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# Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea

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ABSTRACT. The trophic ecology of Konaino Creek, a small mountain headwater stream draining rainforest in the aseasonal tropics on Bougainville Island, Papua New Guinea, was examined and a food web was constructed. The major source of energy in Konaiano Creek was allochthonous detritus, most of which had been terrestrially degraded to fine particulate organic matter rather than entering the stream as leaf litter. This fine detritus was collected by the filter-feeders (mostly Simuliidae and also Hydropsychidae) which formed the dominant functional feeding group (64.4% of the fauna). Thus filterers processed most of the allochthonous detritus and made the energy available to other trophic levels, rather than shredders (1.7% of the fauna) which perform this role in temperate headwater streams. Collector-gatherers made up 22.7% of the fauna, carnivores, mostly Odonata, Decapoda (crabs) and Hydrobiosidae, comprised 2.8% of the fauna and grazer-scrapers made up 7.4%. The latter were inhibited by low instream production owing to heavy shading and the instability and abrasion of the substrate due to frequent spates. In comparison, the trophic ecology of the nearby, coastal, Bovo River (with a catchment mainly in rainforest but mostly cleared with introduced species at the study site) was quite different and it was dominated by collector-gatherers (74%) and grazer-scrapers (15%).

KEYWORDS: Aseasonal tropical trophic ecology, Bougainville Island, food webs

## INTRODUCTION

Trophic relationships are a vital component of community structure in streams, particularly with respect to predation, competition, and resource spiralling. Dietary habits can potentially influence every aspect of the life of stream invertebrates, such as life cycles, choice of habitat and behaviour. Consequently the trophic ecology of invertebrates has received much attention from stream ecologists in temperate regions of the Northern Hemisphere (e.g. Cummins 1973, Hynes 1970, Lamberti & Moore 1984, Merritt & Cummins 1984), and, to a lesser extent, the Southern Hemisphere (Chessman 1986, Winterbourn *et al.* 1984, Yule 1986). Data on the dietary habits of tropical stream invertebrates

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are not common (Burton & McRae 1972, trichopteran predators of simuliids; Dudgeon 1984, a river community; Dudgeon & Wat 1986, a dragonfly; Hearnden & Pearson in press, mayflies; Henderson & Walker 1986, leaf litter communities in the Amazon), particularly for animals in the non-seasonal tropics (Bishop 1973, a river community).

Previous studies of two Bougainville Island streams, Konaiano Creek (a small, pristine mountain stream) and the Bovo River (at a site <2 km from its mouth), showed that the benthic invertebrates all had aseasonal, flexible life cycles (Yule 1993; 1995a,b; Yule, in press; Yule & Pearson, in press), but the fauna of Konaiano Creek exhibited distinct patterns of spatial distribution between the waterfalls, riffles, runs and pools (Yule 1993). This study assesses the dietary habits, functional feeding groups and trophic structure of the benthic invertebrate community of Konaiano Creek and a comparison is made with data from the Bovo River (Yule 1993, 1995b) which arises within 1 km of Konaiano Creek on Mt Negrohead. Since the majority of taxa collected are new to science, and the rest are poorly known, this is the first time their dietary habits have been analysed.

There have been a few studies of the functional organisation of invertebrate communities in the seasonal tropics including those of Dudgeon (1984, 1989, 1992) and Pearson *et al.* (1986). This investigation provides the first opportunity to examine functional feeding groups and to determine the applicability of some of the generalisations of the 'River Continuum Concept' (RCC – Anderson & Sedell 1979, Vannote *et al.* 1980) in the aseasonal tropics. River systems on Bougainville Island tend to lack faunal continuity because, as they rush torrentially down the steep mountains, they become virtually devoid of animals and plants until they reach the flatter coastal plains and hence in this sense they do not follow the predictions of the RCC (Yule 1993, 1995a). Consequently a comparison of the trophic ecology of Konaiano Creek (a headwater stream) with the Bovo River (at a site near its mouth) is of particular interest.

## STUDY SITES

Bougainville Island is the eastern-most province of Papua New Guinea. Konaiano Creek (6° 18′ S and 155° 30′ E; Grid reference: 56MQU759031) arises on a steep ridge extending from the western side of Mount Negrohead (1509 m elevation). It is a small stream, 1.2 km long, flowing through pristine rainforest down the side of the ridge from 1070 to 680 m elevation where it joins the Kawerong River at the town of Panguna.

The catchment of Konaiano Creek lies entirely within lower montane rainforest characterised by many tree ferns and epiphytes. The tallest trees in the valley are 10–15 m in height and include *Casuarina* sp., *Cyathea* sp., *Ficus* sp. and species of Urticaceae with an abundance of vascular and non-vascular epiphytes (particularly orchids, mosses and ferns) as well as vines. The riparian vegetation comprises mostly broad-leaved, succulent trees and shrubs (e.g. *Musa* sp., *Alpinia c.f. oceanica, Saurauia* sp., *Hornstedtia* sp., *Begonia wiegallii, Ophiorrhiza* sp., *Cytosperma bougainvillense*), ferns, mosses and fungi. The dense vegetation shades approximately 70–80% of the stream. The majority of the dicotyledons have large succulent leaves and extensive insect damage is common. Moss and algae grow sparsely in the splash zones of the largest, most stable boulders and bedrock, mostly on the downstream sides, protected from abrasion. Despite the thickly forested catchment intact leaves (mostly still green or yellow rather than the brown, decomposing leaves typical of temperate streams) and leaf packs were rarely seen in the creek. Most of the detritus collected from Konaiano Creek was composed of very fine material with occasional sticks.

The section of Konaiano Creek studied is about 50 m in length, from 0.6 to 3.5 m wide, with an average depth of 20 cm, reaching up to 1.0 m deep below waterfalls (1–2 m high). The substrate consists of bedrock (about 40%), boulders 0.25–1.0 m in diameter (10%), cobbles 0.06–0.25 m in diameter (20%), pebbles 4–60 mm in diameter (10%) and sand less than 4 mm diameter (20%). All but the largest boulders are very unstable.

