SPATIO-TEMPORAL VARIATIONS IN MACROINVERTEBRATE ASSEMBLAGES OF NEW CALEDONIAN STREAMS.

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ABSTRACT

Forty-one sites located on 14 New Caledonian streams were surveyed four times between October 1996 and October 1997 in order to examine the spatial and temporal changes in the structure of the benthic macroinvertebrate communities. About 250 000 invertebrates representing 167 taxa were collected in the streams. Seventy-five percent of identified taxa and 67% of individuals were insects. Major spatial and temporal changes in the composition of the fauna were detected by multivariate analyses (ordination and classification). Overall, the number of individuals was significantly higher in the dry season (October) than in the wetter seasons (January and June). However, a low temporal variability was detected in the structure of benthic communities during the sampling period. A cluster analysis based on taxonomic composition separated five groups of sites in relation with rock type, land use, and geographic characteristics. Several metrics (total invertebrate density, taxon richness, relative abundance of major invertebrate groups, diversity indices) were used to characterize each group of sites. Forested streams, where the highest specific diversity occurred, represented the most speciose habitat for benthic fauna. A less rich and abundant fauna occurred in streams draining ultramafic rocks probably because of their low content in food resources and organic matter.

Key-words : benthic macroinvertebrates, New Caledonia, tropical streams, biodiversity, spatial and temporal variability.

VARIABILITÉ SPATIO-TEMPORELLE DE LA STRUCTURE DES COMMUNAUTÉS DE MACROINVERTÉBRÉS BENTHIQUES DANS LES RIVIÈRES DE LA NOUVELLE-CALÉDONIE.

RÉSUMÉ

Quarante et une stations situées sur 14 cours d'eau répartis sur l'ensemble de la Nouvelle-Calédonie furent périodiquement échantillonnées entre octobre 1996 et octobre 1997. Des analyses multivariées (ordination et classification) permirent d'étudier la variabilité spatio-temporelle de la structure des communautés benthiques. Environ 250 000 invertébrés représentant 167 taxons furent prélevés durant l'étude. Soixante quinze pour cent des taxons identifiés et 67 % des individus prélevés furent des insectes.

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Dans l'ensemble, les densités faunistiques furent significativement plus importantes à l'étiage (octobre) qu'aux autres périodes d'échantillonnage (janvier et juin). Cependant, une faible variabilité temporelle de la structure des peuplements benthiques fut mise en évidence entre octobre 1996 et 1997. Une biotypologie des stations fondée sur la nature géologique des terrains drainés, l'occupation des sols et la localisation géographique est proposée. Plusieurs indices (densité totale, richesse taxonomique, abondance relative des principaux groupes faunistiques, indices de diversité) permettent de caractériser les communautés benthiques des groupes de sites. Les milieux les plus favorables au développement de la macrofaune benthique et qui présentent la diversité spécifique maximale sont les ruisseaux forestiers. Les cours d'eau drainant des péridotites altérées se caractérisent par des peuplements moins abondants et moins diversifiés, probablement en raison de leurs faibles ressources trophiques et de leur contenu en matières organiques peu élevé.

Mots-clés : macroinvertébrés benthiques, Nouvelle-Calédonie, cours d'eau tropicaux, biodiversité, variations spatio-temporelles.

INTRODUCTION

Although benthic invertebrates are numerically important components of lotic ecosystems and represent indicators of environmental degradation, the freshwater invertebrate fauna of South Pacific islands remains largely unknown and undescribed. In New Caledonia, data on freshwater macroinvertebrates is also limited. Available information is derived mostly from the scientific expeditions conducted by SARASIN and ROUX (1913-1926), the Osaka Museum (SATÔ, 1966), the University of Vienna (STARMÜHLNER, 1968), and several American institutions (PETERS, 1981). During these expeditions, large numbers of aquatic insects were collected in both immature and adult stages, and sent to various specialists throughout the world for zoogeographical studies. These expeditions have contributed to the advance of taxonomic knowledge of benthic invertebrates and underlined a highly endemic fauna in New Caledonian rivers and streams (PETERS, 1981).

However, the ecology of invertebrate assemblages has received little attention. Actually, only a few studies have examined benthic community structure in the rivers and streams (STARMÜLHNER, 1968; MARY, 1999; MARY and GAGNEUR, 2000). Information also exists on the distribution of selected groups of molluscs in freshwaters (STARMÜLHNER, 1970; PÖLLABAUER, 1986; HAASE and BOUCHET, 1998). Because of the specificity of New Caledonian aquatic fauna, biological assessment of water quality cannot be made safely by extrapolation from overseas studies. It is therefore important to determine the structure and function of invertebrate communities in order to manage them properly and to preserve local diversity. The aim of this study was to examine, by the means of ordination and classification analyses, the spatial and temporal dynamics of the macroinvertebrate communities in 14 rivers systems located in the main island of New Caledonia.

MATERIAL AND METHODS

Study area

The New Caledonian archipelago (Figure 1) is located in the southeast of the Coral Sea near the Tropic of Capricorn. The archipelago has a subtropical oceanic climate and occupies an area of about 18 500 km^2. Its population is approximately of 200 000 inhabitants. The main island (La Grande Terre) is more than 400 kilometres long and its width seldom exceeds 50 kilometres. A range of high mountains (up to 1 630 m above sea level) divides La Grande Terre into two asymmetrical parts. On the one hand, the east coast, exposed to the wind, gets high rainfall (mean annual precipitation of 2 800 mm) and is characterized by a steep shore. Northeastern streams have particularly steep channel gradients characterized by riffles, cascades, and waterfall features. On the other hand, the west coast is protected from the wind and characterized by a relative dry climate, and plains, which extend over large areas. The average annual rainfall on the west coast is about half (1 300 mm) than that on the steep eastern mountain slopes.

