DIVERSITY PATTERNS IN STREAM BENTHIC INVERTEBRATE COMMUNITIES: THE INFLUENCE OF HABITAT STABILITY[1]

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Abstract. Invertebrate diversity patterns were examined in 11 freshwater habitats (10 streams and a windswept lake shore) of similar physicochemical nature but different thermal and hydrologic stability in the Cass-Craigieburn region, New Zealand. Species richness and density were markedly higher at the more stable sites, but species evenness peaked at sites of intermediate stability. Of the 20 environmental variables examined, a multivariate instability index incorporating temporal variation in depth, temporal variation in current speed, substrate stability, the Pfankuch channel stability index, temperature range, and stream reach tractive force was the single best predictor of the number of species, whereas epilithic pigment concentration was the single best predictor of invertebrate density. The pattern in species richness did not support any of three diversity hypotheses considered. In contrast, the pattern in species evenness suggested competitive exclusion may be occurring patchily and that Huston's dynamic equilibrium model may have some validity, at least at the level of the patch. However, the strong link between productivity and stability apparent in these habitats, and a lack of information on the effects of increased productivity on competition in stream benthic communities makes any firm assessment of the latter model difficult. The observed diversity patterns are, however, consistent with the idea that high diversity is maintained in these habitats by an interaction between low levels of disturbance and habitat patchiness.

Key words: disturbance; disturbance-productivity-diversity model; diversity; Huston's dynamic equilibrium model; intermediate disturbance hypothesis; productivity; species evenness; species richness.

INTRODUCTION

Attempts to explain spatial and temporal patterns of diversity in nature have been (e.g., Thoreau 1860, Clements 1916) and continue to be (May 1986, Walker 1989) a pervading theme of ecological research. Many factors have been linked with observed patterns of diversity (Krebs 1985, Begon et al. 1990), however, the interaction between disturbance and diversity has been one of the most debated issues (for reviews see Thiery 1982, Pickett and White 1985, Resh et al. 1988, Petraitis et al. 1989).

Physical disturbances (sensu White and Pickett 1985) that result in changes to population structure or resource availability, such as increases in discharge, are common in many streams (Power et al. 1988), and are postulated to have strong, possibly overriding influences, on community structure in rivers and streams (Lake and Barmuta 1986, Resh et al. 1988). A large number of observational (e.g., Fisher et al. 1982, McElravy et al. 1989, Scrimgeour and Winterbourn 1989) and experimental lotic studies (e.g., Robinson and Minshall 1986, Malmqvist and Otto 1987, Boulton et al. 1988, Doeg et al. 1989) indicate that disturbances

reduce benthic invertebrate density and diversity, although both may recover quickly.

Nevertheless, although it is clear that severe physical disturbances reduce diversity, the effects of lesser disturbances are unclear. In reviewing the role of disturbance in lotic ecosystems, Resh et al. (1988) discussed three hypotheses relating disturbance regime to community structure: the equilibrium model based on Lotka-Volterra population dynamics (McIntosh 1985), the intermediate disturbance hypothesis (Grime 1973, Connell 1978) and the dynamic equilibrium hypothesis (Huston 1979). Equilibrium models invoke biotic interactions as the principal structuring force in communities, but only seem appropriate in very stable streams or during periods of stable flow (Minshall et al. 1983, 1985, Minshall and Peterson 1985).

Of the three hypotheses considered, only the intermediate disturbance hypothesis (Grime 1973, Connell 1978) has been widely applied in lotic studies (Ward and Stanford 1983, Resh et al. 1988). It predicts that diversity will be greatest at intermediate levels of disturbance, with competitive exclusion and physical elimination leading to species loss at either end of the disturbance continuum. The hypothesis has received support from both theoretical (Petraitis et al. 1989), and some empirical (Stanford and Ward 1983) studies. However, the results of experimental manipulations of substrate patches (Reice 1984, 1985, Robinson and Minshall 1986, Doeg et al. 1989, Lake et al. 1989)

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generally have not supported the hypothesis, although the scale of these experiments may not be appropriate for testing the hypothesis (Minshall 1988, Lake 1990).

Resh et al. (1988) concluded in their review that Huston's (1979) dynamic equilibrium model was the hypothesis most generally applicable to stream communities, but they provided no convincing evidence to support it. This hypothesis considers community structure to be a trade-off between the frequency of population reduction and the rate at which competitive exclusion proceeds, the latter in turn being related to the productivity of the environment. If the interval between disturbance events is shorter than the time required for competitive exclusion to take effect, then initial diversity levels should be maintained. However, when disturbances are infrequent, increases in the population growth rates of strong competitors should lead to decreases in species diversity via competitive displacement.

Therefore, if growth rates (or productivity) are held constant, diversity should peak at sites of intermediate disturbance, although the exact position of the peak along the disturbance continuum will vary with the rate of competitive displacement. If productivity increases as disturbances become less frequent, then this peak will be exaggerated, and if it decreases, highest diversity will occur at the more stable sites.

The disturbance-productivity-diversity model of Hildrew and Townsend (1987) developed empirically from their studies of streams in the Ashdown Forest, southern England, also incorporates an interaction between disturbance and productivity in determining diversity patterns. Their model invokes the intermediate disturbance hypothesis at high levels of productivity, but with the lower diversity in less productive habitats being unaffected by increasing disturbance.

Although the above hypotheses deal equally with biotic (e.g., predation) and abiotic (e.g., substrate movement) disturbances we have followed the approach of Menge and Sutherland (1987) and consider them to be separate. This in itself generates problems, however, because as environmental stability increases, the importance of biotic interactions may also change (Connell 1975, Peckarsky 1983, Menge and Sutherland 1987, Peckarsky et al. 1990, but see Walde 1986). As the impacts and mechanisms of predation per se in stream environments are still poorly understood (Allan 1983, Peckarsky 1984), it is difficult to predict how the effects of predation may alter with increasing stability of the physical environment. However, Menge and Sutherland (1987) predicted a bimodal peak in diversity with declining stability in marine systems.

Clearly, the ways in which disturbances influence benthic invertebrate diversity in stream environments are essentially unresolved. The issue is further complicated by the fact that diversity comprises two components, species richness and species evenness (equitability) (Hurlbert 1971, Magurran 1988), each of which

may respond differently to the effects of disturbance. There also appears to be little information on how overall stability of a habitat, as opposed to the effects of discrete disturbance events (as addressed by most of the studies above) influence biotic diversity in that habitat (Fisher 1987, but see Richards and Minshall 1992). An understanding of this is complicated by the fact that habitat stability can be characterized in a number of different ways, for example, as discharge variability, or as thermal range, features that are not necessarily correlated (Death and Winterbourn 1994). In this paper we assess habitat stability using six different measures of thermal and hydrological stability. We then use these measures to examine invertebrate species richness and evenness in 11 freshwater habitats (10 streams and a windswept lake shore) of similar physicochemical nature but differing stability.

STUDY SITES

The study sites were all on small tributaries of the Waimakariri River, in the Cass-Craigieburn region of the Southern Alps, New Zealand. They occupy three valleys within 18 km of each other, and experience similar climatic conditions (Death 1991). Half the streams arose from either a spring or lake and were relatively stable (both in temperature and discharge), whereas streams with more diffuse origins had more variable flow and temperature regimes and were considered unstable. The stony, wave-washed southwestern end of Lake Grasmere was also included in the study because it appeared to be a stable environment that superficially resembled a stream, with a fauna similar to that of other streams in the region (Stout 1977).

