The intermediate disturbance hypothesis, refugia, and biodiversity in streams

Colin R. Townsend and Mike R. Scarsbrook[1]
Zoology Department, University of Otago, P.O. Box 56, Dunedin, New Zealand

Sylvain Dolédec
ESA CNRS 5023, Ecologie des Eaux Douces et des Grands Fleuves, Université Claude Bernard, Lyon 1, 69622 Villeurbanne Cedex, France

Abstract

The intermediate disturbance hypothesis has been influential in the development of ecological theory and has important practical implications for the maintenance of biodiversity but has received few rigorous tests. We tested the hypothesis that maximum taxon richness of macroinvertebrates will occur in communities subject to intermediate levels of disturbance at 54 stream sites that differed in the frequency and intensity of flood-related episodes of bed movement. Our results support the intermediate disturbance hypothesis, with both highly mobile and relatively sedentary taxa conforming to the predicted bell-shaped curve. Taxon richness was not related to habitat area (stream width), distance from the headwater, or the diversity of microhabitats (particle size categories) but was significantly and negatively related to the proportion of the substratum made up of small particles. Of all the factors measured, however, bed disturbance was by far the best at accounting for variation in taxonomic richness. We also quantified several kinds of potential refugia for invertebrates and found a positive relationship between richness and a refugia axis that combines amount of dead space with proportion of large substratum particles.

The intermediate disturbance hypothesis, whose genesis can be traced back to Hutchinson (1953) and Horn (1975), was proposed by Connell (1978) to account for patterns of diversity in tropical rainforests and coral reefs. It has occupied a central place in the development of ecological theory because all communities are subject to disturbances that exhibit different frequencies and intensities. It also has important practical implications for the maintenance of biodiversity, of which species richness (the number of species present) is the most basic component. The hypothesis is based on the argument that ecological communities seldom reach an equilibrium state, in which the competitively superior species exclude others, because disturbances that kill or damage individuals will continually set back the process of competitive elimination by opening space for colonization by less competitive individuals. For this idea to work, there must be a trade-off between species' colonizing ability and competitive ability, and the habitat must be patchy and dynamic (Wilson 1994). At one extreme, patches that are frequently and/or intensely disturbed are expected to exhibit low species richness because few species are able to colonize during the brief periods between disturbances or tolerate the high intensities of their impact. At the other end of the scale, patches in which disturbances are infrequent and/or of low intensity are expected also to be poor in species because they

become dominated by competitively superior taxa. Richness should be highest at intermediate levels of disturbance because both rapid colonizers and more competitive species co-occur.

Despite its importance, the intermediate disturbance hypothesis has received few rigorous tests. An appropriate test requires, first, a measure of disturbance that is relevant to the organisms and, second, a sufficient number of replicate communities that are similar, in general, but which differ in their disturbance regimes. Streams offer an excellent opportunity for testing the hypothesis (Townsend 1996). Disturbances in streams often take the form of bed movements during periods of high discharge; because of differences in flow regimes and in the substrata of stream beds, some stream communities are disturbed more frequently and to a greater extent than others. We quantified the bed disturbance regime at a number of stream sites and tested whether the pattern of richness in benthic macroinvertebrate taxa conforms to the intermediate disturbance hypothesis.

Refugia, which may act to lessen the effects of disturbance, have been postulated to exist at various spatial scales in streams (Sedell et al. 1990; Townsend 1989; Townsend and Hildrew 1994), but their availability and use by invertebrates have received little study (Scarsbrook and Townsend 1994). Local refugia that may be exploited by benthic invertebrates include large stable substratum particles (Townsend 1989), dead zones (where shear stresses on the bed are always low, even at high discharge) (Lancaster and Hildrew 1993, 1994), and the hyporheic zone (interstitial habitat deep in the stream bed) (Palmer et al. 1992). On a larger scale, areas upstream may act as a refugium for colonizers that drift downstream to disturbed locations (Townsend 1989), nearby tributaries may provide colonists arriving as flying adults (Townsend 1989), and floodplains may provide refugia into which animals move during a flood and then return
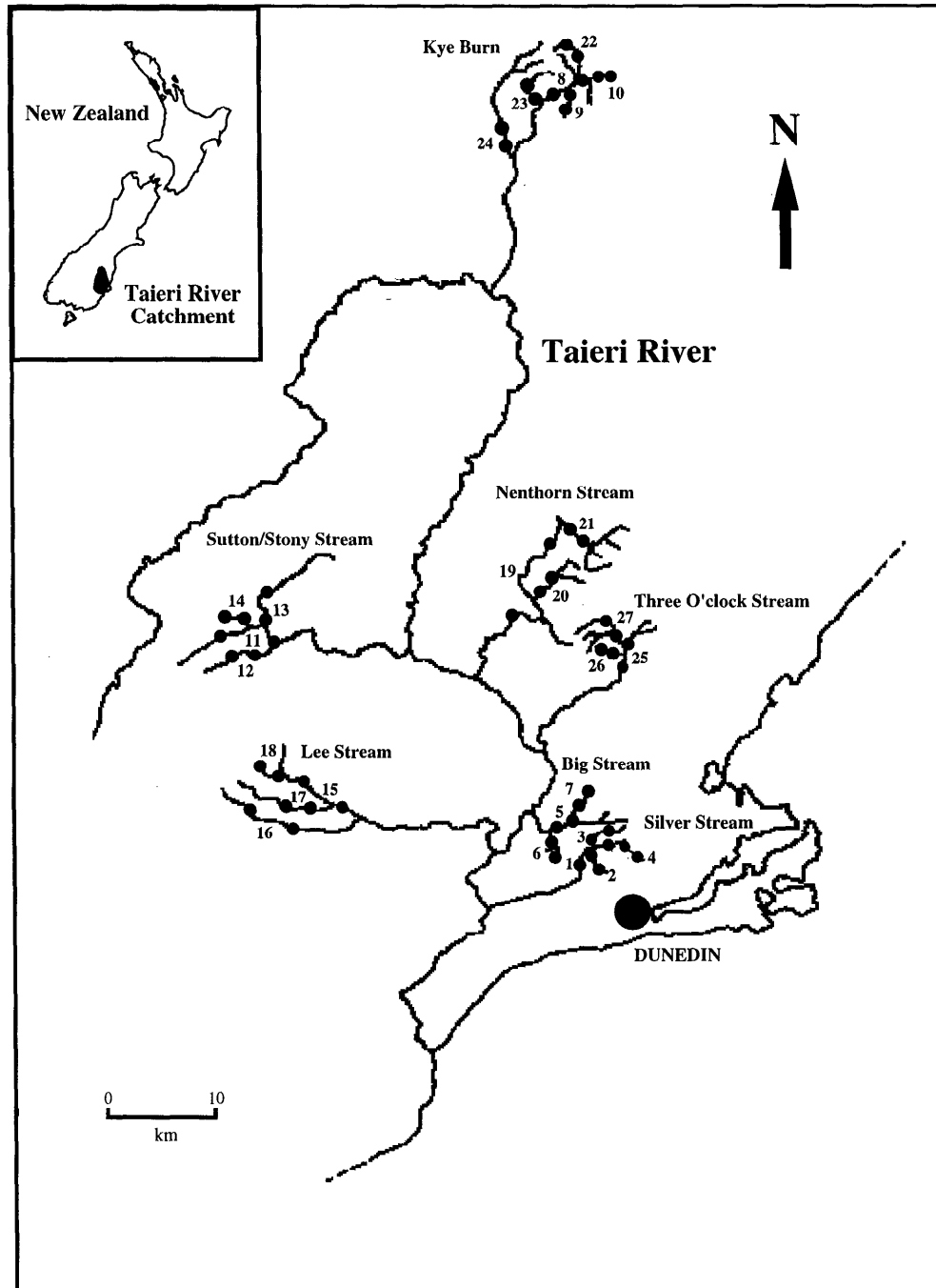
Fig. 1. Location of 54 stream sites in seven subcatchments of the Taieri River. Each number represents a single tributary, within which upper and lower sites (black circles) were sampled.

as discharge subsides (Badri et al. 1987). We attempted to quantify several categories of potential refugia and to determine relationships between their availability and taxon richness.

