Resource partitioning in a tropical stream fish assemblage

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An assemblage of freshwater fishes inhabiting a medium-sized stream in tropical central Vietnam was investigated with respect to spatial and trophic distribution. Point-abundance sampling, gut content analysis and relative intestine length yielded interspecific differences in niche expression. Conspecific juvenile and adult habitat and feeding niches were also distinct. Niche differences arose mainly from differences in current velocity, substrata and foraging preferences. Extreme specializations, such as selective feeding on hard incustrations of cyanobacteria by adult *Annamia normani*, were present. The low niche overlap suggests that this tropical fish assemblage is structured by competitive interactions.   © 2006 The Authors

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Key words: competition exclusion; diet; feeding ecology; habitat use; niche partitioning; Vietnam.

INTRODUCTION

One of the central goals in ecological research is to explain the coexistence of diverse species assemblages in tropical ecosystems. Water bodies, such as streams, are discrete habitats with a limited number of environmental variables, and are ideal for exploring hypotheses to explain the existence of complex species assemblages. Relatively few studies have dealt with the biotic interactions and environmental factors that play a role in structuring tropical freshwater fish assemblages. Published studies on fish communities in tropical streams have reported varying degrees of niche overlap, ranging from high (Knöppel, 1970; Bishop, 1973; Dudgeon, 1987) to low (Zaret & Rand, 1971; Moyle & Senanayake, 1984). There is also evidence that shifts in resource use can occur due to fluctuations in factors such as water level and food availability (Power, 1983; Ross, 1986).

Two main mechanisms are thought to underpin patterns of assemblage diversity. Trade-off-based theories of interspecific resource competition, such

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as the 'Competitive Exclusion Principle' (CEP; Hutchinson, 1965), predict that species assemblages are structured with respect to resource exploitation. Assemblage diversity is explained by the potentially large number of modes of exploitation of resources, corresponding with highly differentiated patterns of habitat use. The CEP focuses on the role of interspecific competition and niche partitioning, leading to equilibria among a high number of specialized species.

In contrast, neutral theories such as 'Connell's Intermediate Disturbance Hypothesis' (CIDH; Connell, 1978) assume that species are ecologically equivalent in their response to environmental constraints and develop without interspecific tradeoffs; diverse assemblages are the result of a balance between speciation, immigration and stochastic extinction. Neutral theories predict no relationship among species in traits related to resource exploitation and corresponding environmental variables. The CIDH specifically predicts that assemblages of highest diversity are maintained at intermediate levels of disturbance, thereby preventing competitively superior species from dominating. Thus, under the CIDH, pronounced niche differentiation is not predicted for the coexistence of species (Tilman, 2004).

A study of a medium-sized tropical stream in central Vietnam was conducted to ascertain the mechanisms that determine assemblage diversity of tropical stream fishes. Resource partitioning among species was analysed based on micro- and mesohabitat use in combination with diet data. The study river is characterized by annual monsoon flooding and high habitat diversity, fulfilling conditions expected for both CEP and CIDH. Species characteristics were compared, with a distinction drawn between juveniles and adults where possible, to test two alternative predictions about niche differentiation among species: (a) low overall niche overlap, supporting the prediction of an assemblage structured by CEP or (b) high or moderate niche overlap as predicted by CIDH.

MATERIALS AND METHODS

STUDY AREA

Fieldwork was conducted during the dry season, from 8–10 May 2000, in the middle reaches of the River Duc My (12°31′ N; 109°02′ E). The River Duc My is a medium-sized coastal river in central Vietnam, entering the South China Sea at Ninh Hoa. The study area was located in the foothills of the eastern slope of the Annamitic mountains. Except for the most mountainous areas, the landscape around the River Duc My has been influenced by agriculture. At the study site, the river is *c.* 25 m wide and characterized by a gentle gradient and a succession of shallow riffles, with short rocky rapids and deep pools. The studied section comprised a heterogeneous micro- and mesohabitat; the river was partly subdivided into two or three channels by small islands; submerged vascular plants were rare, but the submerged parts of emergent vegetation were common. Canopy cover was fragmentary and the shoreline unregulated. The river bottom consisted mainly of gravel and sand. Visible human impacts were restricted to riparian deforestation, damming of one small branch of the river and fishing. During the study maximum water depth was *c.* 1 m, except for a short section that was dammed where the water depth was 1·5 m. Water clarity was high and the river bottom was visible. Water temperature was *c.* 30° C, pH 7·4 and conductivity *c.* 30 μ S cm^{-1}.

SAMPLING

Samples were taken at 1008 sampling points, following a transverse transect intended to give a representative sample of all mesohabitat types. Sampling took place during daylight between 0830 and 1630 hours. A DEKA 3000 portable electrofishing unit with an anode of 15 cm diameter was activated at points selected in a random-stratified manner (Copp & Penaz, 1988; Copp, 1989). The distance between sampling points was 3 m. Sampling points where water depth was >1·1 m water depth were not sampled. Sampling points were approached carefully to avoid disturbance.

At each sampling point, the following quantitative and qualitative microhabitat variables were recorded: water depth, current velocity, distance to shore, substratum and presence of submerged vegetation. Water temperature was measured to the nearest $0·1°$ C, and current velocity measured with a portable anemometer to the nearest 1 cm s^{-1}. The pH and conductivity were measured once at 0900 hours at the start of the survey. Mesohabitats were classified based on current velocity, depth and dominant substratum; rapids were characterized by high current velocity, low depth and gravel and rock substratum; pools by low current velocity, high depth and a substratum composed chiefly of gravel or sand; bays as having no detectable current velocity, low depth and a sand and mud as substratum; runs as a low current velocity, high depth and substratum dominated by sand and gravel.

Microhabitat variables were classified using depth; from ≤10 cm (class 1) to 11–30 cm (class 2) to >30 cm (class 3); distance to shoreline from ≤1 m (class 1) to >1 to ≤3 m (class 2) to >3 to ≤5 m (class 3) to >5 m (class 4); current velocity with 0 cm s^{-1} (class 1) to 1–50 cm s^{-1} (class 2) to >50 cm s^{-1} (class 3); substratum particle size from rock (class 1) to gravel (class 2) to soft sand and mud (class 3).

