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The influence of riparian vegetation on macroinvertebrate community structure and functional organization in six new Guinea streams

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Abstract

Information on the ecology of New Guinea streams is meagre, and data are needed on the trophic basis of aquatic production in rivers such as the Sepik in Papua New Guinea which have low fish yields. This study investigates the relationship between riparian shading (from savanna grassland to primary rainforest), algal and detrital food, and macroinvertebrate abundance and community structure in 6 Sepik River tributary streams. A particular aim was to elucidate macroinvertebrate community responses to changes in riparian conditions. All streams supported diverse benthic communities, but morphospecies richness (overall total 64) was less than in streams on the tropical Asian mainland; population densities of benthic invertebrates, by contrast, were similar to those recorded elsewhere. Low diversity could reflect limited taxonomic penetration, but may result from the absence of major groups (Plecoptera, Heptageniidae, Ephemerellidae, Psephenidae, Megaloptera, etc.) which occur on the Asian mainland. Population densities of all 19 of the most abundant macroinvertebrate taxa varied significantly among the 6 study streams, but community composition in each was broadly similar with dominance by Baetidae and (in order of decreasing importance), Leptophlebiidae, Orthocladiinae, Elmidae and Hydropsychidae. Principal components analysis (PCA) undertaken on counts of abundant macroinvertebrate taxa clearly separated samples taken in two streams from the rest. Both streams contained high detrital standing stocks and one was completely shaded by rainforest. Stepwise multiple-regression analysis indicated that population densities of the majority of abundant taxa (11 out of 19) across streams (10 samples per stream; $n = 60$) were influenced by algae and/or detritus, although standing stocks of these variables were not clearly related to riparian conditions. When regression analysis was repeated on mean counts of taxa per stream (dependent variables) *versus* features of each stream as a whole (thus $n = 6$), % shading and detritus were the independent variables yielding significant regression models most frequently, but pH, total-nitrogen loads and algae were also significant predictors of faunal abundance. Further regression analysis, undertaken separately on samples ($n = 10$) from each stream, confirmed the ability of algae and detritus to account for significant portions of the variance in macroinvertebrate abundance, but the significance of these variables varied among streams with the consequence that responses of individual taxa to algae or detritus was site-specific.

Community functional organization — revealed by investigation of macroinvertebrate functional feeding groups (FFGs) — was rather conservative, and streams were codominated by collector-gatherers (mean across 6 streams = 43%) and grazers (36%), followed by filter-feeders (15%) and predators (7%). The shredder FFG was species-poor and comprised only 0.4% of total macroinvertebrate populations; shredders did not exceed 2% of benthic populations in any stream. PCA of FFG abundance data was characterized by poor separation among streams, although there was some evidence of clustering of samples from unshaded sites. The first 2 PCA axes accounted for 84% of the variation in the data suggesting that the poor separation resulted from the general similarity of FFG representation among streams. Although stepwise multiple-regression analysis indicated that algae and detritus accounted for significant proportions of the variations in population density and relative abundance of some FFGs, the response of community functional organization to changes in riparian conditions and algal and detrital food base was weak – unlike the deterministic responses that may be typical of north-temperate streams.

Introduction

The island of New Guinea is host to a diverse and distinctive assemblage of terrestrial flora and fauna, the great majority of which is of Oriental derivation (Gressitt, 1982). In apparent contrast to the terrestrial biota, there is thought to be a '... general poverty of freshwater animals in New Guinea' (Gressitt, 1982), and '... most rivers ... have a poorly developed aquatic fauna and flora' (Osborne, 1988). Certainly, some major groups of freshwater fish on the Asian mainland (e.g. the Cyprinidae, barring the exotic Cyprinus carpio) are absent from New Guinea, and the fish fauna of the island is quite distinct. A relationship with Australian fish fauna is, however, demonstrated by the fact that two families (Melanotaeniidae and Pseudomugilidae) occur in New Guinea and Australia and are found nowhere else (Allen, 1991). Most New Guinea fishes are either diadromous or permanent (secondary) inhabitants of freshwater derived from marine or estuarine ancestors. Despite the absence of cichlids, silurids and cyprinids, there is a total of 316 native species (Allen, 1991) and the freshwater fish fauna as a whole is not especially species-poor. Limited data on stream invertebrates (Dudgeon, 1990) indicate that benthic communities in New Guinea are not exceptionally depauperate compared to streams elsewhere, but certain lotic taxa (Plecoptera, ephemerellid and heptageniid mayflies) found on the Asian mainland are absent, while others (e.g. naucorid bugs) have diversified. In interesting contrast to the relationship of some of the New Guinea fish fauna with Australia, the freshwater shrimps (Atyidae and Palaemonidae) and mayflies — like much of the terrestrial biota — are of Oriental derivation (Holthuis, 1982; Edmunds & Polhemus, 1990).

There is a conspicuous lack of research on the ecology of New Guinea rivers and streams, and the scant information that is available is derived mostly from studies undertaken to the south of the Central Highlands (Petr, 1983a; Osborne, 1988). The Central Highlands is an important biogeographic barrier to freshwater Crustacea and fishes (Holthuis, 1982; Allen, 1991), and the ecology of rivers on either side of this divide may differ in important ways. The Sepik River, which drains land to the north of the Central Highlands in Papua New Guinea, has a relatively species-poor fish fauna (Coates, 1985; Allen, 1991) although benthic invertebrate communities in tributary streams seem diverse (Dudgeon, 1990). Fish yields from the Sepik are only 10% of what might be expected from floodplain rivers in similar latitudes (Coates, 1985), and over

half the catch is exotic tilapia (Oreochromis mossambicus). The possibility that yields might be increased by further species' introductions (Coates, 1987, 1993) has spurred research on the ecology of the Sepik. Although some taxonomic and ecological research on freshwater algae has been undertaken (Vyverman 1992a, 1992b; and references therein), there is still a need for data on the trophic basis of aquatic production in the system.

The ecology of temperate streams is greatly affected by terrestrial influences — especially riparian vegetation (Hynes, 1975; Vannote et al., 1980; Cummins et al., 1989) — and some geographic differences in the structure and functioning of Nearctic stream communities are associated with differences in terrestrial plant communities (Wiggins & Mackay, 1978). Limited data suggest that riparian vegetation influences tropical stream communities also (Dudgeon, 1988, 1989). Herein, the relationship between riparian shading, algal and detrital food, and macroinvertebrate abundance and community structure of 6 Sepik River tributary streams are analysed in order to determine how their ecology responds to variations in riparian conditions. Of particular interest was the question of whether low fish yields could be attributed to a shortage of animal food resulting from peculiarities in riparian influences upon macroinvertebrate communities.

Study area

The Sepik River system

The 1100 km long Sepik River has a mean discharge in the range of 4000–7000 m^3 s^{-1} (Mitchell et al., 1980; Petr, 1983b and pers. comm.). In terms of area drained (78000 km^2), it is the largest river system in Papua New Guinea. The flood plain is up to 70 km wide (7600 km^2) and consists mostly of backswamps. The Sepik drains the western part of the Central Depression which lies to the north of the Central Highlands and is occupied by the Sepik and Ramu rivers (Fig. 1). The latter is 720 km in length. Gradients in the Central Depression are very gentle (Loffler, 1977) and, during the flood season, the whole region near the mouths of the Sepik and the Ramu is inundated and the rivers are conjoined. Thus for part of the year, the Ramu functions as a major tributary of the Sepik river.

Together, the combined Sepik-Ramu drainage receives water from the Torricelli Mountains in the north, the Finisterre Range in the south east, and the Central Highlands in the south and south west. Each
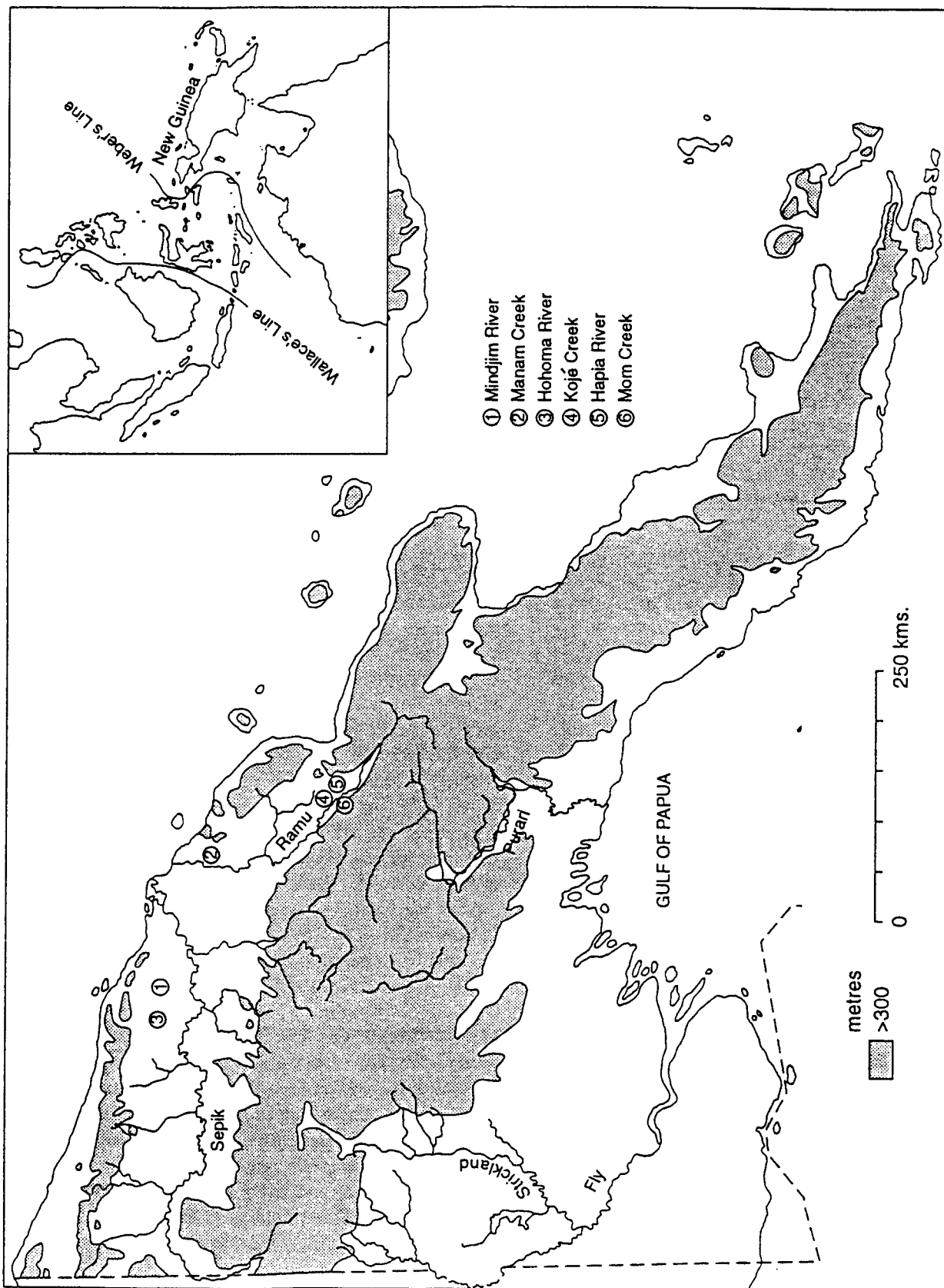
Fig. 1. The Sepik-Ramu River system showing the approximate positions of the six study streams and the location of Papua New Guinea within the region (inset). The shaded area is land above 300 m and includes the Central Highlands separating the region into northern (Sepik/Ramu) and southern drainages.

