Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams

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SUMMARY

1. The physical characteristics of two contrasting streams, and habitat types within these streams, are described in terms of a two-dimensional physical habitat templet in which disturbance frequency and the availability of spatial refugia are the temporal and spatial axes.

2. It is predicted that habitats experiencing a high disturbance frequency and low refuge availability will be characterized by a low invertebrate species diversity, a low biomass of epilithic algae and particulate organic matter and a community made up of mobile, weedy species. Habitats having a low disturbance frequency and high refuge availability will be characterized by a diverse community containing sedentary and specialist species, with high algal and particulate organic matter levels.

3. A lower median substrate particle size and higher shear stress regime in Timber Creek were indicative of a higher disturbance frequency than in the Kyeburn. Substrate diversity was lower in Timber Creek than in the Kyeburn and indicated that the availability of refugia was lower in Timber Creek. In both streams, pools were found to have a higher disturbance frequency and lower availability of refugia than riffles.

4. Invertebrate species diversity, the biomass of epilithic algae and particulate organic matter and the representation of sedentary species, filter feeders and shredders were higher in the more temporally stable and spatially heterogeneous Kyeburn. The community of Timber Creek, frequently disturbed and having low refuge availability, had a high proportion of mobile and weedy species, with the highly mobile, generalist-feeding *Deleatidium* spp. (Ephemeroptera; Leptophlebiidae) being the most dominant organisms.

5. The predictions made about stream community structure and species characteristics in relation to disturbance frequency and the availability of spatial refugia are generally supported. Now a larger scale investigation is required to test the generality of the predictions. We conclude that the habitat templet approach offers a sound framework within which to pose questions in stream ecology.

Introduction

Heterogeneity in both spatial and temporal dimensions is characteristic of running-water systems. The resulting spatiotemporal patchwork, in streams as in other natural systems, exerts powerful influences over the distribution of organisms, their interactions, and their adaptations (Wiens, 1976). Therefore, as we strive to understand and explain the patterns of distribution and abundance of organisms, an approach based on the quantification of environmental patchiness in time and space can be expected to be of value. Southwood (1977, 1988) advocated such an approach stemming from his view that 'the

habitat provides the templet on which evolution forges characteristic life-history strategies' (Southwood, 1988). On an evolutionary timescale, the levels of spatial and temporal variation inherent in a system act as a selective force for species traits conferring the ability to survive in a given environment. In ecological time, the habitat templet acts also to filter out unsuccessful strategists from the potential pool of colonists, thereby controlling community composition. The challenge to the ecologist is to define the axes of the templet at spatial and temporal scales that are readily quantifiable and organism related, so that placement of habitats on the templet is objective and subsequent predictions about biological traits are testable.

The habitat templet provides a promising framework for stream research. The challenge of definition and quantification of the axes is made simpler once stream systems are viewed as being hierarchically organized within a spatiotemporal framework (Frissell *et al.*, 1986). The classification system proposed by Frissell *et al.* (1986) views streams as being spatially nested systems, with lower levels of the hierarchy developing within the constraints set by higher levels. Each level of the hierarchy is controlled and modified by events and processes acting at a certain spatiotemporal scale (Table 1 in Frissell *et al.*, 1986). For example, a stream reach is influenced by physical events such as landslides and channel shifts and may persist for tens to hundreds of years. Pools and riffles, on the other hand, are influenced by flood scour and deposition and thalweg shifts and may persist for only a few years. The physical structure of a stream system and the developmental processes affecting the various scales of the hierarchy (i.e. the levels of spatial and temporal variation inherent in the system) provide a general physical habitat templet upon which species traits and assemblages are selected. However, to make the approach operationally manageable, the axes for the templet need to be made more specific.

Southwood (1988), in a review of habitat templet ideas and research, noted that the definition of the habitat has most commonly been made along the axes of disturbance frequency and level of adversity or harshness of the environment. More recently, and in relation to stream systems, Townsend (1989) defined the axes of spatial and temporal variation as disturbance frequency and habitat heterogeneity.

Poff & Ward (1990), using the habitat templet approach to make predictions about stream community recovery following natural and anthropogenic disturbances, quantified the axes of their templet in relation to the long-term regime of physicochemical variability (disturbance frequency/predictability) and substratum complexity and stability (spatial scale of disturbance). Townsend & Hildrew (in press) define their habitat templet in terms of disturbance frequency and spatial heterogeneity, or more specifically the provision of spatial refugia which lessen the impacts of disturbance.

In this study of community structure and invertebrate species characteristics of two physically contrasting Central Otago (New Zealand) streams, we define the axes of the habitat templet as disturbance frequency and spatial heterogeneity, with the level of spatial heterogeneity being equated with the availability of refugia from disturbance. Disturbance is seen as a major structuring force in stream communities (Resh *et al.*, 1988; Reice, Wissmar & Naiman, 1990), and is defined in general terms as 'any relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species' (Townsend, 1989). Of the many and varied processes causing disturbance to stream communities, the rapid increase in discharge of a flood event with its accompanying substrate movement is perhaps the most striking. Within the stream system hierarchy, flood events most often act as developmental processes at the scale of pool and riffle channel units (Frissell *et al.*, 1986). The disturbance regimes of our two study streams are considered in terms of substrate movement caused by high flow events at the scale of pool and riffle habitat units. We use information on discharges and shear stresses required to move a given proportion of the substrate of each stream to define, in a qualitative manner, the position of the streams on the disturbance axis of the habitat templet. Poff (1992) supported the use of physically based measures of disturbance such as the degree of substrate movement (e.g. Poff & Ward, 1989; Rader & Ward, 1989), as opposed to statistical flow criteria (e.g. Resh *et al.*, 1988), because a physically based measure of disturbance relates more directly to the organism.

Within a spatially heterogeneous environment the impacts of disturbance may be reduced by the

presence of refugia (Townsend, 1989). Such patches, in which the effects of disturbance are lessened or absent, exist at a variety of spatial scales within stream systems (Sedell *et al.*, 1990) and include tributaries (macroscale), the hyporheic zone (mesoscale) and stable substratum patches (microscale). Their presence confers resilience on stream communities, speeding up the recovery process following disturbance by providing sources of recolonists. If the view is taken that temporal heterogeneity generates the demand for refugia and spatial heterogeneity provides the refugia (Townsend & Hildrew, in press), then it can be seen that a templet if formed from the interaction between disturbance frequency and refugia availability.

Along with the definition of disturbance regime and refuge availability, it is the aim of this study to test some general, a priori predictions about community structure and the characteristics of species within communities in relation to the position of the study streams on the habitat templet.

A feature of communities that has received much attention in relation to disturbance regime and spatial heterogeneity is species richness or diversity. In general, species diversity is predicted to increase with habitat heterogeneity (Townsend, 1989) and to decrease as disturbance frequency increases, although diversity may peak at intermediate levels of disturbance (Connell, 1978).

As environmental patchiness increases, especially with respect to disturbance frequency and intensity, the colonizing ability of species is likely to become more important than competitive ability (Townsend, 1989). As disturbance frequency increases further, the ability to move between suitable patches may control community structure. Townsend & Hildrew (in press) predict that high mobility will be characteristic of species in frequently disturbed habitats, and stream communities experiencing a high disturbance frequency are predicted to be dominated by 'weedy' species (Townsend, 1989). Moreover, because sedentary species require stable substrata (e.g. McAuliffe, 1984), they should be 'filtered' out of streams having high disturbance frequencies or a lack of stable substratum patches.

