VERTICAL DISTRIBUTION

AND SECONDARY PRODUCTION

OF INVERTEBRATES IN THREE STREAMS

OF THE CASS BASIN.

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Abstract

The vertical distribution of benthic invertebrates was assessed seasonally in three contrasting streams at Cass, inland Canterbury using freeze core and substrate colonisation techniques. Biomass and production of selected invertebrate taxa were also measured at the three sites that differed in water chemistry, bed stability, and riparian setting.

Densities of aquatic invertebrates differed seasonally, with greatest numbers of most common taxa being present in summer and autumn. Overall, greatest abundances of invertebrates were found in the top 10 cm of the stream beds with densities being lowest at 20-30 cm, the deepest stratum sampled.

Biomass and secondary production were calculated for *Deleatidium* spp., two species of *Olinga* (*O. feredayi* and *O. jeanae*) , and Chironomidae, to determine whether conventional Surber sampling led to underestimations compared with freeze cores to a depth of 30 cm in the hyporheic zone. Results for the two streams for which full data sets were collected indicated that Surber sampling underestimated production of the different taxa to varying degrees although. *Deleatidium* production estimates for both streams were similar when calculated with freeze core data. However, estimates obtained for *Olinga* and Chironomidae were between 6.8 to 9.5 times greater. My findings have important implications for the accurate sampling of stream benthos, and indicate that conventional collection methods that consider only the top 10 cm or so of stream beds may severely underestimate the density and biomass of invertebrates.

Chapter 1

INTRODUCTION

Simplistically, streams and rivers can be viewed as one-way conduits for water and its associated nutrients and energy. However, the visible stream bottom is not the lower boundary of the stream ecosystem (Palmer, 1993; Jones and Holmes, 1996). Also important are longitudinal, lateral and vertical exchanges, which link the stream water and its associated communities with the surrounding environment (Ward, 1992).

Several studies carried out in Canada, Australia, Britain and Europe (Coleman and Hynes, 1970; Williams and Hynes, 1974; Poole and Stewart, 1976; Marchant, 1988; Bretschko, 1990 and Schmid-Araya, 1994) have demonstrated that aquatic invertebrates occur deep within the stream bed or hyporheic zone. This transitional zone between stream and groundwater can be defined as the saturated interstitial spaces of the stream bed and bank, the word hyporheic being derived from the Greek words *hypo* meaning under, and *rheo,* flowing or current. The hyporheos is an important habitat for numerous stream macroinvertebrates. Some are present only during a few stages of their lives (occasional hyporheos). They include some species of Ephemeroptera, Trichoptera and Plecoptera whose aquatic larvae may inhabit the hyporheic zone but whose adults are winged and non-aquatic. Others, such as some hemipterans, crustaceans and molluscs may occur in the hyporheic zone throughout their lives and are described as permanent hyporheos or hypogean organisms (Dahm & Valett, 1996). The depth at which hyporheic invertebrates occur within the streambed is influenced by the size, shape, strength and physiology

of the animals concerned, as well as physicochemical conditions of the subterranean environment (Williams, 1984; Hakenkamp *et al*, 1993; Stanford & Ward, 1993; Valett *et al*, 1993, and Brunke *et al*, 1997). Small larvae with elongate bodies, or hardened exoskeletons (e.g., Elmidae) are likely to be able to burrow deeper than mayflies like *Deleatidium* that have fragile leaf-like gills, or stoneflies such as *Stenoperla* spp. which require high concentrations of dissolved oxygen (Winterbourn, 1974; Marchant, 1995). Not all streams have an extensive hyporheos (Schmid-Araya, 1994). Variations in species presence and density can be related to the geomorphology of the stream, the extent and permeability of alluvial deposits being particularly important factors (Scarsbrook & Halliday, 1996). Storm flows that result in bed movement, and bedrock lying close to the streambed surface can also limit the extent and depth of the hyporheic zone, and as a consequence macroinvertebrate densities can be expected to vary spatially and temporally (Boulton *et al*, 1995; Dole-Olivier *et al*, 1997). Palmer (1993) considered the study of the hyporheic zone to be "the greatest challenge to experimental ecologists" because the potentially great depth and extent of the zone make it extremely difficult to investigate. Furthermore, experimental manipulations inevitably alter essential features of the underground system such as the nature and abundance of microhabitats, nutrient availability and water velocity.

The potential presence of large numbers of 'benthic' invertebrates in the hyporheic zone has important implications for stream ecosystem processes such as nutrient cycling, and potentially provides an important source of recolonists of surface sediments in streams denuded by disturbance events such as floods, drought or pollution (Palmer *et al*, 1992; Scarsbrook, 1995).
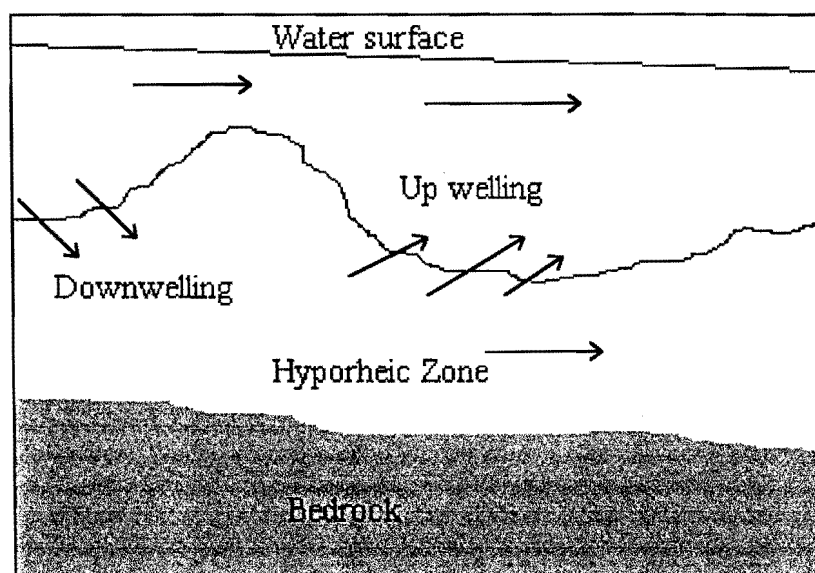
Figure 1.1 Conceptual longitudinal model of a stream showing the relationship between the stream water and hyporheic currents. Arrows indicate direction of water flow.

The passage of water through the hyporheic zone (Fig. 1.1) is influenced by substrate particle size, and the degree to which particles are packed. These factors in turn influence the availability of nutrients such as nitrogen and phosphorus, dissolved gases including oxygen, and the size and availability of interstitial spaces. Sand, for example, provides a poor substrate for most macroinvertebrates because of its instability, tight packing of grains, and consequent paucity of interstitial spaces that limit water, nutrient and oxygen transport.

Down-welling water currents may provide nutrients to the hyporheic zone, thereby influencing microbial growth, and potentially, the composition and size of hyporheic faunal assemblages (Williams, 1984; Hakenkamp *et al*, 1993; Brunke *et al*, 1997).

The first aim of my study was to determine the nature of the hyporheic faunas in three contrasting water courses within the Cass Basin, inland Canterbury, by means

of freeze-coring and a colonisation technique. Seasonal variation in vertical distribution patterns was also examined.

Three main methods are available for quantitative sampling of benthic invertebrates in river beds. They are pumping, substrate colonisation and coring. While pumping is often effective as a method of obtaining invertebrates, it is difficult to obtain accurate quantitative data in this way. It is often hard to estimate the amount of substrate sampled, and not all fauna will be collected equally well (Pugsley and Hynes 1983). For example, invertebrates attached to stone surfaces are likely to be more resistant to pumping than those inhabiting interstitial spaces. Substrate colonisation methods have been used to obtain quantitative data on vertical distribution of invertebrates within stream beds by several workers (Coleman and Hynes, 1970; Williams and Hynes, 1974; Scarsbrook, 1995; Huryn, 1996a) and one such method was included in my study. A limitation of colonisation techniques is that they may result in biased vertical distribution data through providing 'open corridors' to deeper substrates, both through disruption of the stream bed when burying samplers, and through unrepresentative packing of the substrates they contain. Consequently, the arrangement of particles within the sampler is unlikely to be the same as that of the undisturbed stream bed and so will give rise to differences in "microhabitat geometry".

Coring was considered by Pugsley and Hynes (1983) to be the best quantitative method available for sampling hyporheic invertebrates, as it allows simultaneous sampling at a range of depths. Unfortunately, many stony river beds are not easily sampled with mechanical corers which can rarely cope with large stones. Freeze coring was chosen as the principal sampling method in the present study because it

appeared to have several advantages over other methods. There should have been limited disruption of fauna during sampling since sampling pipes were put in place well before sampling, the freezing process was rapid and it did not involve mechanical disruption of the bed. Finally, cores obtained by freezing were able to be accurately divided into sections from which quantitative estimates of faunal abundance were obtained.

Few studies of the hyporheos have been undertaken in New Zealand, and when my study was first proposed, no vertical distribution research appeared to have been done. However, during the course of my study, Scarsbrook (1995) reported the results of experimental work done in Central Otago, New Zealand, using sterile substrate, recolonisation techniques. He showed that while the hyporheic zone may be a substantial potential source of colonists for stream beds disturbed by flood or drought, invertebrate species differ in their ability (related to physiology and anatomy) to benefit from this refuge. More recently, Scarsbrook and Halliday (1996) have given a short, popular overview of the hyporheos, and a brief assessment of the three vertical sampling methods described above.

The second aim of my study was to determine secondary production of selected benthic invertebrates in the three streams using freeze-core and conventional Surber sampling data, in order to assess whether "deep benthos" excluded from Surber samples results in significant underestimation of invertebrate production.

Huryn (1996a) recently addressed this question in the context of the Allen paradox (Allen,1951), which indicated that secondary production of aquatic invertebrates was insufficient to support trout production. The Allen paradox was a significant

outcome of the classic study of a New Zealand trout stream (the Horokiwi River, north of Wellington) and has never been adequately resolved (Huryn, 1996a). Inaccuracies in the calculation of invertebrate production, underestimation of terrestrial prey use by trout, and doubts over the validity of all trout production and fish cannibalism estimates have been implicated as reasons that might partly explain the paradox. However, inadequate sampling of the benthos may be the most important reason for the Allen paradox, if it results in underestimates of invertebrate production. Most faunal sampling programmes assume that all or most animals live close to the surface of the stream bed (within the top 10cm), despite sporadic evidence to the contrary (Williams and Hynes, 1974), but if this is not the case then traditional surface sampling with Surber, and Waters and Knapp (Merrit *et al*, 1996) samplers may result in serious underestimates.

Chapter 2

STUDY AREAS

Introduction

The three study sites were on small to medium sized water courses in the Cass

Basin close to the University of Canterbury Biological Station (map reference, 43°

19'S, 171° 46' E). The three streams are all part of the Waimakariri River system

(Fig. 2.1) but differ in hydrological conditions and bed characteristics.

The Cass Region

Physical description

The Waimakariri catchment was formed as a result of fault movement which

raised the Southern Alps vertically between 12 million and 1 million years ago

(Hayward, 1974). Severe ice action late in this period (late Tertiary - early

Pleistocene era) gouged the major faults into river channels. Five major glaciations

(Gage, 1977) deepened these valleys, and each retreat exposed steep greywacke

and argillite mountain slopes to frost, wind and rain action. Rock fragments moved

downslope to accumulate as screes, or were transported by rivers to give rise to

alluvial fans and terraces. These erosive processes continue in the present time.

Vegetation

As the mountain slopes were eroded, soils were formed and colonised by

vegetation. Climate changes resulted in successional changes in the terrestrial flora

(Schakau, 1993), and by the time of Polynesian occupation most of the region

below 1200 -1400m was forested with beech (*Nothofagus* spp.), podocarp
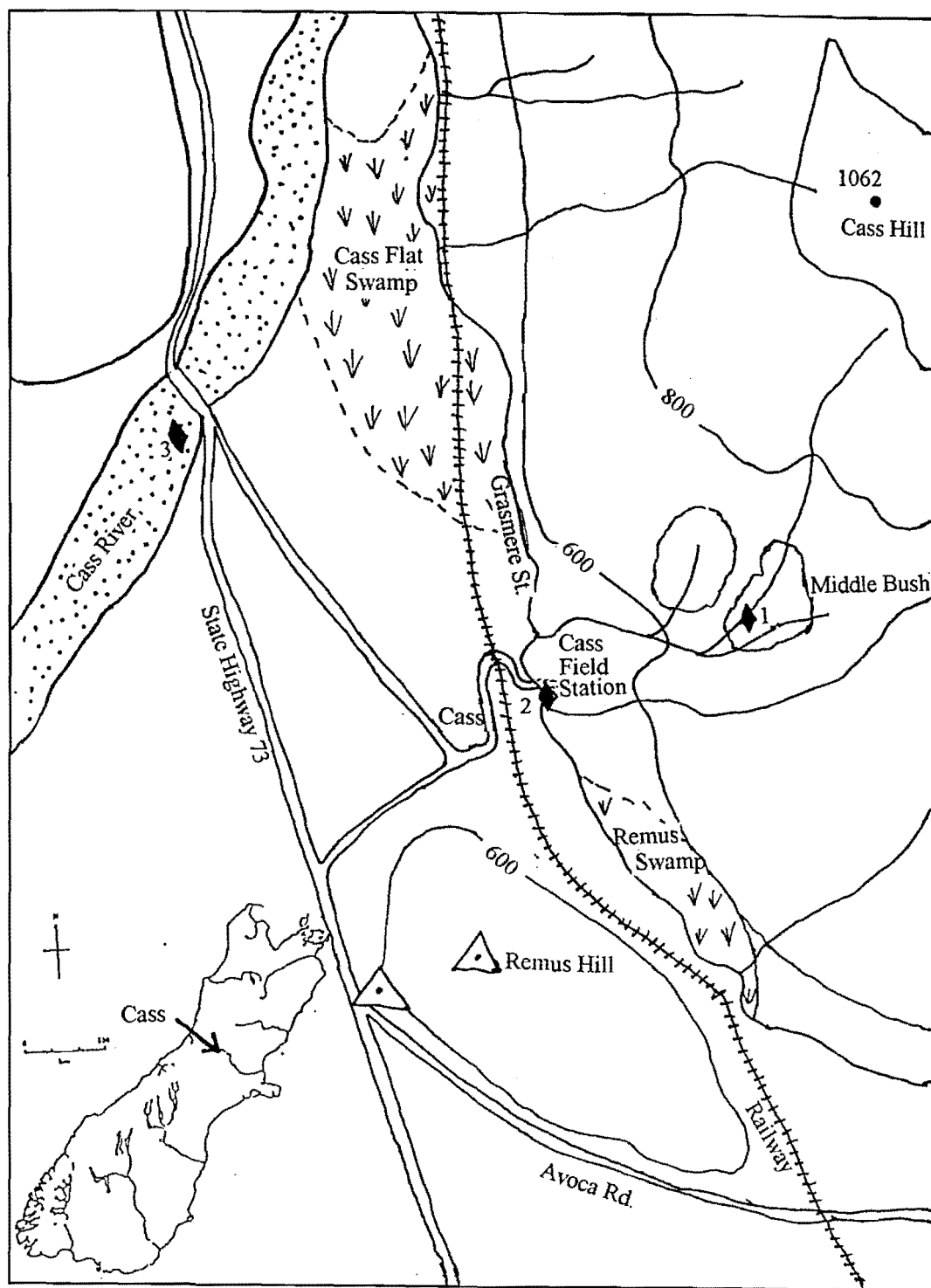
Figure 2.1 Map of the Cass Basin, showing the positions of the three study streams. 1. Middle Bush Stream; 2. Grasmere Stream; 3. Cass River. The insert shows the position of the Cass Basin in inland Canterbury, South Island, New Zealand.

(*Podocarpus* spp.), and kamahi (*Weinmannia racemosa*), kohekohe (*Dysoxylum spectabile*) and tawa (*Beilschmiedia tawa*) (Burrows, 1960; Moar and Lintott, 1977). Human occupation, both Polynesian and European resulted in the loss of this original forest through fire and the introduction of animal pests, exotic plants, and grazers (Relph, 1958; Hayward, 1974). Today the Cass area is characterised by tussock grassland, patches of the formerly widespread forest, especially in gullies, and plantings of exotic trees.

Climate

The surrounding mountains and high altitude (the Field Station is about 600m a.s.l) strongly influence weather patterns in the Cass area (Greenland, 1977). The region experiences high summer temperatures and relatively mild winters (Fig. 2.2). Greenland (1977) noted that annual rainfall at Cass ranged from 924 to 1856 mm between 1951 -1974, and during the 12 month period of my sampling (July 1995 to June 1996) the total precipitation recorded at the Biological Field Station was 1400 mm. Rainfall was lowest in January and February (Fig. 2.3) and snow fell occasionally in winter although it seldom persisted for more than a few days.

