The ecology of an aseasonal tropical river on Bougainville Island, Papua New Guinea

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Abstract

The invertebrate fauna of the Bovo River, a small river on Bougainville Island, was studied over one year. Bougainville is a small, mountainous, volcanic island, mostly covered by tropical rainforest, on the western rim of the Pacific Ocean. The climate is tropical and very equable throughout the year with regard to rainfall, temperature and humidity. The Bovo River arises on Mt Negrohead (1509 m) and flows for 13 km to enter the sea at the town of Arawa. The study site was 2 km from the sea. Flow in the Bovo is very rapid and spates are frequent. The substrate (mostly boulders) at the study site is extremely unstable. Over 10,000 invertebrates, in *ca.* 70 taxa, were collected. Gastropoda, Palaemonidae and Atyidae were diverse and abundant and dominated the invertebrate community in terms of biomass, but an undescribed mayfly, *Caenodes* sp. was the most common species.

The invertebrate community exhibited no pattern of seasonal change with respect to community composition or faunal abundance. The life cycles of two Ephemeroptera, *Prosopistoma sedlaceki* and *Caenodes* sp. were both asynchronous and aseasonal, with continuous hatching and growth. The dietary habits of 40 species of invertebrate in the Bovo were studied. A wide range of energy sources was available including riparian vegetation, benthic algae, semi-submerged grasses, and organic rubbish discarded by humans. The invertebrate fauna was dominated by collector-gatherers (74%), followed by grazer-scrapers (15%), shredders (5%), collector- filterers (3%) and predators (3%).

Introduction

The ecology of stream communities in the humid, aseasonal tropics, where there is no distinct dry season, has rarely been studied. This investigation of the benthic invertebrate fauna of the Bovo River, together with a more intensive study of the ecology of Konaiano Creek, a small mountain stream (Yule 1993 and in press, Yule and Pearson in prep.), represent the first surveys of invertebrate stream communities to be undertaken on Bougainville Island, a small aseasonal tropical island on the western rim of the Pacific Ocean. The life cycles and trophic ecology of the invertebrate fauna of tropical streams remain poorly known in comparison to the wealth of data available for temperate stream communities, yet the ecology of tropical stream invertebrates, particularly in the humid, aseasonal tropics, is likely to be strongly influenced by the very different temperature and flow regimes. Seasonal changes are major influences upon the communities of temperate and seasonally wet-dry tropical streams, but in the aseasonal tropics temperatures and rainfall as well as photoperiod, vary little throughout the year, while spates are likely to be intense but unpredictable. There have been few long term studies of the invertebrate communities of rivers and streams

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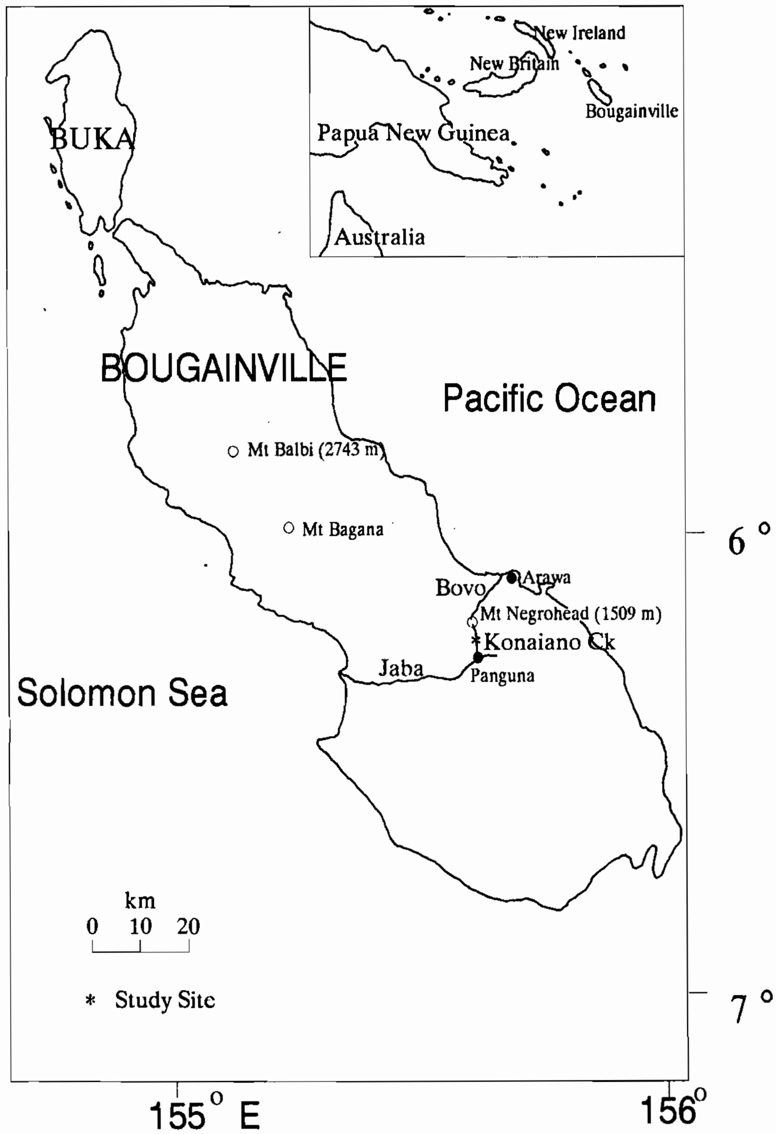


Fig. 1. Location of Bougainville Island and the Bovo River.

in the aseasonal tropics. Bishop (1973) published an extensive study of the Sungai Gombak in Malaysia; Bright (1982) described secondary benthic production in a small stream in the Caroline Islands; and Turcotte and Harper (1982) investigated aspects of a cool Amazon headwater stream in Ecuador. Apart from gathering basic descriptive data, these authors provided some information on invertebrate life cycles in these streams.

The aims of this study were to describe the invertebrate fauna of the Bovo River; to determine whether the community underwent any cyclic changes in species composition or abundance; to investigate the life cycles of two Ephemeroptera (*Prosopistoma sedlaceki* and an undescribed species of *Caenodes* – neither of which had been previously studied); and to examine the dietary habits and trophic ecology of the invertebrate fauna. The study came to a premature close owing to a secessionist rebellion by the Bougainville Republican Army.

