DRIFT OF AQUATIC MACROINVERTEBRATE LARVAE IN MANGANUIATEAO RIVER, CENTRAL NORTH ISLAND, NEW ZEALAND

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ABSTRACT

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Drifting aquatic invertebrate larvae in Manganuiateao River, central North Island, were collected at bi-monthly intervals between January and October 1989 from 2 sites (3 stations per site) over 4 diel periods in 24 h (dawn to mid-morning, mid-morning to mid-afternoon, mid-afternoon to dusk and dusk to dawn). Samples were also collected from 1 station over 1-2 h periods for 24 h in December 1989. A total of 68 aquatic invertebrate taxa were taken in the drift. Chironomidae, *Beraeoptera roria* and *Helicopsyche* spp. were the dominant taxa overall (> 10% of invertebrates on all dates and sites combined) between mid-afternoon and dusk, the only period that complete sets of samples were collected on most dates. Hydrobiosidae, *Deleatidium* spp., *Coloburiscus humeralis*, Plecoptera and *Pycnocentrodes* spp. comprised > 10% of larvae on at least one date. Drift density between mid-afternoon and dusk was highest in March and May (92-151 individuals 100 $m^{-3}h^{-1}$) and lowest in July (18-28 100 $m^{-3}h^{-1}$). Diurnal peaks in drift were evident around dusk and dawn when samples were collected at 1-2 h periods for 24 h, but this pattern was not detected in 2 other months that complete sets of drift samples were collected over 4 continuous periods in 24 h. Densities of *Deleatidium* spp., Plecoptera and Chironomidae larvae in the drift were significantly correlated with the density of invertebrates collected in two sets of comparable benthic samples, suggesting that drift of these taxa could be partly density dependent. Drift density of Chironomidae larvae was inversely correlated with mean flow in the week preceding sampling, but significant positive correlations were detected with preceding flow regime for *Deleatidium* spp., Plecoptera and *Pycnocentrodes* spp. We discuss some factors that are likely to influence invertebrate drift in Manganuiateao River, including the potential role of blue duck predation.

KEYWORDS: aquatic invertebrates - drift - diel periodicity - blue duck - Manganuiateao River.

INTRODUCTION

Drift, the downstream transport of aquatic organisms in the current, is an important mechanism for invertebrate dispersal within rivers, and for recolonisation of denuded areas following natural and anthropogenic disturbances (Elliott 1967, Davies 1976, Minshall & Peterson 1985, Tilley 1989, Doeg & Milledge 1991). Some overseas studies have shown temporal changes in the composition and density of stream drift, with higher densities generally occurring at dusk and lower densities during winter (Elliott 1967, Clifford 1972). Densities of different invertebrate taxa in the drift can also vary at points across the stream channel and on the flow hydrograph. Mechanisms causing drift are thought to include dislodgement by current, pollution, changes in food supply and predation (Brittain & Eikeland 1988).

During 1989, we sampled drift at two sites on a lowland section of Manganuiateao River in the central North Island as part of an investigation into the dynamics of blue duck (*Hymenolaimus malacorhynchos*) food resources which consist primarily of aquatic invertebrates (Kear & Burton 1971, Collier 1991). We were interested in describing seasonal and diel variations of the drift, particularly how these were related to the feeding patterns of blue duck which include diurnal bouts between dawn and mid-morning, and between mid-afternoon and dusk in late summer-autumn (Veltman & Williams 1990). At other times of year, birds feed throughout the day, although recent work indicates that birds also feed at night in February to April (Douglas & Pickard in press). We also investigated the likely roles of discharge preceding sampling and the density of invertebrates in the benthos as factors determining drift patterns in Manganuiateao River.

STUDY AREA

Manganuiateao River drains the western slopes of Mt. Ruapehu, central North Island, New Zealand, and has its flow and water quality protected by a National Water Conservation Order. It supports many native fish species, a nationally significant trout fishery, and one of the largest North Island populations of the threatened blue duck (Cudby & Strickland 1986, Williams 1991).

Average annual rainfall in the catchment is 2 000 mm, although it declines as altitude falls. From its source at about 2 000 m a.s.l. (well above the tree line), the river flows for 80 km in a south-westerly direction to join Whanganui River 11 km upstream of Pipiriki (56 m a.s.l.). The Manganuiateao is the third largest tributary of Whanganui River and has very high water quality (Cudby & Strickland, 1986). During its descent, it passes through alpine slopes, steep gorges and open flats; riparian vegetation includes native and exotic forest, regenerating scrub and pasture.

The section of river sampled consisted of a series of stable pools and riffles with substrata mostly of rounded andesite boulders. Riparian vegetation was primarily silver wattle (*Acacia dealbata*), *Nothofagus fusca*, and podocarps including *Beilschmieda tawa*, *Knightia excelsa* and *Melicytus ramiflorus*. Drift samples were taken from two locations: "Rams", 3 km below the Orautoha Stream confluence and "Meyers", 1 km above the confluence (sites M6 and M8, respectively, of Collier & Lyon 1991 and Collier 1991). These sites were at elevations of 260 and 320 m a.s.l., respectively, were easily accessible, and were representative of the middle section of the river. Mean monthly water temperatures near this section range from 7 to 16°C (Cudby & Strickland 1986).