of these ranges has rather distinct, although complex geology (Loffler, 1977; Blecker, 1983) which will influence water chemistry. The Torricelli Mountains comprises Pliocene fine-grained marine and terrestrial sediments, including raised coral, on a basement of metamorphic rocks. The Finisterre Range is largely made up of a Tertiary volcanics and Miocene limestone. Streams draining limestone empty directly into the sea along the northern coast; those draining volcanic rocks join the Ramu River. The Central Highlands consist of metamorphic rocks derived from the alteration of sedimentary and volcanic rocks of Jurassic and Cretaceous age, along with some intrusive Miocene formations.

Of the six study streams (Fig. 1), two (Hohoma and Mindjim Rivers) drained the Torricelli Mountains, three (Kojé Creek, Manam Creek and Hapia River) drained the Finisterre Range, and one (Mom Creek) drained the Central Highlands. The streams were chosen to represent a range of riparian conditions, from rainforest to savannah, in a narrow altitudinal range (80–200 m). Within logistical constraints set by accessibility and permission to sample, streams were selected to be broadly comparable with regards to physical conditions and general appearance. Data on water chemistry (Table 1) indicate a lack of consistent differences among streams, although Mom Creek appeared to have a generally poorer ionic load and more acid waters than the other sites. For details of the water chemistry of the Sepik-Ramu drainage, see Coates *et al.* (1993).

The study streams

Hohoma River was almost unshaded (less than 10% of the water surface) despite a riparian vegetation of gardens and secondary forest. Width varied between 6 and 11 m; water depths were generally < 40 cm, and only 5–10 cm in runs. Current speeds reached 0.6 m s^{-1} in riffles but rates of 0.2–0.3 m s^{-1} were typical of runs. Leaf packs were rather scarce and, despite a lack of shading, there were no visible accumulations of periphytic algae. The substrate was sand overlain by medium cobbles (<20 cm longest axis). Elevation 160 m; gradient 0.010; univ. grid. ref. 54MYA665870; lat. 3°44'S, long. 143°23'E.

Mindjim River was surrounded by secondary forest, but the canopy above the water was open and only 20% of the water surface was shaded. Current speeds were 0.2–0.3 m s^{-1} in runs which comprised the main biotope; here the substrate was small-medium cobbles

(longest dimension <15 cm) embedded in fine sand. Water depths were 25–40 cm and the river was 10–12 m wide. Leaf packs accumulated close to the banks where current speeds were reduced. Elevation 80 m; gradient 0.003; univ. grid. ref. 54MYA865782; lat. 3°49'S., long. 143°35'E.

Kojé Creek was unshaded, draining secondary forest and gardens. The channel was approximately 5 m wide, but the stream occupied only 1–2 m of this. Water depth was 10–25 cm, and current velocities ranged from 0.3 m s^{-1} in runs up to 0.5 m s^{-1} in riffles. The substrate was small-medium cobbles (longest dimension <15 cm), gravel and fine sand (the latter in areas of slack water). Filamentous algae grew on stony substrates, and some leaf packs were present. Subsequent to this study, an investigation of the effects of rotenone on benthic macroinvertebrates (Dudgeon, 1990) was undertaken here and at Manam Creek (see below). Elevation 160 m; gradient 0.012; univ. grid. ref. 55MCP233867; lat. 5°33'S., long. 145°23'E.

Manam Creek drained rainforest and the water surface was 95–100% shaded. Stream width was approximately 7 m, and topography comprised a number of deep (>1 m) pools separated by runs and small riffles. Current speeds outside pools ranged from 0.2 to 0.5 m s^{-1}. The water in runs was generally <15 cm deep, and as shallow as 2 cm in some localities. The substrate comprised small cobbles (longest dimension <10 cm) of friable, sedimentary rock. Both the bottom sediments and leaf packs seemed rather unstable. Elevation 80 m; gradient 0.029; univ. grid. ref. 55MBQ765960; lat. 4°33'S., 144°59'E.

Hapia River drained savanna grassland with isolated trees, and was unshaded. The river was 8–20 m wide and occupied only a small proportion of the 100-m wide channel. Water depths were <10 cm in runs (where the river was broad) but up to 2 m in pools (where the river narrowed). Current speed was 0.2–0.3 m s^{-1} in runs, increasing to 0.5–0.6 m s^{-1} in riffles. Samples were taken where the river was 9 m wide and 5–20 cm deep. The substrate comprised cobbles (longest dimension <20 cm) firmly embedded in compacted sand; some small boulders (the size of a human head) were present, but the majority of rocks were smaller. The substrate seemed stable, and river discharge was apparently at a dry-season low. Cobbles were coated with a thin film of periphyton (not filamentous algae) and small leaf packs occurred in runs. Elevation 200 m; gradient 0.008; univ. grid. ref. 55MCP470592; lat. 5°47'S., long. 145°37'E.

Table 1. Hydrochemical characteristics of six Sepik River tributaries, Papua New Guinea. Units are mg l^{-1}, except turbidity (= FTU) and conductivity (μS cm^{-1}); SS = suspended solids; Turb = turbidity; SRP = soluble reactive phosphorus; cond. = conductivity. All streams were saturated with oxygen.

	Hohoma River	Mindjim River	Kojé Creek	Manam Creek	Hapia River	Mom Creek
pH	7.0	6.5	7.3	7.0	6.8	6.6
SS	0.9	8.4	26.1	21.9	40.4	2.3
Turb.	0	190	531	248	341 `	22
Cond.	320	187	137	280	270	76
Na$^+$	0.25	1.93	1.57	0.35	0.44	1.88
K$^+$	2.57	1.05	0.75	3.34	1.33	0.41
Mg^{2+}	81.5	34.3	27.7	83.4	47.9	7.1
Ca^{2+}	14.9	10.2	8.6	12.0	12.3	7.4
NH$_4^+$	0.00	0.010	0.00	0.029	0.027	0.009
NO$_2^-$	0.004	0.003	0.007	0.009	0.005	0.006
NO$_3^-$	0.022	0.057	0.059	0.204	0.014	0.093
SRP	0.225	0.060	0.027	0.168	0.200	0.059
SiO$_3$6–	13.91	7.37	2.74	8.03	19.86	5.07
Cl$^-$	3.316	3.56	3.80	5.39	0.94	0.61
HCO$_3^-$	0.0	7.0	0.0	6.0	6.0	0.0
SO$_4^{2-}$	16.15	14.5	7.4	48.7	6.3	13.6

Mom Creek was <20% shaded despite a riparian vegetation of secondary forest. It was situated just above the Ramu floodplain, and local residents reported that the surface water had disappeared for four days during the current (1988) dry season. The substrate of smooth cobbles (longest dimension <25 cm) set in coarse sand was loosely packed and rather unstable. The water was shallow (10–20 cm), with current speeds of 0.3–0.6 m s^{-1} at the sampling site. Although the channel was 8–12 m wide, stream width was only 3–4 m. Elevation 170 m; gradient 0.015; univ. grid ref. 55MCP167642; lat. 5°45'S., long. 145°20'E.

Materials and methods

Field and laboratory procedures

Ten benthic samples were taken from each stream (total samples = 60) by means of a Hess sampler (area 165 cm^2, mesh size 220 μm) constructed according to English (1987). Samples were collected from uniform fast-flowing reaches which appeared typical of each stream as a whole. They were preserved immediately in 5% formalin, and packed in heavy-duty plastic bags for transportation and examination later. A small cobble was collected from the edge of each of the 60 benthic samples for analysis of algal standing stocks. The upper surface of the cobble was placed in a small volume of water and scrubbed vigorously with a toothbrush; cobbles were discarded after length and width had been measured to the nearest mm. Material suspended in the water was concentrated on a membrane filter (0.45 μm pore size) in the field with the aid of a hand-operated pump. Filters were saturated with neutralized 5% formalin and stored in the dark prior to laboratory analysis. Periphytic (i.e. stone-surface) algal biomass was measured in terms of chlorophyll a standing stocks following procedures given by Wetzel & Westlake (1974). Samples were deep frozen for 30 min (to rupture algal cells) and pigments were extracted (at 4 °C) in 90% alkaline acetone; chlorophyll a concentrations were measured with a spectrophotometer.

