Longitudinal and temporal changes in functional organization of macroinvertebrate communities in the Lam Tsuen River, Hong Kong

David Dudgeon
Department of Zoology, The University of Hong Kong

Keywords: River Continuum hypothesis, Hong Kong, functional groups, benthic macroinvertebrates, cultural eutrophication

Abstract

The functional organization of macroinvertebrate communities along the Lam Tsuen River, New Territories, Hong Kong, was investigated in 1976 and 1978–79. Longitudinal changes in functional group representation in 1976 generally matched those predicted by the River Continuum hypothesis, although shredders were poorly represented in the headwaters. This could be attributed to a lack of shading and limited allochthonous inputs from the scrubland watershed.

In 1978–79 community organization was modified by nutrients and organic matter inputs from domestic and agricultural sources. An increase in generalists and the establishment of deposit-feeder populations in the middle and lower course was accompanied by relative declines in collector, filter-feeder and predator diversity. Shredders and scrapers were also adversely affected. Seasonal influences were mediated through the effects of rainfall on river discharge. The river was 'flushed-out' during the wet season and community organization tended toward that seen in 1976. Effects of cultural eutrophication were pronounced during the dry season and marked alterations in middle and lower course functional group representation were noted. Apparently, differing environmental tolerances of individual taxa cause marked changes in functional group representation and community structure in rivers affected by cultural eutrophication.

Introduction

Functional classification of invertebrates according to similarities in resource utilization has several advantages (Hawkins & Sedell 1981; Bahr 1982). The most significant of these are: i) Reduced difficulty in handling poorly known taxonomic groups; ii) A concomitant simplification in community structural data (Hawkins & Sedell 1981), and thus a facilitation of pattern recognition in ecosystems.

The former point has particular relevance to studies undertaken in the tropics; the latter can be a considerable aid in interpretation of the results of non-experimental studies.

Information on benthic invertebrate functional feeding groups in North American inland waters has been synthesized by Merritt & Cummins (1978). Additionally, Cummins (1974) and Vannote *et al* (1980) have developed generalizations regarding invertebrate community organization in lotic habitats. These have been combined in the River Continuum hypothesis which suggests that predictable longitudinal variations in community organization should occur in response to varying hydrological and physical conditions, as well as changes in the resource base.

Hawkins & Sedell (1981) and Minshall *et al* (1983) examined functional group distributions in North American streams. They substantiate the R.C. hypothesis recording that group compositions vary predictably along longitudinal profiles of stream systems arising in wooded environments. Less dramatic seasonal shifts also occurred. Hawkins *et al* (1982) found that functional group organ-

Hydrobiologia 111, 207–217 (1984).

ization could alter from that predicted by the R.C. hypothesis according to riparian vegetation type, substrate and gradient of different streams; the type of canopy surrounding the stream was particularly significant in this respect. Some similar local deviations are noted by Minshall *et al* (1983). To date, however, no comparable information is available from tropical lotic systems, or those receiving significant inputs of nutrients and organic material as a result of man's activities.

Assuming that the R.C. hypothesis provides a scale against which comparisons can be made (Hawkins & Sedell 1983; Minshall *et al* 1983), the following problems can be examined:

i) Do the general predictions of the R.C. hypothesis apply to tropical habitats?

ii) How does the input of organic material and nutrients from agricultural and domestic sources (i.e. cultural eutrophication) affect the functional organization of the benthos as predicted by the R.C. hypothesis?

iii) How are the patterns of functional organization arising from cultural eutrophication affected by seasonal fluctuations in river flow volume?

Investigations were carried out in the Lam Tsuen River, Hong Kong. Previous studies of this river have involved quantification of the distribution and abundance of individual taxa (Dudgeon 1983a, 1983b) with scant attention being paid to their functional role in the benthic community. Subtle taxonomic shifts reflecting the environmental requirements of individual species may result in major changes in community structure; such changes are the focus of attention in the present paper.

Study area

The 9 km long Lam Tsuen River runs from southwest to northeast across central New Territories, Hong Kong, draining an area of approximately 20 km^2. Detailed studies of the water quality, distribution and abundance of the benthic fauna have been published elsewhere (Dudgeon 1983a, 1983b). The present investigation is concerned with the macrobenthos of a series of stations sited in riffle reaches along the river's course. They were first investigated in November 1976 and then at 3-monthly intervals in 1978–79. During both studies quantitative samples of the benthos were taken

Table 1. A comparison of mean values of phosphates at five stations in the Lam Tsuen River in 1976 with levels of this parameter in December 1978.