Mean values for physical and chemical measures made at the study sites between October 1987 and May 1989 are given in Table 1. The streams were small to moderate in size, with all study sites having similar substrate distributions, moderately hard water, circumneutral pH, and low nutrient concentrations. Overall, physical ($F_{8,1} = 23.44$, $P = 0.16$, MANOVA) and chemical characteristics ($F_{3,7} = 2.8$, $P = 0.12$, MANOVA) did not differ between the "stable" and "unstable" site groups.

MATERIALS AND METHODS

Measurement of stability

As none of the study sites has a monitored discharge, and as no single measure can give an accurate assessment of overall stability (Death and Winterbourn 1994) six variables were monitored to evaluate habitat stability. These variables cover a range of hydrological and thermal characteristics that have been shown to affect the distribution and abundance of lotic invertebrates (e.g., Vannote and Sweeney 1980, Winterbourn and Collier 1987). The measured variables included the Pfankuch (1975) stability index, which involves summing the scores assigned to 15 attributes (weighted in

TABLE 1. Physical and chemical characteristics of the study sites. Sites are listed in order from least stable to most stable as measured by their multivariate instability scores. Craigieburn Cutting Stream and Middle Bush Stream have forest canopies; all other streams are open. All streams had nitrate-nitrogen (NO_3-N) and reactive phosphorus (PO_4-P) concentrations below 0.05 mg/L and 0.004 mg/L, respectively.

Sites	Order	Width (m)	Slope	Mean depth (cm)	Mean current velocity (cm/s)	Mean temperature (°C)	Mean particle size (cm)	Mean pH	Mean alkalinity (mg $CaCO_3$/L)
Unstable sites									
Bruce Stream	3	6.3	0.03	34	94	8.8	7.4	7.4	26.1
Kowai River	2	5.3	0.03	29	103	13.0	7.4	7.7	17.8
Dry Stream	2	1.9	0.05	9	44	10.0	5.4	7.6	18.4
Whitewater Stream	3	5.8	0.03	16	75	10.4	7.8	7.5	17.6
Craigieburn Cutting Stream	1	1.1	0.07	8	40	8.9	8.1	7.3	17.7
Stable sites									
Grasmere Stream	1	3.4	0.01	29	85	11.7	4.7	7.4	33.2
Middle Bush Stream	2	0.9	0.14	5	36	8.0	6.4	7.8	35.0
Porter River	2	4.9	0.03	21	90	9.0	6.6	7.5	20.3
Lake Grasmere	NA	NA	NA	29	NA	13.0	5.7	8.0	32.2
Cora Lynn Stream	1	1.3	0.07	11	37	8.6	7.2	7.6	41.6
Slip Spring	1	2.5	0.09	9	46	8.1	8.5	7.2	22.2

relation to their perceived importance) in three regions of the stream channel, i.e., upper banks, lower banks, and stream bottom, according to the observer's evaluation of predetermined criteria (see Pfankuch 1975, Rounick and Winterbourn 1982). Following Winterbourn and Collier (1987) and Death and Winterbourn (1994) we only used the bottom component of the index, which assesses stability of the substrate component of the complete index, and seems more relevant to the scale of lotic invertebrate dynamics. Measurements of temperature range, and the movement of five marked stones in each of three size categories (corresponding to the sizes of stones collected for invertebrate samples) were also made monthly at each site. Temporal variation in depth and current speed were calculated by taking the absolute difference between the value in one month and that in the preceding month. Finally, stream reach tractive force was calculated as detailed by Newbury (1984). This relates channel slope and depth to substrate size distribution and yields a theoretical proportion of particles predicted to be moving in uniform flow conditions within the entire stream reach. It was used to calculate the percentage of substrate predicted to be moving at any given time at the study sites. For further details on the assessment of stability see Death and Winterbourn (1994).

Substrate movement as predicted by tractive force was the only stability measure that did not differ significantly between the "stable" and "unstable" sites. To evaluate overall stability, based on all six variables, the measures were combined into a single, multivariate index of instability using principal components analysis (Death and Winterbourn 1994). Site scores on axis 1 for this analysis accounted for 64% of the variation in the measures and had factor loadings that were approximately equal for all the stability variables except predicted substrate movement. The PCA scores for axis

1 were scaled to give an index where an increase in the multivariate instability score was indicative of decreasing stability. Mean values for each stability measure and the multivariate instability scores are given in Table 2 along with correlations between the instability score and the other stability measures.

Sampling protocol

Collections of invertebrates were made from riffles at the study sites on two or three consecutive days in October 1987 (spring 1), January 1988 (summer), April 1988 (autumn), July 1988 (winter), and October 1988 (spring 2). Fifteen stones were sampled at each site, five stones being selected at random from each of three size classes (maximum linear, planar dimensions 91–180, 60–90, and <60 mm).

Stones were sampled as the collector moved progressively upstream. A 250-μm mesh net was held behind each stone, which was lifted rapidly into it. Adjacent stones were disturbed as little as possible but any fine sediment or detritus immediately below a stone was disturbed and therefore any associated invertebrates were collected. Samples were preserved in 10% formalin. This technique yielded more precise estimates per unit effort for both density and diversity of invertebrates on stones in these streams than Surber sampling (Death 1991). Where possible, invertebrates were identified to species level using available keys. Although some taxa could not be named, they were still differentiated into apparent morphospecies.

Invertebrate densities per 0.1 m^2 were calculated from the stone samples using the technique of Wrona et al. (1986). Densities were calculated by multiplying the mean number of invertebrates in each of the three stone size classes by the mean abundance of stones in that size class in 0.1 m^2 of stream habitat (determined from 10 Surber samples). As this technique cannot be

TABLE 2. Mean stability values calculated from monthly measurements at each of the study sites between December 1987 and May 1989 and their correlations (r_s) with the multivariate instability score. Sites are listed in order from least stable to most stable as measured by their multivariate instability scores.

	Depth variability (cm)	Current variability (cm/s)	Temperature range (°C)	Bottom component Pfankuch index	Stone movement measure (%)	Predicted substrate movement of tractive force (%)	Multivariate instability score (PCA axis 1)
Unstable sites							
Bruce Stream	19	46	9.4	50	96.9	70	2.33
Kowai River	9	44	9.8	50	63.8	72	1.85
Dry Stream	6	35	9.8	42	12.0	50	1.24
Whitewater Stream	4	27	9.8	39	17.2	28	1.03
Craigieburn Cutting Stream	3	18	5.8	44	18.6	66	0.95
Stable sites							
Grasmere Stream	4	34	6.3	36	3.0	13	0.83
Middle Bush Stream	3	11	5.7	42	1.4	68	0.76
Porter River	3	29	2.2	31	0.7	68	0.59
Lake Grasmere	7	NA	8.4	30	0.0	NA	0.52
Cora Lynn Stream	4	13	2.5	31	6.3	76	0.51
Slip Spring	2	18	0.5	31	0.0	63	0.39
Correlations with multivariate instability score	0.85	0.73	0.87	0.89	0.89	0.01	

applied to species number, the total number of species collected on the 15 stones was used as a measure of species richness. As the total number of invertebrates collected on the 15 stones corresponded closely to that calculated for 0.1 m^2 (slope = 1.04, r^2 = 0.96) and as species number within a given site is proportional to the number of individuals collected, this was deemed an appropriate measure of species richness.