During point-abundance sampling, an activated electrode was quickly immersed at the sampling point and placed on the substratum. Fishes immobilized by the electric field were collected immediately in a dip-net by a second operator. Fishes were identified and measured for total length (L_T, tip of snout to the end of caudal fin) to the nearest 1 mm. Representative sub-samples were killed in chlorobutanol (1·1·1·-trichloro-2-methyl-2-propanol) and preserved in 4% formaldehyde for gut content analysis. Specimens of the species collected are archived in the fish collection of the ZFMK (Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany); species, maturity stage and number of recorded specimens are given in Table I. The eight most abundant species, caught with a frequency (mean number of individuals per sample, based on 1008 samples) of >0·015, were used for meso- and microhabitat comparisons.

For *Rasbora paviei* Tirant, (Cyprinidae), *Annamia normani* (Hora) (Balitoridae) and *Schistura namboensis* Freyhof & Serov (Balitoridae), examination of the gonads enabled immature juveniles and sexually mature adults to be differentiated, which permitted detection of intraspecific differences and ontogenetic niche shifts. In *A. normani* and *R. paviei*, adults were >50 mm L_T and in *S. namboensis* >45 mm L_T.

FOOD AND INTESTINE LENGTH ANALYSIS

For the eight most abundant species, except the cobitid loach *Lepidocephalichthys hasselti* (Valenciennes), sub-samples were used for diet and gastro-intestinal tract length analysis. Seven to 30 specimens were examined in each species and stage of maturity (Table II). The body mass of each preserved specimen was measured to the nearest 0·01 g using an electronic balance (Sartorius E2000D) after drying the fish for 1 min between two pieces of tissue paper. Guts were dissected under a binocular microscope. In cyprinids, which do not have a discrete stomach, the anterior third of the intestine was dissected. Specimens in which the stomach (anterior third of intestine in cyprinids) contained no food items were categorized as empty. Gut or stomach contents were embedded in Gelvatol (polyvinylalcohol) and the relative surface area of different food items was estimated for each individual fish. Because food items could not be identified to species they were assigned to broader taxonomic groups. The following 15 categories

TABLE I. Species, maturity stage, number of specimens, index of dispersion (I_D) and abbreviations of fishes caught at 1008 sampling points between 8 and 10 May 2000 in the middle River Duc My

Family	Genus	Maturity stage	n	I_D	Abbreviation
Akysidae	*Akysis calvulus* Ng & Freyhof		4	100	
Anguillidae	*Anguilla marmorata* Quoy & Gaimard		6	133	
Balitoridae	*Annamia normani* (Hora)	Adult	37	351	An
	Annamia normani (Hora)	Juvenile	149	971	Anj
	Schistura namboensis Freyhof & Serov	Adult	14	099	Sn
	Schistura namboensis Freyhof & Serov	Juvenile	20	148	Snj
Chandidae	*Parambassis siamensis* (Fowler)		1	100	
Channidae	*Channa striata* (Bloch)		2	100	
Cobitidae	*Lepidocephalichthys hasselti* (Valenciennes)		33	194	Ln
Cyprinidae	*Osteochilus hasselti* (Valenciennes)		1	100	
	Osteochilus lini Fowler		51	130	Ol
	Poropuntius normani Smith		16	111	Po
	Puntius rhombeus Kottelat		73	216	Pr
	Rasbora paviei Tirant	Adult	29	215	Rp
	Rasbora paviei Tirant	Juvenile	277	362	Rpj
Gobiidae	*Rhinogobius* sp.		25	114	Rs
	Stiphodon sp.		3	100	
Mastacembelidao	*Macrognathus circumcinctus* (Hora)		3	100	
Osphronemidae	*Trichopsis vittata* (Cuvier)		2	100	
Siluridae	*Ompok* sp.		2	100	

I_D, index of dispersion.

were used: Chironomidae larvae, Corixidae, Ephemeroptera larvae, Megaloptera larvae, Simuliidae larvae, Tabanidae larvae, Trichoptera larvae, unidentified aquatic insects, terrestrial arthropods, filamentous algae, cyanobacteria (Nostocales), vascular plant material, detritus, mineral material including sand and gravel and unidentifiable

TABLE II. Relative importance of food items as stomach contents of 10 fish species and total length classes found in River Duc My

Food items	Rashora paviei juveniles			Annamia normani juveniles			Puntius rhombeus			Osteochilus lini			Annamia normani adults		
	V	O	I	V	O	I	V	O	I	V	O	I	V	O	I
Chironomidae larvae	0·17	1	0·01	4·58	6	1·23	0·19	1	0·01				1·68	4	0·4
Corixidae															
Ephemeroptera larvae	3·33	2	0·36				4·44	2	0·45						
Megaloptera larvae															
Simuliidae larvae							3·81	2	0·39						
Tabanidae larvae															
Trichoptera larvae															
Unidentified aquatic insects	9·83	10	5·35				0·74	3	0·11				0·32	2	0·04
Anflug	14·17	8	6·16				0·81	4	0·17	0·91	1	0·08			
Filamentous algae	11·33	9	5·55	5	8	1·79	8·7	7	3·12	0·18	1	0·02	4	8	1·89
Other algae													91·63	18	97·53
Vascular plants	3	2	0·33				7·04	2	0·72						
Detritus	58·17	26	82·24	90·42	24	96·96	74·26	25	95·01	50·27	11	50·78	2·37	1	0·14
Sand										48·64	11	49·12			
Rest															
Number of guts		30			24			27			11			19	
L_T (mm)		34–48			25–49			43–80			61–104			52–106	