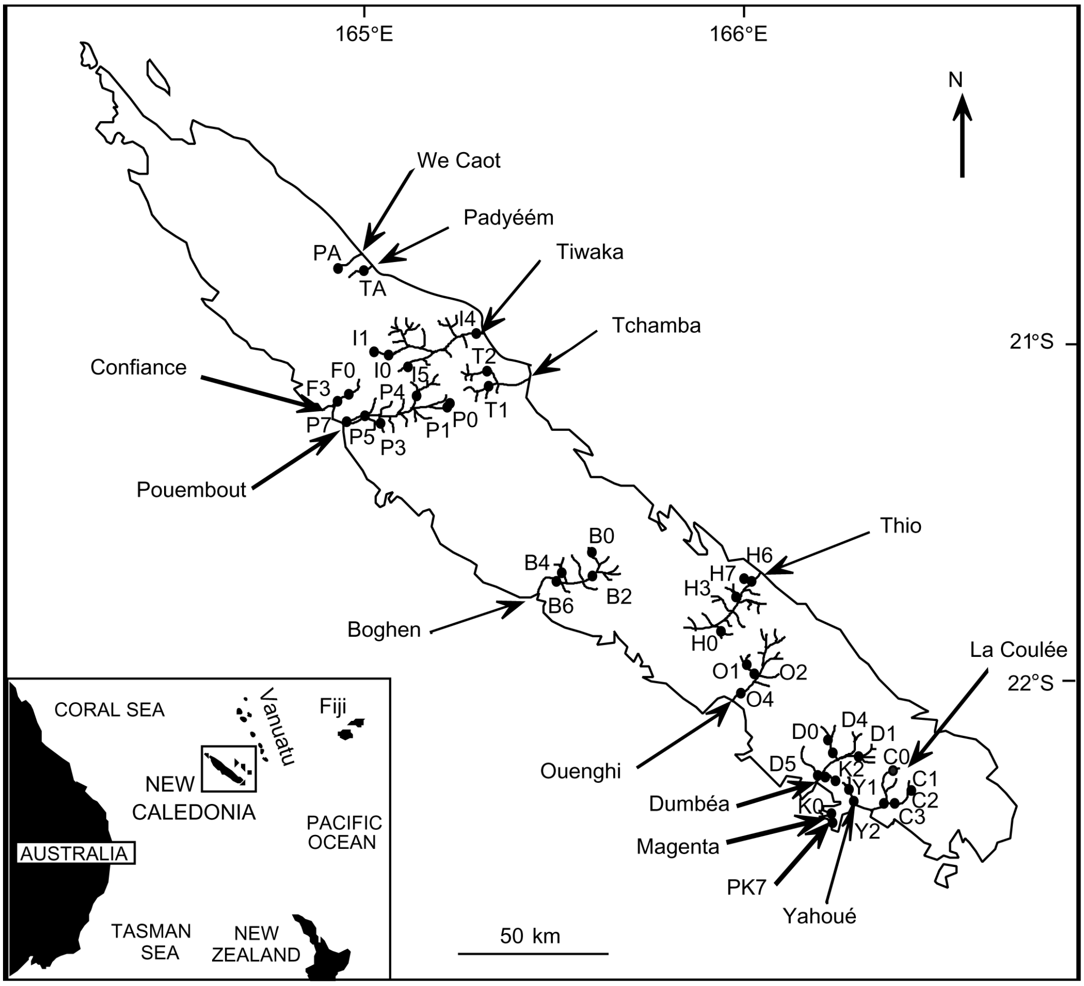

Figure 1
Location of the sampling sites.

Figure 1
Localisation des stations d'étude.

Geologically, the microcontinent of New Caledonia is a « patchwork » of continental terranes and ophiolites formed from Permian to Oligocene (CLUZEL *et al.*, 1994). The main particularity of the geologic evolution is the emplacement of peridotites (ultramafic rocks) in the late Eocene. Peridotites and the laterites that come from peridotite decomposition are rich in metals (mostly iron, nickel and chromium). New Caledonia is the world's third largest producer of nickel. Since 1876, more than 130 million tons of nickel ore have been extracted from ultramafic soils and consequently huge amounts of mine tailings have accumulated. These sterile tailings were dumped into the nearest valleys until 1975 and represented a major pollution to the environment. New techniques are now applied to prevent river and lagoon pollution (PELLETIER, 1990). However, most of the peridotitic lands still show evidence of previous mining activities (erosion, degraded vegetation).

La Grande Terre has a dense hydrographic network. It features many small river systems with short rivers. About 30% of the freshwaters flow on ultramafic rocks, the others on volcanic-sedimentary soils. Water flowing over these substrata is characteristically slightly basic, low in nutrients and dissolved solids, but may have high concentrations of magnesium. New Caledonian streams show low levels of organic pollution, mainly generated by cities (MARY, 1999). The large seasonal fluctuations in precipitation influence the abundance and distribution of the mean annual discharge of freshwaters. In the summer, rainfall from cyclones may cause intense flooding. In contrast, during the dry season, the flow of the streams and rivers may progressively fall, sometimes until they dry up. Generally, the lowest monthly discharges are found in October and November. Precipitation really begins again in December and the highest monthly flows are seen between January and April. The maximum occurs in February or March, according to the river basin geographic position. The flow during this period represents 60 to 70% of the total annual discharge (ORSTOM, 1981).

Streams of the west coast flow through agricultural and pasture lands at the lowest altitudes. The sclerophyll forests, which formerly covered nearly all of the west coast up to 300 m above sea level, have largely disappeared because of numerous fires and clearings. They are nowadays represented only by some isolated fragments, to a total of 350 km^2 (JAFFRÉ *et al.*, 1993). They were replaced by largely widespread savannas of *Melaleuca quinquenervia*, *Psidium guajada* and *Acacia farnesiana* up to 600 m altitude. In the rainiest areas, dense humid forests of *Agathis* sp., *Montrouziera cauliflora* and *Calophylllum neocaledonicum* species often dominate the upper catchments of streams and rivers. Ultramafic rock vegetation consists of heathy formations (« maquis ») represented mainly by *Araucaria* sp., *Agathis ovata* and a large number of endemic species (JAFFRÉ *et al.*, 1994). These climatic, geomorphologic and vegetation features have contributed to a high degree of faunistic endemism within La Grande Terre (CHAZEAU, 1994; HAASE and BOUCHET, 1998).

Study-site selection and sampling protocol

Forty-one sites were chosen in 26 perennial streams and rivers within 14 catchments located on both coasts of La Grande Terre (Figure 1). Sites were selected on the basis of accessibility, proximity to source of pollution, catchment land use, and geological characteristics. The sites represent entire pollution gradients ranging from pristine unimpacted sites to grossly polluted sites (Table I). Most of the unimpacted sites were situated above any major impact point in forested catchments or in relatively unpopulated areas in which pasture, and agriculture are limited. Moderately impacted sites were in areas of diffuse, low intensity, agriculture or rearing, near Melanesian tribes, and/or in area of (previous) mining activities. Severely impacted sites were situated in extensive upstream areas of pasture and agriculture or in Nouméa, where they are subject to large volumes of organic waste (sites M7, MG and Y2).

Selected sites were sampled four times (in October 1996, January, June and October 1997), except for the three sites (PA, F3, P7) which could not be sampled in October 1996 for technical reasons. It seemed important that each site be sampled several times in one year, at regular intervals, to lessen the chances of taxa being missed. Site elevation, channel slope, and distance from source of sites were determined from map series IGN 1:50 000. Some physico-chemical parameters were described at site (catchment's land use, riparian vegetation). Conductivity, pH and water temperature were measured with a CheckMate 90 Mettler-Toledo AG MultiMate.

Table I

Description of the 41 study sites and mean values of some physico-chemical characteristics measured from October 1996 to October 1997 (temp: temperature, cond: conductivity).

Tableau I

Caractéristiques mésologiques des 41 stations d'étude et valeurs moyennes de conductivité (cond.), pH et température (temp.) mesurées entre octobre 1996 et octobre 1997.

