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

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

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

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

Our study suggests that individual communities or assemblages respond independently and asynchronously to environmental factors, a view originally proposed by Gleason (1917). We conclude that the form of community structure in variable habitats remains constant. The species composition and relative abundances can change over time but the relative abundance of the dominant species stays high and the remaining species, regardless of their numbers, make relatively small contributions to the overall community variability pattern.

Introduction

The nature and meaning of community variability has been discussed frequently over the past 25 years (May 1973, McNaughton 1977, Connell and Sousa 1983, Pimm 1991, Micheli et al. 1999). This variability (in space and time) has implications for examining species conservation (Quintana-Ascencio and Morales-Hernández 1997), metapopulation dynamics (Hanski and Gilpin 1997), and assemblage structure (Pimm 1991, Brown et al. 1995). Assemblages or communities are not static but change in species composition and species abundances, both in space (i.e., form location to location) and in time (i.e., from date to date). In this study, we focus on community variability in time. Understanding of community variability demands understanding of its internal and external

causes. For example, changes due to species-specific responses (i.e., competition, predation) or changes due to environmental fluctuations (i.e., weather, stress, disturbance).

Habitat variability is one external mechanism identified as influencing community variability (Pickett and White 1985, Death and Winterbourn 1994). Habitat variability influences the relative abundance of species and species presence in a community and represents a strong structuring force for communities (Death 1995). Deterministic processes that impact community structure, such as competition and predation, are mediated by habitat variability (McAuliffe 1984, Meffe 1984). Several studies show that with an increase in habitat variability, population variability increases and community persistence de-

clines. This applies to stream invertebrates (Death and Winterbourn 1994), fish (Ross et al. 1985, but see Grossman et al. 1982), and non-aquatic insects (Wolda et al. 1992, but see Van Dijk 1986).

Despite attempts to determine the influence of habitat variability (stability) on community properties (i.e., species composition, relative or ranked abundances, etc.), its role remains unclear. Site-specific differences or differences in how habitat stability or variability is defined may confound these inferences. Specifically, defining and measuring habitat variability (stability) has proven problematic (Rykiel 1985). A consensus on what habitat variability means and how to properly measure variability in different ecosystems is lacking. One additional confounding issue is that the impact of habitat variability changes depending on the spatial, temporal, and taxonomic scales used in the study (Rahel 1990, Sale and Guy 1992). One common method to measure habitat variability is to determine the variability in habitat parameters over time, with the two ends of the variability spectrum conveniently categorized as stable or unstable habitats (Death and Winterbourn 1994). A single multivariate variability score representing "overall" habitat variability has been used successfully for streams (Death and Winterbourn 1994).

Measuring community variability has also proven complex (Micheli et al. 1999). Community variability involves changes in species composition and changes in species' relative abundances over time (Magurran 1988). Detecting this variability depends on the measure used (Gaston and McArdle 1994). In this paper, we recognize three components of variability: (a) variability in composition; (b) variability in species rankings (relative abundance); and (c) variability in individual species abundances (as opposed to variability of all species taken jointly). Changes in composition and relative abundances (as evaluated by correlation among ranked abundances of species) are partly independent and may occur in various combinations, which will depend on a variety of factors including species identity (Sankaran and McNaughton 1999), habitat variability, and spatial and temporal scales used in the analyses (Pickett and White 1985, Rahel 1990, Sale and Guy 1992, Death and Winterbourn 1994).

Sometimes geographical or physicochemical variables are more important than habitat variability in determining community structure (e.g., Townsend et al. 1983, Corkum 1989). In aquatic systems, it is important to consider the impact of individual physicochemical variables relative to a combination of these variables that is often used to quantify habitat stability (Death 1995). To fully determine the role of habitat variability, it is useful to use a system from a small geographical area. This minimizes

differences due to large-scale patterns such as weather, biogeography or historical colonization patterns. In this study, we use a system of rock pools to study the effects of habitat variability on community variability, including variability of individual populations and temporal changes in community structure (both species composition and ranked abundances). The system includes 49 pools that span a range of physicochemical properties and are home to communities assembled from a diverse yet shared species pool (Therriault and Kolasa 1999a,b).

It is possible that community and population variability would be greater in pools with higher overall habitat variability. In the most variable pools, those that dry up from time to time or experience more disturbance events, greater extinction rates and random re-colonization events increase the probability for changes in the community composition and in the relative abundance of different species through differential dispersal, increased biotic interactions due to new interactions, and variable intensity of metapopulation dynamics.