TABLE II. Continued

Food items	Rasbora paviei adults			Rhinogobius sp.			Schistura namboensis juveniles			Poropuntius normani			Schistura namboensis adults		
	V	O	I	V	O	I	V	O	I	V	O	I	V	O	I
Chironomidae larvae				28·6	15	38·89	3·16	6	2·03	0·29	1	0·05	5·19	5	1·6
Corixidae				1·6	1	0·15									
Ephemeroptera larvae	5	1	0·86	37·76	13	44·5	51·84	11	61·19				78·19	20	96·53
Megaloptera larvae	2				1	0·18									
Simuliidae larvae	25	1	0·43	9	5	4·08	36·05	9	34·81		1	2·44			
Tabanidae larvae													6·19	2	0·76
Trichoptera larvae				18·8	7	11·93				1·43	1	0·27	7·57	2	0·93
Unidentified aquatic insects	9	5	7·71												
Anflug	36·5	9	56·25												
Filamentous algae	11	4	7·53	0·8	1	0·07				62·86	6	71·7			
Other algae															
Vascular plants	15	3	7·71												
Detritus	18·5	6	19·01	1·2	1	0·11		2	1·92	22·29	6	25·42	2·86	1	0·18
Sand				0·24	2	0·04				0·29	2	0·11			
Rest	2·5	1	0·43												
Number of guts	20			25			19			7			21		
L_T (mm)	49–89			34–48			26–45			41–86			47–71		

O, % occurrence; V, % volume; I, index of food importance; anflug, terrestrial arthropods; rest, unidentifiable material.

material as 'rest'. The term 'detritus' was used to describe fine organic material at different stages of decomposition (Allaby, 1992).

The mean percentage of each food category was calculated for each species. Dietary overlap (O_D) between different species and maturity stages was compared using the index proposed by Schoener (1970): $O_D = 1 - (0 \cdot 5 \sum |p_a - p_b|)100^{-1}$, where p_a = percentage of a food item in species and maturity stage a, and p_b = percentage of a food item in species and maturity stage b. The index produces values between 0 (no overlap) and 1 (complete overlap).

The relative importance of food items was evaluated using the index of food importance (I): $I = 100\ OV\ (\sum OV)^{-1}$, where O = % occurrence and V = % volume.

Food digestibility and diet are related directly to intestine length (Sturmbauer *et al.*, 1992; Kramer & Bryant, 1995*a*, *b*; Delariva & Agostinho, 2001; Pouilly *et al.*, 2003). Length of the uncoiled gastro-intestinal tract was measured from the oesophagus to the anus including stomach if present, following Hugueny & Pouilly (1999). As relative intestine length is known to increase with fish size (Kramer & Bryant, 1995*a*, *b*), data were ln transformed. The Zihler Index (I_Z) (Zihler, 1982) was calculated by dividing the length of the uncoiled gastro-intestinal tract by 10 $M^{0 \cdot 3}$ for 11 species and maturity stages, where M is the fish body mass.

Kramer & Bryant (1995*a*) demonstrated that interspecific comparison of relative intestine length could produce misleading results unless comparisons are made at a common size and account for differences in relative mass. In the present study, size variation among species was high, making direct comparison of similar-sized individuals of all species impossible. Therefore, reduced major axis regressions were used to estimate the interrelationship between relative uncoiled gastro-intestinal tract length of species and maturity stages following the suggestion of Kramer & Bryant (1995*b*). The I_Z allowed an estimate of the influence of different body masses to the species ranking of relative uncoiled gastro-intestinal tract.

HABITAT USE

The mean number of individuals in each species and maturity stage, and the index of dispersion (I_D) ($I_D = S^2 \bar{x}^{-1}$) were calculated following Pilcher & Copp (1997). Species and size class occurrence with respect to meso- and microhabitat variables were visualized using habitat profiles. These are calculated as the difference between the frequency of a species and maturity stage in the group of samples having a given category of environmental variables and the frequency of that species and maturity stage in all samples (Pilcher & Copp, 1997). For each category of environmental variables and species and maturity stages, the relativised electivity E_i^* (Vanderploeg & Scavia, 1979) was calculated, based on semi-quantitative microhabitat classes (Fig. 1). Unlike many alternative indices, E_i^* embodies a measure of occurrence as a function of both the abundance of species and maturity stage at each environmental category and the abundance of other categories present. E_i^* is calculated by: $E_i^* = (W_i - n^{-1})(W_i + n^{-1})^{-1}$, where n is the number of environmental categories available and W_i is determined by: $W_i = (r_i\ p_i^{-1})$ $(\sum r_i\ p_i^{-1})^{-1}$, where r_i and p_i are the percentages of environmental category i used by a species and maturity stage (r_i) and present in the environment, respectively, (p_i); p_i was determined using the composition of all sampling points. E_i^* ranges from −1 to +1, with 0 representing no preference.

Spearman rank correlation coefficients were calculated for microhabitat variables to determine, which environmental variables correlated most with the frequencies of the species and maturity stage.