River basin	Site	Altitude (m)	Distance / source (km)	Stream gradient (%)	Mean temp. (°C)	Mean cond. (μS/cm)	Mean pH	Dominant land use upstream
Boghen	B0	250	3	6	20.0	191	8.1	native forest
	B2	40	20	0.2	24.6	200	7.9	pasture
	B4	110	3	2	23.8	202	8.1	native forest
	B6	15	39	0.07	27.5	221	8.0	pasture, village
Confiance	F0	160	1.25	17	21.6	199	8.1	native forest
	F3	10	3.5	1	22.8	217	8.2	maquis
Coulée	C0	200	2	24	21.7	116	7.9	native forest
	C1	40	3	2	22.1	135	7.9	forest
	C2	10	5	0.75	23.7	146	8.1	maquis, farming
	C3	5	12	0.35	24.4	124	8.0	maquis, farming
Dumbéa	K0	590	0.5	40	19.0	113	7.8	native forest
	K2	40	6	0.6	24.7	129	7.8	forest, farming
	D0	420	0.75	40	22.3	118	7.6	maquis
	D1	150	10.75	1.67	22.3	109	8.0	maquis
	D4	40	12.5	1.3	24.9	160	8.2	maquis, farming
	D5	10	19	0.2	27.2	169	8.2	maquis, farming
Magenta	MG	10	0.5	2	23.6	646	7.4	town
Ouenghi	O1	60	5.5	1	25.3	368	8.0	native forest, pasture
	O2	30	10	0.57	25.3	204	8.2	pasture
	O4	10	23	0.09	26.4	164	8.1	pasture, maquis
PK7	M7	10	1	0.1	22.5	724	7.7	town
We Coat	PA	1360	1.5	52	15.5	26	6.3	native forest
Pouembout	P0	500	0.75	4	18.5	120	7.4	native forest
	P1	490	2	0.8	18.9	149	7.8	native forest
	P3	60	6	1.8	24.6	284	8.5	pasture
	P4	100	20	0.5	25.3	127	7.9	pasture
	P5	40	34	0.13	28.0	180	8.3	pasture
	P7	5	55	0.02	26.8	249	8.1	town
Padyéém	TA	260	4.25	50	22.5	81	7.4	native forest
Tchamba	T1	50	16.5	0.7	25.8	83	8.0	pasture, tribe
	T2	40	4	0.5	27.9	83	7.5	pasture, tribe
Thio	H0	250	2.5	10	22.2	171	8.2	maquis
	H3	40	10.5	0.1	24.8	117	8.1	maquis, tribe
	H6	10	36	0.18	25.8	186	8.2	tribes
	H7	10	6	2	23.8	145	8.0	mining activities
Tiwaka	I0	380	0.5	20	20.8	73	7.5	native forest
	I1	170	7	0.67	23.0	127	8.3	forest, tribe
	I4	5	42	0	25.3	116	7.7	tribes
	I5	300	1.5	4	21.1	137	7.9	native forest
Yahoué	Y1	180	2	28	20.6	66	7.5	native forest
	Y2	15	5.5	1.3	24.9	274	7.5	town

Invertebrate sampling

At each site, the major habitats were sampled in proportion to their occurrence over a 50 to 100 m reach of the stream. Five samples of macroinvertebrates were collected at each site in every season, by means of a « Surber sampler » (0.05 m^2; 250 µm mesh). Individual samples at each site were combined to form one composite sample per season. This total sample comprised an area of 0.25 m^2. Samples were preserved in 5% formaldehyde solution immediately after collection.

Back at the laboratory, macroinvertebrates were sorted from the samples under a stereomicroscope at a magnification of X 40, and preserved in 70% ethanol. Because of the low resolution of taxonomic knowledge for aquatic macroinvertebrates in New Caledonia, particularly for immature insects (most larval-adult associations are unavailable), it was difficult to identify specimens to the species level. The organisms were identified to the lowest practical taxonomic level using available taxonomic keys, publications, and specialist assistance (see acknowledgements). The groups Hydracarina, Ostracoda, Nematoda, Nemertea, Collembola have not been identified to family level and were considered as single taxa. Invertebrate abundances were obtained by counting all individuals in a sample and expressed as number per 0.25 m^2.

Data analysis

All multivariate statistical analyses were performed on Analysis of Data in Ecology software ADE-4 (THIOULOUSE *et al.*, 1997). Species occurring in fewer than 4 samples were considered uncommon and were deleted from the data set, which was reduced to 102 common taxa from a total of 167. Total abundance of each taxon was transformed by Log (x + 1) in order to normalise the data.

Faunistic variables were first organized by between-class PCA so that temporal influence on benthic assemblage structure could be assessed (DOLÉDEC and CHESSEL, 1987; BEFFY and DOLÉDEC, 1991). For this analysis, data were cumulated by date, resulting in a reduced data matrix. All data were then plotted on the PCA diagram to show the fluctuations around the average position of dates. The statistical significance of the between-class PCA was tested with a Monte Carlo permutation test (1 000 permutations).

Secondly, two classification analyses were performed on the faunistic matrix by Ward's method (second order moment criterion method) based on Euclidean distance. The first one allows the detection of site groups on the basis of their taxonomic composition and the second one was performed to obtain taxon associations that better describe the site groups.

Site groups were afterwards characterized by means of univariate procedures, using total abundance, taxon richness, relative abundances of the most dominant groups of invertebrates (Ephemeroptera, Trichoptera, Diptera, and Oligochaeta) and the diversity indices of Shannon Weaver, Margalef, and Simpson. These indices are commonly used in biomonitoring and provide useful ecosystem management tools to assess possible effects of habitat degradation and ecosystem pollution (WASHINGTON, 1984, NORRIS and GEORGES, 1993). Differences in density, taxon richness, and diversity indices of invertebrates among site groups and between seasons were assessed by Kruskall-Wallis one-way analysis of variance by ranks (non-parametric ANOVA) to test the null hypothesis that the average ranks by groups of sites or by season were not significantly different for the variables.

RESULTS

The animals were identified into 167 taxonomic groups. Individuals of all major groups were collected, including Insecta, Gastropoda, Tricladea, Hirudinea, Oligochaeta, and Crustacea. Insecta constituted 67% of the 236 574 sampled invertebrates and 75% of the identified taxa. Diptera (49%), Trichoptera (39%), and Ephemeroptera (10%) accounted for 98% of overall insects collected from all sites. In spite of the large number of taxa present, the benthic community was numerically dominated by a small group of taxa: Oligochaeta Naididae (21% of total invertebrates abundance), Trichoptera Hydropsychidae (15%), Diptera Simuliidae (11%) and Chironomidae Orthocladiinae (7%). The most frequent taxa were the Diptera Chironomidae Orthocladiinae and Tanypodinae (occurring each in 95% of the samples), the Simuliidae (88%), the Coleoptera Hydrophilidae Berosini *N.gen.3* (78%), the Trichoptera Hydropsychidae sp. A1 (70%) and Leptoceridae *Oecetis* spp. (68%), the Ephemeroptera Leptophlebiidae *Paraluma* spp. (65%).

Temporal influence on macroinvertebrate communities

In terms of inertia, 60.1% of the total inertia (PCA) was attributed to the between-site PCA and 5.3% of the total inertia to the between-season PCA. The percentage of the explained variability for F1 and F2 were respectively 79% and 11%, for a total of 90%. Figure 2B shows the position of the sites for all the seasons on the first two axes F1 and F2 of the between-season PCA. Axis F1 of the PCA diagram separated the average positions of dry season (October 1996 and October 1997) from those of the wetter seasons (January and June 1997). However, the 38 sites from each season do not form 4 separate groups, indicating that no general faunal change took place from one season to the other.

The first axis was best explained by the abundance of ubiquitous taxa as Naididae, Hydropsychidae sp. A1, Chironomidae Tanypodiinae, Tanytarsini, Chironomini, and *Rheotanytarsus*, Leptoceridae *Oecetis* and *Triplectides*, Hydroptilidae *Oxyethira* and *Acritoptila*, and Leptophlebiidae *Paraluma cancellata* (Figure 2C). The second axis separates common taxa characteristic of the lower reaches of the less polluted rivers (Chironomidae *Corynoneura*, Leptophlebiidae *Lepeorus*, Hydroptilidae *Caledonotrichia*, *Melanopsis*) from taxa that generally dominated in grossly polluted sites (Chironomidae Orthocladiinae and *Chironomus*, Naididae *Dero*) (pers. obs.).

