (i.e. Dipteran, and cyclopoids).

There are several species that are unique to marine pools, such as the kalyptorhynchid *Polycystis felis*, hydrophilid beetle *Enochrus sp*, midge larvae, Acoela, shrimp 3, ostracod 9 *Cytheromorpha*, and sea anemones. All of these species tolerated marine salinities; however, only kalyptorhynchid *Polycystis felis*, shrimp 3, ostracod 9 *Cytheromorpha sp.2* and sea anemone were associated with highly variable chloride and oxygen conditions over time. Polychaete F (with filtering tentacles) and polychaete 3 (with adhesive posterior end) were exclusive to brackish and marine conditions and were associated with stable salinity. At the micro-spatial and landscape-temporal scale of study, harpaticoid *Nitocra spinipes* Boeck, *Gyratrix* and marine cyclopoid *Metis* were associated with high variability of chloride. However, at the local-temporal scale, they were associated with stability of chloride within the pools over time. *Sesarma miers* associated with high variability of chloride, as well as low variability in temperature. In general, ostracods, copepods and harpacticoids seemed to position around variability in temperature, oxygen, pH, and chloride vectors, indicating that they do better in pools with variability in environmental conditions.

Table 3.9. Summary of marine CCA bi-plot results

Marine	p=	Most important factor on 1st axis	1st axis eigenvalue	Most important factor on 2nd axis	2nd axis eigenvalue
Micro-spatial scale	0.010	Volume	0.54	Variability in temperature	0.30
Local-temporal scale	0.008	Volume	0.34	Variability in chloride	0.17
Landscape-temporal scale	0.004	Variability in temperature and oxygen	0.24	No vectors on 2nd axis	

Figure 3.17. Micro-spatial scale: marine CCA bi-plot of species and environment data ($p = 0.01$).

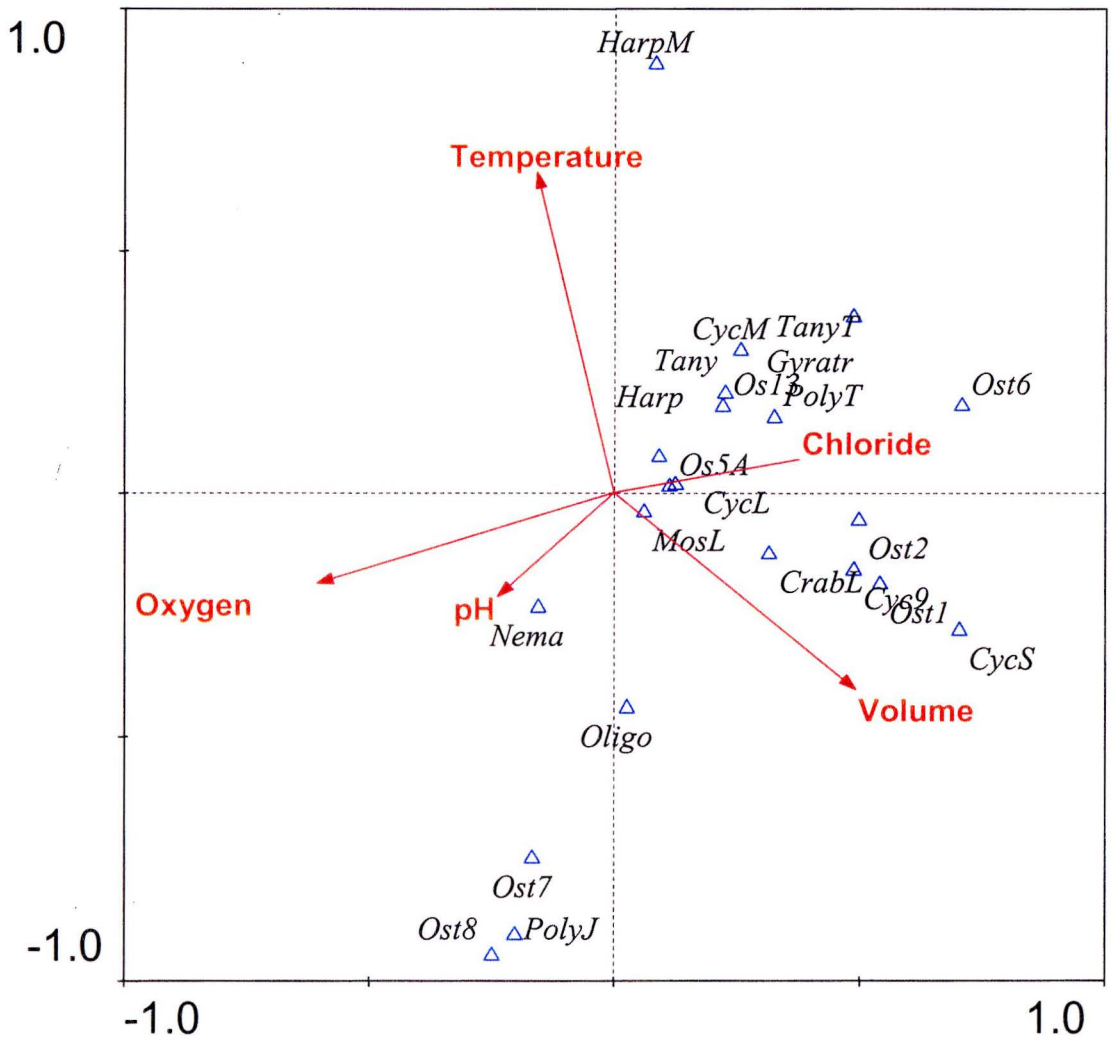

1.0
-1.0
-1.0
1.0
HarpM
Temperature
CycM
TanyT
Tany
Gyratr
Harp
Os12
PolyT
Ost6
Chloride
Os5A
CycL
MosL
Ost2
CrabL
Cyc9
Ost1
CycS
Oxygen
pH
Nema
Volume
Oligo
Ost7
Ost8
PolyJ

Figure 3.18. Local-temporal scale: marine CCA bi-plot of species and environmental data ($p = 0.008$).