It is possible that population variability might influence strongly community variability, especially aggregated measures of it (Micheli et al. 1999). This influence might be further enhanced or dampened by greater habitat variability. Since different populations could impact communities differently (via biotic interactions, trophic cascades, etc.), the strongest effect on community variability should be observed via the impact on habitat generalists (species that have large geographical ranges, usually high abundances). It is clear that a question about the effect of habitat variability on community variability is a complex one and requires examination of variability of several community components. Thus, this paper aims to accomplish this. More specifically we ask the question: does increased habitat variability result in greater community variability, either in species composition or species relative abundances? Also, what impact, if any, do habitat generalists have on community variability and is this impact a result of increased (or decreased) habitat variability?

Materials and methods

Study site

Community and environmental data were collected from 49 natural rock pools located near the Discovery Bay Marine Laboratory on the north coast of Jamaica. Pool locations have been reported elsewhere (Therriault and Kolasa 1999ab). The rock pools are small (most are less than 50 cm deep and 20 to 60 cm in length and wide), erosional in nature, and are located above the high tide

Table 1. Summary of physicochemical and morphological variables made on the 49 rock pools over eight sampling dates.

Variable	Mean (N=49)	Standard Deviation	Minimum Value	Maximum Value
temperature (°C)	26.12	1.14	24.74	29.59
salinity (ppt)	11.24	8.62	0.46	32.08
dissolved oxygen (mg/L)	7.21	2.68	0.95	13.47
pH	8.70	0.57	7.70	10.58
length (cm)	56.71	29.36	14.00	188.00
width (cm)	34.47	33.95	10.00	248.00
depth (cm)	27.92	10.83	5.00	55.00
elevation (cm)	72.79	81.73	1.00	235.00

level. Therefore, most are filled by rainfall but a few pools receive seawater by periodic inflows or occasional wave splash. Physical pool conditions were measured when biotic samples were collected (details below). We measured pool temperature, salinity, dissolved oxygen concentration, and pH. Measurements were completed for all pools within one hour during the morning (starting at ~ 9 a.m.) to eliminate diel differences that may arise due to changing pool conditions over the course of the day.

Data on physical conditions in the pools have been presented elsewhere (Therriault and Kolasa 1999ab), including morphological characteristics (surface area, volume, elevation, etc.). Most of the pools included in these analyses are permanent but a few are ephemeral. A summary of physical and morphological characteristics is reported in Table 1.

Sampling dates were December '89, January '90, January '91, January '92, January '93, January '97, June '97, and January 1998. Due to the small nature of these pools, faunal samples were collected in one day by passing 500 ml of water and sediments from each pool (slightly stirred to dislodge organisms from the pool walls and to homogenize their distribution) through a 63 μm net. Organisms were caught in a collecting container and immediately preserved in 50 – 60 % ethanol. Seventy species were collected including ostracods (20 species); copepods (including harpacticoids and cyclopoids) and cladocerans (10 species); worms (including oligochaetes, polychaetes, and turbellarians; 15 species); aquatic insects (larvae and pupae; 18 species), and other aquatic crustaceans (6 species). Due to the tropical nature of these pools, the aquatic fauna remain largely undescribed with the exception of the microturbellarians (Therriault and

Kolasa 1999b). However, we have used an identification method that separates each of the animals into discrete taxonomic units (i.e., species) based on morphology. Rotifers and gastrotriches were also collected but were not included in the analyses due to difficulties identifying these organisms to the species level and the use of a sampling method not aimed at the collection of such small organisms (the abundance data might have been biased for these species if individuals were able to pass through the net).

Community and population variability

The data used in the analysis include the invertebrate species (excluding rotifers and gastrotriches, see above). Specific information on how species within each pool community interact is largely unavailable (i.e., dominance relations, predatory or competitive interactions). It is important to note that each pool contains its own, specific community, which is a unique combination and a subset of the regional fauna. Community variability represents changes in both species richness and species abundances within each of the 49 pools over time. For each pool and sampling date, we calculated five community metrics, including Simpson's diversity index (1/D; where $D = \Sigma ([n_i\{n_i - 1\}]/[N\{N - 1\}])$; the Shannon-Wiener diversity index (H'; where $H' = -\Sigma p_i \log_2 p_i$); evenness (E; based on the Shannon-Wiener index where $E = H'/\log_2 S'$); Hill's evenness (Hill's $= [\Sigma\{p_I\}^2]^2/\Sigma\{p_I\}^3$); and species richness (S'). Total abundance of all individuals in the community was also determined (transformed as: $\log_{10}[x + 1]$). In the above equations, p_i is the proportion of the ith species; n_i is the number of individuals of the ith species, and N is the total number of individuals in the

sample. Community variability was assessed by calculating the coefficient of variation (CV; where CV = standard deviation/mean) of each community metric based on the eight sampling dates.