Approximately six weeks elapsed between field collection of periphytic algae and chlorophyll extraction in the laboratory. Because phytopigments may be modified by long-term storage, it was necessary to check whether algal standing stocks measured after six weeks storage were correlated with the biomass of stone-surface epilithon. For this reason, one addition-

al cobble was removed along with each algal sample ($n = 10$) at four of the streams (Mindjim, Hohoma, Kojé and Manam); epilithic material was scrubbed from these additional cobbles (each of which was then measured to the nearest mm), concentrated on a pre-ashed glass-fibre filter (0.7 μm pore size), and preserved and stored in the same manner as the algal samples. Approximately six weeks later, the filters and associated epilithon were oven-dried to constant weight at 70°C. Ash-free dry weight of epilithon was determined from weight loss after ignition in a muffle furnace at 450°C for 90 minutes. Regression analysis was used to determine whether there was any relationship between algal biomass (derived from the chlorophyll a data) and epilithon standing stocks on cobbles taken from within the same sampling area (total epilithon samples = 39; one sample was lost).

Benthic samples were elutriated in the laboratory to separate detritus and animals from the inorganic fraction; the latter was discarded after checking for the presence of cased Trichoptera and molluscs. Animals were hand-picked from the detritus, identified and counted. The detritus remaining in each sample was oven-dried to constant weight at 70°C. Specific identification of the majority of macroinvertebrates in New Guinea streams is not possible at present. Animals were therefore sorted to morphospecies and counted. In some cases (e.g. Ephemeroptera) species within a genus were distinguished, but in other cases (e.g. Chironomidae) taxa were recognized at the subfamily level only. Undoubtedly, some cryptic species were missed, and the morphospecies totals given herein must be regarded as conservative. Morphospecies were assigned to functional feeding groups (predators, shredders, collector-gatherers, filter-feeders and grazers: Appendix 1) on the basis of mouthpart morphology, a superficial examination of gut contents, and a knowledge of the habits of related taxa in tropical Asia (Dudgeon, 1992).

Data analysis

All data were log-transformed (for counts) or arcsin-transformed (for proportionate data) prior to statistical analyses, which were undertaken on total numbers of macroinvertebrates per sample, the number of morphospecies per sample, and the abundance of those individual taxa (often comprising several morphospecies; Appendix 1) which were relatively numerous (mean densities ≥ 1 ind. 165 cm^{-2}). The significance of inter-stream differences in the abundance of taxa and functional feeding groups (FFGs) were tested using one-way analysis of variance (ANOVA); where the overall F from an ANOVA was significant, differences among streams were analysed using multiple-range Student-Newman-Kuels (SNK) tests.

Stepwise multiple regression using detrital and algal standing stocks as independent variables were calculated for abundant taxa according to Walpole & Myers (1978), and the coefficient of determination (r^2) was used to explain the proportion of the variance in abundance of macroinvertebrates that could be accounted for by a linear relationship with one, other or both of the two independent variables. The aim was to obtain a minimum of unexplained residual variance in terms of the smallest number of independent variables, and this was achieved by removing any variable which did not reduce a significant ($P<0.05$) independent portion of the variation in macroinvertebrate abundance (*i.e.* where the t values for the partial regression coefficients were insignificant). These regressions were undertaken on the abundance of individual taxa in each stream separately ($n = 10$ for each of the six streams), and on the abundance of individual taxa in all streams combined ($n = 60$).

The results arising from the multiple-regression analysis described above must be interpreted with caution because the data upon which they are based are pseudoreplicated (*sensu* Hurlbert, 1984); *i.e.* the 10 samples from each same stream are not truly independent. Under such circumstances, it may be more appropriate to treat each stream — rather than each benthos sample – as a sampling unit. In this case, therefore, the total sample size for an inter-stream study was equal to 6 rather than 60. Accordingly, stepwise multiple-regression analysis was repeated using a sample size of 6, and features of the stream as a whole (such as % shading and water-chemistry measurements) were included in the analysis. The dependent variables were the mean counts of taxa (plus total individuals and morphospecies richness) and FFGs for each stream; independent variables were mean detrital and algal standing stocks in each stream, % shading, pH and total-nitrogen load (*i.e.* the sum of ammonia, nitrite and nitrate values; Table 1). These variables were selected on the basis of the frequency with which they generated significant correlations within a correlation matrix of all possible independent variables *versus* the abundance of macroinvertebrate taxa.

Principal components analysis (PCA; Gauch, 1982) was employed to group benthos samples (and hence sites) on the basis of species composition in an ordi-

nation diagram, such that sample points with a similar species composition lay close together and those with a different species composition were placed far apart. In essence, this is simply a way of summarizing complex multivariate data in a simple scatter diagram, thereby facilitating communication of results and their interpretation: it provides no statistical test of hypotheses about the data. However, PCA does offer the possibility of indirect gradient analysis (Jongman *et al.*, 1987) whereby the pattern of sample separation on the ordination diagram is matched to known or suspected environmental gradients – such as shading by riparian vegetation. PCA with varimax rotation was undertaken twice: once using a data set comprising the counts of all major taxa (mean densities ≥ 1 ind. 165 cm^{-2}) in each benthic sample, and a second time using a data set made up of the counts of all FFGs in each benthic sample ($n = 60$ in both analyses). Exploratory data analysis using other ordination methods (e.g. deterneded correspondence analysis) did not provide a clearer separation of sites on the oddination diagram, and could not be justified on the basis of the length of ordination axes (<4 S.D.; see Jongman *et al.* 1987).

Results

Inter-stream differences in macrobenthic communities

A total of 64 morphospecies was collected from the six streams (Appendix 1), with an average of 20 morphospecies per stream (Table 2). All but two relatively-scarce taxa (the shrimp *Caridina* and the freshwater crab *Sundathelphusa*) were insects. Kojé Creek and Hohoma River — the richest sites — each yielded a total of 42 morphospecies; 38 were found in Mom Creek, 35 in Manam Creek, 31 in Hapia River, and only 28 in Mindjim River which was relatively species poor. The mean number of morphospecies per sample was greatest in Kojé Creek and Hohoma River also (Table 2), but Mom Creek (not Mindjim River) had both the fewest morphospecies per sample and the lowest population densities. Streams with higher macroinvertebrate population densities generally contained more morphospecies, although densities in Hohoma River were twice those in Kojé Creek without an equivalent increase in morphospecies richness. Hohoma River had the greatest macrobenthic standing stock, followed by Hapia River, and then Manam and Kojé Creeks, with Mom Creek and Mindjim River both supporting significantly lower macroinvertebrate

populations and morphospecies than the other streams (Table 3).

Regression analysis indicated that there was a highly-significant relationship between algal biomass (as estimated following chlorophyll extraction) and epilithon standing stocks ($r^2 = 0.65$, $n = 39$, $P < 0.01$), confirming the assumption that — despite the need to store samples prior to analysis — extracted chlorophyll could be used to compare the standing stocks of periphytic algae in the study streams. However, it should be noted that the absolute amounts of chlorophyll extracted from algal cells, and hence the estimates of algal standing stocks, may have been changed by storage. Indeed, the average algal standing stock across all streams (0.39 mg m^{-2}; Table 2) was low relative to that recorded from streams on the Asian mainland (e.g. Bishop, 1973, Dudgeon, 1988). Algal and detrital standing stocks varied among the study streams (Tables 2 & 3). Detritus was most abundant in Manam and Mom Creeks, and least abundant in Mindjim Creek; mean standing stocks were markedly higher in completely-shaded Manam Creek than in partly-shaded Mom Creek, but there was considerable inter-sample variation in this respect and the difference between these streams was not statistically significant (Table 3). Algal biomass was greatest in Kojé Creek, and lowest in Mom Creek; standing stocks in the remaining four streams did not differ significantly from each other (Table 3).

In overall terms, Baetidae (6 morphospecies) dominated the benthos of the 6 streams (Appendix 1, Table 2), followed (in order of decreasing abundance) by Leptophlebiidae (2 morphospecies), Orthocladiinae, Elmidae (2 morphospecies), Hydropsychidae (5 morphospecies) and Chironominae. Although there were inter-stream differences in their population densities (Table 3), these taxa were generally numerically important (>20 ind. 165 cm^{-2}) and constituted the 5 top-ranked taxa in Hohoma River, Kojé Creek and Hapia River (Table 4). Furthermore, they made up 3 of the 5 top-ranked taxa in Manam and Mom Creeks. Caenidae, Philopotamidae, Tanypodinae and Nymphulinae were also among the 5 top-ranked taxa with Philopotamidae being especially abundant in Manam Creek where Caenidae and Nymphulinae were absent (Tables 2 & 3). Of biogeographic interest was the abundance of Nymphulinae, Naucoridae, Libellulidae and Agrionidae (probably including Megapodagrionidae) in benthic samples. These taxa are scarce in north-temperate streams, and predatory Naucoridae were

Table 2. Mean population densities (± S.D.) of the most abundant taxa in each of six Papua New Guinea streams; data are given only for taxa with densities ≥ 1 individual 165 cm⁻² in a particular stream. Taxa are listed in descending order of overall mean population densities across all six study streams.