The mean density of invertebrates differed significantly according to seasons (ANOVA, $p < 0.05$). More individuals were collected in the dry season (69-27 018 animals/0.25 m^2 in October 1996 and 33-30 338 animals/0.25 m^2 in October 1997) than in the wetter periods (50-5 185 animals/0.25 m^2 in January 1997 and 27-2 841 animals/0.25 m^2 in June 1997). The highest benthic densities of the dry season were found in site T1 and were due to mass occurrence of a single taxon (Oligochaeta Naididae). Mean macroinvertebrates densities at the study sites ranged from 523 to 41 233 animals/m^2.

Likewise, the taxon richness of sites differed significantly among sampling periods (ANOVA, $p < 0.05$). Taxon richness was significantly higher in October 1997 (6-50) than in October 1996 (6-43), January 1997 (2-46) and June 1997 (2-38). Considering all the sites, 137 taxa were collected in October 1997 in comparison to 132 in October 1996, 116 in January and 129 in June 1997. Of all the taxa, 96 were found during all sampling periods.

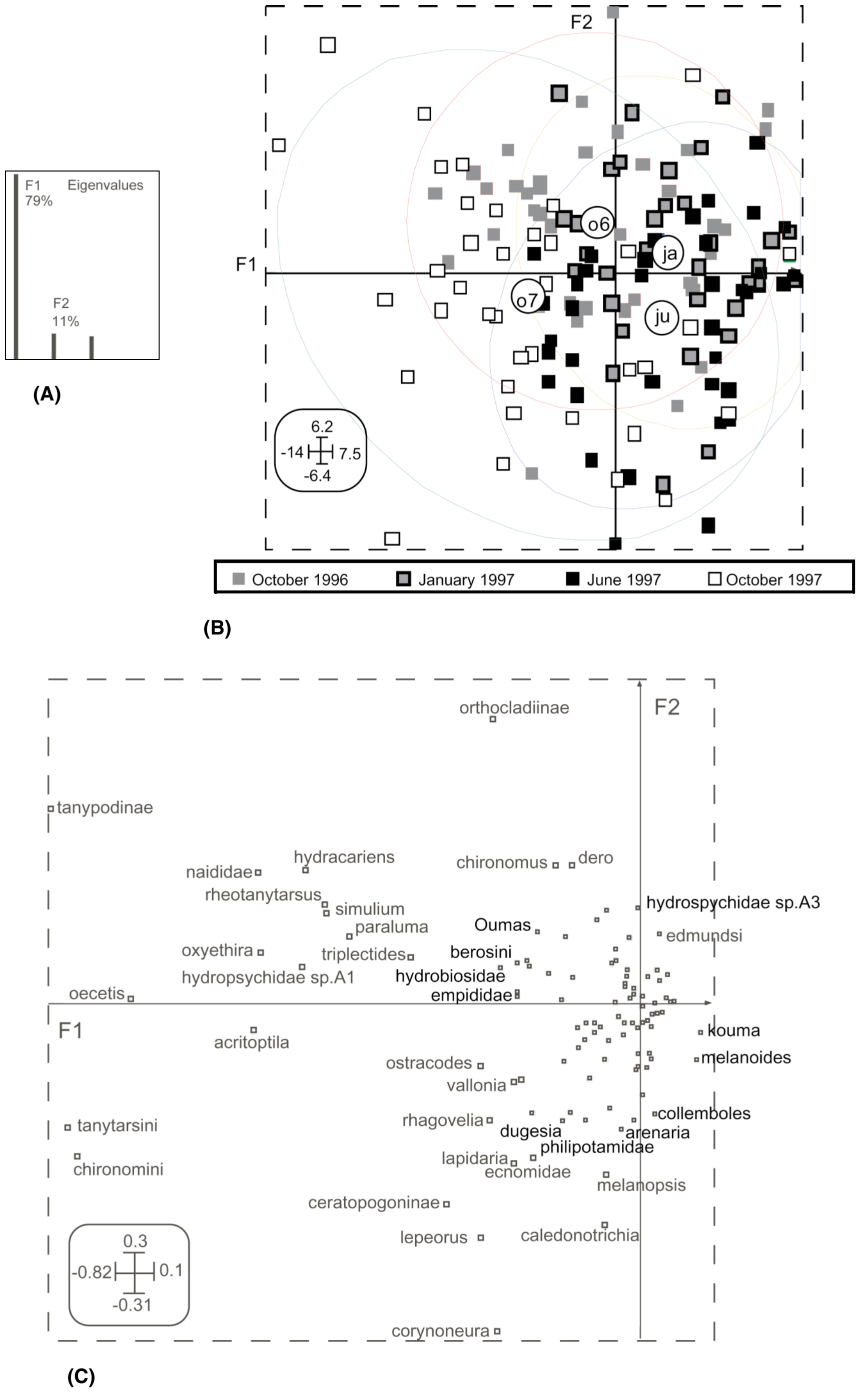

Figure 2

Between-seasons principal component analysis (PCA) ordination of sites based on taxa. A: histogram of eigenvalues. B: F1 X F2 map of the sampling sites. O6, Ja, Ju, and O7, represent, respectively, the average position of the seasons October 1996, January 1997, June 1997, and October 1997. All data from the original matrix were plotted on the PCA diagram. C: F1 X F2 map of taxa.

Figure 2

Résultats de l'ACP inter-dates. A : Graphe des valeurs propres. B : Carte des stations sur le plan factoriel F1 X F2. O6, Ja, Ju, et O7 représentent la position moyenne des dates octobre 1996, janvier 1997, juin 1997 et octobre 1997 respectivement. Les 152 relevés du tableau initial ont été projetés sur le plan factoriel F1 X F2. C : Représentation des taxons sur le plan factoriel F1 X F2.

Macroinvertebrates assemblages

Because of the small effect of season on benthic assemblage structure during the sampling period, the data were pooled for the four sampling periods, leading to a greater statistical significance of between-site comparisons. Clustering of the data matrix (38 sites X 102 taxa) results in five site groups (Nos.1, 2, 3, 4, and 5) (Figure 3) and five macroinvertebrate assemblages (I, II, III, IV, and V), which varied in density and composition (Table II).