Population variability refers to the changes in the abundance of a specific species within each pool over time. Population variability was assessed for three habitat generalists, the harpacticoid copepod (*Nitocra spinipes* Boeck), the cyclopoid copepod (*Orthocyclops modestus* (Herrick)), and the ostracod (*Potamocypris sp.*). These three species were identified as habitat generalists since they occurred in the greatest number of pools spanning the greatest range of physical parameters among all sampling dates. They also had the largest abundances. Due to their broad geographic range (i.e., the number of pools occupied), these species appear to have the best dispersal capabilities in this rock pool system. We assessed population variability of these three generalists in each pool by calculating the coefficient of variation (CV) over the eight sampling dates.

Community structure

Temporal changes in community structure were evaluated using both Kendall's coefficient of concordance (W) and Cochran's Q test. We used Cochran's Q test to evaluate differences in the faunal assemblage composition (presence/absence) among sampling dates and Kendall's coefficient of concordance (W) to assess the constancy in relative abundance of species among the sampling dates. We also considered the effects of rare species on the calculation of both Kendall's W and Cochran's Q. Therefore, we calculated both for each pool using all species, and the 17 most common species (based on abundance and occurrence; Top 17) in order to eliminate rare species. The "Top 17" species had the largest abundances in all pools on all dates and were found in the greatest number of pools on all dates. By eliminating the effects of rare species in this system, we were able to determine the change in community composition (presence/absence) and community constancy (relative abundances) of the "core" species (i.e., species almost always found within a pool, regardless of sampling date). Therefore, this method removed the possibility that changes in species composition or ranked abundances were only due to changes in rare species (i.e., those expected to be more variable over time).

Habitat variability

As explained earlier, habitat variability stands for the changes in physicochemical pool conditions over time and may refer to a single variable or a compound

index such as a multivariate score reflecting variability in several habitat characteristics (i.e., temperature, salinity, dissolved oxygen, or pH) (Death and Winterbourn 1994). For simplicity, we refer to stable habitats as those where the physicochemical variables, either separately or combined, change little over time (e.g., variability is low). In contrast, we define unstable habitats as those where the physicochemical variables change considerably over time (e.g., variability is high). In this study, we used scores of Factor 1 produced by Principal Component Analysis performed on the variability in physicochemical variables (SD of pool temperature, salinity, dissolved oxygen, and pH) over the eight sampling dates. This variability index (PCA Factor 1 + 3; a constant used to eliminate negative numbers in the index), accounted for 52.13 % of the variance in SD of physical variables. In order to eliminate any possible seasonal effects (recall there was one sampling date in June) the June sampling date was eliminated and the analysis re-done (resulting in an explained variance of 48.97 % for Factor 1). Similarly, an argument could be made that the December 1989 sampling date might not be independent of the January 1990 sampling date and it too should be eliminated from the analyses to remove any possible bias (resulting in an explained variance of 49.52 % for Factor 1). Additionally, we examined the effects that variability of individual physical variables (e.g., temperature, salinity, dissolved oxygen, and pH) had on community variability. The variability in these four physicochemical variables was determined for each pool over the eight sampling dates. Analyses were done using all data (June included); all data except June; and all data except June 1997 and December 1989 because summer conditions may slightly deviate from winter ones and because January 1990 sampling was repeated within about a week of the December 1989 sampling. Results from all analyses were similar and the correlation among the resulting community metrics, population data, and habitat data (habitat stability score and SD in physical pool conditions) determined by the three criteria listed above was high (> 88% for community metrics; > 93 % for population measures; and > 70 % for habitat measures). Therefore, for clarity and brevity, only the results from the analyses that excluded both June 1997 and December 1989 sampling dates are shown.

Statistical analyses were completed using Statistica at a significance level of p = 0.05. Regression analyses were used to test the relationships between habitat variability

(either PCA Factor 1 or SD of individual physicochemical variables) and community variability and population variability. Changes in community structure (Kendall's W and Cochran's Q) were also regressed against habitat variability. ANCOVA's were used to evaluate the effects of both habitat and population variability on community variability. For all General Linear Models, residuals were checked for normality and correlation with model terms to validate model assumptions.