Methods

Study sites—Our study involved two sites on each of 27 tributaries of similar order scattered throughout a 2991-km² area in the Taieri River catchment on the South Island of New Zealand (Fig. 1). Each site was approximately 30 m in length and comprised a single pool-riffle sequence. Distance between the upper and lower sites on each tributary ranged from 200 m to 15 km. Sites varied in mean width (1.07–7.25 m—measured as wetted width at baseflow in spring for six cross sections), mean discharge (9–1,760 l s⁻¹; discharge was continuously monitored on the main stem of each catchment from July 1993 to June 1994 by the National Institute

Table 1. Invertebrate taxa identified in this study.

Higher taxonomic group	Family	Taxon
Ephemeroptera	Ephemeridae	*Ichthybotus bicolor* Tillyard
	Leptophlebiidae	*Austroclima* spp.
		Deleatidium spp.
		Neozephlebia scita (Walker)
		Zephlebia spectabilis
	Oligoneuriidae	*Coloburiscus humeralis* (Walker)
	Siphlonuridae	*Ameletopsis perscitus* (Eaton)
		Nesameletus spp.
		Oniscigaster wakefieldi McLachlan
Plecoptera	Austroperlidae	*Austroperla cyrene* (Newman)
	Eusteniidae	*Stenoperla prasina* (Newman)
	Gripopterygidae	*Megaleptoperla* spp.
		Zelandobius spp.
		Zelandoperla spp.
Trichoptera	Conoesucidae	*Beraeoptera roria* Mosely
		Olinga feredayi (McLachlan)
		Pycnocentrodes sp.
	Helicopsychidae	*Helicopsyche albescens* Tillyard
	Hydrobiosidae	*Costachorema* spp.
		Hydrobiosis spp.
		Neurochorema spp.
		Psilochorema spp.
		Tiphobiosis sp.
	Hydropsychidae	*Aoteapsyche* spp.*
	Hydroptilidae	*Oxyethira albiceps* McLachlan
		Paroxyethira sp.
	Leptoceridae	*Hudsonema amabilis* (McLachlan)
		Triplecides obsoleata (McLachlan)
	Philopotamidae	*Hydrobiosella stenocerca* Tillyard*
	Polycentropodidae	*Polyplectropus* sp.*
Coleoptera	Dytiscidae	*Liodessus plicatus* (Sharp)
		Antiporus sp.
	Elmidae	*Hydora* spp.
	Hydraenidae	Hydraenidae
	Hydrophilidae	*Berosus* sp.
	Ptilodactylidae	*Byrrhocryptus* sp.
	Scirtidae	Scirtidae
Diptera	Tipulidae	*Aphrophila neozelandica* (Edwards)*
		Eriopterini
		Paralimnophila skusei Hutton
		Limonia nigrescens (Hutton)
		Zelandotipula sp.
	Ceratopogonidae	
	Chironomidae	Tanypodinae
		Non-tanypod Chironomidae
	Empididae	
	Muscidae	*Limnophora* sp.
	Psychodidae	
	Simuliidae	*Austrosimulium australense* gp.*
	Tabanidae	
	Tanyderidae	*Mischoderus* sp.
Hemiptera	Corixidae	*Sigara* sp.
Mecoptera	Nannochoristidae	*Nannochorista philpotti* (Tillyard)
Megaloptera	Corydalidae	*Archichauliodes diversus* (Walker)
Odonata	Anisoptera	Anisoptera
	Zygoptera	Zygoptera

Table 1. Continued.

Higher taxonomic group	Family	Taxon
Mollusca	Planorbidae	*Gyraulus corinna* (Gray)
	Lymnaeidae	*Lymnaea* sp.
	Physidae	*Physa acuta* (Draparnaud)
	Hydrobiidae	*Potamopyrgus antipodarum* (Gray)
	Sphaeriidae	*Sphaerium novaezelandiae* (Deshayes)*
Crustacea	Amphipoda	Amphipoda
	Isopoda	Isopoda
	Ostracoda	Ostracoda
	Decapoda	*Paranephrops zealandicus* (White)
Platyhelminthes		Platyhelminthes
Acarina		Acarina
Oligochaeta		Oligochaeta

* Taxa that are relatively sedentary.

of Water and Atmospheric Research Ltd. while each tributary had maximum flow indicators and was regularly gauged to allow the correlation of flows in the tributaries with those of the mainstem), stream slope (0.11% to 9.92%—measured over a 30-m reach with an Abney level), distance from furthest headwaters (0.65–45.15 km—estimated from topographical maps) and median particle size (medium gravel, 16 mm diameter, to large cobble, 256 mm diameter—assessed from 100 randomly chosen particles). Diversity of particle sizes at a site was measured as the evenness of representation of 12 substratum size classes ($E = H'/\ln S$ with S as the number of size classes); all were present at every site so that evenness is a measure of the extent to which many microhabitats are available in substantial quantities.

Assessment of disturbance—To assess bed disturbance during high discharge events, particles taken from the immediate area of each study reach and corresponding to the 50th, 75th, and 90th percentiles of the substratum size distribution (excluding bedrock) were painted and arranged on the surface of the stream bed in regular arrays (five rows of three particles in each of the three size classes randomly assigned to transects placed 1 m apart). The movement of these particles was monitored on five occasions from September 93 to June 1994, a period when some unusually large discharge events occurred. On each occasion, particles that had moved were noted and replaced. Mean intensity of bed disturbance at a site was calculated as the average of the percentage of the painted tracer particles of all size classes combined that moved between consecutive sampling occasions (log-transformed). Frequency of disturbance was taken to be the proportion of periods (of the five) during which at least an arbitrarily chosen 40% of particles moved (all size classes combined).