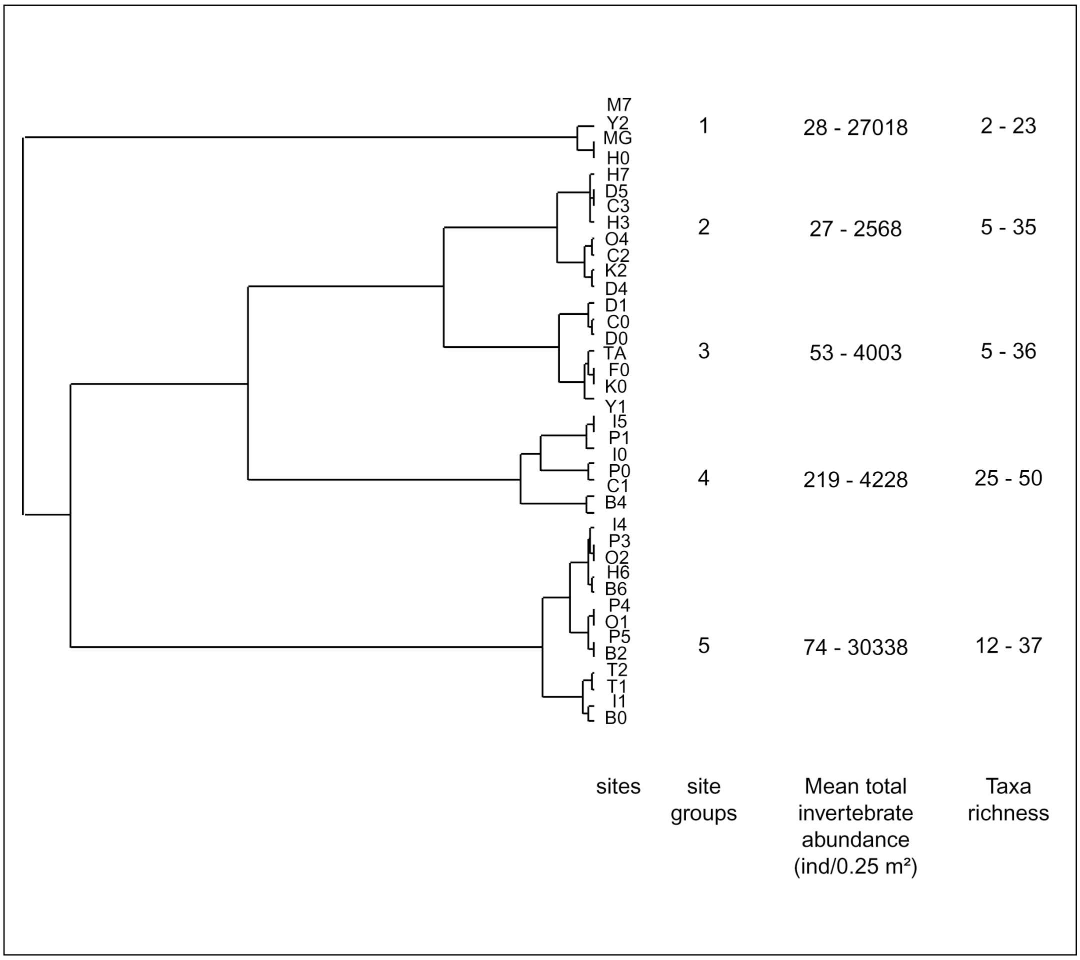

Figure 3
Dendrogram for hierarchical clustering of the 38 study sites of La Grande Terre on the basis of 102 taxa (euclidean distances, Ward's method).

Figure 3
Résultats de la classification hiérarchique (distances euclidiennes, méthode de Ward) réalisée sur les données faunistiques cumulées des 38 stations (102 taxons considérés).

Table II

Classification of sites and taxa. Distribution of taxa: • < 25% of sites; •• 25-49% sites; ••• 50-74% sites; •••• > 75% of sites. Mean density: · 1-19 individuals/0.25 m²; • 20-99 individuals/0.25 m²; ● > 100 individuals/0.25 m².

Tableau II

Classification des sites et des taxons. Fréquence d'apparition des taxons : • moins de 25 % des sites ; •• 25 à 49 % des sites ; ••• 50 à 74 % des sites ; •••• > 75% des sites. Densité moyenne : · 1 à 19 individus/0,25 m² ; • 20 à 99 individus/0,25 m² ; ● plus de 100 individus/0,25 m².

	Site groups / Groups of taxa	**1** (Y2, M7, MG)	**2** (H0, H3, H7, D5, C3, C2, K2, O4)	**3** (DO, D1, D4, C0, Ta, FO, K0)	**4** (I0,P0, Y1,I5, P1, B4, C1)	**5** (O1, O2, P3, P4, P5,I4, H6, B6,B2, T1, T2, I1, B0)
I	Hydracarina		···	····	••••	••••
	Celiphlebia spp.		●●●●	••••	●●●	···
	Lepeorus spp.		••••	●●	••••	●●●●
	Paraluma		●●●	••	••••	●●●●
	Chironomini		••••	····	●●●●	●●●●
	Corynoneura spp.		••••	••••	●●●●	••••
	Tanytarsini	··	••••	••••	●●●●	●●●●
	Tanypodinae		••••	••••	●●●●	●●●●
	Acriptoptila spp.		••••	··	····	●●●●
	Caledonitrichia spp.		···	••••	••••	••••
	Oxyethira spp.		••••	···	••••	●●●●
	Oecetis sp.1		●●●●	···	••••	●●●●
	Berosini NG 3 spp.		••••	··	••••	••••
II	Naididae	●●●	··	·	●●●	●●●●
	Orthocladiinae	●●●●	●●●●	••••	●●●●	●●●●
	Rheotanytarsus	•••	•••	···	●●●●	●●●●
	Simulium neornatipes	●●●	●●●●	••••	●●●●	●●●●
	Hydropsychidae sp. A1		●●●●	··	●●●	●●●●
III	*Leptophlebiidae NG4*			···	●●●●	·
	Notachalcus corbassoni		·	···	●●●●	··
	Synthemis fenella		···	··	····	···
	Rhagovelia		··	··	••••	···
	Ceratopogoninae		····	····	····	····
	Harrisius spp.		····	····	••••	··
	Tipulidae	··	··	···	••••	···
	Tabanidae		····	···	···	····
	Ecnomidae		••••	····	····	·
	Arenaria		··		●●●	···
	Lapidaria		•••	••••	••••	·
	Vallonia		·	•••	●●●	
	Xanthochorema spp.		····	····	····	··
	Hydropsychidae sp. B2		••	··		••
	Triplectides spp.		···	···	••••	··
	Gracilipsodes spp.		•••	•••	•••	•••
IV	Achète sp.1	··			·	··
	Nématodes	●●●●				
	Lumbricidae	•••			·	••
	Gyraulus spp.				·	··
	Melanoides spp.	··			·	•••