Station	PO_4 (mg l^{-1})		Magnitude of change
	1976	1978	
1	0.14	0.04	-3.5
2	0.05	0.10	2.0
3	0.50	1.35	2.7
5	0.85	1.00	1.2
6	1.83	3.25	1.77

but monitoring of hydrological parameters was more intensive in 1978–79. Comparing 1978–79 and 1976 (see Dudgeon 1983a), a general increase in cultural eutrophication is indicated reflecting increased rearing of livestock (pigs, ducks and chickens) in the watershed. For example, phosphate concentrations along the river increased by an average of over 250% (Table 1). Such effects were, however, confined to the middle and lower reaches of the river. The two uppermost sites, draining sparsely populated scrubland, were relatively unchanged between 1976 and 1978–79 and had soft, slightly acidic waters (pH 6.80–7.00, $\bar{x} = 6.92$) which were rich in silicates (4.0–8.2, $\bar{x} = 6.13$ mg l^{-1}), but relatively poor in phosphates (0.40–0.62, $\bar{x} = 0.24$ mg l^{-1}), nitrites (0.00–0.05, $\bar{x} = 0.02$ mg l^{-1}) and nitrates (0.03–0.23, $\bar{x} = 0.10$ mg l^{-1}). Dissolved oxygen concentrations always exceeded 8 mg l^{-1} ($\bar{x} = 8.92$ mg l^{-1}) and B.O.D.$_5$ values were less than 2.85 mg O_2 l^{-1} ($\bar{x} =$ 1.13 mg O_2 l^{-1}. Seston loads (suspended organic material) varied between 0.10 and 0.55 mg l^{-1} ($\bar{x} =$ 0.38 mg l^{-1}). Along the river as a whole, water temperatures over the study period ranged between 17.5 and 30.0 °C. Further details of the river and watershed can be found elsewhere (Dudgeon 1983a).

Methods and materials

The study sites were designated 1–6 (Station 5b, established in 1976 only, was located between 5 and 6); Station 1 was a boulderstrewn headwater torrent while Station 6, in the lower course, was characterized by extensive aquatic macrophyte growths. Hydrological parameters were measured following standard procedures (APHA 1975; Dudgeon 1982). Stratified quantitative samples (Dudgeon 1983a) of the benthos were taken at six sites along the river in

June, September and December 1978, and March 1979, corresponding to the onset of the wet season (June), the end of the wet season (September), and the middle and end of the dry season (December and March, respectively). Samples were also taken from the same sites (and one additional station) in late November 1976 when the river showed little sign of cultural eutrophication.

Benthic samples were sorted to the highest possible taxonomic level (using letters and numbers to designate morphotypes within taxonomic units) and counted. Animals were assigned to functional categories at the generic level following Merritt & Cummins (1978). Gut content analyses were carried out on taxa where published information on feeding methods was inadequate.

Results

Lam Tsuen River hydrology changed markedly during the study. Eutrophication increased between 1976 and 1978 (Table 1 and Dudgeon 1983a), and seasonal changes, summarized in Fig. 1, were apparent during 1978–79. Phosphates, nitrates, nitrites, suspended organic matter (SOM) and B.O.D.$_5$ levels were generally higher in the middle and lower course (Stations 4–6) than upstream (Stations 1 and 2). Conditions at Station 3 depended upon the season; high levels of phosphates, nitrates, nitrites and B.O.D.$_5$ prevailed during the dry season. Thus in March 1979, Station 3 closely resembled downstream sites with respect to hydrology. By contrast, during the wet season (June to September), this site was more closely akin to the headwaters.

Functional group representation also varied considerably (Fig. 2). The 119 benthic taxa recorded were assigned to 8 functional groups (Table 2). Certain taxa could not be placed into discrete categories; for example *Chironomus* cf. *plumosus*, classified as a collector/filter-feeder, was treated as

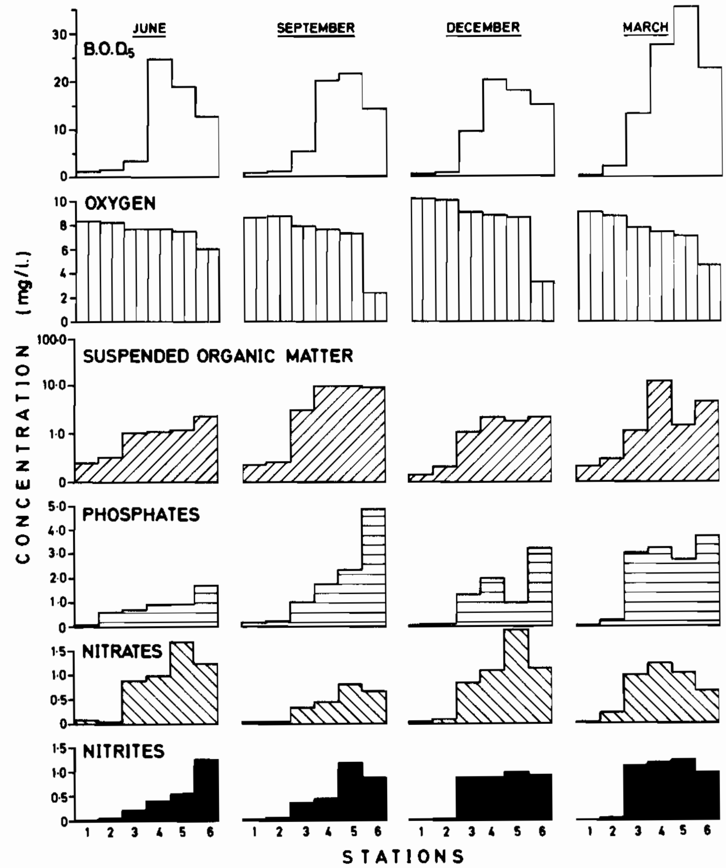

Fig. 1. Hydrological conditions prevailing at sites along the Lam Tsuen River, 1978–79.

Table 2. Species list and functional feeding group classification used in this study.