Epilithic and particulate carbon

To estimate productivity at the study sites, photosynthetic pigments (chlorophyll a and phaeophytin a) were extracted with 90% acetone from five cobbles (mean diameter = 6 cm) collected on each sampling occasion. Total pigment concentrations (chlorophyll a + phaeophytin a) were calculated using the method of Moss (1967a, b) and corrected for stone surface area determined by wrapping stones with aluminium foil of known mass per unit area.

Similarly, stone surface organic carbon was determined on each sampling occasion from five stones (mean diameter = 3 cm) with the micro-dichromate oxidation technique (Maciolek 1962, Newell 1982) using heat-by-dilution, as modified by Collier (1987).

Coarse (>1 mm) and fine (5 μm–1 mm) particulate organic material (POM) was measured from five core samples (4.5 cm diameter and 6 cm deep) of substrate collected at each site seasonally. Organic content was determined by ashing material (dried to constant mass) at 550°C for 6 h and taking the difference in mass before and after ashing. Similarly, particulate material associated with the invertebrate stone samples was weighed after drying to constant mass and expressed on an areal basis using the technique of Wrona et al. (1986).

Measurement of diversity

Many indices have been used to measure species diversity. However, despite having been extensively reviewed (e.g., May 1975, Pielou 1975, Southwood 1978, Washington 1984, Ludwig and Reynolds 1988, Magurran 1988) there is still little consensus as to which measure or measures are best. The choice of an index is complicated by the fact that diversity comprises two components, species richness and species evenness or equitability, and although some indices combine both components, this can obscure potentially useful information.

We used several indices, each of which measures a slightly different aspect of diversity. They are all easy to interpret biologically, and have received consistent support in reviews on the topic. They are:

1) Species number (S).

2) Margalef's index (Clifford and Stephenson 1975), a simple measure of species richness given by:

$$D = (S - 1)/\ln N$$

where N = the total number of individuals collected.

3) The log series alpha index (Taylor 1978), which is also essentially a measure of species richness and is given by:

$$\alpha = \frac{N(1 - x)}{x},$$

where x is estimated from the iterative solution of:

$$S/N = (1 - x)/x[-\ln(1 - x)].$$

4) The Berger-Parker dominance index (Berger and Parker 1970), which is a simple measure of evenness (or dominance) given by:

TABLE 3. Results of a stepwise regression analysis of the number of species collected in each season at all study sites against 20 biological, physicochemical, and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Parameter estimate	Partial r^2	Total r^2
Spring 1			
Intercept	43.28		
Multivariate instability score	−12.82	0.75	0.75
Mean conductivity	0.14	0.15	0.90
Summer			
Intercept	62.19		
Multivariate instability score	−19.28	0.88	0.88
Autumn			
Intercept	61.37		
Multivariate instability score	−19.46	0.80	0.80
Winter			
Intercept	55.61		
Multivariate instability score	−19.52	0.81	0.81
Spring 2			
Intercept	4.24		
Epilithic carbon conc.	2.05	0.60	0.60
Spot conductivity	0.13	0.16	0.77
Stone associated POM	1.30	0.12	0.89
All seasons combined			
Intercept	40.71		
Multivariate instability score	−12.38	0.65	0.65
Epilithic carbon conc.	0.36	0.070	0.72
Stone associated POM	0.47	0.04	0.76
Spot conductivity	0.05	0.02	0.78

$$D = N_{max}/N,$$

where N_{max} = the number of individuals in the most abundant species and N = the total number of individuals collected.

5) Simpson's index (1949), which is also a measure of evenness and has the form:

$$D = \sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right),$$

where n_i = the number of individuals in the ith species and N = the total number of individuals collected. Simpson's index is strongly weighted towards the most abundant species, but is advocated by a number of authors including May (1975) and Washington (1984), because it better reflects the entire species abundance distribution than other indices of the same general form (e.g., the Shannon index).

The Berger-Parker and Simpson's indices were expressed as reciprocals, so that in all indices, an increase in the index indicates an increase in diversity.

Data analysis

Data were analyzed with the regression, stepwise regression, and Spearman rank correlation procedures of SAS (1985). Regression lines are plotted as seasonal means (± 1 SE) of diversity or density vs. stability mea-

sures but analysis was carried out using the entire data set in an analysis of covariance (ANCOVA) design. Regression equations are for this ANCOVA analysis, not the plotted seasonal means. Stepwise regression of diversity variables was undertaken using 20 of the biological, chemical, physical, and stability measurements listed in Table 4; stability measures used to calculate the multivariate instability scores were excluded to remove singularity problems. Spot measurements are those made at the time of collection, or during the month prior to the collection of samples. The critical probability level for addition and removal of variables to or from the model was set at 0.05. The same variables were used in the correlation analysis.

RESULTS

Species number

A total of 185 species was collected in the seasonal sampling program, with any one collection (i.e., all the stones collected in each season at a site) containing between 7 and 64 species. The number of species collected at a site declined in a linear fashion as overall environmental stability (i.e., the multivariate instability scores) decreased (Fig. 1) ($F_{1,45} = 130.99$, $P < 0.001$, $r^2 = 0.78$).

The number of species collected also differed significantly between seasons ($F_{4,45} = 5.67$, $P < 0.001$), although this difference existed primarily between the spring 2 sample and the others. Significantly fewer species occurred in spring 2 than in all other seasons except winter (the only other significant difference in species number was between winter and summer). The lower species numbers in spring 2, and to a lesser extent winter, were probably the result of an increase in the size and severity of spates during these seasons (Death and Winterbourn 1994) when even some of the more stable sites (especially Cora Lynn and Middle Bush) were mildly disturbed. Life history patterns could also have accounted for the absence of some taxa in spring 2 and in winter, although New Zealand invertebrates in general have poorly synchronized life histories and occur throughout the year (Towns 1981).

The nature of the relationship between the number of species present and the stability of the sites (i.e., the slope of the graph) did not change with season ($F_{4,45} = 0.49$, $P = 0.74$). This was surprising given that during spring 2 and winter, conditions in many of the streams were considerably more unstable than at other times of the year. During spring 2 and winter, one might have expected communities at the unstable sites to be more severely affected by increases in disturbance, and to have lost proportionately more species than the stable sites. If so, the slopes of the regression lines would have been steeper in spring 2 and winter. This was not found (Fig. 2), and only two sites of intermediate stability showed signs of proportionately greater declines in species number during spring 2 and winter.

TABLE 4. Correlation (r_s) of six diversity measures with biological, hydrological, and chemical parameters measured in the study streams. The hydrological and chemical parameters were monthly measurements made at the study sites between October 1987 and May 1989. The biological parameters were those collected at the time of invertebrate sampling.