METHODS

SAMPLING PROTOCOL

Samples were taken at 3 stations per site, from stable boulder banks where blue duck were known to feed (Veltman & Williams 1990). At each site, drift was collected continuously for 24 h with nets being changed at mid-morning (*c*. 1000-1120 h), mid-afternoon (*c*.1400-1510 h), dusk and dawn (all times are NZST). There were thus 4 unequal sampling periods in the 24 h. This sampling regime was carried out at approximately bi-monthly intervals from January to October 1989. On 12-13 December, we collected samples at 1-2 hour intervals over a 24 h period to verify conclusions concerning diel drift periodicity drawn from the longer diel sampling periods.

Each site was sampled on successive days during the 6 bi-monthly trips, except on July 11 when floods meant only the afternoon and night samples could be obtained from one site. A second trip on 18-19 July was also disrupted by floods, and a complete set of samples was collected from the alternate site only for the period mid-afternoon to dusk. Six of the samples collected in September were not sorted because they were clogged with flower heads from riparian wattle trees, and 4 samples were lost in January and March. Discharge at the time of sampling (recorded 1.5 km downstream of Rams) ranged from 3.3 to 13.0 $m^3.s^{-1}$.

DRIFT SAMPLING

We collected drift using samplers similar to those described by Field-Dodgson (1985) except that replicate nets were placed on separate stands so that samples could be taken from a wider range of locations at each site. Samplers consisted of a rectangular Marley guttering sump (sampling area = 0.0053 m^2) to which a one metre long net (0.5 mm mesh) was attached. These were tied individually around boulders and were supported by metal stakes on the river bed so that samples were collected half way between the river bottom and the water surface (range of depths from water surface to top of sampler = 22-50 cm). The downstream end of the net consisted of a short segment of downpipe enclosed by a piece of net secured with a hose clip. Samples were removed from this end net after each sampling period and preserved in 4% formalin. Water velocity at the mouth of each sampler was measured over a ten second interval using a Scientific Instruments Model 1205 mini meter fitted with a Stewart Stream Gauging Counter. This was done at the beginning and end of each sampling period, and the mean of the two counts was used to calculate velocity using the appropriate equations. Flows less than about 0.2 $m.s^{-1}$ could not be measured accurately in January, March and part of the May trip.

Invertebrates were sorted and identified at 10-40x magnification under a stereoscopic microscope using the keys of Winterbourn & Gregson (1989), McFarlane (1951) and Towns (1983). Some of the less abundant taxa were grouped together in genera, families or orders for analysis. Terrestrial invertebrates and aquatic mites, oligochaetes and nematodes comprised only a small proportion of the invertebrates collected and were not considered in analyses.

BENTHIC INVERTEBRATE SAMPLING

Aquatic invertebrates were collected from large stones in the middle of the dawn to mid-morning and mid-afternoon to dusk drift sampling periods at the site from which drift was not being collected. These data were used to compare proportions and densities of invertebrate taxa in the benthos with those in the drift. Five stones (total surface area 0.04-0.13 m^2; estimated by wrapping them in foil of known weight per unit area or by the method of Graham *et al.* (1988)) were randomly selected from each site during each diel period. The upper surfaces of stones were brushed in situ into a 0.5 mm mesh net, and the stones were then taken in another net to the bank where their lower surfaces were brushed.

RESULTS

SEASONAL CHANGES IN DRIFT DENSITY AND COMPOSITION

A total of 68 aquatic invertebrate taxa were recorded in the drift and 63 taxa were taken in benthic samples (Appendix 1). Most taxa collected in the drift were Trichoptera (35% of taxa), Ephemeroptera (21%) or Plecoptera (18%). Fourteen taxa were collected in drift samples but not in benthic samples, whereas 9 taxa were taken only from the benthos (Appendix 1).

Table 1. Results of non-parametric analysis of variance of total invertebrate drift density. July data were excluded because sampling was disrupted by floods. DF = degrees of freedom

	DF	Value	Probability
Month	4	13.37	<0.001
Site	1	0.04	0.847
Month x site	4	2.46	0.054
Diel period	3	55.12	<0.001
Month x diel period	1	24.14	<0.001
Site x diel period	3	1.63	0.190
Month x site x diel period	1	0.57	0.831

Non-parametric analysis of variance (Table 1) showed that total drift density was not significantly different between sites, but that it varied significantly between months (excluding July when floods disrupted sampling). Drift density peaked at Meyers in March (92 larvae 100 $m^{-3}.h^{-1}$) and at Rams in May (151 100 $m^{-3}.h^{-1}$). At both sites an initial increase in drift density occurred between January and March, a distinct decrease was observed in July, and an increase occurred in September. September and October drift densities were similar. Benthic densities at both sites during mid-afternoon to dusk were highest in September (12 821-13 283 m^{-2}), and were lowest in January at Rams and in October at Meyers (Fig. 1). Benthic densities were low at Meyers in July when sampling followed a large flood, but were high at Rams in the same month because samples were collected before the flood (Fig. 1).