Hydroidea	
Hydra sp.	P
Oligochaeta	
Limnodrilus spp.	D
Branchiura sp.	D
Hirudinea	
Glossiphonia weberi (Blanchard)	P
Barbonia weberi (Blanchard)	P
Bivalvia	
Corbicula fluminea (Müller)	F
Gastropoda	
Brotia hainanensis (Brot)	Sh
Melanoides tuberculata (Müller)	G
Sinotaia quadrata (Benson)	G
Physella acuta (Draparnaud)	G
Hippeutis cantonensis Yen	G
Biomphalaria straminea (Dunker)	G
Ferrissia baconi (Bourguignat)	Sc
Cladocera	
Simocephalus L_1, L_2	CoF
Ostracoda	
Cypris L_1	CoF
Cypridae sp. indet. L_2	CoF
Decapoda	
Caridina lanceifrons Yu	Co
Neocaridina serrata (Stimpson)	Co
Macrobrachium hainanense (Parisi)	P
Potamon sp.	G
Ephemeroptera	
Baetis T_1, T_2, T_3, T_4, T_5, L_6, L_7, L_8 & cf. T_3	CoSc
Centroptilium L_1	CoSc
Pseudocloeon T_1, T_2, L_3	CoSc
Compsoneuria T_1, T_2	CoSc
Epeorus T_1, T_2	CoSc
Iron sp.	CoSc
Thalerosphyrus T_1	CoSc
Choroterpes T_1	CoSc
Choroterpes (*Euthraulus*) L_1	CoSc
Isca sp.	CoSc
Ephemerella T_1, T_2, L_3	CoSc
Ephemera sp.	Co
Caenis T_1, T_2, L_2, L_3	Co
Odonata	
Protosticta sp.	P
Euphea decorata (Selys)	P
Protoneura sp.	P
Anax guttatus (Burmeister)	P
Ictinogomphus pertinax (Selys)	P
Heliogomphus T_1, T_2	P
Onychomphus sinicus Chao	P
Zygonyx iris (Kirby)	P
Brachydiplax flavovittata Ris	P
Orthetrum sabina (Drury)	P
Plecoptera	
Amphinemura sp.	Sh
Perlidae spp. indet.	P
Heteroptera	
Aphelochirus T_1	P
Sphaerodema rusticum (Fabricius)	P
Pleidae sp. indet	P
Megaloptera	
Neochauloides boweringi (McLachlan)	P
Trichoptera	
Rhyacophila T_1	P
Himalopsyche L_1	P
Agapetus T_1	Sc
Chimarra T_1, L_4	F
Hydropsyche T_s, T_v, T_y, L_w, L_x, L_y, L_z & sp. indet	F
Cheumatopsyche L_x, L_y, L_z & sp. indet.	F
Hydropsychidae genus indet. Ch	F
Psychomyia T_1	Co
Pseudoneureclipsis TA_1, TA_2, TA_3	Co
Psilotreta T_1	CoSc
Hydroptila sp	Pr
Coleoptera	
Enochrus sp.	Co
Hydrophilidae genus indet. T_2	Co
Helodes T_1	CoSc
Stenocolus sp.	Sh
Eubrianax sp.	Sc
Psephenus sp.	Sc
Psephenoides sp.	Sc
Elmidae genus indet. T_1	CoSc
Elmidae genus indet. T_2	CoSc
cf. *Zaitzevia* sp.	CoSc
cf. *Limnius* sp.	CoSc
Stenelmis T_1	CoSc
Elmidae spp. indet.	CoSc
Diptera	
Chironomidae spp. indet	CoF
Chironomus cf. *plumosus* (L.)	CoF
Polypedium (Polypedium) sp.	CoF
Dicrotendipes sp.	CoF
Microspectra sp.	CoF
Tanypodinae spp. indet.	P
cf. *Thienemannimyia* sp.	P
Simulium T_1, $T_{2(D)}$, L_3, L_4 & S_6	F
cf. *Pedicia* sp.	P

Key to functional groups:

Co	Collectors
Sc	Scrapers
CoSc	Collector/Scrapers
Sh	Shredders
F	Filter-feeders
CoF	Collector/Filter-feeders
P	Predator
G	Generalist
Pr	Piercers – suckers of plant cells
D	Deposit-feeders.