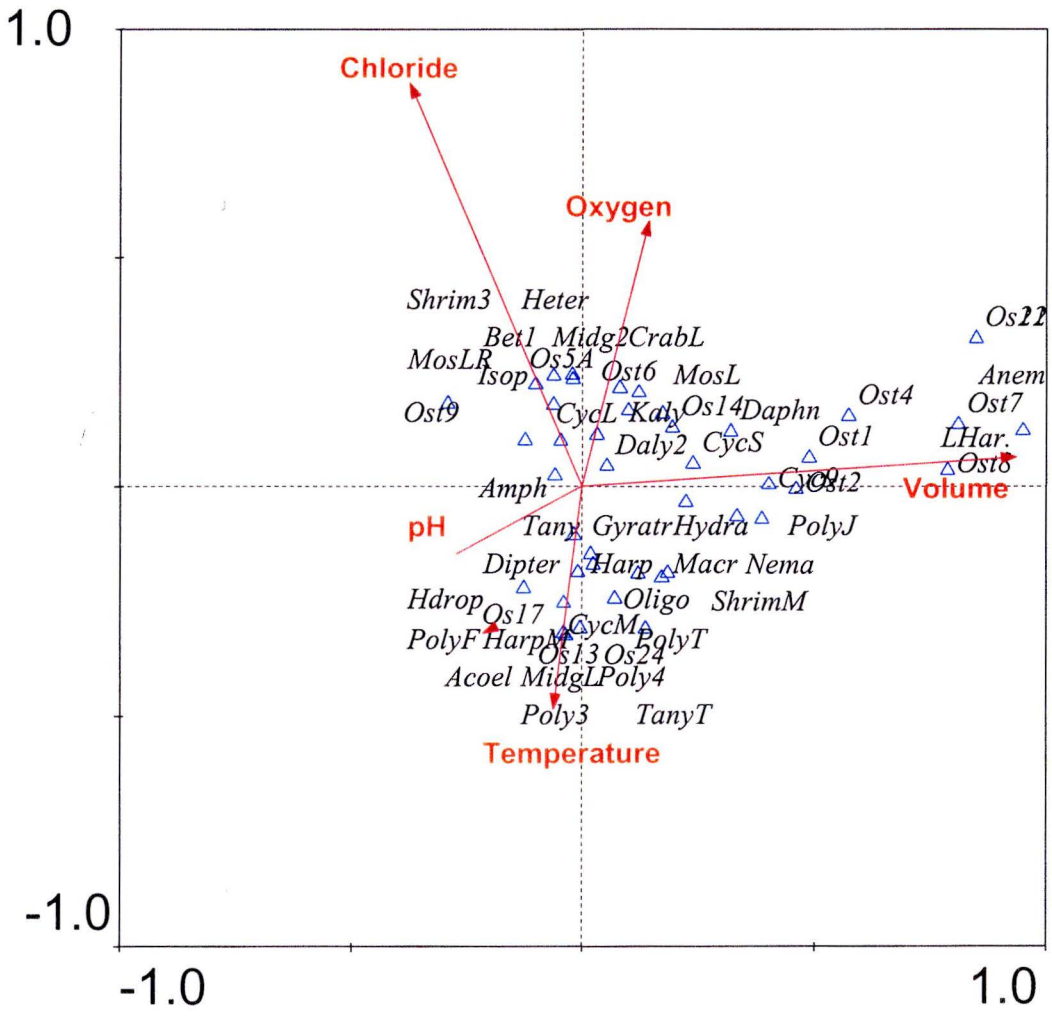
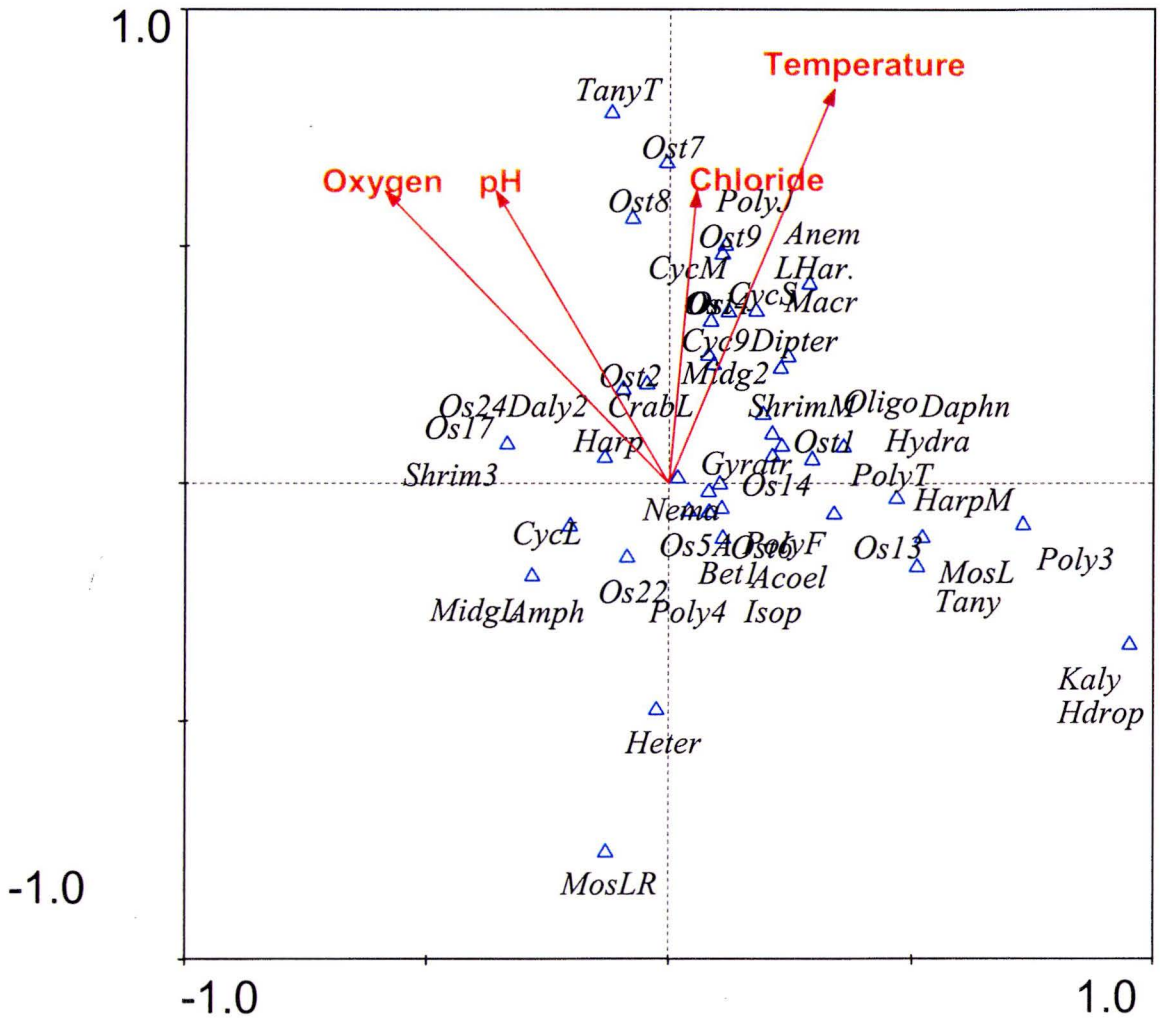

1.0
-1.0
-1.0
1.0
Chloride
Oxygen
pH
Volume
Temperature
Shrim3
Heter
Bet1
Midg2
CrabL
MosLR
Os5A
Ost6
MosL
Isop
Ost9
CycL
Kal
Os14
Daphn
Ost4
Ost7
Anem
Daly2
CycS
Ost1
LHar.
Ost8
Amph
Ost2
Tany
Gyratr
Hydra
PolyJ
Dipter
Harp
Macr
Nema
Hdrop
Os17
Oligo
ShrimM
CycM
PolyF
HarpM
PolyT
Os13
Os24
Acoel
MidgL
Poly4
Poly3
TanyT

Figure 3.19. Landscape-temporal scale: marine CCA bi-plot of species and environmental data ($p = 0.004$).


1.0
-1.0
-1.0
1.0
Temperature
Oxygen
pH
Chloride
TanyT
Ost7
Ost8
PolyJ
Ost9
Anem
CycM
LHar.
Macr
Cyc9Dipter
Ost2
Midg2
Os24Daly2
CrabL
ShrimM
Oligo
Daphn
Os17
Harp
Ostl
Hydra
Shrim3
Gyratr.
Os14
PolyT
HarpM
Nema
CycL
Os5A
PolyF
Os13
Poly3
Bet1
Acoel
MosL
Os22
Tany
MidgL
Amph
Poly4
Isop
Kaly
Hdrop
Heter
MosLR

CCA: Comparison between Plots with and Without the Variability of Chloride Data

CCA: Freshwater Pools

In freshwater pools, at the micro-spatial and landscape-temporal scales, the CCA vectors and species ordination were similar when the chloride vector was removed from the CCA bi-plot. Thus, variability in chloride was not an important factor in the relationship between species data and environmental data in fresh water pools. However, at the local-temporal scale, the addition of the chloride vector (variability in chloride) changed the positions of where the species ordinate, and also slightly rotated the vectors in relation to each other and the axes (Appendix 2, Fig. 1). Thus, when all freshwater pools are considered together, over time, variability in chloride becomes less important. Likewise, within individual pools at the micro scale, variation in chloride is less traumatic for species than at the local-temporal scale, because they can move to other areas of the pool that are suitable to their salinity tolerances. Conversely, over time, the variability in chloride is important in shaping the species patterns within individual pools. If each individual freshwater pool becomes variable in salinity, then the freshwater communities must adapt and change to varying chloride conditions.

CCA: Brackish Pools

In brackish pools, at the micro-spatial scale, the vector for chloride variability was an important factor in the relationship between species data and environmental data. At the micro-spatial scale, the addition of chloride vector changed the length of the other

vectors. For example, volume and the variability of oxygen became more important and the variability of temperature and pH became less important (Appendix 2, Fig. 2).

At the landscape-temporal scale of study, the addition of the chloride variability vector shifted the ordination of species in relation to the axes and in some cases in relation to each other. Overall, there were no major changes in the CCA plot, but the minor changes did suggest that the variability of chloride was a factor to consider in the relationship between species data and the environmental data (Appendix 2, Fig. 3).

CCA: Marine Pools

At all scales of study, the addition of the chloride vector did not significantly change the general ordination of species and the vector loadings. Therefore, the variability of chloride did not have an effect on the patterns of species ordination within the CCA bi-plot.

Chapter 4:

Discussion

Discussion

Although there were no significant relationships between univariate (Table 3.1) or composite (Table 3.3) measures of environmental variability and community metrics, the multiple regression analysis (Table 3.2), at the local-temporal scale, and the CCA (using the composite measure of environmental variability) showed that local species richness and species performance were associated with environmental variability (Fig. 3.1, 3.3, 3.5). These results suggest that while environmental variability may not be a primary determinant of community structure in rock pools, environmental variability does play a role in determining species compositions and the abundances of particular species in the pools (Townsend *et al.*, 1983; Corkum, 1989).