The Study Sites

Introduction

The study streams differed in source, size, disturbance events, and the rate and patterns of flow (see Death, 1991). They were chosen because they differed in these characteristics, and so were likely to provide contrasting hyporheic environments. Preliminary sampling also indicated that the three streams had some
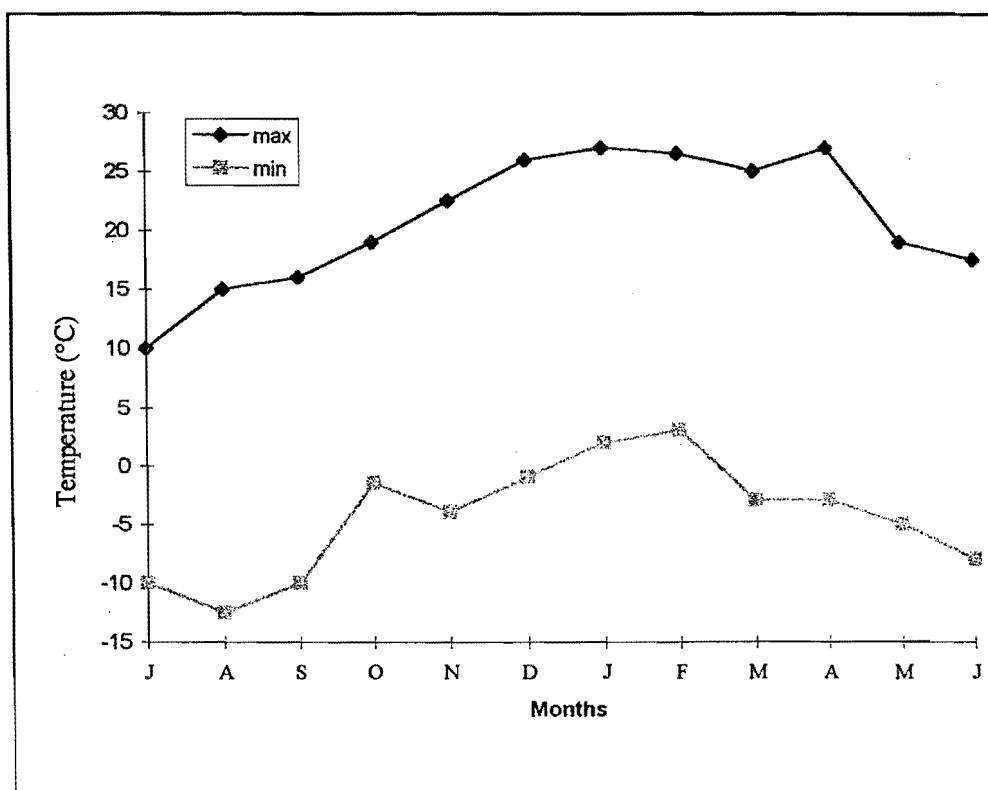
Figure 2.2 Monthly maximum and minimum air temperatures recorded at Cass
Field Station from July 1995 to June 1996.
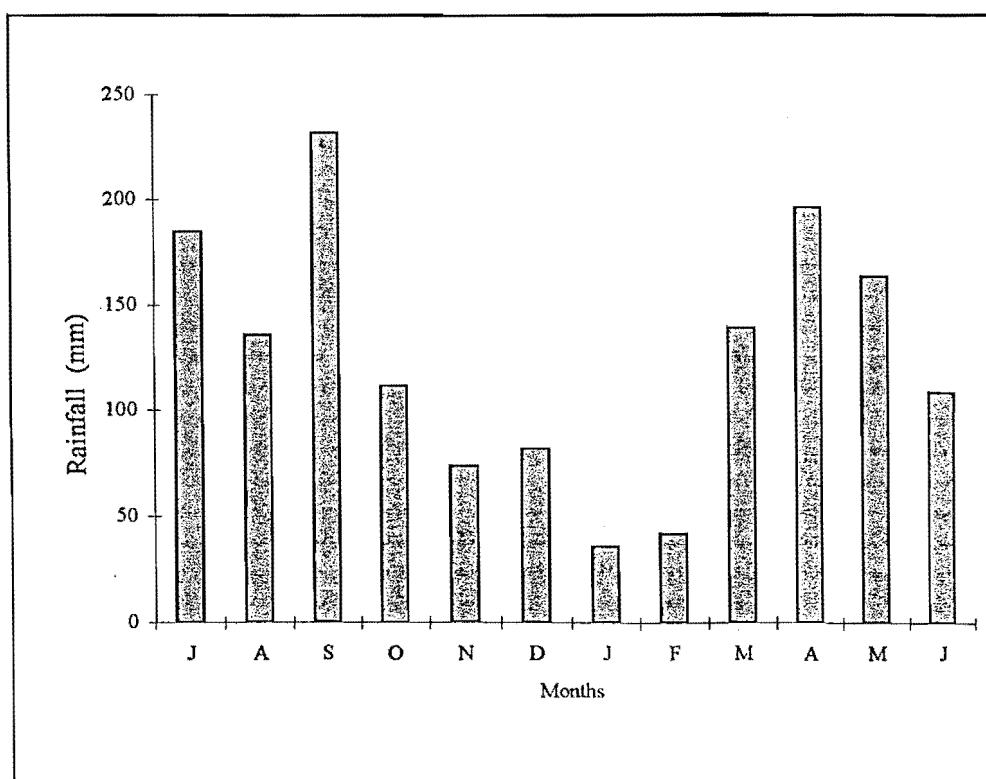
Figure 2.3. Monthly rainfall recorded at Cass Field Station from July 1995 to June 1996.

benthic invertebrate taxa in common (e.g., *Deleatidium* and Chironomidae) and would therefore provide the opportunity to make some specific faunal comparisons.

Middle Bush Stream

The smallest of the three water courses, Middle Bush Stream (Fig. 2.4A) is a first order stream on the south side of Cass Hill, and although spring fed, its discharge is strongly influenced by rainfall events. This stream drains a 28ha catchment of subalpine scrub, tussock and bare scree (Winterbourn, 1977) and flows down a relatively steep-sided valley through mixed scrub, before entering a stand of mountain beech (*Nothofagus solandri* var. *cliffortioides*). The sampling site was situated within the beech forest, where the shaded stream bed was littered with branches and leaves that are trapped in pools and amongst boulders. The gradient of the stream at the sampling site was approximately 7°, and the stony bed comprised poorly defined riffles and pools. Allochthonous litter input occurs year round although the maximum leaf fall occurs in the summer half of the year (Winterbourn, 1978). The benthic community has been the subject of several studies (see Death, 1991; Winterbourn, 1995).

Grasmere Stream

This stream (Figure 2.4B) is the outlet of Lakes Sarah and Grasmere, two glacial lakes south of the Biological Station. It flows through tussock grassland for most of its length, but passes through a bed of flax (*Phormium tenax*) and rushes (*Typha orientalis*) just above the study site. Grasmere Stream has a low gradient

Figure 2.4 Photographs of the three streams showing the physical characteristics, and surrounding terrain. A. Middle Bush Stream, a mountain bush stream; B. Grasmere Stream, flowing though tussock grassland; and C. Cass River, above State Highway 73, with Mt. Misery in the background.

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(2°) and a stable bed of gravel and cobbles with no well-defined riffle/pool sequences. An obvious growth of epilithic algae occurs for most of the year, along with some patches of *Nasturtium* sp. Grasmere Stream has been the site of several recent studies of benthic invertebrates (Death, 1991; Winterbourn and Harding, 1993; Shearer, 1995).

Cass River

This is a gravel-bed river (Figure 2.4C) with a meandering braided channel. One major braid is usually present but even it may dry up in the lower reaches of the river during summer. At the study site, upstream of the bridge on Highway 73, the gradient of the river is 3°, and the channel positions are continually fluctuating. The broad flood plain of the river drains a catchment of predominantly subalpine tussock, pasture, bare scree and remnant patches of mountain beech. Although much of the river bed is dry for long periods, it is periodically inundated so that little terrestrial vegetation is present. No previous studies have been made on the benthic invertebrate fauna of the Cass River.

Physicochemical Characteristics

Introduction

A number of parameters were measured seasonally so that physical and chemical differences between the sites could be documented.

Materials and Methods

Physical characteristics

Depth and current velocity were measured in each stream immediately adjacent

to each sample collection point. Measurements were averaged to give a mean value

for each season. Water velocity was measured midway between the water surface

and the stream bed using a Hydrological Services meter, model OSS-PCI equipped

with a 50 mm propeller. Water temperature was determined on each sampling

occasion with a hand-held thermometer. Substrate composition was assessed for

each stream and each depth category (0-10 cm, 10-20 cm, 20-30 cm) by separating

all freeze core samples into predetermined substrate categories and determining their

average percentage composition by weight. This procedure was performed in the

laboratory concurrently with faunal separation and identification procedures.

Chemical characteristics

Conductivity and pH of stream water were measured in the field or on water

samples immediately on return to the laboratory. Water samples were collected in

opaque polyethylene bottles and stored at $7°$ C. Conductivity (μS cm^{-1}) was

measured at $25°C$ with a Hanna HI 8333 conductivity meter, and pH was measured

with a Metrohm E488 meter and electrode. Alkalinity was determined by titration

of 100 ml samples with 0.01N HCl to an endpoint at pH 4.5 (Mackereth, 1963)

and is reported as mg l^{-1} CaCO$_3$.

The Pfankuch technique (1975) was used to evaluate stream channel stability. The method involves the subjective rating of 15 variables in three regions of the stream channel; upper banks, lower banks and stream bed, relative to descriptors on a standard evaluation form (Appendix 1). Summing of all selected scores gives an overall stability rating (SR) which can range from 36 to 154. The lower the rating the more stable the site. SR indicates the capacity of a particular reach to resist bed and bank material detachment, and to recover from hydrological disruption. Pfankuch stability scores, especially the streambed component, were correlated with taxonomic richness and/or abundance of benthic invertebrates in other South Island stream studies (Rounick & Winterbourn, 1982; Death, 1991; Collier, 1992).

Results and Discussion

Physical and chemical characteristics

Middle Bush and Grasmere Streams occupied well defined channels, whereas the braided Cass River channels changed position and size between each sampling date. It ranged in width from 2.5 to 8m on the four sampling days, but depth was always 10 to 16 cm. Middle Bush Stream was the narrowest and shallowest stream in all seasons, whereas Grasmere Stream was always the deepest (Table 2.1). Cass River showed the least seasonal variation in water temperature (range 8.5 to 10.5 °C), whereas Grasmere Stream and Middle Bush Stream were considerably warmer in summer than in other seasons. Grasmere Stream was the fastest flowing of the three streams, followed by the Cass River and Middle Bush Stream.

The pH of all three streams was circumneutral (Table 2.2) and ranged from 7.2 at Middle Bush Stream to 7.9 at both Grasmere Stream and Middle Bush Stream.

Alkalinity varied between the streams (Table 2.2) ranging from 18 mg L^{-1} $CaCO_3$ (Cass River) to 44 mg L^{-1} $CaCO_3$ (Middle Bush Stream).

The mean conductivity of the three streams was 102 (Middle Bush Stream), 68 (Grasmere Stream) and 48 μS cm^{-1} (Cass River) and small differences were found seasonally (Table 2.2). Conductivity measures are indicative of ionic concentration and like alkalinity probably reflect differences in the origins of the water, and in the geology of the catchments. The conductivities of the three streams fall within the range of values reported by Death (1991) for eleven streams in the Cass- Porters Pass region.

There was little variation in substrate composition either between the streams, or between depth categories within streams (Fig. 2.5). All levels were dominated by large cobbles (>9 mm) in all streams, with small cobbles (3 - 9 mm) the next most abundant category (Table 2.3). Consequently, similar habitat niches should be available to benthic invertebrates throughout the 30 cm study depth in all three streams.

Table 2. 1. Water temperature readings, and mean width, depth and current velocity measurements for Grasmere Stream, Middle Bush Stream and Cass River on four occasions between July 1995 and June 1996.

Site	Season	Water temperature (°C)	Width (m)	Depth (cm)	Velocity (m/s)
Grasmere Stream	Spring	11.5	4.4	40	0.74
	Summer	19	3.7	32	0.86
	Autumn	11	3.6	26	0.51
	Winter	8.5	4.5	50	0.98
Middle Bush Stream	Spring	5	0.9	10	0.47
	Summer	18	0.8	5	0.27
	Autumn	9	0.9	7	0.19
	Winter	6	0.4	10	0.42
Cass River	Spring	9	4.9	12	0.62
	Summer	10.5	2.5	11	0.51
	Autumn	10	5	16	0.64
	Winter	8.5	8	11	0.64

Table 2.2 Water chemistry value for the three study streams for the period July 1995 to June 1996.

Site	Season	Alkalinity mg/l $CaCO_3$	Conductivity $\mu S\ cm^{-1}$	pH
Grasmere Stream	Spring	39	53	7.8
	Summer	32	68	7.4
	Autumn	37	72	7.3
	Winter	37	81	7.9
Middle Bush Stream	Spring	42	96	7.7
	Summer	43	103	7.9
	Autumn	44	101	7.6
	Winter	36	110	7.2
Cass River	Spring	24	44	7.7
	Summer	20	48	7.6
	Autumn	21	49	7.4
	Winter	18	52	6.8

Table 2.3 Substrate material greater than 3 mm diameter presented as a percentage of total mass for the three study streams.

Site	Depth (mm)	Cobble size		
		>9 mm	3 - 9 mm	Total >3 mm
Grasmere Stream	0-100	59	17	76
	100-200	48	20	68
	200-300	43	22	65
Middle Bush Stream	0-100	61	15	76
	100-200	51	19	69
	200-300	50	17	67
Cass River	0-100	63	16	79
	100-200	47	20	67
	200-300	38	22	60

A.
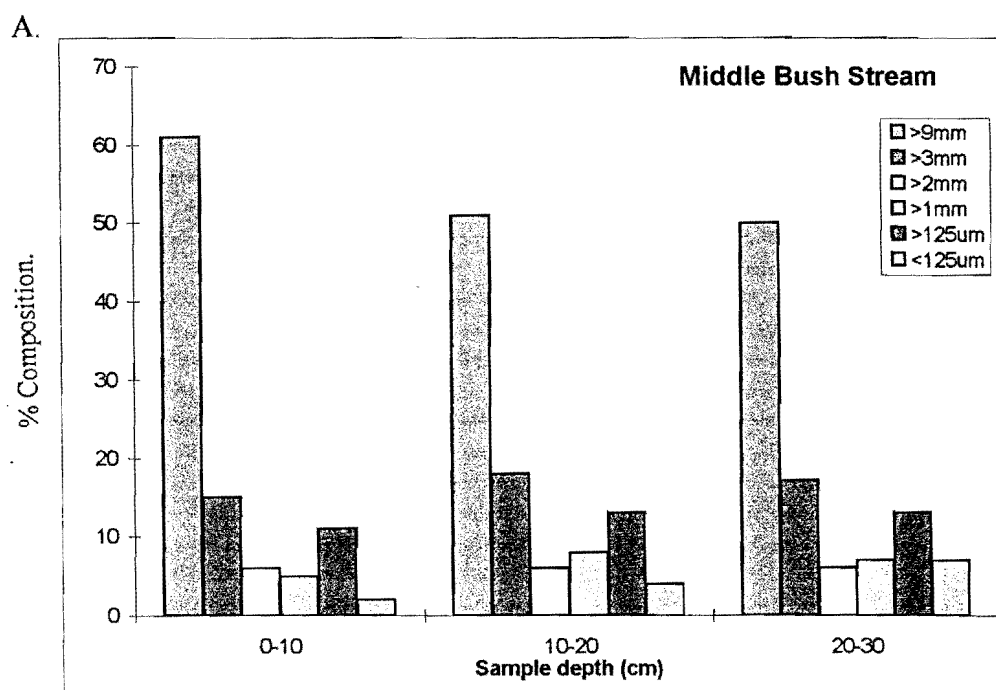
Figure 2. 5. Percentage substrate composition for the three study sites and three depth categories sampled during the period July 1995 to June 1996. A. Middle Bush Stream, B. Grasmere Stream, C. Cass River.