	Mindjim River	Manam Creek	Hohoma River	Kojé Creek	Hapia River	Mom Creek	Mean across all streams
Baetidae	20.6±15.8	33.4±14.2	440.1±131.4	47.6±15.8	156.5±43.1	16.0±6.1	119.0±162.1
Leptophlebiidae	2.7±1.8	151.2±29.9	7.1±2.7	34.4±8.4	42.5±16.6	2.1±2.42	40.0±54.4
Orthocladiinae	6.3±2.3	–	56.4±12.3	71.5±29.9	48.7±20.4	31.1±24.4	35.8±31.5
Elmidae	18.3±8.1	24.1±17.2	66.5±28.6	58.0±25.3	7.5±6.1	3.8±3.7	29.7±29.6
Hydropsychidae	15.2±10.0	6.9±4.1	48.5±24.2	25.0±18.2	80.6±42.6	2.2±1.8	29.6±34.6
Chironominae	7.0±5.2	5.6±4.4	44.0±10.6	27.5±11.4	33.5±19.7	13.4±7.7	21.8±17.8
Caenidae	10.2±7.3	–	13.5±10.1	5.5±8.9	10.1±8.7	5.5±3.7	7.5±8.3
Philopotamidae	–	26.3±21.3	11.8±14.2	–	1.2±2.0	–	6.8±14.0
Glossosomatidae	7.0±4.3	–	–	1.1±1.2	27.4±13.8	2.1±3.2	6.4±11.4
Tanypodinae	1.6±2.0	2.0±1.1	9.2±4.8	12.8±9.3	2.8±1.5	4.2±3.2	5.4±6.1
Nymphulinae	8.6±5.5	–	3.0±3.6	6.3±2.5	10.5±5.4	–	4.7±5.4
Libellulidae	–	–	5.4±3.2	–	8.3±5.9	1.1±1.0	3.5±5.7
Hydroptilidae	1.6±1.4	4.2±5.7	5.9±7.4	–	8.3±5.9	–	3.0±2.3
Hydrophilidae	3.7±3.3	–	–	3.3±1.4	4.0±1.7	–	2.6±3.9
Naucoridae	–	–	2.7±1.4	5.8±3.2	5.4±3.0	–	2.6±3.0
Simuliidae	–	7.1±7.0	1.1±1.9	–	7.0±11.7	–	2.6±6.3
Agrionidae	–	6.9±4.6	1.3±1.2	–	–	–	2.5±3.1
Ceratopogonidae	–	1.1±1.0	–	2.7±2.4	–	2.7±2.8	1.3±1.9
Tipulidae	1.6±2.0	1.7±1.3	2.0±1.6	–	–	–	1.3±1.6
Total individuals	109.7 ±44.2	227.3 ±77.5	721.2 ±140.1	306.5 ±83.9	456.5 ±120.3	94.1 ±41.9	327.5 ±233.8
Number of morphospecies	19.2±3.5	17.8±2.7	24.4±1.4	22.3±3.2	22.9±1.5	16.0±3.7	20.4±4.0
Detritus (g DW 165 cm⁻²)	0.23±0.18	1.74±2.05	0.36±0.19	0.61±0.46	0.37±0.31	0.85±0.86	0.69±1.04
Algae (mg m⁻²)	0.23±0.21	0.27±0.16	0.21±0.14	1.22±1.20	0.29±0.14	0.10±0.07	0.39±0.62

unusually well-represented in the New Guinea samples (see also Dudgeon, 1990).

There were strongly-significant inter-stream differences in the abundance of the 19 taxa with densities ≥1.0 ind. 165 cm⁻¹ (Table 3), despite the overall similarity in the composition of the 5 top-ranked taxa (Table 4). PCA of the counts of major macroinvertebrate taxa in each benthic sample provided a convenient method of displaying the differences in community composition among the study streams (Fig. 2). In this ordination the first two PCA axes accounted for 45% of the variation in the data: axis 1 accounted for 26% and axis 2 accounted for an additional 19%. The ordination diagram shows that the community composition of Manam Creek — the only stream completely shad-ed by riparian forest — was markedly different from other sites. Mom Creek samples were also rather distinct and both streams had similar axis-1 scores as well as comparable standing stocks of detritus (Table 3). Hapia and Hohoma Rivers were located at the opposite end of axis 1 from Manam and Mom Creeks on the ordination plot, and samples from the former two sites (which were largely unshaded) were alike – a feature that is underscored by the similar rankings of these two rivers for many of the analyses in Table 3. Note that the standing stocks of periphytic algae were uncorrelated with the sample scores of axes 1 and 2, but detrital standing stocks were strongly correlated with axis 2 scores ($r^2 = 0.13$, $n = 60$, $P = 0.004$).

Table 3. Inter-stream differences in the population densities of the most abundant taxa in six Papua New Guinea streams as revealed by one-way ANOVA and S.N.K. tests. Data are given only for taxa with mean densities >1 individual 165 cm^{-2} across the six study streams, and taxa are listed in descending order of overall mean population densities across all streams. Abbreviations: Mi = Mindjim River; Ma = Manam Creek; Ho = Hohoma River; K = Kojé Creek; Ha = Hapia River; Mo = Mom Creek.

	$F_{(5.54)}$	P	Abundance rankings
Baetidae	83.64	<0.0001	Ho>Ha>Ko>Ma>Mi, Mo
Leptophlebiidae	117.41	<0.0001	Ma>Ko, Ha>Ho>Mi, Mo
Orthocladiinae	10.07	<0.0001	Ho, Ko, Ha>Mo>Mi>Ma
Elmidae	32.24	<0.0001	Ho, Ko>Mi, Ma, Ha, Mo
Hydropsychidae	37.92	<0.0001	Ho, Ha>Ko, Mi>Ma>Mo
Chironominae	23.51	<0.0001	Ho>Ko, Ha>Mo>Mi, Ma
Caenidae	17.79	<0.0001	Mi, Ho, Ha>Ko, Mo>Ma
Philopotamidae	22.00	<0.0001	Ma, Ho>Ko, Ha, Mi, Mo
Glossosomatidae	39.53	<0.0001	Ha>Mi>Ho, Ko, Ma, Mo
Tanypodinae	13.09	<0.0001	Ko, Ho>Mo, Ha>Mi, Ma
Nymphulinae	37.52	<0.0001	Ha, Mi, Ko>Ho>Ma, Mo
Libellulidae	34.90	<0.0001	Ho, Ha>Mi, Mo, Ma>Ko
Hydroptilidae	5.63	0.0003	Ha, Ho, Ma>Mi>Ko, Mo
Hydrophilidae	21.67	<0.0001	Mi, Ko, Ha>Ho, Ma, Mo
Naucoridae	22.45	<0.0001	Ko, Ha>Ho>Mi, Ma, Mo
Simuliidae	8.61	<0.0001	Ma, Ha>Ho, Ko, Mi, Mo
Agrionidae	22.09	<0.0001	Ma>Ho, Ko>Ha, Mi, Mo
Ceratopogonidae	5.82	0.0002	Ko, Mo>Ma, Ho, Ha>Mi
Tipulidae	7.11	<0.0001	Mi, Ma, Ho>Mo, Ko, Ha[1]
Total individuals	56.27	<0.0001	Ho>Ha>Ma, Ko>Mi, Mo
Number of morphospecies	13.59	<0.0001	Ho, Ko, Ha>Mi, Ma, Mo
Detritus	3.52	0.008	Ma, Mo>Ko, Ho, Ha>Mi[2]
Algae	6.51	0.0001	Ko>Mi, Ma, Ho, Ha>Mo

[1] Multiple comparison revealed that tipulid densities were generally greater ($P<0.05$) in Mi, Ma & Ho than they were in Mo, Ko & Ha, except that there was no significant difference in densities between Mo and Ho.

[2] Multiple comparison revealed interstream differences ($P<0.05$) in detrital standing stocks as indicated, but Ko did not contain significantly less detritus than Mo.

To what extent can the variations in community composition among streams be related to responses of macroinvertebrate taxa to differences in the quantities of algae and detritus in the benthic environment? Stepwise multiple regression analysis of the 19 most abundant taxa, as well total individuals and total morphospecies per sample (Table 5), indicated that overall abundance and morphospecies richness were unaffected by either independent variable, but 11 of the 19 taxa

tested (including 3 of the 5 top-ranked taxa) were influenced significantly ($P\leq0.016$). Detritus accounted for a significant proportion of the variation in the abundance of 8 taxa, and algae influenced 6 taxa; the abundance of 3 taxa was related to a combination of both variables (Table 5). The relationship between macroinvertebrate abundance and algal standing stocks was positive in the 6 regression models that included algae as a predictor; the relationship with detritus was nega-

Table 4. Dominant benthic taxa (based on mean population densities) arranged in order of descending rank in each of six Papua New Guinea streams; data are given only for taxa with densities >1 individual 165 cm^{-2} in a particular stream.

Mindjim River	Manam Creek	Hohoma River	Kojé Creek	Hapia River	Mom Creek
Baetidae	Leptophlebiidae	Baetidae	Orthocladiinae	Baetidae	Orthocladiinae
Elmidae	Baetidae	Elmidae	Elmidae	Hydropsychidae	Baetidae
Hydropsychidae	Philopotamidae	Orthocladiinae	Baetidae	Orthocladiinae	Chironominae
Caenidae	Elmidae	Hydropsychidae	Leptophlebiidae	Leptophlebiidae	Caenidae
Nymphulinae	Simuliidae	Chironominae	Chironominae	Chironominae	Tanypodinae
Glossosomatidae	Hydropsychidae	Caenidae	Hydropsychidae	Glossosomatidae	Hydraenidae
Chironominae	Agrionidae	Philopotamidae	Tanypodinae	Nymphulinae	Elmidae
Orthocladiinae	Chironominae	Tanypodinae	Nymphulinae	Caenidae	Ceratopogonidae
Hydrophilidae	Hydroptilidae	Leptophlebiidae	Naucoridae	Hydroptilidae	Hydropsychidae
Leptophlebiidae	Athericidae	Hydroptilidae	Caenidae	Libellulidae	Glossosomatidae
Tipulidae	Tanypodinae	Libellulidae	Hydrophilidae	Elmidae	Leptophlebiidae
Hydroptilidae	Tipulidae	Nymphulinae	Ceratopogonidae	Simuliidae	Calamoceratidae
Tanypodinae	Ceratopogonidae	Naucoridae	Glossosomatidae	Naucoridae	Libellulidae
Naucoridae		Prosopistomatidae	Agrionidae	Hydrophilidae	
		Tipulidae		Tanypodinae	
		Agrionidae		Philopotamidae	
		Simuliidae			

tive in 4 cases and positive in 4 cases, but was negative in the 3 regression models which included both algae and detritus as independent variables.