Canonical correspondence analysis (CCA) was applied to evaluate multivariate fish-habitat relationships, using the programme CANOCO for Windows Version 4·02 (ter Braak & Smilauer, 1997). To perform CCA, null-samples were eliminated. The bivariate plot derived from this analysis illustrates the main pattern of variation in assemblage composition as accounted for by the environmental variables as well as the species and maturity stage distribution along each environmental variable. Arrow length representing an environmental variable is equal to the rate of change in the
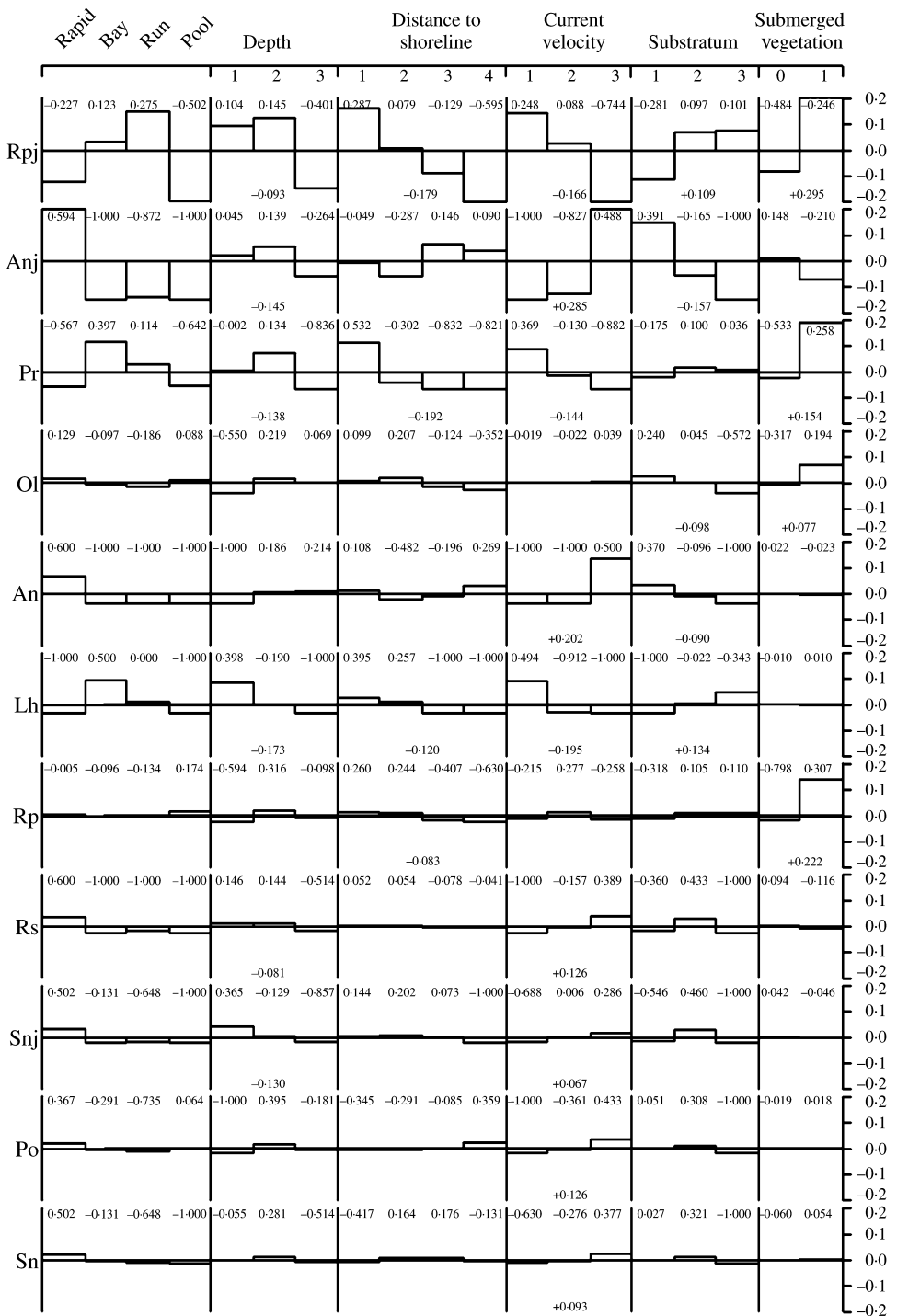
FIG. 1. Environmental profiles calculated as the difference between the frequency of a species and maturity stage in the group of samples having a given category of environmental variable and the

weighted average as inferred from the biplot and is thereby a measure of how much the species distribution differs along that environmental variable; position of the species and maturity stage centre along the ordination axes represents their main occurrence (ter Braak, 1986; Chessel *et al.*, 1987; Pilcher & Copp, 1997). The non-null data were subsequently used to perform a Dunnett-T3 comparison test of averages to compare meso- and microhabitat use between species and maturity stages.

RESULTS

A total of 748 specimens, representing 17 species (Table I), were caught at 327 sampling points. Juvenile *R. paviei* and juvenile *A. normani* were the most abundant fishes and, along with adult *A. normani*, exhibited the greatest tendency for aggregation (Table I). The eight most abundant species, represented by 724 specimens, were chosen for analysis.

Species and maturity stages were found to segregate according to meso- and microhabitat variable (Fig. 2). The average O_D between species and maturity stages reached *c.* 20% of the total possible overlap (Table III), with 0·016 between *Osteochilus lini* Fowler and *Rhinogobius* sp., to 0·794 between juvenile *A. normani* and *Puntius rhombeus* Kottelat.

Distinct differences in habitat use and diet were detected. At the mesohabitat level, two major groups were separated according to their tendency to occur in rapids or in one of the other mesohabitats. A strictly rheophilous group, comprising *Rhinogobius* sp., *A. normani*, *S. namboensis* and *Poropuntius normani* Smith can be distinguished (Table IV and Fig. 1). Within this group, *A. normani* was separated at the microhabitat level from *S. namboensis* and *Rhinogobius* sp. by its tendency to occupy rocks rather than gravel substratum. Juvenile and adult *A. normani* were further distinguished as inhabiting different water depths. Adult *A. normani* occupied rapids and fed selectively on cyanobacteria (Tables II and III), whereas juveniles were detrivorous.

Schistura namboensis and *Rhinogobius* sp. both foraged on aquatic insects, but on different taxa. Ephemeroptera larvae were found to be the almost exclusive food item of adult *S. namboensis*, whereas Simuliidae larvae were also an important component in the diet of juveniles. In contrast, *Rhinogobius* sp. fed on larvae of Ephemeroptera and Chironomidae in nearly equal proportions. The cyprinid *P. normani* was clearly distinguished from the other species studied by its feeding habit, being the only herbivorous species (Table II).

Lepidocephalichthys hasselti was found to be associated with soft-substratum bays; this cobitid was distinguished from all other species by its absence from sites with a measurable current (Table IV and Fig. 1). *Osteochilus lini*, *P. rhombeus* and both juvenile and adult *R. paviei* were found to occur at sites characterized by submerged vegetation. Like *L. hasselti*, *P. rhombeus* showed a high electivity for bays, which were avoided by most other species (Fig. 1). In addition to its occurrence at sites with high current velocity, *P. rhombeus* was