The climate of Bougainville Island is tropical and very equable throughout the year with regard to temperature, rainfall and humidity. Rainfall is high (mean annual rainfall at Panguna for 1968–1990 was 4367 mm) and tends to fall in intense cloudbursts throughout the year in contrast to the more predictable monsoons of the wet-dry tropics. Consequently the rivers and streams are characterised by extreme short-term variability in flow. Every month receives an average of over 200 mm of rain. The mean temperature at Panguna ranges from 22.8 to 24.0°C. The diurnal range is much greater than the monthly variation: the average daytime temperature is 26.4–28.2°C, while at night it is 19.0–19.8°C. The temperature of Konaiano Creek is constantly high with little variability (range 19–24°C). Humidity is always high, averaging between 78 and 90%. Photoperiod on Bougainville changes little throughout the year as the annual variation in day length is only 36 min. Konaiano Creek site is further described in Yule (1993, 1995a).

The physical characteristics, flora and fauna of the Bovo River have been described by Yule (1993, 1995a, b). The upper catchment of Bovo River is very similar to that of Konaiano Creek and consists mostly of rainforest. The original riparian vegetation along the Bovo River at the study site, in the town of Arawa, has largely been cleared and replaced with introduced and native species (*e.g. Cocos nucifera, Caesalpinia* sp., *Cassia* sp., *Ficus benghalensis, Artocarpus altilis, Musa* spp.). Herbs and grasses grow thickly along the banks, many of them being partially submerged. Filamentous green algae (*Spirogyra* sp.), and moss grow sparsely on larger boulders. Under normal flow conditions, Bovo River is about 10 m wide and between 0.2 and 1.0 m deep at the study site. The flow is always very fast and turbulent and the substrate, mostly large boulders, is extremely unstable.

## METHODS

Konaiano Creek was sampled monthly from July 1987 until April 1989 (except for January 1989). The benthic invertebrate fauna was quantitatively sampled using a Surber sampler 20 cm × 20 cm (400 $cm^2$) in size, with a 300 μm mesh. Samples were preserved in 70% alcohol and sorted under a microscope at a magnification of × 20. Species were identified as far as possible by the various experts listed in the acknowledgements. Few, however, had been previously described.

The dietary habits of all the species in the January–December 1988 samples represented by five or more specimens with at least partly filled guts, were determined by means of gut analysis and *in situ* observations of feeding behaviour. Specimens of different instars/sizes were examined for each species to detect any dietary shift (*e.g.* from collector-gatherer to predator) with increasing size.

The foreguts were dissected out and the contents squashed (for very small specimens, the entire animal was squashed) on a microscope slide and mounted in polyvinyl alcohol lactophenol mountant. The slides were examined under an Olympus microscope at magnifications of ×200 and ×400. Six major categories of food were present in the guts. These were: (1) Fine particulate organic matter (FPOM) <1 mm. (2) Coarse particulate organic matter (CPOM) >1 mm. Often the CPOM could not be identified, although sometimes leaf fragments, tiny pieces of wood or pollen grains were evident. (3) Fungal hyphae and conidia. (4) Vascular plant tissue. Leaf and wood fragments usually lacking fungi. Typically of only one species per gut. (5) Diatoms. A variety of species were observed. (6) Animals or parts thereof.

Gut contents were quantitatively assessed in the following manner. Each gut was considered to be 100% full. An evaluation was made of the amount of material in each of the food categories for each gut. This assessment was subjective but consistent. The animals were assigned to functional feeding groups, *i.e.* predators, shredders, scrapers, collector-gatherers and collector-filterers (Merritt & Cummins 1984) depending on their gut contents (and also their method of feeding determined by field and laboratory observations and examination of mouthparts). Some taxa occupied more than one functional feeding group because they had a mixed diet or else they underwent a dietary shift with increasing size. Consequently these taxa were allocated to all the appropriate functional feeding groups. Where analysis required enumeration, the relative abundance of specimens in each functional group was determined.

All the detritus collected in each Surber sample was oven-dried at 70°C for 24 h and then weighed. Correlation coefficients (r) were calculated to determine whether there was a statistically significant relationship between the abundance of individual taxa in each sample and the amount of detritus.

Methods used in the Bovo River are described in Yule (1993, 1995b). Gut analyses were performed upon the benthic invertebrates and the fauna were assigned to functional feeding groups. Their dietary habits are also described in Yule (1993, 1995b).

## RESULTS

*Dietary habits of individual taxa (Table 1)*

*Odonata. Lieftinckia kimminsi* Lieftinck (Megapodagrionidae) was a predator. The guts of late instar larvae contained mostly chironomids as well as simuliids, mayflies, caddisflies, beetles, tipulids and copepods (Figure 1). *L. kimminsi* inhabited the undersides of cobbles where chironomids congregated, rather than the upper surfaces favoured by the more abundant simuliids. A *Lieftinckia* larva was the only invertebrate found to have eaten a dragonfly larva, in this case a