Assessment of refugia—Our assessment of refugia is tentative because it has not generally been determined whether invertebrates actually use the refugia proposed by theorists. We have measured six variables that we consider to be potential indices of potential refugia. (1) The proportion of 100 randomly selected substratum particles from the streambed

that were large (diameter > 128 mm). (2) The amount of dead space on the stream bed, assessed as the percentage of 100 random shear stress measurements, taken at base flow in summer, which were less than $0.771 \times 10 \ \mu N \ cm^{-2}$. This value corresponds to the critical shear stress required to move a hemisphere (3.85 cm radius) with density 1.015 g cm^{-3}, the lightest in a set of 24 hemispheres differing only in density which are used to estimate near-bed shear stress (Statzner and Müller 1989; Statzner et al. 1991). It was not possible to estimate shear stress under high discharge conditions. (3) An index of the potential depth of the hyporheos (interstitial space in the bed inhabited by invertebrates), obtained by averaging the depths to which a metal sounding rod (16 mm diameter, 1.5 m length) could be hammered into the substratum at 10 randomly chosen points. Invertebrates occur in loose bed material to the depths measured (pers. obs.), whereas none can occur at a depth where bedrock exists close to or at the bed surface. (4) An index of the drift refugium, measured as the length in km of all stream channels upstream of the site. (5) An index of the aerial refugium, measured as the length in km of stream channels within an arbitrary 1 km of the site. (6) An index of floodplain availability, classified into four classes according to the angle of the upper streambank; 1—highly constrained channel with minimal floodplain (bank gradient >50°), 4—unconstrained channel with maximal floodplain (bank gradient <30°), 2 and 3 are intermediate.

Sampling of invertebrates—While the physical measurements at each site were taken during 1993–1994, invertebrates were sampled in two periods. On tributaries 1–21, four Surber samples (area 0.06 m², 300 μm mesh, two each in a pool and a riffle) were taken from random locations in the 30-m study reaches in the austral summer between 2 January and 7 February 1990 as part of a large-scale, long-term study of sites within the Taieri River system (Townsend et al. 1997). Size-class composition of the bed material and other physical conditions at these sites did not change between 1990 and 1994 (pers. obs. on frequent site visits). Thus, the indices of disturbance and refugia availability derived in 1993/1994 can provide an acceptable comparative

representation of conditions in 1990. Macroinvertebrates at sites in tributaries 22–27 were sampled, using the same techniques, between 17 January and 1 March 1994, a few weeks after some uncharacteristically large floods in the Taieri catchment, the largest of which ($1{,}467.2$ m^3 s^{-1} measured below the confluence of tributaries 5–27; see Fig. 1) had a return period of about 30 yr (National Institute of Water and Atmospheric Research, Dunedin, New Zealand, pers. comm.). In contrast, the 1990 sampling dates followed a period of low flow without major flood disturbances (mean discharge for the period 30 November 1989 to 31 March 1990 = 6.2 m^3 s^{-1}, maximum discharge = 110.3 m^3 s^{-1}). This presented an opportunity to assess the influence of the timing of the most recent major disturbance on invertebrate richness.

Invertebrate samples were preserved in the field in 70% ethanol. In the laboratory, animals were removed from the samples and identified to species wherever possible, using the keys of Winterbourn and Gregson (1989) for Insecta, Winterbourn (1973) for Mollusca, and Chapman and Lewis (1976) for Crustacea and Acarina. When specific names could not be reliably assigned, taxa were identified to the genus level. Likewise where species have not been formally described, family or subfamily names are given. A list of taxa is provided in Table 1. Taxon richness was calculated as the number of invertebrate taxa recorded at each site.

Treatment of data—The relationships among physical variables were explored by correlation analysis (Pearson's r), applying Bonferroni-adjusted probabilities to provide protection for multiple tests.

The relationships between invertebrate taxon richness at the 54 stream sites and our a priori indices of disturbance were explored using regression analysis. Simple and stepwise multiple linear regressions were used to discover the models that produced the highest coefficients of determination (R^2). Moreover, because the intermediate disturbance hypothesis predicts a bell-shaped curve we repeated the exercise using polynomial regression models.

The relationships between taxon richness and the availability of each of our postulated refugia were also investigated by regression analysis. In addition, we constructed combined refugia axes as follows. Each variable was scaled between 0 and 1 using: $x_{ij} = (z_{ij} - \min)/(\max - \min)$ where z_{ij} is the value of the jth variable for the ith site, min is the smallest value of the jth variable, and max is the highest value of the jth variable. A noncentered principal components analysis then ordered the sites according to their refugia availability. This analysis takes into account the potential synergistic effects of the refugium variables. All combinations of refugia variables were investigated for their relationships with taxon richness.

The significance of regression coefficients (slopes and intercepts) against 0 was tested using analysis of variance (null hypothesis rejected if $F_{obs} \geq F_{1-0.05}$). The use of linear regression models requires data to be distributed normally and homoscedastic. Tests of normality (Lilliefors 1967) and the examination of residuals showed that log transformations were needed to meet these assumptions for intensity of bed disturbance, distance to the furthest headwater, index of hy-

porheos, percentage of large particles, in drift refuge, aerial refuge and combined abundance of invertebrates.

Results

The relationships among physical variables are shown in Table 2. The intensity and frequency of disturbance were positively correlated. The percentage of particles that were small (8–32 mm in diameter) was positively correlated with the intensity and frequency of disturbance and hyporheos depth. Drift refugium, aerial refugium, and distance to the furthest headwater were strongly positively correlated with each other. Deadspace was negatively correlated with frequency of disturbance, drift refugium, and distance to the furthest headwater.

Taxon richness was highest at intermediate intensities and frequencies of disturbance (Fig. 2), conforming to the intermediate disturbance hypothesis. The overall relationship between richness and the intensity of disturbance (IoD) was well described by a second-order quadratic regression [richness = 177.0 (± 63.2, 95% CL) log IoD $- 61.2$ (± 21.1) log IoD$^2 - 102.3$ (± 46.8); regression line shown in Fig. 2; 95% confidence limits are significantly different from zero at $P < 0.0001$]. The coefficient of determination for the quadratic regression model ($R^2 = 0.42$, $P < 0.0001$) was much greater than that obtained from a simple linear regression model ($R^2 = 0.04$, $P = 0.16$). The possibility that site 15 was an outlier biasing the overall result (see Fig. 2) was tested by reanalyzing the data after excluding the datum for this site; the quadratic relationship remained highly significant ($R^2 = 0.38$, $P < 0.0001$). The relationship between richness and frequency of disturbance also conformed to the predicted bell-shaped curve (ANOVA of richness in six frequency categories, F-value = 10.08, $P < 0.0001$). (A Tukey HSD multiple comparison test demonstrated significantly lower taxon richness for FoD = 0.0 than 0.4, and also for FoD = 0.2 than either 0.4 and 0.6; taxon richness was significantly higher for FoD = 0.4 than any of 0.6, 0.8, and 1.0.) The relationships with richness for IoD and FoD are essentially the same because intensity and frequency of disturbance were strongly correlated in our study. Results presented in the rest of this paper are restricted to intensity of disturbance.

Relationships between taxon richness and the intensity of disturbance were similar in the upper and lower sets of sites from the 27 tributaries but the percentage of variance explained was somewhat higher in the upper set of sites [upper sites: richness = 200.1 (± 81.0, 95% CL) log IoD $- 70.5$ (± 28.4) log IoD2 $- 115.2$ (± 57.3); $R^2 = 0.52$, $P < 0.0001$; 95% CL are significantly different from zero at $P < 0.0005$, $P < 0.0001$, and $P < 0.0001$, respectively; lower sites: richness = 196.0 (± 143.1, 95% CL) log IoD $- 66.1$ (± 46.0) log IoD2 $- 120.1$ (± 109.7); $R^2 = 0.36$, $P = 0.005$; 95% CL at $P < 0.01$, $P < 0.007$, and $P < 0.04$, respectively]. In both cases the coefficients of determination for quadratic regression models (*see above*) were greater than those obtained for simple regression models (upper: $R^2 = 0.00$, $P > 0.95$; lower: $R^2 = 0.12$, $P = 0.08$). Perusal of Fig. 2 also shows that the 1994 (postflood) subset of sites (tributaries 22–27) conformed to the overall relationship just as well as the 1990 subset (tributaries 1–21).