Overall, the drift was dominated by Chironomidae, *B. roria* and *Helicopsyche* spp. (>10% of total drift on all dates combined), although *Deleatidium* spp., *C. humeralis*, Hydrobiosidae (most were *Hydrobiosis parumbripennis*, *Costachorema* spp. and unidentifiable small larvae), *Pycnocentrodes* spp. and Plecoptera (mostly *Zelandoperla* species) were relatively abundant (> 10%) in some months (Fig. 2). Of the remaining invertebrates, *O. feredayi* comprised 0-9.7% of the drift and all other taxa combined (*ie.*, "Other" in Fig. 2) made up 0.3 - 21.4% in different months. The relative abundance of taxa in the drift fluctuated throughout the year.

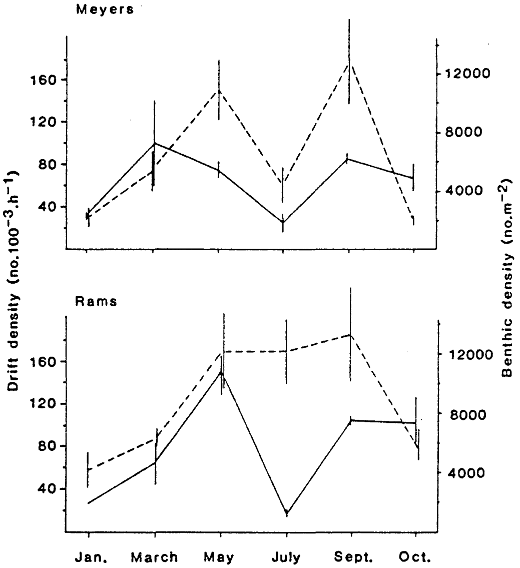

Figure 1. Densities of total invertebrates (x ± 1 SE) in the drift (solid line) and the benthos (broken line) during the mid-afternoon to dusk sampling period on 6 dates at 2 sites on Manganuiateao River. Only the mid-afternoon to dusk samples were used in this analysis as they provided the most complete data set. n=5 for benthic samples and 3 for drift samples except at Rams in January when n=1 for drift.

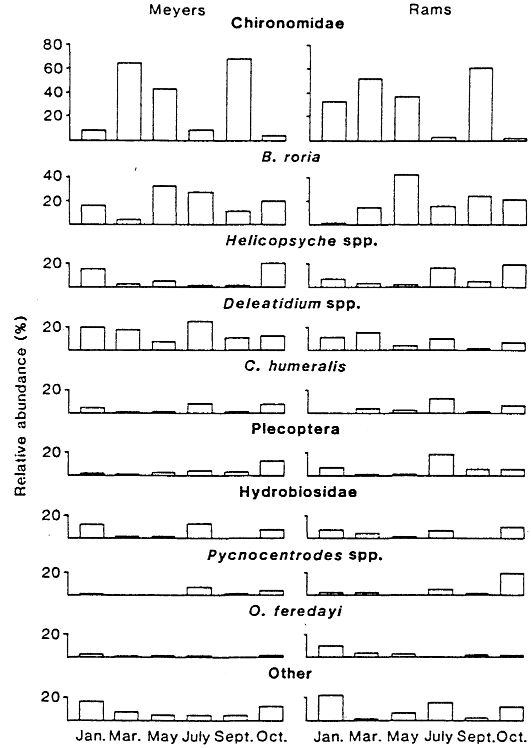

Figure 2. Relative abundances of 10 common invertebrate groups in the drift during the mid-afternoon to dusk sampling period on 6 dates at 2 sites on Manganuiateao River.

Chironomid larvae comprised over 50% of total drift in March and September, but constituted much lower percentages (3-10%) at both sites in July and October. Relative abundances of *O. feredayi*, *Helicopsyche* spp. and *B. roria* larvae were greatest in January, October and May, respectively.

DIEL CHANGES IN DRIFT DENSITY

Significant differences in total drift density were detected between diel periods when data for all months (excluding July) and sites were combined (Table 1). Drift density was consistently highest during the mid-afternoon to dusk or the mid-morning to mid-afternoon time periods in May and October (Fig. 3) the only months complete sets of replicate samples were obtained over 24 h. Differences were statistically significant (Kruskal-Wallis, $P<0.05$) at both sites in both months except for Meyers in October (Fig. 3). When more intensive 24 h sampling was carried out in December, peaks in drift were evident at dusk, 2 h after dusk, and around dawn (Fig. 4). Drift densities between 0800 and 1800 h were low (<75 100 m^{-3}. h^{-1}; Fig. 4) in this month.