B.
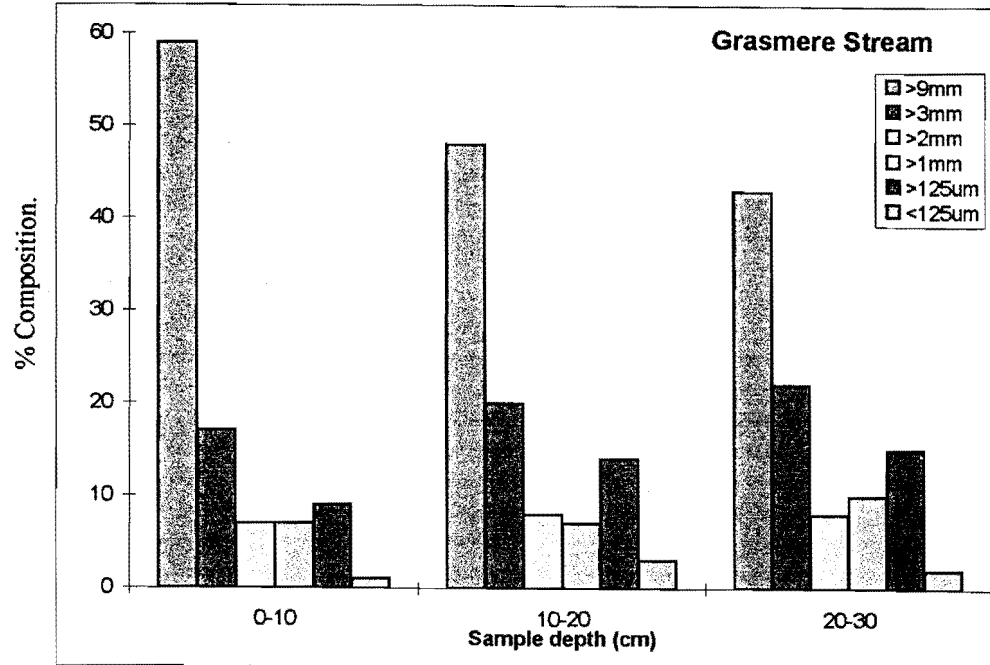
C.
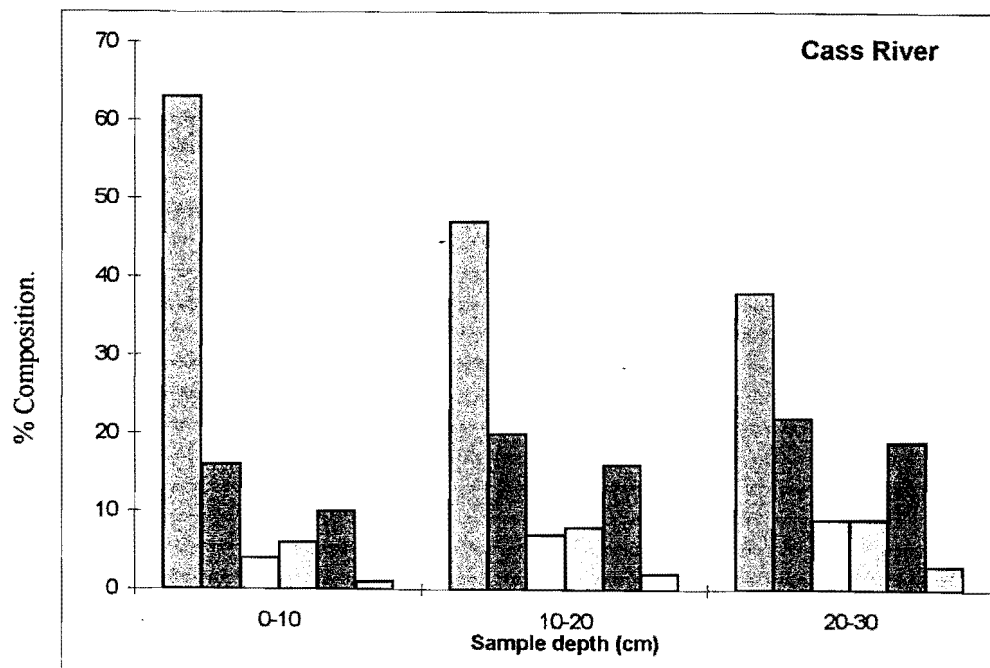
Figure 2. 5.(contd).

Stream stability evaluation

The Pfankuch stability scores indicated that Grasmere Stream, with its low gradient and constant water flow, was more stable than Middle Bush Stream, which in turn was more stable than Cass River (Table 2.4).

Table 2.4. Pfankuch stability scores for the three study streams.

Site	Total score	Upper Bank	Lower Bank	Bottom Component
Grasmere Stream	59	15	21	23
Middle Bush Stream	100	33	29	38
Cass River	120	17	44	59

The scores for the lower banks and bottom components ranked the three sites in the same order, but the ranking was different for the upper banks. These were vegetated in tussock grass at Cass River and Grasmere Stream but forested at Middle Bush Stream (the Pfankuch method was designed for forest stream evaluation). Bank stability and large debris potential were therefore greater at Middle Bush Stream, and contributed substantially to the higher upper bank score there. Grasmere Stream, a lake outlet with a constant water flow showed little evidence of scouring and deposition of fine materials and therefore had a much lower bed score than the other two streams.

In summary, the three streams were exposed to similar climatic conditions, and had almost identical pH. However, they showed differences in some aspects of their water chemistry (alkalinity and conductivity), physical characteristics (stream

width, depth, current velocity, and water temperature), stream stability and channel gradient at the sampling sites. All three streams had beds formed from greywacke sandstone, and had similar particle size distributions both at the surface (top 10 cm) and deeper in the bed (10-20 and 20-30 cm).

Chapter 3

THE VERTICAL DISTRIBUTION
OF AQUATIC INVERTEBRATES WITHIN
THREE STREAM BEDS

Introduction

It has long been recognised that the hyporheic zone, i.e., the saturated

interstitial spaces within the stream bed, is a dynamic habitat (Ward, 1992; Palmer,

1993; Allan, 1995) with benthic invertebrates occurring to depths of at least 70 cm

(Coleman and Hynes, 1970; Williams and Hynes, 1974; and Marchant, 1988,

1995). Consequently, use of conventional samplers (e.g., Surber sampling) which

allow penetration of the stream bed to a depth of only 5-10 cm almost certainly

leads to inaccuracies in benthic invertebrate density estimations in many instances.

Research on the vertical distribution of aquatic invertebrates has been carried

out in North America (Hynes, 1974; Williams and Hynes, 1974; Godbout and

Hynes, 1982; Pugsley and Hynes, 1983), Europe (Efford, 1960; Hynes *et al*, 1976;

Morris and Brooker, 1979; Bretschko, 1990), Malaysia (Bishop, 1973), and

Australia (Marchant, 1988, 1995; Marchant and Lilywhite, 1989). At the

commencement of my study, no vertical distribution work was known from New

Zealand, but Scarsbrook (1995) has since described hyporheic research in two

tributaries of the Taieri River, Otago, and Huryn (1996a) examined the depth

distribution of invertebrates in Sutton Stream, Otago.

Generally, the above studies concluded that the percentage of invertebrates

occurring in the top 10 cm of stream substrate is variable, with physical and

chemical factors being important in determining vertical distributions (Williams, 1984; Scarsbrook, 1995). However, Marchant (1988) found that the majority (72-84%) of the fauna sampled during summer in Thomson River (Victoria, Australia) occurred within the 0-10 cm depth range. Scarsbrook's New Zealand work showed that while species composition was similar between the benthos and hyporheos, several benthic species were absent, or present in reduced numbers in the hyporheic zone.

The need for quantitative sampling of the hyporheos has led to the investigation of alternative sampling methods. I considered three options, but quickly eliminated mechanical corers, which have limitations in stony riverbeds, due partly to grainsize of the sediments, and partly to the disruptive forces associated with using them (Williams and Hynes, 1974).

My first choice was freeze-coring, which overcomes the disruptive problems associated with mechanical corers. Originally, freeze corers collected a frozen sample **within** the sampling tube (Efford, 1960), but now more commonly, the "core" is frozen to the **outside** of the pipe (Pugsley and Hynes 1983; Marchant and Lilywhite 1989).

Freeze coring has its own drawbacks, in that it may underestimate benthic faunal densities close to the surface of the stream bed due to non-retrieval of loose rocks and their attached fauna from the bed surface (Marchant, 1988). Bretschko (1990) also questioned the accuracy of abundance estimations and depth distribution data because of the rapid escape reactions (starting less than 15 seconds after the beginning of the perturbation) of some benthic invertebrates

during the freezing process. However, an important advantage of the freeze coring method is the short time required to sample compared with colonisation tubes, which were the second method I chose.

Substrate colonisation using perforated tubes packed with clean (fauna free) substrate of similar particle size to the recipient stream bed, and sunk into the bed to a predetermined depth is the technique that has been used by a number of stream ecologists to study vertical distribution (Coleman and Hynes, 1970; Williams and Hynes, 1974; Scarsbrook, 1995; Huryn, 1996a). Several problems are associated with this method (Williams and Hynes, 1974; Rosenberg and Resh, 1982), including inadequate packing of substrate in the tube giving rise to vertical 'corridors', and loss of fine material during insertion and retrieval of the tubes. The time required for complete recolonisation of artificial substrates is also a matter of debate, with 28 days being considered acceptable by many workers (e.g., Coleman and Hynes, 1970; Williams and Hynes, 1976; Kramer, 1982). However, Scarsbrook (1995) left his hyporheic samplers in place for three months, and Huryn (1996) allowed a colonisation period of 3 months or more.

For my study, three sampling techniques were attempted in three streams; two hyporheic sampling methods to study the vertical distribution of benthic invertebrates, and Surber sampling to provide additional data for secondary production estimates.

Sampling program

Surface sampling

Conventional sampling of the stream bed involves disrupting and scraping the upper bed sediments and catching released material in a net. While the area sampled can be standardised to a certain extent by using a quadrat to sample within, the depth to which the area can be sampled may not be consistent unless the tool used for scraping is suitably calibrated.

A Surber sampler ($0.09m^2$, 0.5 mm mesh) was used to collect five samples from the top 10 cm of substrate in each of four seasons. Samples were preserved in 70% ethanol, and returned to the laboratory for sorting, counting and measurement of invertebrates.

Vertical sampling

Freeze corers

Freeze-coring was attempted at all three study sites, with varying degrees of success. At the Cass River, it was not possible to produce a complete set of cores in all seasons, because of the nature of the substrate and the inconsistency of water flows. On two occasions, the standpipes were driven into place, and within 24 hours the river level rose to such an extent that it was unsafe to proceed with the freezing process.

The equipment used for freeze-coring was based on that of Marchant & Lilywhite (1989), but modified to use dry ice as the freezing agent rather than liquid CO_2 or liquid nitrogen. This decision was based on safety, and on storage limitations at the Cass Field Station.

The standpipes were made from 35 mm internal diameter galvanised pipe, with a conical steel driving tip welded on to the lower end (Fig. 3.1A). The pipes were 1.04 m long, and had two steel rings welded to their outer surfaces. The upper ring supported the steel driving cap (Fig. 3.1C) which protected the top of the pipe when it was being driven into the substrate. The lower one supported the separate lifting assembly (Fig. 3.1B) which was held in position by a metal pin inserted through holes bored in the lifting assembly and the standpipes. Solid CO_2 (dry ice) was transported in polystyrene boxes ('chillybins') and stored in a conventional freezer until used.

In the field, the standpipes were hammered vertically 30 cm into the stream bed with a sledge hammer. The depth of penetration was measured with a graduated rod from a predetermined point on the driving cap. Rubber bungs were inserted in the top and side holes of the standpipes to prevent the entry of moisture that would interfere with the freezing process. The pipes were left for 24 hours before freezing to allow the fauna to recover from any disturbance associated with the hammering (Marchant & Lilywhite, 1989). Thick rubber tubing was placed around the outside of the tubes to reduce the likelihood of heating by water flowing past during the freezing operation. The freezing procedure involved pouring dry ice pellets into the standpipe through a funnel. A rod was used to gently tamp these down. Timing of the operation began once the pellets were packed in to just below the level of the lifting assembly anchor holes. Satisfactory cores were usually frozen on to the outside of the pipe within 20 minutes, but the

Figure 3.1 Freeze-coring equipment. A: Standpipes with one jack used for lifting; B. Close-up of the lifting gear on standpipe; and C. The driving caps used to protect the top of the standpipe during hammering.

time needed was influenced by the temperature of the air and the water. To

remove a standpipe and core, the lifting assembly was fitted over the pipe, two

halves of a steel split sleeve were fitted under the lower ring and a steel pin was

inserted to secure the apparatus. Two jacks (Fig. 3.1 A) were then fitted into the

loops on the assembly and the whole apparatus was jacked vertically out of the

stream bed. The frozen sediment core (Fig. 3.2) was removed from the pipe in

10 cm lengths using a bolster and hammer, and the sections were bagged

separately and kept frozen until processing could be undertaken in the laboratory.

In the laboratory, each section of core was weighed and its volume

determined. Each section was then placed on a 120 μm mesh sieve and all fine

mud and silt was washed through it into a container. The fauna were separated

from the remaining substrate by elutriation. Animals were sorted, identified to

species level where possible (Winterbourn & Mason, 1983; Winterbourn &

Gregson, 1989), and counted in a Bogorov sorting tray. Sediments were passed

through a series of sieves, dried and weighed (see Chapter 2, substrate analysis).

Colonisation samplers

In addition to freeze core sampling, the hyporheic zone of each stream was

sampled seasonally with perforated re-colonisation samplers dug into the

substrate.

Figure 3.2 Frozen core on standpipe.
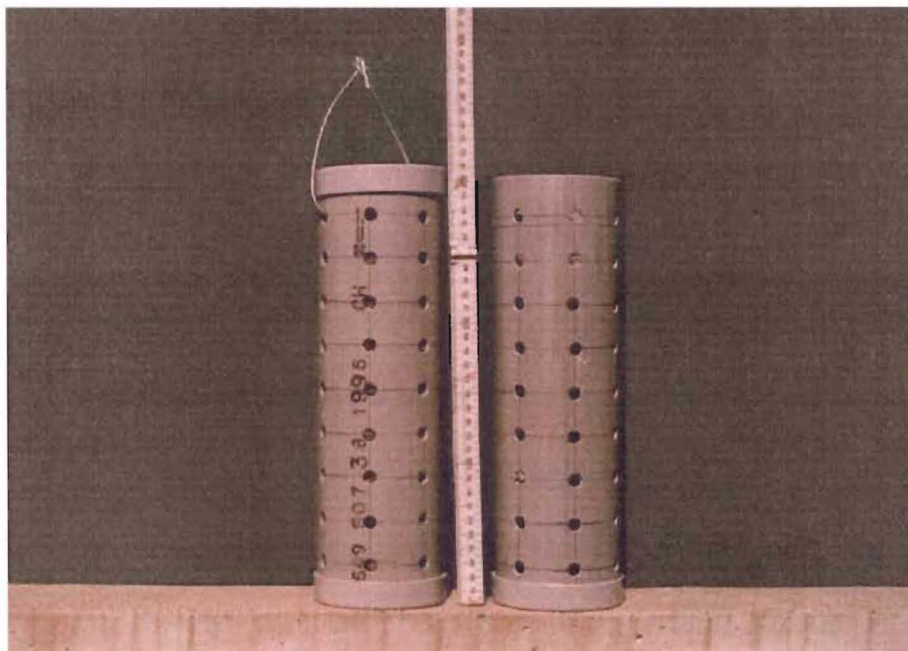
Figure 3.3 Perforated colonisation tubes, one with cap and lifting wire in place.

My original intention was to dig perforated samplers into the substrate of all three streams, and to retrieve them after 1 month each season. However, the Cass River site was eliminated after the pipes could not be found at the end of the first recolonisation period because of substantial bed movement, and when it was not possible to penetrate the substrate to the required depth the following season.

The technique involved digging three perforated samplers into each stream bed to a depth of 30 cm. The samplers (Fig. 3.3) were manufactured from PVC pipe (110 mm diameter, 300 mm long) with nine rows of 10 mm holes drilled along their lengths, 63 holes in all. The bottom end of each pipe was sealed with a plastic cap, and a similar removable cap was used to close the top. The tubes were packed with clean substrata of similar composition to that of the appropriate stream bed, and plastic mesh discs (1 cm mesh size) were inserted into them 10 and 20 cm from the bottom so they were divided into three equal portions but . A piece of number 8 fencing wire was threaded through the top third of the pipe as a lifting device, and a length of rope with a marker tag attached was tied to it. Holes were dug in the stream bed by hand, and the pipes were inserted until the level of the top plastic cap was level with the stream bottom. The pipes were left in position for 28 days to allow invertebrates to colonise (Coleman and Hynes, 1970; Williams and Hynes, 1974; Kramer 1982). The pipes were removed from the substrate by lifting them vertically with the wire handle. On the bank, each gravel core was separated into three 10 cm sections using the mesh dividers as guides. Each section was preserved using 70% ethanol .