Resh *et al.* (1988) predicted that streams experiencing frequent disturbance will have less epilithic algae and benthic particulate organic matter than more stable streams. Differences in food source availability caused by the disturbance regime will have consequences for community functional feeding group structure. Thus, less stable streams are predicted to have fewer specialist grazers, filter feeders and shredders, and more generalist feeders. Specialist grazers are generally considered lacking in New Zealand streams (Winterbourn, Rounick & Cowie, 1981) and the term browser (Cowie, 1980) has been applied to generalists that use the layer of detritus, bacterial, algal and fungal cells covering surfaces as their primary food source.

Many stony streams throughout New Zealand are inhabited by a common core of invertebrate taxa, with the leptophlebiid mayfly genus *Deleatidium* often being dominant (Winterbourn *et al.*, 1981; Rounick & Winterbourn, 1982). Several authors have commented on the 'weediness' of this highly mobile generalist (Winterbourn *et al.*, 1981; Scrimgeour & Winterbourn, 1989; Mackay 1992), which is a suitable species with which to test the prediction that more highly disturbed systems will be more strongly dominated by weedy species.

Perhaps the most frequently stated prediction concerning species traits in relation to environmental variability is that concerning age at first reproduction. In highly disturbed stream habitats, there should be a shift to small size and rapid growth to a reproductive age (Townsend & Hildrew, in press). Because of the importance of *Deleatidium* spp. in New Zealand stream ecosystems, size spectra of this taxon were measured to determine whether differences in the position of streams on the templet were accompanied by the predicted shift in size of *Deleatidium*.

It is the aim of this paper, first, to determine the location of the two study streams (and pool and riffle habitats within them) on the habitat templet and, second, to test the predictions brought together in Table 1.

Study sites

In a comparative study such as this it is important to choose streams that are similar in all aspects except for the feature of interest (Resh *et al.*, 1988). With this in mind we chose to study two adjacent third-order streams above their confluence; they are similar in catchment vegetation and land use (upland indigenous tussock grassland grazed by sheep) but contrast in geomorphology. The differences in geomorphology

	Highly disturbed and/or spatially homogeneous	Temporally stable and/or spatially heterogeneous
Invertebrate diversity	Low	High
Representation of:		
Mobile species	High	Low
Sedentary species	Low	High
Weedy species	High	Low
Availability of:		
Epilithic algae	Low	High
Particulate organic matter	Low	High
Representation of:		
Browsers	Low	High
Filterers	Low	High
Shredders	Low	High
Generalists	High	Low
Deleatidium size	Small	Large

Table 1 Specific predictions made in relation to contrasting positions on the habitat templet

can be expected to influence the physical structure of the streams at all levels of the hierarchy (Frissell *et al.*, 1986) and to directly influence the disturbance regime and its impact on the stream communities (Resh *et al.*, 1988).

Timber Creek (catchment area 13.86 km^2) drains an area dominated by semischist. The nature of this rock type, the presence of a fault line shear zone, the steep topography and wind action, combine to provide a large-scale input of fine gravel and sand (Bishop, 1976), resulting in the braiding of the stream in unconstrained reaches. The upper Kyeburn (catchment area 9.43 km^2) has a more stable geology, dominated by quartzofeldspathic and pelitic schist. The stream is constrained to a single well-defined channel until below its confluence with Timber Creek (NZMS 260 I41 993795).

Three pools and three riffles (all within 2 km of the confluence) were chosen as study sites in each stream. Pools were defined as reach subsystems having a low water surface slope and a maximum water depth greater than 25 cm. Riffles were defined as having a water surface slope intermediate to that of pools and cascades and had a maximum depth of less than 25 cm. In Timber Creek the input of large amounts of sediment resulted not only in the braiding of the stream but also in the virtual loss of pool—riffle structure. Thus, there were few well-defined pools in Timber Creek; the pools chosen for study were lateral scour pools (Bisson *et al.*, 1982). The Kyeburn had a greater range of habitat types, and pools (lateral

scour type) and riffles were chosen to correspond to the habitats available in Timber Creek.

Physical and biological sampling were carried out on four occasions corresponding to autumn, winter, spring and summer.

Materials and Methods

Physical characteristics

Discharge was monitored continuously in both streams over the course of the study (May 1990—April 1991). Water height was recorded on Foxboro pen/chart recorders which were set up on each stream immediately above the confluence. Ratings curves for each stream (DSIR Water Resources Survey, unpublished data) allowed discharge to be estimated from the Foxboro recordings. Means and coefficients of variation of flow (ls^{-1}) were calculated for each stream using 6-hourly discharge values over the 12-month period.

The substrate size distribution of the streambed surface was estimated from fifty particles chosen at random from each pool and riffle site using the method of Wolman (1954). The collector paced across the sampling area with eyes closed and picked up the first particle encountered with the index finger when it was extended to the streambed. Particle size was estimated by comparing it with square holes corresponding to 1-1 sieve sizes between 8 and 256 mm (-3 to -8 phi, in 0.5 phi increments) cut in an alumi-

nium plate (Mosely, 1982). Median substrate particle size and substrate diversity were calculated for pool and riffle habitats in both streams. Substrate diversity, used here as a measure of substrate heterogeneity (Minshall, 1984), was estimated using Simpson's diversity index (SDI):

$$SDI = 1/\Sigma(n_i(n_i-1))/(N(N-1))$$

where n_i = the number of individuals in the ith species and N = the total number of individuals (Magurran, 1988).

A set of Fliesswasserstammtisch hemispheres (Statzner and Müller, 1989) was used to estimate shear stress at the streambed. On each of the four sampling occasions shear stress was estimated at twenty-four points chosen randomly in each stream, corresponding to the points in the pools and riffles where benthic samples were taken. Analysis of the shear stress data was by three-way ANOVA. A $\log(x + 1)$ transformation of the data was required to satisfy the ANOVA assumptions of normality and homoscedasticity. Shear stress diversity (estimated using SDI) was measured for each sampling occasion and analysed using a two-factor ANOVA.

Bed movement was estimated using the empirical formula of Carling (1983), as presented by Komar (1987), for threshold flow stress. The relationship between particle diameter and the critical shear stress required for incipient motion of that particle was constructed from data gathered in an upland, gravel-bedded stream (Carling, 1983). Although Wilcock (1992) has some criticisms of this approach it is an important advance in the sediment transport field since the relationship is for selective entrainment from deposits of mixed sizes (Komar, 1988).

Biological characteristics

Four Surber samples ($0.06\,m^2$, 300-μm mesh) were collected at random from each pool and riffle site on each of the four sampling occasions. The samples were preserved in 70% ethanol and returned to the laboratory where invertebrates were removed from the samples in a well-lit, white sorting tray. The samples were then checked under ×7 magnification for any invertebrates passed over in the sorting process. Aquatic invertebrates were identified to genus, or species where possible.

Invertebrate drift was sampled in both streams on the same four sampling occasions. Two nets were set at the downstream end of each pool and riffle site and left for 20–24 h. Flow velocity through the nets was estimated using a timed release of fluorescein dye at the mouth of the net. Average depth at each site was measured to allow calculation of drift variables. The samples were preserved in 70% ethanol and counted and identified as for Surber samples.