FACTORS AFFECTING DRIFT

The relationship between densities of invertebrate taxa in the drift and benthos was investigated for the morning and afternoon diel periods by calculating Spearman rank correlation coefficients (Table 2). This analysis was carried out on data for all months combined except for July when water temperatures were low (Cudby & Strickland 1986) and floods disrupted sampling. Total density and densities of *Deleatidium* spp., Plecoptera and Chironomidae in the drift and benthos were significantly correlated for both diel periods whereas densities of *Pycnocentrodes* spp. and Hydrobiosidae were significantly correlated in one diel period only (Table 2). This analysis suggests that drift of *Deleatidium*, Plecoptera and Chironomi-

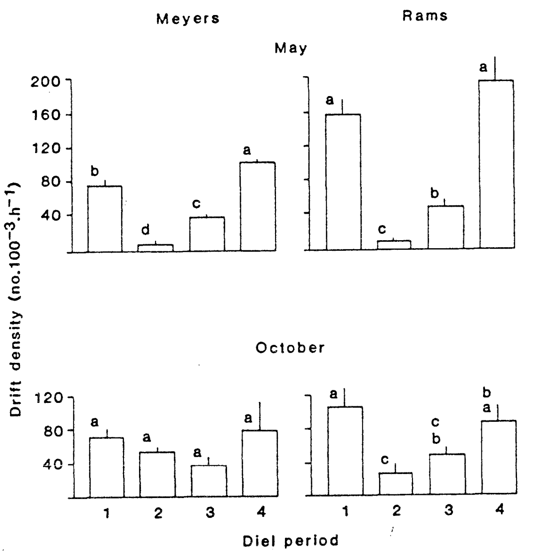

Figure 3. Drift density (x ± 1 SE, n = 3) of total invertebrates at 2 sites during the 4 diel sampling periods in May and October, the only months for which complete data sets were available. Bars with the same letters above them are not significantly different (Kruskal-Wallis followed by Student-Neuman-Keuls test on ranks, $P<0.05$). For diel periods, 1 = mid-afternoon to dusk, 2 = dusk to dawn, 3 = dawn to mid-morning, 4 = mid-morning to mid-afternoon.

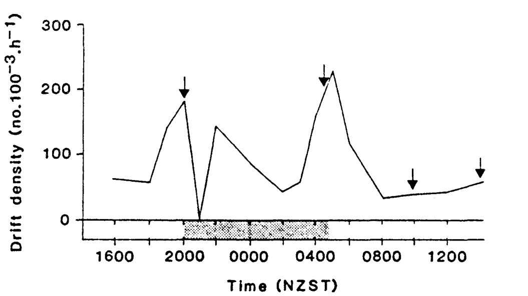

Figure 4. Total invertebrate drift density in mid-water for one sampling station on 12-13 December 1989 at Rams, Manganuiateao River. Stippled bar at bottom of graph indicates the period of darkness. Arrows indicate approximate times of routine sample collections on other dates.

dae in particular could be partly density dependent, although seasonal factors may have influenced these correlations.

Correlation coefficients between relative abundance of most taxa in the drift and benthos were similar for upper and total stone surfaces for most invertebrate taxa (Table 2). This suggests that invertebrate activity on upper surfaces was not a major factor affecting their relative abundance in the daytime drift during the 5 sampling months examined.
All correlations were positive except for *B. roria* which showed a weak tendency not to enter the drift from upper stone surfaces.

Temporal variations in drift density of some taxa during the mid-afternoon to dusk period appeared to be related partly to the flow regime preceding sampling (Table 3). Thus, drift densities of Chironomidae were inversely correlated with mean flow in the week prior to sampling determined from daily spot readings at a downstream gauging station. In contrast, densities of *Deleatidium* spp., Plecoptera and *Pycnocentrodes* spp. were positively correlated with mean flow preceeding sampling, although not all relationships were statistically significant (Table 3).

For some invertebrate taxa, relationships between preceeding flow regime and benthic densities differed from those observed for drift densities (Table 3). Flow was significantly and inversely correlated with densities of *B. roria* in the benthos but not in the drift. In contrast, preceeding flow regime and densities of *Pycnocentrodes* spp. larvae were significantly and positively correlated in the drift but not in the benthos (Table 3). The reasons for these differences are not understood.

DISCUSSION

COMPOSITION AND DENSITY OF THE DRIFT

Studies of aquatic invertebrate drift in New Zealand have been conducted in a variety of habitats ranging from a limestone cave stream (Death 1988) to large, braided rivers (Pierce 1986, Sagar & Glova 1988). The composition of the drift reported in different studies has been correspondingly variable, although chironomids and *Deleatidium* are frequently amongst the dominant taxa (Table 4). Elmidae, Oligochaeta and various taxa of caddisflies have also been reported to comprise large proportions of the drift in several studies (see Table 4 and Irvine & Henriques 1984, Watson 1971). Many of these taxa were also common in the drift in Manganuiateao River, and we also found high relative abundances of *Helicopsyche*, Plecoptera and *C. humeralis* larvae on some dates. Relative abundances of drifting *Helicopsyche* larvae elsewhere in New Zealand have ranged from

Table 2. Spearman rank correlation coefficients between density and % composition of common invertebrate taxa in the drift and benthos (mean of all stone surfaces or upper surfaces only) from dawn to mid-morning (no parentheses, n=24-26) and mid-afternoon to dusk (parentheses, n=28-30) for all dates (excluding July) combined. * $P<0.05$, ** $P<0.01$, *** $P<0.001$. -, not applicable.