Overall, the lack of clear or strong relationships between environmental variability and community metrics (Table 3.1 and Table 3.3), for all 49 pools together, at the local-temporal and landscape-temporal scales of observation, suggests that the processes determining species richness and abundance in rock pools are more complex than simply environmental variability. One possible explanation for these complex patterns could be caused by scaling effects. Patterns and processes are scale dependent phenomena (Wiens, 1989) and our view of any system depends on the scale of observation. Thus, the combinations of environmental and biotic factors that might determine community structure would also change depending on the scale of observation. For example, at the micro-spatial scale, predation or competition, are mechanisms that may affect diversity (Pianka, 1994). At the local-temporal scale, local extinction and re-colonization events may affect patterns of diversity. At the landscape-temporal scale,

large scale processes that affect all the pools, such as dispersal mediated by wind or rainfall, may affect species richness and abundance (Therriault, 2000).

Using multiple regression analyses (Table 3.2), Therriault and Kolasa (1999) suggested that physical variables have a greater impact on the number of species present in a rock pool than on community abundance. Likewise, the multiple regression analysis in this study, found that at the local-temporal scale of observation, environmental variability was significantly correlated with species richness but not with community abundance.

At the micro-spatial scale, the species-environment ordination suggested that invertebrate community composition and abundance was strongly influenced by pool salinity (Fig. 3.1). This finding agrees with Williams *et al.* (1997) whom identified a strong relationship between groundwater spring taxon occurrence and chloride concentrations. In the rock pools, those species that preferred variability in salinity were marine species, such as the marine cyclopoid and marine harpacticoid. Whereas, those species that favored stable environmental conditions were freshwater species, for example daphnids (Pennak, 1989). Clearly, the observed community composition and abundance was determined by the variability of salinity in the pools (Fig. 3.1).

While the micro-spatial scale of observation had significant effects on which mechanism was seen as important in structuring rock pool communities (i.e. salinity), a possible explanation for the lack of any strong relationships at the local-temporal and landscape-temporal scale of observation, between community metrics and environmental variability, is that the 49 pools represented distinct communities (Fig. 3.3, 3.5). The

processes determining species richness and abundance in these different communities were masked when all 49 pools are analyzed together. I speculated that patterns between environmental variability and community metrics would emerge more clearly when pools were grouped based on salinity, as the species composition of the pools is strongly dependent on pool salinity (As seen at the micro-spatial scale of observation, figure 3.1) (Hutchinson, 1967; Timms, 1983; Therriault and Kolasa, 1999; Therriault, 2000). Not surprisingly, by analyzing the role of environmental variability in freshwater, brackish, and marine pools separately, a more complete picture of the effects of environmental variability on community structure emerged.

In freshwater pools, the regression analysis suggested that as environmental variability increased, species richness decreased (Fig. 3.7). Species inhabiting these rock pools are freshwater organisms and therefore are only able to tolerate low variability in environmental conditions. Once environmental conditions exceed the tolerance limits of organisms, then species are unable to survive and therefore species richness decreases (Hutchinson, 1967; Therriault and Kolasa, 1999).

Freshwater pools usually contain species originating from only freshwater, whereas brackish pools contain a combination of taxa, some originating from freshwater pools and others originating from the marine pools, or the ocean (Therriault, 2000). Thus, it is not surprising that the linear regression analyses in figures 3.8 and 3.9 indicate that as environmental variability increases, both species richness and abundance increase, because the brackish pool community is a mixture of both freshwater and marine species. Therefore, there is potential for more species to survive in variable environments. Those

that can tolerate more variable environments can exploit the resources and thereby increase in abundance (Therriault, 2000). Likewise, in marine pools, the positive relationship observed in the regression between the abundance and environmental variability (Fig. 3.10), indicates that some species are able to exploit unstable pool conditions, and their abundances increase accordingly (Therriault and Kolasa, 1999; Romanuk, 2002).

Temperature was the most important CCA vector in freshwater communities at the micro-spatial and landscape-temporal scales (Fig. 3.11, 3.13). Temperature in aquatic ecosystems has two effects it causes thermal stratification in water bodies and affects the rates of chemical reactions and biological processes (Lind, 1985; Klugh, 1924). Rock pools are small and shallow and therefore thermal stratification of the water column within the pool is not as important of a factor as in large bodies of water; however, the regulation of chemical reactions and biological processes is still applicable to this system. Varying temperatures over time and space can cause organisms to either speed up their metabolic wheels, or slow down and use much less energy (Horne and Goldman, 1994). Changes in temperature from location to location and through time not only affect an organism's metabolic rate, but also how soluble the water is to oxygen (Horne and Goldman, 1994).

Volume was also an important determinant of species performance in freshwater, brackish and marine pools, particularly at the micro-spatial scale of observation (Fig. 3.11). This is not surprising as pools with greater volume have a greater probability of the pool supporting more individuals and a lower probability of extinction. (Hanski and

Gyllenberg, 1993; Tonn *et al.*, 1995). Furthermore, evaporation leads to higher variability in temperature, salinity, and pH (Van Dam, 1988), which can have negative effects on species richness and abundance. Thus, it is not surprising that at the micro-spatial scale organisms that usually prefer stable environmental conditions, such as worms (*Gyratrix*), are positively associated with moderate to high volume in freshwater pools (Pennak, 1989; Romanuk 2002).

Variability in pH was not the primary factor in determining species performance in any of the rock pools, despite the role of pH on the physiology of invertebrates and on food resources (Townsend *et al.*, 1983). The lack of strong effects of variability in pH in rock pools is likely due to the composition of the pools. Rock pools are created from limestone and thus the calcium bicarbonate buffers the alkalinity or acidity that enters the pool from photosynthesis, respiration, biotic waste and or rain water (Lind, 1985; Horne and Goldman, 1994). Thus, variability in pH in rock pools is likely low in comparison with other small aquatic systems. pH and oxygen are strongly correlated (Therriault and Kolasa, 1999; Romanuk and Kolasa, 2002); as a result, it is not surprising that variability in oxygen was also not a factor that determined species patterns in any of the rock pools.

Similarly, variability in salinity was not a factor in shaping the patterns of species composition and abundance in freshwater pools at the micro-spatial scale or the landscape-temporal scale (Fig. 3.11, 3.13). However, variability in salinity did play a role in determining species performance in individual pools (local-temporal scale, Fig. 3.12). Temporal variation in salinity can be a major determinant of whether a species can persist in a pool (Therriault and Kolasa, 1999). If salinity is changing over time, species that are

adapted to freshwater conditions may not be able to persist. At the micro-spatial scale and the landscape-temporal scale variability in salinity was very low and thus unlikely to have a strong effect on species performance in freshwater pools.

In brackish pools, there was no one factor responsible for shaping the patterns of species data across all scales. Instead, at different scales, different environmental factors were important. This is not surprising, as biological and physical processes change with scale and new properties may appear at different scales (Allen and Hoekstra, 1991; Legendre *et al.*, 1986). As such, variability in salinity at the micro-spatial scale (Fig. 3.14), pool volume at the local-temporal scale (within each pool over time, Fig. 3.15), and variability in temperature at the landscape-temporal scale (Fig. 3.16), were the most important factors in shaping species patterns in brackish pools. Indeed, brackish pools were more complex with respect to describing species patterns because the environment was much more variable than that of freshwater or marine pools (Diesel *et al.*, 2000).

Variability in salinity was important at the micro-spatial scale and to a lesser extent at the landscape-temporal scale (Fig. 3.14, 3.16); however, at the local-temporal scale (Fig. 3.15), variability in salinity was not an important factor shaping the patterns of brackish water species. In brackish pools at the micro-spatial scale, half of the species were associated with variability in salinity and the other half were negatively associated with variability in salinity. This could result from the brackish water community being composed of both marine and freshwater species, with the marine species associated with variability in salinity, and the freshwater species associated with stable salinity (Palmer and Dixon, 1990).

Generally, lower volume/desiccation causes detrimental cascading effects on environmental pool conditions. Moreover, desiccation occurring in pools that are already environmentally variable to start with, such as brackish pools, is devastating to freshwater species that are desiccation intolerant (Van Dam, 1988). Adapting and surviving in low volume brackish pools is difficult because it affects the ability of freshwater species, such as polychaetes, oligochaetes and daphnids, from encysting, or persisting (Wiggins *et al.*, 1980; Pennak, 1989). Therefore, in order for freshwater species to exist in brackish pools, at the local-temporal scale of observation (Fig. 3.15), the volume level in individual pools must remain moderate to high. Conversely, turbellarians, such as dalyelloid *Gieysztoria reggae* and dalyelloid *Gieysztoria rastafari*, as well as marine cyclopoids are desiccation tolerant species (Pennak, 1989) and can encyst and persist in environmentally variable conditions within brackish pools. Thus, species that are able to tolerate a pool with variable environmental conditions are able to successfully survive in brackish pools at the local-temporal scale.

Likewise, in marine pools, at the local-temporal scale, volume effects increased species richness (Fig. 3.18). With higher volume levels, rare species could inhabit the pools because there was more available niche space and more stable environmental conditions for rare species to enter the saline environment. These species include rare ostracods, *Nitocra spinipes* harpacticoids, kalyptorhynchid (*Polycystis felis*), hydrophilid beetle and sea anemones.