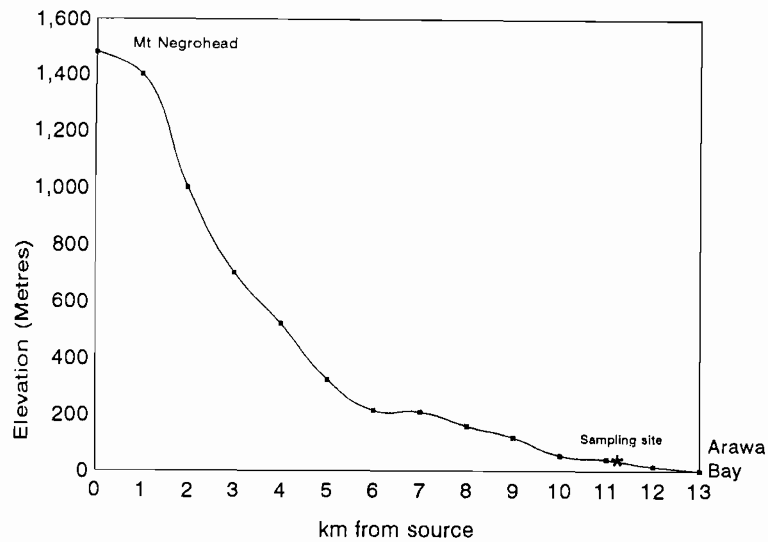


Fig. 2. Stream profile of Bovo River.

Study Site

Bougainville Island is the eastern-most province of Papua New Guinea. Bovo River arises on the eastern slope of Mt Negrohead (1509 m elevation) with major tributaries from Mount Kupara (1593 m) further to the east (Figs. 1, 2). It is roughly 13 km long, yet despite its brief length it is quite large by the time it reaches the coast, at the town of Arawa, where the study site was situated (6° 115' 1S., 155° 33' E; Grid Reference: 56MQU831105).

The upper catchment of Bovo River consists mostly of montane and lower montane rainforest with occasional clearings for shifting agriculture. Most of the original riparian vegetation along the Bovo River at the study site, in the town of Arawa, has been cleared and replaced with introduced and native species (*e.g. Cocos nucifera, Caesalpinia* sp., *Cassia* sp., *Ficus benghalensis, Artocarpus altilis, Musa* spp., as well as herbs and grasses). Filamentous green algae (*Spirogyra* sp.), and moss grow sparsely on larger boulders. Moss occurs mostly in the splash zone in areas protected from abrasion. Lichen grows on the largest boulders above the water line.

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, (Table 1) is extremely unstable. The river has large accumulations of rubbish, washed in from the adjacent streets and left by the numerous people who use the river for washing (clothes, cooking utensils and themselves), swimming and fishing.- The relatively high pH recorded in the Bovo River (Table 1) is also reflected in the high level of alkalinity and is typical of a coastal river. Despite the proximity to the sea (< 2 km downstream), conductivity was quite low, indicating negligible estuarine influence at this point. The turbidity was quite high. Again this is typical of coastal rivers and it was influenced by town drainage and bank disturbance, but much higher levels were evident when the river was in spate.

The climate of Bougainville Island is tropical and very equable throughout the year with regard to temperature, rainfall and humidity (Fig. 3). Rainfall is high and tends to fall mainly in intense cloudbursts throughout the year in contrast to the more predictable monsoons of the wet-dry tropics. Consequently the rivers and streams are characterized by extreme short-term variability in flow. The Bovo is subject to sudden, intense spates since it receives very high runoffs from its very wet mountain catchment. The weather at the coast at Arawa, is relatively drier, warmer and less

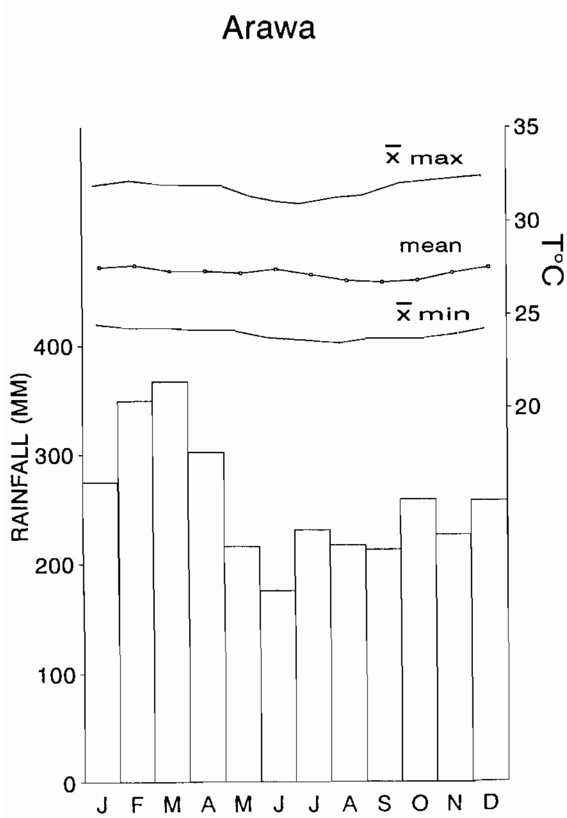


Fig. 3. Mean monthly rainfall and temperature at Arawa (1958 – 1989).

predictable than in the mountains (Table 1). Photoperiod on Bougainville changes little throughout the year as the annual variation in day length is only 36 minutes.

Methods

The Bovo River was sampled monthly on 11 occasions between May 1988 and April 1989 (except for January 1989). Quantitative sampling was not possible because of the large size of the boulders which dominated its substrate and also the extremely rapid flow rate (children are often drowned in the Bovo). Two qualitative kick samples for approximately 5 min. each were taken using an F.B.A. net (175 μm mesh) each month. Samples were preserved in 70% alcohol and sorted under an Olympus SZH stereomicroscope at a magnification of 20X. Adults were collected by sweeping the riparian vegetation and also by light trapping approximately 300 metres from the river.