Table 2. Matrix of Pearson correlation coefficients among physical variables. Statistically significant coefficients (after Bonferroni correction) are shown by asterisks: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Key: IoD—intensity of disturbance, FoD—frequency of disturbance, SUBSDIV—substrate diversity, DIST—distance to the furthest headwater, SMALPAR—% of small particles 8–32 mm, LARPAR—% of large particles >128 mm, DEADSP—deadspace, HYPORH—hyporheos depth, DRIFT—drift refugium, AERIAL—aerial refugium, FLOODP—floodplain availability.

	IoD	FoD	SUBSDIV	WIDTH	DIST	SMALPAR	LARPAR	DEADSP	HYPORH	DRIFT	AERIAL
FoD	0.889***										
SUBSDIV	0.084	0.138									
WIDTH	0.360	0.382	0.290								
DIST	0.196	0.305	-0.106								
SMALPAR	0.559***	0.584***	0.170	0.406	0.181						
LARPAR	-0.301	-0.368	0.320	0.006	-0.177	-0.532**					
DEADSP	-0.424	-0.479*	0.079	0.315	-0.631***	-0.119	0.121				
HYPORH	0.358	0.314	0.368	-0.322	0.098	0.457*	-0.182	-0.080			
DRIFT	0.203	0.337	-0.073	0.217	0.953***	0.142	-0.166	-0.689	0.128		
AERIAL	0.134	0.144	0.027	0.395	0.519**	0.039	0.134	-0.380	0.135	0.602***	
FLOODPL	-0.013	0.052	-0.305	0.344	-0.208	-0.094	-0.080	0.217	-0.140	-0.177	-0.140

The number of sampled organisms differed from site to site (Fig. 3a) and samples containing more individuals are expected to contain more taxa. To check the possibility that the pattern of richness might be an artifact arising through a relationship between abundance and disturbance, we investigated the ratio of taxon richness to abundance (log-transformed) and found a second-order quadratic relationship between this ratio and intensity of disturbance similar to that between richness and disturbance [Fig. 3b; richness/abundance = 48.9 ($\pm$20.4, 95% CL) log IoD − 17.0 ($\pm$6.9) log IoD^2 − 26.9 ($\pm$15.2); R^2 = 0.37, $P < 0.0001$; 95% CL all at $P < 0.0001$]. The R^2 value resulting from the quadratic regression model was again higher than that obtained from a simple regression model ($R^2 = 0.05$, $P = 0.09$).

The Shannon diversity index ($H' = -\Sigma_{i-1}^{s} p_i \ln p_i$, where p_i is the proportional abundance of the ith taxon) also showed a quadratic relationship with intensity of disturbance [Shannon diversity = 10.1 ($\pm$7.7, 95% CL) log IoD − 3.8 ($\pm$2.9) log IoD^2 − 3.9 ($\pm$5.7); R^2 = 0.27, $P < 0.001$; 95% CL at $P < 0.015$, $P < 0.005$, and $P = 0.27$, respectively] (Fig. 3c). This index has two components—richness and the evenness of the distribution of individuals among taxa. Evenness ($E = H'/\ln S$ with S as the richness of invertebrate taxa) was negatively, linearly correlated with the intensity of disturbance [evenness = 0.9 ($\pm$0.2, 95% CL) − 0.2 ($\pm$0.1) log IoD, R^2 = 0.13, $P < 0.008$; 95% CL at $P < 0.0001$ and $P < 0.008$, respectively] (Fig. 3d). A quadratic regression model was not appropriate in this case (quadratic term not significantly different from zero).

Invertebrate taxa may be divided into those that are mobile and those that are more or less sedentary (Table 1). Figure 4 shows that both mobile and sedentary taxa conform to the pattern predicted by the intermediate disturbance hypothesis [mobile taxon richness = 156.2 ($\pm$55.9, 95% CL) log IoD − 54.4 ($\pm$18.7) log IoD^2 − 90.0 ($\pm$41.5); R^2 = 0.44, $P < 0.0001$; 95% CL all at $P < 0.0001$; sedentary taxon richness = 20.8 ($\pm$15.2, 95% CL) log IoD − 7.1 ($\pm$5.1) log IoD^2 − 12.0 ($\pm$11.3); R^2 = 0.14, $P = 0.021$; 95% CL at $P < 0.01$, $P < 0.01$, and $P < 0.04$, respectively]. The R^2 values resulting from quadratic regression models were again higher than those obtained from simple regression models (mobile: R^2 = 0.06, $P = 0.07$; sedentary: R^2 = 0.01, $P = 0.55$).

Taxon richness was not significantly related to stream width (Fig. 5a), distance to the furthest headwater (Fig. 5b), or the diversity of particle sizes at a site (Fig. 5c). When individual particle size classes were considered, however, richness decreased with an increase in the proportion of the substratum composed of small particles [richness = 26.7 − 0.14X, where X = proportion of particles 8–32 mm in diameter; R^2 = 0.13, $P < 0.009$; 95% confidence limits 2.8 ($P < 0.0001$) and 0.1 ($P = 0.009$), respectively].