On each sampling occasion abundance of epilithic algae was estimated from the amount of phytopigments extracted from a sample of five gravel particles collected from each study site. The samples were immediately placed on ice and transported to the laboratory in black plastic bags. The samples remained frozen for not more than 2 weeks before analysis. After removal from the freezer the five stones from each site were placed in buffered 90% ethanol (pH > 7), scrubbed with a toothbrush and left for 24 h in black plastic bags, in a 4°C refrigerator. After this extraction period, the total volume of the ethanol homogenate was measured before three 10-ml aliquots were taken from a filtered 40-ml subsample. The absorption in the three aliquots was measured at 665 nm and 750 nm using a spectrophotometer (Shimadzu UV-120-01). After acidification of the aliquots with 10 μl 2 M HCl absorption readings were repeated (Nusch, 1980). Chlorophyll *a* and phaeophytin were calculated using the equations of Lorenzen (1967). Total stone surface area for each sample was calculated by wrapping the five stones in aluminium foil of known weight per unit area and weighing the foil. Finally the estimates of chlorophyll *a* and phaeophytin were converted to phytopigments m^{-2}, for stone surface area.

Benthic particulate organic matter collected in the Surber samples was sorted into coarse particulate organic matter (CPOM, >1 mm) and fine particulate organic matter (FPOM, <1 mm) by wet sieving. To determine organic content, all fractions were dried at 55°C for 24 h, weighed, ashed at 550°C for 1 h, rewet, redried at 55°C for 24 h and reweighed.

A three-way ANOVA incorporating stream, season and habitat factors was used to analyse differences in several invertebrate community benthic and drift characteristics, and in the amounts of epilithic algae and particulate organic matter present in the systems. In order to satisfy the assumptions of population normality, and homoscedasticity and additivity of variances, proportional and count data were transformed. Proportional data were transformed using

the arcsin $\sqrt{x}$ transformation (Zar, 1984), and count data were transformed by $\log(x + 1)$ transformation. Results are expressed as non-transformed means.

In order to estimate the size frequency of the *Deleatidium* population in each stream through time, ten Surber samples were taken monthly from May 1990 to April 1991 in each stream from a 100-m reach that included the six study sites used for other aspects of the study. The samples were taken from all major habitat types and were pooled and preserved in 70% ethanol. Fifty *Deleatidium* larvae were picked at random each month from a 10% subsample taken with a vacuum pump, except in July 1990 when only ten individuals were found in the ten pooled samples. The head capsule width (mm) of each individual was measured under ×7 magnification using an Olympus microscope fitted with an eyepiece micrometer.

Results

Physical characteristics

Both mean flow and coefficient of variation of flow were higher in Timber Creek than in the Kyeburn (Fig. 1). The erosion in the Timber Creek catchment and less extensive tussock cover may play a role in the high variability of flow in this stream. The ability of snow tussock grasslands to hold precipitation and release it slowly as baseflow rather than quickflow · (spates) is well known (Pearce, Rowe & O'Louglin, 1984; McSaveney & Whitehouse, 1988). Although large floods, associated with passing storm fronts, had the same frequency in both streams, smaller spates were less common in Kyeburn than in Timber Creek (personal observation of M.R.S.).

The median particle size in Timber Creek was smaller than in the Kyeburn (Fig. 2; $P < 0.05$, median test; Zar, 1984), and in both streams median particle size was greater in riffles than pools. Substrate diversity was highest in Kyeburn pools (SDI = 13.62), intermediate in riffle habitats (Kyeburn higher than Timber Creek, SDI = 10.39, 9.82, respectively) and lowest in Timber Creek pools (SDI = 8.55).

Shear stress varied significantly between streams (being higher in Timber Creek; $P < 0.0001$), between season (highest in winter; $P = 0.0001$) and between habitats (higher in riffles than pools; $P = 0.0001$) (Fig. 3a). No significant differences in shear stress diversity (Fig. 3b) were found between streams or habitat types.
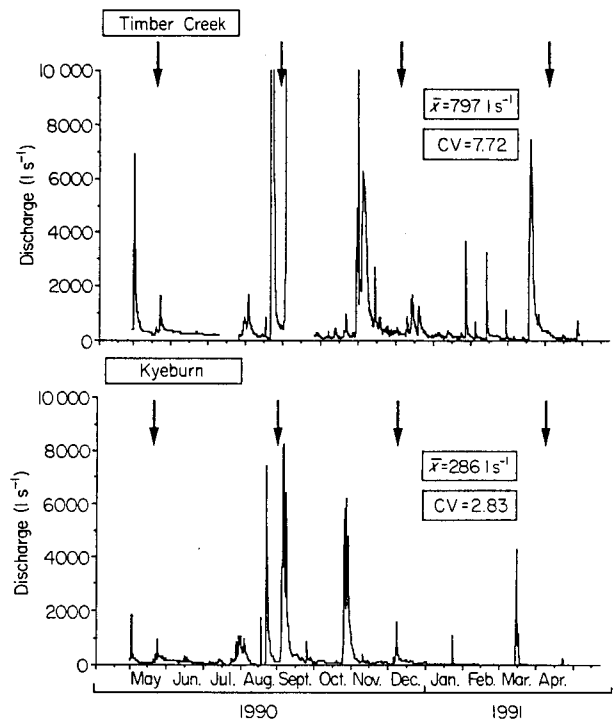

Fig. 1 Hydrographs of Timber Creek and the Kyeburn from May 1990 to April 1991. Mean ($\bar{x}$) and coefficient of variation (CV) of discharge are shown. Arrows indicate the times of biological and physical sampling. Note: gaps in the hydrograph of Timber Creek occurred due to equipment failure.