Taxon	Densities	% on all stones surfaces	% on upper stone surfaces
Chironomidae	0.73***	0.78***	0.82***
	(0.59**)	(0.50**)	(0.70***)
B. roria	0.18	-0.08	-0.22
	(0.15)	(-0.16)	(-0.28)
Helicopsyche spp.	-0.07	0.36	0.40*
	(0.12)	(0.44*)	(0.47**)
Deleatidium spp.	0.58**	0.66***	0.58**
	(0.72***)	(0.67***)	(0.74***)
C. humeralis	0.17	0.41*	0.30
	(0.18)	(0.16)	(0.29)
Plecoptera	0.45*	0.34	0.32
	(0.46*)	(0.37*)	(0.35)
Hydrobiosidae	0.00	0.65***	0.41*
	(0.43*)	(0.60***)	(0.67***)
Pycnocentrodes spp.	0.41*	0.50**	0.34
	(0.33)	(0.62***)	(0.59***)
O. feredayi	0.3	0.21	0.29
	(0.24)	(0.41*)	(0.15)
Total	0.41*	-	-
	(0.52**)	-	-

0.2-0.8% of total drift (Fechney 1988, Glova & Sagar 1989b) compared with up to 49% in our samples. This may reflect high benthic densities of *Helicopsyche* spp. (325-3193 m^{-2}) in Manganuiateao River, although we did not detect a significant correlation between benthic and drift densities (Table 2).

Mid-water drift densities in boulder banks of Manganuiateao River ranged from 0 to 229 invertebrates 100 $m^{-3}.h^{-1}$ during the course of our study (see Fig. 4). Where possible, we have standardised the unit of drift density (no. 100 $m^{-3}.h^{-1}$) from some other New Zealand studies to enable comparisons with our work (Table 4). This shows that maximum drift density in our study was lower than the maximum densities reported for some South Island rivers by McLay (1968) and Sagar & Glova (1992), but considerably higher than the drift densities recorded in 3 flood-prone Westland streams by Graesser (1988). Densities in Manganuiateao River were similar to those recorded in Ryton River by Sagar & Glova (1992; Table 4).

SEASONAL AND DIEL DRIFT PATTERNS

Drift density in temperate rivers is generally lowest in winter (McLay 1968, Clifford 1972, Brittain & Eikeland 1988, Bayly 1990), and cool water temperatures affecting invertebrate activity patterns may be one reason for this phenomenon (Watson 1971, Pierce 1986, Death 1988, Bayly 1990). Our finding of low drift densities in winter when water temperatures average 7-8°C is consistent with this pattern. However, we also recorded very low densities in summer (Fig. 1). Boothroyd (1988) also reported low densities of drifting chironomid pupal exuviae in a Waikato stream in late summer through to July. Other factors (see later discussion) can be superimposed on seasonal trends thereby influencing invertebrate drift patterns.

Variations in drift over a 24 h period can give rise to diel periodicity (Brittain & Eikeland 1988).

Table 3. Spearman rank correlation coefficients between mean daily discharge in the week prior to sampling and densities (mid-afternoon to dusk) of 9 invertebrate taxa in the drift (no parentheses, n = 15-18) and benthos (parentheses, n = 30) at 2 sites on Manganuiateao River (all dates combined). *, $P<0.05$; **, $P<0.01$, ***, $P<0.001$.

	Meyers	Rams
Chironomidae	-0.36	-0.52*
	(-0.27)	(-0.02)
B. roria	0.22	-0.08
	(-0.52**)	(-0.59***)
Helicopsyche spp.	0.11	-0.08
	(-0.26)	(-0.28)
Deleatidium spp.	0.37	0.56*
	(0.27)	(0.56**)
C. humeralis	0.40	0.17
	(0.14)	(0.36*)
Plecoptera	0.51*	0.46
	(0.36)	(0.41*)
Hydrobiosidae	0.20	0.27
	(-0.13)	(-0.04)
Pycnocentrodes spp.	0.56*	0.59*
	(-0.15)	(0.06)
O. feredayi	0.04	-0.41
	(-0.25)	(0.27)

Most studies of diel variation in the drift have detected greater drift densities during the hours of darkness, particularly just after dusk (Elliott 1967, McLay 1968, Clifford 1972, Death 1988, Bayly 1990). Other workers have detected drift peaks later at night (Sagar & Glova 1988, Glova & Sagar 1989a, b). In some New Zealand studies high drift densities have also been reported during the day. Glova & Sagar (1989a) detected a diurnal rise in drift in Ryton River, Canterbury, although this followed a noctural peak. Death (1988) recorded diurnal peaks in the drift of Chironomidae and *Pycnocentrodes* larvae outside the cave of Cave Stream, and Watson (1971) found that *Pycnocentrodes* was more active in the drift during the day in a stream near Auckland.

Another cased caddisfly (*Pycnocentria*) and Chironomidae were dominant in the drift of Dalgety Stream, Canterbury, during the day whereas *Deleatidium* and *Olinga* dominated the nocturnal drift (Fechney 1988). In contrast, Cadwallader (1975) found *Pycnocentria* larvae mostly at night in another Canterbury river, and *Pycnocentrodes*, *Beraeoptera*, Elmidae and chironomid pupae were collected mostly during the day.

