



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

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Abstract

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

Introduction

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

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

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

Methods and materials

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

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

Physical variables describing pool conditions including temperature, dissolved oxygen, salinity and

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

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

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

Results

Independent dates

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

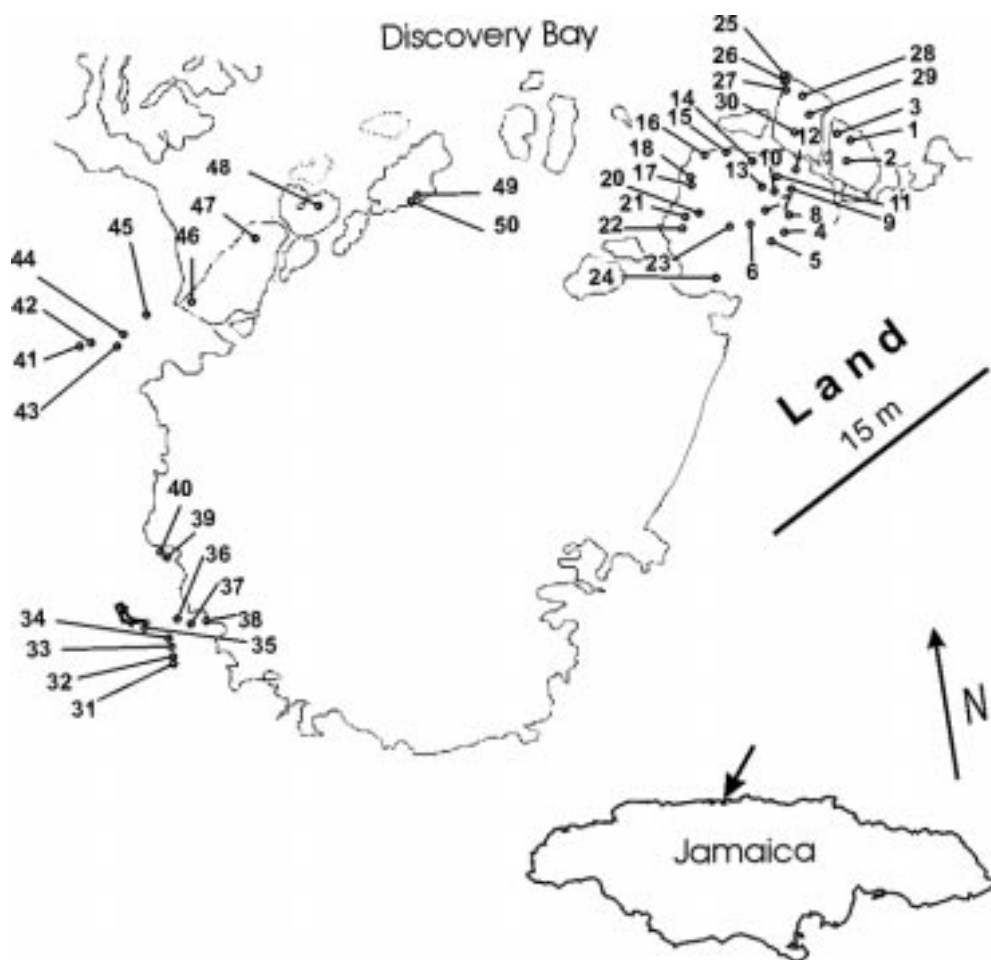


Figure 1. Location of the rock pool communities used in this study. The outline differentiates the backreef area of Discovery Bay and the coastal rocks upon which the pools are found. An arrow on the map of Jamaica indicates the location of Discovery Bay.

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

Stepwise regressions were conducted using both the physical and morphometric variables used in the simple regressions. However, the explained variance (R^2) was low for species richness (18.37%), total abundance (4.48%), species biomass (10.16%), Shannon-Wiener diversity index (13.44%), evenness

(5.62%), and Simpson's diversity index (2.95%). In addition, of the 10 variables included in the stepwise regression (temperature, salinity, dissolved oxygen, pH, pool length, width, depth, surface area, volume, and elevation), no more than two were significant in any one model despite the fact that all of the models were significant ($p < 0.05$).