Only two species of insects from the Bovo River, the mayflies *Prosopistoma sedlaceki* and *Caenodes* sp., were collected in sufficiently large numbers to enable life cycle studies. Although the chironomid *Rheocricotopus* sp. was also very common, discrimination of the early instars proved too difficult. The gastropods, *Neritina* sp. and *Neritilia rubida* were also abundant but the large specimens were not sampled; suffice to say that specimens of all sizes were continually present in the river. The head capsule widths of all the prosopistomatids and 50 *Caenodes* larvae in each monthly collection were measured using an ocular micrometer of 0.015 mm units at a magnification of 64X.

The data were analysed to determine whether there was any seasonal change exhibited by the Bovo invertebrate community with respect to the species present and the relative abundance of each taxon in each monthly sample. The relative abundances of the taxa present each month were compared by determining Spearman's rank correlation coefficient (Elliott 1977: $r_s = 1 - 6\Sigma d^2/n(n^2 -1)$, where d = the difference between each pair of ranked values and n = the number of taxa) between each pair of months, that is between May and every other month, between June and every other month and so on. The monthly samples were also compared on the basis of their similarity with respect to species composition using Sorensen's Index of Similarity (Hellawell 1978:- $S = 2C(A + B)^{-1}$ where A and B are the number of species each month and C is the number of species common to both months).

The dietary habits of several specimens of each of the most abundant species, were determined by means of gut analysis, study of the mouthparts and *in situ* observations of feeding behaviour. Specimens of all the common species were examined from each of the monthly samples in order to detect any possible seasonal change in the diets. Where possible, specimens of different instars/ sizes were examined for each species to determine whether a dietary shift occurred (*e.g.* from collector-gatherer to predator) with increasing size. Specimens of

Table 1. Physical characteristics of the study site.

SUBSTRATE

Type Diameter	Boulders (0.25–3m)	Cobbles (0.06–0.25m)	Pebbles (4–60mm)	Sand (<4mm)
% of stream bed	50%	20%	20%	10%

WATER CHEMISTRY Results of a single sample

pH	Alkalinity as CaCO	Conductivity μS	Turbidity NTU	SO 2 (mg/l)	Cl (mg/l)
7.93	53*	83	28.4	14	1.5

* 1.24 ml of 0.025N HCl to pH 4.3

CLIMATE (recorded at Arawa; 1953–1990)

Mean daily Air temperature °C	Max. recorded Air temp. °C	Min. recorded Air temp. °C	Water temp. °C	Mean annual rainfall (mm)	Average humidity	Mean rain days/month	Av. sunshine hours/day
26.7–27.6	38.5	18.1	24–26	3093.7	72–81%	16–21	4.1–5.5

some species were sent away for taxonomic study and so were unavailable for dietary analysis.

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 compound microscope at magnifications of X200 and X400. Eight 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. The presence of fungal hyphae indicated that this matter was probably mostly dead and decaying when ingested.
3. Fungal hyphae and conidia.
4. Vascular plant tissue – mostly grass. Given the absence of fungal hyphae this was probably live material growing partially submerged along the river banks.
5. Wood.
6. Diatoms. A variety of species were occasionally observed.
7. Filamentous green algae.
8. Animals or parts thereof.

Mineral particles were common in the guts of animals which scraped organic matter from rocks, filtered the water column or gathered detritus from substrate surfaces. 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. It is possible that rare food items were over-estimated. The animals were assigned to functional feeding groups, *i.e.* predators, shredders, scrapers, collector-gatherers and collector-filterers (Merritt and Cummins 1984) depending on their gut contents (and also their method of feeding determined by field and laboratory observations and examination of mouthparts). Taxa with mixed diets, and those which underwent a dietary shift with increasing size, were allocated to all the appropriate functional feeding groups. Where analysis required enumeration, the relative abundance of specimens in each functional group was determined. For species common to both Konaiano Creek and Bovo River, results from a more intensive study of Konaiano Creek (Yule 1993 and in prep.) were used to corroborate the Bovo data, particularly when few specimens were available from the Bovo.

Results

A. Composition of the Fauna

About 10,000 invertebrates, in approximately 70 taxa (only 12 of which were identified to species), were collected from the Bovo River (Appendix). A wide variety of fish were frequently caught in the kick net and also caught by local anglers, but these were not studied. Gastropods and prawns (the latter poorly sampled with the kick net) were diverse and abundant and dominated the invertebrate community at the study site in terms of biomass, yet were absent from its mountain catchment streams. An undescribed mayfly, *Caenodes* sp., was the most common invertebrate, with over 4000 specimens collected. It is the first record of *Caenodes* from the Solomon Island chain (W. Peters pers.comm.). Apart from the Gastropoda and Decapoda (which are of marine origin) only one of the invertebrates found in the Bovo River had been described before (*Prosopistoma sedlaceki*) and many of the species appear to be unique to Bougainville Island.

The young volcanic mountains of Bougainville are very steep sided (Fig. 2) thus the middle reaches of the Bovo River are extremely torrential and the boulder strewn substrate is very unstable. No benthic invertebrates were found in this region although the higher mountain headwater streams supported a diverse and abundant fauna (Yule 1993). The animals of marine origin, such as fish, prawns, and gastropods, inhabited the lower reaches of the Bovo but appeared unable to colonize the mountain headwater streams owing to the impassable nature of the middle stretches. Forty invertebrate taxa, all insects with flying adult stages, were collected from both the coastal river and the headwater streams.

B. Life Cycles

The relative abundances of the fauna (Fig. 4) and species composition was very stable from month to month. The major differences between the months were due to the presence or absence of rarer taxa. Spearman's rank correlation coefficients between each of the monthly samples ranged from 0.953 (between the September and October samples) to 0.98 (between June and December and between November and April), showing a very highly significant ($p < 0.001$) similarity in relative abundance of the taxa. Sorensen's Coefficient of Similarity were determined between each pair of months and also showed high similarity between the months. The mean coefficient for all the months was 0.65 with a range of 0.51, between the June and August samples, and 0.87, between the November and February samples (where 0 = no taxa in common and 1 = identical faunal composition).