Although multiple-regression models involving detritus and algae as independent variables were frequently highly-significant 'predictors' of macroinvertebrate abundance, interpretation of these data must be made with caution because they are pseudoreplicated. Accordingly, multiple stepwise regression analysis of the dependent variables in Table 5 was repeated with a sample size of 6 (the number of streams studied), and including detrital and algal standing stocks, % shading, pH and total-nitrogen load as independent variables. (Other independent variables were excluded on the basis of low r values in a correlation matrix of dependent versus independent variables.) As was the case for the algae plus detritus regressions (Table 5), neither total individuals nor number of morphospecies was significantly related to the independent variables (Table 6). The abundance of 9 out of 19 taxa was influenced significantly by the independent variables, although they included only 1 (Orthocladiinae) of the 5 top-ranked taxa. Of the 13 independent variables incorporated in the 9 regression models, shade and detritus were included 4 times each, pH and total-nitrogen were included twice, and algae was included

once. The regression coefficient for detritus was negative in all four cases (Table 6). Note that the coefficient of determination (r^2) for significant regressions (i.e. the proportion of variation in the dependent variables 'explained' by the independent variables) in Table 6 were much higher (0.675–0.991) than for the regression models involving algae and/or detritus in Table 5 (0.072–0.217). In part, this reflects the fact that a significant regression can be obtained even if r^2 is rather low provided that (as in Table 5, where $n = 60$) the sample size is large enough. However — as Table 6 (where $n = 6$) shows — the proportion of inter-stream variation in the abundance of some macroinvertebrates accounted for by different combinations of shade, detritus, pH, total-nitrogen and algae was surprisingly high.

Inter-stream differences in functional feeding groups

Although there were differences in the abundance of all major macroinvertebrate taxa among the study streams, the effects of these differences on community functioning will depend upon concomitant changes in functional group representation. When considered together, the streams were co-dominated by collector-gatherers and grazers (means of 42.7% and 36.3% respectively); filter-feeders made up 14.7% of the
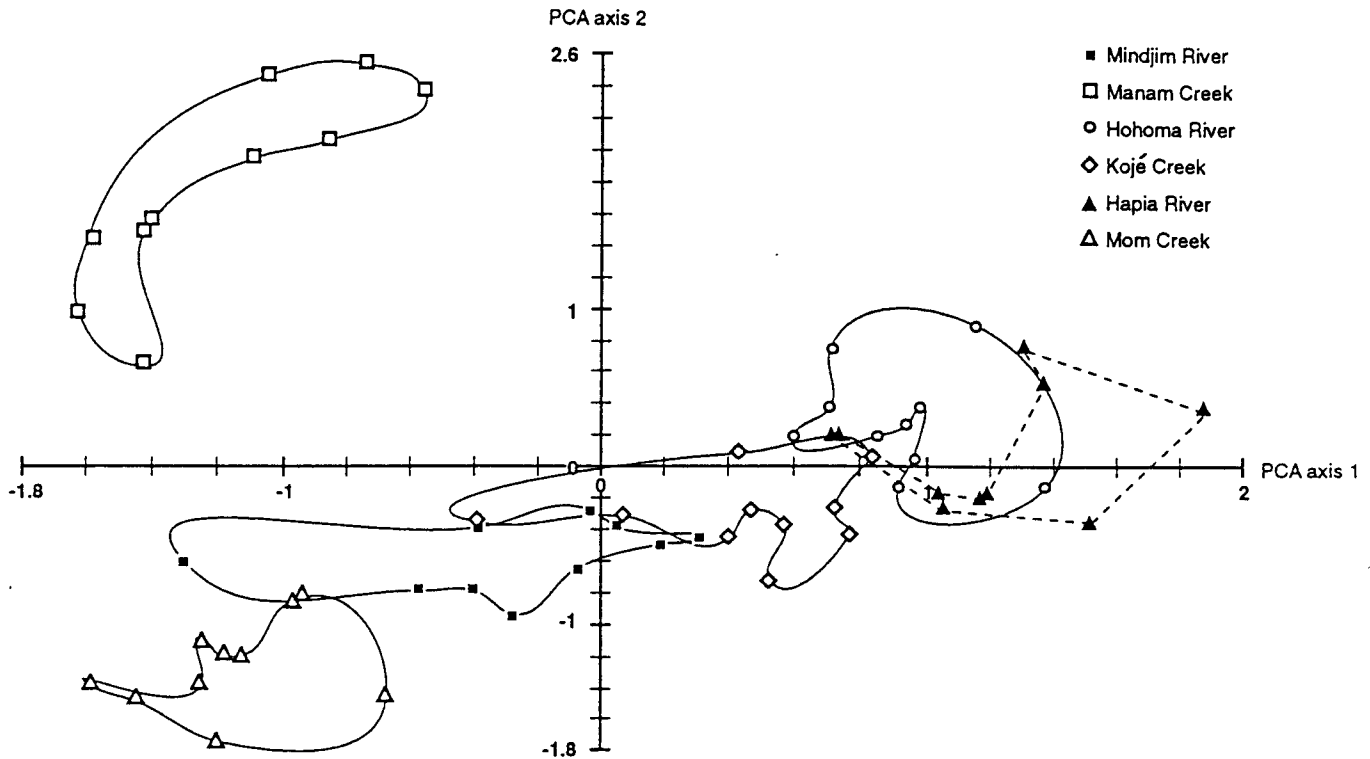
PCA on Major Taxa

Fig. 2. Ordination diagram arising from principal components analysis undertaken on counts of macroinvertebrate taxa in each of 60 samples from 6 New Guinea streams. Solid lines or broken lines have been drawn around samples from the same stream as an aid to visual interpretation; the use of a solid or broken line has no significance except to clarify the ordination diagram.

macrobenthos, while predators (7.0%) and especially shredders (0.4%) comprised a small fraction of the community (Table 7). In terms of population densities, collector-gatherers, grazers and filter-feeders were most abundant in Hohoma River which had the greatest macroinvertebrate populations (Table 3). However, filter-feeders reached similar densities in Hapia River, while predators were equally abundant in Hohoma River, Hapia River and Kojé Creek (Tables 7 & 8). Shredders were most numerous in Mom Creek, although — even here — they made up only 2.0% of the macrobenthos. In terms of relative abundance, Manam Creek contained significantly more collector-gatherers and fewer grazers than the other five streams (Tables 7 & 8). Interstream differences in the proportion of filter-feeders were rather minor, while Mindjim River, Mom Creek and Kojé Creek had approximately twice the proportions of predators as the other 3

streams, although this FFG never exceeded 10.1% of total macroinvertebrate standing stocks.

PCA of the FFG abundance data produced an ordination diagram (Fig. 3) which could be characterised by a generally poor separation among sites. Mom Creek and Mindjim River occupied the left of the ordination diagram, Manam Creek was in the centre and samples from the three remaining sites were poorly distinguished from each other and grouped towards the right. It is notable that those sites grouped on the right of the ordination diagram had low standing stocks of detritus and were almost completely unshaded, but the grouping of samples from other sites was not easily interpreted on the basis of environmental data; Mindjim River, for example, was partly shaded but contained less detritus than any other stream (Table 3). Despite difficulties in using environmental gradients to interpret the pattern of separation, the first two PCA axes accounted for a large proportion (84%) of the

Table 5. Results of multiple-regression analysis in which algae and detritus are assumed to be determinants of the population densities of the most abundant taxa in six Papua New Guinea streams. Data are given only for taxa with mean densities >1 individual 165 cm^{-2} across the six study streams, and taxa are listed in descending order of overall mean population densities across all streams. Abbreviation: n.s. = neither independent variable yielded a significant (P <0.05) regression model.

	Variables	r^2	F	d.f.	P	Regression coefficient
Baetidae	n.s.	—	—	—	—	—
Leptophlebiidae	Detritus	0.119	7.9	1,58	0.007	0.520
Orthocladiinae	Detritus, algae	0.135	4.5	2,57	0.016	−0.378, 0.621
Elmidae	Algae	0.072	4.5	1,58	0.038	0.519
Hydropsychidae	n.s.	—	—	—	—	—
Chironominae	n.s.	—	—	—	—	—
Caenidae	Detritus	0.133	8.9	1,58	0.004	−0.360
Philopotamidae	Detritus	0.161	11.1	1,58	0.002	0.503
Glossosomatidae	n.s.	—	—	—	—	—
Tanypodinae	Algae	0.148	10.1	1,58	0.002	0.518
Nymphulinae	Detritus, algae	0.175	6.1	2,57	0.004	−0.360, 0.444
Libellulidae	n.s.	—	—	—	—	—
Hydroptilidae	n.s.	—	—	—	—	—
Hydrophilidae	Detritus, algae	0.137	4.5	2,57	0.014	−0.202, 0.322
Naucoridae	Algae	0.164	11.4	1,58	0.001	0.530
Simuliidae	Detritus	0.143	9.67	1,58	0.003	0.353
Agrionidae	Detritus	0.217	16.1	1,58	0.0002	0.359
Ceratopogonidae	n.s.	—	—	—	—	—
Tipulidae	n.s.	—	—	—	—	—
Total individuals	n.s.	—	—	—	—	—
Number of morphospecies	n.s.	—	—	—	—	—

variation in the data: Axis 1 accounted for 62% and Axis 2 accounted for an additional 22%.