Physicochemical/biological parameter	Species number	Total number of individuals	Margalef's index	Log series alpha index	Berger-Parker dominance index	Simpson's index
Biological						
Epilithic pigment conc.	0.72*	0.82*	0.23	0.04	0.11	0.07
Epilithic carbon conc.	0.79*	0.81*	0.38*	0.20	0.19	0.18
Coarse POM	−0.08	−0.22	0.20	0.25	0.08	0.11
Fine POM	0.03	−0.17	0.23	0.22	0.06	0.07
Total POM	−0.10	−0.28*	0.20	0.25	0.04	0.08
Stone POM	0.70*	0.39*	0.72*	0.63*	0.46*	0.49*
Chemical						
Spot conductivity	0.24	0.12	0.23	0.19	0.23	0.19
Spot pH	0.17	−0.01	0.23	0.20	0.31*	0.22
Mean Conductivity	0.21	−0.07	0.33*	0.31*	0.28*	0.32*
Mean pH	0.11	0.001	0.14	0.12	0.20	0.14
Mean alkalinity	0.46*	0.18	0.38*	0.29*	0.21	0.30*
Physical						
Spot current velocity	−0.34*	−0.20	−0.33*	−0.28*	0.06	0.03
Spot depth	−0.22	−0.06	−0.39*	−0.37*	−0.002	0.02
Spot temperature	0.35*	0.40*	0.14	−0.02	0.23	0.15
Mean current velocity	−0.39*	−0.12	−0.49*	−0.47*	−0.14	−0.15
Mean depth	−0.24	0.05	−0.53*	−0.56*	−0.17	−0.21
Mean temperature	−0.17	0.16	−0.37*	−0.35*	−0.03	−0.13
Stability						
Spot temperature range	−0.45*	−0.32*	−0.40*	−0.32*	−0.08	−0.17
Mean temperature range	−0.64*	−0.42*	−0.53*	−0.42*	−0.23	−0.34*
Current variation	−0.52*	−0.27*	−0.56*	−0.51*	−0.22	−0.21
Depth variation	−0.50*	−0.26	−0.60*	−0.55*	−0.26	−0.31*
Spot stone movement	−0.67*	−0.70*	−0.38*	−0.22	−0.21	−0.19
Mean stone movement	−0.76*	−0.73*	−0.41*	−0.23	−0.26	−0.24
Pfankuch bottom comp.	−0.75*	−0.71*	−0.40*	−0.25	−0.14	−0.09
Tractive force	−0.15	−0.34*	0.07	0.11	−0.06	0.02
Instability score	−0.77*	−0.65*	−0.51*	−0.37*	−0.15	−0.16

* $P < 0.05$.

This decline in species number at the sites of intermediate stability is seen to be more pronounced if a measure of substrate movement is used as the independent variable (the stability measure next most high-
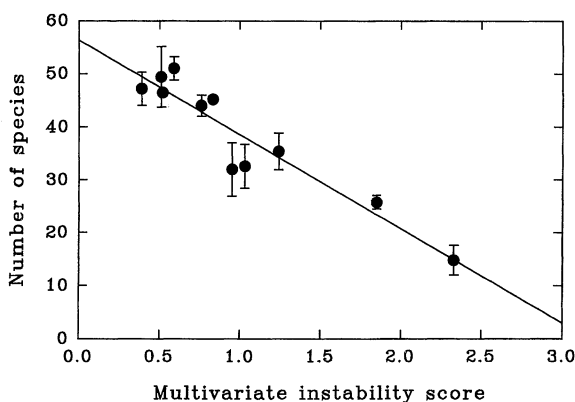
FIG. 1. Number of species collected at each site as a function of overall stability (multivariate instability score). Plotted values are site averages (±1 SE) over all seasons of the total number of species collected on each sampling date. Regression equation: $y = 48.10 - 16.83\ x$, $r^2 = 0.78$.

ly correlated with species number), rather than the multivariate instability score (Fig. 3). The slope of the regression line does not change if all sites are included, but if the two most unstable sites are ignored (dashed lines) the slope of the relationship increases in seasons with more unstable conditions ($F_{4,35} = 3.85, P = 0.01$), the predicted response. The number of species present at the highly unstable sites (Kowai River and Bruce Stream) appeared to be largely unaffected by increasingly disturbed conditions, and it was only at sites of intermediate stability that a distinct reduction in species number in response to increased disturbances was observed.

Huston's dynamic equilibrium model also incorporates productivity as an important determinant of diversity, so we also examined the relationship between species number and chlorophyll concentration (an estimate of algal biomass and therefore a rough indicator of productivity). Species number increased as epilithic biomass increased (Fig. 4) ($F_{1,45} = 30.01, P < 0.001$, $r^2 = 0.53$), although the relationship was not as strong as that with overall stability. A quadratic model for the relationship only improved the fit by 9%. However, epilithic biomass was also negatively correlated with
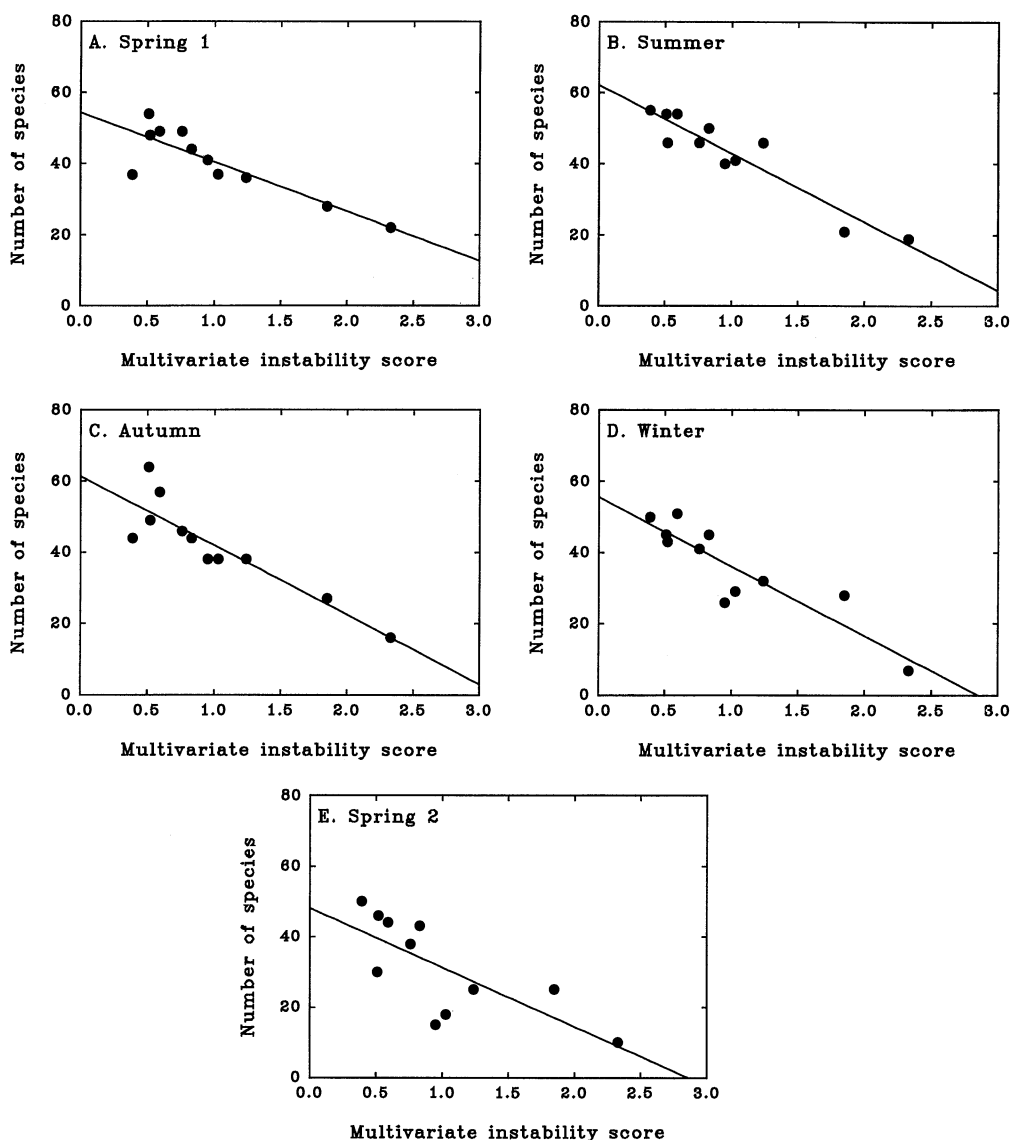
FIG. 2.   Total number of species collected in each season as a function of overall stability (multivariate instability score).

the instability score ($r_s = -0.74$, $P < 0.001$). To examine the effect of stability independently of productivity we selected the five sites with similar levels of algal biomass (0.59–1.60 μg chl a/cm²) and examined the relationship between species number and stability at these sites. Again species number decreased as the stability of the site decreased (Fig. 5) ($F_{1,15} = 15.05$, $P = 0.002$, $r^2 = 0.73$).