Fig. 4 shows the relationship between threshold flow stress and the percentage of the bed of each stream moved under those conditions. Taking an arbitrary value of 50% bed movement as a working definition of disturbance (cf. Rader & Ward, 1989), we see that this requires a smaller threshold flow stress in Timber Creek than in the Kyeburn. In both streams, pools required a lower shear stress to exceed the threshold of incipient substrate movement than riffles. Since Timber Creek had a higher shear stress regime than the Kyeburn, disturbance to the bed of the stream resulting from increases in discharge and accompanying increases in shear stress at the stream bottom will be more frequent in Timber Creek. With respect to the pool/riffle comparison, matters are less straightforward. Shear stress values were higher in riffles (erosional habitats) than pools (depositional habitats) during the sampling occasions. During high flows the relationship is expected to reverse, however, resulting in higher shear stresses and substrate movement in pools than in riffles (Richards, 1976; Church & Jones, 1982).
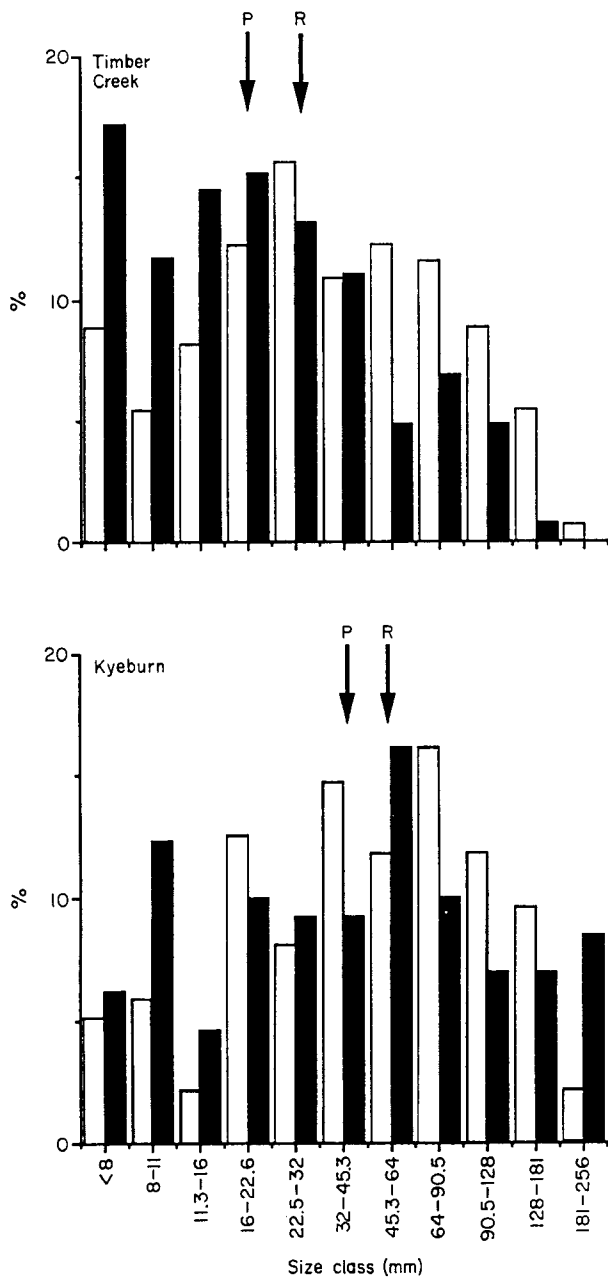
Fig. 2 Size distribution of surface particles in riffle and pool habitats. Arrows show the median (D_{50}) particle size for pool (P) (■) and riffle (R) (□) habitats.
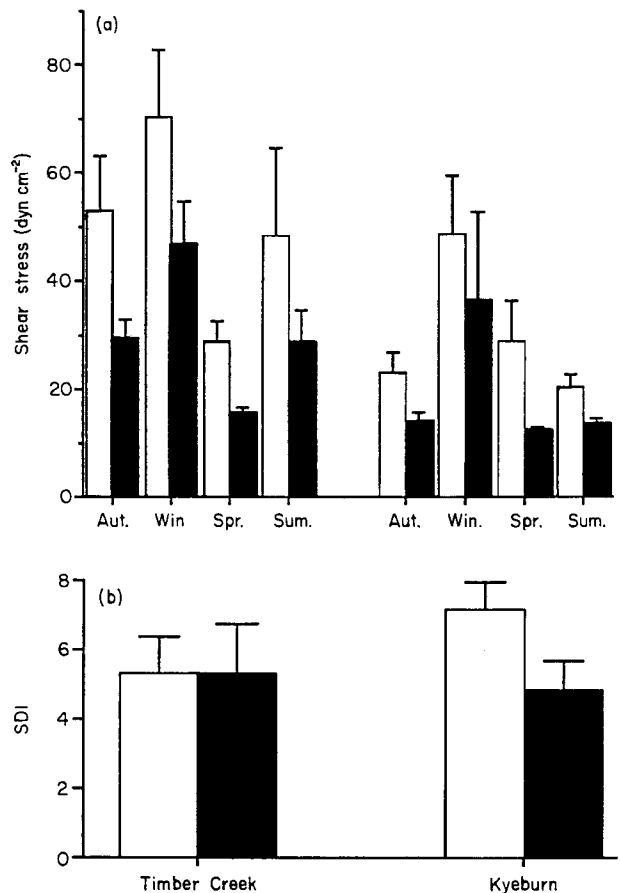

Fig. 3 Characteristics of the shear stress regime in Timber Creek and the Kyeburn. (a) Mean shear stress values in Timber Creek and the Kyeburn. (b) Shear stress diversity (SDI). Error bars are standard errors of mean seasonal shear stress diversity. □, Riffle; ■, pool.

Biological characteristics

Invertebrate species richness differed significantly with respect to stream ($P = 0.0001$), season ($P = 0.0001$) and habitat ($P = 0.009$) (Fig. 5). In the Kyeburn, mean species richness ranged from 15.5 in the winter to 19.2 in the summer, whereas Timber Creek had a mean species richness ranging from 7.1 (winter) to 14.6 (summer). The significant interaction between stream and habitat type ($P = 0.015$) can be explained by the lack of a significant difference in species richness between riffle and pool habitats in Timber Creek (Fig. 5). All taxa found in Timber Creek were also found in the Kyeburn. In contrast, several species found in the Kyeburn (e.g. *Stenoperla prasina* (Newman) (Plecoptera: Eustheniidae), *Potamopyrgus antipodarum* (Gray) (Gastropoda: Hydrobiidae) and *Coloburiscus humeralis* (Walker) (Ephemeroptera: Oligoneuriidae)) were never found in Timber Creek samples. The species assemblage in Timber Creek can therefore be thought of as a subset of that found in the Kyeburn.

Invertebrate species diversity (SDI) varied significantly between streams ($P = 0.0001$) and season ($P = 0.0001$), but was not significantly different between riffles and pools. The difference seen between streams was dependent on season ($P = 0.0001$). Invertebrate diversity was higher in the Kyeburn
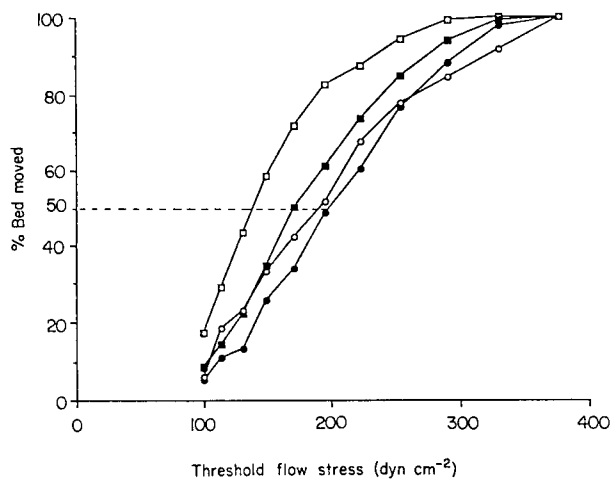
Fig. 4 Percentage of the stream bed predicted to move at given threshold flow stress values. Dashed line shows the shear stress required to move 50% of the bed. □, Timber Creek — pool; ■, Timber Creek — riffle; ○, Kyeburn — pool; ●, Kyeburn — riffle.
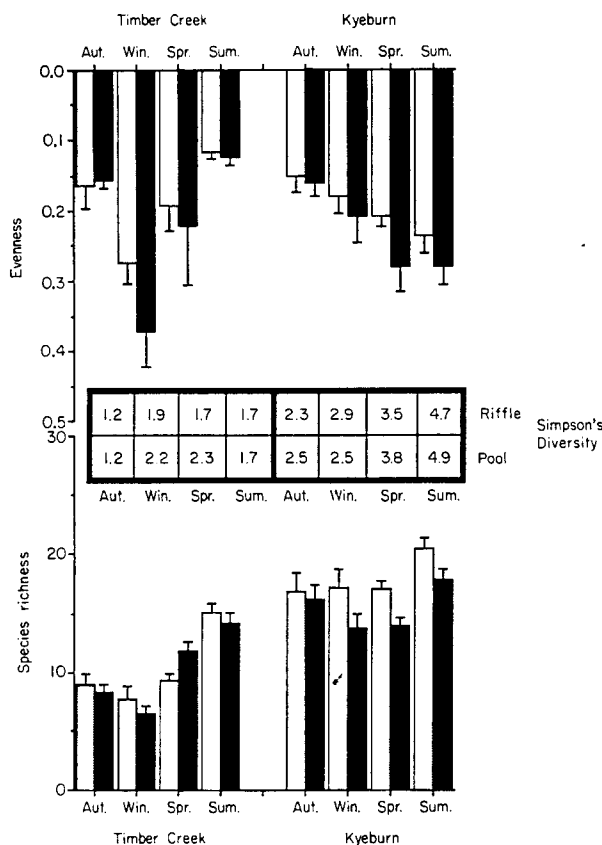