If physical and environmental conditions are highly variable, there usually exists a particular suite of species that are well adapted to surviving highly variable conditions

(Death, 1995). Marine species were quite tolerant to harsh conditions (Lind, 1985) they were able to persist in pools with high temporal variability in both temperature and salinity as well as persist in pools with high internal differentiation in temperature and salinity. At both the micro-spatial scale and landscape-temporal scale, the most important environmental factor shaping the patterns of species in marine pools was the variability in temperature (Fig. 3.17, 3.19). Stable dissolved oxygen conditions were also an important factor for species performance in marine pools. Dissolved oxygen participates in many important chemical and biological reactions. It is continually consumed in respiration by both plants and animals but is produced by plant photosynthesis, when sufficient light and nutrients are available (Horne and Goldman, 1994). Indeed, the observed trend of species being able to tolerate variable temperature and salinity in marine pools, but not variability in dissolved oxygen (Fig. 3.17, 3.18), could be the result of stress due to physiological stress from suboptimal amounts of dissolved oxygen (Ziv, 1998; Horne and Goldman, 1994).

At both the micro-spatial and landscape-temporal scales, salinity was not a dominant factor shaping species performance in marine pools (Fig. 3.17, 3.19). Since the marine pools already have a high salinity it is not surprising that variations in salinity would have little effect. Salinity is usually a major determinate of community structure in coastal marine systems (Jorcin, 1999), and in rock pools, salinity is one of the primary variables determining species composition (Therriault and Kolasa, 1999). However, while salinity *per se* is important in determining patterns of species richness, abundance,

and identity across all rock pools, variability in salinity across and within the marine pools is very low.

At all three scales of observation and throughout all pools, the species-environment ordinations indicated that *Nitocra spinipes* Harpacticoids were able to out compete other organisms in freshwater rock pools because they are able to tolerate both salinity and variable environmental conditions. Thus, they were able to tolerate a wide range of environmental conditions and therefore could exploit the resources within most of the pools. Because of their tolerance ranges, *Nitocra spinipes* Harpacticoids were the most abundant species in the rock pool system and were found in the majority of the pools (Romanuk, 2002; personal observation). Also, most insects (i.e. mosquitoes) are able to out compete other rock pool organisms because they are able to breathe air and therefore are not confined to certain freshwater pools (Pennak, 1989). Indeed, varying environmental conditions do not limit insects or *Nitocra spinipes* harpacticoids in terms of abundance. Overall, these species are considered "generalists" because they have large geographical ranges and high abundances (Romanuk, 2002; Therriault and Kolasa, 2000; Therriault, 2000). Similarly, *Cypridopsis* sp. and *Potamocypris* sp. exist in freshwater, brackish and marine pools and are second to *Nitocra spinipes* harpacticoids in terms of abundance.

Conversely, specialists are those species that have narrow tolerance ranges and lower abundances (Therriault, 2000). Species such as *Forcipomyia*, rotifers and *Pseudosmittia* sp. species are specialized to freshwater. Kalyptorhynchid *Polycystis felis*, hydrophilid beetle *Enochrus sp*, sea anemones, and midge larvae are specialists restricted

to marine water although they can tolerate harsh environmental conditions including variability in salinity.

Overall, the scale that describes the most explained variance between environmental data and species data is the micro-spatial scale of observation. Based on the spread of the biotic data in the CCA bi-plots, and the overall high eigenvalues for each bi-plot, the micro-spatial scale of observation shows that the species are most reacting to environmental data at this scale. Unlike other studies done on rock pools, the species seem to be most affected and perceive the environment at the micro-spatial scale. This is a result of other studies only observing species patterns at the local-temporal scale (Romanuk and Kolasa, 2002; Therriault and Kolasa, 2000; Schuh and Diesel, 1995; Diesel *et al.*, 2000). Unlike the local-temporal scale and landscape-temporal scale where environmental variability was found to only have had a minor role on the patterns of species, the micro-spatial scale indicates that abiotic factors help to exert control on the persistence and presence of species. Although the micro-spatial scale cannot prove that larger scale patterns, such as the local-temporal and landscape-temporal scales, have the same causes, it can demonstrate which factors actually operate in order to produce species patterns.

Conclusion

Overall, there are complex patterns and relationships between species and environmental variability in rock pools. Variability in temperature was the most important factor that positively affected the species patterns. Ecological scaling becomes important when different processes affect species at different spatio-temporal dimensions (Ricklefs, 1987). In this study, scale of observation had strong effects in most of the analyses, with the environmental factors associated with species patterns changing depending on the scale of analysis. Identifying and understanding scale dependent changes in community patterns is a prerequisite for predicting the consequences of changes in ecological systems induced by variability in environmental factors (Allen and Hoekstra, 1991; Legendre *et al.*, 1986).

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Appendix 1:

Biotic Data

Biotic Data

Crustacea

Amph=amphipod (sideswimmer)

Daph=*Ceriodaphnia rigaudi*

CopS=copepod with short antennae

CopL=copepod with long antennae

Acant=*Leidygia acanthocercoides*

CopM=marine (red) copepod

Leid=*Leidygia leydigi*

ShrimM=Shrimp with Mantis like claws

Alon=*Alona davidi*

ShrimT=Shrimp with thin claws

PHar.= Predatory "Harpacticoid"

LHar.= Long "Harpacticoid"

Isop= Isopod

Rotif=Rotifer

Worms

PolyT= Thin Polychaete w/o cuticular jaws

PolyJ= Polychaete w/ culticular jaws

Poly3 = Polychate with adhesive posterior end

Poly4 = Polychaete with serrated jaws & massive parapedia

PolyF = Polychaete with tentacles ("filtering")

Macr=*Macrostomum* sp indet.

MacrB = *Macrostomum balticum*

OligoB=oligochaete with long bristles

Gyratr=*Gyratrix* (Kalyptorynchid)

Kaly = Kalyptorhynchid (*Polycystis felis*)

Daly=Dalelloid *Gieysztoria reggae*

Daly2=Dalyelloid *Gieysztoria rastafari*

Insects

MidgeL = midge larvae or Midge1; two eyes

Midg2= midge with one flat central tooth (photo) and very short antennae

Midge3=midge with one pointed central tooth and long antennae; one eye
Psmit=Pseudosmittia

Psych = Psychodid fly

Dipt = non-midge like diptera: Dolichopodid larva

Forci = Forcipomyia

Heter= heteropteran bug

Tany = 'tanypodid' fly larvae (probably ceratopogonid)

TanyT = true tanypodid

Bet1= Beetle 1

Bet2= Beetle 2

Bet3= Beetle 3

Hdrop = Hydrophilid beetle: *Eochrus sp.*

OdonL = Odonata Larva

MosL=Mosquito Larva

Mos2=Mosquito Larva with long bristles all over the body

Appendix 2:

Chloride measurements

Chloride Measurements

The chloride measurements, taken by the Lazar labs micro chloride probe, for the January 2002 spatial data were consistent; however, the values were not similar to the average values obtained by the YSI data sonde taken in January of 2002. In order to check for accuracy in the spatial chloride values, contour plots of the data were created using both SYSTAT 10.2 (examples of plots shown in Fig.1-3) and STASTICA 6.0 (examples of plots shown in Fig 4-10); however, the STATISTICA plots better display the data. From these plots, it could be determined if there was a drift in the probe, for example it could be determined if the instrument would start recording high salinity values and then slowly drift to low salinity values as the probe was moved from one location of the pool to another. Although the values recorded were not correct, the contour plots suggested that the instrument did not drift and that the probe was taking consistent measurements. Also, the depth versus chloride value bar graphs (examples of graphs shown in Fig. 11-16), indicate that both fresh water and marine water pools have mostly uniform salinity throughout the pools. Freshwater has much less salinity than marine pools. Also, the box whisker graphs (one way ANOVA) for brackish water pools indicate that an increase in depth shows that there is an increase in salinity, because saline water sinks beneath fresh water. Since there is confidence in the chloride data, it was then manipulated (Table 1) in order to maintain the consistency, but to bring the values closer to the average salinity values previously recorded over various sampling dates.