Caenodes sp.

Caenodes sp., a caenid mayfly, was very abundant in the Bovo River. Nymphs of all stages of development were present in every sample collected and adults were often collected in a light trap situated several hundred metres from the river (Fig. 5a). The life cycle is clearly aseasonal and development would certainly be very rapid given its tiny size and the high temperatures in the Bovo. Marchant (1982) studied another caenid, *Tasmanocaenis* sp. from billabongs along Magela Creek in the Northern Territory of Australia. This much larger species (mean length 40% greater than *Caenodes* sp.) had a mean life span of about 4 weeks, but at times it may have been as short as 2 weeks.

Prosopistoma sedlaceki

There was no evidence of seasonality exhibited in the life cycle of this prosopistomatid mayfly, with larvae of all size ranges being collected in almost every sample (Fig. 5b). A similar lack of cyclical variation was exhibited by *P.sedlaceki* in Konaiano Creek, near the headwaters of the Bovo (Yule 1993, Yule and Pearson in prep.). This small mayfly is

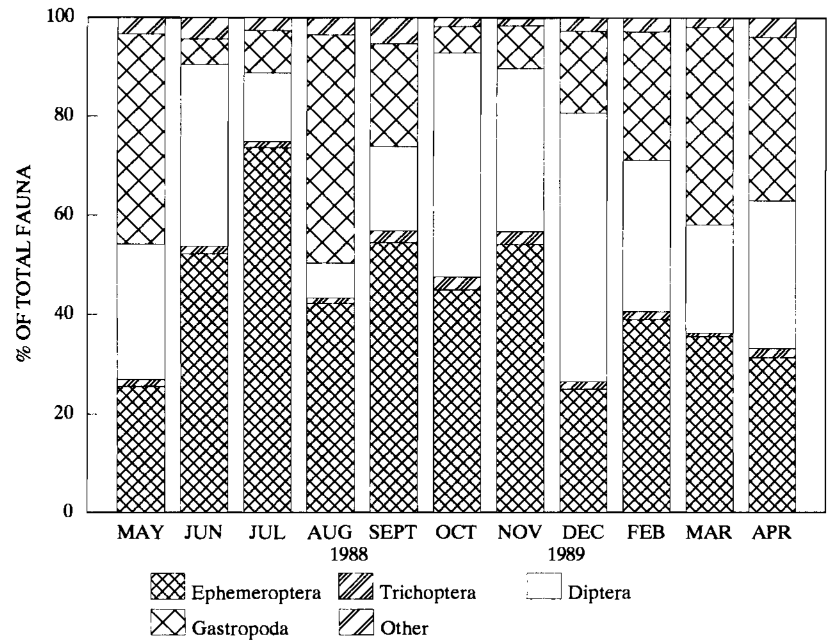


Fig. 4. Relative abundances of the major invertebrate groups recorded from the Bovo River during the sampling period.

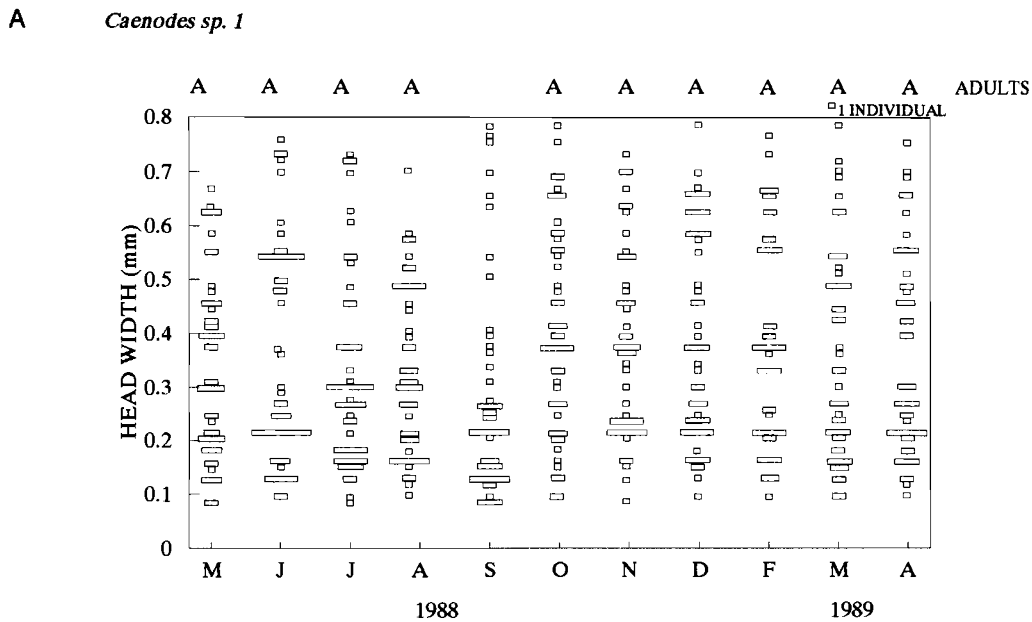
almost certainly multivoltine with continuous hatching and emergence.

C. Dietary Habits

The gut contents of most of the Bovo River invertebrates are listed in Table 2, and their allocation to functional feeding groups is depicted in Figure 6. Dietary shifts with increasing size were exhibited by many species, particularly the predators. The most common carnivorous invertebrate in the Bovo is the small prosopistomatid, *Prosopistoma sedlaceki.* Guts contained a range of animals, particularly chironomids as well as simuliids, baetid mayflies, and other unidentified insects. Early instar prosopistomatids consumed FPOM, with an increasingly carnivorous diet from about the fourth instar upwards. All the odonatans in the Bovo River are carnivores, although early instars of all the species consume FPOM. Aeshnidae sp. 1 eats chironomids, mayflies, simuliids, ostracods and oligochaetes. Corduliids eat large numbers of the mayfly *Caenodes* sp.. The few coenagrionids available for study were found to contain ostracods and mayflies.