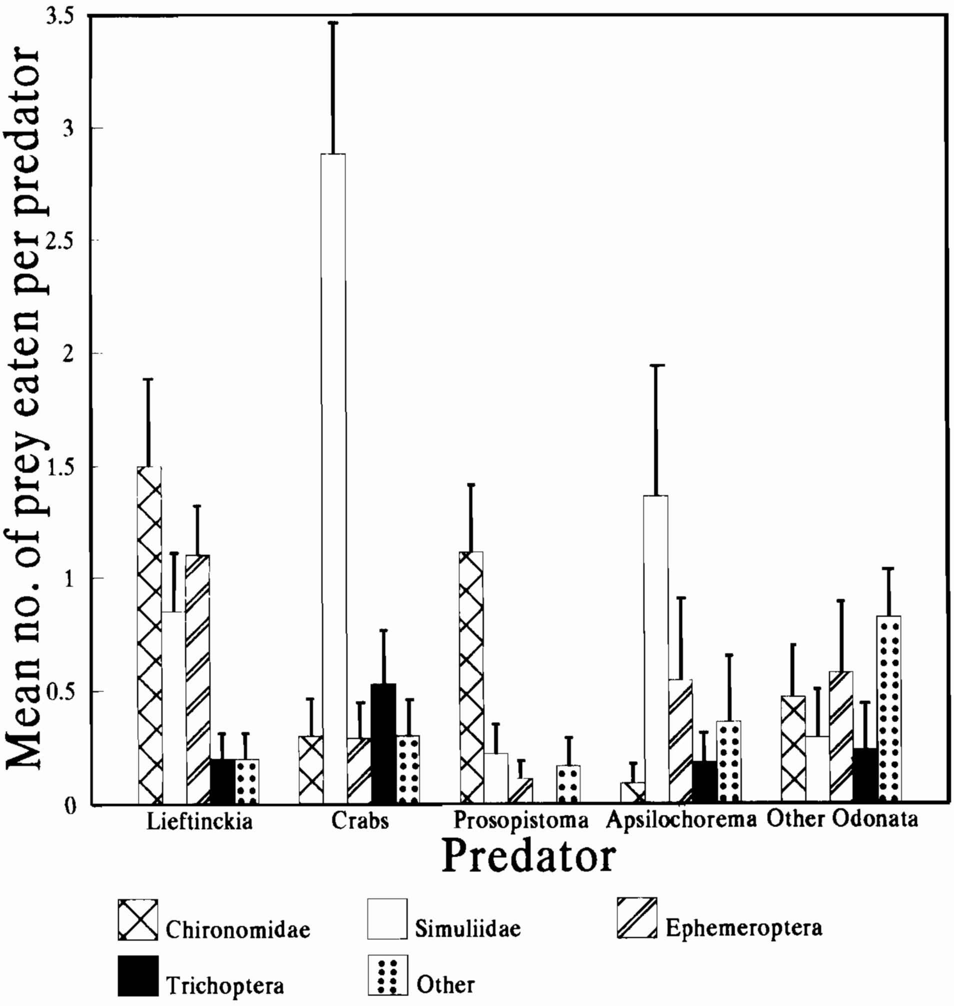


Figure 1. Predator diets in Konaiano Creek, Bougainville Island. Mean number (±SE) of prey eaten by each of the common predators.

Table 1. Summary of analyses of digestive tract contents of late instar specimens collected from Konaiaino Creek, Bougainville Island.

| | SPECIES | % of standing crop | Mean % composition of gut contents: CPOM | FPOM | Fungi | Diatoms | Leaf Litter | Wood | Animals | No. of Specimens |
|---|---|---|---|---|---|---|---|---|---|---|
| EPHEMEROPTERA | | | | | | | | | | |
| Prosopistomatidae | *Prosopistoma sedlaceki* | 0.27 | | | | | | | 100 | 27 |
| Leptophlebiidae | *Barba* sp.1 | 1.61 | 13.3 | 29.2 | 1 | 0.5 | 56 | | | 9 |
| Baetidae | *'Pseudocloeon'* sp. 1 | 2.52 | 5.5 | 94 | 0.5 | | | | | 5 |
| | *Baetis* sp. 1 | 5.82 | 56 | 42 | 1 | 1 | | | | 6 |
| | *Baetis* sp. 2 | 0.05 | 60 | 32 | 5 | 3 | | | | 5 |
| ODONATA | | | | | | | | | | |
| Megapodagrionidae | *Lieftinckia kimminsi* | 0.36 | | | | | | | 100 | 83 |
| | Megapodagrionidae sp. 1 | 0.03 | | | | | | | 100 | 8 |
| Coenagrionidae | *Ischnura* sp. 1 | 0.01 | | | | | | | 100 | 5 |
| Platycnemidae | Platycnemidae sp. 1 | 0.05 | | | | | | | 100 | 10 |
| Aeshnidae | Aeshnidae sp. 1 | 0.08 | | | | | | | 100 | 7 |
| TRICHOPTERA | | | | | | | | | | |
| Hydropsychidae | Hydropsychinae sp. 1 | 6.19 | 62.9 | 36.1 | 1 | | | | | 12 |
| | Hydropsychinae sp. 2 | 2.35 | 47.5 | 49.5 | 3 | | | | | 7 |
| Leptoceridae | nr *Triaenodes* sp. 1 | 0.11 | | | | | 100 | | | 5 |
| | nr *Triaenodes* sp. 2 | 0.42 | | | | | 100 | | | 5 |
| | 'Leptoceridae' sp. 3 | 0.05 | | | | | | | 100 | 4 |
| Philopotamidae | *Chimarra* sp. 1 | 0.66 | | 99.8 | 0.1 | 0.1 | | | | 5 |
| | Philopotamidae sp. 1 | 0.3 | | 100 | | | | | | 8 |
| Calamoceratidae | *Anisocentropus* sp. 1 | 0.23 | 26.8 | 20.2 | 5.5 | | 48 | | | 19 |
| Hydrobiosidae | *Apsilochorema* sp. 1 | 0.2 | | | | | | | 100 | 18 |
| Goeridae | Goeridae sp. 1 | 0.13 | 34 | 30 | | 36 | | | | 3 |
| Polycentropodidae | *Nyctiophylax* sp. 1 | 0.29 | | 100 | | | | | | 13 |
| Hydroptilidae | *Orthotrichia* sp. 2 | 0.21 | | | | | | | 100 | 10 |
| | *Niuginitrichia* sp. 1 | 0.03 | | 56 | 1 | 43 | | | | 6 |
| | *Scelotrichia* sp. 1 | 0.03 | | 100 | | | | | | 4 |

Table 1. Continued.