In the laboratory, the samples were washed on a 120 μm mesh screen to remove fine material, and invertebrates were elutriated from the remainder. Animals were identified to species level where possible and counted.

Eight groups of invertebrates, incorporating taxa that were common to all streams, and were comparable to categories used in research elsewhere, were selected for analysis of vertical distributions. *Cristaperla fimbria* (Plecoptera) occurred only at Middle Bush Stream, but was included because it occurred in all three depth strata. The invertebrate categories were:

(1) Total invertebrates

(2) Total Ephemeroptera

(3) *Deleatidium* spp.

(4) Total Trichoptera

(5) *Olinga feredayi* (Grasmere Stream), and *O. jeanae* (Middle Bush Stream)

(6) Total Plecoptera

(7) *Cristaperla fimbria*

(8) Chironomidae

Statistical analysis of distribution data obtained with both hyporheic sampling methods was performed using two-way ANOVA (SAS) on log transformed data with depth and season as fixed factors. Invertebrate densities at three depth levels and four seasons were compared.

Results

Sixty aquatic invertebrate taxa were identified from the three streams over

the twelve month sampling period (Table 3.1). Middle Bush Stream had the most

diverse fauna with 44 taxa present, followed by Grasmere Stream with 35,

Table 3.1. Taxa taken from at the three streams, July 1995 to June 1996.

	Middle Bush Stream	Grasmere Stream	Cass River
Neuroptera			
Kempynus sp.	+		
Mecoptera			
Nannochorista philpotti	+		
Megaloptera			
Archichauliodes diversus	+		
Ephemeroptera			
Coloburiscus humeralis		+	
Nesameletus sp.	+		+
Oniscigaster wakefieldi			+
Deleatidium spp.	+	+	+
Plecoptera			
Stenoperla prasina	+	+	+
Austroperla cyrene	+		
Zelandoperla fenestrata	+		+
Zelandobius furcillatus	+	+	+
Acroperla trivacuata	+		
Cristaperla fimbria	+		
Spaniocerca zelandica	+		
Trichoptera			
Aoteapsyche colonica		+	+
Aoteapsyche tipua	+		
Oxyethira albiceps		+	+
Psilochorema sp.	+	+	
Hydrobiosis parumbripennis	+	+	
Polyplectropus sp.	+	+	
Hydrobiosella stenocerca	+	+	+
Zelandopsyche ingens	+	+	
Hudsonema amabilis	+	+	+
Philoreithrus agilis	+		+
Pycnocentria sylvestris	+		
Pycnocentria evecta		+	+

Table 3 contd.

	Middle Bush Stream	Grasmere Stream	Cass River
Pycnocentrodes sp.		+	+
Beraeoptera roria			+
Olinga feredayi		+	+
O. jeanae	+		
Hemiptera			
Microvelia macgregori	+		
Coleoptera			
Elmidae	+	+	
Hydraenidae	+		+
Scirtidae	+		+
Staphylinidae			+
Ptilodactylidae	+	+	
Hydrophilidae		+	
Diptera			
Aphrophila neozelandica		+	
Eriopterini	+		+
Ceratopogonidae	+	+	
Other Tipulidae	+	+	+
Tabanidae	+		
Tanypodinae			+
Neocurupira sp.			+
Nothodixa sp.	+		
Austrosimulium spp.	+	+	+
Chironomidae	+	+	
Stratiomyidae	+	+	
Coelenterata			
Hydrida	+	+	+
Platyhelminthes			
Neppia montana	+	+	
Annelida			
Oligochaeta	+	+	+
Hirudinea		+	
Mollusca			
Potamopyrgus antipodarum	+	+	
Physa acuta		+	
Crustacea			
Copepoda	+	+	+
Cladocera		+	+
Ostracoda	+	+	+
Amphipoda	+	+	
Other Arthropoda			
Acarina	+		
Collembola	+	+	

and Cass River with 28. Some taxa were found at all sites e.g., *Deleatidium* spp.,

Chironomidae, Oligochaeta and Copepoda, while others such as *Aoteapsyche*

tipua and *Olinga jeanae* occurred only at Middle Bush Stream.

Freeze cores

Results of a two-way ANOVA comparing depth and seasonal density

variations based on 9 litre sample volumes are summarised in Table 3.2 for

Grasmere Stream, and Table 3.3 for Middle Bush Stream.

In Grasmere Stream (Table 3.2) significant differences (P<0.05) in density

with depth were found for three of the selected invertebrate taxa (total

invertebrates, total Ephemeroptera, *Deleatidium* spp.), whereas Chironomidae

showed a significant depth*season interaction.

Figures 3.4 and 3.5 show mean seasonal densities (± 1 SE) for the three

depth categories and the eight selected taxonomic groups. At Grasmere Stream

(Fig. 3.4A) approximately 70% of invertebrates occurred in the top 10 cm of

substrate in winter and spring, but they were more evenly distributed within the

cores in the other two seasons. Total density peaked in autumn. Mean densities

for the other seven selected taxa (Fig. 3.4B) showed various distribution patterns.

Chironomid densities did not differ seasonally (Table 3.2), but greatest numbers

were found at a depth of 20-30 cm. Most Ephemeroptera (70%) occurred in the

top 10 cm of stream bed, with little seasonal variation in total density, a pattern

repeated within this group by the dominant taxon *Deleatidium*. Total density of

Trichoptera showed little seasonal variation, and most animals occurred in the top

10 cm, except during winter when they were evenly distributed through the 30 cm

cores. Within this group, *Olinga feredayi* had a fairly even distribution, with an

autumn density peak in the top 10 cm. Plecoptera occurred in summer, mainly at

20-30 cm depth, and were very small larvae, probably of *Zelandobius*.

Table 3.2. Summary of two-way ANOVA comparisons of invertebrate density (season, df =3, depth, df =2) for freeze core data from Grasmere Stream. Sample volume was 9L. Significant P values are shown in bold.

|	**Source**	**F ratio**	**P**
Total invertebrates	Season	1.87	0.15
	Depth	3.88	**0.03**
	Season*depth	0.91	0.5.
Total Ephemeroptera	Season	1.41	0.26
	Depth	5.97	**0.005**
	Season*depth	1.37	0.25
Deleatidium spp.	Season	1.18	0.33
	Depth	4.57	**0.02**
	Season*depth	1.07	0.40
Total Trichoptera	Season	1.08	0.37
	Depth	2.91	0.07
	Season*depth	0.27	0.95
Olinga feredayi	Season	0.37	0.78
	Depth	1.04	0.36
	Season*depth	0.64	0.70
Total Plecoptera	Season	0.77	0.52
	Depth	0.08	0.93
	Season*depth	1.36	0.26
Chironomidae	Season	0.6	0.62
	Depth	0.17	0.85
	Season*depth	2.36	**0.05**
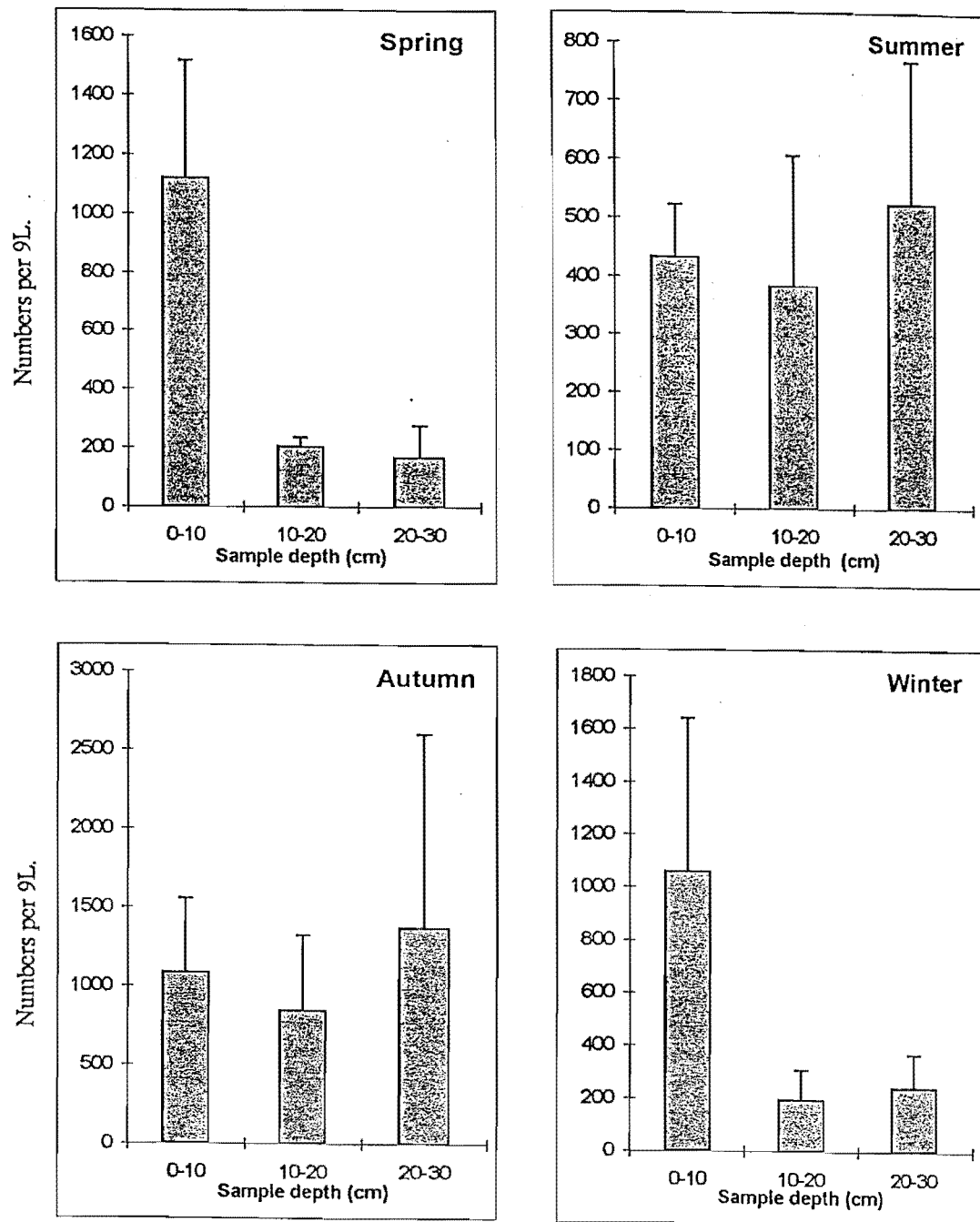
Figure 3.4A. Mean densities (± 1SE) of total invertebrates at Grasmere Stream in four seasons, sampled by freeze coring.
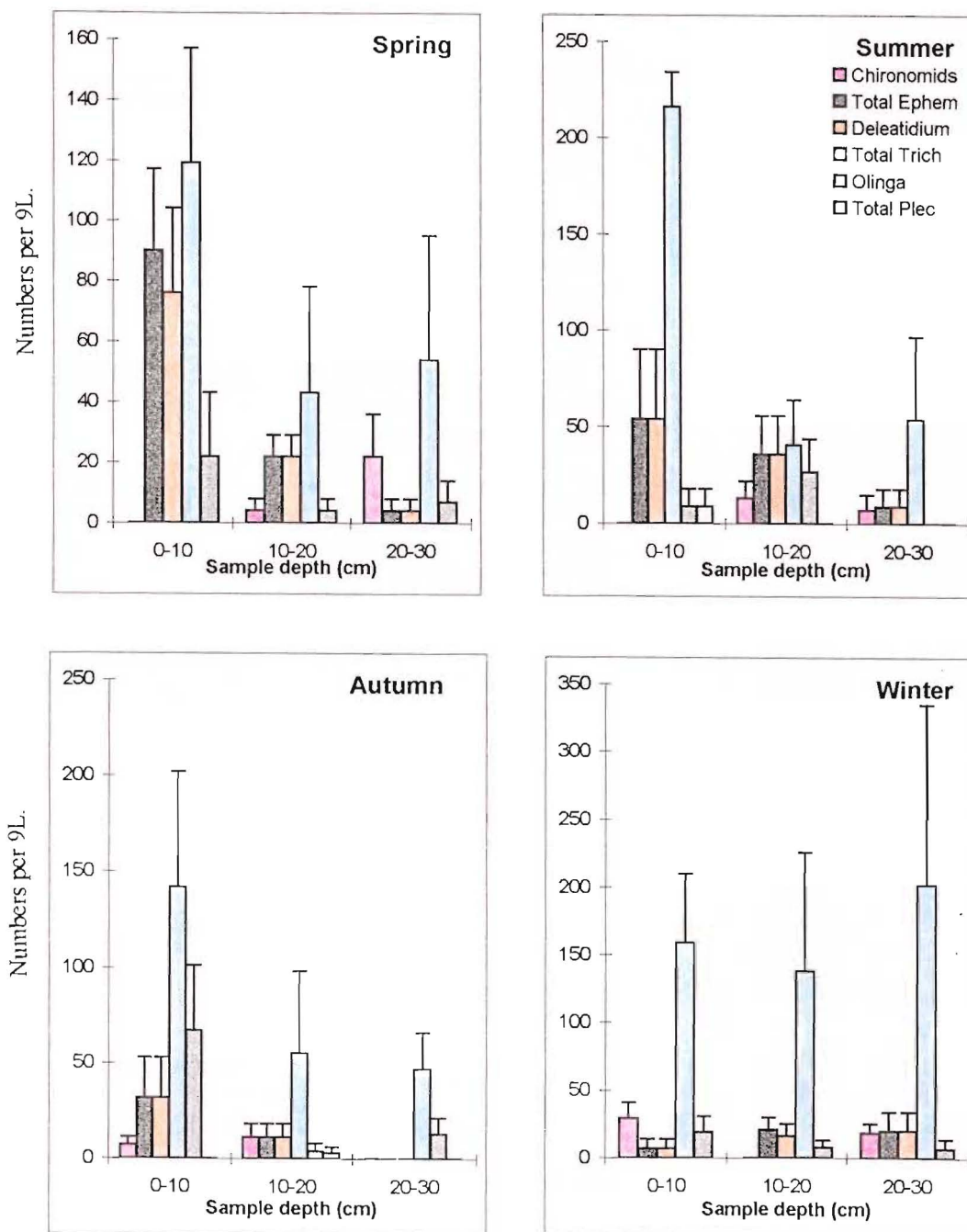
Figure 3.4B Mean densities (± 1SE) of selected taxa from Grasmere Stream in four seasons, sampled by freeze coring.

Table 3.3 Summary of two-way ANOVA comparisons of invertebrate density (season, df =3, depth, df =2) for freeze core data from Middle Bush Stream. Sample volume was 9L. Significant P values are shown in bold.