A dietary shift was also seen in the leptophlebiid *Barba* sp. 1 which is a collector-gatherer in its early instars consuming mostly CPOM with some FPOM and fungal hyphae. Late instars also shred woody material and leaves. The common caenid, *Caenodes* sp. consumes mostly FPOM, together with fungal hyphae, but larger specimens occasionally eat small amounts of CPOM. The first four instars of the collector- filterer *Chimarra* sp. 1, a philopotamid, only contained FPOM, while final instars also consumed small amounts of fungal spores, pollen grains and diatoms.

The two hydropsychids are both collector-filterers, consuming mostly CPOM (particularly leaf fragments), as well as FPOM, fungal hyphae, pollen grains, insect eggs and fern spores. Leptoceridae nr *Triaenodes* sp. 2 shreds leaves. No fungal hyphae were seen, indicating that the material consumed was fresh. 'Leptocerid' sp. 3 is a predator. Larval guts contained chironomids and unidentified insect remains. *Anisocentropus* shredded leaves such as grass or small pieces of



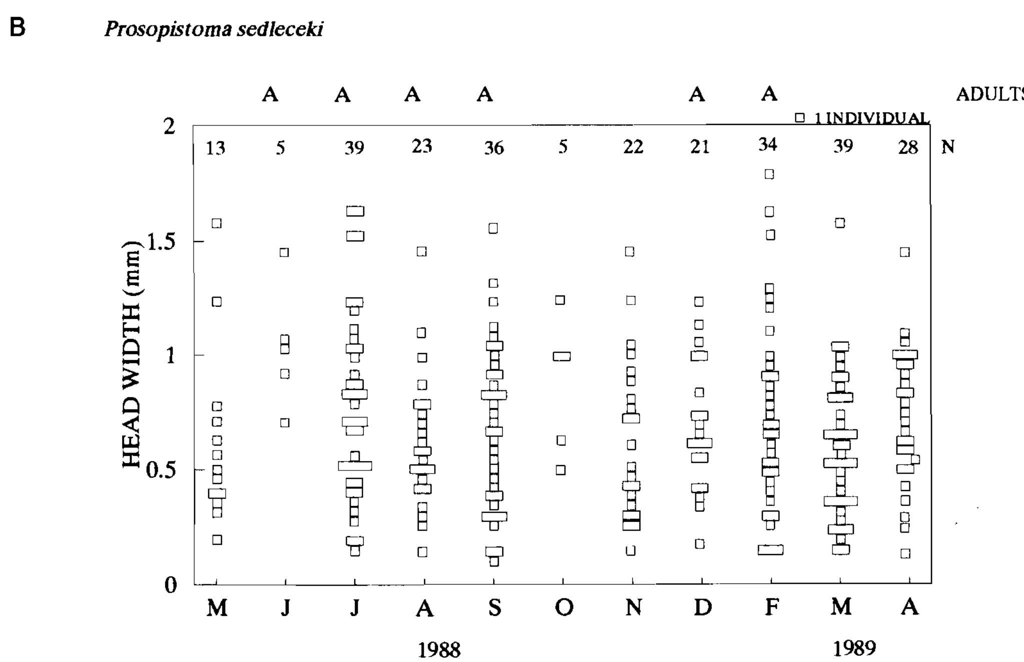


Fig. 5A. Caenodes sp. Monthly larval size distributions (N = 450).
Fig. 5B. Prosopistoma sedlaceki. Monthly larval size distributions.

wood. Some of the guts of the tiny hydroptilid larvae, *Orthotrichia* sp. 2, contained FPOM; however, mostly they had unidentifiable gut contents. Wells (1985) reports Australian *Orthotrichia* larvae 'graze' upon insect egg masses on the undersurfaces of rocks. It is likely that invertebrate eggs also form an important part of the diet of this Bougainvillean species. The hemipteran, Veliidae sp. 1 has piercing-sucking mouthparts. The gut contents were unidentifiable apart from occasional setae and bristles, but appeared to be animal in origin.

Tipulidae sp. 2 is a shredder. Individual larvae in Konaiano Creek usually contained leaf fragments from a single species (Yule 1993). Fungal hyphae were rare and thus the material consumed was presumably fresh. Most of the chironomids consume FPOM, collected either by gathering or filtering, however, *Stenochironomus* sp., shredded grass, while *Rheocricotopus* and nr *Glyptotendipes* occasionally ate filamentous green algae.

The most abundant gastropod in the Bovo River, *Neritina* sp. had a very varied diet, consuming filamentous green algae, diatoms, fungi, grass and other vascular plant material, FPOM and CPOM. This snail can thus function as a shredder, a scraper-grazer and a collector-gatherer. The radula in this species has three kinds of teeth: fine brush-like outer teeth which could be used to collect fine detritus; sharp inner rows which could shred leaves; and stubby middle teeth which could scrape algae from rocks. *Neritilia rubida* is the second most common species. It uses its fine-toothed, brush-like radula for collecting fine detritus – FPOM, fungal hyphae and mineral particles. It is a collector-gatherer. The third species examined, *Melanoides lutosa* is a scraper-grazer, eating filamentous green algae, diatoms, FPOM and CPOM which it consumes from the surfaces of the boulders and cobbles where it lives. All the large prawns collected in the Bovo River were sent away for identification and so were unavailable for gut analysis. Smaller specimens all contained FPOM and occasionally fungal hyphae and mineral particles. They appear to be collector-filterers.

D. Trophic Structure

The Bovo fauna is mostly made up of collector-gatherers (74%), followed by grazer-scrapers (15%), shredders (5%), collector- filterers (3%) and predators (3%) (Figs. 6 and 7). A diagram of the major trophic pathways in the Bovo is given in Figure 6. Fish species would almost certainly occupy several of the functional feeding groups and would probably exert their greatest impact through predation and through grazing of the filamentous algae. The fish would certainly form an extra trophic level by preying upon the carnivorous invertebrates, while the top predators, forming yet another trophic level, were humans who consumed both fish and prawns. The composition of the benthic invertebrate fauna, with respect to functional feeding groups, exhibited very little change from month to month (Fig. 7) apart from an increase in the proportion of grazer-scrapers in August 1988.