FIG. 1. (Continued) frequency of that species and maturity stage in all samples for meso- and microhabitat variables of 11 fish species and maturity stages (see Table I) in River Duc My. Electivity indices (E_i^*) are given above the bars, significant (95% level) Spearman rank correlation factors below.
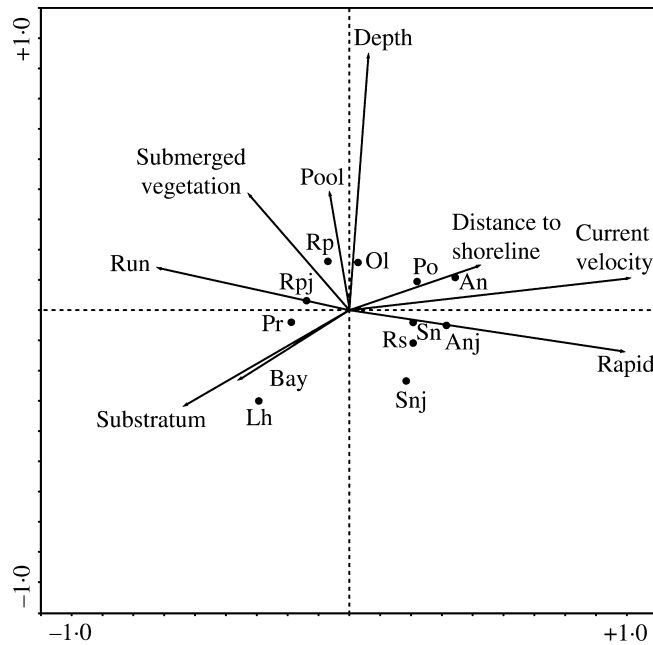
FIG. 2. Canonical correspondence analysis plot of micro- and mesohabitat use of 11 fish species and maturity stages (see Table I) from River Duc My, Vietnam. Arrow length is proportional to the relative importance of that environmental variable. The position of a species, (●), is a composite of all species-species and species-variable interactions, with its position along a given vector (→) generally reflecting the preference of that species relative to other species.

distinguished from *L. hasselti* by occupying deeper water (mainly 11–30 cm, compared to <11 cm). No significant intraspecific differences in habitat use were found between juvenile and adult *R. paviei* (Table IV). Likewise, significant interspecific differences were absent between both stages of *R. paviei*

TABLE III. Dietary overlap between 10 species and maturity stages (see Table I) represented by the Schoener-Index (O_D), ranging from 0 = no overlap to 1 = total overlap

Species and maturity stage	Po	Ol	Pr	Rpj	Rp	Rs	Snj	Sn	Anj
An	0·067	0·026	0·069	0·069	0·067	0·037	0·041	0·041	0·081
Anj	1·276	0·505	0·794	0·633	0·235	0·066	0·121	0·074	
Sn	0·046	0·029	0·075	0·064	0·079	0·517	0·579		
Snj	0·221	0·089	0·174	0·124	0·164	0·511			
Rs	0·13	0·016	0·104	0·055	0·095				
Rp	0·32	0·196	0·427	0·59					
Rpj	0·338	0·514	0·749						
Pr	0·35	0·513							
Ol	0·228								

TABLE IV. Between species and maturity stage (see Table I) comparison (Dunnett-T3 comparison test of mean) of meso- and microhabitat use of the 11 most abundant fish species and maturity stages of the River Duc My

		Anj	Pr	Ol	An	Lh	Rp	Rs	Snj	Po	Sn
Rpj	Mesohabitat	<0·001	NS	NS	<0·001	NS	NS	<0·001	<0·001	NS	<0·001
	Depth	NS	NS	NS	NS	<0·001	NS	NS	NS	NS	NS
	Distance to shoreline	NS	0·022	NS	NS	NS	NS	NS	NS	NS	NS
	Current velocity	<0·001	NS	NS	<0·001	<0·001	NS	<0·001	0·028	0·001	0·013
	Substratum	<0·001	NS	<0·001	0·001	0·02	NS	NS	NS	NS	NS
	Submerged vegetation	<0·001	NS	NS	0·005	NS	0·004	NS	NS	NS	NS
Anj	Mesohabitat		0	<0·001	NS	<0·001	NS	NS	NS	NS	<0·001
	Depth		NS	0·003	0·013	NS	NS	NS	NS	NS	NS
	Distance to shoreline		<0·001	NS	NS	<0·001	NS	NS	NS	NS	0·023
	Current velocity		<0·001	<0·001	NS	<0·001	<0·001	NS	NS	<0·001	0·002
	Substratum		<0·001	NS	NS	<0·001	0·009	0·001	0·001	NS	NS
	Submerged vegetation		0·038	NS	NS	NS	0·005	NS	NS	NS	NS
Pr	Mesohabitat			NS	<0·001	NS	NS	<0·001	<0·001	NS	<0·001
	Depth			0·001	0·013	0·035	NS	NS	NS	NS	NS
	Distance to shoreline			0·028	0·013	NS	NS	NS	NS	001	0·023
	Current velocity			0·015	<0·001	0·001	NS	<0·001	0·003	<0·001	0·002
	Substratum			0·01	0·002	NS	NS	NS	NS	NS	NS
	Submerged vegetation			NS	NS	NS	NS	NS	NS	NS	NS
Ol	Mesohabitat				<0·001	NS	0·002	0·031	0·002	NS	0·03
	Depth				NS	<0·001	NS	NS	0·003	NS	NS
	Distance to shoreline				NS	NS	NS	NS	NS	NS	NS
	Current velocity				<0·001	<0·001	NS	0·049	NS	0·014	NS
	Substratum				NS	<0·001	NS	NS	NS	NS	NS
	Submerged vegetation				NS	NS	NS	0·01	NS	NS	NS
An	Mesohabitat					<0·001	0·002	NS	NS	NS	NS
	Depth					<0·001	NS	NS	0·003	NS	NS
	Distance to shoreline					0·021	NS	NS	NS	NS	NS
	Current velocity					<0·001	<0·001	0·009	0·016	NS	NS
	Substratum					<0·001	0·022	NS	0·033	NS	NS
	Submerged vegetation					NS	0·006	NS	NS	NS	NS