	Source	F ratio	P
Total invertebrates	Season	0.93	0.433
	Depth	6.82	**0.003**
	Season*depth	1.97	0.092
Total Ephemeroptera	Season	1027	0.297
	Depth	2.54	0.091
	Season*depth	0.88	0.521
Deleatidium spp.	Season	1.3	0.286
	Depth	2.44	0.099
	Season*depth	0.91	0.496
Total Trichoptera	Season	1.72	0.179
	Depth	7.97	**0.001**
	Season*depth	0.51	0.768
Olinga jeanae	Season	0.80	0.502
	Depth	5.18	**0.0001**
	Season*depth	0.53	0.779
Total Plecoptera	Season	4.43	0.009
	Depth	4.86	**0.013**
	Season*depth	0.64	0.700
Cristaperla fimbria	Season	10.8	**0.0001**
	Depth	1.04	0.363
	Season*depth	0.55	0.765
Chironomidae	Season	1.0	0.404
	Depth	5.47	**0.008**
	Season*depth	2.21	0.061

In Middle Bush Stream significant (P<0.05) differences in density with depth

were found for total invertebrates, total Trichoptera, *Olinga*

Figure 3.5A. Mean densities (+\- 1SE) for total invertebrates and Chironomidae at Middle Bush Stream in four seasons sampled by freeze cores.
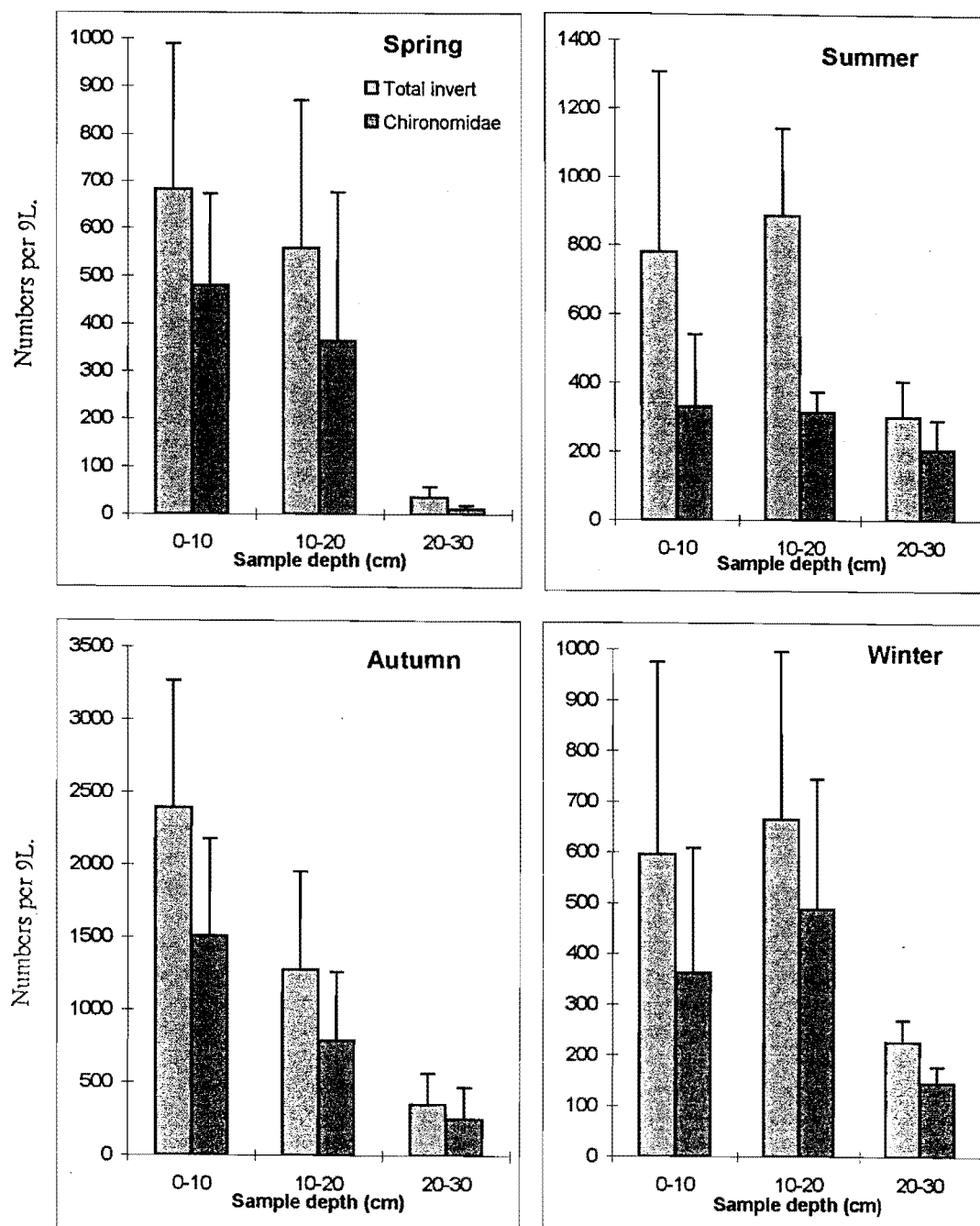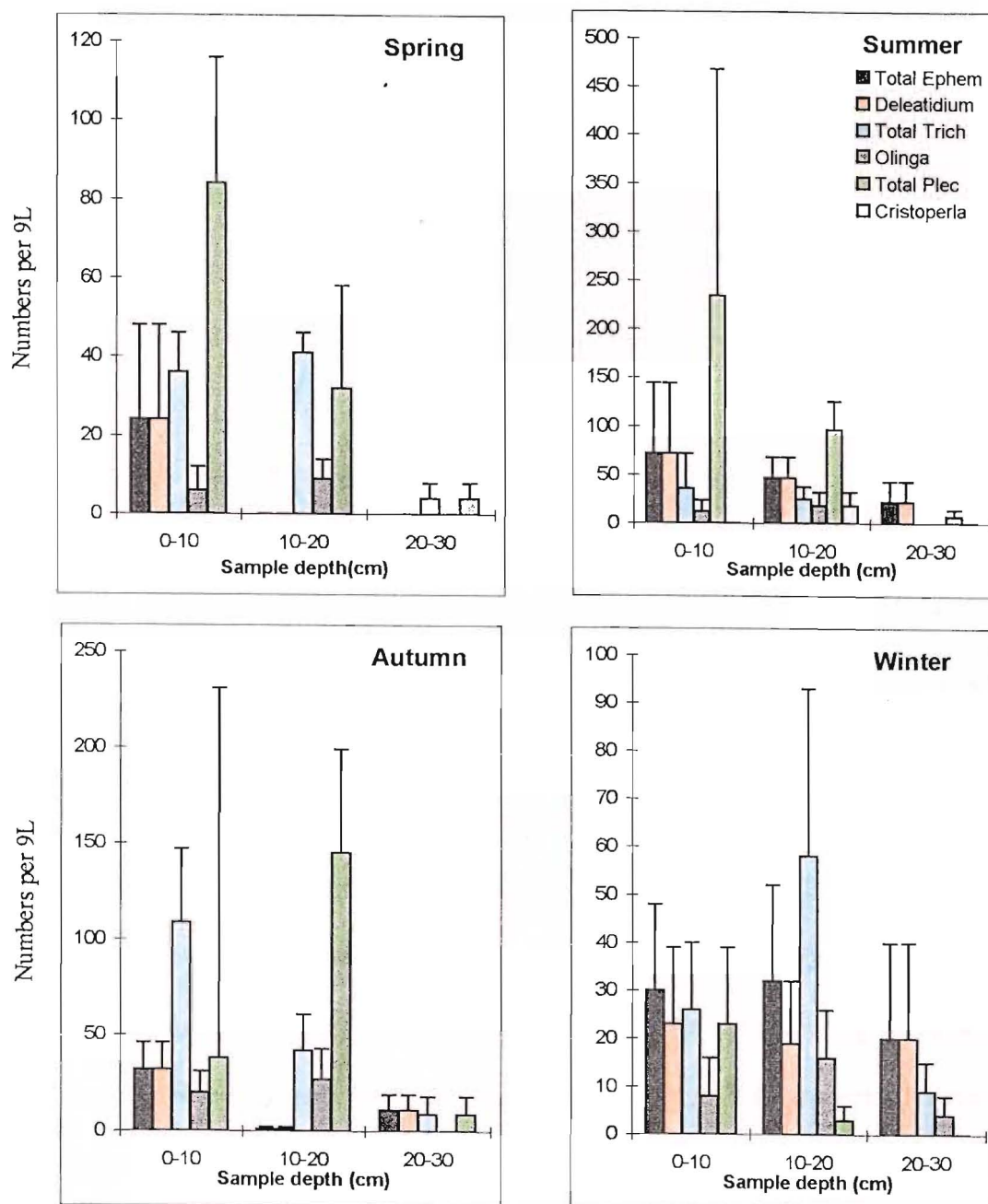
Figure 3.5B. Mean densities (+\- 1SE) for selected taxa at Middle Bush Stream in four seasons sampled by freeze cores

feredayi , total Plecoptera, and Chironomidae (Table 3.3). A seasonal difference was shown for *Cristaperla fimbria*.

In Middle Bush Stream, invertebrate density peaked in autumn (Fig, 3.5 A) when most animals were in the top 10 cm of substrate. For the rest of the year, densities remained relatively similar throughout the cores. Chironomidae also showed an autumn density peak, with most larvae occurring in the 0-10 cm zone. During winter, the density of Chironomidae was reduced, and a greater proportion of animals occurred below 10 cm.

As at Grasmere Stream, the remaining taxa groups (Fig. 3.5B) showed variable distribution patterns. Total ephemeropteran densities peaked in summer, and were more evenly spread within the cores in winter than in the other seasons, a pattern repeated by *Deleatidium*. Total trichopteran densities were similar year round, but the depth distribution of caddis larvae varied, with highest densities occurring in the 10-20 cm layer. *Olinga jeanae* exhibited a similar distribution pattern to total Trichoptera. Plecoptera were present at higher densities than at Grasmere Stream, with most animals occurred in the top 10 cm during spring and summer, and at 10-20 cm during autumn. Small numbers of *Cristaperla fimbria* were present during summer at the 10-20 cm level.

Colonisation samplers

Results obtained for Grasmere Stream (Table 3.4) showed no depth differences, but significant (P<0.05) seasonal differences in density were obtained for all taxa groups except total Plecoptera and *Zelandobius furcillatus*.

Table 3.4 Summary of two-way ANOVA comparisons of invertebrate density (season, df =3, depth, df =2) for colonisation sampler data from Grasmere Stream. Sample volume was 9L. Significant P values are shown in bold.

	Source	F ratio	P
Total invertebrates	Season	26.36	**0.001**
	Depth	0.08	0.92
	Season*depth	1012	0.38
Total Ephemeroptera	Season	25.42	**0.001**
	Depth	1.56	0.23
	Season*depth	1.39	0.26
Deleatidium sp.	Season	21.37	**0.001**
	Depth	1.01	0.38
	Season*depth	1.07	0.41
Total Trichoptera	Season	41.08	**0.001**
	Depth	2.44	0.100
	Season*depth	0.39	0.88
Olinga feredayi	Season	6.98	**0.001**
	Depth	0.97	0.393
	Season*depth	1.03	0.428
Total Plecoptera	Season	1.78	0.178
	Depth	0.33	0.719
	Season*depth	2.11	0.089
Zelandobius furcillatus	Season	1.78	0.178
	Depth	0.33	0.719
	Season*depth	2.11	0.089
Chironomidae	Season	15052	**0.001**
	Depth	0.02	0.98
	Season*depth	0.64	0.698

The corresponding data for Middle Bush Stream (Table 3.5) indicate significant

($P < 0.05$) seasonal differences in density for seven of the eight taxa, *Olinga jeanae*

being the exception. Significant depth differences were recorded for total

invertebrates, total Trichoptera, and Chironomidae. Total Ephemeroptera, total

Trichoptera, and *Deleatidium* sp. showed significant depth*season interactions.

Table 3.5 Summary of two-way ANOVA comparisons of invertebrate density (season, df =3, depth, df =2) for colonisation sampler data from Middle Bush Stream . Sample volume was 9L. Significant P values are shown in bold.

|	Source	F ratio	P
Total invertebrates	Season	16.05	**0.001**
	Depth	6.96	**0.004**
	Season*depth	0.94	0.485
Total Ephemeroptera	Season	13.06	**0.001**
	Depth	0.37	0.69
	Season*depth	3.59	**0.011**
Deleatidium spp.	Season	13.06	**0.001**
	Depth	0.37	0.69
	Season*depth	3.59	**0.011**
Total Trichoptera	Season	4.02	**0.019**
	Depth	4.00	**0.032**
	Season*depth	4.00	**0.007**
Olinga jeanae	Season	2.22	0.112
	Depth	0.48	0.627
	Season*depth	3.5	**0.013**
Total Plecoptera	Season	3.13	0.045
	Depth	0.56	0.58
	Season*depth	2.04	0.099
Cristaperla fimbria	Season	11.44	**0.0001**
	Depth	1.43	0.259
	Season*depth	1.5	0.221
Chironomidae	Season	10.75	**0.001**
	Depth	4.53	**0.022**
	Season*depth	0.65	0.688
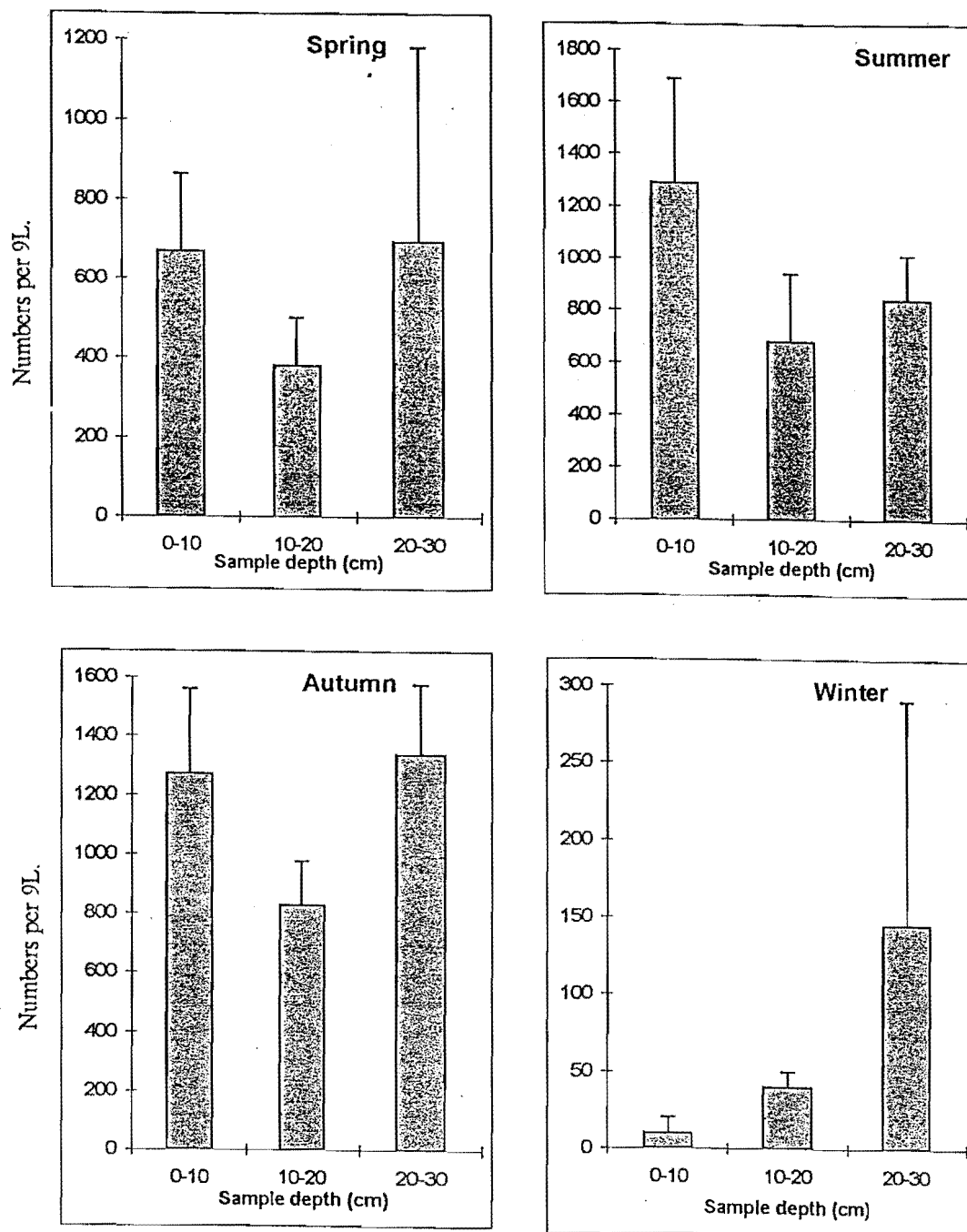
Figure 3.6A. Mean densities (+\- 1SE) of total invertebrates at Grasmere Stream in four seasons sampled with colonisation tubes
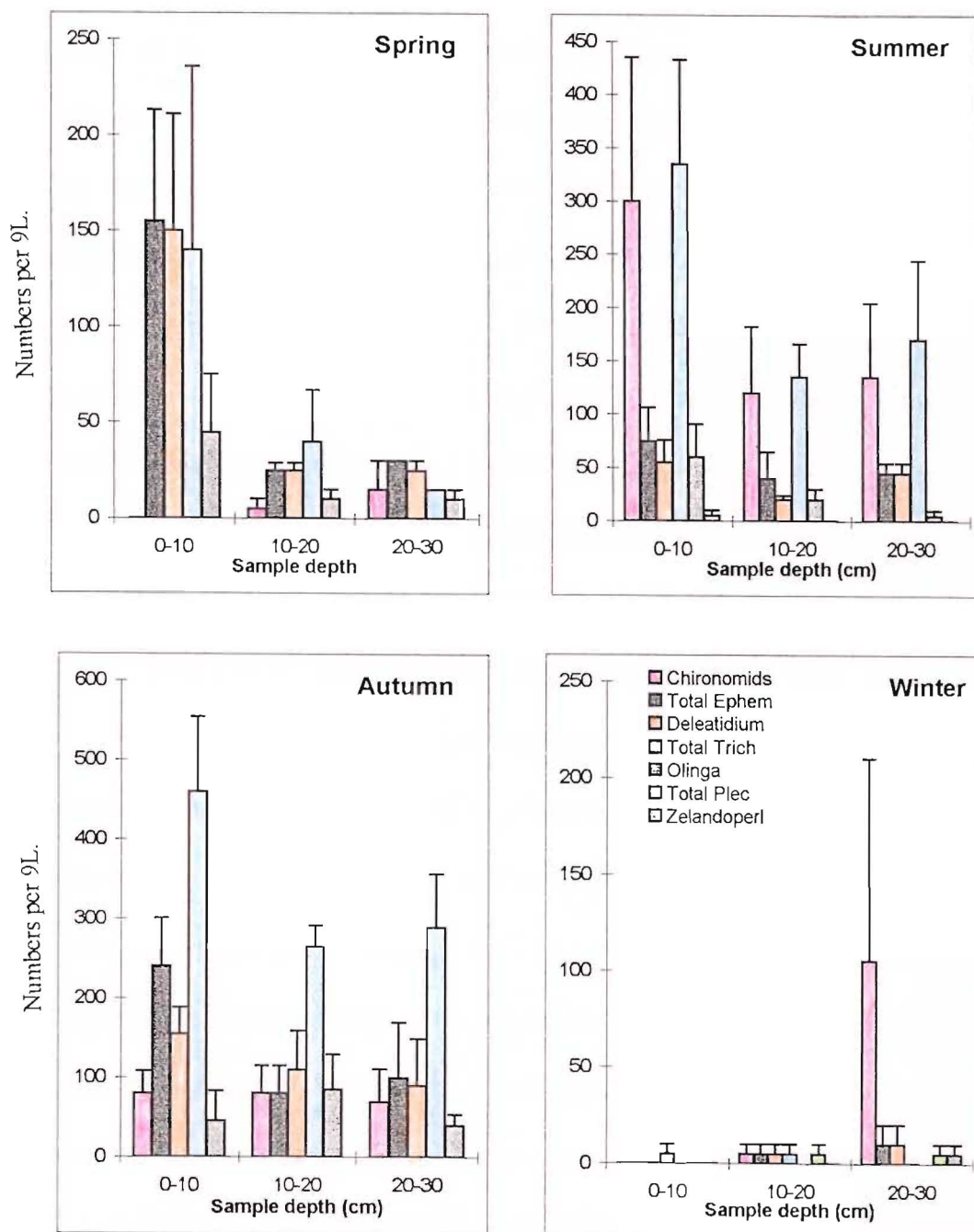
Figure 3.6B. Mean densities (+\- 1SE) of selected taxa at Grasmere Stream in four seasons sampled with colonisation tubes