Table 1. Conversion of raw chloride data (ppm) into corrected chloride data (ppm)

Chloride **reading,** (ppm)	Chloride **Pool mean** (ppm), YSI data sonde	**Product 1**	Corrected chloride data value, (ppm)
		Reading * Pool Mean	Product 1 * Ratio of Pool mean to mean of product 1
		Reading * Pool Mean	Product 1 * Ratio of Pool mean to mean of product 1
		Reading * Pool Mean	Product 1 * Ratio of Pool mean to mean of product 1
		Mean of product 1	

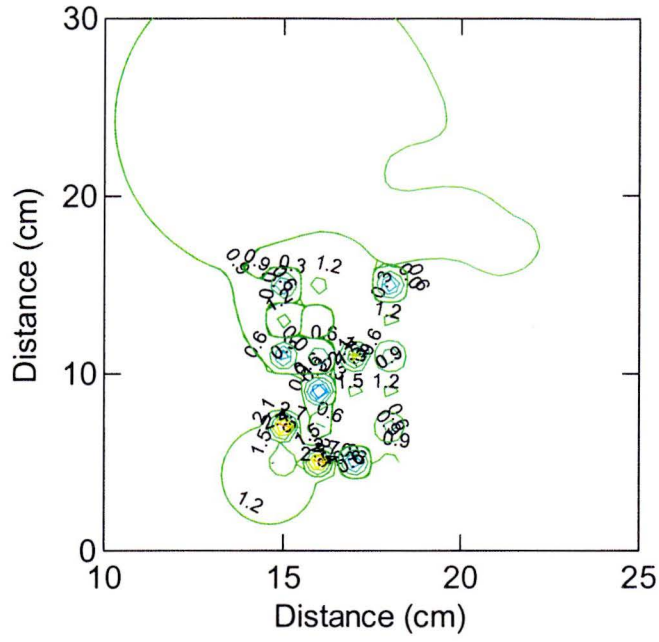

Figure 1. Pool 3 (freshwater) variability of chloride contour plot: Depth 1 cm below surface

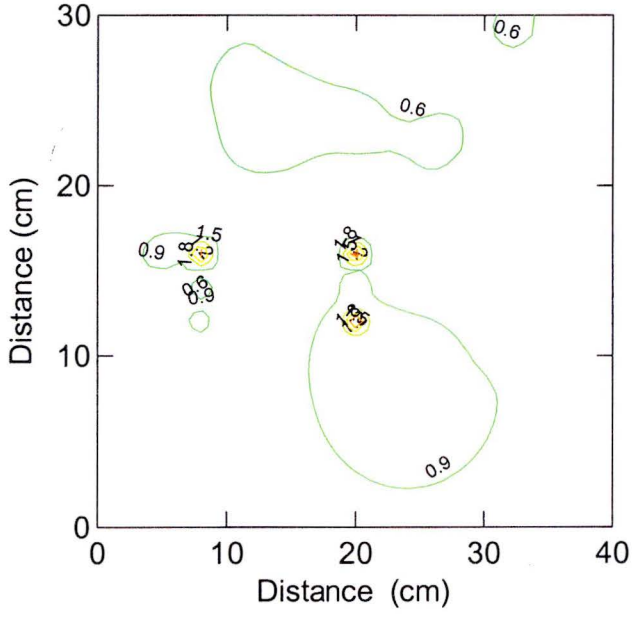

Figure 2. Pool 8 (brackish) variability of chloride contour plot: Depth 1 cm below surface

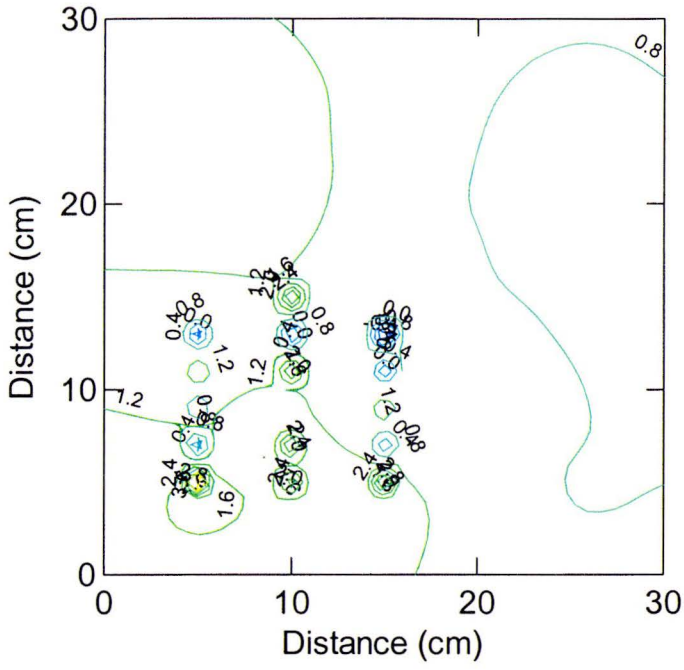

Figure 3. Pool 26 (marine) variability of chloride contour plot: Depth 1 cm below surface

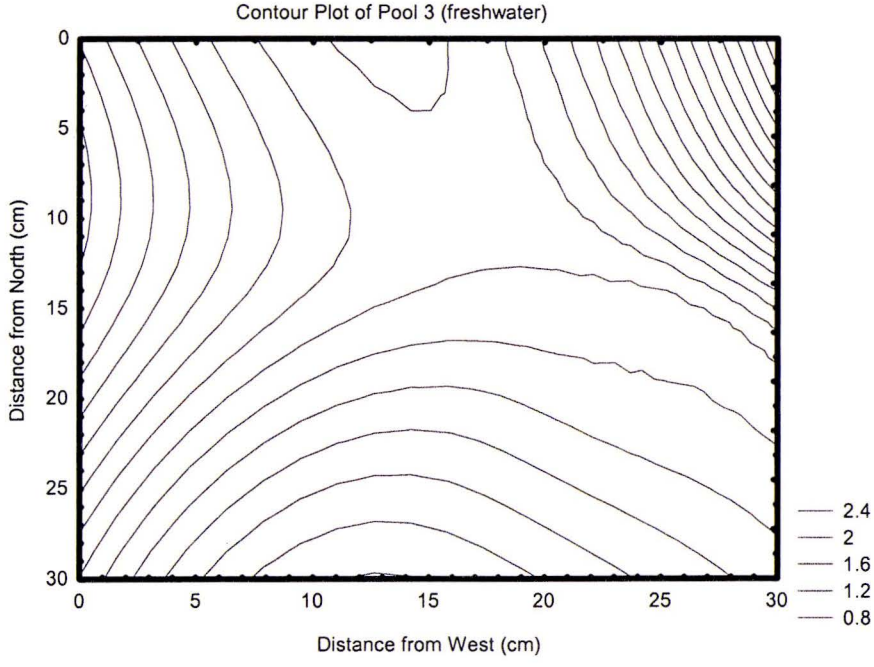

Figure 4. Pool 3 (freshwater) variability of chloride contour plot: 1cm below surface

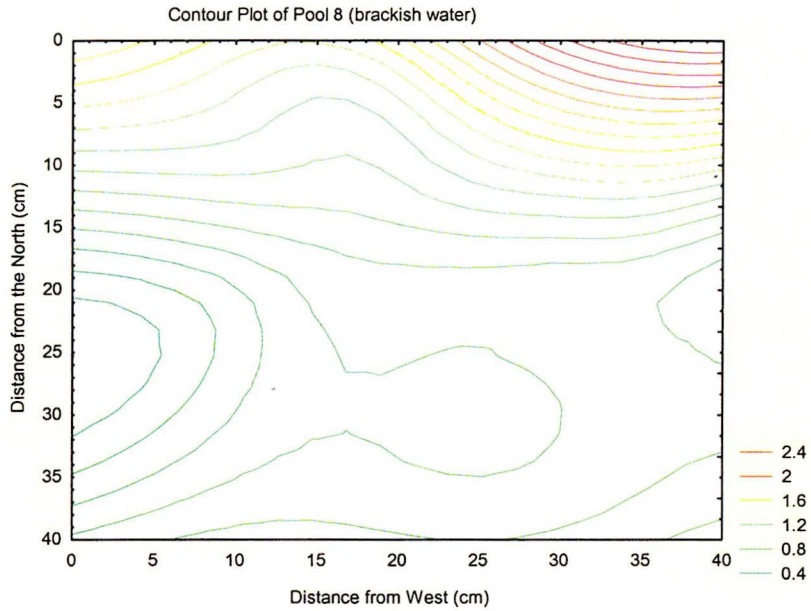

Figure 5. Pool 8 (brackish) variability of chloride contour plot: 1 cm below surface