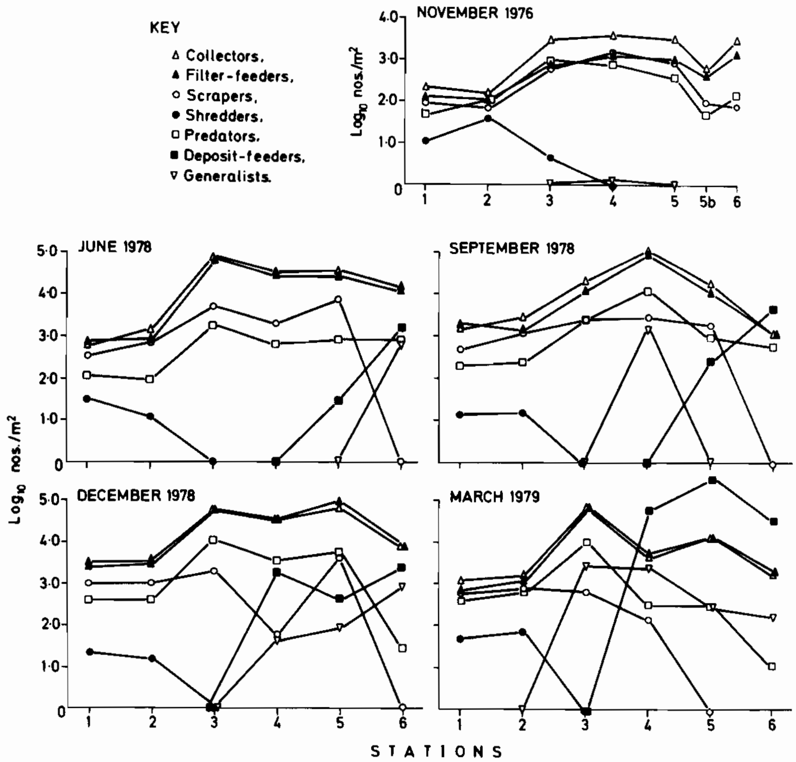

Fig. 2. Population densities of macroinvertebrate functional groups at sites along the Lam Tsuen River, 1976 and 1978–79.

one-half collector and one-half filter-feeder in all calculations.

Some functional groups increased in abundance during the study. The most obvious was the incidence of deposit-feeders, which were not recorded in 1976, but were abundant in 1978–79. Generalists were also more numerous in the later survey, occurring at Stations 3–6 during the dry season. Shredders were restricted to the upper course of the river (Stations 1–3 in 1976, Stations 1 and 2 in 1978–79), but collectors, filter-feeders and predators were found at all sites. Collectors and filter-feeders were generally the most abundant groups at each station, although deposit-feeders were more numerous at Stations 4–6 in March 1979. Scrapers were collected at all sites except Station 6.

Throughout the study, macroinvertebrate abundance increased downstream. The trend was magnified in 1978–79 when population densities exceeded 1976 levels. At this time a change in the community composition was apparent with greater numbers of filter-feeders, collectors, generalists and deposit feeders, and a relative decline in predator abundance. Predator:prey ratios (Fig. 3) were highest in 1976 and gradually declined downstream. Ratios were lowest during the 1978 wet season and did not

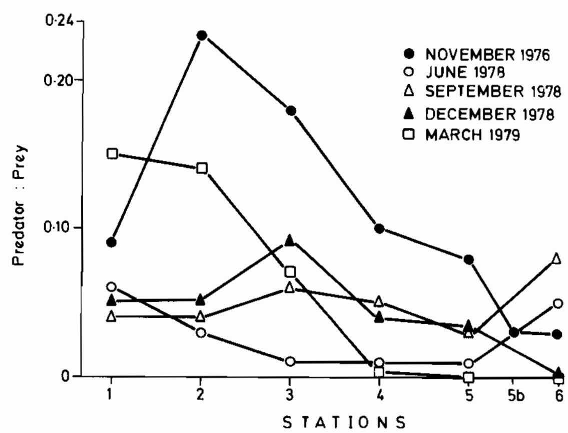

Fig. 3. Ratio between predator and total macroinvertebrate population densities at sites along the Lam Tsuen River, 1976 and 1978–79.

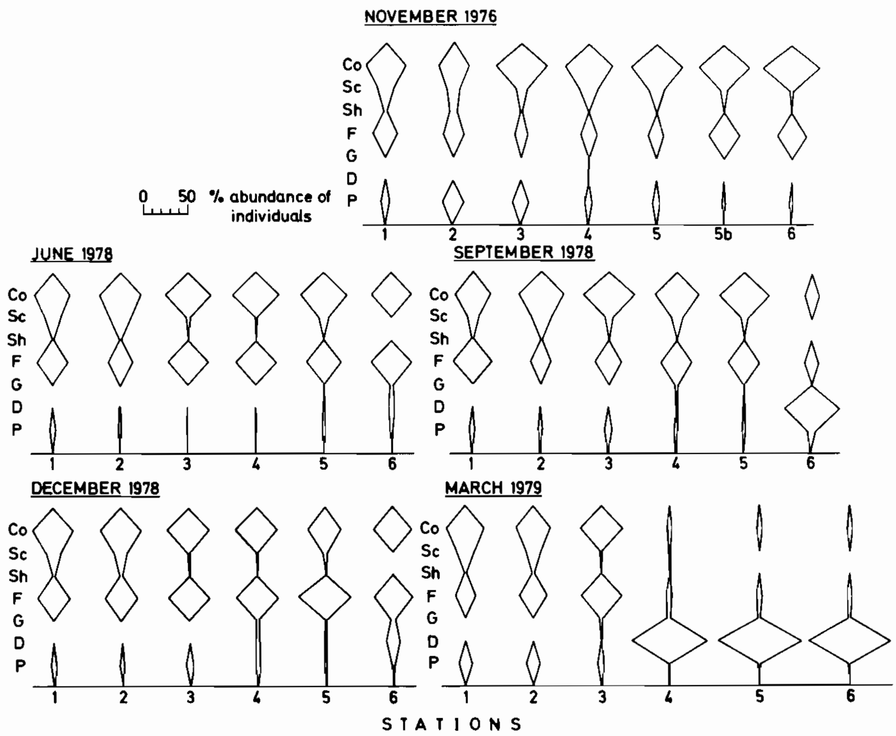

Fig. 4. Relative abundance of macroinvertebrate functional groups at sites along the Lam Tsuen River, 1976 and 1978–79.