Data obtained from colonisation samplers in Grasmere Stream indicated a fairly even depth distribution of total invertebrates (Fig. 3.6A), with densities peaking in summer and autumn. Distributions of the remaining taxa are shown in Figure 3.6B. Chironomidae also had density peaks in summer and autumn, and most animals occurred in the upper 10 cm of stream bed. Greater numbers were present below 10 cm in spring and winter. Total Ephemeroptera showed a significant seasonal difference in density (P<0.001) which peaked in autumn and was lowest in winter. Depth distribution of mayfly larvae, including the dominant taxon *Deleatidium*, was very even. Total Trichoptera showed summer and autumn density peaks and an even depth distribution, as did *Olinga feredayi*. Plecopterans were present only during winter, with some very small animals probably *Zelandobius*, occurring in the 20-30 cm zone.

Total numbers of invertebrates in colonisation samplers at Middle Bush Stream (Fig. 3.7A) also peaked in summer and autumn. Chironomidae followed a similar pattern to total invertebrates with greatest numbers being found in summer. Total Ephemeroptera had a significant autumn peak (P<0.001) in density, with larvae evenly distributed through the full depth range in each season. *Deleatidium* had an identical distribution pattern. Total Trichoptera increased in density through spring and summer, and peaked in autumn. Seventy per cent of this group occurred in the upper 10 cm except in winter when almost all larvae were found between 10 and 30 cm (Fig. 3.7B). *Olinga jeanae* was most abundant in winter between 10 and 30 cm. *Cristaperla fimbria* was present during winter and spring, and was most abundant in the 10-20 cm range.
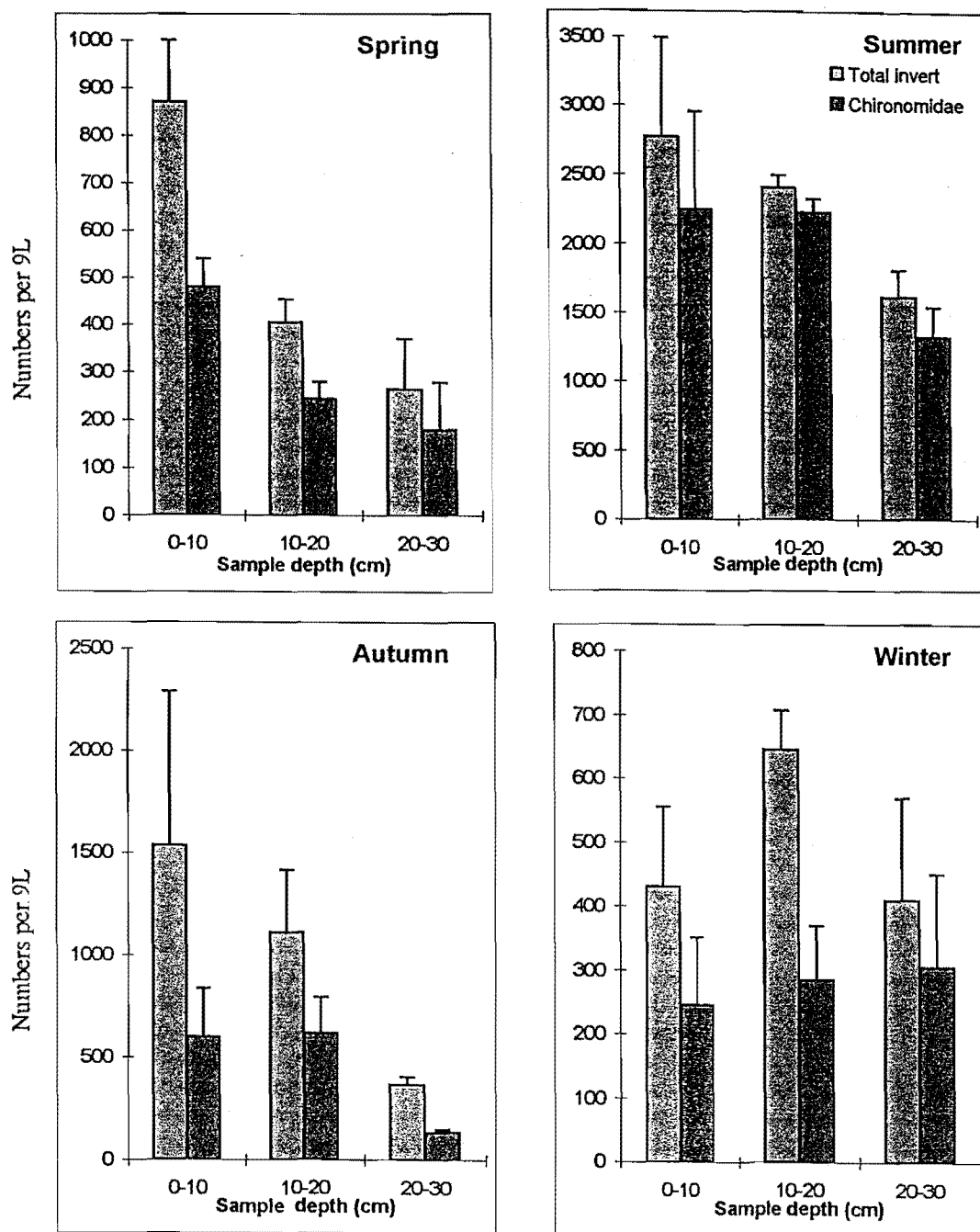
Figure 3.7A. Mean densities (+/- 1SE) of total invertebrates and Chironomidae at Middle Bush Stream in four seasons, sampled with colonisation tubes.

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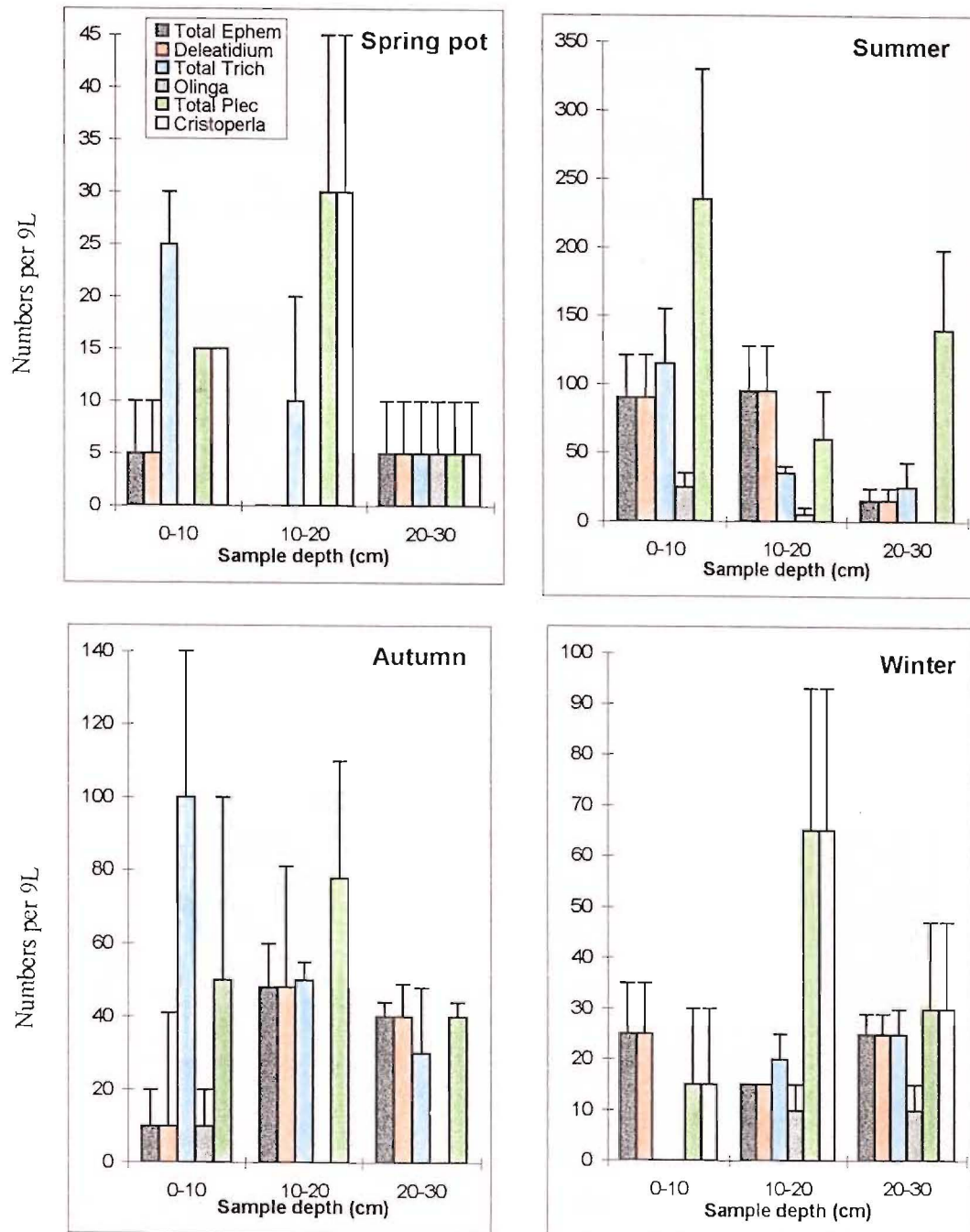
Figure 3.7B. Mean densities (+/- 1SE) of selected taxa at Middle Bush Stream in four seasons, sampled with colonisation tubes. Where there are no error bars, SE =0.

Table 3.6 summarises the results of one-way ANOVAs carried out on Cass

River data.. As a full data set covering the four seasons was not collected at this

site, it was possible to look at depth variations only for winter and spring. No data

were available for this site for colonisation samplers.

Table 3.6 One-way ANOVA summary (depth, df =2) for freeze-cores at Cass River. (A) Winter, and (B) Spring. Sample volume 9L.

A: Winter

	F Ratio	P
Total invertebrates	0.04	0.957
Total Ephemeroptera	0.70	0.528
Total Trichoptera	0.07	0.936
Chironomidae	2.8	0.128

(B) Spring

	F Ratio	P
Total invertebrates	0.02	0.98
Total Ephemeroptera	1.23	0.35
Total Trichoptera	1.22	0.35
Total Plecoptera	1.22	0.35
Chironomidae	0.05	0.95

No significant differences (P>0.05) in vertical distribution were observed with the

limited Cass River data.

Discussion

Samplers that characteristically collect animals to a depth of about 10 cm have been widely used to sample benthic invertebrates in streams, and have provided data for studies of population dynamics, community interactions and ecosystem processes. It has also been recognised for some time that aquatic invertebrates are not necessarily confined to the top 10 cm of the stream bed (Williams and Hynes, 1974; Pugsley and Hynes, 1983; Marchant, 1988, 1995), and that use of surface samplers may not give a true representation of invertebrate densities, especially in water courses with extensive hyporheic zones.

Studies carried out in North America, (Hynes, 1974; Williams and Hynes, 1974; Pugsley and Hynes, 1983) and Australia (Marchant, 1988, 1995; Marchant and Lilywhite, 1989) have shown that the vertical distribution of the hyporheos is highly variable, both seasonally, and in degree of penetration of the fauna into the substrate, and may be related to the nature of the hyporheic zone (Williams, 1984). Several factors, including the type of substrate, influence the likelihood that this zone will be colonised. Solid bedrock close to or on the surface of the stream bed means that no hyporheic zone can be present, while very fine-grained substrates such as clay that lack interstitial spaces cannot be colonised by many animal groups (Bourass and Morin, 1995). Compaction of the substrate also influences water flow through the hyporheic region, and as a consequence, the species composition of invertebrate assmblages. Other factors that affect the hyporheic zone as habitat include temperature, the absence of light, and chemical features such as pH,

alkalinity, presence or absence of organic material, and the concentrations of dissolved oxygen and carbon dioxide (Williams, 1984).

In the present study, particle size distribution of the hyporheic zones in all three streams was quite similar, and it is clear from my results that interstitial spaces were sufficiently abundant to a depth of at least 30 cm for a diverse range of species to colonise it . However, no measurements of chemical factors were made in my study, so their effects on the hyporheos are unknown.

Vertical distribution patterns of invertebrates have been shown to vary seasonally (Williams and Hynes, 1974; Godbout and Hynes, 1982; Marchant, 1995), with faunal densities usually decreasing with increasing depth, and maximum numbers of invertebrates occurring at a depth of approximately 10- 20 cm (Williams and Hynes, 1974). The workers listed above found peak densities of invertebrates in either winter, spring or autumn when most stream species were actively growing, and lowest numbers in summer, the emergence period for many insect species. However, individual taxa show different distributional and temporal patterns: some Trichoptera have been found at depths of at least 30- 40 cm; mayfly species (Ephemeroptera) vary in their ability to use the hyporheic zone depending on their size and robustness; and Plecoptera occur deep within the streambed mainly in early larval instars. A remarkable and extreme example of hyporheic existence is provided by two genera of stoneflies in Montana that occur to depths of >10 m (Stanford and Ward, 1988).

The results of my study in three Cass Basin streams were consistent with overseas findings and those of recent New Zealand studies by Scarsbrook (1995)

and Huryn (1996) which have shown that aquatic invertebrates occur deep into the substratum, and that distributional patterns vary between taxa. In general, faunal densities decreased with depth, but larvae of Ephemerotpera, Plecoptera, Trichoptera and Chironomidae all occurred down to 30 cm, the depth limit of my sampling. Peak densities of invertebrates in the hyporheic zone of Grasmere and Middle Bush Streams tended to be in autumn when many new generation larvae are known to be present (Winterbourn, 1978, 1995; Winterbourn and Harding, 1993).

Differences in the vertical distribution patterns of selected taxa were also apparent between the two streams. These variations were probably related to differences in the nature of the hyporheic zone, for although the two streams had similar water chemistry and substrate composition, they differed in flow regime and bed stability. The latter factor affects bed compaction, which in turn is recognised as a limiting factor for invertebrate penetration of the substrate as indicated above. Middle Bush Stream is subjected to greater and more frequent water velocity fluctuations than Grasmere Stream (Death, 1991), and because its surface sediments are more severly disturbed, invertebrates may make greater use of the hyporheic zone as a refuge, as suggested by my density data.