Discussion

The invertebrate fauna of the Bovo River consists of many undescribed species of insects (mostly collector-gatherers) and previously described decapods and gastropods of marine origin. Studies by Yule (1993 and in press) of Konaiano Creek, a small mountain stream close to the headwaters of the Bovo, revealed a very different fauna, lacking the groups of marine origin (including fish) and dominated by filter-feeding simuliids and hydropsychids. Yule (in press) hypothesized that species lacking a flying stage or unable to crawl terrestrially (such as crabs) were unable to colonize high mountain streams because of the torrential, barren nature of the mid-mountain streams which sharply divide the headwater streams from the lowland rivers on Bougainville Island.

Community structure and insect life cycles in the Bovo exhibited no pattern of seasonal change. There was continuous hatching, growth and insect emergence which parallel the results from Konaiano Creek where the 15 species examined all had flexible non-seasonal life cycles (Yule 1993, Yule and Pearson in prep.). Apart from Konaiano

Table 2. Analyses of potential food items in gut contents of the invertebrate fauna.

	MEAN % OF GUT CONTENTS									
	FPOM	CPOM	Leaf Litter	Fungi	Diatoms	Algae	Wood	Grass	Animals	No. of specimens
EPHEMEROPTERA										
Caenodes sp 1	96	3		1						15
Prosopistoma sedlaceki	13.5			0.5					86	16
'Pseudocloeon' sp 1	90	9		1						10
Baetis sp 3	50	47	2		1					1
Barba sp 1	21	40	25.5	1.2		0.3	12			5
ODONATA										
Corduliidae sp 1									100	5
Aeshnidae sp 1									100	5
Coenagrionidae sp 1									100	2
TRICHOPTERA										
Hydropsychinae sp 1	24	70		1						10
Hydropsychinae sp 2	38	60		2						10
Chimarra sp 1	99			0.5	0.5					10
Leptoceridae sp 2			100							2
Leptoceridae sp 3									100	5
Anisocentropus sp			71	0.7			28.3			9
Polycentropodidae sp 2	100									10
Orthotrichia sp 2									100	5
DIPTERA										
Ablabesmyia sp	99			1						5
Polypedilum sp	99			1						10
Stenochironomus sp								100		10
nr Pedionomus sp	100									10
Rheocricotopus sp	79			1		20				5
nr Glyptotendipes sp	49			1		50				5
Corynoneura sp	100									5
nr Paraphaenocladius sp	99			1						3
Empididae sp 1	100									5
Simuliidae sp 3	59	40		1						10
Psychodidae sp 1	98			2						1
Psychodidae sp 6	100									2
Tipulidae sp 2			100							1
HEMIPTERA										
Veliidae sp 1									100	3
LEPIDOPTERA										
Pyralidae sp 1	60			5	35					2
GASTROPODA										
Neritina sp	46	2.5		0.5	3.25	2.5		45.25		8
Neritilia rubida	80			20						6
Melanoides lutosa	58	7		1	0.3	27.3		6.4		5
DECAPODA										
spp	98			2						12
OLIGOCHAETA										
Tubificidae sp 1	100									5
Enchytraeidae sp 1	79	20		1						5
nr Pristinella sp	100									5

Creek, the author knows of no other stream recorded in the literature totally lacking species with life cycles showing some cyclic pattern. The climate of Bougainville Island is aseasonal: mean monthly temperatures fluctuate less than daily temperatures and rainfall is continuously high throughout the year, while proximity to the equator decreases variation in photoperiod. Consequently there is a lack of environmental cues to engender synchronization of life history stages. It was further hypothesized (Yule 1993, Yule and Pearson in prep.) that the occurrence of very frequent but unpredictable spates would promote asynchrony of life cycles so that, should the spates be catastrophic, at least some members of a population of a species would survive.

The trophic ecology of the Bovo River is similar to its temperate lowland counterparts in that a large proportion of the energy is derived from autochthonous production by algae and diatoms and it has a reduced reliance upon allochthonous detritus (Vannote *et al.* 1980, Minshall *et al.* 1985), although the results must be interpreted with some caution because instream production and assimilation of digestive contents were not examined. The Bovo has a broad range of energy inputs with the presence of partially submerged grasses and other vegetation along the banks, abundant growths of filamentous green algae and large quantities of human organic rubbish, particularly food scraps and sewage (Fig. 6). Although human waste does enter the river, the fast flow and mainly organic nature of the refuse mean that such pollution appears not to have an adverse effect on the fauna. It seems likely that the invertebrate community is strongly influenced by competition with, and predation by fish. A thorough understanding of trophic relationships in the Bovo cannot be accomplished without a study of the fish fauna which is large and diverse.

The trophic structure of the Bovo River fits the predictions of the River Continuum Concept (Vannote *et. al* 1980) with regard to the relative proportions of the functional feeding groups in a lowland river with its large proportions of collector-gatherers (74%) and grazer-scrapers (14%). Thus even though the Bovo is not a typical lowland river with regard to substrate and flow, the trophic ecology is governed by the energy inputs. Dudgeon (1984, 1992) also found that functional group representation along the lower reaches of a Hong Kong River (in the wet-dry tropics) generally followed those predicted by the River Continuum Concept. It would be useful to study changes in functional organization of the fauna of a river on Bougainville Island along its entire length, particularly since the functional organization of Konaiano Creek diverges markedly from that typified in the River Continuum Concept as it is heavily dominated by filter feeders and has very few shredders (Yule 1993 and in prep.).

The trophic relationships of benthic invertebrates within Bovo River exhibited no temporal change apart from minor changes in species composition with respect to less abundant taxa. The lack of seasonal change in the functional feeding groups between the monthly samples indicates that there was no seasonal change of energy supply such as often occurs in temperate streams where there may be seasonal input of leaf litter or seasonal algal blooms.

Further studies of Bougainvillean rivers and streams are clearly warranted. The aseasonal climate provides ideal conditions for testing hypotheses in the absence of variations imposed by seasonal change. Many of the high crater lakes and mountain streams are still pristine and the freshwater invertebrate fauna is largely unsurveyed and undescribed. It is to be hoped that peace will soon return to the island and that scientific studies may be resumed.