Stepwise multiple regressions of FFG abundance (absolute and relative) using algae and detritus as independent variables (Table 9), showed that the absolute abundance (population densities) of predators and shredders was positively related to algal and detrital standing stocks respectively, while the relative abundance (%) of collector-gatherers and grazers was influenced by detritus. This relationship was positive for collector-gatherers and negative for grazers. Neither detritus nor algae had a significant effect on filter-feeder abundance. Multiple stepwise regression analysis of FFGs (mean values from Table 7 for each of the 6 streams) including detrital and algal standing stocks, % shading, pH and total-nitrogen load as independent variables yielded significant values for collector-gatherer relative abundance (which was related to

detritus: $r^2 = 0.844$; $F_{(1,4)} = 21.6$, $P = 0.001$, regression coefficient = 0.158) and grazer relative abundance (which was negatively influenced by detritus: $r^2 = 0.779$; $F_{(1,4)} = 14.1$, $P = 0.019$; regression coefficient = −0.150) only. These results matched the outcome of regression models for the relative abundance of collector-gatherers and grazers in benthic samples across all streams (Table 9).

Within-stream differences in macrobenthic communities

The results of stepwise multiple regressions of the abundance of major taxa and FFGs in individual streams ($n = 10$ for each stream), using algae and detritus as independent variables, were of interest because it was possible that inter-patch variations in algae and/or detritus could determine distribution and abun-

Table 6. Results of multiple-regression analysis in which algal and detrital standing stocks, percentage shading by riparian vegetation, pH and total nitrogen load (total-N) are assumed to be determinants of the population densities of the most abundant taxa in six Papua New Guinea streams. Data are given only for taxa with mean densities >1 individual 165 cm^{-2} across the six study streams, and taxa are listed in descending order of overall mean population densities across all streams. Abbreviation: n.s. = neither independent variable yielded a significant ($P<0.05$) regression model.

Variables		r^2	F	d.f.	P	Regression coefficient
Baetidae	n.s.	—	—	—	—	—
Leptophlebiidae	n.s.	—	—	—	—	—
Orthocladiinae	Shade	0.675	8.3	1,4	0.044	−2.302
Elmidae	n.s	—	—	—	—	—
Hydropsychidae	n.s.	—	—	—	—	—
Chironominae	n.s.	—	—	—	—	—
Caenidae	Detritus	0.816	17.8	1,4	0.014	−1.213
Philopotamidae	Shade	0.735	11.1	1,4	0.029	2.115
Glossosomatidae	n.s.	—	—	—	—	—
Tanypodinae	pH, total-N	0.978	67.5	2,3	0.003	1.436, 0.752
Nymphulinae	Detritus	0.691	8.95	1,4	0.040	−1.265
Libellulidae	n.s.	—	—	—	—	—
Hydroptilidae	n.s.	—	—	—	—	—
Hydrophilidae	pH, detritus, algae	0.991	230.0	3,2	0.0004	−2.738, −1.514, 0.821
Naucoridae	n.s.	—	—	—	—	—
Simuliidae	n.s.	—	—	—	—	—
Agrionidae	Shade	0.906	38.5	1,4	0.003	1.355
Ceratopogonidae	Total-N	0.675	8.3	—	0.045	0.719
Tipulidae	Shade, detritus	0.970	49.2	2,3	0.005	1.121, −0.577
Total individuals	n.s.	—	—	—	—	—
Number of morphospecies	n.s.	—	—	—	—	—

dance within a stream — notwithstanding the presence or absence of a significant relationship with these variables across habitats. This is demonstrated by the fact that 3 significant regressions were obtained for Baetidae (Table 10), although the abundance of these mayflies across all streams was not predicted by either independent variable (Table 5). Of 35 significant regression models, 23 included detritus, 18 included algae, and 6 included both detritus and algae (Table 10). The relationship with detritus was negative in 7 cases (in Mindjim and Hohoma Rivers) and positive in 16 cases (in Hapia River and Manam, Kojé and Mom Creeks), while that with algae was negative in 9 cases (in Mindjim and Hapia Rivers) and positive in 9 cases (in Hapia River, Kojé Creek and Mom Creek). These data suggest that algae was not important as a

predictor in Hohoma river, but that it was associated with reduced macroinvertebrate abundance in Mindjim and Hapia Rivers and enhanced abundance within the 3 remaining streams. Detritus was associated with reduced macroinvertebrate abundance in Mindjim and Hohoma Rivers and enhanced densities within the 4 remaining sites. Clearly, the effects of detritus and algae on macroinvertebrate abundance varied among sites, but it could not be related to riparian shading or terrestrial vegetation in any straightforward fashion.

In this context it is notable that the independent variables which accounted for a significant proportion of the variance in the abundance of particular macroinvertebrate groups changed from stream to stream. For example, Baetidae was influenced by detritus in one stream and by algae in two (Table 10), while collector-

Table 7. Mean (±S.D.) population densities (n 165 cm^{-2}) of macroinvertebrate functional feeding groups in each of six Papua New Guinea streams; the relative abundance (%) of each functional group are given in parentheses. Functional groups are listed in descending order of overall mean population densities across all six study streams.

	Mindjim River	Manam Creek	Hohoma River	Kojé Creek	Hapia River	Mom Creek	Mean across all streams
Collector-gatherers	30.1±16.4 (27.3±6.7)	172.1±34.2 (63.9±10.1)	290.2±56.0 (40.4±2.2)	114.1±29.6 (37.4±3.6)	171.8±41.7 (37.9±4.3)	40.6±19.6 (43.1±5.6)	136.5±95.6 (41.7±12.6)
Grazers	49.8±20.2 (46.0±8.7)	45.7±23.3 (16.1±5.2)	326.7±75.3 (45.1±3.4)	126.0±37.6 (41.2±7.3)	156.3±35.9 (35.0±5.6)	31.8±15.1 (34.1±7.1)	122.7±109.6 (36.3±11.9)
Filter-feeders	19.3±11.7 (17.1±7.0)	43.2±33.1 (14.0±8.5)	80.4±30.0 (11.2±3.3)	40.1±23.4 (12.4±4.5)	105.9±55.9 (22.2±8.3)	9.8±4.1 (11.4±3.4)	49.8±45.1 (14.7±7.1)
Predators	10.4±6.2 (9.5±5.3)	15.4±5.4 (5.7±1.4)	23.3±8.2 (3.5±1.6)	26.1±12.8 (8.4±3.7)	22.4±6.9 (4.9±1.2)	10.0±5.9 (10.1±3.8)	17.9±9.4 (7.0±3.9)
Shredders	0.3±0.3 0.2±0.2	0.9±1.0 (0.3±0.4)	0.3±0.4 (0.03±0.05)	0.6±0.6 (0.2±0.2)	0.2±0.3 (0.04±0.10)	2.0±2.8 (1.7±2.2)	0.7±1.4 (0.4±1.1)

Table 8. Inter-stream differences in the abundance of macroinvertebrate functional feeding groups in six Papua New Guinea streams as revealed by one-way ANOVA and S.N.K. tests. Inter-stream differences in the relative abundance (%) of these groups are given in parentheses. Functional groups are listed in descending order of overall mean population densities across all six study streams. Abbreviations: Mi = Mindjim River; Ma = Manam Creek; Ho = Hohoma River; K = Kojé Creek; Ha = Hapia River; Mo = Mom Creek.

	$F_{(554)}$	P	Abundance rankings
Collector-gatherers	72.80 (38.62)	<0.0001 (<0.0001)	Ho>Ma, Ha>Ko>Mi, Mo (Ma>Mo>Ho, Ko, Ha>Mi)
Grazers	54.33 (31.48)	<0.0001 (<0.0001)	Ho>Ha, Ko>Mi, Ma, Mo (Mi, Ho, Ko>Ha, Mo>Ma)
Filter-feeders	16.87 (4.04)	<0.0001 (0.003)	Ha, Ho>Ko, Ma>Mi>Mo[1] (Ha, Mi>Ma, Ko, Mo, Ho)
Predators	7.76 (7.71)	<0.0001 (<0.0001)	Ko, Ho, Ha>Ma, Mi, Mo (Mi, Mo, Ko>Ma, Ha, Ho)
Shredders	2.96 (5.08)	0.02 (0.0007)	—[2] (Mo>Mi, Ma, Ho, Ko, Ha)

[1] Filter-feeder population densities in Ko & Mi were significantly different, but densities in Ma & Mi (and in Ko & Mi) were not.
[2] Intersite differences were marginally significant ($P<0.1$) only.

gatherers were influenced by a combination of algae and detritus in two streams (although the relationship was negative in one and positive in the other) and by algae and detritus alone in one stream each.

Discussion

The species richness of the New Guinea streams was lower than streams on the Asian mainland. For example, in an investigation of four Hong Kong streams using broadly-similar sampling methods, Dudgeon
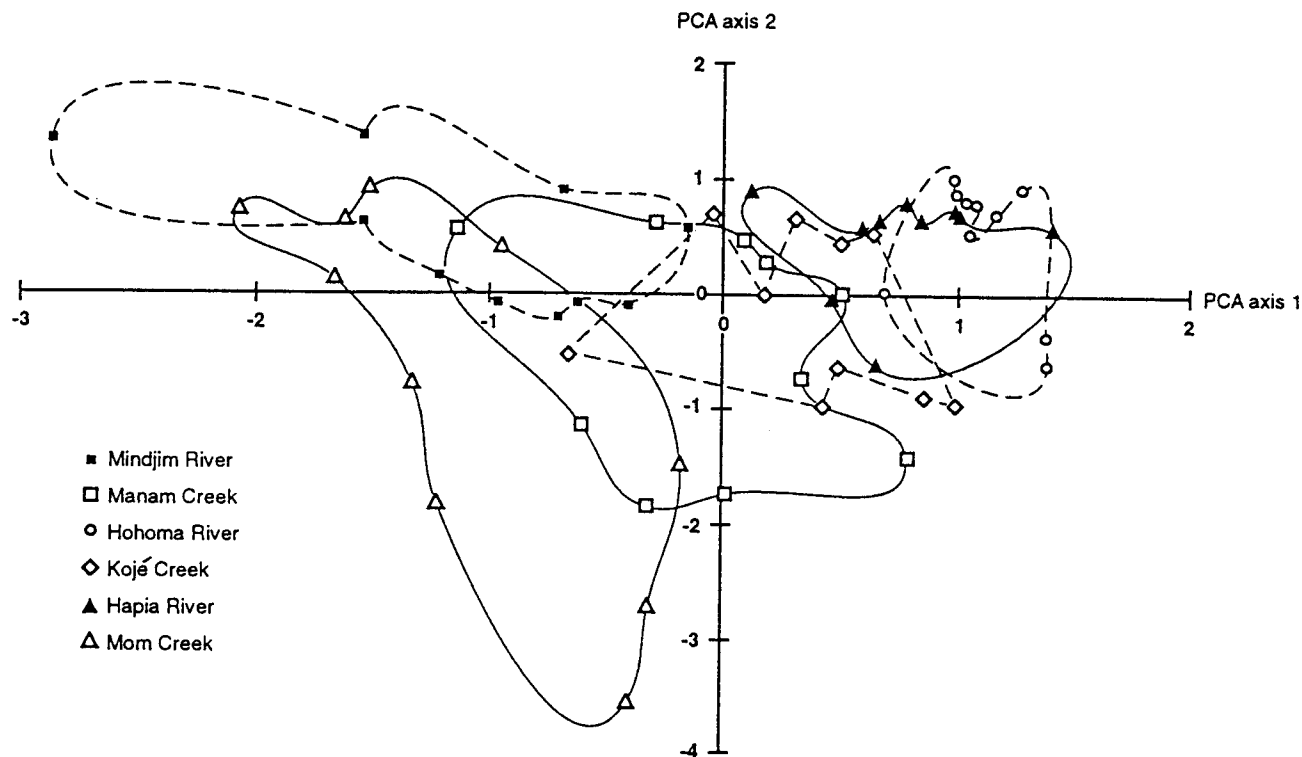
PCA on Functional Groups