Finally, it was very apparent in this study that the two hyporheic sampling techniques resulted in different vertical distribution patterns for several taxa. These differences can be explained by the fact that substrate filled tubes provide vertical corridors which allow animals to move down to greater depths and as a result achieve a more uniform distribution through the substrate. For example, freeze coring at Grasmere Stream indicated density differences with depth for

Ephemeroptera, *Deleatidium*, and total invertebrates, but the colonisation samplers did not. Similarly, in Middle Bush Stream the distribution of *Olinga jeanae* differed with depth in freeze cores but not in colonisation tubes whereas the depth distributions of some other taxa (e.g., Chironomidae) were found to be similar with both methods. In this regard, my findings with the two species of *Olinga* are of particular interest, as surprisingly *Olinga feredayi* had been recorded down to 40 cm in colonisation tubes by Scarsbrook (1995) and Huryn (1996a). The latter calculated that 46% of *Olinga feredayi* annual production occurred in the hyporheic zone (below 10 cm). The comparable figure from my freeze cores at Grasmere Stream was 71 %, with 68 % for *O. jeanae*, in Middle Bush Stream (see Chapter 4). My work therefore confirms that larvae of *Olinga* do indeed penetrate the stream bed to considerable depths and that the findings of Scarsbrook and Huryn are not merely methodological artefacts.

Chapter 4

SECONDARY PRODUCTION

Introduction

Secondary production is defined by Benke (1996, 1984) as "the living organic matter, or biomass, that is created or produced by an animal population during an interval of time". It combines measures of biomass, growth and survivorship in a single parameter, and as such is a useful comparative measure of population or community success (Benke, 1984).

The objective of this part of my research was to determine the secondary production of selected taxa in the benthos of the three streams using freeze-core and Surber sampling techniques. In particular, I was interested to know whether "deep benthos" excluded from Surber samples results in significant underestimates of secondary production. Allen's study (1951) of brown trout production in the Horokiwi Stream (near Wellington) indicated that secondary production of aquatic invertebrates was insufficient to support trout production, and has been referred to as the Allen paradox (Huryn, 1996a). A number of factors including inaccuracies in the calculation of invertebrate production, and underestimates of terrestrial prey use by trout have been implicated as partial reasons for the paradox, while Gerking (1962) suggested that Allen's annual production estimates for trout were too high due to varying food requirements of the trout at different growth stages. Even if these various suggestions are correct, it is likely that inadequate sampling of the benthos may be a major reason for obtaining underestimates of invertebrate production. Traditional collection methods such as the use of Surber, and Waters

and Knapp samplers assume that all or most animals live close to the surface of the stream bed (within the top 10 cm), and do not sample deeper layers. However, evidence now exists that some invertebrates can penetrate and reside deep (up to 70cm) in the hyporheic zone (Williams and Hynes, 1974; Huryn, 1996; this thesis). Vertical distribution studies (Bishop, 1973; Williams and Hynes, 1974; Godbout and Hynes, 1982; Pugsley and Hynes, 1983; and Bretschko and Klemens, 1986) have indicated that the percentage of fauna within the top 10cm of substratum is variable, and Australian research (Marchant, 1988 and 1995) showed that the vertical distribution of invertebrates within the stream bed could vary seasonally. Thus, Marchant found that 70-80% of the benthic invertebrates in the Thompson and Acheron Rivers were located in the top 10 cm of substrate during summer, but in other seasons about 50% of the fauna was below 10 cm.

I used two sampling methods, freeze coring and Surber sampling, to make comparative estimates of secondary production of three invertebrate taxa in Grasmere Stream and Middle Bush Stream, and obtained some more limited data for Cass River. The taxa were *Deleatidium*, a mayfly, which could not be identified to species and may have been represented by different species at the three sites, larval Chironomidae (non-biting midge larvae) that were considered at family level, and the cased caddisfly *Olinga*. The latter genus was represented by *O. feredayi* in Grasmere Stream, and *O. jeanae* in Middle Bush Stream.

A number of factors have made the measurement of secondary production of New Zealand aquatic invertebrates difficult. These include incomplete knowledge of life histories, difficulties in following growth and mortality rates of distinct cohorts, and the occurrence of weakly seasonal or non-seasonal life cycles in many

species (Winterbourn, 1974; Hopkins, 1976; Towns 1981 & 1983; Collier and Winterbourn, 1990; Scrimgeour, 1991; Huryn, 1996b). Nevertheless, estimates of secondary production of stream invertebrates have been made by a number of stream ecologists in New Zealand, since the pioneering work of Allen (1951) who estimated total secondary production of aquatic invertebrates in the course of his study on brown trout (*Salmo trutta*) production in the Horokiwi Stream.

Production of *Deleatidium* sp. has been estimated in at least eight New Zealand stream studies (Winterbourn, 1995), with annual values ranging from 0.2 to 7.4 g $AFDW.m^{-2} y^{-1}$. The highest value (7.4 g $AFDW.m^{-2} y^{-1}$) was for a site on the braided Ashley River in North Canterbury (Marchant and Scrimgeour, 1991), and the lowest for a brown water stream flowing into Lake Mapourika in Westland (Graesser, 1988). More recently, Armstrong (1996) obtained production estimates ranging from 0.43 to 2.9 g DW $m^{-2} y^{-1}$, for *Deleatidium* populations in twelve South Island rivers, the higher values being found in those rivers with the more stable beds. Harding and Winterbourn (1993) investigated the life history and production of another ephemeropteran (*Coloburiscus humeralis*) at two sites near Cass and reported production estimates of 2.42 and 3.62 g DW $m^{-2} y^{-1}$.

Several production estimates have been obtained for species of New Zealand Trichoptera including *Olinga feredayi* . Hopkins (1976) reported annual production of 1.2 g DW $m^{-2} y^{-1}$ for *O. feredayi* in the Hinau River, North Island, and Shearer (1995) obtained values of 0.11, 0.2, and 0.55 g DW $m^{-2} y^{-1}$ for three streams in the Cass- Porters Pass region of Canterbury. Her estimate of 0.11 g DW $m^{-2} y^{-1}$ for *O. feredayi* in Grasmere Stream can be compared directly with my results as sampling was undertaken at exactly the same site. Production estimates have also

been obtained for other New Zealand caddisflies including *Aoteapsyche colonica*

(Winterbourn & Harding (1993), *Pycnocentria forcipata* and *Oeconesus maori*

(Linklater and Winterbourn, 1993), and *Zelolessica cheira* (Graesser, 1988) and

ranged from 0.13 to 7.15 g DW m^{-2}. All the above studies used 'surface' sampling,

whereas Huryn (1996a) obtained annual production estimates from 40 cm deep

cores for a number of invertebrates including *A. colonica* (1.17 g DW m^{-2}),

Hydrobiosis (0.08 g DW m^{-2}), and *Coloburiscus* (0.16 g DW m^{-2}).

Lastly, numerous calculations of production have been obtained for

Chironomidae in various parts of the world, but the only estimates for New Zealand

midges are those of Hopkins (1976) and Huryn (1996a). Production values that

have been reported vary from less than 1.0 g DW m^{-2}y^{-1} to nearly 100 g DW m^{-2}y^{-1}

(Tokeshi, 1995), and New Zealand estimates range from 0.07 to 0.69 g DW m^{-2}y^{-1}.

Methods

Because a decision to study secondary production was made part way through

the sampling programme, larvae preserved in alcohol for some months would

have lost variable amounts of weight through the extraction of lipids (Donald &

Paterson, 1977, Howmiller, 1972, and Meyer, 1989). All dry weights of larvae

were therefore estimated using the regression formulae provided by Tower *et*

al.(1994). The general equation used was

$$Log_e \text{ n DW} = Log_e \text{ n a} + Log_e \text{ n b.L}$$

where DW = dry weight (in mg),

L = body length (in mm),

and a, b are regression constants (provided by Towers *et al*, 1994) (Table 4.1).

Secondary production was calculated from Surber sample and freeze core data for

populations of *Deleatidium* , *Olinga fereday*, *O. jeanae* and Chironomidae at the

Grasmere Stream and Middle Bush Stream sites. Because larval abundances were

low, and because freeze core sampling was only partially successful in the Cass

River, production estimates were obtained there only for populations of *Deleatidium*

and Chironomidae in Surber samples, and Chironomidae in whole cores.

Table 4.1 Values for the constants Log n a and Log n b obtained from the regressions performed by Towers et al (1994) on body lengths of *Deleatidium* sp., *Olinga feredayi* and Chironomidae. SE is the standard error of the estimate.

Species	Log na ± SE	Log n b ± SE
Deleatidium sp.	-5.38 ± 0.27	3.06 ± 0.14
Olinga feredayi	-6.57 ± 0.24	3.42 ± 0.18
Chironomidae	-3.88 ± 0.17	2.72 ± 0.16

Annual production (P), biomass (B) and the turnover ratio (P/B) were

calculated using the size frequency method (Benke, 1984) from Surber sample and

freeze core data collected from July 1995 to June 1996 . For the freeze-core data,

production was calculated for all depth levels separately, and then summed.

The size frequency method assumes that average size frequency distributions

calculated from samples taken over a year will approximate the average survivorship

of a hypothetical average cohort (Benke, 1984). A cohort production interval (CPI)

of one year was assumed for all three taxa when making these calculations, although

it is likely that some *Deleatidium* and Chironomidae species may have shorter generations than this. Huryn (1996b) estimated the length of the larval stage for *Deleatidium* sp was likely to range between 107 and 273 days; Winterbourn's (1974) work on the Selwyn River suggested that a short summer generation of *Deleatidium* may occur, and Towns (1983) found that the life histories of several *Deleatidium* species studied near Auckland varied in length up to a year. On the other hand, Greig (1976) obtained clear evidence of a one year life cycle for *Deleatidium vernale* in Lake Grasmere, close to the three sites used in my study. Winterbourn (1982) considered that monthly size distributions of three chironomid species found in Middle Bush Stream indicated that they probably had annual lifecycles, but Huryn (1996a) estimated larval lifespans of 74 to 174 days for a species of *Maoridiamesa* (Diamesinae) (summer/autumn cohort) in Sutton Stream, Otago.

Because the principal objective of my study was to compare sampling methods, not species, inaccuracies in estimating life history duration are not critical but will simply introduce a systematic error. Population densities, biomass and production estimates are presented for 9 litres of stream sediment for Surber samples, whereas the total volume of a frozen core is 27 litres (i.e. three 9 litre sections relative to the three depth categories sampled). This enables direct comparison of Surber samples with core samples from different depths and with somewhat variable configurations that were always of a lesser surface area than Surber samples. Nine litres is the approximate volume of sediment disturbed during Surber sampling (i.e., 0.09 m^2 x 10 cm deep).

Results

Two worked examples of production calculations are provided in Table 4.2.

The first is for Chironomidae in Grasmere Stream, and the second for *Olinga*

jeanae in Middle Bush Stream. Note that in calculating production, negative values

in the final column have been ignored, (and considered to be zero) as recommended

by Benke (1984).

Table 4.2. Two examples of production calculation by the size frequency method as recommended by Benke (1984).

(A) Chironomidae at Grasmere Stream based on Surber samples. Values are per 9 litres of streambed*.

Size class (mm)	Mean density	Total biomass (mg)	ΔN	Mean Wt (W) mg	ΔN*W Wt lost	x8
1-2	0.6	0.12				
			-0.45	1.57	(-0.71)	
2-3	1.05	3.1				
			-1.6	3.09	(-4.94)	
3-4	2.65	14.9				
			1.25	7.01	8.76	70.1
4-5	1.4	11.7				
			-0.05	9.73	-0.49	-3.9
5-6	1.45	16.1				
			0.6	12.45	7.47	59.8
6-7	0.85	11.7				
			0.35	15.17	5.31	42.5
7-8	0.5	8.3				
			0.25	17.89	4.47	35.8
8-9	0.25	4.8				
					4.81	38.5
		Σ= 70.8 mg/yr				Σ= 242.6 mg/yr

* Area of Surber sampler = $0.09m^2$; depth of sampling = 10cm; $\therefore$ Volume of stream bed sampled = 9 litres.

(B) *Olinga jeanae* at Middle Bush Stream based on freeze core sampling at depth 10-20 cm. Values are per 9 litres of sediment.

Size class (mm)	Mean density	Total biomass (mg)	ΔN	Mean Wt(W) mg	$\Delta N*W$ Wt lost	x6
0-1.4	0	0				
			-17.96	-1.89	(-33.9)	203.7
1.5-2.9	17.9	8.06				
			7.98	3.11	24.8	148.9
3-4.4	9.9	57.78				
			9.98	8.3	82.83	497
4.5-5.9	0	0				
			0	13.32	0	0
6-7.4	0	0				
			-0.3	18.33	-5.5	-33
7.5-8.9	0.3	6.25			6.25	37.5
		Σ =72.09				Σ=854 mg/yr

Production estimates for *Deleatidium* sp, *Olinga feredayi*, *O. jeanae* and Chironomidae from Grasmere Stream and Middle Bush Stream are shown in Tables 4.3 and 4.4.

Results obtained from Surber samples and freeze cores are given in each table.

Table 4.3. Biomass and secondary production estimates for three depth levels of freeze core samples and for Surber samples at Grasmere Stream. Note that values for total core are for a volume of 27 litres.

	Freeze core sample depths (cm)			Surber sample	Σ Total Core	Core: Surber sample ratio
	0-10	10-20	20-30			
Deleatidium sp.						
Density (9L^{-1})	124	48	21	166	193	1.2: 1
Biomass (mg DW. 9L^{-1})	241	87	45	326	373	1.2:1
Production (mg DW. 9L^{-1}.y)	558	271	103	968	932	1:1
P:B	2.3	3.1	2.3	2.9	2.5	
Olinga feredayi						
Density (9L^{-1})	153	78	61	53	292	5.5:1
Biomass (mg DW. 9L^{-1})	499	1105	318	105	1922	18.3:1
Production (mg DW. 9L^{-1}.y)	1635	3090	914	632	5639	8.9:1
P:B	3.3	2.8	2.9	5.9	2.9	
Chironomidae						
Density (9L^{-1})	114	37	33	35	184	5.3:1
Biomass (mg DW. 9L^{-1})	170	41	69	71	280	3.9:1
Production (mg DW. 9L^{-1}.y)	1171	131	484	243	1786	7.4:1
P:B	6.9	3.2	7.0	3.4	6.4	

Table 4.4. Biomass and secondary production estimates for the three depth levels of the freeze cores and for Surber samples at Middle Bush Stream. Note that values for total core are for a volume of 27 litres.

	Freeze core sample depths (cm)			Surber sample	Σ Total Core	Core: Surber sample ratio
	0-10	10-20	20-30			
Deleatidium sp.						
Density (9L^{-1})	274	22	28	123	324	2.6:1
Biomass (mg DW. 9L^{-1})	162	28	23	186	213	1.1:1
Production (mg DW. 9L^{-1}.yr)	848	98	55	844	1001	1.2:1
P:B	5.2	3.5	2.4	4.5	4.7	
Olinga jeanae						
Density (9L^{-1})	57	113	16	19	186	9.8:1
Biomass (mg DW. 9L^{-1})	62	72	0.02	31	134	4.3:
Production (mg DW. 9L^{-1}.yr)	403	854	0.13	185	1257	6.8:1
P:B	6.4	11.8	7	5.9	9.4	
Chironomidae						
Density (9L^{-1})	1186	921	489	165	2596	15.7:1
Biomass (mg DW. 9L^{-1})	1359	805	365	253	2529	10:1
Production (mg DW. 9L^{-1}.yr)	5190	3624	1641	1104	10455	9.5:1
P:B	3.8	4.5	4.5	4.4	4.1	

Biomass and production estimates for the three depth levels sampled using freeze coring (Tables 4.3 and 4.4) decreased with depth in both Grasmere Stream and Middle Bush Stream for *Deleatidium* sp. and Chironomidae. Biomass and production of the *Olinga* species was greatest at 10-20 cm in both streams, and a very low density of larvae was found at 20 -30 cm in Middle Bush Stream. P:B ratios for *Deleatidium* sp. ranged from 2.4 to 3.1 at Grasmere Stream and 2.4 to 5.2 at Middle Bush Stream. For *Olinga feredayi* and *O. jeanae* they were 2.8 to 3.3 and 6.4 to 11.8, respectively, for Chironomidae 3.2 to 7.1 in Grasmere Stream and 3.8 to 4.5 in Middle Bush Stream. The relatively high P:B of 11.8 for *O. jeanae* at 10-20 cm is probably explained by the occurrence of small sized larvae only at that depth.

