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## Discussion paper\*

# Are New Zealand stream ecosystems really different?

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**Abstract** New Zealand stream ecosystems differ from many of their North American counterparts, on which general stream ecosystem models are based, in several ways. In New Zealand, large particle detritivores (shredders) are poorly represented, and the dominant invertebrates are browsers which feed on fine particulate organic matter and stone-surface organic layers. In contrast with the river continuum concept of Vannote et al. (*Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137, 1980), representation of functional feeding groups shows little change downstream and a temporal continuum of synchronous species replacements is not found. Many common benthic invertebrates are ecologically flexible species with poorly synchronised life histories. These differences appear to be associated with the non-retentive, climatically unpredictable nature of the stream environment. The idea that stream communities are highly structured entities is questioned, as is the generality of the river continuum concept.

**Keywords** stream ecosystems; river continuum concept; ecology; functional feeding groups; organic layers.

## INTRODUCTION

The river continuum concept of Vannote et al. (1980) has focussed attention on stream ecosystems as predictably organised units, and attempts to provide a conceptual framework of their organisation. It extends the idea that streams possess

Received 20 March 1981; revised 29 June 1981

\*Comments, brief and to the point, are welcomed by the Editor and may be published as "Letters to the Editor". The authors of the Discussion Paper will be given the right of reply

assemblages of species, which respond to physical gradients, to include functional relationships. Community structure and function are seen as adjusting to changes in certain geomorphic, physical, and biotic variables, such as stream flow, channel morphology, detritus loading, size of particulate organic material, characteristics of autotrophic production, and thermal regime, to achieve a state of dynamic equilibrium. Since downstream communities are considered to be dependent on those upstream for at least part of their energy income, Vannote et al. (1980) hypothesised that they will become structured in a predictable manner to utilise this material most efficiently.

Although it is based primarily on North American experience, Vannote et al. inferred that their model is a universal one and, therefore, by implication applicable to New Zealand river systems. The results of our studies and those of colleagues in this country are at odds with several specific criteria of the river continuum concept, and have led us to ask the question: Are New Zealand stream ecosystems really different? If they are, why should this be so, and if not, is there something wrong with the North American model?

Since the river continuum concept has attempted to draw together many of the recent developments in stream ecology, it is appropriate for us to consider New Zealand streams in its light.

## NEW ZEALAND STREAM ECOSYSTEMS

### Physical background

New Zealand is a small country with a complex, diverse landscape including prominent mountain ranges. Peaks in the Southern Alps range up to 3764 m (Mt Cook), and although they are lower in the North Island (maximum 2797 m, Mt Ruapehu), they offer much steep, finely dissected relief. In common with other Southern Hemisphere land masses the timber line is low (1200-1500 m), and consequently extensive river catchments occur above the forests in terrain which is often steep and barren. Scree slopes are a continual source of the sediments carried down mountain streams and may be a striking feature of the landscape, as in the Cass-Arthur's Pass region of the South Island. Since heavy rainfalls occur

WAG 04/13

unpredictably and frequently in mountainous areas, it is not surprising that sediment yields measured in several New Zealand rivers are among the highest reported in the world (Griffiths 1979).

River continua in New Zealand are short, with major rivers having a stream order (sensu Strahler (1957)) of only 6 or 7 compared with 12 for a long river like the Mississippi. Mountain streams typically are turbulent and fast-flowing with shifting and unstable beds and poor debris retention characteristics. The extensive, evergreen beech and podocarp-hardwood forests, often with poorly developed subcanopy vegetation (notably in beech forests), and a paucity of deciduous, riparian trees, provide streams with only small quantities of woody debris compared with many elsewhere. Thus, in New Zealand it is rare for more than 5-10% of forest stream beds to hold wood debris, whereas in parts of western North America it is common for up to 50% of stream bed area to be covered with wood and associated materials (Sedell & Triska 1977) and debris dams can remain intact for over 100 years (Swanson et al. 1976).