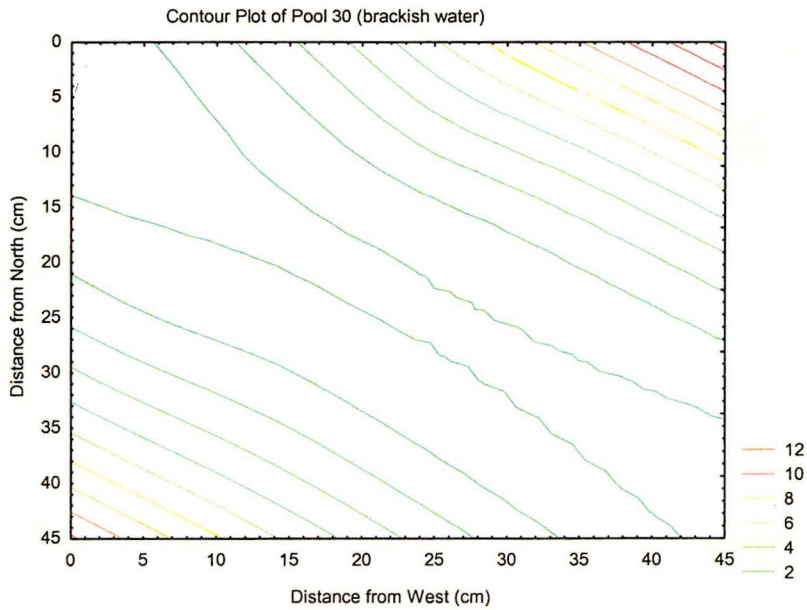

Figure 6. Pool 30 (brackish) variability of chloride contour plot: 1 cm below surface

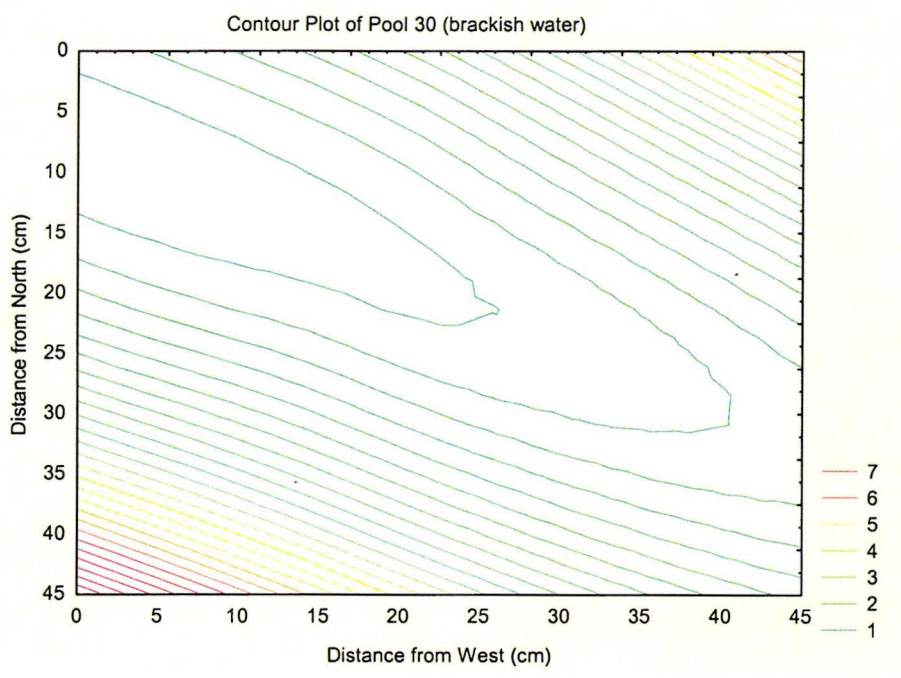

Figure 7. Pool 30 (brackish) variability of chloride contour plot: 6 cm below surface

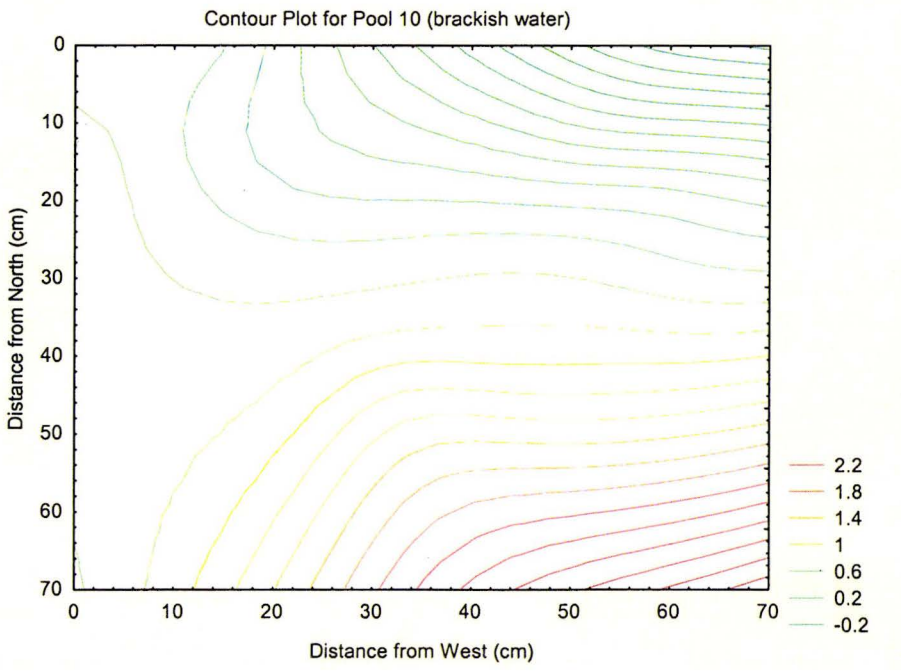

Figure 8. Pool 10 (brackish) variability of chloride contour plot: 1 cm below surface

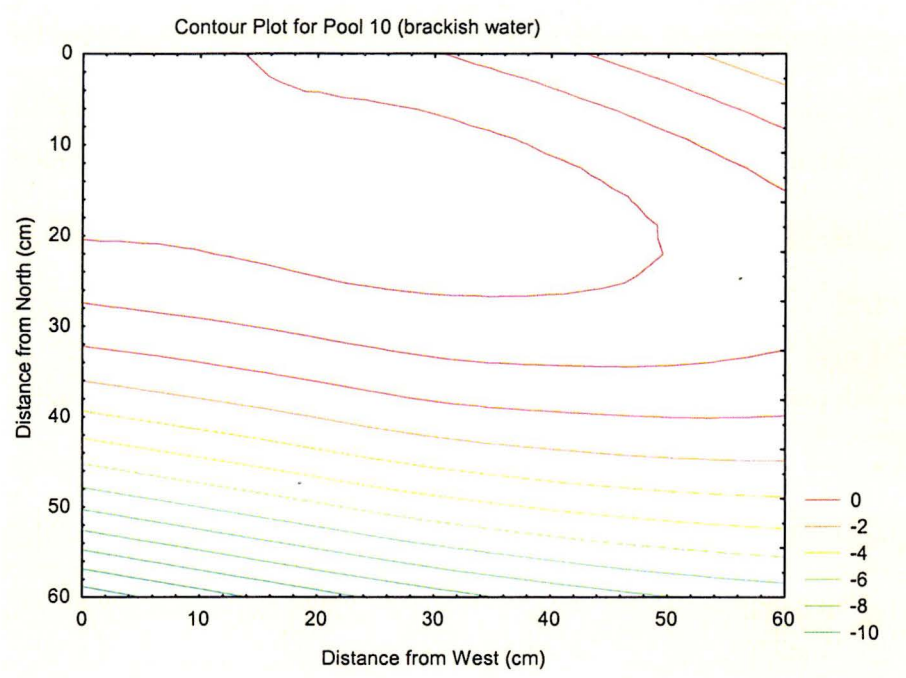

Figure 9 Pool 10 (brackish) variability of chloride contour plot: 6 cm below surface

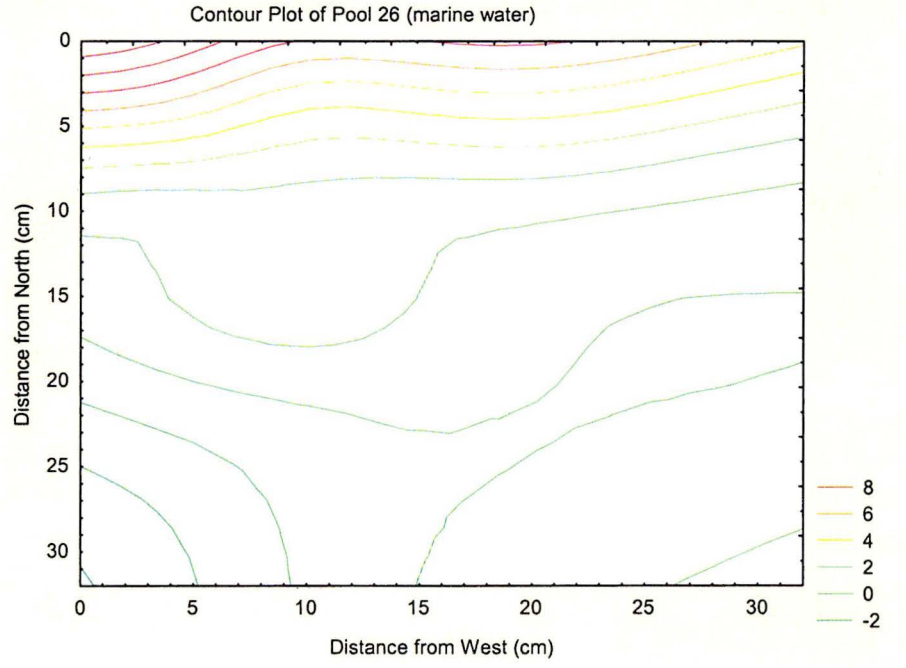

Figure 10. Pool 26 (marine) variability of chloride contour plot: 1 cm below surface