| | SPECIES | % of standing crop | Mean % composition of gut contents: CPOM | FPOM | Fungi | Diatoms | Leaf Litter | Wood | Animals | No. of Specimens |
|---|---|---|---|---|---|---|---|---|---|---|
| DIPTERA | | | | | | | | | | |
| Blephariceridae | *Apistomyia* sp. 1 | 0.49 | 6.6 | 73 | 2 | 18.4 | | | | 5 |
| Simuliidac | *Simulium (Morops)* sp. 1 | 30.1 | 61.5 | 37 | 1.5 | | | | | 10 |
| | *Simulium (Morops)* sp. 2 | 26.1 | 65 | 32 | 3 | | | | | 10 |
| Tipulidae | Tipulidae sp. 1 | 0.05 | | 20 | | | | | 80 | 5 |
| | Tipulidae sp. 2 | 0.04 | | | | | 100 | | | 5 |
| | Tipulidae sp. 3 | 0.01 | | 100 | | | | | | 5 |
| Tabanidae | Tabanidae sp. 2 | 0.01 | | 100 | | | | | | 4 |
| Psychodidae | Psychodidae sp. 1 | 0.06 | 99 | | 1 | | | | | 3 |
| | Psychodidae sp. 6 | 0.02 | | 100 | | | | | | 3 |
| Empididae | Empidid sp. 2 | 0.06 | | 100 | | | | | | 6 |
| Ceratopogonidae | nr *Atrichopogon* sp. 1 | 0.04 | | 100 | | | | | | 4 |
| Chironomidae | *Paramerina* sp. 2 | 0.04 | | 100 | | | | | | 6 |
| | *Polypedilum nr watsoni* | 0.6 | | 99 | 1 | | | | | 5 |
| | *Tanytarsus inextensis* | 0.23 | | 100 | | | | | | 5 |
| | *Paralauterborniella* sp. 1 | 0.19 | | 100 | | | | | | 5 |
| | *Stenochironomus* sp. 1 | 0.07 | | | | | 60 | 40 | | 4 |
| | *Rheocricotopus* sp. 2 | 0.29 | | 100 | | | | | | 5 |
| | *Thienemanniella* sp. 2 | 0.07 | | 100 | | | | | | 5 |
| | *Corynoneura australiensis* | 0.01 | | 100 | | | | | | 6 |
| HEMIPTERA | | | | | | | | | | |
| Veliidae | Veliidae sp. 1 | 0.02 | | 100 | | | | | | 5 |
| LEPIDOPTERA | | | | | | | | | | |
| Pyralidae | Pyralidae sp. 1 | 0.02 | | 50 | 20 | 30 | | | | 5 |
| CRUSTACEA | | | | | | | | | | |
| Decapoda | *Sendlaria salomonis and Rouxana? minima* | 0.11 | | 13.1 | 1 | | 32 | 33.8 | 53 | 26 |
| OLIGOCHAETA | | | | | | | | | | |
| Naididae | nr *Pristina* sp. 1 | 0.68 | | 100 | | | | | | 5 |

small corduliid. *L. kimminsi* was the largest insect in Konaiano Creek and, since fish and other vertebrates were absent from the stream, it was a top predator in the food web. The distribution of L. *kimminsi* was positively correlated with the distribution of detritus in the stream ($r = 0.230$, $n = 184$, $P < 0.05$). This association could be related to the presence of prey species amongst the detritus.

All the other odonates in Konaiano Creek were also carnivores, but they were uncommon and so few specimens were available for study. Megapodagrionidae sp. 1, a very similar species to *L. kimminsi*, had a similar diet, preying upon simuliids and chironomids. The Aeshnidae ate chironomids, mayflies, simuliids, ostracods and oligochaetes. The few coenagrionids (*Ischnura* sp.) available for study had eaten ostracods and mayflies. Platycnemidae sp. 1 captured chironomids, caddisflies, simuliids, and mayflies. Some specimens also contained insect eggs.

*Ephemeroptera.* The mayfly *Prosopistoma sedlaceki* Peters (Prosopistomatidae) was a predator, consuming mostly chironomids and some simuliids and baetids, but not caddisflies which are probably too large (Figure 1). Early instars consumed FPOM, with an increasingly carnivorous diet from about the 4th instar.

The leptophlebiid *Barba* sp. 1 was a collector-gatherer, its early instars consuming mostly FPOM with some CPOM, fungal hyphae and mineral particles. Late instars also shredded woody material and leaves. The gut contents of specimens comprised up to 15% mineral particles. The abundance of *Barba* nymphs was positively correlated with the distribution of detritus ($r = 0.214$, $n = 931$, $P < 0.05$).

'*Pseudocloeon*' sp. 1 (Baetidae) was a collector-gatherer, with a diet primarily of FPOM and some CPOM and fungi. Up to 8% of gut contents were filled with mineral particles. Despite its dietary habits there was no correlation between the distribution of '*Pseudocloeon*' and the distribution of detritus. *Baetis* spp. 1, 2 and 3 were grazer-scrapers consuming FPOM, CPOM, diatoms and fungi. The guts of all the baetids examined contained large amounts of mineral particles (up to 50%). The distribution of *Baetis* sp. 1 nymphs was strongly correlated with the distribution of detritus ($r = 0.341$, $n = 3755$, $P < 0.001$). Possibly detrital deposits were a refuge from predation.

*Trichoptera.* The most abundant caddisflies in Konaiano Creek were two hydropsychids, Hydropsychinae sp. 1 and sp. 2. Both were collector-filterers, consuming a wide variety of food items. Hydropsychid nets were a common feature of the stream, particularly on the bedrock surfaces of waterfalls. Larvel guts were filled mostly with CPOM (particularly leaf fragments), as well as FPOM, fungal hyphae, pollen grains, insect eggs and fern spores. Although leaf fragments were commonly seen in guts, they were invariably from a variety of sources rather than from a single leaf that would have indicated that the larvae were shredding the leaves. A single chironomid head capsule was found in the gut of a 4th instar sp. 2 larva but was probably an exuvium discarded following moulting.

*Chimarra* sp. 1 (Philopotamidae) was another collector-filterer. Larval guts all contained very fine detritus. Final instar specimens also consumed small amounts of fungal spores, pollen grains and diatoms. The distribution of *Chimarra* sp. 1 larvae was positively correlated with the distribution of detritus in the stream ($r = 0.228$, $n = 432$, $P < 0.05$). All the guts examined of Philopotamidae sp. 1 also contained FPOM collected using a fine net, but the distribution of larvae was not correlated with detrital abundance.

Species of polycentropodid in the genus *Nyctiophylax* have been recorded as predators, shredders and collector-filterers (Chessman 1986, Australia; Wiggins 1984, U.S.A.). The species in Konaiano Creek was a collector-filterer with all instars consuming only very fine FPOM, which they obtained using fine nets. The distribution of this species was positively correlated with the abundance of detritus ($r = 0.242$, $n = 179$, $P < 0.05$).

Leptoceridae nr *Triaenodes* sp. 1 and 2 were shredders. The guts of all the specimens examined contained leaf fragments. No fungal hyphae were seen, even in foregut material, indicating that the material consumed was fresh. The abundance of nr *Triaenodes* sp. 2 larvae in Konaiano Creek was strongly positively correlated with the distribution of detritus in the stream ($r = 0.259$, $n = 238$, $P < 0.01$). 'Leptocerid' sp. 3 is a predator. Larval guts contained chironomids and unidentified insect remains.