Acknowledgements

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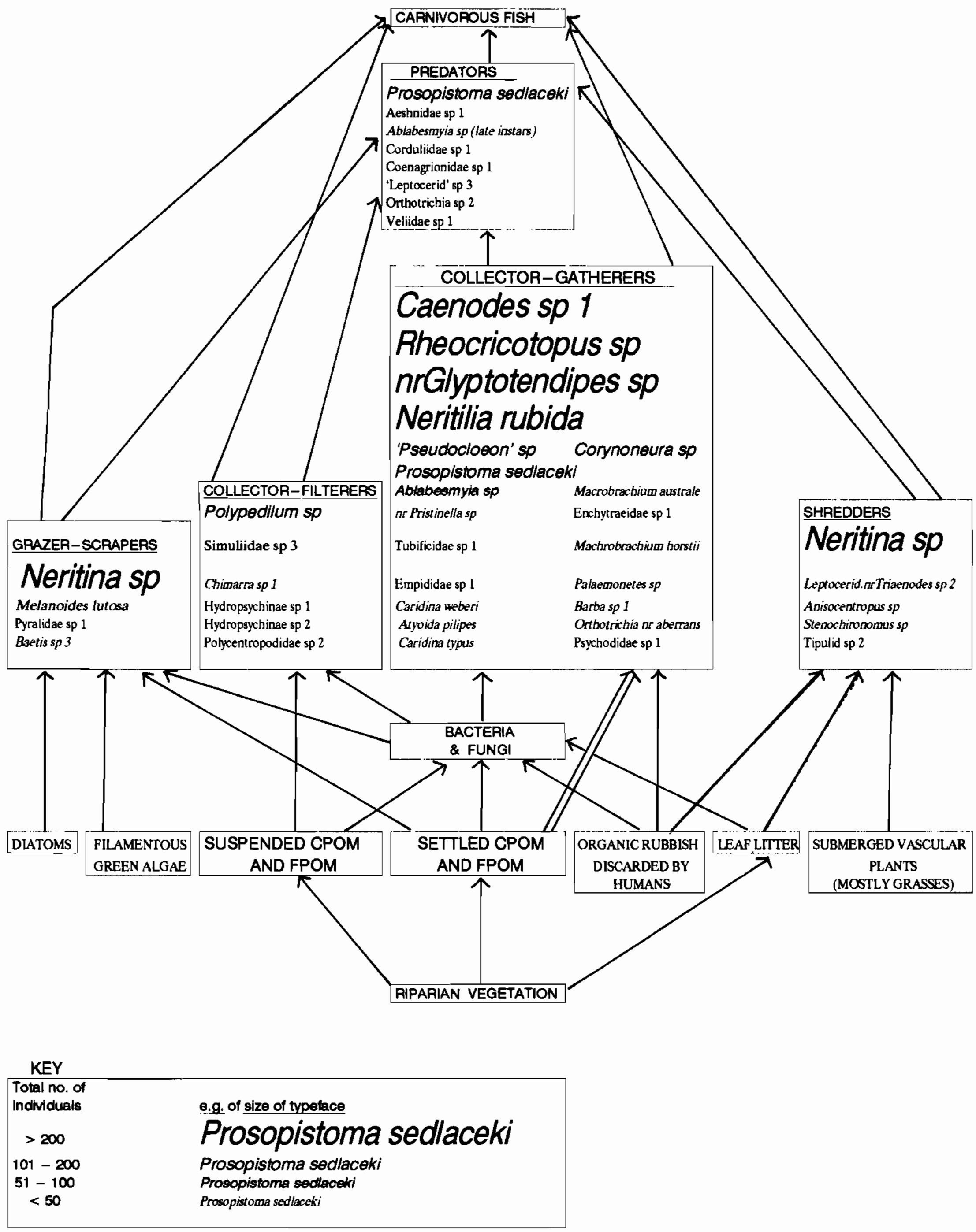
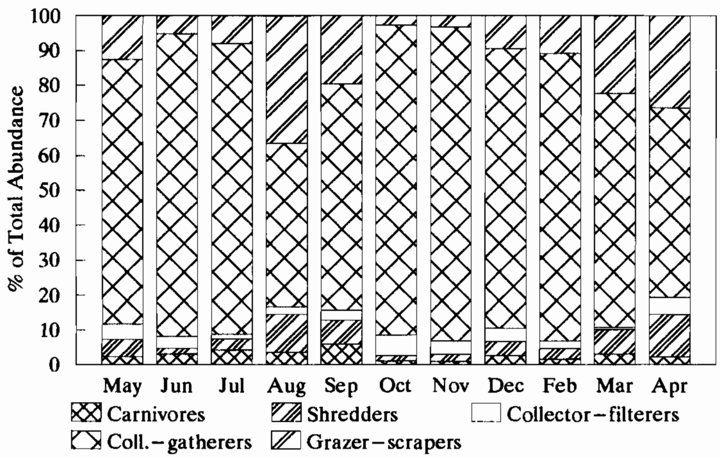


Fig. 6. Major trophic pathways in the Bovo River. N.B. All functional feeding groups contribute to settled and suspended CPOM and FPOM through defecation and death. The role of bacteria and fungi is assumed.

A.



B.

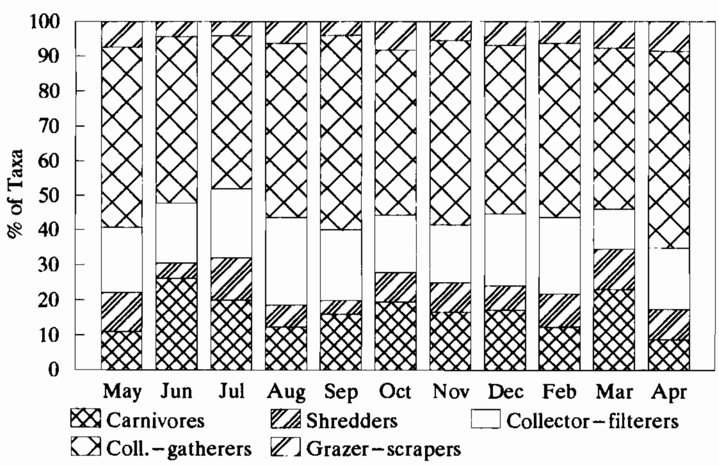


Fig. 7A Monthly variation in the composition of the benthic invertebrate community with respect to the proportion of the total number of individuals in each of the functional feeding groups.