Where they pass through foothills and over plains, many New Zealand rivers, particularly in the South Island, have extensive braided channels and gravel beds which may be dry at the surface in summer and muddy torrents after heavy rain or snowmelt. Not all our rivers are as physically imposing as this, however, but unfortunately, from the point of view of this discussion, many of the smaller, lower gradient streams and rivers now drain agricultural and urban catchments and are subject to varying degrees of enrichment or other modification. This brief description has stressed the instability and unpredictability of New Zealand stream environments, features which must be kept clearly in mind when trying to understand the nature of their biological communities.

#### Characteristics of the invertebrate fauna

At the higher taxonomic levels (family or subfamily and above), New Zealand stream faunas show numerous differences from their Northern Hemisphere counterparts, although in some groups (e.g., Oligochaeta) there is a predominance of cosmopolitan species. The dominant mayflies are Leptophlebiidae and Siphonuridae, and the best represented stoneflies are Gripopterygidae and Notonemouridae. Large stoneflies equivalent to the familiar perlids, perlodids, and pteronarcids of the Northern Hemisphere are poorly represented. Chironomidae and to a lesser extent Tipulidae and Simuliidae are the most abundant lotic Diptera, and Elmidae, Hydracnidae, and Helodidae are the commonest beetles. Several other groups typically

associated with running waters have few representatives in New Zealand; thus there is only one megalopteran (a corydalid), and very few Odonata, Gastropoda, or Crustacea. In contrast, caddisflies are well represented in New Zealand's running waters, but like the stoneflies most are rather small. Species of Coenocricidae, Hydropsychidae, Rhyacophilidae (Hydrobiosinae), and Hydropsilidae are best represented, and apart from a few species of Oeconesidae and Leptoceridae whose larvae are typical shredders there are no ecological equivalents of the Northern Hemisphere Limnephilidae, Lepidostomatidae, and Odontoceridae, or of the algal-scraping Glossosomatidae.

#### Benthic invertebrate communities

Throughout New Zealand, unmodified streams tend to have remarkably similar faunas with a nucleus of common genera (*Deleatidium*, *Coloburiscus*, *Nesameletus* (Ephemeroptera); *Stenoperla*, *Zelandoperla*, *Zelandobius* (Plecoptera); *Hydrobiosis*, *Psilochorema*, *Pycnocentria*, *Olinga*, *Aoteapsyche* (Trichoptera); *Archichauliodes* (Megaloptera); *Potamopyrgus* (Gastropoda)) and species. This faunal similarity extends to streams in exotic plantations as well as in native forest and grassland, a point of significance for stream management and one that is contrary to the appealing idea that stream insects may show close adaptation to forest vegetation. Although frequently mentioned, this is an unresolved issue, and a careful reading of Ross (1963), the authority most frequently cited in this respect, shows that many of the statements attributed to him exaggerate his suggestion that "the forest itself superimposes certain ecological conditions upon the streams originating in it and running through it, ecological conditions necessary for the survival of the caddisflies."

Changes in community structure along unperturbed montane streams in New Zealand appear to be related primarily to physical factors, especially stream size, slope, and stability, and secondarily to the nature of the energy sources available to the fauna (Cowie 1980). Highly unstable stream beds may support a diverse insect fauna, but our work suggests that the most diverse faunas are associated with the more stable stream channels exhibiting a high degree of substrate heterogeneity. This is in accordance with Minckley's (1963) contention (expanded by Bishop (1973)) that increasing heterogeneity promotes faunal diversity, but is contrary to the suggestion of Vannote et al. (1980) that physical stability may be equated with low diversity. Cowie's (1980) work on West Coast streams also showed that although severe floods were frequent and temporally unpredictable, they had little apparent effect on species richness or

relative abundance at his more stable sites. Perhaps this is not surprising given the climatic and physiographic conditions prevailing in New Zealand.

Winterbourn (1976) and Davis & Winterbourn (1977) suggested that species diversity in New Zealand streams is poor compared with that found in many streams elsewhere, but the comprehensive studies of Towns (1976) and Cowie (1980), in kauri and beech forest streams respectively, indicated that this is not necessarily so. Nevertheless, it is true that several major faunal groups have only a few common species whose distributions show that they have broad ecological requirements. Amongst the Ephemeroptera and Plecoptera, for example, the one or two species of *Coloburiscus*, *Nesameletus*, *Stenoperla*, and *Spaniocerca* are widely distributed and often abundant in different kinds of rivers and streams. On the other hand, considerable diversity is shown by Trichoptera (notably Rhyacophilidae and Hydropsychidae) and Diptera, orders possessing holometabolous development which might be expected to have aided in the evolution of more precise larval adaptation to specific habitats. Despite this radiation, differences in ecological niches of related or potentially competitive species have proved difficult to define (Devonport & Winterbourn 1976, Winterbourn 1978b), although some rhyacophilids show altitudinal distribution patterns (McFarlane 1938) and some species of Hydropsychidae, Oeconesidae, Rhyacophilidae, and Calocidae are restricted either to open or forested streams.