Although the principal aim of this study was to investigate the effect of habitat stability on species diversity, numerous other variables were recorded concurrently, both in characterizing overall stability and in describing habitats, so we also examined these variables for any relationship with species number. Stepwise regression analysis indicated that of the 20 measured variables, the overall instability score was the

single best predictor of the number of species at a site in all seasons but one (spring 2) ($r^2 = 0.75$–0.88), and for all seasons combined ($r^2 = 0.65$) (Table 3). In spring 2, epilithic carbon concentration was the best predictor ($r^2 = 0.60$).

Number of species was also positively correlated with epilithic pigment concentration, epilithic carbon concentration, and stone-associated particulate organic matter (POM) biomass, and with the exception of tractive force was negatively correlated with all the stability measures (Table 4). Several physical and chemical variables such as current velocity were more weakly correlated with species number.

Total number of individuals

The total number of animals collected from the 15 stones at each site in any one season ranged from 16
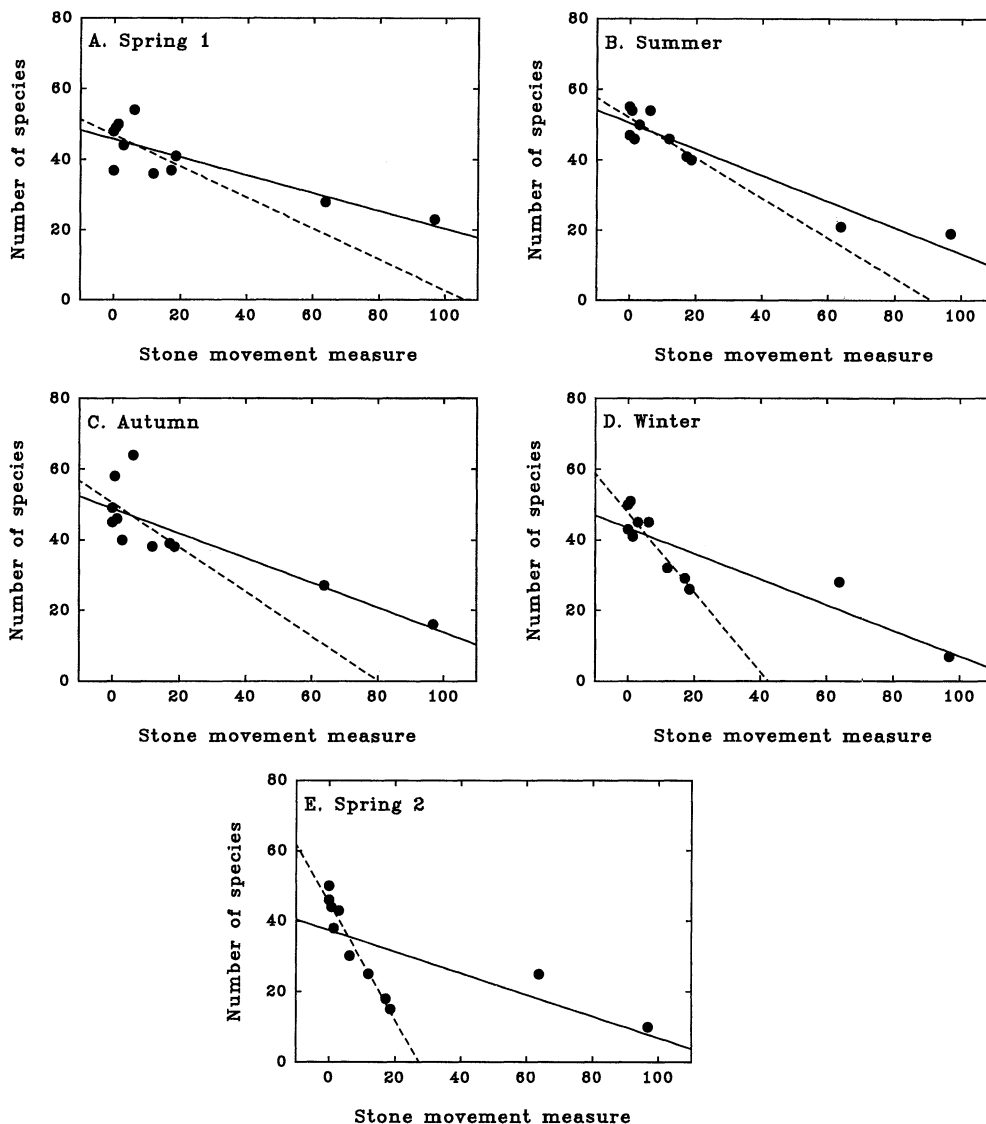
FIG. 3.   Total number of species collected in each season as a function of mean stone movement. Solid regression lines include the two most unstable streams (Kowai River and Bruce Stream) in the analysis; dashed regression lines exclude these two sites.

at Bruce Stream to 16 047 at Slip Spring. Seasonal patterns in the total numbers of animals appeared to be similar at both stable and unstable sites with peaks of abundance in the first spring and summer (Death 1991). Seasonal differences in density were significant ($F_{4,45}$ = 4.84, P = 0.003), with spring 1, summer, and autumn having significantly higher densities than winter and spring 2, probably because many of the streams experienced more disturbed conditions during the latter two seasons.

The total number of invertebrates was considerably lower at the less stable sites (Fig. 6) ($F_{1,45}$ = 48.22, P < 0.001, r^2 = 0.62), with the slope of the relationship being similar in all seasons ($F_{4,45}$ = 0.98, P = 0.43). However, stepwise regression analysis indicated that

epilithic pigment concentration was the best predictor of the total number of individuals in each of the seasons (r^2 = 0.64–0.87) and for all seasons combined (r^2 = 0.54) (Table 5). As with species number, total invertebrate abundance was also positively correlated with epilithic carbon concentration and stone-associated particulate organic matter (POM), and negatively correlated with all but one stability measure (depth variation) (Table 4).