The hydrobiosid *Apsilochorema* sp. 1 was a predator (Figure 1). Guts of 2nd to final instar larvae contained a variety of prey items including mayflies, chironomids, simuliids and caddisflies. Simuliids, and to a lesser extent mayflies were clearly favoured over other invertebrates. First instar larvae ate FPOM.

The calamoceratid, *Anisocentropus* sp. 1 was sometimes as collector-gatherer, consuming FPOM, CPOM, and fungal hyphae and sometimes it shredded leaf litter (shown by guts filled with leaf material from a single plant species). The gut of one 4th instar larva was filled with fungal hyphae and conidia. The abundance of *Anisocentropus* larvae was very strongly correlated with the distribution of detritus in Konaiano Creek ($r = 0.493$, $n = 110$, $P < 0.001$).

Goeridae sp. 1 was a grazer-scraper, consuming CPOM, FPOM, diatoms (up to 30% of early instar gut contents) and mineral particles (up to 40%). Some of the guts of the hydroptilid larva, *Orthotrichia* sp. 2, contained FPOM; however, mostly the contents were unidentifiable.

*Niuginitrichia* sp. 1, another hydroptilid, was a scraper, with a diet consisting mostly (up to 80%) of a variety of species of diatoms as well as FPOM. Larvae of *Scelotrichia* sp. 1 ate very fine FPOM.

*Diptera*. The most common benthic invertebrates in Konaiano Creek (55% of the total animals collected), *Simulium (Morops)* sp. 1 and sp. 2 (*Simuliidae*) were both collector-filterers, eating CPOM, FPOM and fungal hyphae. Mineral particles formed a very small proportion of the gut contents. The blephariceridae

*Apistomyia* sp. 1 was a scraper-grazer. Guts examined contained FPOM, a variety of species of diatoms, fungal hyphae and a large proportion of mineral particles (up to 60% of gut contents). One specimen contained some plant fragments, possibly moss. *Apistomyia* was mostly found on bedrock surfaces of waterfalls.

Tipulidae sp. 1 had a partly carnivorous diet in its later instars, eating FPOM and diatoms as well, while small specimens consumed FPOM. Thus it underwent a dietary shift from being a collector-gatherer to being a predator/collector-gatherer. Tipulidae sp. 2 was a shredder. Individual larvae usually contained leaf fragments from a single species, while guts of specimens in the same sample often contained the same leaf species, suggesting that they were all feeding on the same leaf. Fungal hyphae were rare and thus the material consumed was presumably fresh. Tipulidae sp. 3 was a collector-gatherer consuming FPOM. Empididae sp. 2 and Tabanidae sp. 2 consumed FPOM and were collector-gatherers. The abundance of Empididae sp. 2 was strongly correlated with the distribution of detritus ($r = 0.407$, $n = 331$, $P < 0.001$). Psychodidae spp. 1 and 6 were collector-gatherers although sp. 1 ingested CPOM together with fungal hyphae, while sp. 6 ate FPOM.

Most of the chironomids consumed FPOM, collected either by gathering or filtering. One species, *Stenochironomus* sp., shredded wood and leaves. None of the chironomids in Konaiano Creek appeared to be grazer-scrapers. Taxonomic problems precluded extensive analysis of chironomid dietary habits.

*Lepidoptera*. Pyralidae sp.1 larvae were scrapers, consuming diatoms, FPOM, and fungi.

*Crustacea*. The two crab species, *Sendlaria salomonis* (Roux) and *Rouxana? minima* (Roux) shredded large amounts of wood and leaves and they also ate animals such as simuliids, caddis larvae (particularly Hydropsychinae sp. 1), chironomids and terrestrial insects. One specimen contained eight simuliid larvae as well as leaf fragments. Simuliid larvae were the most common prey items (Figure. 1). Small specimens consumed FPOM as well as leaves, wood and animals.

*Oligochaeta*. Only one species of oligochaete, a naidid *nr Pristina* sp., was found in Konaiano Creek. Like most other oligochaetes, it was a collector-gatherer, consuming FPOM.

*Functional organisation of the community*

The major trophic pathways in Konaiano Creek are depicted in Figure 2 and the major trophic pathways in the Bovo (a nearby coastal river lined with semi-submerged grasses and with a relatively high level of autochthonous production) are presented in Figure 3. The collector-filterers dominated Konaiano Creek, followed by the collector-gatherers, the grazer-scrapers, the carnivores and the shredders (Figure 4a, Table 2). The filterers included relatively