Larvae of most New Zealand aquatic insects also show little evidence of food specialisation. Carnivorous species examined (*Stenoperla*, *Archichauliodes*, *Polypectropus*, *Hudsonema*, *Microchorista*, several Rhyacophilidae) appear to be generalists taking suitably sized prey more or less in proportion to its abundance and availability (Winterbourn 1974, 1978b, Crosby 1975, Devonport & Winterbourn 1976, authors' unpubl. data), while most browsers are also food generalists, feeding predominantly on fine particulate organic matter and the organic layers present on the surfaces of stones (see below). There is little evidence of food partitioning, and several surface-browsing stoneflies and caddis (species of *Spaniocerca*, *Zelandobius*, *Zelandoperla*, *Olinga*) can act as opportunistic shredders (Davis & Winterbourn 1977, Cowie 1980). Similarly, all New Zealand Hydropsychidae appear to construct similar nets which capture a mixture of detrital and animal foods, whereas in many other parts of the world it seems to be common for species to partition food resources through the use of nets differing in mesh size (Wallace 1975).

In addition to their broad habitat requirements and apparent lack of feeding niche differentiation,

many New Zealand stream insects possess flexible, poorly synchronised life histories (Winterbourn 1978a, Towns 1981). These can vary in the length of the larval period (e.g., 1-3 years in *Stenoperla prasina* (Cowie 1980)), exhibit non-seasonal or weakly seasonal patterns of development, and include extended flight and egg-hatching periods. Temporal segregation of taxonomically or functionally related species through staggering of their development and emergence periods as described by Mackay (1969), Kerst & Anderson (1974), Vannote & Sweeney (1980), and others in North America does not occur. This contrasts with the contention of Vannote et al. (1980) that the biological communities of natural streams should incorporate a temporal continuum of synchronised species replacements associated with seasonal variations in the nature of the food base, thereby enabling the efficient utilisation of inputs over time. Instead, because of their broad, ecological flexibility, e.g. possession of wide ecological niches, single New Zealand species appear to be functionally equivalent to several sequentially appearing North American species. Whether this implies that seasonal variations in the nature of energy inputs and physical conditions are minimal, as the argument of Vannote et al. (1980) suggests, is an interesting point which is touched upon below. Regardless of this, it is our belief that abiotic factors have been of paramount importance in shaping the nature of New Zealand stream communities. In particular, the prevalence of steep, unstable streams and the unpredictability of the physical environment appear to have favoured selection for opportunism, while the risks of unseasonal insect emergence or larval cohort losses have been spread by the evolution (or maintenance of what may be the primitive, generalised condition) of poorly synchronised life histories.

#### STREAMS AS ECOSYSTEMS

The importance of coarse particulate organic matter (CPOM) (principally autumn-shed leaves) as a major source of energy to small forest stream communities has been emphasised by North American stream ecologists (e.g., Cummins 1974), and numerous studies have focussed on the mechanisms of litter breakdown and decomposition (e.g., Petersen & Cummins 1974, Hart & Howmiller 1975, Padgett 1976, Triska & Sedell 1976, Davis & Winterbourn 1977, McCammon 1980). The role played by microorganisms in conditioning CPOM, thereby increasing its nutritive value and palatability to many detritivores, is also well established (Kaushik & Hynes 1971, Barlocher & Kendrick 1973, Cummins 1974, Iversen 1974). Hyphomycetous fungi appear to be the key colonists of dead leaves in many streams (Barlocher & Kendrick

**Table 1** Percentage of New Zealand trichopteran genera in 4 functional feeding categories and a comparison with some overseas caddis faunas. Feeding categories of Northern Hemisphere and Chilean (in part) faunas based mainly on summaries by Merritt & Cummins (1978); where information not available we assigned genera to the trophic class of closely related genera. Placement of Tasmanian genera and southern element of Chilean fauna inferred from our knowledge of their New Zealand relatives.