Fig. 5 Invertebrate species richness and evenness with table showing species diversity (SDI). Standard errors of means are shown on the bar graphs. □, Riffle; ■, pool.

in autumn, spring and summer, but not in winter (Fig. 5 inset). Analysis of species evenness (where evenness = SDI/the total number of species present) showed a significant difference between streams ($P = 0.0001$) and seasons ($P = 0.0001$). There was a significant interaction between stream and season, with evenness being higher in the Kyeburn in summer (0.26 v 0.12), higher in Timber Creek in winter (0.32 v 0.19) and not significantly different in autumn and spring.

Deleatidium was abundant in both streams (average seasonal densities ranged from 533 to 4031 m^{-2} in Timber Creek, and from 1502 to 2088 m^{-2} in the Kyeburn), however it made up a greater proportion of the community in Timber Creek than in the more stable Kyeburn. The difference between streams was dependent on season ($P = 0.0001$) (Fig. 6). In autumn, spring and summer *Deleatidium* was proportionally more dominant in Timber Creek than in the Kyeburn. However, in winter *Deleatidium* dominance in Timber Creek was lower and was not significantly different from the Kyeburn. No significant differences were found between the degree of dominance of *Deleatidium* in pool and riffle habitat.

Drift density (no. m^{-3}) of all invertebrate species combined differed significantly between streams ($P = 0.0001$) and seasons ($P = 0.0001$) (Fig. 7a). Differences in total drift density between streams were dependent on season ($P = 0.0001$), with Timber Creek having much higher drift densities than the Kyeburn in autumn (5.32 v 0.35 m^{-3}), spring (2.70 v 0.36 m^{-3}) and summer (4.51 v 0.88 m^{-3}), but not in winter (1.63 v 1.27 m^{-3}). Drift samples were dominated by *Deleatidium* in both streams. The density of
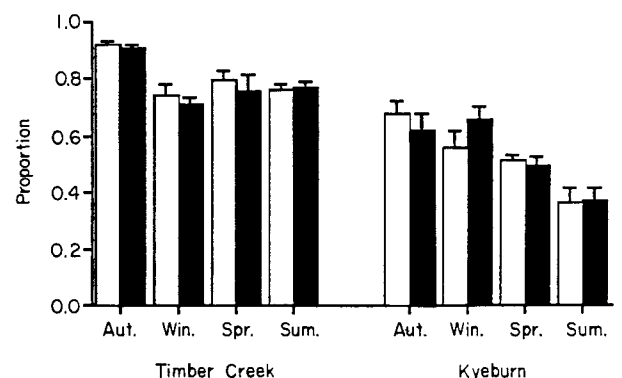

Fig. 6 The dominance of *Deleatidium* (expressed as proportion of total invertebrates) in the benthos. Standard errors of the means are shown. □, Riffle; ■, pool.
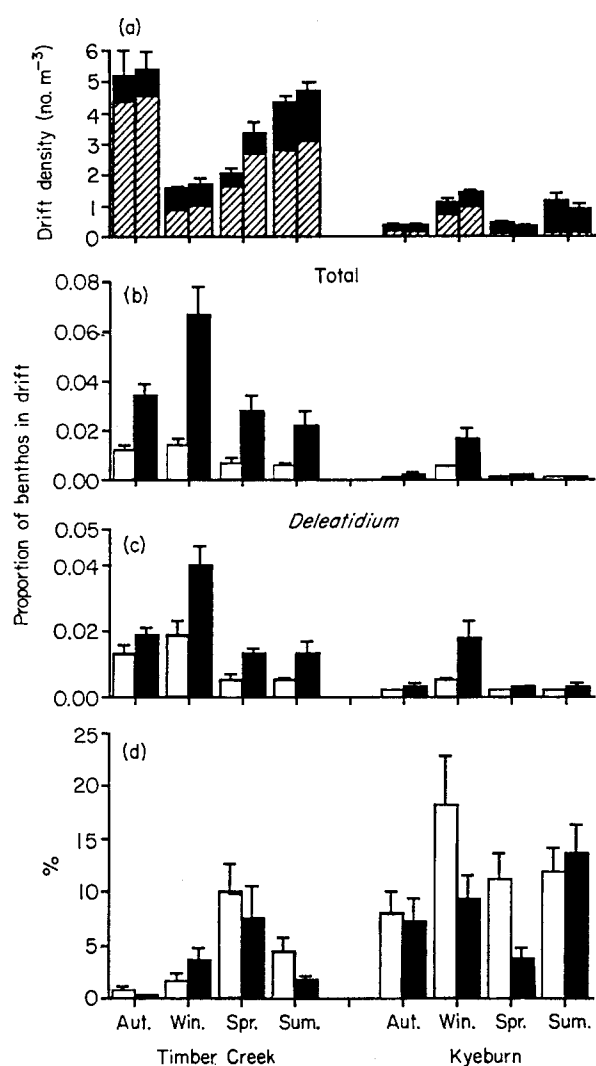
Fig. 7 (a) Invertebrate drift density: ▨, *Deleatidium*; ■, total. Paired bars are riffle and pool means. (b) Proportion of the total invertebrate community in the drift at any one time. (c) Proportion of the benthic *Deleatidium* population in the drift at any one time. (d) Percentage of the community made up by taxa classified as sedentary. Error bars are standard errors of the mean. □, Riffle, ■, pool.

Deleatidium in drift samples was significantly higher in Timber Creek than the Kyeburn in autumn, spring and summer ($P = 0.05$). The drift density of *Deleatidium* was higher in pools than riffles ($P = 0.009$).

The proportion of the benthos in the drift at any one time was calculated from the equation of Elliott (1967), both for the total invertebrate community and for *Deleatidium*. The percentage of the total benthos in the drift at any one time was significantly greater in Timber Creek than in the Kyeburn (P = 0.0001), was higher in pools than riffles ($P = 0.0001$) and

showed a significant seasonal effect ($P = 0.0001$) (Fig. 7b). In Timber Creek the percentage of the benthos in the drift ranged from 0.009 to 0.03%, whereas in the Kyeburn it ranged from 0.003 to 0.012%. The seasonal effect was also seen with respect to the propensity of the *Deleatidium* population to drift ($P = 0.0001$). The difference between streams was dependent on habitat type ($P = 0.0001$), with the proportion of *Deleatidium* in the drift being greater in pools than riffles in both Timber Creek and the Kyeburn (Fig. 7c).

Members of the invertebrate fauna in the two streams were classified as either mobile or sedentary. Species classified as sedentary included net-spinning Trichoptera, tube-dwelling Chironomidae and filtering Simuliidae. The proportion of the community made up of sedentary species was dependent on season ($P = 0.0001$). Autumn, winter and summer samples showed significant differences between streams (Kyeburn greater than Timber Creek), whereas the spring sample did not ($P = 0.621$) (Fig. 7d). Riffles had a significantly higher proportion of sedentary species than pools ($P = 0.009$).