	Melanopsis spp.		•	●●	●●●●	•••
	Hydrobiidae				••	•
	Amphipoda			•	●●●	•
	Paratya sp.1				••	
	Caridina novaecaledoniae		•	•	•••	••
	Caridina longirostris				•	••
	Caridina serratirostris					••
	Caridina typus		•	•		
	Caridina spp.		••	••	•	••
IV	*Odiomaris pilosus*		•			•
	Collembola	•••	••	••	•••	••
	Kouma annulata			•••	●●●●	
	Lepegenia lineata		•	●●		•
	Oumas spp.			••	••	
	Amoa spp.			••	●●●●	
	Leptophlebiidae NGA sp.1			•		
	Ounia loisoni		•	••	•••	
	Poya brunnea			•	●●	
	Simulacala spp.		•	•••	••••	•
	Tenagophila spp.		••	•••	••	•
	Tindea cochereaui			••	••	
	Synthemis spp.		•	••	••	•••
	Coenagrionidae	••			•	•
	Isosticta spp.		•	••	••••	•
	Diplacodes spp.	••	••		••	••••
	Caledopteryx sarasini			•••		•
	Caledargiolestes uniseries				••	
	Rhagovelia novacaledonica		••	••	•••	••
	Paltostominae NG1		•	●●		
	Forcipomyiinae		••		•••	•
	Culicidae			•	••	•
	Dixidae			••	••••	
	Hemerodromia spp.		•••	••••	••	••
	Edmundsi			●	●●●	
	Hydropsychidae sp. A2		•••	●●●	•	
	Hydropsychidae sp. A3				●●	●
	Hydropsychidae sp. B1		•			●●
	Hydropsychidae sp. C1		•	●		
	Hydropsychidae sp. D1			●	•	
	Hydropsychidae sp. D2				●●	
	Hydropsychidae sp. G1				●●	
	Hydropsychidae sp. G2		••			
	Leptoceridae NGA		•	●	•	
	Leptoceridae NGB		••		••	•
	Symphitoneuria spp.		••	●●	●●●	
	Philopotamidae		••	••••	••••	•
	Polycentropodidae sp.1		••	•••	•••	
	Hydrophilidae unidentified	••	•		•	•
	Scirtidae			•	•	•
	Hydraena spp.		•	••	•••	•
V	*Dugesia pinguis*	●●	•	••	●●●●	●●●●
	Barbronia sp.1	●●●				•
	Prostoma sp.1				••	●●●●
	Dero spp.	●●●●			•	
	Tubificidae	●●●●			•••	●●●●
	Physastra spp.	●●●	•	•	••	•••
	Ostracoda	●●●		•	●	●●●
	Chironomus spp.	●●●●	•		••	••
	Psychodini spp.	●●●●				•
	Hydroptila losida	••	•		••	●●●
	Hydropsychidae sp.B3		●	•	•••	●●●

Site group 1 included only 3 sites located in Nouméa and heavily organically-enriched (MG, M7, and Y2). Taxa groups II and V that contained pollution-tolerant taxa such as Oligochaeta Naididae *Dero* and Tubificidae, Diptera Chironomidae *Chironomus*, Psychodidae, Syrphidae, Stratiomyinae, and Gastropoda *Physastra* characterized this first site group.

Almost all the sites in groups 2 and 3 were located in streams draining ultramafic rocks. The second site group comprised 6 sites (C2, C3, H0, H3, H7) moderately influenced by human occupation (Melanesian tribes and farms) and/or pasture (site O4) whereas the third site group contained pristine sites (DO, D1, D4, C0, F0, K0, TA). Site groups 2 and 3 had quite similar taxa assemblages varying in density. They were characterized by ubiquitous taxa of groups I and II (Ephemeroptera Leptophlebiidae *Celiphlebia*, *Lepeorus*, *Paraluma*, Trichoptera Hydroptilidae *Caledonotrichia*, Leptoceridae *Oecetis* sp.1, *Hydropsychide* sp. A1, Diptera Simuliidae *Simulium neornatipes* and Chironomidae Orthocladiinae, Tanypodiinae, *Corynoneura* and Tanytarsini) as well as specific taxa of groups III and IV (Leptophlebiidae *Lepegenia*, Hydropsychidae sp. A2, sp. C1 and sp. G2, Ecnomidae, Hydrobiosidae, Leptoceridae *Gracilipsodes*).

Site group 4 consisted of forested unimpacted streams flowing on volcanic-sedimentary soils (Y1, P0, P1, I0, I5, B4, C1). The streams were generally fast flowing, with beds dominated by boulders and cobbles. They were inhabited by communities of insects Trichoptera Hydropsychidae spp., Helicopsychidae *Helicopsyche*, Leptoceridae *Symphitoneuria and Triplectides;* Ephemeroptera Leptophlebiidae *Notachalcus*, *N.gen.4*, *Amoa*, *Kouma*; Odonata Megapodagrionidae. Some taxa, which generally occurred in low numbers, such as Leptophlebiidae *Tindea*, *Poya*, *Oumas*, *Helicopsyche* of group *Edmundsi*, Diptera Dixidae occurred in pristine sites of groups 3 and 4.

The 13 sites of group 5 (I1, I4, P3, P4, P5, O1, O2, H6, B0, B2, B6, T1, T2) were located in middle and lower reaches of streams flowing over volcanic-sedimentary lands. The sites were influenced by nutrient/organic input of pastures, tribes and/or towns. Their macrofaunal assemblages were dominated by ubiquitous taxa (groups I and II) as Leptophlebiidae *Celiphlebia*, *Lepeorus* and *Paraluma*, Hydroptilidae *Acritoptila*, *Caledonotrichia* and *Oxyethira*, Leptoceridae *Oecetis*, *Hydropsychide* sp. A1, Simuliidae *Simulium neornatipes* and Chironomidae Orthocladiinae, Tanypodiinae, *Corynoneura* and Tanytarsini, Gastropoda *Physastra* spp. Some taxa of group V such as Nemertea, Tricladia *Dugesia pinguis*, Hydroptilidae *Hydroptila* were also abundant in site group 5.

Kruskall-Wallis non-parametric analysis of variance indicated significant differences between site groups for mean density of invertebrates, taxon richness, relative abundance of Ephemeroptera, Trichoptera, and Oligochaeta, and diversity indices of Simpson, Shannon, and Margalef. Time had a significant effect on invertebrate density, taxon richness, and Margalef's indices, but did not affect the relative abundance of major invertebrate groups, nor the Simpson's and Shannon's indices (Figures 4 and 5).

Total invertebrate abundance was significantly lower in site groups 2 and 3 in comparison to site groups 1 and 5 (Figures 3 and 4). For example, the mean values ranged from 28 to 27 000 animals/0.25 m^2 for the sites of group 1 and from 74 to 30 340 animals/0.25 m^2 for the sites of group 5 whereas it varied from 27 to 2 570 animals/0.25 m^2 for the site group 2 and from 54 to 4 000 animals/0.25 m^2 for the site group 3. Likewise, during each season, taxon richness was significantly higher in forested sites of group 4 (25-50) in comparison to sites of rivers draining ultramafic rocks (groups 2 and 3) where taxon richness ranged from 5 to 36, and grossly polluted sites of group 1 (generally < 10 taxa).