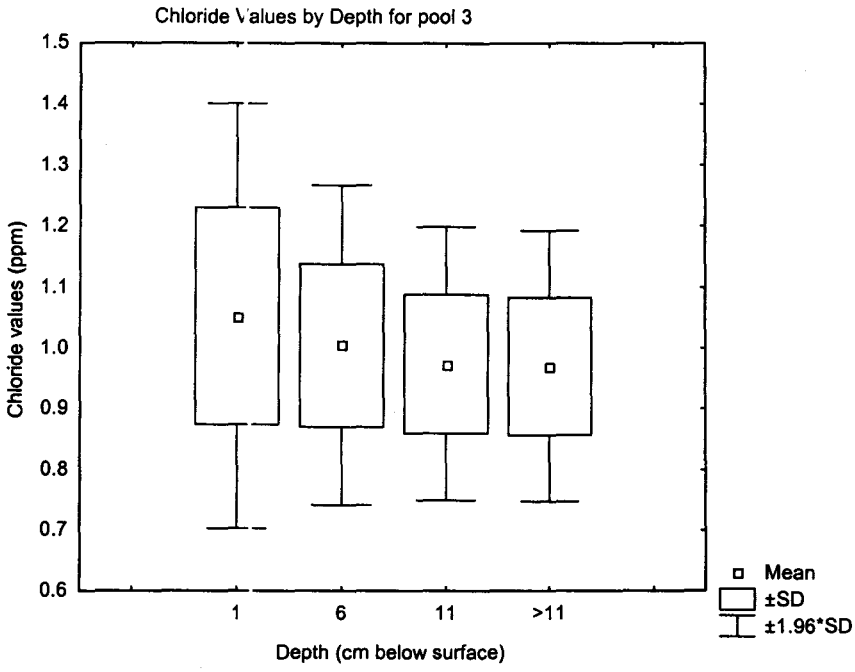

Figure 11. Chloride values by depth for pool 3 (freshwater)

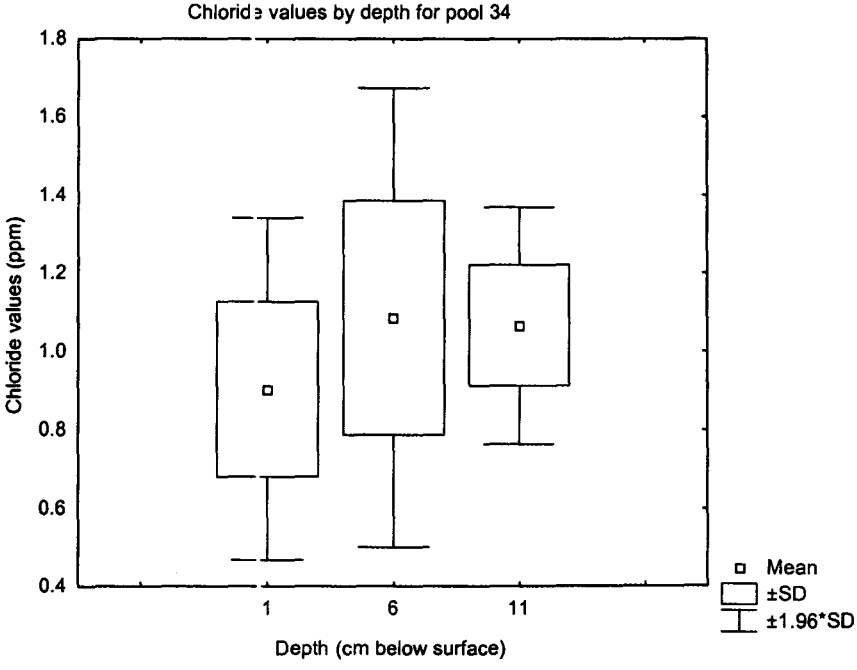

Figure 12. Chloride values by depth for pool 34 (freshwater)

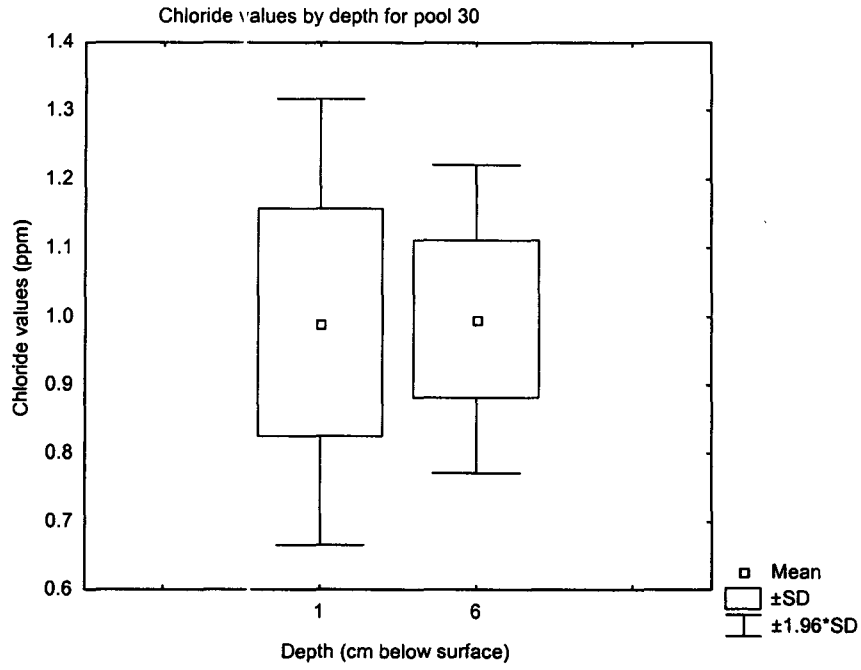

Figure 13. Chloride values by depth for pool 30 (brackish)

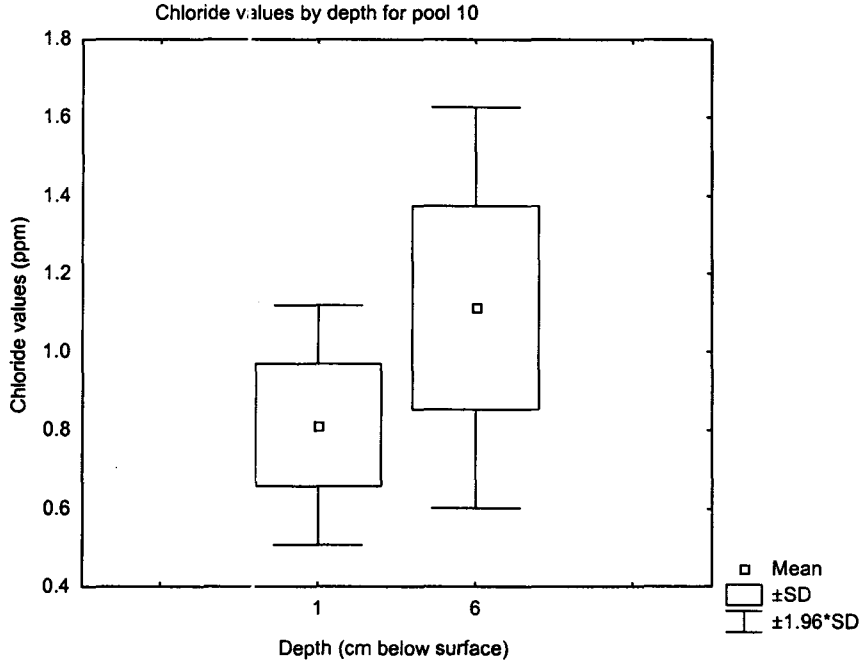

Figure 14. Chloride values by depth for pool 10 (brackish)