The relationships between taxon richness at the 54 stream sites and the availability of each of the six postulated refugia are shown in Fig. 6. Taking the variables separately, only the amount of dead space showed a significant relationship with richness [richness = 15.8 ($\pm$4.8, 95% CL) + 0.5 deadspace ($\pm$0.3) − 0.005 ($\pm$0.004) deadspace^2, R^2 = 0.19, $P < 0.005$; 95% CL at $P < 0.0001$, $P < 0.008$, and $P = 0.03$, respectively]. A refugia axis that combines the amount of
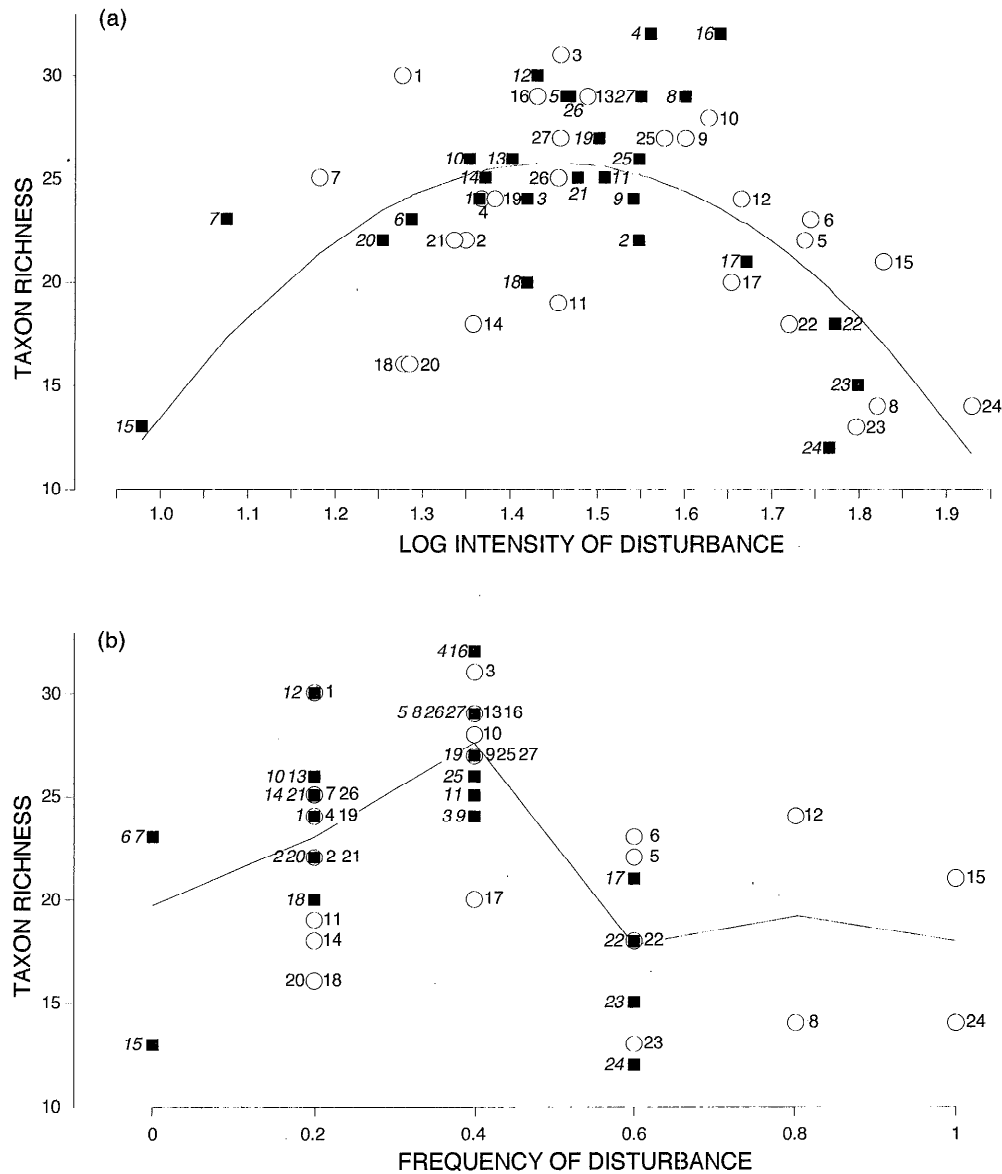
Fig. 2. Richness of invertebrate taxa in relation to (a) intensity of disturbance and (b) frequency of disturbance at 54 stream sites in the Taieri River. The invertebrate communities of tributaries 1–21 and 22–27 were sampled in the summers of 1990 and 1994, respectively. In each tributary two sites were selected; lower sites are shown as open circles; upper sites as black squares (numbers are in italic). A second-order quadratic regression line is fitted in a; lines are drawn between means for five frequency categories in b.

dead space with the proportion of large substratum particles was positively and linearly related to taxon richness [richness = 19.1 (±4.3) + 6.9 (±5.7) refuge; R^2 = 0.13; P < 0.008; 95% CL at P < 0.0001 and P = 0.016, respectively].

A stepwise multiple regression involving all of the physical variables failed to detect a combination of variables that could explain more of the variation in taxon richness than was accounted for by the intensity of disturbance alone.

Discussion

There are two approaches to testing the intermediate disturbance hypothesis, each with inherent advantages and dis-

advantages. The first, used here, concentrates on patterns in natural communities and seeks to establish whether taxon richness peaks, as predicted, at intermediate levels of disturbance. Because it deals with natural situations this approach has the advantages of realism and, perhaps more important, utility. Support for the hypothesis may provide the knowledge to engineer the maintenance or enhancement of biodiversity by, for example, manipulating discharge regimes. The disadvantages are that the mechanisms underlying the intermediate disturbance hypothesis are not directly addressed and, furthermore, that a relationship between richness and disturbance may result from the effect of another
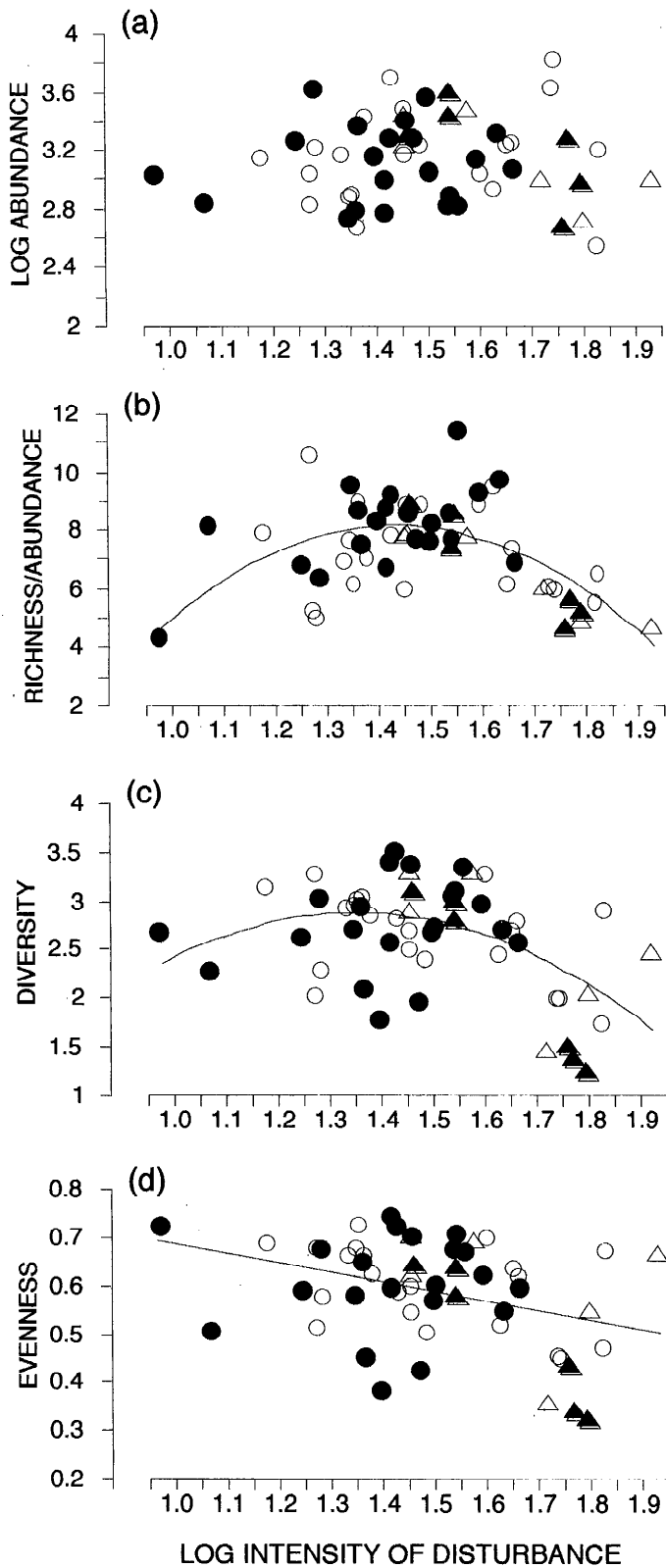
Fig. 3. Relationships of intensity of disturbance with (a) invertebrate abundance (m⁻²), (b) richness/log abundance, (c) Shannon diversity index, and (d) evenness. Sites sampled in 1990 are shown as circles and in 1994 as triangles; lower sites as open symbols and upper sites as closed symbols.
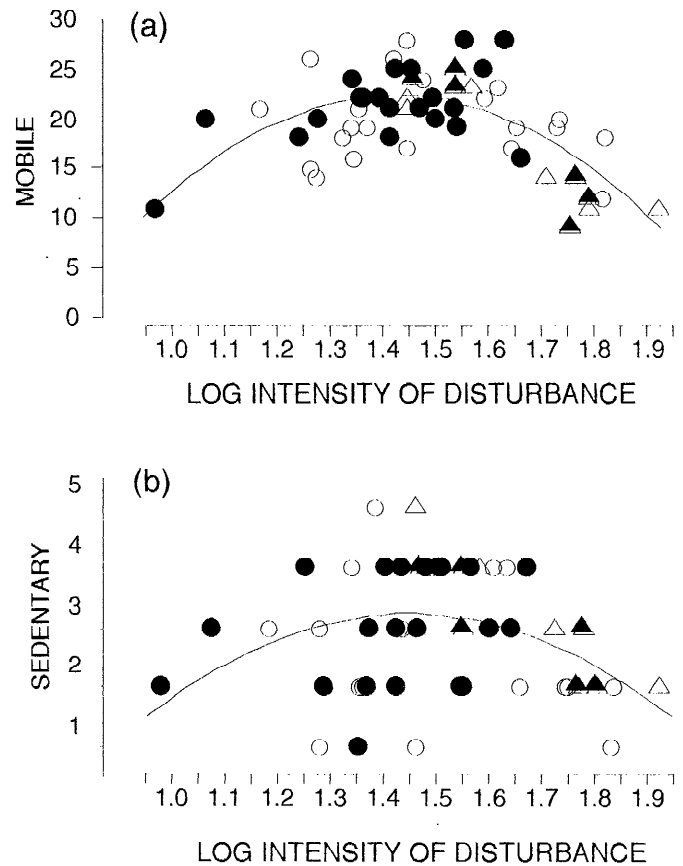