Apparently, diel drift patterns can vary for different invertebrate taxa and in different rivers. Nocturnal peaks in drift were not evident in Manganuiateao River in May and October when we collected complete 24 h data sets over 4 diel drift periods. However, drift peaks were evident around dusk and dawn in December when more intensive 24 h sampling was carried out. Drift began to increase well before dusk when the channel became shaded by adjacent hills. If this diel pattern is representative of other months, then our routine sample collections which coincided with dusk and dawn would have included the peaks in drift. This would explain our finding in May and October of high drift densities during mid-afternoon to dusk, and emphasises the importance of collecting samples frequently when elucidating diel drift periodicity (see also Elliott 1969).

Effects of preceding flow regime

In our study, preceding flow regime was implicated as a factor affecting the drift and benthic densities of some taxa. Higher mean daily flow in the week prior to sampling (implying the recent occurrence of spates) was associated with lower

Table 4. Summary of the results of several New Zealand drift studies in different rivers. -, no data or not calculable. *, includes terrestrial invertebrates.

Location	Sampling interval	Dominant aquatic taxa	Drift density (no.100^{-3}.h^{-1})	Reference
Kakanui R., Otago	0.5h	*Deleatidium* Chironomidae	280-9260	McLay 1968
Glentui R., Canterbury	1h	*Deleatidium* *Pycnocentrodes* *Olinga*	-	Cadwallader 1975
Cave Stm., Canterbury	-	Hydrobiosidae Elmidae Simuliidae	-	Death 1988
Dalgety Stm., Canterbury	-	*Deleatidium* Chironomidae	-	Fechney 1988
Westland streams	sunset and sunrise	*Deleatidium* Chironomidae	0-3*	Graesser 1988
Rakaia R., Canterbury	1-4h	*Deleatidium* Chironomidae *Aoteapsyche* *Hydrobiosis*	11-895	Sagar & Glova 1992
Ryton R., Canterbury	3.5-9h	Chironomidae *Austrosimulium* *Oxyethira*	42-206	Sagar & Glova 1992
Hawkins R., Canterbury	1-5h	*Deleatidium* *Olinga* *Austrosimulium*	108-768	Sagar & Glova 1992
Deep Ck., Canterbury	5-6h	*Deleatidium* Chironomidae	879-1890	Sagar & Glova 1992
Weydon Burn, Otago	1-12h	*Deleatidium* Hydora	186-3409	Sagar & Glova 1992
Manganuiateao R., central N.I.	1.0-14.6h	Chironomidae *Helicopsyche*	0-229	This study

drift and lower benthic densities of chironomids and *B. roria*, respectively, but with higher drift and/or benthic densities of *Pycnocentrodes* spp., *C. humeralis*, Plecoptera and *Deleatidium* spp. The strength of some relationships varied between sites, and this may have been partly because the July samples were collected at the 2 sites on different dates, before and after a large flood.

Irvine and Henriques (1984) found that numbers of drifting chironomids, oligochaetes and caddisflies (mainly *O. albiceps*) were higher during artifically induced spates in Hawea River, Otago. Patterns of abundance for these taxa in the drift were similar to those for the biomass of drifting periphyton, suggesting that most invertebrates were associated with periphyton dislodged by high flows (see also McLay 1968). In Manganuiateao River, the biomass of periphyton mats that accumulated on rocks during periods of stable flow were noticeably reduced after high flows, and this may have resulted in depletion of the associated chironomid fauna. This would at least partly explain the negative correlations observed between preceding flow regime and the density of chironomid larvae in the drift.

McLay (1968) also found that chironomid densities decreased following a flood in Kakanui River, whereas densities of *Deleatidium* and other taxa increased in the drift and benthos. He suggested that those taxa which increased in abundance following floods sought shelter deep in the bed and were therefore able to survive periods of high flow. This is also likely to occur in Manganuiateao River where the bed consists predominantly of stable boulders and large cobbles, and interstitial spaces are reasonably large. Retreat into these interstices during periods of high flow and subsequent dispersal and recolonisation of surface substrates after floods could partly explain the significant positive correlations observed between preceding flow regime and drift densities of *Pycnocentrodes* spp., Plecoptera and *Deleatidium* spp. larvae.

BIOTIC FACTORS AFFECTING DRIFT

The drift of many invertebrate taxa has been found to be correlated with their densities in the benthos indicating that drift could be density dependent. Some workers have suggested that this is the result of excess secondary production in a river leading to competition for food and/or space (see references in Brittain & Eikeland 1988). However, density dependence is complicated by other factors such as current velocity, substrate type and seasonal factors which also influence the density and composition of drift (Brittain & Eikeland 1988).