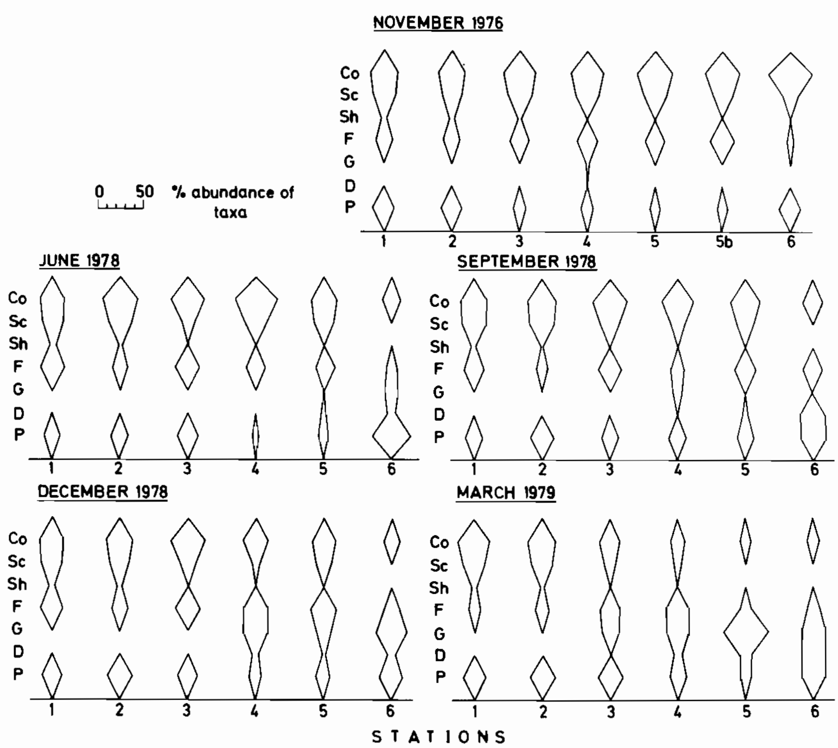

Fig. 5. Relative numbers of taxa composing macroinvertebrate functional groups at sites along the Lam Tsuen River, 1976 and 1978–79.

exhibit regular downstream changes; a reflection of the influence of spates on the benthic fauna (Dudgeon 1983a). Predator:prey ratios remained depressed during the dry season and were extremely low at Stations 4–6 in March 1979. High nitrite and phosphate levels prevailed in the lower course of the river at this time (Fig. 1).

The relative abundance of function groups and the number of taxa comprising them are shown in Figs. 4 & 5. Predators were a small part of the benthic community although generally more numerous in 1976 (Fig. 4). In terms of the number of taxa, however, they were well represented at all sites (Fig. 5). Shredders, by contrast, showed both low relative abundance and low taxonomic representation. Filter-feeders and collectors were relatively numerous throughout this study except in March 1979. However, there were fewer taxa in downstream sites. This trend was particularly marked in filter-feeders but was not apparent in 1976.

Scrapers declined downstream in both the abundance of individuals and taxa, while deposit-feeders increased in the lower course. This increase was in terms of individual numbers; taxonomic diversity was restricted. By contrast, generalists were relatively species-rich in March 1979, although comprising a small proportion of the macrobenthic community in numerical terms.

The relative abundance of functional groups can be considered in terms of Functional Group Ratios (FGR), where

$$FGR_a = \frac{\text{population density of } a \text{ at Station}_n \text{ on time}_t}{\text{population density of all taxa at Station}_n \text{ on time}_t}$$

and a represents any single functional group.

For the purposes of the present study, FGRs for each functional group at each site on the 5 sampling dates have been calculated and plotted as a mean FGR value in Fig. 6, thus providing a summary of the relative abundance of each group along the river. Collectors were clearly the most abundant category, followed by filter-feeders. Predators were less well represented than scrapers and were the least common regularly occurring group. Shredders and generalists were typically minor community components but deposit-feeders attained some significance in the lower course.

As a measure of temporal changes in the relative

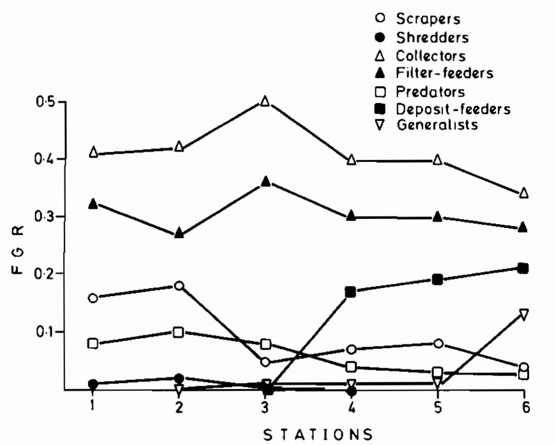

Fig. 6. Mean values of functional group ratios (FGR) at sites along the Lam Tsuen River, 1976 and 1978–79.

abundance and taxonomic diversity of each functional group along the river, the relationship between FGR and the number of taxa in each functional group was plotted for every Station on all sampling dates, and a best fitting line derived by the method of least mean squares (Fig. 7). Best-fitting lines which cross the X-axis at an angle of approximately 45° or less indicate functionally diverse communities with a large number of taxa comprising those categories with high FGRs. Those lines crossing at a greater angle (especially $> 90°$) are characteristic of functionally less diverse communities where functional groupings composed of few taxa comprise a major part of the macrobenthos.