Fauna	No. of genera	Percentage of				Source
		Shredders	Filterers (collectors)	Browsers	Predators	
New Zealand	41	12	12	44	32	Wise (1973)
South Island forest streams	26	15	8	38	38	Authors' studies
Tasmania	62	14	8	43	34	Neboiss (1977)
Chile	57	35	5	21	38	Flint (1974)
Eastern deciduous forest biome, North America	88	34	23	32	11	Wiggins & Mackay (1978)
Western montane forest biome, North America	59	37	15	37	10	Wiggins & Mackay (1978)
Northwestern Europe	86	35	10	31	10	Svensson & Tjeder (1975)

1975), although bacteria can also play this role, as on *Fagus* and *Nothofagus* leaves in Danish and New Zealand streams respectively (Iversen 1973, Davis & Winterbourn 1977).

Not surprisingly, recent discussions of stream ecosystem structure and function have emphasised the important role of shredders (CPOM feeders), an attitude summed up in Hynes's (1975) phrase that shredder feeding lay "at the base of almost all the biotic activity in the water".

In New Zealand, shredders are poorly represented in the fauna and frequently may be absent from forested headwater streams. Their relative scarcity is illustrated in Table 1, in which the feeding modes of larval Trichoptera (one of the principal orders containing shredders elsewhere) are analysed. In New Zealand and Tasmania—a land mass of similar climate and topography to New Zealand—only 12 and 14% of genera are classified as shredders compared with 34–37% in parts of North America and Europe. In Chile, much of whose fauna has strong phylogenetic links with those of southeastern Australia and New Zealand rather than the rest of South America (Flint 1974), the relatively high representation of shredders can be accounted for by the presence of Sericostomatidae (9 genera) and Limnephilidae (6 genera), northern families which are absent from New Zealand (although one limnephilid genus occurs in Tasmania). On the other hand, predators are over-represented in Southern Hemisphere faunas, reflecting in large part the radiation of Hydrorhynchidae (Rhyacophilidae) in New Zealand (9 genera), Tasmania (10 genera), and Chile (17 genera).

For shredders to occur, a stream must be able to retain CPOM. This often happens in small, low

gradient tributaries where even in New Zealand shredders can be common (Graynoth 1979, authors' unpubl. data). Evidence that retention is of major significance was shown by our experiments with larvae of the caddisfly *Zelandopsycha ingens* which were caged for 3 months in an unretentive stream with no resident caddis population, yet survived and grew (utilising leaf litter from the recipient stream as food) as well as larvae kept under identical conditions within the donor stream. Peckarsky (1980) has suggested, and Young et al. (1978) have inferred, that shredders are essentially opportunistic species occurring where conditions allow. Clearly, this is so in New Zealand where they do not play a fundamental role in organic matter processing or energy flow in streams.

A fundamental part of the river continuum concept (Vannote et al. 1980) is that as one moves from headwaters to mouth, adjacent watershed vegetation will have a decreasing direct influence on the river ecosystem (an extension of the ideas of Ross (1963)), while detrital inputs from upstream tributaries and in situ algal production become increasingly important. The theory implies that downstream communities depend on upstream areas for a proportion of their energy in the form of fine particulate organic matter (FPOM), at least some of which is derived from CPOM through the feeding activities of shredders. Thus, Cummins (1975), in describing headwater streams as "CPOM-fungi-shredder-FPOM-bacteria-collector systems", implied that shredders were significant producers of collector food, Anderson & Cummins (1979) stated that "much of it [FPOM] is fecal material produced by shredders and other functional groups", and Short & Maslin (1977) contended that "shredders are of great importance ... with regard to nutrient

availability to the various collector species". We would be surprised to find that FPOM of shredder origin was a major source of collector food, except perhaps in highly retentive headwater streams, and note that, despite their authoritative ring, surprisingly little evidence has been forthcoming to substantiate claims such as those quoted above.