Results

Habitat variability effects

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

It is possible that the variability of specific physicochemical variables (i.e., SD for pool temperature, salinity, dissolved oxygen, and pH) are more important when considered independently rather than when combined into an index, such as the habitat variability index. No measure of community variability was significantly affected by the variability in either pool temperature or pool pH (regression, p>0.05). However, the variability in species richness was negatively related to the variability in pool dissolved oxygen concentration ($F_{1,47} = 12.82$; $p = 0.0008$) and the variability in Simpson's index was negatively related to the variability in pool salinity ($F_{1,47} = 4.73$; $p = 0.0348$). Also, the variability in pool salinity was positively related to the variability in the Shannon-Wiener index ($F_{1,47} = 5.65$; $p = 0.0216$) and the variability in evenness based on the Shannon-Wiener index ($F_{1,46} = 17.91$; $p = 0.0001$).

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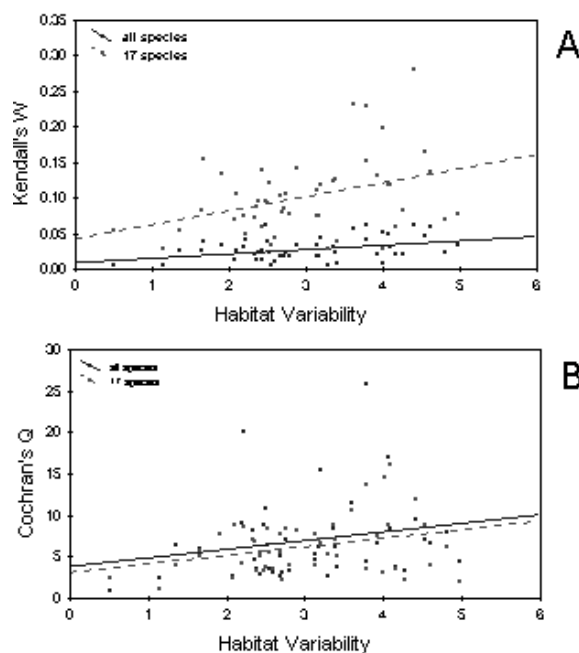

Figure 1. Relationship between habitat variability and variability in community structure among sampling dates for: (A) Kendall's coefficient of concordance (W); and (B) Cochran's Q. Solid lines indicate the relationships when all species were included and dashed lines indicate the relationships when only the 17 most common species were used.

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

Community, population, and habitat variability

When we considered community variability with respect to population variability of the three habitat generalists (harpacticoid copepod, cyclopoid copepod, and the ostracod species) and habitat variability, we found several patterns. The variability in the ostracod species did not significantly affect the variability of any of the community metrics used in this study. The variability in evenness (based on the Shannon-Wiener index) was negatively related to the variability in harpacticoid copepod populations ($F_{1,43} = 9.31$; $p = 0.0039$). The cyclopoid copepods had the greatest effect on community variability. The

Table 2. ANOVA table showing the relationships among the variability in evenness (based on the Shannon-Wiener index), habitat variability, and population variability of the three habitat generalists, the harpacticoid copepod (*Nitocra spinipes* Boeck), the cyclopoid copepod (*Orthocyclops modestus* Herrick), and the ostracod (*Potamocypris sp.*).

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

variability in species richness, the variability in the Shannon-Wiener index, and the variability in evenness (based on the Shannon-Wiener index) were all positively related to the variability in cyclopoid populations ($F_{1,44} = 29.25$; $p < 0.0001$; $F_{1,44} = 29.36$; $p < 0.0001$; and $F_{1,43} = 13.31$; $p = 0.0007$, respectively) while the variability in evenness (based on Hill's index) was negatively related to the variability in cyclopoid populations ($F_{1,44} = 5.98$; $p = 0.0185$).

The variability in evenness (based on the Shannon-Wiener index) showed several interesting patterns that require further explanation. This measure of community variability was significantly related to each of the three habitat generalists (i.e., the harpacticoid copepod, the cyclopoid copepod, and the ostracod; Table 2; Fig. 2). The variability in evenness was negatively related to harpacticoid variability but positively related to both ostracod and cyclopoid copepod variability (Fig. 2), implying that population variability strongly affects species ranking. Habitat variability was also negatively related to the variability in evenness (Fig. 2B).