Table IV. Continued

		Anj	Pr	Ol	An	Lh	Rp	Rs	Snj	Po	Sn
Lh	Mesohabitat						NS	<0.001	<0.001	NS	<0.001
	Depth						<0.001	NS	NS	<0.001	NS
	Distance to shoreline						NS	NS	NS	0.016	0.035
	Current velocity						<0.001	<0.001	<0.001	<0.001	<0.001
	Substratum						NS	<0.001	0.001	<0.001	0.001
	Submerged vegetation						NS	NS	NS	NS	NS
Rp	Mesohabitat							0.038	0.009	NS	0.031
	Depth							NS	0.038	NS	NS
	Distance to shoreline							NS	NS	NS	NS
	Current velocity							0.033	NS	0.009	NS
	Substratum							NS	NS	NS	NS
	Submerged vegetation							0.031	NS	NS	NS
Rs	Mesohabitat								NS	NS	NS
	Depth								NS	NS	NS
	Distance to shoreline								NS	NS	NS
	Current velocity								NS	NS	NS
	Substratum								NS	NS	NS
	Submerged vegetation								NS	NS	NS
Snj	Mesohabitat									NS	NS
	Depth									0.029	NS
	Distance to shoreline									NS	NS
	Current velocity									NS	NS
	Substratum									NS	NS
	Submerged vegetation									NS	NS
Po	Mesohabitat										NS
	Depth										NS
	Distance to shoreline										NS
	Current velocity										NS
	Substratum										NS
	Submerged vegetation										NS

NS, non-significant.

and *O. lini*, except for the predominant use of coarse substratum in *O. lini* contrasting with fine substratum in juvenile *R. paviei* (Table IV and Fig. 1). In addition, juvenile *R. paviei* were most prominent in runs, whereas adults exhibited a slight preference for pools (Figs 1 and 2). Adult *R. paviei* and *O. lini* were underrepresented in habitats with shallow water (Fig. 1). The feeding habits of adult *R. paviei* were clearly distinct from those of *O. lini* and juvenile *R. paviei*; the diets of both *O. lini* and juvenile *R. paviei* were dominated by detritus, with *O. lini* feeding exclusively on detritus (Table II).

Clear patterns were evident in relative gastro-intestinal tract length (Figs 3 and 4 and Table V). The highest relative uncoiled gastro-intestinal tract length was found in the detrivorous *O. lini*, followed by *P. normani*, adult and juvenile *A. normani* and *P. rhombeus*. Lower values were shown by both maturity states of *R. paviei*, followed by *Rhinogobius* sp. and adult *S. namboensis*. Juvenile *S. namboensis* possessed a conspicuously low relative uncoiled gastro-intestinal tract length. The I_Z (Table V) based on body mass widely supported this succession.

DISCUSSION

Kramer & Bryant (1995a) demonstrated for tropical stream fishes in Panama that relative intestine length of fishes increases from insectivores and omnivores to herbivores. Bowen (1983) ranked relative intestine development in relation to diet as: carnivores < omnivores < herbivores < detrivores, which is generally interpreted as a reflection of the resistance of different foods to digestion. A corresponding pattern of intestine length relative to both body length and mass is present in River Duc My (Table V). Based on the I_Z, species feeding mainly on aquatic insect larvae (*S. namboensis*, *Rhinogobius* sp.) have the shortest relative gastro-intestinal tract length, whereas species feeding mainly on detritus, algae or cyanobacteria (*O. lini*, *P. normani* and *A. normani*) possess the longest. In the context of diet plasticity of tropical fishes (Zaret & Rand, 1971; Lowe-McConnell, 1975), these results suggest trophic specialisation does occur in the fish communities of tropical streams. Differences in trophic ecology broadly correspond to morphological adaptations of the feeding apparatus. For example, the position of the mouth is superior in terrestrial insect feeding *R. paviei*, terminal in drift-feeding *Rhinogobius* sp., inferior in the cyanobacteria-grazing *A. normani* and sub-terminal to inferior in species feeding on detritus (*O. lini* and *P. rhombeus*) vascular plants (*P. normani*) or invertebrates in gravel (*S. namboensis*).