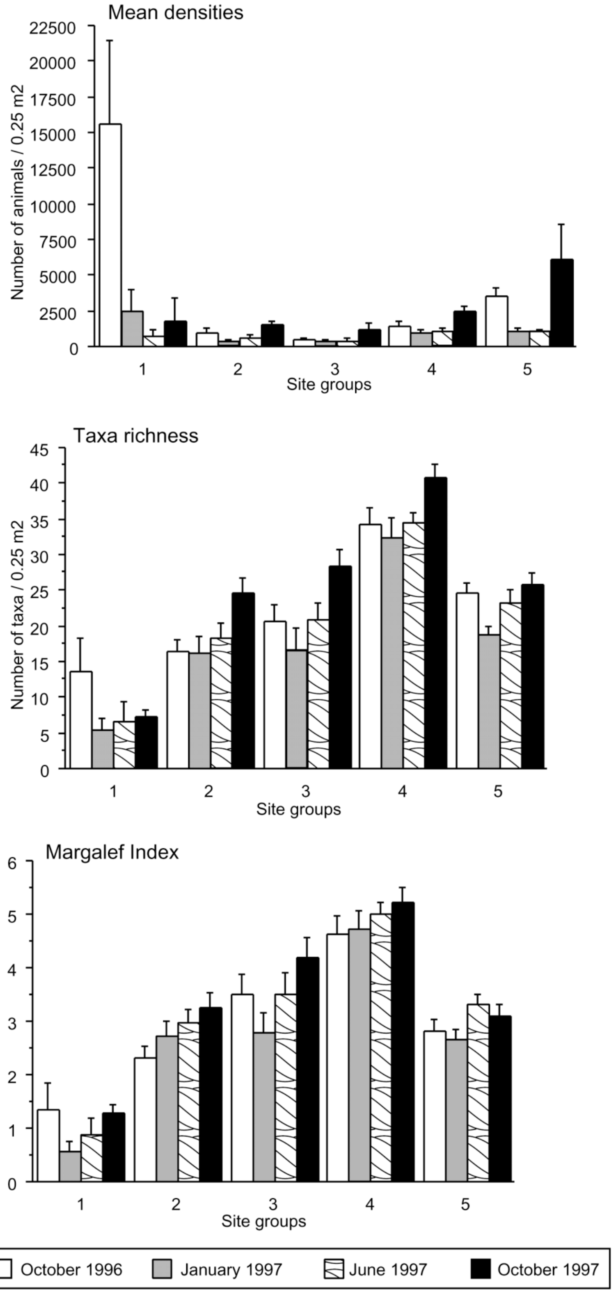

Figure 4

Mean invertebrate densities, taxon richness, and Margalef indices (x ± SE) in reaches of the five site groups for the four seasons. Results of the Kruskall-Wallis one-way analysis of variance by ranks. Densities: between site groups H = 34.57, *p < 0.0001*, between seasons H = 33.72, *p < 0.0001*; Taxon richness: between site groups H = 75.74, *p < 0.0001*, between seasons H = 14.70, *p < 0.005*; Margalef index: between site groups H = 80.92, *p < 0.0001*, between seasons H = 8.02, *p < 0.05*.

Figure 4

Comparaison des densités moyennes, des richesses taxonomiques et des indices de diversité de Margalef (x ± SE) pour les 5 groupes de stations, à l'aide de tests non paramétriques de Kruskall-Wallis. Densités : inter-groupes H = 34,57, *p < 0,0001*, inter-dates H = 33,72, *p < 0,0001* ; richesses taxonomiques : inter-groupes H = 75,74, *p < 0,0001*, inter-dates H = 14,70, *p < 0,005* ; indices de Margalef : inter-groupes H = 80,92, *p < 0,0001*, inter-dates H = 8,02, *p < 0,05*.

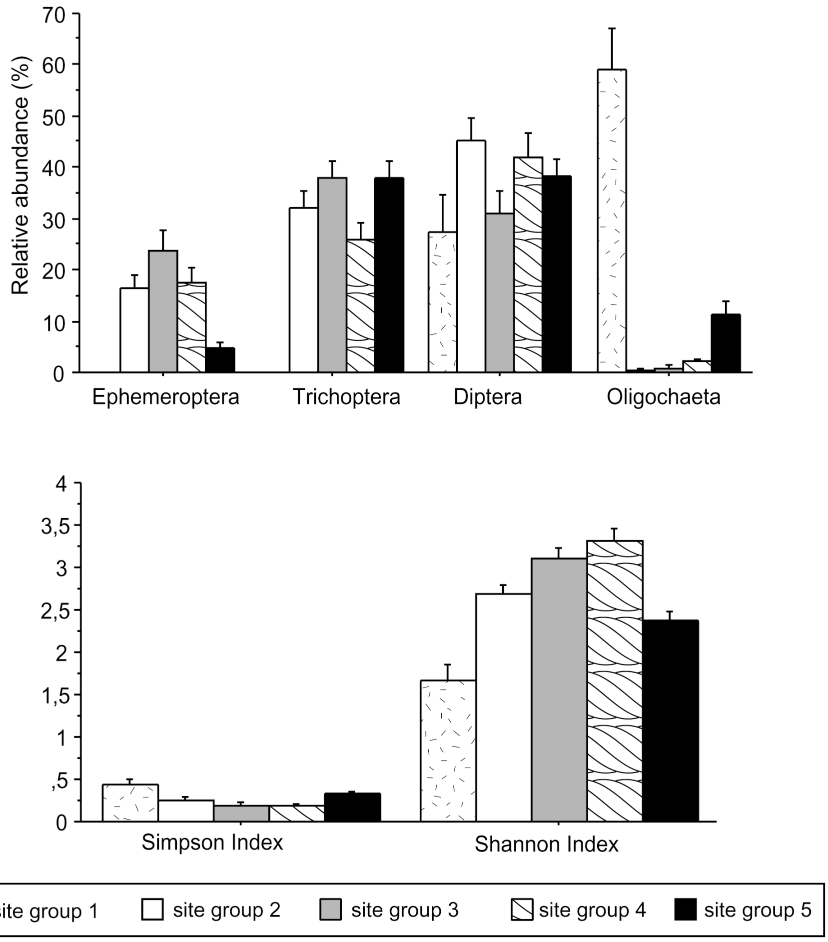

Figure 5

Comparison of relative abundance of major groups of invertebrates, and diversity indices of Simpson and Shannon (x ± SE) between site groups. Results of the Kruskall-Wallis one-way analysis of variance by ranks; Ephemeroptera: H = 55.42, *p < 0.0001*; Trichoptera: H = 38.97, *p < 0.0001*; Diptera: H = 9.56, *p < 0.05*; Oligochaetes: H = 82.03, *p < 0.0001*; Simpson index: H = 37.70, *p < 0.0001*; Shannon index: H = 48.01, *p < 0.0001*.

Figure 5

Comparaison des abondances relatives des principaux groupes d'invertébrés benthiques et des indices de diversité de Simpson et de Shannon (x ± SE) entre les 5 groupes de stations, à l'aide de tests non paramétriques de Kruskall-Wallis; Ephéméroptères : H = 55,42, *p < 0,0001* ; Trichoptères : H = 38,97, *p < 0,0001* ; Diptères : H = 9,56, *p < 0,05* ; Oligochètes : H = 82,03, *p < 0,0001* ; indice de Simpson : H = 37,70, *p < 0,0001* ; indice de Shannon : H = 48,01, *p < 0,0001*.

Trichoptera and Ephemeroptera were scarce in, or absent from site group 1 but predominant in groups 2, 3 and 4 (Figure 5) whereas Oligochaeta were significantly higher in streams of group 1 (9-90%) in comparison to streams of groups 2 and 3 (0-13%). Site group 5 was dominated by Diptera and Trichoptera. There were generally no significant differences in the relative abundance of Ephemeroptera, Trichoptera and Diptera between site groups 2, 3, 4 and 5.

Macroinvertebrate communities of site groups 3 and 4 had the highest Margalef (> 4) and Shannon (> 3.5) indices and the lowest Simpson values (< 0.3) due to high taxon richness, and high relative abundance of Ephemeroptera and Trichoptera (Figure 5). Communities of groups 2 and 5 had intermediate Margalef (2.5-4) and Shannon (2.5-3.5) indices. Finally, sites of group 1 had the lowest Margalef (< 2) and Shannon (< 2.5) indices and the highest Simpson values (> 0.4) due, essentially, to a lower number of taxa and a higher relative abundance of Oligochaetes.