Discussion

Habitat variability

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

Other variables could be added to this study but, due to biotic and abiotic dependency among them, the vari-

ability index would be unlikely to change substantially. For example, desiccation frequency, productivity, or DOC (dissolved organic carbon) are all, in principle, related to the variables we have already included in the analysis. Similarly, Death and Winterbourn (1994) used a multivariate index to characterize "overall" habitat variability and included several, but not an exhaustive set, of variables.

Two consistent patterns emerged that differ from other studies and thus require an explanation: (a) species abundance ranks changed less over time in high variability (unstable) pools than in low variability (unstable) ones (Fig. 1A); and (b) stable pools had more persistent community structure than unstable pools (Fig. 1B). It is possible that high habitat variability is responsible for the reduced temporal variation in population size by restricting the population growth. Communities in highly disturbed environments (i.e., high habitat variability) have lower species richness (Connell 1978, Reynolds et al. 1993, Wilson 1994, Reynolds 1995) and tend to be dominated by a few "weedy" species (Scarsbrook and Townsend 1993). Invertebrate and fish studies have suggested that stability and persistence of communities is greater in moderately disturbed environments (low habitat variability, low levels of disturbance) than in highly disturbed environments (Ross et al. 1985) and that abiotic factors can affect community persistence over time (Townsend et al. 1987). Furthermore, Death and Winterbourn (1994) showed that, for invertebrate communities in lotic ecosystems, communities tended to diverge compositionally as habitat variability increased (habitat stability decreased). This may indicate that, in this system, unstable pools are dominated by a few taxa that have good dispersal and colonization abilities thereby maintaining high community similarity over time. Given that pools with high habitat variability tend to dry out more frequently than pools
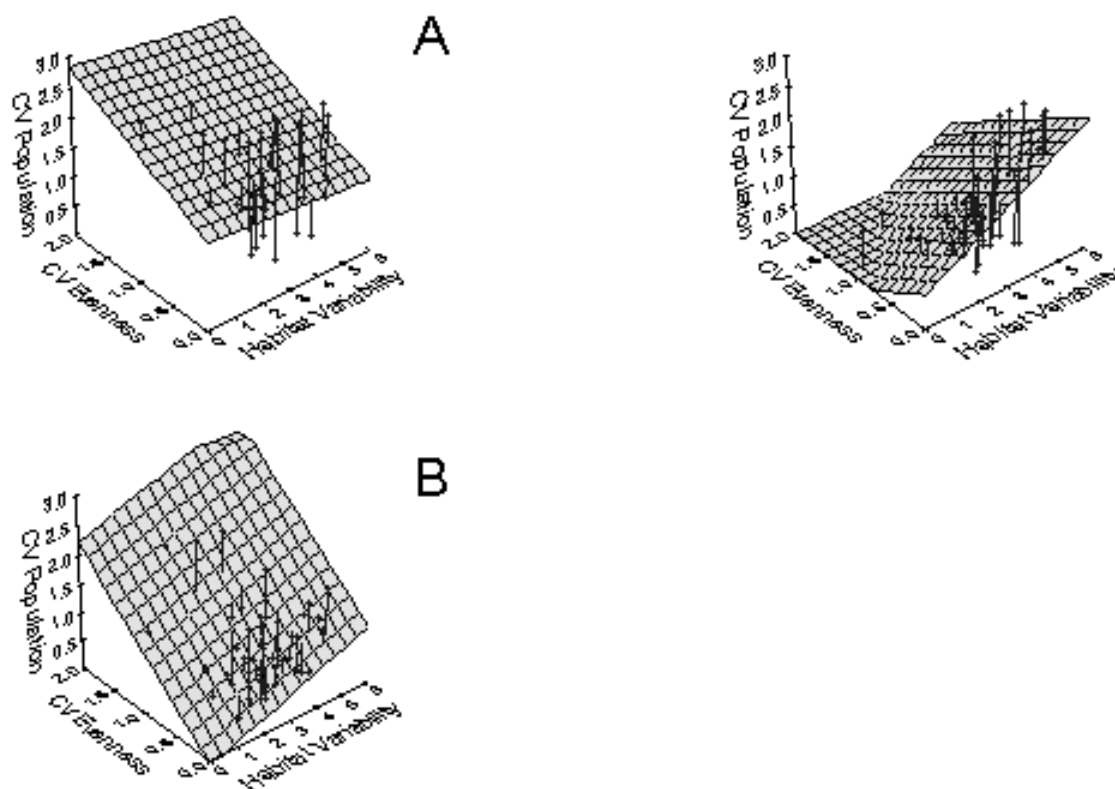
Figure 2. Relationships among variability in evenness (based on the Shannon-Wiener index), habitat variability and the three habitat generalists: (A) the ostracod (*Potamocypris sp.*); (B) harpacticoid copepod (*Nitocra spinipes* Boeck); and (C) cyclopoid copepod (*Orthocyclops modestus* Herrick).