The gut contents of insect larvae from the headwaters and lower reaches of a wide range of New Zealand rivers and streams indicate that FPOM is indeed the major particulate material ingested, but since shredder feeding is negligible it must have other origins. We suspect that much of this material (Table 2) enters our streams already in fine particulate form, via wind blow, surface runoff, and bank erosion, and suggest that such sources are also of considerable importance in many streams elsewhere. Since many New Zealand rivers begin in the mountains high above the tree line where typically eroded, windswept conditions prevail, it is likely that primary tributaries receive extensive fine particulate inputs, and at least seasonally may support considerable primary production. Even where shredders are conspicuous, as in Manson Creek (Table 2) or Middle Bush Stream, Cass (Winterbourn 1978a), it is most unlikely that they are the main source of FPOM ingested by insect larvae since the sizes and shapes of most particles found in insect guts are quite unlike those of faecal fragments produced by shredders inhabiting the streams. It might be argued that faecal fragments break down further before reingestion, but *Nothofagus* leaves (the main materials ingested in beech forest streams) are notably tough and lignified, and this seems inherently unlikely. In shallow gradient, non-forested streams, aquatic macrophytes and/or algae also may represent a major source of the FPOM ingested by benthic insects. However, since few if any of our stream-dwelling invertebrates eat living macrophyte tissue directly, animal feeding again cannot be of importance in FPOM production; therefore we presume that breakdown and decomposition occur primarily by microbial and mechanical means.

As well as being food items in their own right, fine particles also form an important component of the organic layers which occur on the surfaces of stones, logs, and leaves in streams (Madsen 1972, Calow 1975, Pennak 1977). Traditionally, stream biologists have focussed on the algal (autotrophic) component of attached stone-surface communities (e.g., Nielsen 1950, McIntyre 1973), and although we agree with Minshall (1978) that the importance of autotrophic production should not be underestimated, we believe that heterotrophic elements which are not restricted to well lit surfaces may play a major part in the transfer of energy to benthic invertebrate communities.

**Table 2** Particle size distribution (percent dry weight) of fine particulate organic matter (< 1 mm diameter) present in sediment samples from 3 sites along Manson Creek, a beech forest stream in the Craigieburn Range, South I. Mar 1980. Shredders were absent from the first order tributary (Site a), but present (*Zelandopsycha ingens*) at Site b; extensive filamentous algae present at Site c. Shredders produce particles mainly in the size range marked \*, whereas particles in guts of browsers are much smaller (\*\*).

Particle size class (µm)	Sites		
	a 1st order tributary in forest	b 3rd order stream in forest	c 3rd order stream in open
501–1000	22	28	72
251–500*	25	27	19
91–250	16	25	5
46–90**	15	8	2
< 46	22	12	1

The emphasis placed on shredder-feeding pathways by Cummins and co-workers (e.g., Cummins 1974, Petersen & Cummins 1974) has turned the attention of stream ecologists away from stone-surface communities, and even when the former are obvious we would still expect to find well developed organic layers supporting significant secondary production.

In fast-flowing natural streams, fungi and bacteria—the main living heterotrophs within the organic layer—obtain much of the carbon required for their growth and maintenance in dissolved form from the surrounding water (McDowell & Fisher 1976, Iversen & Madsen 1977, Geesey et al. 1978, Dahm 1981). Its exact source is unclear, but is assumed to include algal exudates and leaf leachates as well as dissolved materials in groundwater, throughfall, surface runoff, and other CPOM leachates (Lock & Hynes 1976, Dahm 1981). We contend that organic layers and associated FPOM are the main food sources of benthic invertebrates in fast-flowing New Zealand streams. About 85% of the non-carnivorous insects in South Island streams surveyed by Cowie (1980) and J. S. Rounick (unpubl. results) fed in this way, and detrital particles, rather than intact algal cells, predominated in gut contents of most species from both open and forested streams.

CPOM, when it occurs, may be important primarily as a source of dissolved organic matter utilised by microorganisms forming part of the organic layers which represent one of the most stable (Cowie 1980), and hence reliable, carbon sources in the lotic environment.