Diversity indices

The two other indices of species richness, Margalef's index and the log series alpha index, both showed a significant linear decrease with a decline in the multivariate instability score (Fig. 7) ($F_{1,45}$ = 49.59, P <
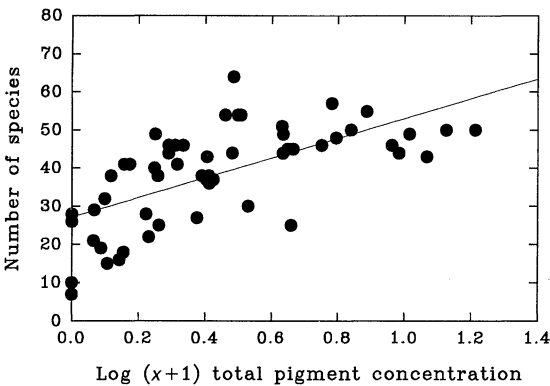
FIG. 4. Total number of species collected at each site in each season as a function of total pigment concentration (μg/cm^2). Regression equation: $y = 19.16 + 27.73 \log x$, $r^2 = 0.53$.

FIG. 6. Total number of individuals collected at each site as a function of overall stability. Plotted values are site averages (± 1 SE) over all seasons of the total number of individuals collected on each sampling date. Regression equation: $\log y = 3.55 - 0.71 x$, $r^2 = 0.61$.

0.001, $r^2 = 0.55$, and $F_{1,45} = 10.44$, $P = 0.002$, $r^2 = 0.24$, respectively). In contrast, the Berger-Parker dominance index and Simpson's index (Fig. 7) indicated peaks in diversity (i.e., minimum dominance) at sites of intermediate stability, and a similar degree of evenness at very stable and unstable sites. Polynomial regression of the evenness indices against a log-transformed instability score yielded a cubic function as the best model for both indices ($F_{7,47} = 2.92$, $P = 0.01$, $r^2 = 0.30$ and $F_{7,47} = 3.40$, $P = 0.005$, $r^2 = 0.34$ for the Berger-Parker and Simpson's indices, respectively).

Correlation of the species richness and evenness indices with physicochemical, stability, and biological variables also revealed different patterns for the two components of diversity (Table 4). The two species richness indices were negatively correlated with most of the stability measures and several physical variables, including mean depth, current velocity, and temperature, and positively correlated with several biological

and chemical variables, including stone-associated POM, conductivity, and alkalinity. In contrast, the two evenness measures were poorly correlated with all variables except stone-associated POM, with which they were positively correlated. Stepwise regression anal-

TABLE 5. Results of a stepwise regression analysis of the total numbers of individuals collected in each season at all study sites against 20 biological, physicochemical, and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

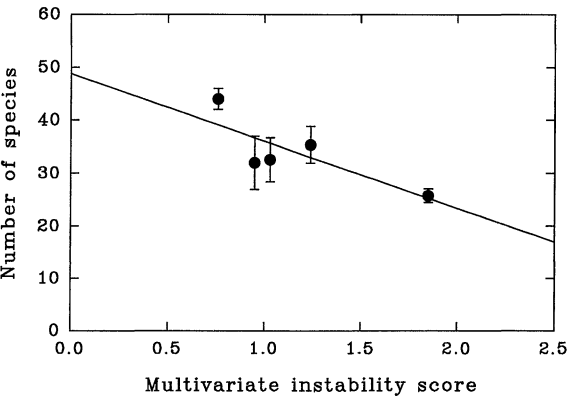| Variable entered	Parameter estimate	Partial r^2	Total r^2
Spring 1			
Intercept	1047.38		
Epilithic pigment conc.	1563.32	0.64	0.64
Summer			
Intercept	11 395.18		
Epilithic pigment conc.	1660.87	0.84	0.84
Total POM	−7383.09	0.07	0.91
Spot stone movement	−54.96	0.06	0.96
Autumn			
Intercept	683.99		
Epilithic pigment conc.	1131.07	0.78	0.78
Winter			
Intercept	27 268.21		
Epilithic pigment conc.	669.97	0.87	0.87
Spot pH	−3617.91	0.08	0.95
Spring 2			
Intercept	−2996.17		
Epilithic pigment conc.	1027.39	0.84	0.84
Mean current velocity	37.24	0.08	0.91
All seasons combined			
Intercept	3833.71		
Epilithic pigment conc.	478.08	0.54	0.54
Epilithic carbon conc.	202.09	0.15	0.70
Mean conductivity	−75.24	0.06	0.76
Stone POM	287.00	0.03	0.79
Total POM	−1392.65	0.04	0.82
Spot conductivity	31.52	0.04	0.86

FIG. 5. Number of species as a function of overall stability for sites with mean epilithic biomass between 0.59 and 1.60 μg chl. a/cm^2. Plotted values are site averages (± 1 SE) over all seasons of the total number of species collected on each sampling date. Regression equation: $y = 27.79 - 3.08 x$, $r^2 = 0.73$.
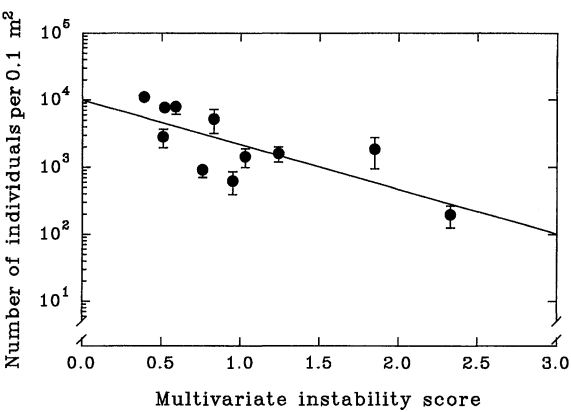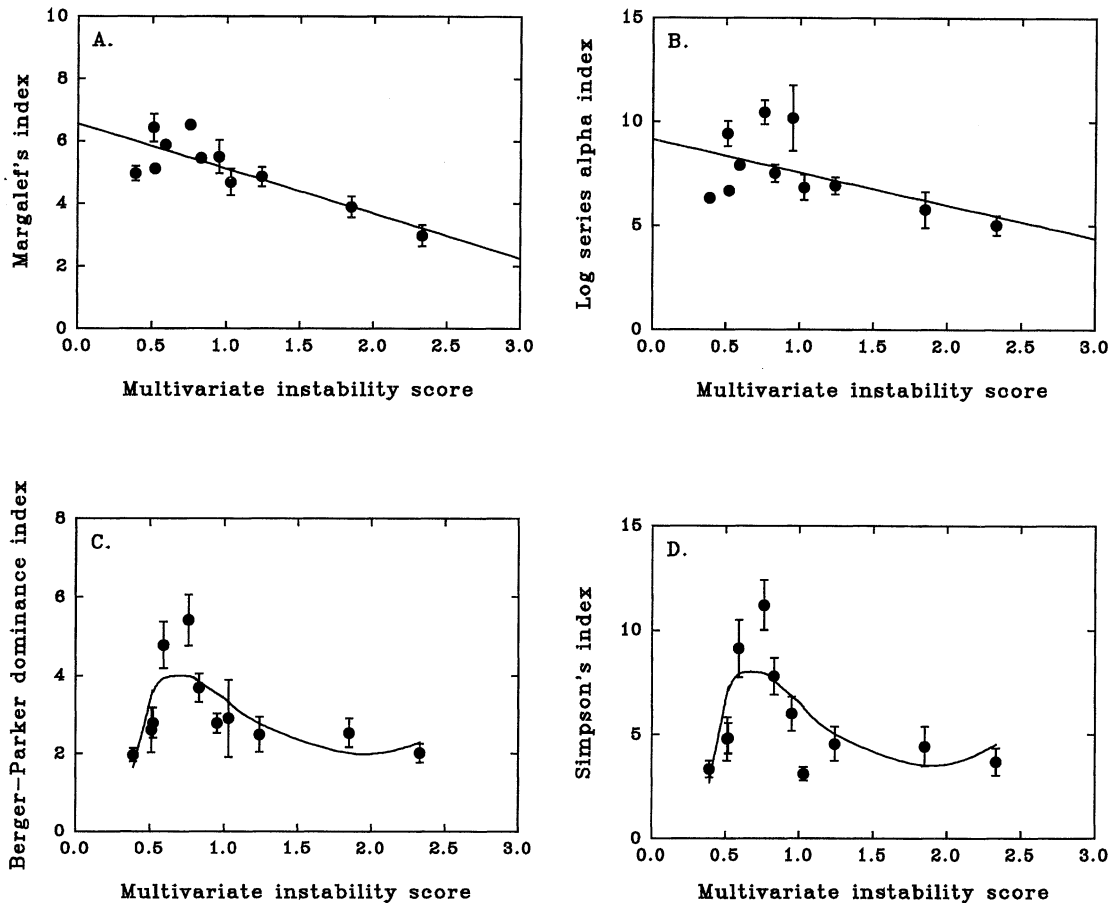
FIG. 7.   Margalef's index (A), log series alpha index (B), Berger-Parker dominance index (C), and Simpson's index (D) as a function of overall stability. Plotted values are site averages (± 1 SE) over all seasons of the index scores recorded on each sampling date. Regression equations: (A) $y = 6.18 - 1.55\ x$, $r^2 = 0.55$, (B) $y = 9.06 - 1.90\ x$, $r^2 = 0.24$, (C) $y = 3.40 - 6.42 \log x - 7.51 (\log x)^2 + 45.50 (\log x)^3$, $r^2 = 0.30$, (D) $y = 6.51 - 15.36 \log x - 14.29 (\log x)^2 + 112.57 (\log x)^3$, $r^2 = 0.34$.