Benthic communities were functionally diverse along the river in 1976 although there was a tendency for higher FGRs to consist of fewer taxa in the lower course. In 1978–79, the trends were altered. Stations 1 and 2 were relatively diverse and similar to each other, buth the remaining sites exhibited tendencies toward community dominance by one or more species – poor functional groups. This was especially apparent at Station 6 in June and December 1978, and Stations 4 and 5 in March 1979. Stations along the river were most similar (and functionally diverse) in September 1978.

Reasons for changing functional group representation along the Lam Tsuen River during the study period cannot be unequivocally determined from the results of the present study. However, correlation analysis can give an indication of factors

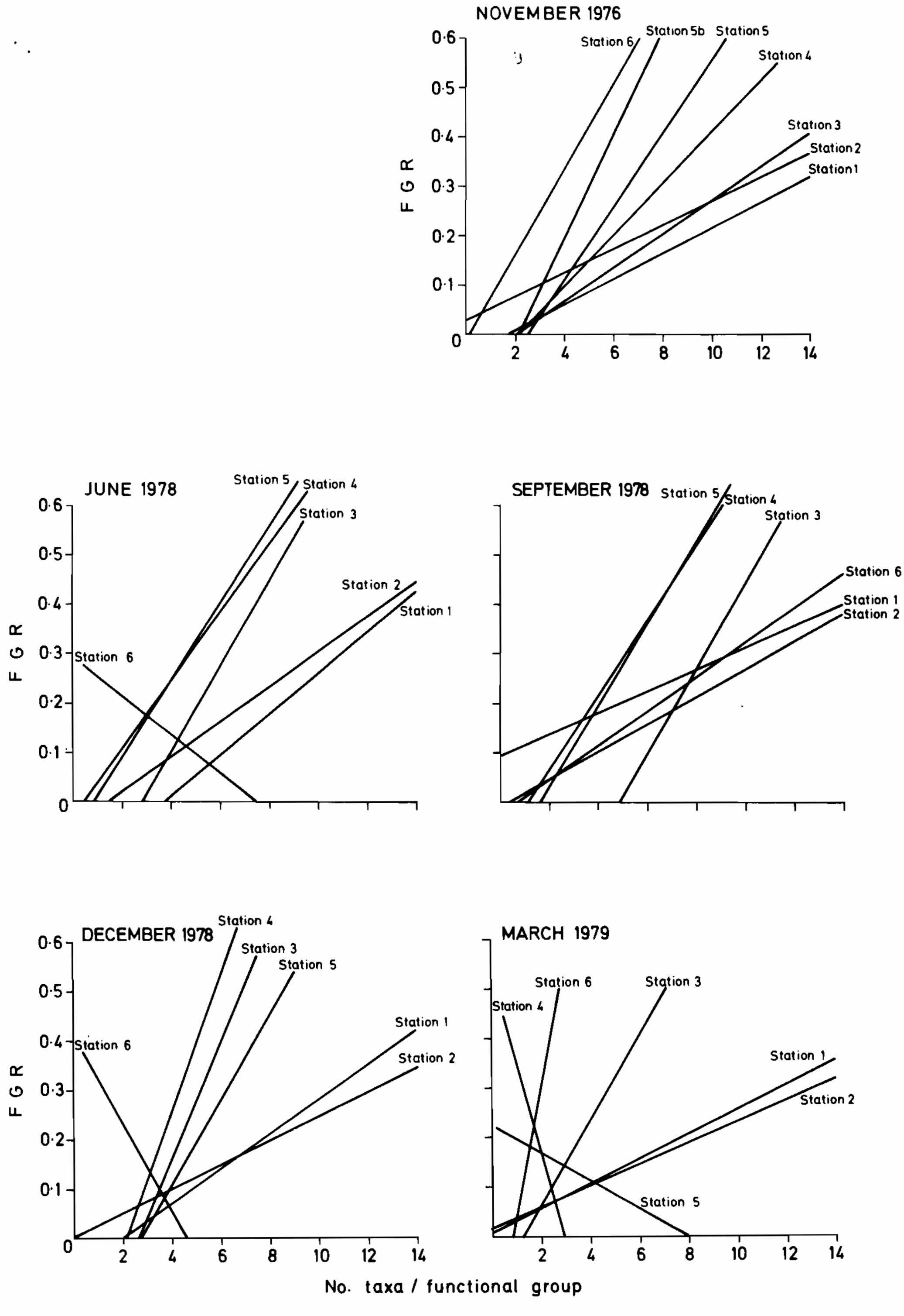

Fig. 7. Best fitting lines for the relationship between FGR and the number of taxa comprising each functional group at sites along the Lam Tsuen River, 1976 and 1978–79.

Table 3. Correlation analysis of functional group population densities against biotic and hydrological parameters in the Lam Tsuen River.