Fig. 3. Ordination diagram arising from principal components analysis undertaken on counts of macroinvertebrate functional feeding groups (FFGs) in each of the 60 samples from 6 New Guinea streams. Solid lines or broken lines have been drawn around samples from the same stream as an aid to visual interpretation; the use of a solid or broken line has no significance except to clarify the ordination diagram.

(1988) recorded species totals of between 70 and 94 per stream (overall total 126), compared to totals of 28–42 (overall total 64) in the present study. In both studies the vast majority of taxa were insects. These differences may be ascribed to differences in taxonomic penetration, greater knowledge of the Hong Kong fauna, as well as the isolation of New Guinea and the absence of major groups (e.g. Plecoptera, Heptageniidae, Ephemerellidae, Ephemeridae, Rhyacophilidae, Psephenidae and Megaloptera) which are abundant in streams on the mainland of tropical Asia. Although the absence of some taxa may have been compensated for by radiation in others (e.g. Naucoridae), groups which were present in Hong Kong and New Guinea were less diverse in New Guinea. For example, 4 streams in Hong Kong yielded 19 elmid beetle morphospecies (Dudgeon, 1988); 6 New Guinea streams sampled in an equivalent manner yielded only 2. A more wide-ranging survey of Kojé and Manam Creeks using different sampling methods (Surber samples and

drift nets; Dudgeon, 1990) did increase the total number of morphospecies collected (to 60 and 48 respectively), but the same collecting methods in Hong Kong streams would have uncovered additional species also. On the basis of present information, it can be stated that the benthos of streams in the Sepik drainage of Papua New Guinea is diverse, but less diverse that of tropical streams on the Asian mainland. In terms of mayflies, at least, New Guinea lacks a number of major families and seems to have a poor fauna for a land mass of its size and topographic complexity; in this regard it resembles an oceanic more than a continental island (Edmunds & Polhemus, 1990).

Although these New Guinea streams appeared to be somewhat poorer in macroinvertebrate species than streams on the Asian mainland, there was no evidence that standing stocks were reduced. Dudgeon (1988) has recorded population densities from 2408–6658 ind. m^{-2} in Hong Kong hillstreams, and values of 3583–5277 ind. m^{-2} from unpolluted sec-

Table 9. Results of multiple-regression analysis in which algae and detritus are assumed to be determinants of the population densities of macroinvertebrate functional feeding groups in six Papua New Guinea streams. Results of regressions where the relative abundance (%) of functional groups were used as dependent variables are given in parentheses. Functional groups are listed in descending order of overall mean population densities across all streams. Abbreviation: n.s. = neither independent variable yielded a significant ($P<0.05$) regression model.

	Variables	r^2	$F_{(1,58)}$	P	Regression coefficient
Collector-gatherers	n.s. (Detritus)	— (0.086)	— (5.47)	— (0.023)	— (0.037)
Grazers	n.s. (Detritus)	— (0.207)	— (15.2)	— (0.0003)	— (−0.058)
Filter-feeders	n.s. (n.s.)	— (−)	— (−)	— (−)	— (−)
Predators	Algae (n.s.)	0.076 (−)	4.7 (−)	0.034 (−)	0.318 (−)
Shredders	Detritus (Detritus)	0.110 (0.073)	7.2 (4.6)	0.009 (0.036)	0.161 (0.041)

tions of the Lam Tsuen River, Hong Kong (Dudgeon, 1984a). Bishop (1973) gives similar figures (2609–8921 ind. m^{-2}) from sites along the Sungai Gombak in Malaysia, although greater numbers of invertebrates (40346 ind. m^{-2}) were recorded at an organically-enriched site. Macroinvertebrate densities in the Sepik tributary streams (5702–43704 ind. m^{-2}) are within the same order of magnitude as the Hong Kong and Malaysian figures, and there is no evidence that the New Guinea streams are deficient in this regard. These data suggest that low fishery yields from the Sepik River and its tributaries (Coates, 1985; Van Zwieten, 1990) cannot be attributed to a shortage of invertebrate food for fishes.

There were significant differences in the population densities of all of the most abundant macroinvertebrate taxa in the study streams, and there were some differences in benthic community composition among them. Nevertheless, there was broad similarity in the representation of the most abundant species across streams, and three streams — Kojé Creek, Hohoma River and Hapia River — were dominated by the same 5 taxa. Multiple regression showed that inter-stream differences in the abundance of macroinvertebrate taxa could be related to algae and detritus, but the extent of shading, pH and total-nitrogen loads strongly influenced the abundance of some taxa also. An ordination dia-

gram based on counts of abundant taxa in the study streams (Fig. 2) accounted for approximately half of the variation in the data, and showed that the macroinvertebrate community of Manam Creek — the only completely-shaded stream and the only one situated in primary rainforest — was distinct from that of the other streams. The ordination diagram also indicated a general separation of Mom and Manam Creek samples which may be attributable to macroinvertebrate responses to relatively high detrital standing stocks in these streams.

Surprisingly, algal and detrital standing stocks in the study streams were not clearly correlated with riparian conditions: for example, Kojé Creek had significantly higher algal standing stocks than Hohoma and Hapia Rivers yet all three were unshaded, while standing stocks of algae in shaded Manam Creek were no less than in Hohoma and Hapia Rivers. Similarly, Manam and Mom Creeks contained comparable quantities of detritus but the former was completely shaded while the latter was <20% shaded. While detrital standing stocks will be influenced by the development of riparian vegetation and the extent of shading, they can also be affected by the retentiveness of the stream (Cummins *et al.*, 1989; Prochazka *et al.*, 1991). It is possible that a highly-retentive stream receiving low inputs could contain equivalent standing stocks of detritus to

Table 10. Results of multiple regressions of population densities of the most abundant macroinvertebrate taxa and functional feeding groups in each of six Papua New Guinea streams; detritus and algae were used as predictor variables. Taxa are listed in descending order of overall mean population densities across all six study streams. Only those taxa of functional groups which yielded at least one significant predictor variable are included. Abbreviations; n.s. = not significant; * $P<0.05$; ** $P<0.01$; $P<0.001$ (where $n = 10$); −ve and +ve refer to the sign of the regression coefficient in the best-fit model.

	Mindjim River	Manam Creek	Hohoma River	Kojé Creek	Hapia River	Mom Creek
Baetidae	Detritus,-ve, *	Algae, +ve, *	n.s.	n.s.	n.s.	Algae, +ve, *
Leptophlebiidae	n.s.	n.s.	n.s.	Detritus, +ve, *	Algae, -ve, *	n.s.
Orihocladiillae	Algae, -ve, ***	n.s.	n.s.	n.s.	Detritus, +ve, *	n.s.
Elmidae	Detritus & algae, -ve & -ve, *	n.s.	n.s.	n.s	n.s.	n.s.
Hydropsychidae	n.s.	Detritus & algae, +ve	n.s. +ve, **	n.s.	Detritus, +ve, *	n.s.
Chironominae	n.s.	Algae, +ve, **	Detritus, -ve, *	Detritus, +ve, ***	n.s.	Detritus, +ve, *
Caenidae	n.s.	n.s.	n.s.	n.s.	n.s.	Detritus, +ve, **
Philopotamidae	n.s.	Algae, +ve, **	n.s.	n.s.	n.s.	n.s.
Libellulidae	n.s.	n.s.	n.s.	n.s.	n.s.	Detritus, +ve, *
Hydroptilidae	n.s.	Algae, +ve, *	n.s.	n.s.	n.s.	n.s.
Hydrophilidae	Algae,-ve, *	n.s.	n.s.	n.s.	n.s.	n.s.
Naucoridae	n.s.	n.s.	Detritus, -ve, ***	n.s.	Detritus, +ve, *	n.s.
Simuliidae	n.s.	Algae, +ve, **	n.s.	n.s.	Detritus, +ve, *	n.s.
Total individuals	Detritus & algae, -ve & -ve, **	n.s.	n.s.	n.s.	n.s.	n.s.
Number of morphospecies	n.s.	Detritus, +ve, **	n.s.	n.s.	n.s.	n.s.
Collector-gatherers	Detritus & algae, -ve & -ve, *	n.s.	n.s.	Detritus & algae, +ve & +ve, *	Algae, -ve, *	Detritus, +ve, *
Grazers	Detritus & algae, -ve & -ve, **	n.s.	n.s.	n.s.	n.s.	n.s.
Filter-feeders	n.s.	Algae, +ve, **	n.s.	Detritus, +ve, *	Detritus, +ve. *	n.s.
Predators	Algae, -ve, **	n.s.	n.s.	n.s.	n.s.	n.s.
Shredders	n.s.	n.s.	n.s.	n.s.	n.s.	Detritus, +ve, ***

a stream with high inputs but low retention. Unfortunately, there are no data on the retentiveness of the New Guinea streams considered here, but it is notable that Manam Creek had the highest gradient of the six study streams and (all other things being equal) might have been the least retentive. If correct, this might explain why completely-shaded Manam Creek contained no more detritus than Mom Creek.