ysis carried out on each of the four diversity indices was not particularly revealing, and significant predictors of each of the diversity indices were either absent or inconsistent between seasons.

DISCUSSION

In the present study, species number declined as overall stream stability decreased, and of 20 environmental variables examined, overall stability (i.e., the multivariate instability score) was the single best predictor of the number of species at a site. This is consistent with the results of Robinson and Minshall (1986) who found that the number of species on artificial substrata decreased as the frequency of disturbance increased. Other experimental manipulations in streams (Clifford 1982, Doeg et al. 1989) and studies of flood events (Fisher et al. 1982, McElravy et al. 1989, Scrimgeour and Winterbourn 1989) have also shown that disturbances lower species richness, and suggest that frequent disturbances (at least those above

a particular threshold) will lead to the maintenance of low species diversity.

In contrast, Reice (1984, 1985) found no impact of disturbance frequency on species number or "diversity" (i.e., the Shannon index) in experimentally disturbed baskets of substrate. Lake et al. (1989) also found that similar numbers of species recolonized disturbed patches whether they had been disturbed once or three times prior to monitoring community recovery. We suspect that increasing disturbance frequency in streams acts on species diversity primarily by reducing the time available for recolonization following disturbance events. In the study of Lake et al. (1989), the time between the last disturbance and monitoring recovery was the same for all treatments. In contrast, Robinson and Minshall (1986) used an increasing disturbance regime over a fixed time period so that time since the last disturbance increased with a decrease in disturbance frequency. The results of Robinson and Minshall (1986) and those of our field experiments on

disturbance frequency (Death 1991) are consistent with the hypothesis that time since the last disturbance rather than the number of disturbances a patch experiences per se is more important in determining species richness.

It should be noted that most of the studies discussed above considered the effects of discrete disturbance events, whereas we examined the effects of habitat stability, as assessed by changes in the environment, not the frequency, intensity, or impact of individual disturbance events (Death and Winterbourn 1994). For example, a large amount of substrate movement in any one month could have resulted from a single large disturbance, or from several smaller, but more frequent disturbances. Whether increases in frequency or intensity of disturbance have similar effects on stream biotas and how they may interact (e.g., with respect to the area affected by a disturbance) awaits investigation.

The strong linear relationship found between species number and habitat stability is not consistent with the intermediate disturbance hypothesis unless our most stable sites are considered to represent intermediate levels of disturbance in a broader perspective. We consider this unlikely, as few running water habitats are likely to be more stable than the upper reach of a spring-fed stream. Petraitis et al. (1989), in their theoretical review of diversity models, suggested that the nature of the relationship between disturbance and diversity will depend on the balance between immigration and extinction rates as patch recolonization proceeds following a disturbance. The scenario of the intermediate disturbance hypothesis will only eventuate if the extinction rate exceeds the immigration rate as recolonization occurs. If extinction and immigration rates form an equilibrium, or if both decrease to zero, then more stable patches will have greater diversity. What factors control immigration and extinction rates in stream habitats, and how they interact to generate diversity patterns, are essentially unanswered questions in stream ecology (but see Sheldon 1984).

To invoke the intermediate disturbance hypothesis it is also necessary to demonstrate that competitive exclusion occurs in streams, and that if it does, that there is a trade-off between superior competitive ability and the ability to colonize newly available habitat (Petraitis et al. 1989). Competitive exclusion, at least at the patch scale, is known to occur in some streams (e.g., McAuliffe 1984, Hemphill 1988, Dudley et al. 1990), but whether this is a general phenomenon or not is far from clear (Reice 1985). Similarly, there are instances where species that colonize newly created patches are replaced as time since disturbance increases. For example, Hemphill and Cooper (1983) observed that the larvae of *Simulium virgatum* colonized bare stones following a disturbance, but were eventually replaced by the competitively superior *Hydropsyche oslari*. Likewise, McAuliffe (1984) found that *Parargyractis confusalis* could colonize overturned stones more quickly

than *Leucotrichia pictipes,* thereby preventing *Leucotrichia* establishing the monopoly it held on undisturbed stones. In contrast, neither Reice (1984, 1985) nor Doeg et al. (1989) found evidence of a specialized "colonizing" fauna in their experimental studies. Whether stream invertebrates exhibit any trade-off between competitive and colonizing ability is still therefore far from clear and in need of further investigation.

Support for Huston's (1979) dynamic equilibrium model is difficult to assess without knowing, if competitive displacement is occurring, whether the rate at which it is occurring differs among sites. Huston's model predicts a peak in diversity at medium levels of productivity (at least at a fixed level of disturbance) and although we found that species richness levelled off as periphyton biomass increased there was no suggestion of it declining. Huston reasoned that high productivity would increase the rate of competitive exclusion, therefore given the scenario of increasing stability and productivity a peak in diversity at some intermediate level of disturbance (and productivity) would be predicted. In Fig. 8 we plotted number of species against stability and periphyton biomass within the framework of Huston's model. Clearly the data do not fit within the predicted pattern for increasing stability and productivity. Species number is greatest at the sites of highest stability and does not decline at sites with high productivity as the model would suggest.