with low habitat variability, recolonization abilities are likely to determine the observed community composition (but not structure). Provided recolonization of these empty patches is somewhat variable, community structure will change slightly over time, resulting in different assemblages in pools with high habitat variability, especially when compared to pools with low habitat variability that are less likely to be affected by colonization. Interestingly, there was no significant relationship between mean species richness (among dates) and habitat variability (p = 0.3943; R^2 = 1.55%), indicating that pools with high habitat variability (unstable) could support as many species as pools with low habitat variability (stable). Wilson (1990) suggested that for plant communities, intermediate timescale disturbances might be responsible for maintaining high diversity if the environment supported patches of different disturbance-ages in order to maintain among-patch diversity. In this system, it is likely that among-patch dynamics are important to the maintenance of some metapopulations, especially given the close proximity of pools to each other.

The community assemblage changed more in pools with greater habitat variability (Fig. 1B). Additionally,

one possible explanation for the differing trends in community constancy (Kendall's W) between stream and rock pool systems is the number of taxa. Death and Winterbourn (1994) report finding 42 – 92 taxa present at each stream site. The number of taxa present in the rock pool system ranges from 0 – 16 species per pool (Therriault and Kolasa, pers. obs.), although the system contains 70 species or more. Greater species richness has been suggested as one possible mechanism that can stabilize community structure and thus potentially lower community variability (Tilman 1996).

Community variability differed between pools with high and low habitat variability but depended on the measure of community variability considered: one based on species presence or one based on relative abundance. Simpson's index gives higher weight to dominant species than does the Shannon-Weaver index, while species richness gives equal weighting to rare and dominant species (Magurran 1988). Generally, community variability increased with increased population variability. This indicates that rare species are important in determining overall community variability and community structure. A negative relationship between habitat variability and

population variability on one side and variability in evenness on the other indicates that, as habitats become more variable and as population variability increases, community structure tends to become fixed. Higher variability in diversity with decreased habitat variability suggests that communities in high variability environments are more persistent. It is possible that communities in these highly variable habitats are structured more by stochastic processes than deterministic processes (sensu Townsend et al. 1987). Given the often-unpredictable (i.e., weather driven) nature of variable habitats, species surviving in such habitats should show high extinction rates and high dispersal and colonization rates, due to their adaptations to disperse. If the species composition of variable pools is restricted, the variability in diversity will be low simply because the same few species return to the available habitat via repeated colonization events (Connell 1978), possibly in proportion to their occupancy of landscape patches (Hanski and Gilpin 1997). These results suggest that the form of community structure in variable habitats remains constant. The species composition and relative abundances can change over time (i.e., be variable) but the relative abundance of the dominant species will be high and the remaining species, regardless of their numbers, will remain relatively unimportant in the overall community makeup. Although the exact mechanisms remain unclear, variable habitats are dominated by a few species, likely those well adapted to take advantage of brief suitable periods.

Community variability

An important finding was the relationships among population variability and community variability. It is possible that at larger spatial scales, the variability in the meta-community is relatively low compared to the variability of individual communities. Such an effect would be produced if the individual communities responded independently and asynchronously to environmental factors or if environmental factors were independent and asynchronous in individual pools (cf. Micheli et al. 1999). In addition, metapopulation dynamics of the three habitat generalists (harpacticoid copepod, cyclopoid copepod and the ostracod) may contribute to the observed community variability. Although the exact mechanisms of dispersal for these animals are poorly understood, these organisms are typically the first to colonize and establish populations in open patches (Therriault, unpubl.).
In conclusion, there is a clear positive link between habitat variability and community variability. Habitat generalists are expected to contribute substantially to community variability given their likely contributions to inter- and intra-pool dynamics, either through in-

fluences on colonization or through biotic interactions such as trophic dynamics. Habitat generalists have broad geographic distributions and good dispersal and colonization abilities. They may therefore determine the colonization sequence of open patches, or may contribute significantly to the observed assemblage structure via effects on other species in the community (i.e., resource partitioning, niche pre-emption, niche packing). If habitat generalists are variable over time, then rare species should also vary in response to the habitat generalists, thereby exasperating community variability.

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