Notwithstanding the fact that algae and detritus accounted for inter-stream differences in the abundance of many taxa, and that the benthic community of shaded Manam Creek was distinct from that of partially-shaded or unshaded streams, investigation of FFGs is needed to ascertain whether the trophic struc-

ture of the study streams changed in response to variations in shading, algae and detritus. An obvious feature of the New Guinea streams discussed here was the paucity of shredders (mean = $0.4 \pm 1.1\%$ of total abundance; 0.7 ± 1.4 ind. 165 cm^{-2}), and a total of only 5 morphospecies which fed wholly or partially as shredders was recorded (Appendix 1). Hong Kong streams are likewise poor in shredders (Dudgeon, 1984b, 1989, 1992), with approximately 5–7 species per stream, and examination of macroinvertebrate species lists from the Sungai Gombak (Bishop, 1973) suggests that this paucity is a feature of Malaysian streams also. In New Zealand too, there is a general deficiency of shredders (Winterbourn et al., 1981), and even retentive streams

Appendix 1. List of taxa (number of morphospecies per taxon is given in brackets), their functional feeding group assignment, and mean population densities (n 165 cm^{-2} ± 1 S.D.) across six New Guinea streams. Co = collector-gatherers, Gr = grazers, Ff = filter-feeders, Pr = Predators, and Sh = shredders; Co/Gr were treated as one-half collector-gatherers and one-half grazer in all calculations, and other mixed feeding groups (Co/Sh, Co/Ff) were dealt with likewise.

DECAPODA		0.32± 0.89
Ca/Sh	Atyidae: *Caridina*	0.25± 0.88
Sh	Sundathelphusidae: *Sundathelphusa*	0.07± 0.25
EPHEMEROPTERA		166. 8±160.32
Co/Gr	Baetidae (6): *Baetis, Liebebiella*	119.0±162.12
Co	Caenidae	7.48± 8.25
Co	Leptophlebiidae (2): *Barba, Nonnullidens*	40.0± 54.38
Gr	Prosopistomatidae: *Prosopistoma*	0.42± 1.76
ODONATA		4.20± 4.76
Pr	Agrionidae: (including Megapodagrionidae)	2.53± 3.13
Pr	Libellulidae	3.67± 4.13
HETEROPTERA		2.62± 2.96
Pr	Gelastocoridae: *Nerthra*	0.02± 0.13
Pr	Naucoridae (3)	2.60± 2.95
LEPIDOPTERA		
Gr	Nymphulinae (2)	4.73± 5.36
TRICHOPTERA		46.75± 44.16
Gr	Hydroptilidae (2): *Hydroptila, Orthotrichia*	3.47± 5.74
Gr	Glossosomatidae: *Agapetus*	6.42± 11.36
Ff	Philopotamidae: *Chimarra*	6.78± 13.98
Ff	Hydropsychidae (5): *Macrostemum, Hydropsychodes, Herbertorossia, cf. Hydropsyche*	29.57± 34.55
Sh	Calamoceratidae: *Anisocentropus*	0.33± 1.14
Co/Sh	Leptoceridae (3)	0. 60± 0. 84
COLEOPTERA		33.17± 29.43
Pr	Dytiscidae	0.18± 0.47
Co/Gr	Hydraenidae (2): *cf. Hydraena*	0.68± 2.27
Pr	Hydrophilidae (4): *Enochrus* type	3.02± 2.33
Co/Gr	Dryopidae (2)	0.22± 0.64
Gr	Elmidae (2)	29.70± 29.60
Co	Helodidae (2)	0.05± 0.22
Sh	Ptilodactylidae: *cf. Epilichas*	0.03± 0.18
Pr	Lampyridae	0.07± 0.52

contain only 4–6 shredder species (Linklater & Winterbourn, 1993). These data contrast with a report of up to 23 shredder species in a single Virginian (USA) headwater stream (Roeding & Smock, 1989), the observation that shredders constitute 22% of benthic biomass in forested reaches of a Kansas (U.S.A.) stream (Gray & Johnson, 1988), and a recent model predicting tight deterministic responses of shredders to riparian vegetation and litter inputs (Cummins *et al.*, 1989). A paucity of shredders in New Zealand, New Guinea and tropical Asian streams could reflect biogeography, because of the virtual or complete absence of many groups of aquatic invertebrates that include numerous shredder species (e.g. certain plecopteran and trichopteran families), but other factors such as a low retentiveness of streams for coarse detritus (Winterbourn *et al.*, 1981) could play a role. However, given that the physical form of streams would not be expected to vary across latitudes, it is unlikely that an overall lack of retentiveness can explain the general scarcity of shredders in tropical Asian and New Zealand streams. Low retentiveness is also unlikely to provide an explantation for

Appendix 1 cont.. List of taxa (number of morphospecies per taxon is given in brackets), their functional feeding group assignment, and mean population densities (n 165 cm^{-2} ± 1 S.D.) across six New Guinea streams. Co = collector-gatherers, Gr = grazers, Ff = filter-feeders, Pr = Predators, and Sh = shredders; Co/Gr were treated as one-half collector-gatherers and one-half grazer in all calculations, and other mixed feeding groups (Co/Sh, Co/Ff) were dealt with likewise.

DIPTERA		68.97± 49.64
Pr	Tipulidae (3)	1.25± 1.55
Co	Psychodidae	0.03± 0.18
Co	Dixidae: *Dixa*	0.03± 0.18
Ff	Simuliidae: *Simulium*	2.60± 6.28
Pr	Chironomidae: Tanypodinae	5.43± 6.06
Co/Gr	Chironomidae: Orthocladiinae	35.75± 31.51
Co/Ff	Chironomidae: Chironominae	21.83± 17.84
Pr	Ceratopogonidae (4): *cf. Bezzia, cf. Culicoides*, Dasyheilinae	1.33± 1.93
Pr	Athericidae	0.55± 1.10
Pr	Empididae	0.18± 0.43
Co/Gr	Ephydridae	0.02± 0.13
Total = 64 morphospecies		327.50±233.75

a deficiency of shredders in monsoonal streams since litter accumulates in these habitats outside the rainy season (Dudgeon, unpublished observations).

Grazers and collector-gathers dominated the study streams, and the most obvious inter-stream difference in FFGs was the relative abundance of collector-gatherers and shortage of grazers in Manam Creek. A scarcity of grazers might be predicted from the degree of shading at this site, although algal standing stocks in this stream were not exceptionally low. The results of regression analysis employing algae and detritus as independent variables indicated that detritus was an important predictor of the relative abundance of collector-gatherers, grazers and shredders across all streams, although it had a significant effect on the population densities of shredders only. When the analysis was repeated using mean values for each stream as independent variables, the relationship between collector-gatherers and detritus was positive — perhaps indicating consumption of fine detritus by collectors — while that between grazers and detritus was negative. The latter is not surprising if we accept the assumption that sites which are rich in detritus will tend to be shaded and thus unsuitable feeding sites for grazers, but may also reflect that fact that Mom Creek — with the lowest algal biomass had (along with Manam Creek) the highest standing stocks of detritus. An ordination diagram of sites based on FFG abundance (Fig. 3) did not show the clear separation of Manam

Creek that was apparent when the ordination was based on the abundance of major taxa, and the only 'interpretable' aspect of the ordination was close grouping of samples taken from streams with little or no shade and small amounts of detritus (Hohoma River, Hapia River and Kojé Creek). However, the success of the PCA in accounting for over 80% of the variation in the data suggests that the lack of separation of sites on the ordination diagram results from the general similarity of FFG representation among the study streams, and perhaps a weak response to changes in riparian conditions, rather than inadequate characterization of the data by the multivariate analysis. The poor site separation reflects the general dominance of all communities by collector-gatherers and grazers, the paucity of shredders, and the relatively stable representation of predators in the 6 study streams.

An interesting finding of the present study was the difference in the importance of algae and detritus in best-fit regression models calculated for the abundant taxa within each stream. In two streams (Mindjim and Hohoma Rivers) significant regression models including detritus were negative, while they were positive in Hapia River and Manam, Kojé and Mom Creeks. Regression models including algae were negative in Mindjim and Hapia Rivers, and positive in Manam, Kojé and Mom Creeks. These differences were not related in any obvious way to quantities of algae or detritus in the streams: for example, Mindjim River,

Hapia River and Manam Creek had similar amounts of algae (Table 3) yet this variable was correlated with enhanced faunal abundance in two of the streams and reduced abundance in the third. Likewise, Hohoma and Hapia rivers contained comparable quantities of detritus, but the response of macroinvertebrates to variations in this factor were different. In the absence of other data which might account for these differing responses, speculation is unlikely to be fruitful. The data presented here suggest that macroinvertebrate communities in Papua New Guinea streams — like those in other regions — are influenced by riparian vegetation as well as standing stocks of detritus and algae. However, the responses of individual taxa, FFGs and the community as a whole are not straightforward: FFG responses appear to be weak, while the influence of detritus and algae upon individual taxa can vary among streams. This suggests that the explicit deterministic responses of stream invertebrates to riparian vegetation that have been proposed for north-temperate regions (e.g. Cummins *et al.*, 1989) will require modification before they can be applied to streams elsewhere.

Acknowledgments

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