In *R. paviei*, the finding that detritus-feeding juveniles possess a shorter relative uncoiled gastro-intestinal tract than adults, which feed on terrestrial insects, raises the question of whether the samples present were representative. Moreover, there is no difference between gradients in the major axis regression between juveniles and adults (Fig. 4). Therefore, detritus cannot be excluded as a temporary diet in juvenile *R. paviei*, as proposed by Bowen (1983) and Lowe-McConnell (1975) for other tropical freshwater fish species. As *R. paviei* has a superior mouth, it is unlikely to be specialized for benthic detritus. Instead, dietary analysis suggests that it is euphagic, feeding mainly on drifting items during the juvenile stage and later switching to allochthonous material.
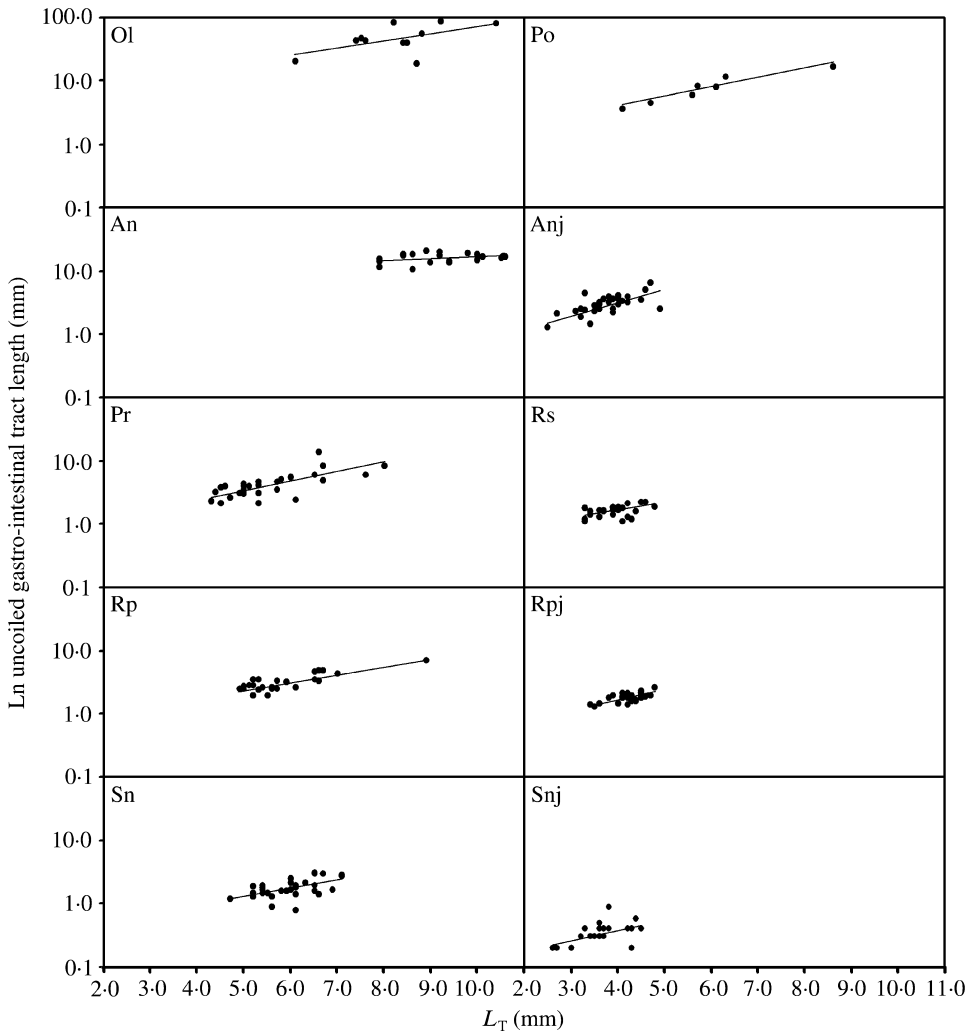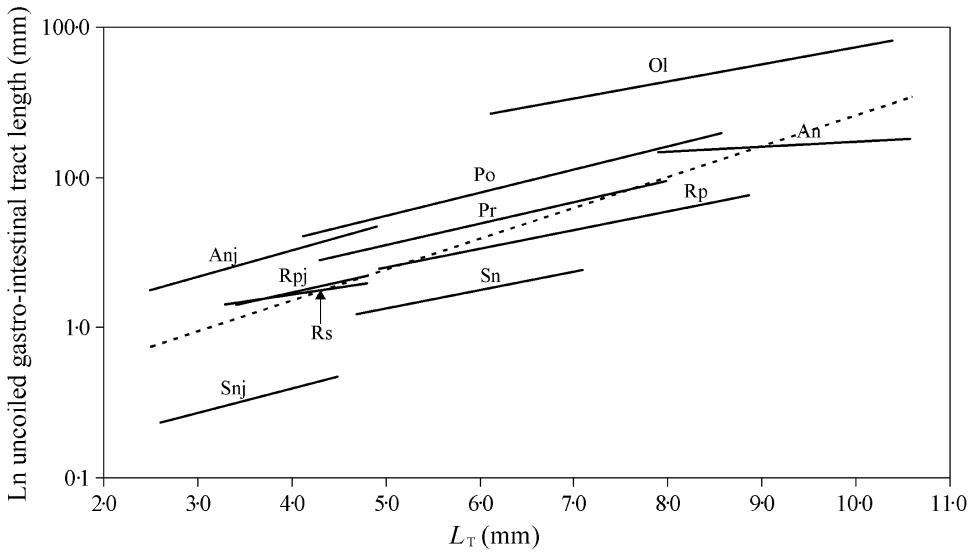
FIG. 3. Relationship between uncoiled gastro-intestinal length and total length for 10 fish species and maturity stages (see Table I) from River Duc My, representing different feeding types from cyanobacteriovor (*Annamia normani*) and detrivor (*Osteochilus lini*) to insectivor (*Schistura namboensis*), with different graduations. ●, individual specimens. Lines are the reduced major axis regression lines: Ol, $y = 5.4751e^{0.2574x}$ ($r^2 = 0.314$); Po, $y = 0.909e^{0.3586x}$ ($r^2 = 0.907$); An, $y = 8.8765e^{0.0645x}$ ($r^2 = 0.096$); Anj, $y = 0.6374e^{0.411x}$ ($r^2 = 0.437$); Pr, $y = 0.6795e^{0.3241x}$ ($r^2 = 0.520$); Rs, $y = 0.6883e^{0.2163x}$ ($r^2 = 0.208$); Rpi, $y = 0.6032e^{0.2805x}$ ($r^2 = 0.685$); Rpj, $y = 0.4835e^{0.3143x}$ ($r^2 = 0.458$); Sn, $y = 0.3283e^{0.2806x}$ ($r^2 = 0.272$); Snj, $y = 0.0846e^{0.3818x}$ ($r^2 = 0.280$).

The prevalence of debris in the diet of *R. paviei* might indicate that food was limited during the study.

Puntius rhombeus appeared to be a specialized detritivore, although its relative gut length was the lowest of the non-insectivorous species (Table V). Detritus might serve as a temporary dietary item when its preferred food is

FIG. 4. Relationship between uncoiled gastro-intestinal length and total length for 10 fish species and maturity stages from River Duc My. Lines are the combined reduced major axis regression lines from Fig. 3. (---), the total major axis regression line for all species and maturity stages $y = 0.217e^{0.4833x}$ ($r^2 = 0.581$). Regression lines demonstrate potential intersections and restricted data comparability.

not available, a pattern known to occur in several omnivorous species (Lowe-McConnell, 1975; Bowen, 1983). Detritus can be an important nutritional component in the diets of fishes in tropical freshwater ecosystems (Bowen, 1983; Lowe-McConnell, 1987). It is most important in backwaters and floodplain pools of lower river sections. In the River Duc My, detrivory also appears to be important in the lotic environment. Surprisingly, even the rheophilous juveniles of *A. normani* were found to feed on detritus, perhaps grazing detritus that accumulates on cyanobacteria incrustations and rock surfaces. *Annamia*

TABLE V. Intestine length in relation to total length (mean relative ln intestine length) and body mass (mean Zihler Index, I_Z) for 10 species and maturity stages (see Table I)

Species	Mean relative ln intestine length	I_Z
Ol	0·467	27·107
Po	0·341	6·194
An	0·303	10·008
Anj	0·288	5·005
Pr	0·251	3·522
Rp	0·193	2·633
Rpj	0·141	2·160
Rs	0·12	2·009
Sn	0·092	1·507
Snj	−0·316	0·505

normani was previously considered as insectivorous (Rainboth, 1996). Present results suggest adult *A. normani* to be a rare example of a freshwater fish that specializes on grazing cyanobacteria, a feeding strategy rarely mentioned in the literature (Gerking, 1994) and not commonly known for inhabitants of rapids. Nostocale cyanobacteria form hard encrustations on the surfaces of rocks in regions where current velocities are high (pers. obs.). For the species encountered, this food item is probably only accessible to large *A. normani* specimens, which are able to bite pieces out of these encrustations. Juveniles of the same species ingest detritus particles in shallower areas of the same mesohabitat.