Comparison of the total core values with those for Surber samples shows that at Middle Bush Stream, density, biomass and production values were 4.3 to 15.7 times higher for *O. jeanae* and Chironomidae for the total cores. Similarly at Grasmere Stream, density, biomass and production of *O. feredayi* and Chironomidae were 3.9 to 18.3 times greater in cores. However, *Deleatidium* sp. values were almost identical in cores and Surber samples.

Table 4.5. Mean density, biomass and production values and turnover ratios for *Deleatidium* sp. (Surber samples only) and Chironomidae from Cass River, July 1995 to June 1996. Values are units per 9 litres of sediment.

	Surber sample	Freeze core 0 -30 cm
(a) *Deleatidium* sp		
Density $(9L^{-1})$	20	no data
Biomass $(mg\ DW.\ 9L^{-1})$	117	"
Production $(mg\ DW.\ 9L^{-1}.y)$	757	"
P:B	6.5	"
(b) Chironomidae		
Density $(9L^{-1})$	4	5
Biomass $(mg\ DW.\ 9L^{-1})$	19	4
Production $(mg\ DW.\ 9L^{-1}.y)$	80	11
P:B	4.2	2.8

Cass River data (Table 4.5) were not used to compare the efficiencies of the two sampling methods in assessing secondary production. However, it was possible to make a limited comparison of secondary production for *Deleatidium* sp. and Chironomidae between the three streams. Density, biomass and secondary production of Chironomidae at Cass River was much lower than in the other two streams, however, the *Deleatidium* population was very similar in size and production to that in Middle Bush Stream.

Discussion

Secondary production has been calculated by numerous stream ecologists (see Allan, 1951, 1971; Hamilton, 1969; Rigler *et al*, 1969; Benke, 1984, 1993,1996; and Huryn, 1996a) in conjunction with studies of life histories and population dynamics of aquatic invertebrates. However, as I stated above, the question has arisen as to whether Surber sampling, which is a convenient and long established sampling technique, may lead to the underestimation of densities, biomass and production of macroinvertebrates living in the beds of streams. When using a Surber sampler the stream bed is rarely disturbed below a depth of 10 cm, but recent studies (Palmer et al, 1993; Ward, 1992; Boulton, 1993; Boulton et al, 1995; Fraser et al, 1996; Brunke et al, 1997) have demonstrated that the hyporheic zone is a dynamic region that provides habitat for significant numbers of macroinvertebrates (Marchant, 1988, 1995; Schmid- Araya, 1994).

In order to address the question of underestimation, I sampled streams with a Surber sampler and using freeze coring techniques which enabled all invertebrates to be collected to a depth of 30 cm. To compare the values for the full 30 cm depth of freeze coring with Surber sampling it is important to translate the values from units per volume of sediment to units per specific area, in this case 0.09 m^2, the area of the Surber sampler. When viewed this way, my results indicate that Surber sampling did underestimate density, biomass and production quite markedly, with freeze core production values for *O. jeanae* and Chironomidae from Middle Bush Stream being 6.8 and 9.5 times greater than those for Surber sampling . Even when equal sized volumes of surface sediments (upper 10 cm) were compared for the two methods, freeze core production values for these two taxa were two to three times

greater than obtained by Surber sampling. There are several reasons for Surber sampling having short-comings. Thus, standardisation of sampling depth depends on the skill of the person sampling, and even when the scraping tool is calibrated for the required depth, large rocks/bedrock can mean that this level is not achieved over the full sampling area. Also, animals may be lost around the sides of the net, and very small ones may pass through the mesh.

Although production estimates for *Olinga* and Chironomidae were higher when based on 30 cm deep cores than Surber samples at both Middle Bush Stream and Grasmere Stream, relative differences in values obtained with the two techniques were not consistent between streams. Production estimates for *Deleatidium* at Grasmere Stream and Middle Bush Stream using Surber sampling were similar to those calculated from the total freeze core samples. The reasons for these differences between taxa are unclear, but could indicate subtle differences in the placement of samplers within and between the streams which differed in bed morphology.

In both streams, production estimates for *Olinga* and Chironomidae were between 6.8 and 9.5 times greater for freeze cores than Surber samples, and may at least in part be a consequence of the behaviour of the animals. Neither taxon is likely to flee during freezing, but larvae may be less efficiently collected by Surber sampling because of their tube-dwelling habit (most of the chironomid species present) or moderately heavy larval case (*Olinga*).

My results also confirm the findings of Huryn (1996a) and Scarsbrook (1995) that the larvae of *Olinga* occur within the hyporheic zone. Thus, production estimates for the 10 -20 cm deep region of the stream bed were twice those

calculated for the top 10 cm in both streams, but declined at 20 -30 cm depth. In contrast, production estimates for *Olinga feredayi* in Sutton Stream (Huryn, 1996a) were greatest in the top 10 cm of substrate, with production in the deeper strata (below 10 cm) being about three-quarters of this value. Shearer's (1995) production estimate of 0.11 g DW $m^{-2} y^{-1}$ for *Olinga feredayi* in Grasmere Stream is six times smaller than the estimate of 0.63 g DW $m^{-2} y^{-1}$ obtained for this taxon using Surber sampling in this study, while the freeze core production value (5.6 g DW $m^{-2} y^{-1}$) is nearly fifty times greater than her result.

It could be assumed that Surber sampling should not seriously underestimate secondary production for filter feeding invertebrates such as *Coloburiscus humeralis* and hydropsychid caddisflies that live and feed predominantly at the bed surface. However, by including the hyporheic component through the use of deeper sampling techniques, higher (and more accurate) secondary production estimates will be achieved for other taxa. Similarly, where bed sediments are too closely packed (e.g., very fine clay) to allow faunal penetration, or where bedrock is close to the surface (within 10 cm) Surber sampling data should provide accurate assessments of density, biomass and secondary production, as long as sampling is performed with care and consistency. Conversely, in loose alluvial gravel river beds such as occur on the Canterbury Plains, very deep penetration of the fauna might be expected, and therefore marked underestimations of secondary production can be anticipated with Surber sampling.

My results highlight the importance of considering the hyporheic zone when assessing production budgets, and it may well be that underestimation of invertebrate production partly explains the Allen paradox (Huryn, 1996a). However,

the extent of the underestimation in Allen's original production study (Allen, 1951)

cannot be inferred from my results, as it is not known whether the vertical

distribution, abundance and biomass of the hyporheos in the Horokiwi Stream

would have been similar to that of the streams at Cass.

Chapter 5

SYNOPSIS

The hyporheic zone is the subject of on-going studies by stream ecologists. Overseas research has centred on physical (Bourassa and Morin, 1995; Jones and Holmes, 1996), chemical (Fraser *et al.*, 1996) and biotic (Coleman and Hynes, 1970; Williams and Hynes, 1974; Poole and Stewart, 1976; Marchant, 1988, Bretschko, 1990; and Schmid-Araya, 1994) components of this zone, and the nature of hydrological exchanges between surface water and interstitial spaces (Boulton, 1993; Brunke and Gonser, 1997). Ecological research on the hyporheos has only been undertaken recently in New Zealand, however, the most detailed study being that of Scarsbrook (1995) who examined the vertical distribution of invertebrates in two Otago streams in relation to catchment geomorphology, and considered the hyporheic zone as a potential refuge from disturbance. Subesquently, Huryn (1996a) included the hyporheic component in a comprehensive production budget for a tributary of the Taieri River, Otago, and Scarsbrook and Halliday (1996) have briefly described and assessed several vertical sampling methods.

Why do invertebrates inhabit the hyporheic zone, especially when water flow, dissolved oxygen and light availability are likely to suboptimal? Advantages include reduced predation, protection from fast currents, ameliorated water temperatures, and enhanced food supplies, but most important is likely to be survival at times of adverse environmental conditions, such as during spates and droughts (Williams & Hynes, 1976; Poole and Stewart, 1976).

My research focused on the vertical distribution of aquatic invertebrates in the stream bed, and the possible consequences of including data from deeper regions on production estimates. The streams selected for study were chosen because they differed in bed stability, flow patterns, and surrounding terrain, and because they had several factors in common. These included similar geology and particle size composition of stream substrata, and faunas that included *Deleatidium*, Chironomidae and some other taxa in common.

All three sites were located in the Cass Basin about 600 m above sea level. Taxonomic richness and invertebrate densities varied between the streams, with the forested Middle Bush Stream having most taxa, and the lake-fed Grasmere Stream the highest densities. The braided Cass River had fewest taxa and lowest densities of invertebrates.

My seasonal studies undertaken with freeze coring and substrate colonisation techniques, produced results that were consistent with those obtained in several overseas (Williams and Hynes, 1974; Godout and Hynes, 1982; Marchant, 1995), and New Zealand investigations (Scarsbrook 1995; Huryn 1996a) in showing that invertebrates occurred deep within the substrata, and that taxa differ in their distributional patterns. In addition, differences in vertical distribution patterns were noted between my two main streams, and were probably related to differences in the bed stability and flow regime of these streams. Another important result of my study was the finding of differences in vertical distribution patterns by the two hyporheic sampling methods. Because the colonisation tubes, with their wide-meshed spacer discs, were packed with stones and did not sample 'undisturbed' bed substrata, they probably provided vertical 'corridors' that enabled deeper

penetration by some invertebrates. Thus, Ephemeroptera, *Deleatidium* and total invertebrates were found more evenly distributed within tubes at Grasmere Stream in contrast to freeze cores where density differences with depth were apparent. Clearly, the deployment of colonisation tubes is questionable if accurate information on natural depth distributions is required, and the method cannot be recommended.

Finally, secondary production estimates were obtained for selected taxa using freeze core and Surber sampling data, the objective being to determine whether 'deep benthos' excluded by Surber sampling resulted in significant underestimations of secondary production. Estimates obtained using both sets of data varied between the streams, and were larger for *Olinga* and Chironomidae with freeze coring in both Grasmere and Middle Bush Streams. *Deleatidium* estimates were similar with freeze coring and Surber sampling at both Middle Bush and Grasmere Streams. Production estimates for *Olinga* and Chironomidae were much higher for 30 cm freeze cores than for Surber sampling, and even comparisons between equal volumes of sediment in the top 10 cm of stream bed resulted in differences between the methods. Thus, freeze core estimates for *Olinga* and Chironomidae were two to three times higher than with Surber sampling in both streams. While *Deleatidium* estimates at Middle Bush Stream were very similar, at Grasmere Stream, the Surber sampler value was nearly twice that for freeze coring. These findings imply that Surber sampling can also result in losses of individuals or inadequate collection, and consequently underestimation of densities, biomass and production.

It is clear from my results that sampling of the hyporheic zone is very desirable if accurate assessments of density, biomass and production are to be obtained for many

invertebrate taxa in many streams. However, the depth of the hyporheic zone differs considerably among streams and rivers, and the ability of invertebrates to colonise it will also vary greatly because of differences in substrate composition and compaction, water chemistry, and the ecological requirements of individual taxa.

To summarise, it is clear that stream ecologists need to appreciate that in many streams invertebrate populations will extend to varying degrees into the hyporheic zone, and that if this 'deep' fauna is ignored, then quantitative studies of the benthos, including secondary production estimates, can be subject to considerable error.

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Appendix 1. *Stream channel stability evaluation form (after Pfankuch, 1975).*

Item Rated	Stability Indicators by Classes							
UPPER BANKS	**EXCELLENT**		**GOOD**		**FAIR**		**POOR**	
Landform slope	Bank slope gradient <30%	(20)	Bank slope gradient 30-40%	(4)	Bank slope gradient 40-60%	(6)	Bank slope gradient 60%+	(8)
Mass-wasting (existing or potential)	No evidence of past or any potential for future mass-wasting into channel.	(3)	Infrequent and/or very small. Mostly healed over. Low future potential.	(6)	Moderate frequency and size, with some raw spots eroded by water during high flows.	(9)	Frequent or large, causing sediment nearly year-long OR imminent danger of same.	(12)
Debris jam potential (floatable objects)	Essentially absent from immediate channel area.	(2)	Present but mostly small twigs and limbs.	(4)	Present, volume and size are both increasing.	(6)	Moderate to heavy amounts, predominantly larger sizes.	(8)
Vegetative bank protection	90%+ plant density. Vigor and variety suggests a deep, dense, soil binding root mass.	(3)	70-90% density. Fewer plant species or lower vigor suggests a less dense or deep root mass.	(6)	50-70% density. Lower vigor and still fewer species form a somewhat shallow and discontinuous root mass.	(9)	<50% density plus fewer species and less vigor indicate poor, discontinuous and shallow root mass.	(12)
Channel capacity	Ample for present plus some increases. Peak flows contained. W/D ratio <7.	(1)	Adequate. Overbank flows rare. Width to Depth (W/D) ratio 8 to 15.	(2)	Barely contains present peaks. Occasional overbank floods. W/D ratio 15 to 25.	(3)	Inadequate. Overbank flows common. W/D ratio >25.	(4)
LOWER BANKS								
Bank rock content	65%+ with large, angular boulders 12"+ numerous.	(2)	40 to 65%, mostly small boulders to cobbles 6-12".	(4)	20 to 40%, with most in the 3-6" diameter class.	(6)	<20% rock fragments of gravel-sizes, 1-3" or less.	(8)
Obstructions Flow deflectors Sediment traps	Rocks and old logs firmly embedded. Flow pattern without cutting or deposition. Pools and riffles stable.	(2)	Some present, causing erosive cross currents and minor pool filling. Obstructions and deflectors newer and less firm.	(4)	Moderately frequent, moderately unstable obstructions and deflectors move with high water causing bank cutting and filling of pools.	(6)	Frequent obstructions and deflectors cause bank erosion year-long. Sediment traps full, channel migration occurring.	(8)
Cutting	Little or none evident. Infrequent raw banks less than 6" high generally.	(4)	Some, intermittently at outcurves and constrictions. Raw banks may be up to 12".	(6)	Significant. Cuts 12-24" high. Root mat overhangs and sloughing evident.	(12)	Almost continuous cuts, some over 24" high. Failure of overhangs frequent.	(16)
Deposition	Little or no enlargement of channel or point bars.	(4)	Some new increase in bar formation, mostly from coarse gravels.	(8)	Moderate deposition of new gravel and coarse sand on old and some new bars.	(12)	Extensive deposits of predominantly fine particles. Accelerated bar development.	(16)
BOTTOM								
Rock angularity	Sharp edges and corners, plane surfaces roughened.	(1)	Rounded corners and edges, surfaces smooth and flat.	(2)	Corners and edges well rounded in two dimensions.	(3)	Well rounded in all dimensions, surfaces smooth.	(4)
Brightness	Surfaces dull, darkened or stained. Gen. not "bright".	(1)	Mostly dull, but may have up to 35% bright surfaces.	(2)	Mixture, 50-50% dull and bright, ±15%, i.e. 35-65%.	(3)	Predominantly bright, 65%+, exposed or scoured surfaces.	(4)
Consolidation or particle packing	Assorted sizes tightly packed and/or overlapping.	(2)	Moderately packed with some overlapping.	(4)	Mostly a loose assortment with no apparent overlap.	(6)	No packing evident. Loose assortment, easily moved.	(8)
Bottom size distribution and percent stable materials	No change in sizes evident. Stable materials 80-100%.	(4)	Distribution shift slight. Stable materials 50-80%.	(8)	Moderate change in sizes. Stable materials 20-50%.	(12)	Marked distribution change. Stable materials 0-20%.	(16)
Scouring and deposition	Less than 5% of the bottom affected by scouring and deposition.	(6)	5-30% affected. Scour at constrictions and where grades steepen. Some deposition in pools.	(12)	30-50% affected. Deposits and scour at obstructions, constrictions, and bends. Some filling of pools.	(18)	More than 50% of the bottom in a state of flux or change nearly year-long.	(24)
Clinging aquatic vegetation (moss and algae)	Abundant. Growth largely moss-like, dark green, perennial. In swift water too.	(1)	Common. Algal forms in low velocity and pool areas. Moss here too and swifter waters.	(2)	Present but spotty, mostly in backwater areas. Seasonal blooms make rocks slick.	(3)	Perennial types scarce or absent. Yellow-green, short term bloom may be present.	(4)
	COLUMN TOTALS							

Add the values in each column for a total reach score here (E___ + G___ + F___ + P___ = ___).

Reach score of: <38 = Excellent, 39-76 = Good, 77-114 = Fair, 115+ = Poor.

Appendix 2. Raw data set for invertebrate densities, July 1995 to June 1996 is held on disc available at the Secretaries' Office, Zoology Department, University of Canterbury.

Files are saved under Exel. Abbreviations used:

MBS - Middle Bush Stream
GS - Grasmere Stream
CR - Cass River