Connell (1978) similarly found no support for the corollary of this situation (i.e., the maintenance of high species diversity by low productivity) in tropical rain forests or coral reefs. Whether low productivity should reduce the likelihood of competitive exclusion because population growth rates are depressed, or enhance its likelihood because resources are more limiting is, however, unclear (McGuinness 1987). Theoretical studies on the interaction between productivity and diversity (Tilman 1982, Abrams 1988) suggest both increases and decreases can occur with increasing productivity depending on the nature of the resources and the way in which they are utilized. Given the paucity of knowledge on resource usage by lotic invertebrates (Dudley et al. 1990), it is difficult to predict from these theoretical studies how productivity should affect benthic invertebrate diversity. There is similarly little empirical evidence with which to judge the effects of increased productivity on diversity, except in artificially enriched streams (Hildrew and Townsend 1987).

At the scale of the stream reach our data provide no suggestion that competitive exclusion was occurring at any of the sites if it is assumed that immigration rates did not increase during recolonization, and it seems unlikely rates would increase. If competition was occurring, then it had not resulted in the exclusion of any taxa even at the most stable sites. The higher species number at the more stable sites may simply be a consequence of longer periods for colonization between
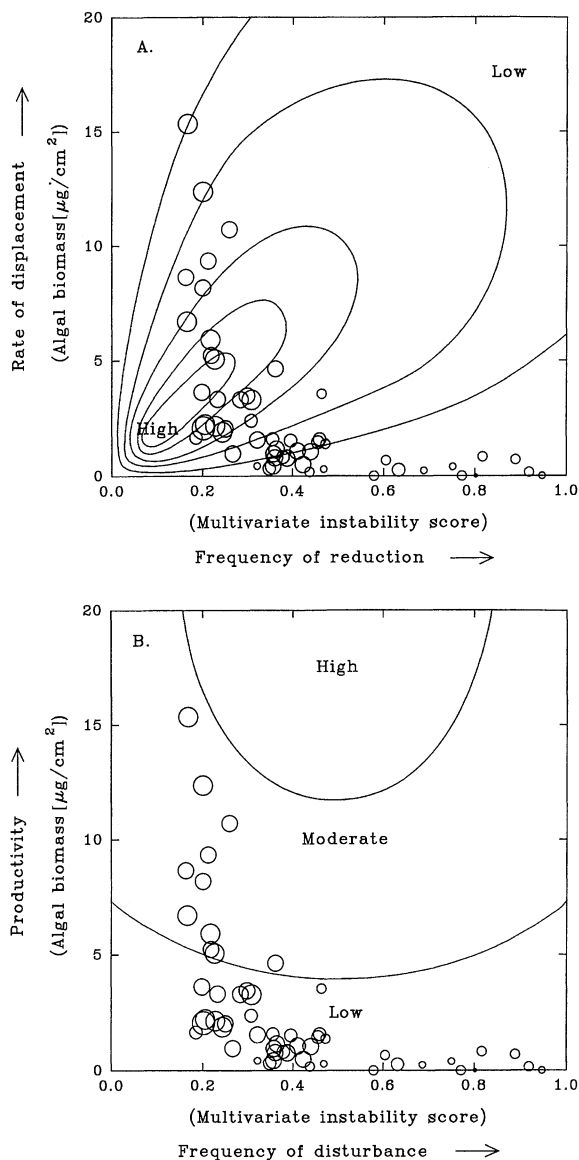
FIG. 8. Number of species collected at each site as a function of stability (multivariate instability score) and periphyton biomass within the framework of (A) Huston's dynamic equilibrium model (1979) and (B) the disturbance-productivity-diversity model (Hildrew and Townsend 1987). The terms high, moderate, and low indicate diversity levels predicted by the models at those points on the plotted framework with contour lines indicating areas of change. Circle size indicates number of species collected: ○ 0–9, ○ 10–19, ○ 20–29, ○ 30–39, ○ 40–49, ○ 50–59, ○ 60–69 species.

disturbances, during which few or no species become extinct.

Similarly, when our data are plotted within the framework of the disturbance-productivity-diversity model (Hildrew and Townsend 1987) the predictions of the model are not supported (Fig. 8). Except in streams of high productivity, Hildrew and Townsend's model predicts fixed levels of diversity, dictated by

productivity, that are unaffected by increased disturbance frequency. Clearly this is not the case in our streams with high species richness in the more stable streams irrespective of their periphyton levels. Therefore, in contrast to the Hildrew and Townsend model, where productivity is the major determinant of diversity patterns, in our streams stability seems to be the major factor.

The nature of the relationship between stability and species number remained remarkably constant over all seasons, despite the stability of some sites decreasing during winter and spring 2. This was largely because both stable and highly unstable sites maintained proportionally similar numbers of species, although sites of intermediate stability exhibited a greater relative decrease in species number in the more unstable seasons. Our finding that species richness in the most unstable streams was largely unaffected by increasingly severe disturbances, in some of which entire stream channels were displaced 20 m or more, is remarkable. It suggests that the fauna is not only highly resilient but that some species are also able to resist such conditions, as some of the streams were in flood during sampling. Several authors have provided evidence that stream faunas in New Zealand and elsewhere are able to cope with severe physical disturbances (e.g., Gray 1981, Reice 1985, Sagar 1986, Scrimgeour and Winterbourn 1989), but whether this is via resilience or resistance to flood events almost certainly depends on the particular species involved.

Total faunal density also showed a negative relationship with habitat stability, although it may have been more closely linked with the concomitant decline in periphyton biomass at these sites. This complicates the relationship between stability and species richness, for as the number of individuals increases so too does the number of species. Distinguishing whether species number increases simply as a result of a higher density of individuals or whether it is determined by stability per se was not possible. In theory, rarefaction analysis could circumvent this problem, but because of differences in the underlying species abundance distributions among sites (Death 1991) this would be misleading (Peet 1974, May 1993). This in itself suggests that species richness does not increase with stability solely as a result of increases in total abundance. It is not simply a case of rare species being collected as the number of individuals sampled increases; the entire distribution of individuals among species also changes as stability increases.

Species evenness or dominance, in contrast to species richness, did not exhibit a linear relationship with stability, but peaked at sites of intermediate stability, and was lower but similar at both very stable and unstable sites. This suggests that Huston's (1979) dynamic equilibrium hypothesis may apply. Thus, competitive displacement of species may occur at very stable sites, but it may proceed so slowly that total exclusion of a

species does not occur. Alternatively, given the very patchy nature of stream environments, it may be that a particular species can be removed from many patches by competitive exclusion, but is able to survive in others, either because conditions ameliorate competitive effects or, simply through continual movements of the fauna. Thus, although some successful competitors may dominate in highly stable environments they do not completely eliminate other species. There is certainly considerable theoretical support for the idea that high species diversity can be maintained in the face of strong competitive (e.g., Levins and Culver 1971, Hanski 1983, Kishimoto 1990) or predatory interactions (Caswell 1978) by habitat patchiness. Consequently, when viewed at the level of the patch, the dynamic equilibrium model may apply, although it certainly doesn't seem appropriate at the stream reach level in our study.

In summary, we found a strong relationship between environmental stability and the diversity of benthic invertebrate stream communities. However, the two components of diversity responded differently; species richness peaked at sites of greatest stability, whereas evenness peaked at sites of intermediate stability. How these relationships are maintained is difficult to assess as stability may not only affect diversity (and density of invertebrates) directly, but may also interact with other factors, such as habitat heterogeneity and productivity (or periphyton biomass) whose effects on competitive exclusion in streams are in turn unclear. Nevertheless, the diversity patterns observed in these streams are consistent with the idea that high diversity is maintained by an interaction between low levels of disturbance and habitat patchiness.

ACKNOWLEDGMENTS

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