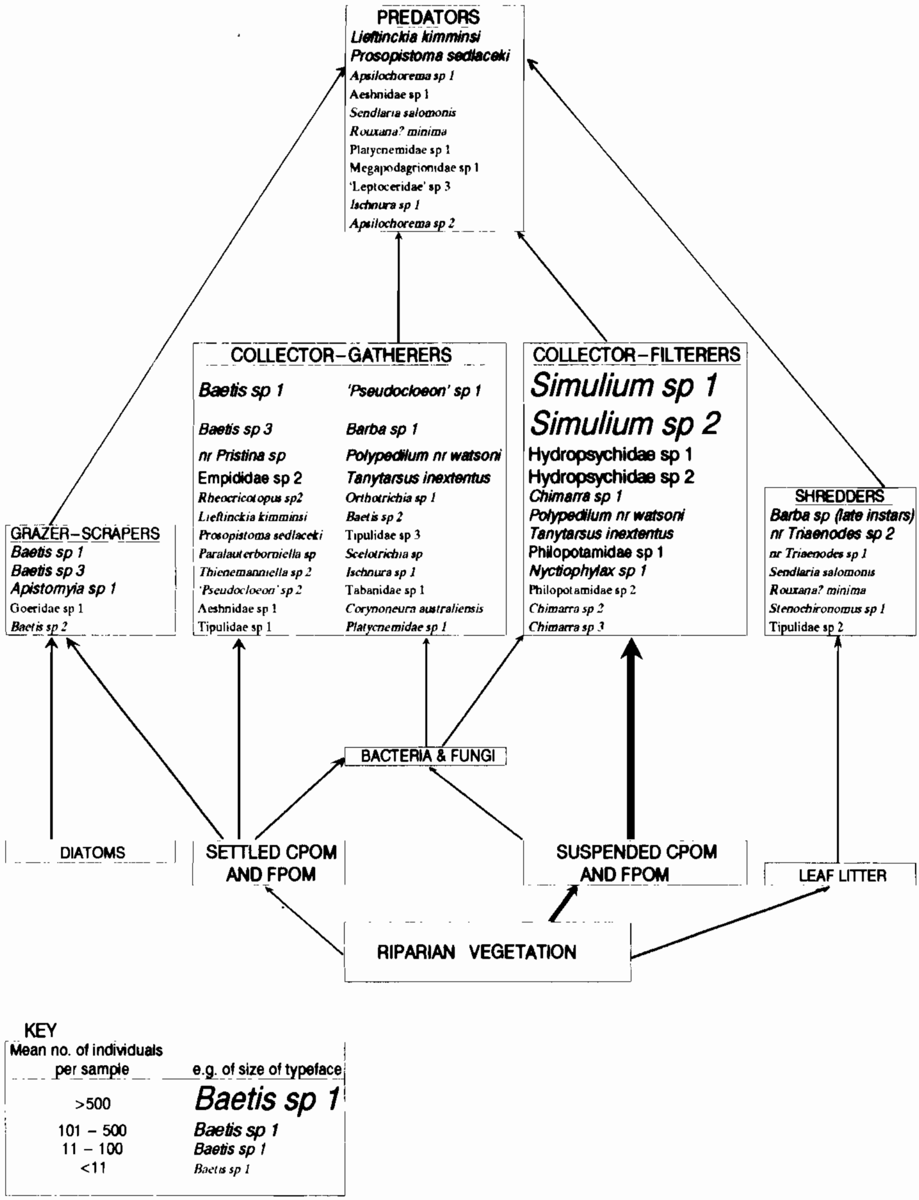


Figure 2. Major trophic pathways in Konaiano Creek, Bougainville Island. N.B. All functional feeding groups contribute to settled and suspended CPOM and FPOM through defecation and death. The role of bacteria and fungi is assumed.

few species, being dominated by *Simulium* spp. 1 and 2, and the two hydropsychids, while the collector-gatherers comprised the highest proportion of the species and the grazer-scrapers the least (Figure 4b). The composition of the Bovo River community (Yule 1993, 1995b) was very similar to that of Konaiano Creek with respect to the relative numbers of taxa in each functional feeding

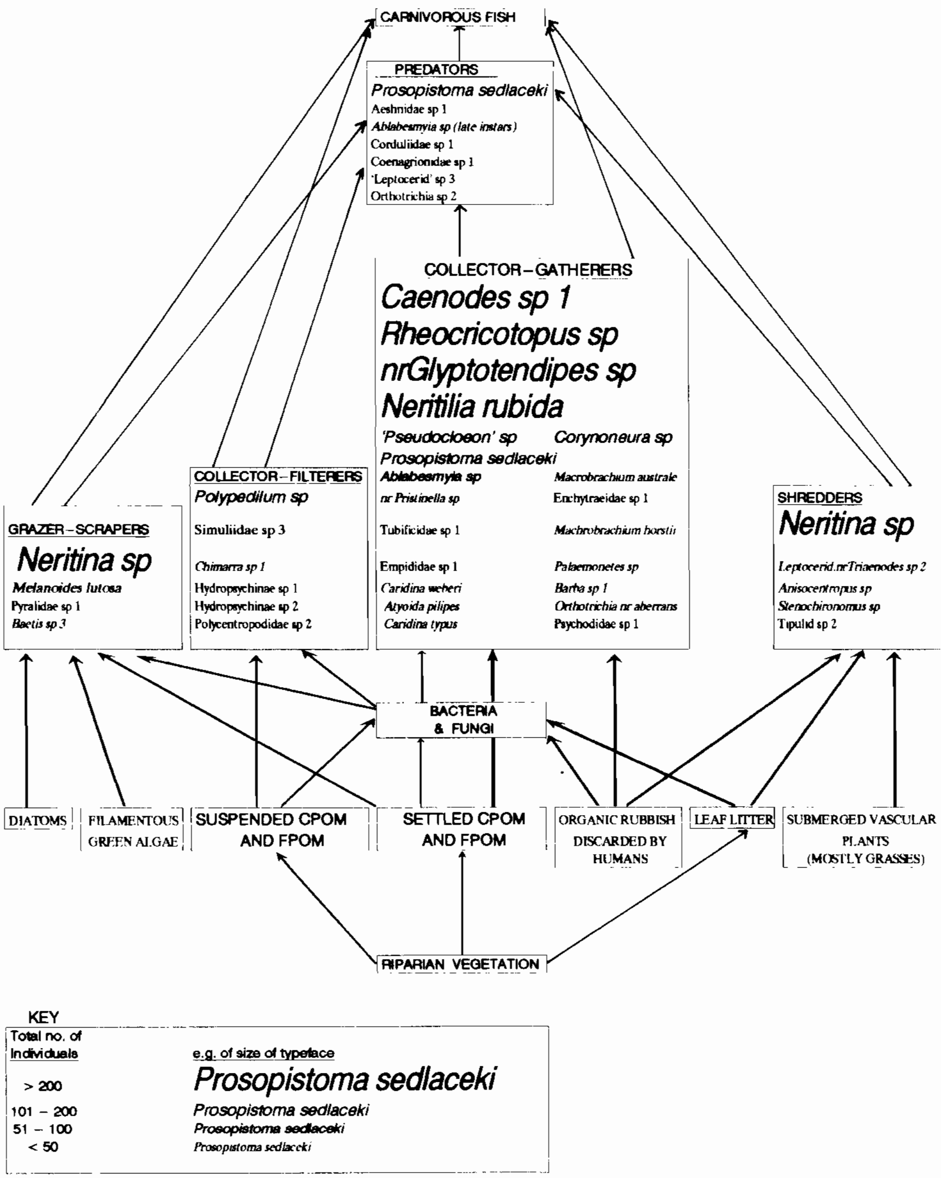


Figure 3. Major trophic pathways in the Bovo River, Bougainville Island. N.B. All functional feeding groups contribute to settled and suspended CPOM and FPOM through defecation and death. The role of bacteria and fungi is assumed. (From Yule 1993, 1995 b)

group, but the relative abundances of animals in each feeding group was quite different (Figure 3, Table 2). Whereas Konaiano Creek is numerically dominated by the filterers, the Bovo fauna is mostly made up of collector-gatherers. The presence of a large population of fish in the Bovo (observed whilst sampling but not studied) would have a great influence on its trophic ecology, but they were not present in Konaiano Creek.