	Log_{10} total population density	Log_{10} Co population density	Log_{10} F population density	Log_{10} P population density
Log_{10} P population density		0.68***	0.64***	0.49*
SOM	0.03	0.14	0.13	0.34
$PO_4 + NO_2 + NO_3$	0.03	0.42*	0.35	0.53**
$PO_4 + NO_2 + NO_3$ + SOM	0.05	0.26	0.22	0.47*
$PO_4 + NO_2 + NO_3$ + SOM + BOD_5	0.03	0.43*	0.39	0.68***
BOD_5	0.01	0.49*	0.44*	0.73***

Significance levels:
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

worthy of investigation in future experimental studies. Correlation of the population densities of total macroinvertebrates, as well as those of individual functional groups, against various parameters, indicated that B.O.D.$_5$ levels were strongly associated with high total population densities ($P < 0.001$) (Table 3). A similar result was attained for the relationship between total population densities and combined total load of phosphates, nitrates, nitrites, SOM and B.O.D.$_5$. There was, however, no correlation between SOM and total population density, or with the densities of collectors or filter-feeders. Predator abundance was strongly correlated with numbers of filter-feeders and collectors, but the correlation was less strong with total population densities. The results of other correlation analyses are shown in Table 3.

Discussion

Data collected from the Lam Tsuen River in 1976 provide the best record of natural functional group distribution in a Hong Kong lotic habitat. Despite some minor enrichment of the lower reaches (Dudgeon 1983a), the river supported functionally diverse communities along its course (Fig. 7). This trend was disrupted in 1978–79 when the effects of cultural eutrophication were superimposed upon natural seasonal changes in river discharge. In 1976, however, functional group distribution broadly followed the predictions of the River Continuum hypothesis (Vannote *et al* 1980), as investigated by Hawkins & Sedell (1981), Hawkins *et al* (1982) and Minshall *et al* (1983). According to the hypothesis, shredders and collectors (including collector-gatherers + filter-feeders) are codominant in headwaters. Scraper dominance follows shifts in primary production, and is maximized in midsized rivers, whereas with increasing stream size and a reduction in detrital particle size, collectors (collector-gatherers + filter-feeders) will increase in importance and dominate macroinvertebrate assemblages of larger rivers (Vannote *et al* 1980).

Shredders were restricted to the upper Lam Tsuen River but did not attain codominance of the benthic community. Shredder abundance reflects the influence of riparian vegetation (Vannote *et al* 1980); in the upper Lam Tsuen Valley this comprises scrub and grassland and contributes little shading or allochthonous material to the river. Consequently, collectors and scrapers are more numerous and diverse functional groups. This community organization was maintained at Stations 1, 2 and 3 in 1976 where diverse predator assemblages were recorded.

Deviations in the relative abundance of upper Lam Tsuen River functional groups from predictions of the R.C. hypothesis can be anticipated from the studies of Haefner & Wallace (1981), Murphy *et al* (1981) and Hawkins *et al* (1982) who noted that functional group organization varied according to riparian vegetation type. Towns (1981) has recorded significant effects on functional group organization in response to shading in a New Zealand stream. However, whether the effects of local environmental vagaries alter the overall tendency towards gradual change in biotic conditions within a river system remains open to question (cf. Winterbourn *et al* 1981).

The lower course of the Lam Tsuen River in 1976 was dominated by collectors. Scrapers were well represented at Stations 4, 5 and 5b but scarce at Station 6; this is in broad agreement with the predictions of the R.C. hypothesis. Filter-feeders had a similar pattern of distribution and, like scrapers, may have been poorly represented at Station 6 due to an unsuitable substratum (Dudgeon 1983a) or reduced current velocity. As predicted by Vannote *et al* (1980), the predator component changed little in relative abundance along the river.

Overall, there was general agreement between predicted and actual functional group distribution along the Lam Tsuen River in 1976. A good match with the R.C. hypothesis can be seen in Bishop's (1973) study of a Malaysian river (although again shredders seemed poorly represented), indicating that such generalizations about lotic community organization may apply to both tropical and temperate lotic systems. However, inference that the Vannote *et al* (1980) model is a universal one is contentious (Winterbourn *et al* 1981) and requires further extensive study.

Cultural eutrophication of the Lam Tsuen River altered the functional organization of macrobenthic communities in 1978–79. Changes were confined to the middle and lower reaches (Stations 3–6) where generalists and deposit-feeders became locally abundant. The latter were new colonizers and, although lacking in taxonomic diversity, dominated lower course communities in March 1979. Collectors and filter-feeders increased in population density and relative abundance; this was offset by a reduction in taxonomic diversity which was particularly apparent at Station 4 (immediately downstream of a large duck farm) and, in the case of collectors, at Station 6. By contrast, shredders were eliminated from Station 3, while scraper distribution and diversity was reduced. The latter was especially apparent for Heptageniidae, Leptophlebiidae (Ephemeroptera) and Psephenidae (Coleoptera), and can be attributed to growths of filamentous algae (*Cladophora* and other Chlorophyceae), and in some places *Sphaerotilus* (Chlamydobacteriales), smothering rock surfaces thus rendering them unsuitable for scrapers. Predator diversity and relative abundance also declined in 1978–79, being particularly marked in the lower course where only leeches and Tanypodinae (Diptera: Chironomidae) were regularly recorded. As a result, the predator: prey ratio declined along the river and can be interpreted as a disruption in a community structure.