Fig. 4. Relationships of intensity of disturbance with (a) number of mobile taxa and (b) number of sedentary taxa. A second-order quadratic regression is fitted.

factor correlated with disturbance; correlation does not prove causation. We have tried to deal with the potential confounding effects of intercorrelated factors in our analytical approach; however, of all the factors measured, bed disturbance accounted for the most variation in taxonomic richness. The second approach seeks to check the veracity of the mechanisms underlying the intermediate disturbance hypothesis; that is, the trade-off between competitive and colonizing ability under contrasting disturbance regimes (e.g. Sommer 1995). Such an approach can be informative but is unsatisfying unless it has been established that the predicted pattern in richness actually exists and that the proposed mechanism is actually at work in the natural environment. The ideal study, which has not yet been performed, will combine both approaches. One reason for this lack of a combined approach is the enormous amount of work required either to determine the pattern or to establish the mechanism. To provide evidence of competitive exclusion among just a pair of stream invertebrate species requires a substantial effort (e.g. Hemphill and Cooper 1983). The extension of pairwise competition studies to large species assemblages, and the incorporation of investigations of colonizing as well as competitive abilities of taxa, provides a major challenge for the future.

In our study, it is likely that low taxon richness at high frequencies and intensities of disturbance reflects the poor
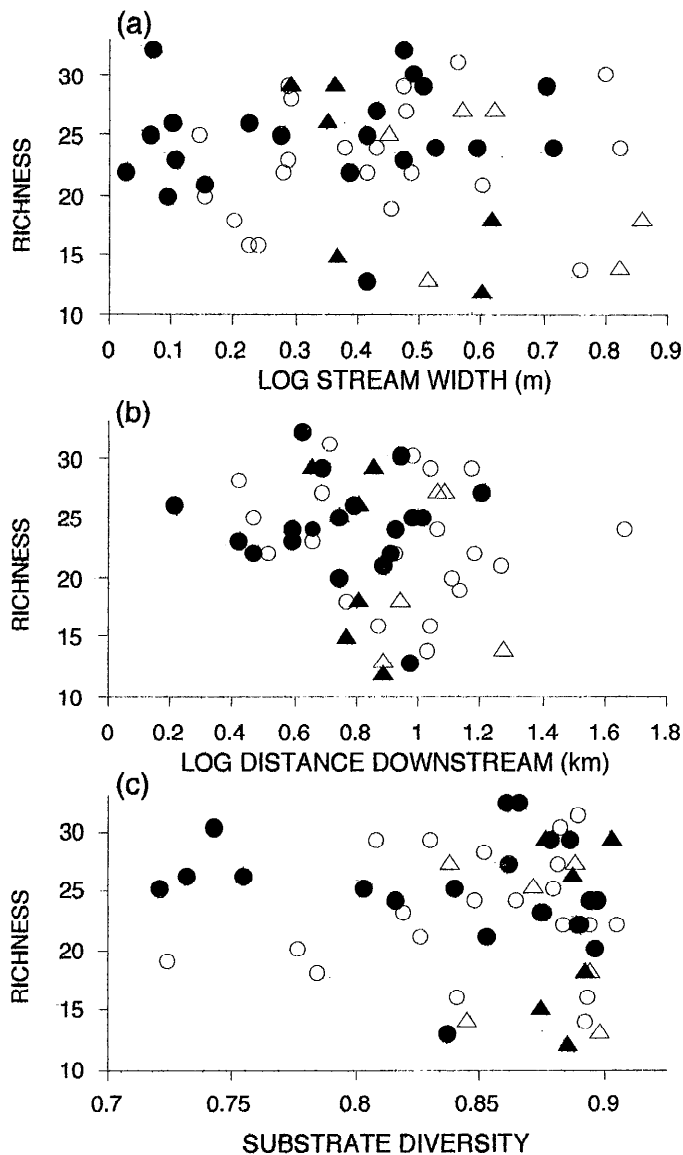
Fig. 5. Relationships between richness of invertebrate taxa and (a) stream width, (b) distance downstream (distance from furthest headwater to sampling site), and (c) substratum diversity (measured as the evenness of representation of 12 substratum size classes).

ability of some stream invertebrates to colonize or persist in such situations. Whether low richness at low frequencies and intensities of disturbance is due to competitive exclusion, as proposed in the intermediate disturbance hypothesis, is uncertain. Competitive exclusion in streams is expected to be more likely between species that are relatively sedentary and compete for space (Hemphill and Cooper 1983; McAuliffe 1984; Frid and Townsend 1989). However, in the River Taieri both sedentary and highly mobile taxa conform to the intermediate disturbance pattern, indicating that competition between mobile taxa (e.g. Kohler 1992) may be more influential than previously thought. The finding that evenness was higher in less disturbed sites is consistent with the hypothesis that competitive forces structure these communities by eliminating rare species, but the pattern is also consistent with

some rare taxa gaining more members. Further work will be needed to resolve these conflicting hypotheses.

The upper and lower sites in each tributary often differed substantially in their disturbance regimes because of increased discharge between them and/or differences in the size class composition of their substrata. The predicted quadratic relationships were similar in the two sets of sites, but with the percentage of variance explained somewhat higher in the upper set of sites. It is possible that the tendency of invertebrates to drift downstream (Brittain and Eikeland 1988) confounds the relationship between taxon richness and disturbance regime at downstream sites.