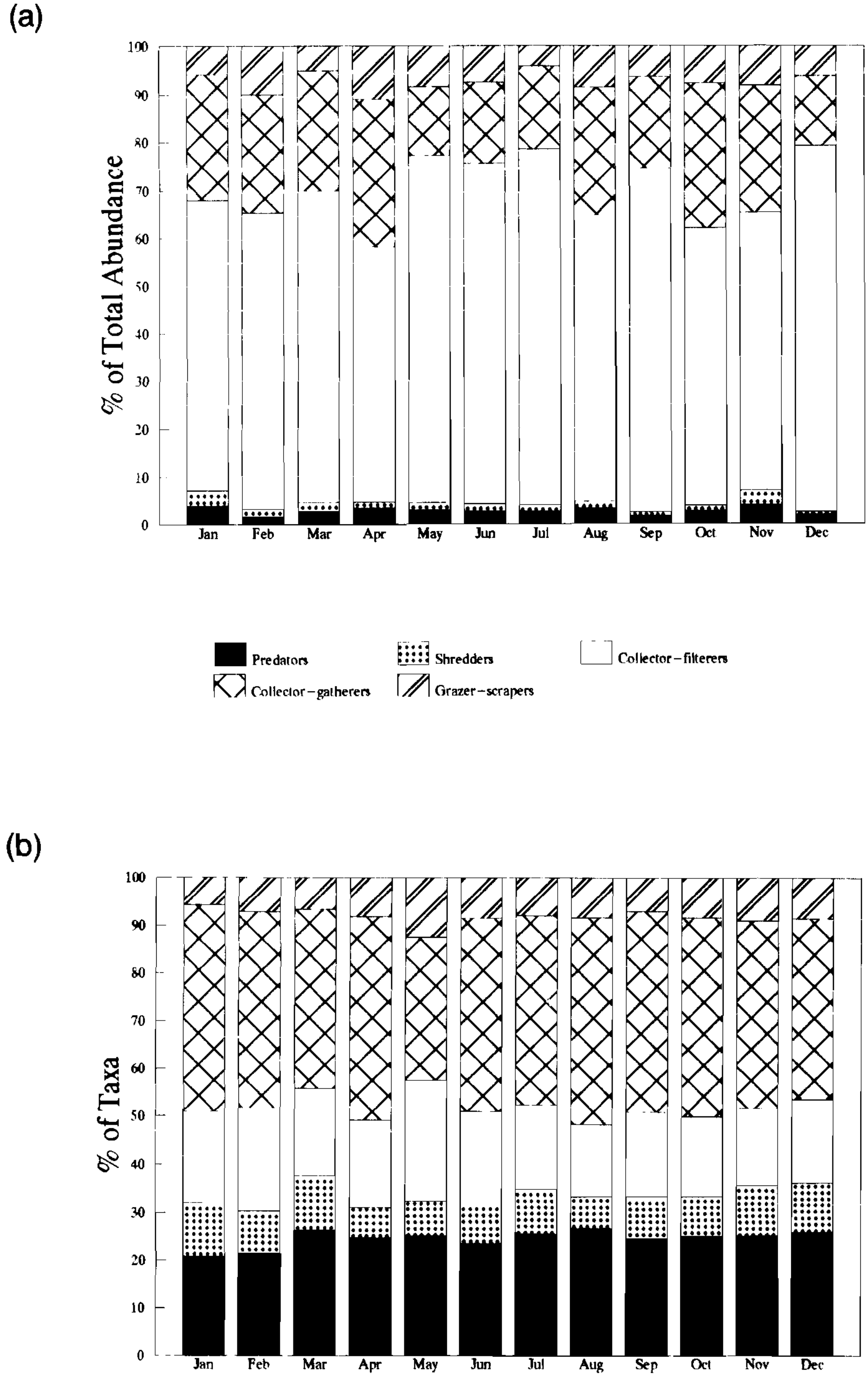


Figure 4. Monthly variation in the composition of the Konaiano Creek, Bougainville Island, benthic invertebrate community with respect to the proportion of (a) the total number of individuals in each of the functional feeding groups and (b) the taxa in each of the functional feeding groups.

Table 2. Comparison between average proportions of each functional feeding group in Konaiano Creek and the Bovo River, Bougainville Island, with respect to faunal abundance and numbers of taxa (±1 S.E.).

| | Konaiano Creek | | Bovo River | |
|---|---|---|---|---|
| | % by numbers | % by species | % by numbers | % by species |
| Predators | 2.82 (±0.23) | 24.5 (±0.52) | 2.74 (±0.44) | 16.7 (±1.6) |
| Shredders | 1.72 (±0.23) | 9.05 (±0.48) | 5.22 (±1.12) | 8.26 (±0.8) |
| Collector–Filterers | 65.39 (±2.2) | 18.37 (±0.76) | 3.21 (±0.47) | 18.7 (±1.05) |
| Collector–Gatherers | 22.67 (±1.7) | 39.9 (±1.06) | 74.1 (±4.4) | 50.1 (±1.19) |
| Grazer–Scrapers | 7.4 (±0.57) | 8.14 (±0.48) | 14.7 (±3.2) | 6.31 (±0.51) |

The composition of the benthic invertebrate fauna in Konaiano Creek exhibited little monthly change with respect to functional feeding groups (Figure 4) and there was no evidence for any seasonal change in faunal dietary habits.

## DISCUSSION

Almost all the benthic invertebrates in Konaiano Creek consumed particulate organic matter and leaf litter originating from the riparian vegetation while instream autochthonous production was of little importance in their diets (Figure 2). Konaiano Creek thus resembles forest streams in temperate regions that are also typically dependent upon an input of allochthonous detritus (Minshall 1967, Cummins 1974). The creek was numerically dominated by the collector-filterers (65% of all the benthic invertebrates collected), mostly simuliids but also hydropsychids. It thus has a similarity with lake or dam outlet fauna where large numbers of filter-feeders take advantage of the outflowing plankton and fine detritus (Boon 1984, Crosskey 1990, Wallace & Merritt 1980). This indicates the presence of a large amount of suspended organic material in the stream. Collector-gatherers (mostly mayflies) made up 22% of the fauna, and thus almost 90% of the fauna of Konaiano Creek was directly reliant upon particulate organic matter. Autochthonous production was very low in Konaiano Creek because of shading and substrate instability, and so the fine material must have been of riparian origin. The RCC predicts that FPOM in forested headwater streams is largely the result of instream processing of leaf litter by shredders, but such processing did not appear to occur to any large extent in Konaiano Creek.