Combined dates

It was believed that the relationships between species diversity and abiotic variables might be clearer if inter-annual variability was reduced. Therefore, we calculated the mean value of each diversity measure for each pool. Similarly, we calculated the mean, minimum, and maximum values for physical pool conditions including temperature, salinity, dissolved oxygen, and pH. The morphometric measures, when

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

Response variable	Morphometric variables	Mean physical measures	Minimum physical measures	Maximum physical measures	All measures combined
Mean species richness	0.2829 (2) $p=0.00048$	0.4616 (4) $p=0.00001$	0.5021 (4) $p<0.000001$	0.3060 (3) $p=0.00085$	0.6303 (9) $p<0.000001$
Mean abundance	No terms (0)	0.0799 (2) $p=0.14737$	0.1407 (2) $p=0.03058$	0.1762 (1) $p=0.00268$	0.4058 (5) $p=0.00032$
Mean biomass	0.0706 (1) $p=0.06501$	0.0715 (2) $p=0.10819$	0.2026 (4) $p=0.18174$	0.4086 (9) $p=0.03747$	0.4086 (9) $p=0.00826$
Shannon-Wiener index	0.2860 (2) $p=0.00043$	0.3493 (2) $p=0.00005$	0.4364 (3) $p=0.00001$	0.1975 (1) $p=0.00138$	0.5929 (8) $p=0.00001$
Evenness	0.0438 (1) $p=0.14877$	0.1915 (2) $p=0.00752$	0.2363 (1) $p=0.00040$	0.1799 (3) $p=0.02904$	0.4863 (9) $p=0.00091$
Simpson's diversity index	0.1481 (2) $p=0.02502$	0.2263 (2) $p=0.00273$	0.2943 (3) $p=0.00121$	0.1320 (2) $p=0.03856$	0.4925 (8) $p=0.00032$

added by stepwise regression, indicated that pool depth from the lip and elevation tended to be important variables for determining diversity. However, the explained variance of these models was low (Table 1). When considering the mean, minimum, or maximum measures of the physical pool conditions alone, the explained variance was substantially higher (Table 1). In fact, the highest explained variance was noted when the minimum values of physical measures were used with respect to the diversity measures (species richness, Shannon-Wiener index, evenness, and Simpson's diversity index). Maximum values of physical measures explained more variance in mean pool abundance and mean pool biomass.

Not surprisingly, the compound models resulting from stepwise regression explained the most variance for all of the dependent variables (Table 1), ranging from 41% for mean abundance and biomass to 63% for mean species richness. It is important to determine the correlation between the variables and to ensure that the observed relationships are not biased due to statistical properties of the data (i.e. environmental variables that are highly correlated). As expected, some variables were highly correlated with others (Table 2). Thus, we were able to exclude mean pool temperature and mean

pool salinity from the model by retaining minimum and maximum measures of these variables. Similarly, pool volume can be excluded if both pool length and surface area are included. The high correlation coefficients between the measures of pool dissolved oxygen and pool pH indicate that maximum dissolved oxygen and minimum pH will suffice as measures of pool productivity in the optimized model.

When the correlated variables were removed, the resulting model for mean species richness did not sacrifice any explained variance ($R^2=0.6301$; $p<0.0001$). A similar observation was made for the model explaining the mean Shannon-Wiener diversity index ($R^2=0.5894$; $p<0.0001$) and the model explaining mean species abundance ($R^2=0.3847$; $p=0.0006$). The variables included in the species richness and the Shannon-Wiener models were the same and included minimum pH and temperature, minimum and maximum salinity, maximum dissolved oxygen, elevation, length, and pool depth from the lip. Differences were noted in the models for biomass ($R^2=0.1845$; 3 terms; $p=0.0258$); evenness ($R^2=0.2627$; 2 terms; $p=0.0009$); and Simpson's diversity index ($R^2=0.3710$; 5 terms; $p=0.0010$). A closer examination of the variables that were added to the biomass model indicated that ini-