In summary, the main departures from the R.C. hypothesis caused by cultural eutrophication were: elimination of shredders, decline in predators and scrapers, an increase in collectors and filter-feeders accompanied by declining numbers of taxa, and an increase in generalists and deposit-feeders. The latter reflected greater food availability in the enriched river with biological processing no longer being completed in the water column (Minshall *et al* 1983). Consequently food accumulating in the bottom sediments provided an energy source for deposit feeders. Significantly, high levels of sedimentary organics were recorded from sites where deposit-feeders were abundant (Dudgeon 1983a).

Seasonal changes in community organization reflected suppression or amplification of the effects of cultural eutrophication on functional group representation. Life cycle events played little or no role in such changes; freshwater invertebrates in tropical regions generally exhibit continuous patterns of growth and recruitment (Petr 1970; McLachlan & McLachlan 1971; Bishop 1973; Marchant 1982). Decreased river discharge in the dry season was accompanied by high nutrient and B.O.D.$_5$ levels and greater abundance of deposit-feeders and generalists. Other functional groups declined in relative abundance, and reduced taxonomic richness was inadequately compensated by the diverse generalist grouping (Dudgeon 1983b). The generalists were typically lentic species which were able to establish themselves during periods of low discharge, but were swept away upon the onset of the summer rains. These rains 'flushed-out' the river causing declines in nutrient levels, sedimentary organics (Dudgeon 1983a) and deposit-feeders. In consequence, a degree of the original community organization was re-established, with increased predator:prey ratios in the lower course, a greater representation of scrapers in downstream sites, and a general increase in collectors and filter-feeders at sites from which they were excluded in the dry season. Thus functional organization in June and September 1978 tended to approach that recorded in 1976. However, by December community alteration was already underway and became most apparent in March 1979, at the end of the dry season.

Seasonal effects, acting by way of changing Lam Tsuen River discharge volume, altered the magnitude of community disruption induced by cultural eutrophication. The causal elements in this disruptive process cannot be identified with certainty, but strong correlations between total benthic population densities and $B.O.D._5$ loading, as well as combined nutrient, SOM and $B.O.D._5$ loading, indicate that these parameters have, at least, some influence on population size. Curiously, there was no correlation between SOM and filter-feeder abundance although Hawkins & Sedell (1981) were able to relate these parameters in Oregon streams. A certain degree of complex inter-group interaction in the Lam Tsuen River is indicated by the strong correlations between densities of predator populations and those of collector-gatherers and filter-feeders, but not with those of total benthic populations. Such variations may result from species-specific hydrological tolerance limits as well as other environmental influences, and have the overall effect of favouring certain functional groups at the expense of others requiring different conditions.

References

American Public Health Association, 1975. Standard methods for the Examination of Water and Waste Water. 14th Edition. Am. Publ. Health Assoc., Washington. 1193 pp.

Bahr, L. M., Jr., 1982. Functional taxonomy: an immodest proposal. Ecol. Modelling 15: 211-233.

Bishop, J. E., 1973. Limnology of a Small Malayan River Sungai Gombak. Dr. W. Junk Publ., The Hague, 485 pp.

Cummins, K. W., 1974. Structure and function of stream ecosystems. BioScience 24: 631-641.

Dudgeon, D., 1982. Aspects of the hydrology of Tai Po Kau Forest Stream, New Territories, Hong Kong. Arch. Hydrobiol. Suppl. 64: 1-35.

Dudgeon, D., 1983a. Seasonal and long-term changes in the hydrobiology of the Lam Tsuen River, New Territories, Hong Kong, with special reference to benthic macroinvertebrate distribution and abundance. Arch. Hydrobiol Suppl. 69: 55-129.

Dudgeon, D., 1983b. Spatial and temporal changes in the distribution of gastropods in the Lam Tsuen River, New Territories, Hong Kong, with notes on the occurrence of the exotic snail Biomphalaria straminea. Malac. Rev. 16: 91-92.

Haefner, J. D. & J. B. Wallace, 1981. Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. Can. J. Fish. aquat. Sci. 38: 353-359.

Hawkins, C. P. & J. R. Sedell, 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology 62: 387-397.

Hawkins, C. P., M. L. Murphy & N. H. Anderson, 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63: 1840-1856.

Marchant, R., 1982. Life spans of two species of tropical mayfly nymph (Ephemeroptera) from Magela Creek, Northern Territory. Aust. J. mar. Freshwat. Res. 33: 173-179.

McLachlan, A. J. & S. M. McLachlan, 1971. Benthic fauna and sediments in the newly created Lake Kariba. Ecology 52: 800-809.

Merritt, R. W. & K. W. Cummins, 1978. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publ., Iowa, 441 pp.

Minshall, C. W., R. C. Peterson, K. W. Cummins, T. L. Bott, J. R. Sedell, C. R. Cushing & R. L. Vannote, 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monogr. 53: 1-25.

Murphy, M. L., C. P. Hawkins & N. H. Anderson, 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. am. Fish. Soc. 110: 469-478.

Petr, T., 1970. The bottom fauna of the rapids of the Black Volta River. Hydrobiologia 35: 399-418.

Towns, D. R., 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. N.Z. J. mar. Freshwat. Res. 15: 185-192.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Can. J. Fish. aquat. Sci. 37: 130-137.

Winterbourn, M. J., J. S. Rounick & B. Cowie, 1981. Are New Zealand stream ecosystems really different? N.Z. J. mar. Freshwat. Res. 15: 321-328.

Received 25 July 1983; accepted 22 September 1983.