Fig. 7B. Monthly variation in the composition of the benthic invertebrate community with respect to the proportion of the taxa in each of the functional feeding groups.

(James Cook University), Arturs Neboiss, John Dean and David Cartwright (Melbourne and Metropolitan Board of Works). Ephemeroptera – Bill Peters and R.W. Flowers (Florida A & M University, U.S.A.). Simuliidae – Roger Crosskey (British Museum Natural History). Decapoda – L.B. Holthuis (Natuurhistorisch Museum, Leiden, The Netherlands). Meteorological data were obtained from the Hydrology Section, Bougainville Copper Limited. This research was supported by a Gordon Lewis Fellowship, for which I am very grateful.

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APPENDIX

List of species recorded from Bovo River.

Mean, average of total monthly abundance; s.e., average of monthly s.e.; C.V., coefficient of variation of monthly means.

			MEAN	S.E.	C.V.(%)
EPHEMEROPTERA	Caenidae	*Caenodes sp 1*	378.45	105.67	88.29
	Prosopistomatidae	*Prosopistoma sedlaceki*	22.64	3.79	52.92
	Baetidae	*'Pseudocloeon' sp 1*	8.91	1.89	66.91
		Baetis sp 3	0.09	0.09	316.23
	Leptophlebiidae	*Barba sp 1*	0.71	0.33	144.22
ODONATA	Corduliidae	sp 1	0.91	0.31	109.54
	Aeshnidae	sp 1	3.27	0.81	78.27
	Coenagrionidae	sp 1	0.18	0.12	212.13
TRICHOPTERA	Hydropsychidae	Hydropsychinae sp 1	3.27	1.75	169.42
		Hydropsychinae sp 2	2.91	1.32	143.95
	Philopotamidae	*Chimarra sp 1*	3.73	1.47	124.32
	Leptoceridae	sp 2	0.27	0.14	163.30
		sp 3	0.82	0.26	101.84
		sp 3 pupae	0.09	0.09	316.23
	Calamoceratidae	*Anisocentropus sp 1*	1.64	0.53	101.84
	Polycentropodidae	sp 2	3.73	1.38	116.72
	Hydroptilidae	*Orthotrichia sp. aberrans gp*	0.09	0.09	316.23
		Orthotrichia sp 2	0.73	0.27	118.59
DIPTERA	Chironomidae	Unidentified larvae	27.91	7.16	81.13
		Unidentified pupae	5.55	1.68	95.53
	Tanypodinae	*Ablabesmyia sp 1*	4.82	1.23	80.54
	Chironominae	*Polypedilum sp 1*	11.36	4.86	135.31
		Stenochironomus sp 1	1.73	1:10	200.69
		nr Pedionomus sp 1	0.91	0.51	178.33
	Orthocladinae	*Rheocricotopus sp 1*	179.45	58.46	103.00
		nr Glyptotendipes sp 1	38.91	11.17	90.74
		Corynoneura sp 1	11.09	4.61	131.31
		nr Paraphaenocladius sp 1	0.63	0.31	158.75
	Empididae	sp 1	1.64	0.68	131.00
	Simuliidae	sp 3	5.55	1.28	73.09
		sp 3 pupae	0.36	0.20	176.78
	Ceratopogonidae	sp 5	0.09	0.09	316.23
	Psychodidae	sp 1	0.09	0.09	316.23
		sp 6	0.18	0.12	212.13
		sp 7	0.18	0.12	212.13
		sp 8	0.45	0.37	254.56
	Canaceidae	sp 1	0.09	0.09	316.23
	Tipulidae	sp 2	0.09	0.09	316.23
		sp 9	0.18	0.12	212.13
		pupae sp a	0.18	0.12	212.13
		Unident. larvae sp 9	0.18	0.12	212.13
		Unident.pupae sp 5	0.18	0.12	212.13
		Unident.pupae sp 14	0.09	0.09	316.23
COLEOPTERA	Hydraenidae	adults sp 1	0.09	0.09	316.23
		Unident. larvae sp 10	0.27	0.19	226.08
		Unident. larvae sp 3	0.09	0.09	316.23
HEMIPTERA	Veliidae	sp 1	0.27	0.27	316.23

APPENDIX (CONT.)

			MEAN	S.E.	C.V.(%)
LEPIDOPTERA	Pyralidae	sp 1	0.18	0.18	316.23
HYDRACARINA	Hygrobatidae	*Australiobates sp. 1*	0.36	0.15	132.29
		Axonopsella sp. 1	1.64	0.41	79.35
	Oribatidae	spp	0.45	0.28	195.96
	Mesostigmata	spp	0.55	0.25	143.37
		Unidentified sp 5	0.09	0.09	316.23
GASTROPODA	Neritidae	*Neritina sp 1*	95.09	19.57	65.09
		Neritilia rubida	72.73	24.77	107.68
	Thiaridae	*Thiara scabra*	0.18	0.12	212.13
		Melanoides lutosa	3.45	1.31	119.90
	Septariidae	*Septaria macrocephala*	1.00	0.65	204.49
	Assimineidae	*Assiminea crosseana*	0.09	0.09	316.23
	Hydrobiidae	*Fluviopupa pupoidea*	0.27	0.19	226.08
DECAPODA	Atyidae	*Atyoida pilipes*	1.91	0.64	105.84
		Caridina typus	1.36	0.49	113.92
		C.weberi	2.36	0.58	77.12
	Palaemonidae	*Macrobrachium australe*	1.36	0.45	104.99
		M. horstii	0.64	0.24	121.22
		Palaemonetes sp 1	0.82	0.82	316.23
	Ostracoda	spp	0.36	0.15	132.29
	Copepoda	spp	0.27	0.14	163.30
HIRUDINEA		sp 1	0.64	0.24	121.22
OLIGOCHAETA	Tubificidae	sp 1	1.73	0.56	102.06
	Enchytraeidae	sp 1	1.18	0.35	94.21
	Naididae	*nr Pristinella sp 1*	2.09	0.87	131.30
NEMATODA		spp	0.27	0.14	163.30