Cummins (1992) states that in headwater streams at least 30% of the processing of coarse litter into FPOM is due to shredders. However, shredders were far fewer in number in Konaiano Creek (only 1.7% of faunal abundance) than in northern temperate streams where they form about 10% of the fauna (Cummins *et al.* 1989), and so they were unlikely to be responsible for the large quantities of FPOM and CPOM consumed by the collectors. Their low abundance is partly due to the low levels of leaf litter in the stream – a mean of 0.04–0.23 kg dry wt $m^{-2}$ compared with 0.2–0.9 kg $m^{-2}$ reported for northern temperate streams (Cummins *et al.* 1989) and up to 0.74 kg $m^{-2}$ reported for a wet-dry tropical stream in Hong Kong (Dudgeon 1982). Dudgeon (1984, 1989, 1992) found low numbers of shredders in the headwaters of the Hong Kong stream despite a relatively large standing crop of detritus. Stout (1989) suggested that shredders are inhibited in tropical streams by the higher proportion of toxic condensed tannins in the leaves of tropical plants.

Shredders were most abundant in the Bovo River where they comprised over 5% of the benthic invertebrates collected and commonly ate the semi-submerged bankside grasses that lined the river (Yule 1993, 1995b). There appeared to be little material available for shredders in Konaiano Creek as most of the detritus was composed of very fine material with occasional sticks, while intact leaves were rarely seen. Leaf packs typically accumulate in pools in temperate streams, but in Konaiano Creek, the pools tended to fill with large deposits of particulate organic matter. Low leaf litter input into Konaiano Creek can be partly explained by low leaf litter production in the catchment owing to the constantly high rainfall (leaf shedding is an adaptation to drought; Longman & Jenik 1987) and the low rates of leaf turnover of the dominant climax forest trees (W. F. Laurance, pers. comm.).

Konaiano Creek lies in a steep-sided valley, in a pristine rainforest, with a rough bed, and so it would be expected to retain leaf litter efficiently according to the criteria of Cummins *et al.* (1989), but it is subject to the frequent disturbance of spates. Several temperate studies have found leaf retention in streams to be inversely proportional to discharge (Ehrman & Lamberti 1992, Jones & Smock 1991), but in a seasonal tropical stream Dudgeon (1982) found that fine detritus and leaf litter exported by spates were replaced by transport from upstream or washed in from the banks. Further, litter would be expected to accumulate between spates, yet there was no evidence of this. Instead the pools became filled with particulate organic matter. It can be concluded that most of the leaf litter that enters Konaiano Creek from the surrounding rainforest is already broken down to finer particles, except for the sticks and twigs that are more resistant to decomposition. Most of the intact leaves in the stream originate from the overhanging riparian vegetation.

Complete terrestrial breakdown of leaf litter in temperate regions may take up to several years because of the seasonal restrictions of low temperatures and dry conditions for much of the year and the scarcity of shredders (Cummins *et al.* 1989, Deshmukh 1986). However, in the humid tropics terrestrial leaf litter may be completely broken down in only a few weeks (Deshmukh 1986, Mabberly 1983) as it is constantly warm and wet – ideal conditions for both invertebrate shredders and decomposing bacteria and fungi. In tropical rainforests much of the shredding occurs in the canopy where vertebrate and invertebrate herbivores abound and green leaves are typically very 'moth-eaten'. Most of the suspended FPOM and CPOM caught (no intact leaves were captured) in a drift net placed in Konaiano Creek during the day was green, indicating that it had been mechanically broken down, probably by herbivores in the canopy (thus it was largely composed of frass fall), rather than decomposed by bacteria and fungi. In the wet-dry tropics of Zimbabwe most leaf material is processed by terrestrial detritivores during the dry season, reducing it to fine particles by the time the rains come and there is a consequent reduction of instream shredders (Minshall *et al.* 1985).

Another distinction between temperate and tropical forests is that in the latter the leaf litter and other organic matter tend to lie on top of the mineral soil layer rather like a carpet. Tropical forests lack the digging animals such as oligochaetes which, in temperate forests, cause a thorough mixing of the organic layer with the inorganic material below (Fittkau & Klinge 1973). Thus finely decomposed leaf litter tends not to be incorporated into the soil in tropical forests and so may be more readily washed into streams, such as Konaiano Creek, when it rains.

The high proportion of filter-feeders in Konaiano Creek has important implications on the trophic ecology of the stream. Filter-feeders, particularly simuliids and hydropsychids, can reduce the suspended organic loads of streams (McCullough *et al.* 1979), they convert this material to finer material in faeces that may then be available to collector-gatherers, and they also convert the filtered organic material to animal tissue providing an energy source for predators (simuliids were particularly frequent prey items) and for collectors upon death. They also recycle material egested by other benthic invertebrates upstream. The collector-filterers in Konaiano Creek ingest large quantities of fine material that largely enters the stream from the surrounding rainforest as FPOM and CPOM, rather than as leaf litter. I hypothesise that given the continuously fast flows in the stream, it is unlikely that much of this fine material would settle out in the absence of the filter-feeders and thus without them the major energy source for Konaiano Creek would be unavailable to other benthic invertebrates.

Konaiano Creek does not fit in with the prediction of the 'River Continuum Concept' for a typical headwater stream, since the allochthonous energy supply entering from the riparian vegetation is in the form of fine detritus which is captured and passed on to other feeding groups by the very abundant collector-filterers rather than the shredders common in forested temperate and wet-dry tropical headwater streams. The trophic ecology of the coastal Bovo River fitted the predictions of the RCC for a lowland river more closely with a greater input from autochthonous production. There is clearly a need to study the composition of organic stream inputs, particularly looking at levels of suspended particulate organic matter, in Konaiano Creek. It would be interesting to compare other headwater streams in the aseasonal tropics to see whether the large input of particulate organic matter rather than leaf litter is a typical phenomenon.

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