The 1990 samples were taken after a period of low flow without major floods, whereas the 1994 samples were taken a few weeks after some large floods. We might have expected the 1994 samples to contain fewer species, being dominated by a few, rapidly colonizing species. It is of interest, therefore, that the relationship for the 1994 subset conforms to the overall relationship just as well as the 1990 subset, indicating that the timing of the most recent major disturbance had little impact on the pattern of taxon richness.

Other proposed patterns of species richness in streams were investigated but not supported. Thus, there were no significant relationships between species richness and habitat area (assessed as stream width) (Townsend and Hildrew 1994) or distance downstream (Vannote et al. 1980), nor was there a relationship between species richness and the diversity of substrata (microhabitats) available at a site (Townsend 1991). Richness, however, was observed to decrease with an increase in the proportion of the substratum made up of small particles (8–32 mm diameter). Because sites with smaller particles will experience a higher level of disturbance for a given discharge event, the decrease in richness observed from intermediate to high disturbance levels might conceivably be due to a substratum size effect and not to disturbance per se. However, while intensity of disturbance explains more than 42% of the variance in richness, the variance explained by small substratum was only 12.5%. In addition, the relationship with substratum particle size cannot explain a decrease in richness from intermediate to low disturbance levels.

Whether frequency or intensity of disturbance is the more influential in determining species richness in our streams is a moot point. A greater frequency of disturbance may reduce richness by excluding taxa that cannot quickly recolonize in the intervals between disturbances and a lesser frequency may permit competitive exclusion of species that are capable colonists but poor competitors. An intermediate frequency allows both sets of species to co-occur. On the other hand, a greater intensity of disturbance may exclude species because local refugia become inoperative (even large particles, dead space and the hyporheos are disturbed) whereas large-scale refugia (drift, aerial, floodplain) predominate and may provide sources of long-distance colonists. A lesser intensity of disturbance may lead to low richness because most of the bed is relatively stable over the long term and competitive exclusion occurs. Finally, an intermediate intensity of disturbance permits coexistence of a wider variety of species because of the presence of a range of local and large-scale refugia. In operational terms, it may be impossible to dis-
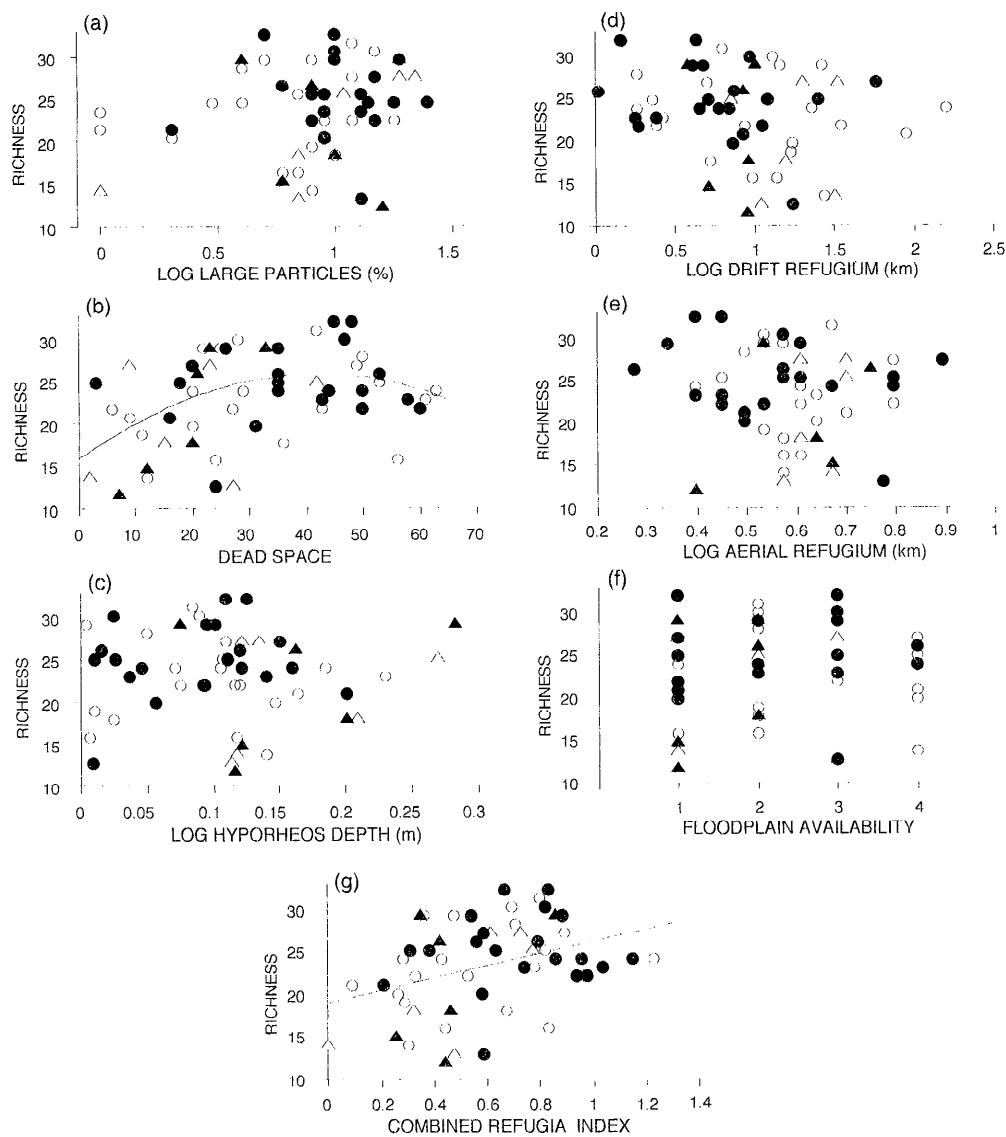
Fig. 6. Relationships between richness of invertebrate taxa and various possible refugium categories: (a) proportion of streambed substratum particles that were large (diameter > 128 mm), (b) potential amount of dead space (percentage of the streambed where shear stress was negligible, measured at base flow in summer), (c) potential depth of hyporheos, (d) potential extent of drift refugium, (e) potential extent of aerial refugium, (f) potential availability of floodplain refugium (1—highly constrained channel with minimal floodplain, 4—unconstrained channel with maximal floodplain), and (g) a refugia axis that combines dead space and proportion of large substratum particles. The relationships were statistically significant in b (second-order quadratic regression fitted) and g (simple linear regression fitted).

entangle frequency and intensity when intensity is measured as the percentage of space disturbed and frequency as the number of occasions when more than an arbitrarily defined percentage of area is disturbed. More frequently disturbed stream sites are also more intensely disturbed.

The central importance of disturbances in the development of ecological theory (Begon et al. 1996) places a high premium on finding appropriate ways to measure disturbance. Our measures of disturbance are undoubtedly imperfect, particularly because the tracer particles were placed on the streambed when, in reality, much of the substratum consists

of embedded particles that are less likely to move at a given discharge than surface particles. Moreover, other potentially influential aspects of disturbance for benthic invertebrates, such as abrasion and high shear stress, are ignored. Nevertheless, our a priori choices of disturbance measures were related to taxon richness as predicted by the intermediate disturbance hypothesis. The method provides a comparative index that may be of general value in studies of disturbance in streams. Tests of disturbance theory require that disturbance be defined relative to the organisms of interest. Thus, for example, the measurement in streams of the frequency

with which certain sizes of discharge event occur (Resh et al. 1988) is not likely to be appropriate for organisms that inhabit the streambed because the impact of these events also will vary with substratum composition. Disturbance needs to be assessed in terms of bed movement itself.