Significant differences were found in phytopigment concentrations between streams ($P = 0.0001$), seasons ($P = 0.0001$) and habitat types, with riffles having higher amounts than pools ($P = 0.0001$) (Fig. 8a). Differences in phytopigment concentrations between streams were dependent on season ($P = 0.0001$); Kyeburn had higher concentrations of phytopigments than Timber Creek in autumn ($P = 0.0001$), winter ($P = 0.0001$) and summer ($P = 0.0001$). Amounts of phytopigment did not differ significantly between streams in the spring sample, which was taken after a period of stable flow (cf. Fig. 1).

The amounts of coarse particulate organic matter (CPOM) taken in benthic samples were significantly higher in the Kyeburn than in Timber Creek ($P = 0.0001$). Riffles contained greater amounts of CPOM than pools ($P = 0.001$) and CPOM levels varied significantly between seasons ($P = 0.001$) (Fig. 8b).

Differences in the amounts of fine particulate organic matter (FPOM) were not significant between streams or habitat types, but FPOM varied significantly between sampling occasions ($P = 0.0001$) (Fig. 8c). Furthermore, there was a significant interaction between stream and season ($P = 0.001$), with significant differences between streams in winter ($P = 0.008$), spring ($P = 0.048$) and summer
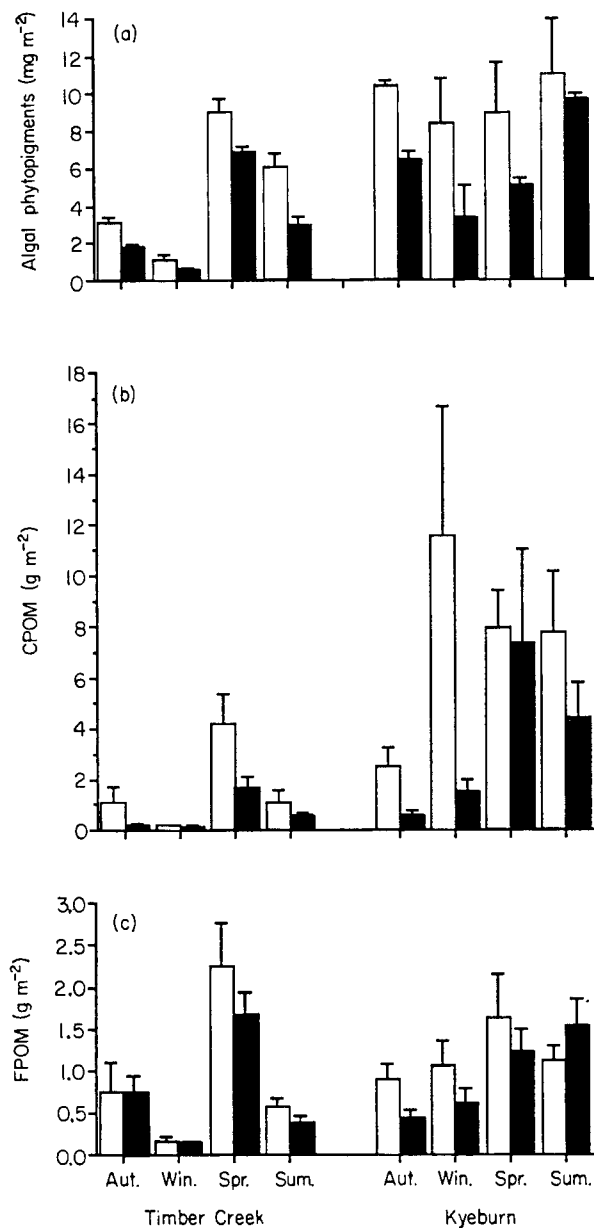
Fig. 8 Availability of food sources for primary consumers in Timber Creek and the Kyeburn. (a) Epilithic algae, (b) coarse particulate organic matter, and (c) fine particulate organic matter. □, Riffle; ■, pool.

$(P = 0.001)$, but not autumn. The data indicate that the biomass of FPOM was more constant in the Kyeburn than in Timber Creek.

The invertebrate community of each stream was separated into four functional feeding groups (browser, filterer, shredder and predator), according to the classification scheme of Cowie (1980). The proportion of the community made up by browsers varied significantly between streams $(P = 0.0001)$,

seasons $(P = 0.0001)$ and habitat types $(P = 0.0001)$ (Fig. 9). However, a significant interaction effect was found between stream, season and habitat type $(P = 0.016)$. Significant differences in the proportion of filterers were found between streams $(P = 0.0001)$, seasons $(P = 0.0001)$ and habitat types $(P = 0.0001)$. The difference between streams was dependent on season with Kyeburn having a significantly higher percentage of filterers than Timber Creek in autumn $(P = 0.0001)$, winter $(P = 0.0001)$ and spring $(P = 0.001)$ but not in summer. Riffles in both streams had higher proportions of filterers than did pools. The percentages of the community made up of both predators and shredders were significantly higher in Kyeburn in autumn, spring and summer, but did not differ in winter. Relative abundances of shredders and predators did not differ significantly between habitat types.

As well as differences in the proportions of functional feeding groups between streams, differences in the species make up of the functional feeding groups were found. In Kyeburn the major invertebrate predators were *Archichauliodes diversus* (Walker) (Megaloptera: Corydalidae), *Stenoperla prasina* and Tanypodinae (Diptera: Chironomidae). In Timber Creek the major predators were members of the family Hydrobiosidae with *Archichauliodes diversus* being rare and both *Stenoperla prasina* and Tanypodinae absent. Filterers in Timber Creek were almost exclusively blackflies of the *Austrosimulium australense* group (Diptera: Simuliidae), whereas the filtering guild of the Kyeburn was made up of a
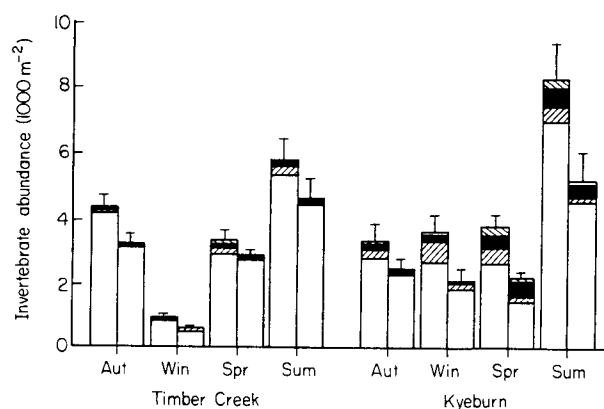

Fig. 9 Total invertebrate abundance and abundance of functional feeding groups shown for riffle/pool pairs. Standard errors of the total invertebrate mean abundances are given. □, Browser; ▨, filterer; ■, predator; ▨, shredder.

number of taxa, including *Austrosimulium australense* group and the larvae of a hydropsychid caddis, *Aoteapsyche colonica* (McLachlan), both of which were very common.

Obligate shredders were rare in both streams. However, the conoesucid caddis, *Olinga feredayi* (McLachlan), a facultative shredder (Ryder & Scott, 1988), was common in the Kyeburn at times.

The major difference in the browser guild between the two streams was in the relative abundance of non-predatory chironomids belonging to the sub-families Chironominae, Diamesinae and Orthocladiinae. Chironomids were uncommon in Timber Creek, whereas in the Kyeburn they were the dominant taxon on some occasions.