Finally, Vannote et al. (1980) have suggested that stream communities evolve to utilise energy inputs

with a high degree of efficiency and temporal uniformity, and according to Vannote & Sweeney (1980) they are highly structured entities. We see this as a contentious proposal, given the naturally heterogeneous and unpredictable nature of stream environments. Cummins's (1974) paper on stream ecosystem structure and function, although written from a limited data base, has been influential in popularising such a viewpoint—typified by Richardson's (1980) statements that "in woodland streams where leaf inputs are the chief plant materials available there is a strikingly complex set of species interactions", and "the species of each stage are clearly dependent on the species of all previous stages of leaf breakdown". As Richardson pointed out, animals and decomposers lend themselves to such organismic (i.e., community-as-organism) notions of the community, a view fostered by modern emphases on ecosystems, energy flow, and biotic influences on community structuring. Vannote & Sweeney (1980) and Vannote et al. (1980) apparently accepted this dogma when they suggested that stream communities have evolved to utilise energy inputs in a very efficient manner, a view implying (it seems to us) that natural selection operates at the community level!

On the face of it, stream ecosystems appear to be anything but integrated, closed systems displaying light, or complex (cohesive) organisation, feedback loops, and so on. Rather, they are dominated by continual, but not necessarily predictable, recruitment of materials and organisms from outside (energy, nutrients, structural elements such as logs, invading insects) and losses or displacement of some of these downstream, and it is only the continual nature of their supply which serves to perpetuate stream communities. Physically controlled communities, especially those in unstable and unpredictable environments—as are New Zealand streams—are likely to be highly individualistic (as opposed to organismic) in nature, consisting of species geared towards colonising and saturating a physically demanding habitat, and not towards fine-tuned accommodation with co-existing species (Richardson 1980).

In addressing the problem of how to approach community-level phenomena in streams, Reice (1980) concluded that stream communities were very fluid and could best be interpreted as the transitory result of many individual population dynamics—a view with which we are in sympathy. Extending this to Vannote & Sweeney's (1980) contention that streams contain "highly structured communities" in a state of dynamic equilibrium (Vannote et al. 1980) must be considered a giant and tenuous step.

## EPILOGUE

Let us return to the questions posed at the start of this paper. By now it should be clear that New Zealand streams do differ in a number of respects from those which have been intensively studied in North America and from which the river continuum concept has been developed. Why are they different? We suggest that to a large extent this is a function of the generally steep and youthful topography of New Zealand, the heavy and temporally unpredictable rainfall, and the nature of our upland catchments with their low timberlines, low biomass native forest, and paucity of deciduous trees. These features have resulted in New Zealand streams having poor retention characteristics and, consequently, biological communities centred around the direct utilisation of CPOM energy sources can rarely exist. In terms of the Cummins (1975) and Vannote et al. (1980) continuum models they are essentially decapitated systems, the equivalent, regardless of stream order, of Cummins's (1975) intermediate-sized rivers.

Finally, how realistic is the river continuum concept of Vannote et al. (1980) as a summary of river ecosystem structure and function as currently understood? Whereas in general it may be a fair description of those North American streams on which it is largely based, we would be surprised if some of the points and reservations raised above did not apply to them too. Clearly, considerably more work and data collection are required to test the concept adequately.

We predict that rivers arising high in the American Rockies and many other alpine regions will have ecosystem characteristics essentially like those in New Zealand, whereas those of ephemeral Australian waterways, English chalk streams, and the brown-water rivers of northern Canada are likely to be quite different and also poorly accommodated by the schemes of Vannote and his colleagues.

The river continuum concept, like so many generalisations, is bound to have numerous exceptions. The question then becomes: Are the exceptions so many as to invalidate the generality of the scheme? We are inclined to think so.

## ACKNOWLEDGMENTS

Much of our research on which this paper is based was supported by research grants from the New Zealand Forest Service. In particular, we thank Dr Colin O'Loughlin (Forest Research Institute, Christchurch) for much appreciated advice and assistance. We also thank our colleague, Robin McCammon, for valuable discussions which have aided the development of our ideas.

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## ERRATUM

**Volume 15, Number 2, p. 125 and 127:** J. L. McKOY and D. B. ESTERMAN, Growth of rock lobsters (*Jasus edwardsii*) in the Gisborne region, New Zealand. Figures 4 and 5, but not their captions, should be transposed.