Floods with their associated bed movements can have a severe impact on the community of organisms in streams and rivers (Siegfried and Knight 1977; Scrimgeour and Winterbourn 1989; Giller et al. 1991; Flecker and Feifarek 1994). Despite the sometimes catastrophic effects of floods, community recovery can be very rapid, resulting in a community structure similar to that preceding the disturbance (Fisher et al. 1982; Molles 1985; Townsend et al. 1987; Scrimgeour et al. 1988). The presence of a range of refugia, each likely to be used by different sets of species, must be largely responsible for this resilience. Our analysis of the potential importance of refugia in maintaining biodiversity is very preliminary but indicates that the availability of large substratum particles and dead space may be influential. Dolédec and Statzner (1994) have also recorded a positive relationship between species richness in habitats of the Rhône river and a spatial variability index defined partly by grain size.

The preservation (or restoration) of natural and diverse communities in our streams and rivers is likely to depend on identifying and protecting (and enhancing) refugia. Moreover, an intermediate level of disturbance may often itself be responsible for generating some of the richness of communities, as indicated here. Patterns of abstraction or impoundment of river water for human benefit will need to consider these patterns if we wish to achieve the objective of maintaining high biodiversity.

References

BADRI, A., J. GIUDICELLI, AND G. PRÉVÔT. 1987. Effects of flood on the benthic macroinvertebrate community in a mediterranean river, the Rdat (Morocco). Acta Ecol. Ecol. Gen. **8:** 481–500.

BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1996. Ecology: Individuals, populations and communities, 3rd ed. Blackwell Science.

BRITTAIN, J. E., AND T. I. EIKELAND. 1988. Invertebrate drift—a review. Hydrobiologia **166:** 77–93.

CHAPMAN, A., AND M. LEWIS. 1976. An introduction to the freshwater Crustacea of New Zealand. Collins.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199:** 1302–1310.

DOLÉDEC, S., AND B. STATZNER. 1994. Theoretical habitat templets, species traits, and species richness: 548 plant and animal species in the Upper Rhône River and its floodplain. Freshwater Biol. **31:** 523–538.

FISHER, S. G., L. J. GRAY, N. B. GRIMM, AND D. E. BUSCH. 1982. Temporal succession in a desert stream following flooding. Ecol. Monogr. **52:** 93–110.

FLECKER, A. S., AND B. FEIFAREK. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. Freshwater Biol. **31:** 131–142.

FRID, C. L. J., AND C. R. TOWNSEND. 1989. An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. Oikos **56:** 137–141.

GILLER, P. S., N. SANGPRADUB, AND H. TWOMEY. 1991. Catastrophic flooding and macroinvertebrate community structure. Verh. Int. Ver. Limnol. **24:** 1724–1729.

HEMPHILL, N., AND S. D. COOPER. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. Oecologia **58:** 378–382.

HORN, H. S. 1975. Marckovian processes of forest succession, p. 196–213. *In* M. L. Cody and J. M. Diamond [eds.], Ecology and evolution of communities. Belknap.

HUTCHINSON, G. E. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. Phila. **105:** 1–12.

KOHLER, S. L. 1992. Competition and the structure of a benthic stream community. Ecol. Monogr. **62:** 165–188.

LANCASTER, J., AND A. G. HILDREW. 1993. Characterizing instream flow refugia. Can. J. Fish. Aquat. Sci. **50:** 1663–1675.

———, AND ———. 1994. Flow refugia and the microdistribution of lotic macroinvertebrates. J. N. Am. Benthol. Soc. **12:** 385–393.

LILLIEFORS, H. W. 1967. On the Kolmogorov–Smirnov test for normality with mean and variance unknown. J. Am. Stat. Assoc. **64:** 387–389.

MCAULIFFE, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community Ecology **65:** 894–908.

MOLLES, M. C., JR. 1985. Recovery of a stream invertebrate community from a flash flood in Tesuque Creek, New Mexico. Southwest. Nat. **30:** 279–287.

PALMER, M. A., A. E. BELY, AND K. E. BERG. 1992. Response of invertebrates to lotic disturbance: A test of the hyporheic refuge hypothesis. Oecologia **89:** 182–194.

RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. C. WISSMAR. 1988. The role of disturbance in stream ecology. J. N. Am. Benthol. Soc. **7:** 433–455.

SCARSBROOK, M. R., AND C. R. TOWNSEND. 1994. Stream community structure in relation to spatial and temporal variation: A habitat templet study of two contrasting New Zealand streams. Freshwater Biol. **29:** 395–410.

SCRIMGEOUR, G. J., R. J. DAVIDSON, AND J. M. DAVIDSON. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. N. Z. J. Mar. Freshwater Res. **22:** 337–344.

———, AND M. J. WINTERBOURN. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. Hydrobiologia **171:** 33–44.

SEDELL, J. R., G. H. REEVES, F. R. HAUER, J. A. STANFORD, AND C. P. HAWKINS. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. Environ. Manage. **14:** 711–724.

SIEGFRIED, C. A., AND A. W. KNIGHT. 1977. The effects of washout in a Sierra foothill stream. Am. Midl. Nat. **98:** 200–207.

SOMMER, U. 1995. An experimental test of the intermediate disturbance hypothesis using cultures of marine phytoplankton. Limnol. Oceanogr. **40:** 1271–1277.

STATZNER, B., F. KOHMANN, AND A. G. HILDREW. 1991. Calibration of FST-hemispheres against bottom shear stress in a laboratory flume. Freshwater Biol. **26:** 227–231.

———, AND R. MÜLLER. 1989. Standard hemispheres as indicators of flow characteristics in lotic benthos research. Freshwater Biol. **21:** 445–459.

TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. **8:** 36–50.

———. 1991. Community organization in marine and freshwater environments, p. 125–144. *In* R. S. K. Barnes and K. H. Mann [eds.], Fundamentals of aquatic ecology. Blackwell Sci. Publ.

———. 1996. Concepts in river ecology: Pattern and process in

the catchment hierarchy. Arch. Hydrobiol. **113**(suppl. 10): 3–21.

———, T. A. CROWL, C. J. ARBUCKLE, AND M. R. SCARSBROOK. 1997. The relationship between land use and physicochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: A hierarchically scaled approach. Freshwater Biol. **37:** 177–192.

———, AND A. G. HILDREW. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biol. **31:** 265–275.

———, ———, AND K. SCHOFIELD. 1987. Persistence of stream invertebrate communities in relation to environmental variability. J. Anim. Ecol. **56:** 597–613.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37:** 130–137.

WILSON, J. B. 1994. The 'intermediate disturbance hypothesis' of species coexistence is based on patch dynamics. N.Z. J. Ecol. **18:** 176–181.

WINTERBOURN, M. J. 1973. A guide to the freshwater mollusca of New Zealand. Tuatara **20:** 141–159.

———, AND K. L. D. GREGSON. 1989. Guide to the aquatic insects of New Zealand. Bull. N.Z. Entomol. Soc. **9.** 95 p.