In New Zealand, McLay (1968) and Watson (1971) have observed correlations between densities of invertebrates in the drift and benthos, although patterns in Kakanui River were influenced by behavioural differences between taxa. In contrast, Graesser (1988) found no relationship between drift and benthic densities (all of which were low) in 3 flood-prone Westland streams. Our results in Manganuiateao River suggest that drift of Chironomidae, *Deleatidium* and Plecoptera could be partly density dependent, although seasonal factors may be superimposed on this pattern. Activity of invertebrates on upper stone surfaces during the day did not appear to be a major factor influencing the propensity of taxa to drift.

Finally, Peckarsky (1980) suggested that the relative abundance and periodicity of some invertebrate larvae in the drift may be partly explained by predator evasion behaviour. In Manganuiateao River, blue ducks are important invertebrate predators and drift from localised patches of the benthos could be initiated by their presence. Birds may dislodge invertebrates while foraging, or invertebrates may actively swim into the water column in response to visual, hydrodynamic or olfactory cues (*eg.*, Williams 1990).

However, given the size of their territories (around 1 km long, Williams 1991), it is unlikely that predation by blue duck has a major effect on invertebrate drift patterns in Manganuiateao River. Observed diel patterns are probably the result of a combination of factors including innate invertebrate rhythms, specific activities of individuals and localised changes in light levels. Differences in drift of many taxa between sampling months can be partly attributed to seasonal changes in conditions (*eg.*, water temperatures), and to dispersal and re-colonisation of bed substrata following floods.

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REFERENCES

Bayly, I.A.E. (1990). Abundance and drift of the larval micro-caddis, *Oxyethira albiceps* (McLachlan), in the Waikato River near Lake Taupo. *New Zealand Entomologist* 13: 52-54.

Boothroyd, I.K.G. (1988). Temporal and diel emergence of Chironomidae (Diptera: Insecta) from a New Zealand stream. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1399-1404.

Brittain, J.E. & Eikeland, T.J. (1988). Invertebrate drift: a review. *Hydrobiolgia* 166: 77-93.

Cadwallader, P.L. (1975). Feeding habits of two fish species in relation to invertebrate drift in a New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 9: 11-26

Clifford, H.F. (1972). A years study of the drifting organisms in a brown water stream of Alberta, Canada. *Canadian Journal of Zoology* 50: 975-983.

Collier, K.J. (1991). Invertebrate food supplies and diet of blue duck in rivers of two regions of the North Island, New Zealand. *New Zealand Journal of Ecology* 15: 131-138.

Collier, K.J. & Lyon, G.L.L. (1991). Trophic pathways and diet of blue duck (*Hymenolaimus malacorhynchos*) in Manganuiateao River: a stable carbon isotope study. *New Zealand Journal of Marine and Freshwater Research* 25: 181-186.

Cudby, E.J. & Strickland, R.R. (1986). The Manganuiateao River Fishery. Fisheries Environmental Report No. 14, Fisheries Research Division, N.Z. Ministry of Agriculture and Fisheries, Turangi, New Zealand.

Davies, B.R. (1976). The dispersal of Chironomidae larvae: a review. *Journal of the Entomological Society of South Africa 39*: 39-62.

Death, R.G. (1988). Drift distance, periodicity and frequency of benthic invertebrates in a cave stream. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1446-1450.

Doeg, T.J. & Milledge, G.A. 1991. Effect of experimentally increasing concentrations of suspended sediment on macroinvertebrate drift. *Australian Journal of Marine and Freshwater Research* 42: 519-526.

Douglas, M.J. & Pickard, C.R. (in press). Telemetry of body tilt for automatic data-logging blue duck behaviour. *In*: Priede, I.G. & Swift, S.M. (eds.), Wildlife telemetry. Proceedings of the 4th European conference on wildlife telemetry, Aberdeen, Scotland, U.K. 16-20 September, 1991. Ellis Horwood, Chichester, U.K.

Elliott, J.M. (1967). Invertebrate drift in a Dartmoor stream. *Archiv für Hydrobiologie* 63: 202-237.

Elliott, J.M. (1969). Diel periodicity in invertebrate drift and the effect of different sampling periods. *Oikos* 20: 524-528.

Fechney, L.R. (1988). The summer diet of brook trout (*Salvelinus fontinalis*) in a South Island high-country stream. *New Zealand Journal of Marine and Freshwater Research* 22:163-168.

Field-Dodgson, M.S. (1985). A simple and efficient drift sampler. *New Zealand Journal of Marine and Freshwater Research* 19: 167-172.

Glova, G.J. & Sagar, P.M. (1989a). Feeding in a nocturnally active fish, *Galaxias brevipinnis*, in a New Zealand stream. *Australian Journal of Marine and Freshwater Research* 40: 231-240.

Glova, G.J. & Sagar, P.M. (1989b). Prey selection by *Galaxias vulgaris* in the Hawkins River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 153-161.

Graesser, A.K. (1988). Invertebrate drift in three flood-prone streams in South Westland, New Zealand. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1422-1426.

Graham, A.A., McCaughan, D.J. & McKee, F.S. (1988). Measurement of surface area of stones. *Hydrobiologia* 157: 85-87.

Irvine, J.R. & Henriques, R.R. (1984). A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 18: 283-290.

Kear, J. & Burton, J.K. (1971). The food and feeding apparatus of blue duck *Hymenolaimus*. *Ibis* 113: 483-493.