Poropuntius normani was found to be the only strictly herbivorous fish species in this study (Table II). Although the species is herbivorous, only filamentous algae, no vascular plant material, were found in its gastro-intestinal tract. This finding also does not agree with Rainboth (1996) who described two species of this genus, possibly not the species studied here, as feeding primarily on insect larvae.

The finding that *Rhinogobius* sp. fed on aquatic invertebrates agrees with Sone *et al.* (2001) who reported that Japanese species of this genus feed mainly on drifting aquatic invertebrates. The stomach contents of *Rhinogobius* sp. in the present study contained 85% Ephemeroptera, Trichoptera and Chironomidae (Diptera) (Table II), which are known to be common among drifting invertebrates (Dudgeon, 1983; Sone *et al.*, 2001). Coarse substrata such as gravel, which are found where current velocities are relatively high are preferred by *Rhinogobius* sp. and the density of drifting invertebrates increases with current velocity (Allan & Russek, 1985). Thus, habitat use by *Rhinogobius* sp. appears to correspond with the occurrence of drifting invertebrates. The foraging behaviour of this goby is facilitated by its ventral sucking-disc, allowing the fish to maintain its position in rapid currents (pers. obs.).

The loach *S. namboensis* fed more selectively on Ephemeroptera larvae than did *Rhinogobius* sp.; this fish has been observed to move actively within the interstitial spaces of gravel substrata. These observations agree with the results of Dudgeon (1983), who found *Schistura hingi* (Herre) [as *Shistura fasciolata* (Nichole & Pope); Freyhof & Serov, 2001] in a Hong Kong stream feeding mainly on benthic, and occasionally on drifting insects. In *S. namboensis*, juveniles possess a conspicuously low relative intestine length (Figs 3 and 4), suggesting juveniles of this loach may feed on invertebrates from an early stage.

Like allochtonous vegetable material, the quantity of terrestrial arthropods reaching the stream surface may depend on the extent of riparian cover, which might explain the minor role of terrestrial arthropods in the diets of fishes in the River Duc My. In contrast, the majority of fishes in Amazonian waters appear to depend on terrestrial arthropods (Saul, 1975).

Lowe-McConnell (1987) characterized fish feeding habits in seasonal environments such as streams as either facultative or specialized mostly in the lower trophic levels. She argued that under conditions of seasonal change, fishes have to feed on whatever is available at that time, which precludes specialization. There was no definitive evidence for this pattern in the present study. *Puntius rhombeus*, *O. lini* and juvenile *A. normani* feed selectively on detritus, *P. normani* on filamentous algae and adult *A. normani* on cyanobacteria. Equally distinct feeding and habitat preferences were shown by insectivorous species.

Niche overlap leads to competition if resources are limited. In the present study, there was little evidence for niche overlap in terms of habitat use or diet. Spatially, all species could be classified as either rheophilous or stagnophilous. Habitat use could further be differentiated based on substratum preferences and other microhabitat variables. With respect to foraging, a wide variety of strategies, ranging from specialized cyanobacteria feeding, to detritus feeding, to specialization on terrestrial arthropods suggested niche partitioning. In addition to interspecific niche differences, there were differences between conspecifics belonging to different maturity stages. These distinct intra- and interspecific niche differences suggest that trade-off-based mechanisms driven by competition structure the fish assemblage of the River Duc My. The CEP, which focuses on competition for limited resources, may explain the observed patterns. In contrast, the sympatric coexistence of species and maturity stages that exhibited distinct patterns of resource exploration does not match the assumptions of neutral theory; there was no indication of similar patterns of resource exploitation among species.

The present data, however, are purely observational. Direct tests for competition would require extensive removal experiments in the field, which are not accomplishable for a complex tropical stream. Nevertheless, consistent results of stomach content analysis and relative intestine length, corresponding to feasible patterns in micro- and mesohabitat choice, support the hypothesis of differentiated adaptations. Understanding of the forces structuring this community, however, would benefit from inclusion of the factors daytime and season, both of which would require multiple higher numbers of samples. In this context and due to the absence of comparative studies in small south-east Asian rivers, the possibility cannot be excluded that niche overlap does occur during different seasons, as suggested by Zaret & Rand (1971) for neotropical streams. Since competition is the best explanation for the observed pattern of niche partitioning, however, competitive mechanisms have to be considered as the force most likely structuring the fish assemblage of River Duc My.

The CIDH and the CEP are concepts that focus on opposing mechanisms for community structure. Combinations of both mechanisms may exist, *e.g.* in ecosystems influenced by both stochastic events and competition. The River Duc My may be a system where both factors operate: water level and thereby resources fluctuate markedly among seasons.

The present results accord with previous studies that suggest habitat choice and resource partitioning are mechanisms for the coexistence of different species in the same environment (Connell, 1978; Whitham, 1980; Moyle & Vondracek, 1985; Ross, 1986; Sone *et al.*, 2001). The findings of Gorman & Karr (1978), Owen & Karr (1978) and Fausch (1984) suggest habitat specialization as a key factor that structures stream fish communities, with foraging specialization depending on food abundance and differentiated feeding efficiency. Zaret & Rand (1971) refer directly to the CEP in explaining the structure of an assemblage of fishes in a Central American stream. A number of additional studies have led to similar conclusions (Dudgeon, 1987).

Dudgeon (1987) explained conspicuous niche overlap of fishes in a Hong Kong stream on the basis of disturbance-related mortality and disruption of the assemblage during the monsoon season. Several additional studies have

reported minimal niche differentiation in tropical stream fish communities (Knöppel, 1970; Bishop, 1973; Saul, 1975; Goulding *et al.*, 1988) suggesting that assemblages of tropical stream fishes can reflect stochastic processes during the wet season. In the River Duc My, however, distinct patterns in habitat and feeding preference with low niche overlaps between different species and between juvenile and adult conspecifics suggest a community structured by trade-off-based mechanisms, such as competition exclusion.

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