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

	Mean temperature	Mean salinity	Mean oxygen	Mean pH	Minimum pH	Maximum pH	Volume
Minimum temperature	0.8849						
Maximum temperature	0.7291						
Minimum salinity		0.8399					
Maximum salinity		0.8465					
Minimum oxygen			0.8101	0.7226	0.7799		
Maximum oxygen			0.9104	0.7411		0.8138	
Mean pH			0.8378				
Minimum pH				0.9171		0.7513	
Maximum pH			0.8460	0.9285			
Length							0.7376
Surface area							0.9042

tially nine variables (including several that were correlated with each other) were added but once the correlated variables were eliminated from the analyses, only three variables contributed to the final model. A similar observation was made for the evenness model with nine variables included initially (again, several were correlated with each other) and two remaining in the final model. The model for Simpson's diversity index was intermediate and initially contained 3 additional terms (2 were highly correlated with other variables), which is why the explained variance dropped by only 10%. For each of the above models, residuals were examined and were normally distributed. There was no evidence of trends, thereby confirming model linearity.

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

The models (regardless of the dependent variable) are influenced predominately by physical measurements rather than morphometric measurements. Meas-

ures of pool temperature, salinity, dissolved oxygen and pH were more correlated (higher R^2) than morphometric measures and were always added first using the stepwise approach.

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

Discussion

The 49 pools are located within close proximity and most are no further than 50 cm from a neighbor. A total of 70 species was identified from all the samples, but a maximum of 16 species was found in any one pool during any one sampling event. There is much variation in species richness, both between pools and between years. By calculating the mean over seven

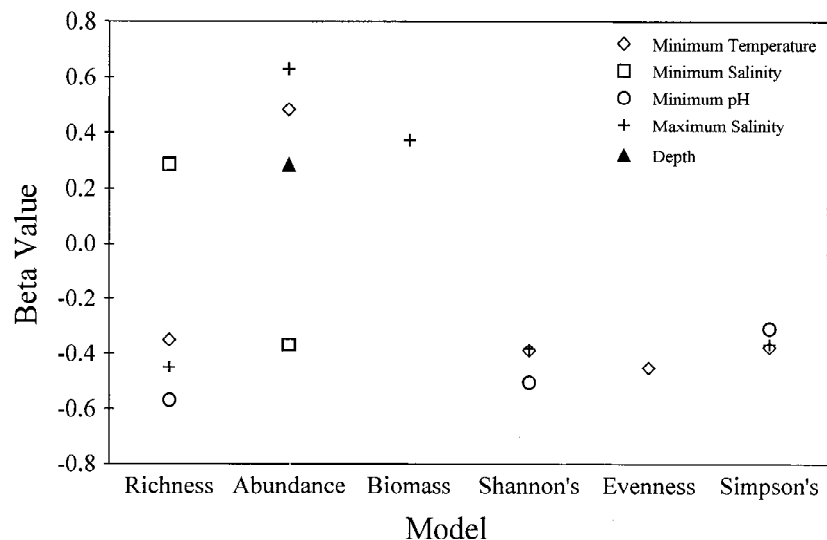


Figure 2. Beta values for the significant variables retained in the stepwise regression approach for the mean diversity/abundance models. Variables retained in at least one model include minimum temperature, minimum salinity, minimum pH, maximum salinity and pool depth.

sampling events, this variability is reduced and patterns become more apparent. King et al. (1996) found that species assemblages varied among pools within the same site and not all species occurring at a site were found within a single pool.

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

The stepwise regression models that accounted for correlation between variables developed for mean species richness and mean Shannon-Wiener index had similar levels of explained variance (around 60%) and included the same variables. This is not surprising considering that both of these measures of diversity are strongly affected by richness (Magurran, 1988). This also means that dominant and rare spe-

cies contribute equally to these measures of diversity. The model for the Simpson's diversity index included fewer terms and explained less of the variance (about 37%) than the species richness or Shannon-Wiener models. Magurran (1988) indicates that this measure of diversity is strongly influenced by dominance and, thus, dominant species contribute more to the calculation of this index than rare ones. These findings indicate that physical and morphometric variables have a greater impact determining the number of species present in aquatic communities but have less impact in determining community abundance structure. Furthermore, the abundance models developed in this study had considerably lower explained variance (R^2) than richness or diversity models (Table 1). These results suggest that, while the physical conditions set the limits to distribution (i.e. presence and absence of species), it may be the biotic factors, acting at population and community levels, that have a greater impact on species abundances.

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

icates a few species are able to exploit warmer water conditions and their abundances increase accordingly.

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

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

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

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

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