Analysis of the monthly *Deleatidium* size frequency data showed that mean monthly head capsule width was not significantly different between individuals from Timber Creek and the Kyeburn. However, individuals in the Kyeburn attained a significantly greater monthly maximum head capsule width ($P = 0.0001$, paired t-test) than those from Timber Creek. Variation in mean monthly head capsule width was also significantly greater in Kyeburn than Timber Creek (F-test, $P < 0.05$). Head capsule widths of individuals in the Kyeburn ranged from 0.4 to 3.6 mm, whereas in Timber Creek they ranged from 0.4 to only 3.0 mm (Fig. 10).

Discussion

The first step in the habitat templet approach is to decide where the study streams (and pool and riffle habitats within them) are to be located on the two axes of relative disturbance frequency and refuge availability. We considered bed movements caused by increases in shear stress during high discharge events to be disturbances. The results show that stream community structure was disturbed more often in Timber Creek than in the Kyeburn because of the lower shear stresses required to move significant proportions of the bed in the former. Pools can be expected to be disturbed more often than riffles (Frissell *et al.*, 1986) and the lower shear stresses required to move 50% of the bed in pools compared to riffles (Fig. 4) supports this contention. The higher variability of flow in Timber Creek also points to a higher disturbance frequency than in the Kyeburn. Even small storms, that brought about no increase
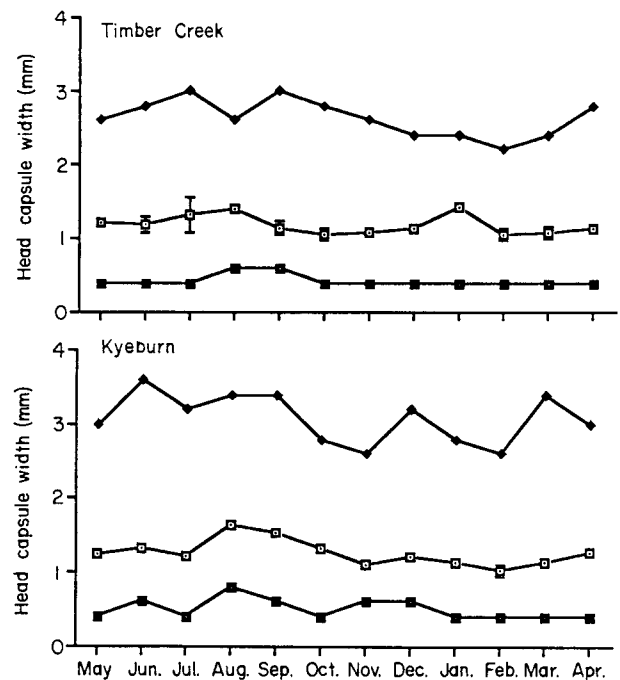

Fig. 10 Mean (▫), maximum (◆) and minimum (■) head capsule widths of *Deleatidium* larvae taken from monthly samples.

in discharge in the Kyeburn, caused an increase in discharge and sediment transport in Timber Creek.

The availability of refugia, provided by habitat heterogeneity, confers resilience on a stream community and reduces the impact of a given disturbance event. Substrate diversity, a measure of habitat heterogeneity, is lower in Timber Creek than in the Kyeburn. Riffles in Timber Creek were higher in substrate diversity than pools, but the opposite situation was found in the Kyeburn. Although shear stress diversity was not significantly different between streams or habitat types the shear stress regime at high flows, when heterogeneity really matters, was not studied, and would be impossible to study with the methodology used here. As well as microscale refugia, both streams possessed other potential refuge areas at larger spatial scales. At an intermediate scale the hyporheic zone may act as a refuge. The wide alluvial floodplain in unconstrained reaches of Timber Creek is consistent with the presence of an extensive hyporheic zone (cf. Stanford & Ward, 1988). However, the inputs of find sand and gravel from areas of erosion probably make this potential refuge unavailable to all but the smallest of invertebrates. The coarse-grained bed of the Kyeburn may provide

a more readily accessible hyporheic zone. It is note-worthy that a recent study by Palmer, Bely & Berg (1992) showed little evidence for the availability and use of the hyporheic zone as a refuge for meiofauna from flood disturbance in a sand-bottomed stream; stream ecologists cannot assume that the hyporheic zone serves as a flood refuge for fauna in all streams. At the macroscale, headwater tributaries may act as refugia from disturbance if they turn out to be impacted to a lesser extent than mainstream sections by high discharge events, and if invertebrates possess the high mobility necessary to utilize such a large-scale refuge. Further study is required to elucidate this point.

Fig. 11 shows the placement of the various habitats on the templet as an illustration of the conclusions drawn above regarding disturbance frequency and refuge availability in Timber Creek and the Kyeburn. The axes of the templet are dimensionless since rigorous quantification of the axes, especially dis-turbance frequency, was not possible in this study.

Roughly speaking, Timber Creek conforms to the 'highly disturbed, spatially homogeneous' case in Table 1 and the Kyeburn to the 'temporally stable, spatially heterogeneous' situation. The placement of Timber Creek and the Kyeburn on the templet now enable us to test the predictions made in the introduction.

As predicted, invertebrate species richness was . greater in the Kyeburn on all occasions and diversity was higher on three of the four sampling occasions. In winter, Timber Creek had very low invertebrate abundance, with *Deleatidium* having dropped in numbers after a long low-flow period. Species rich-ness was low during this period, but because of the

Disturbance frequency ———————▶

Fig. 11 Placement of study streams on the habitat templet.

absence of large numbers of *Deleatidium*, evenness was high and, consequently, diversity was relatively high. The expected difference between habitat types, with lower diversity in pools than in riffles in Timber Creek and higher diversity in pools than riffles in the Kyeburn, was not seen.

Invertebrate drift is a major source of recolonists following disturbance. It was predicted that drift density would be higher in Timber Creek than in the Kyeburn and this was found on three of the four sampling occasions, with the winter sample again showing no difference. Drift density of *Deleatidium* was much higher in Timber Creek than in the Kyeburn and was higher in pools than riffles.

Invertebrate mobility was predicted to be higher in Timber Creek than in the Kyeburn because of a lack of microscale refuges in Timber Creek. The pro-portion of the benthos found in the drift was indeed higher in Timber Creek than in the Kyeburn, and a greater proportion of benthos from pools than riffles was found in the drift. The results for *Deleatidium* alone were the same. The high drift densities and greater drift propensity of invertebrates in Timber Creek can be expected to speed up the recolonization process following disturbance in this system where microscale refugia are lacking.

Sedentary species were predicted to be more com-mon in the Kyeburn than in Timber Creek because of the presence of microscale refugia provided by stable substrate patches. This was true in autumn, winter and summer, but not in spring when both communities had similar proportions of sedentary filter feeders. A greater proportion of sedentary species were found in riffles than pools.

In general, the community of the more frequently disturbed, spatially homogeneous Timber Creek was dominated, as predicted, by the highly mobile browser, *Deleatidium*. The low availability of micro-scale refugia in Timber Creek may have selected for species traits which allow the use of macroscale refuges such as stable headwater tributaries.