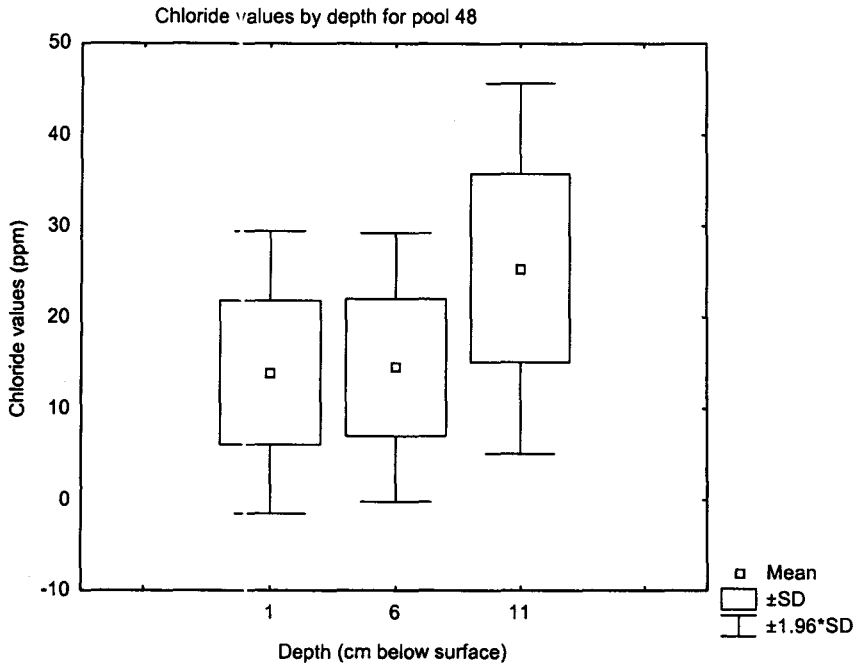

Figure 15. Chloride values by depth for pool 48 (marine)

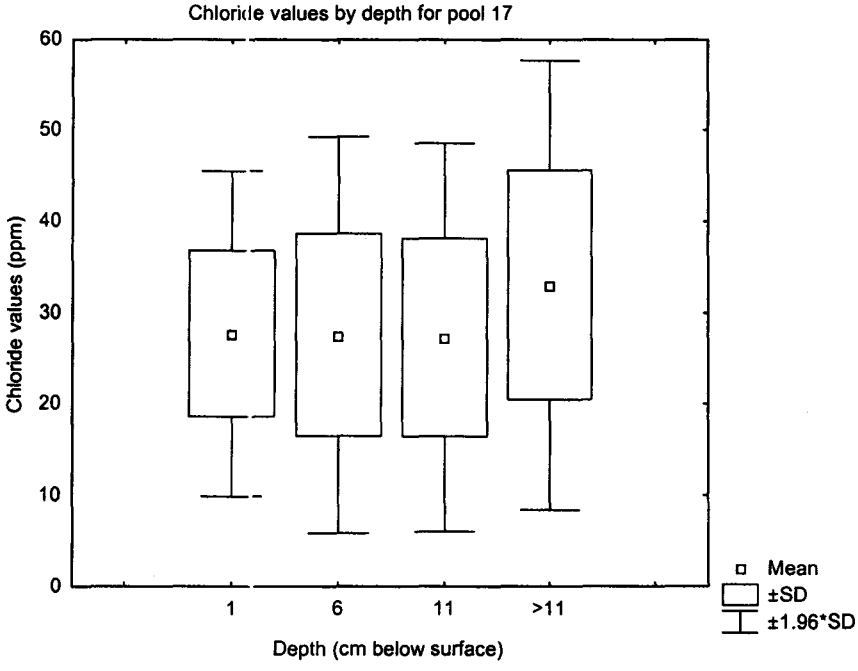

Figure 16. Chloride values by depth for pool 17 (marine)

Appendix 3:

CCA bi plots that do not include the "variability of chloride" vector

CCA bi-plots: Variability of chloride values not included

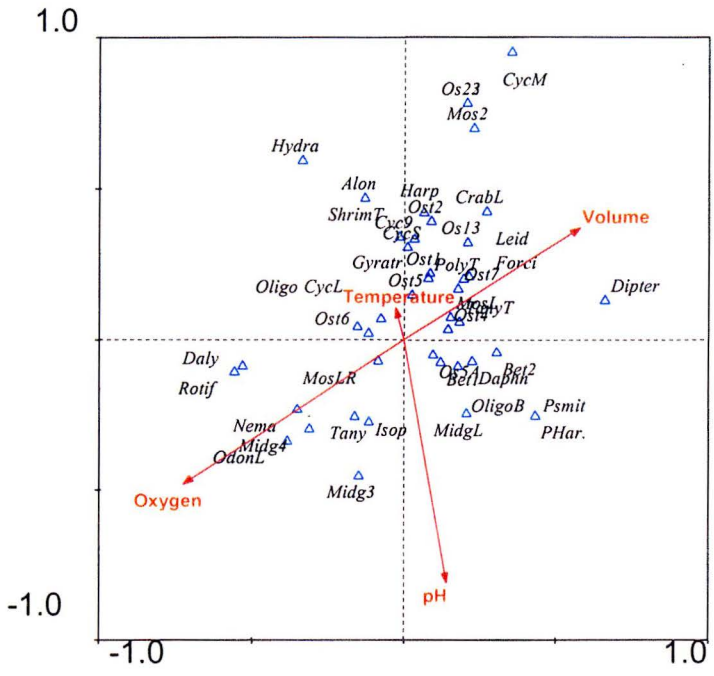

Figure 1. Freshwater CCA bi-plot of species and environmental data: local-temporal scale($p = 0.05$)

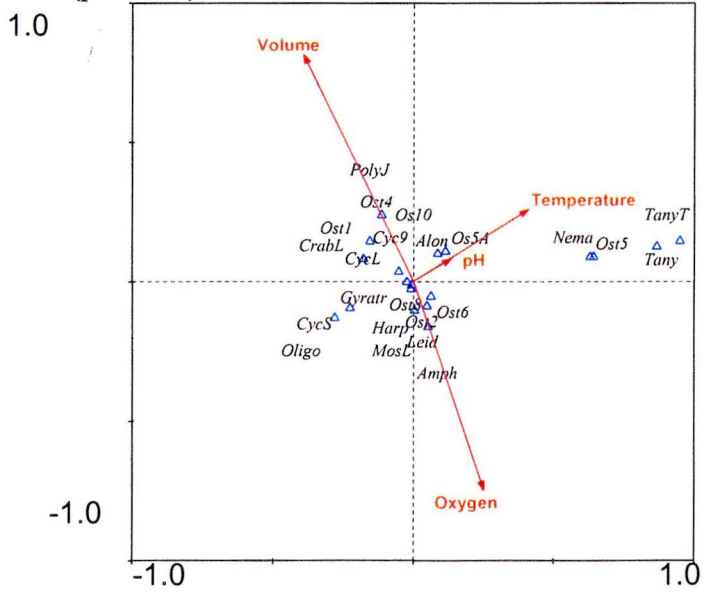

Figure 2. Brackish CCA bi-plot of species and environmental data: micro-spatial scale ($p = 0.03$)

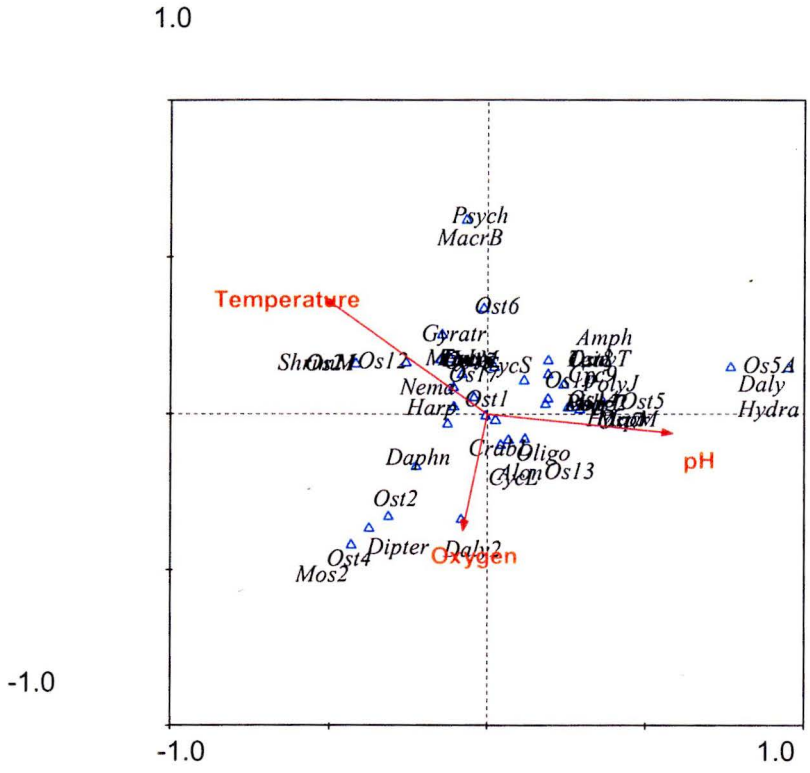

Figure 3. Brackish CCA bi-plots of species and environmental data: landscape-temporal scale (p = 0.03)