DISCUSSION

Abundance and community composition

Mean macroinvertebrates densities at our study sites (523 - 41 233 animals/m^2) were within the same order of magnitude as that reported by several authors in Papua New Guinea. For example, YULE (1996) reported benthic densities ranging from 5 000 - 13 000 animals/m^2 in a small river of Bougainville Island, and DUDGEON (1994) found benthic densities ranging from 5 700 to 43 700 animals/m^2 in six Sepik River tributary streams. However, all these abundance values were very high when compared to that reported from several small Pacific islands. For example, a study in Fiji found benthic densities ranging from 50 to 346 individuals/m^2 (HAYNES, 1987); BRIGHT (1982) collected between 320 and 620 individuals/m^2 in Palau (Caroline Islands), and TINA LIU and RESH (1997) reported mean densities ranging from 30 to 100 individuals/m^2 in Moorea (French Polynesia). These low values may be explained by the relatively limited insect fauna in the Pacific oceanic islands, compared to that of continental islands. Molluscs and shrimps are generally major components of the macrofauna in the oceanic islands streams in terms of biomass, and sometimes numerically (RESH and DE SZALAY, 1995).

Insect communities of New Caledonian freshwaters were dominated by Diptera, Trichoptera, and Ephemeroptera. This kind of pattern is similar to the composition reported by YULE (1995) for a stream of Bougainville Island, Papua New Guinea. In term of relative abundance, we found that insect assemblages were dominated by filter-feeding Trichoptera Hydropsychidae and Diptera Simuliidae as was also found by YULE (1996).

Temporal changes in the structure of benthic communities

Overall, the number of individuals and taxa of the study sites were significantly higher during the dry season (October 1996 and 1997) than during the wetter seasons (January and June). However, ordination analysis showed no consistent change in assemblage structure between the four seasons. Some similar results have been demonstrated by YULE and PEARSON (1996) who pointed out an absence of seasonal change in faunal abundance and species composition in a small aseasonal tropical stream on Bougainville Island. They noticed that all species exhibited asynchronous life cycles with continuous hatching, growth and insect emergence. This strategy appeared to be in response to the lack of environmental cues to enable synchronisation of hatching, growth and emergences, since the climate of Bougainville island is remarkably constant throughout the year with regard to temperature, rainfall, and photoperiod (YULE and PEARSON, 1996).

These results suggest that precipitation, climatic changes and subsequent high water discharge could be the main factors defining seasonal variability in the structure of benthic community in New Caledonian rivers and streams. We attribute variations in abundance of macroinvertebrate assemblages to changes in stream discharge with high discharge during the wetter months affecting invertebrate populations, which showed decreasing abundance. More research is needed to better understand the seasonal faunal dynamics.

Spatial variation

Our study has proposed a stream typology based on assemblages of taxa recurring under similar environmental conditions. This typology represents a basis for better understanding and managing freshwater biota for water quality assessment. Five types of sites were distinguished, in relation to their rock type, land use, and location:

- sites in densely populated areas subjected to large volumes of organic waste (group 1);

- moderately polluted sites of streams draining ultramafic rocks (group 2);

- cascades of north-eastern coast and pristine streams draining ultramafic rocks (group 3);

- unimpacted sites in forested catchments (group 4);

- moderately organically enriched sites of rivers flowing over volcanic-sedimentary rocks (group 5).

Taxonomically diverse Ephemeroptera and Trichoptera dominated communities of forest streams (group 4). These streams where large amount of coarse particulate organic matter was observed, were rich in shredders and highly favourable for the benthic community.

At the other extreme, severely impacted sites of group 1 were characterised by low-diversity communities with few if any Ephemeroptera and Trichoptera, and a predominance of molluscs, oligochaetes, and chironomids. Some of them were characterized by taxa that can survive anaerobic conditions by means of air-breathing, such as Syrphidae. These taxa were commonly found in polluted sites (TUFFÉRY, 1980; JACQUES *et al.*, 1986; MATAGI, 1996; SLEPUKHINA, 1984).

Organically-enriched sites of group 5 were rich in oligochaetes, molluscs, and filter-feeding taxa (Hydropsychidae, Simuliidae), most of which were scarce or poorly represented in streams draining ultramafic rocks (site groups 2 and 3), regardless of the season. We also noted lower densities in streams draining ultramafic rocks compared to streams flowing on volcanic-sedimentary lands. These consistent reductions in density and abundance of saprobe taxa suggest that food resources and organic matter were limited in stream draining ultramafic rocks. Actually, ultramafic rock vegetation consist on sclerophyll, sempervirent vegetation with limited inputs of leaf litter to the streams. Previous mining activities and wildfire have degraded upstream forests of many river systems whereas they provided considerable inputs of detritus to the streams. Moreover, through deforestation, road construction, and rock extraction, mining activities have induced soil erosion on a large spatial scale, increasing siltation and sedimentation in stream channels. These results are in agreement with those of MARY and MARMONIER (2000) who studied the interstitial fauna of 15 New Caledonian streams. They noticed a high sensitivity of interstitial fauna to peridotitic substratum, with significantly lower abundance and lower taxonomic richness in interstitial communities when the percentage of peridotitic substratum in the stream catchment increased. For them, « the physical and chemical consequences of substratum geology seem to control abundances and richness of fauna » in New Caledonian streams.

Some taxa such as Leptophlebiidae *Lepegenia*, and Hydropsychidae sp. C1 and sp. G2 occur only in peridotitic lands. PETERS *et al.* (1978) and CHAZEAU (1994) suggested a specific endemism of fauna to ultramafic rocks. For example, PETERS *et al.* (1978) examined the distribution of Ephemeroptera Leptophlebiidae *Lepeorus* over

La Grande Terre and showed that the subspecies *Lepeorus calidus notialis* and *L. goyi australis* were restricted to the ultramafic South region of La Grande Terre, whereas the subspecies *Lepeorus calidus calidus* and *L. goyi goyi* occur everywhere else.

HAASE and BOUCHET (1998) also pointed out the uniqueness of New Caledonian fauna and explained the distribution of endemic species of Hydrobiidae (Gastropoda) by geological influences. They described the radiation of 54 species of spring Hydrobiidae within La Grande Terre and showed that the majority of the species occurred in very restricted areas. They noted that the hydrobiid diversity of west coast drainages was much higher than that of river systems draining the east coast and explained this variation by differing precipitation regimes and geological conditions of the areas considered. The west coast receives much less rainfall so that in continuous periods of drought, the area of a species would be fragmented by drying up of springs and consequently, gene flow between the remaining populations reduced, enhancing speciation. Moreover, the insular ultramafic mountains of the west coast hamper dispersal along the west coast (HAASE and BOUCHET, 1998).

CONCLUSION

Spatial variation appeared as the most important feature influencing faunal communities over La Grande Terre, with seasonal dynamics being of secondary importance. The type of rocks over which the streams flow is a major factor affecting the composition of macroinvertebrate assemblages, with fewer individuals generally occurring in rivers from ultramafic lands than from volcanic-sedimentary soils. The low level of detritus accumulation and food resources in streams draining ultramafic rocks is likely to reduce the number of benthic invertebrates living in these habitats. These data indicate that autochthonous and allochthonous energy sources are of primary importance in determining the structure of benthic communities in New Caledonian streams. Further investigations of the relative importance of detritus as habitat and food source for macroinvertebrates are required. In addition to rock type, catchment land use represented a factor directly influencing community composition and taxonomic richness.

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