McFarlane, A.G. (1951). Caddis Fly Larvae (Trichoptera) of the Family Rhyacophilidae. *Records of the Canterbury Museum* 5: 267-289.

McLay, C.L. (1968). A study of the drift in the Kakanui River, New Zealand. *Australian Journal of Marine and Freshwater Research* 19: 139-149.

Minshall, G.W. & Peterson, R.C. (1985). Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv für Hydrobiologie* 104: 49-76.

Peckarsky, B.L. (1980). Predator-prey interactions between stoneflies and mayflies: behavioural observations. *Ecology 61*: 932-943.

Pierce, R.J. (1986). Foraging responses of stilts (*Himantopus* spp.: Aves) to changes in behaviour and abundance of their invertebrate prey. *New Zealand Journal of Marine and Freshwater Research* 20: 17-28.

Sagar, P.M. & Glova, G.J. (1988). Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fish Biology* 33: 643-653.

Sagar, P.M. & Glova, G.J. (1992). Diel changes in the abundance and size composition of invertebrate drift in five South Island, New Zealand, rivers. *New Zealand Journal of Marine and Freshwater Research*. 26: 103-114.

Tilley, L.J. (1989). Diel drift of Chironomidae larvae in a pristine Idaho stream. *Hydrobiologia* 174: 133-149.

Towns, D.R. (1983). A revision of the genus *Zephlebia* (Ephemeroptera: Leptophlebiidae). *New Zealand Journal of Zoology* 10: 1-52.

Veltman, C.J. & Williams, M. (1990). Diurnal use of time and space by breeding blue duck. *Wildfowl* 41: 62-74.

Watson, G.W. (1971). Drift of stream invertebrates. *Tane* 17: 197-212.

Williams, D.D. (1990). A field study of the effects of water temperature, discharge and trout odour on the drift of stream invertebrates. *Archiv für Hydrobiologie* 119: 167-181.

Williams, M.J. (1992). Some social and demographic characteristics of blue duck. *Wildfowl* 42: 65-86.

Winterbourn, M.J. & Gregson, K.L.D. (1989). Guide to the Aquatic Insects of New Zealand. Bulletin of the Entomological Society 9.

APPENDIX 1 List of invertebrate taxa recorded in drift and benthic samples collected from the Manganuiateao River on six dates in 1989. Those taxa found only in the drift (*) or benthos (**) are indicated.

Phylum Arthropoda
Class Insecta
Order Ephemeroptera.
- *Coloburiscus humeralis*
- *Nesameletus* sp.
- *Deleatidium* spp.
- *Mauiulus luma*
- *Austroclima sepia*
- *A. jollyae*
- *Ameletopsis perscitus*
- *Neozephlebia scita*
- *Zephlebia versicolor*
- *Z. dentata*
- *Z. spectabilis*
- *Z. inconspicua*
- *Atalophlebioides cromwelli* *
- *Ichthybotus hudsoni* *
- *Acanthophlebia cruentata* **

Order Plecoptera.
- *Austroperla cyrene*
- *Megaleptoperla grandis*
- *M. diminuta* *
- *Stenoperla prasina*
- *Acroperla trivacuata*
- *Acroperla* sp.
- *Zelandobius confusus*
- *Z. furcillatus*
- *Zelandoperla decorata*
- *Z. fenestrata*
- *Z. agnetis*
- *Halticoperla* sp. *

Order Trichoptera.
- *Helicopsyche* spp.
- *Beraeoptera roria*
- *Olinga feredayi*
- *Confluens hamiltoni*
- *Pycnocentria funerea*
- *P. evecta*
- *P. sylvestris* **
- *Pycnocentrodes* spp.
- *Hudsonema aliena* *
- *H. amabilis*
- *Triplectides* sp.
- *Oecetis* sp. **
- *Alloecentrella ?magnicornis* *
- *Zelolessica cheira*
- *Oxyethira albiceps*
- *Aoteapsyche* spp.
- Ecnomidae sp.
- *Neurochorema forsteri*
- *N. confusum*
- *Hydrobiosis parumbripennis*
- *H. ?clavigera*
- *H. ?frater* **
- *Costachorema* sp.
- *C. ?xanthoptera*
- *C. ?psaroptera*
- *Psilochorema* sp.
- Hydrobiosidae indet
- *Polyplectropus puerilis* **
- *Plectrocnemia maclachlani* **

Order Megaloptera.
- *Archichauliodes diversus*

Order Coleoptera.
- Elmidae
- Hydraenidae
- Hydrophilidae *
- Dytiscidae sp. *
- *Liodessus deflectus* *

Order Hemiptera
- *Sigara* sp.

Order Diptera.
- Chironomidae
- *Aphrophila neozelandica*
- Eriopterini **
- *Paralimnophila skusei* **
- Muscidae
- Ephydridae *
- Empididae
- Culicidae *
- Tanyderidae *
- Psychodidae *
- Blephariceridae *
- *Austrosimulium* sp. **

Phylum Mollusca,
Class Gastropoda.
- *Potamopyrgus antipodarum*
- *Latia neritoides*