As predicted, epilithic algal biomass was lower in the unstable Timber Creek than in the Kyeburn (except in spring) and biomass was higher in riffles than pools in both streams, possibly reflecting the more strongly disturbed nature of pools. The timing of the sampling events (cf. Fig. 1) may help explain the significant differences found in the two streams. The spring sample occurred at the end of a low-flow
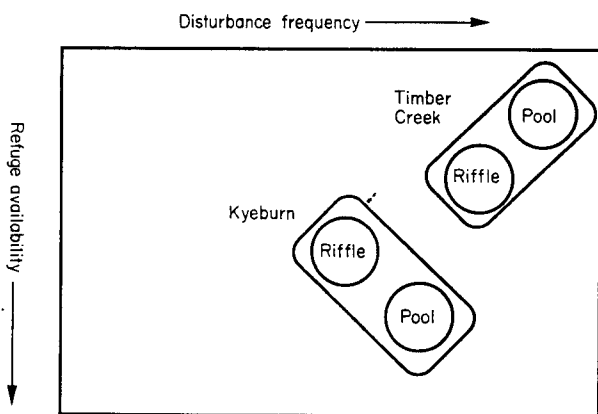
period. The algal communities of the two streams may be very resilient and the disturbance frequency may not act at a temporal scale necessary to drive selection for differences between the streams.

Coarse particulate organic matter was more abundant in the Kyeburn than Timber Creek and in riffles compared to pools, as predicted. In these snow tussock grasslands it is the leaves of the snow tussock *Chionochloa rigida* (Zotov) which form the dominant source of CPOM. Short-term retention of these leaves is higher in the Kyeburn than in Timber Creek (unpublished data). Long-term retention of these leaves, and their subsequent availability to shredding invertebrates, is lower in Timber Creek which has a more unstable bed.

On three of the four sampling occasions Timber Creek had less FPOM than the Kyeburn, as predicted. In contrast to the clear differences between habitat types with respect to the availability of CPOM, the amounts of fine particulate organic matter showed no difference between pool and riffle habitats. At low flows, pools are depositional habitats, gaining FPOM, and riffles are erosional habitats, losing FPOM (Moon, 1939). During high flows, however, there is a reversal of this situation, although there would most likely be a net loss of FPOM from both habitat types.

As predicted there were differences between the streams with respect to the representation of the different functional feeding groups. The expected difference between streams with respect to the proportion of the community made up by browsing invertebrates was complicated by an interaction with habitat type and season. However, there were major differences between the streams with respect to the species making up this feeding group. The dominant browser in Timber Creek was *Deleatidium*, a generalist feeder. In contrast, chironomids, rare in Timber Creek, were very common in the Kyeburn, especially in summer. This supports the predictions that specialist feeders will be more common in the stable Kyeburn and generalists will be more common in the unstable Timber Creek.

Filter feeders were more common in the Kyeburn on all sampling occasions except summer. Thick mats of golden diatoms were present in the Kyeburn over summer and may have reduced the space available for filterers, leading to the lower relative abundances of this group. As expected filter feeders were more common in riffles than pools.

As predicted, invertebrates classified as shredders were more common in the Kyeburn than in Timber Creek in the autumn, spring and summer samples, but not in the winter.

Finally, we predicted that *Deleatidium* individuals would be smaller in the more frequently disturbed Timber Creek and attain a smaller maximum size. Although mean monthly size was not significantly different, maximum monthly size was. There could be several alternative hypotheses for the observed absence of the largest size classes of *Deleatidium* individuals from Timber Creek. Giberson & Rosenberg (1992) found that temperature and food quantity were the most important factors affecting life-history traits of two burrowing mayfly species. Temperature was not continuously recorded in this study but differences between the two streams would have been very small (spot temperature measures support this contention). Although the biomass of epilithic algae, a major food source of *Deleatidium*, was lower in Timber Creek there was no evidence that it was limiting, and the study of Scrimgeour (1991) suggests that *Deleatidium* has the ability to thrive on low-quality organic layers left on stones following disturbance. Flannagan, Flannagan & Chapman (1992) suggested that different species of *Deleatidium* may inhabit streams of differing stability; in this study larvae in both streams belonged to the informal *myzobranchia* group (Winterbourn & Gregson, 1989).

Community structure in the Kyeburn reflects the more stable nature of the system, with its low disturbance frequency and apparent availability of spatial refugia. This environment may have selected for species able to utilize the available micro-scale refugia. However, as Townsend & Hildrew (in press) have pointed out, organisms with traits suitable for a more variable environment are not necessarily selected against in constant environments. For example, *Deleatidium* is also common in the more stable Kyeburn. Characteristics that allow survival in the harsh environment of Timber Creek may have been selected for at the cost of competitive ability. Biotic interactions, including interspecific competition, may be predicted to be of greater importance in a stream such as the Kyeburn than in Timber Creek (Townsend, 1989). However, there is no evidence that *Deleatidium* is outcompeted at any times of the year.

The results of this limited study of two habitat

types in two streams indicate that the habitat templet approach set in a patch dynamics framework has promise as a generator of testable, realistic predictions in stream ecology. What are needed now are larger scale investigations involving many streams, together with a more rigorous classification and quantification of the axes of spatial and temporal variation in an organism-related sense. The frequency of disturbance, used here as a descriptor of the disturbance regime, is only one aspect of disturbance (White & Pickett, 1985). Predictability is another, and this is beginning to receive attention from stream ecologists (e.g. Resh *et al.*, 1988; Poff, 1992). In the studies of both Poff & Ward (1989) and Rader & Ward (1989) disturbance predictability was estimated using the method of Colwell (1974) which requires long-term flow records (not available for the two streams in this study).

As far as refuge availability is concerned we require detailed mechanistic explanations of how habitat heterogeneity provides refugia that may increase the resilience of benthic communities in the face of disturbances (Hildrew & Giller, in press). Disturbances caused by increases in discharge are patchy in their effects and this needs to be more fully understood. Moreover, bed movement has a spatial component which has largely been ingnored by both hydrologist/geomorphologists and stream ecologists. The relative stability of substrate patches, although of prime importance to the study of disturbance and refugia in streams, is not understood, and information is needed on this to allow quantification of microscale refuge availability. Ultimately, quantification of invertebrate patchiness before and after disturbance events coupled with physical measurements will provide valuable information on the links between invertebrate retention and patch characteristics.

Refuge availability can be expected to vary with the intensity of disturbance. As the areal extent of disturbance increases, refuge availability will decrease as microscale and mesoscale refugia are lost and only macroscale refugia are available. As a result, community recovery following large, rare disturbance events may take much longer than after smaller, more frequent disturbances. In systems where spatial refugia are largely unavailable, because of features of geomorphology or the high frequency of large-scale disturbances, temporal refugia (e.g. extended flight periods of aerial adults) will assume greater import-

ance. A good example of such a system is described by Gray (1981) and Gray & Fisher (1981); a high proportion of the fauna of desert streams, subjected to unpredictable, high-intensity floods, and often having low spatial heterogeneity, show extended flight periods and very rapid generation times.

The predictions made and tested in this study serve as a test of the templet approach itself. Since our simple predictions were largely supported, the testing of more complex predictions should be a next step. Species traits such as body form, potential life span, potential size and many others have been linked to the habitat templet (Townsend & Hildrew, in press). Another prediction, which directly relates to disturbance regime and refuge availability, concerns refugee categories. Species composition may be predictable if we know the species capable of utilizing particular refugia and the availability of refugia in a system.

The original aim of Southwood (1977) in proposing a habitat templet for species characteristics was to provide us with the basis for an ecological 'periodic table'. Although this goal is a long way off, and even if it is never successful, the templet approach nevertheless provides a valuable framework within which to pose questions.

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