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Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes

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Analysis of stomach contents of larvae, juveniles and adults of three closely related armoured catfishes in coastal plain swamps of Suriname, South America, revealed major ontogenetic diet shifts. Larvae of *Hoplosternum littorale*, *H. thoracatum* and *Callichthys callichthys* showed a restricted diet of rotifers and microcrustacea. Diets of juveniles and adults were more diverse, but large volumes of microcrustacea, aquatic insect larvae and detritus were always present. In all three species diet overlap was especially low between larvae and adults. The proportion of detritus in the stomach was positively related to fish size, which probably reflected the inability of larger size classes to separate effectively benthic invertebrate prey from bottom substrata, and not a specialization towards detritivory. Adults showed only minor seasonality in diet composition, and no effect of season on diet breadth. Interspecific diet overlap among larvae, juveniles and adults did not differ significantly from 1 (complete overlap). Lack of food partitioning was probably related to a similar morphology of the three catfishes. Intraspecific between-size class diet overlap was considerably lower than interspecific within-size class overlap. It is suggested that large interspecific diet overlap occurred because food was not limiting the populations of these catfish. However, the nest habitats of the three species differed.

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Key words: *Hoplosternum littorale*; *Hoplosternum thoracatum*; *Callichthys callichthys*; resource partitioning; diet breadth; seasonality; Suriname.

INTRODUCTION

Alpha diversity, the number of species that occur together in a particular biotope, is characteristically very high in many tropical freshwater fish communities (Lowe-McConnell, 1987). Two central questions in neotropical fish ecology are: what factors determine how many different species are able to coexist in the same community, and how do they divide or share the available resources?

In a recent review of resource partitioning in fish communities, Ross (1986) observed greatest separation of species along the diet axis (57%), followed by habitat (32%) and time of activity (11%). As Goulding (1980) pointed out, investigation of the use of food is probably the best starting point for understanding how fish communities function. Studies on neotropical freshwater fish have shown marked seasonality in diet composition and feeding level (Lowe-McConnell, 1964; Zaret & Rand, 1971; Goulding, 1980), ontogenetic diet shifts (Angermeier & Karr, 1983; Winemiller, 1989), size-related fat storage potential (Gouding, 1980; Junk, 1985) and (lack of) resource partitioning

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(Knöppel, 1970; Zaret & Rand, 1971; Goulding, 1980; Angermeier & Karr, 1983; Winemiller, 1989).

Conclusions on the importance of food resource partitioning derived from the studies mentioned above are radically different. Knöppel (1970) was unable to detect significant differences in the diet composition of fishes in Amazonian rainforest streams. Zaret & Rand (1971) found low diet overlap in the dry season among fishes of a rainforest stream in Panama. Angermeier & Karr (1983), also working with Panamanian stream fish in the dry season, found large diet overlap within feeding guilds. Goulding (1980) reported important feeding specializations in large floodplain fishes in the wet season, although resource partitioning was much less distinguishable between closely related species. In the Venezuelan Llanos, Winemiller (1989) found low dietary overlap among piscivores throughout the year.

According to the 'competitive exclusion principle' two species occupying identical ecological niches cannot coexist indefinitely in the same place, one will ultimately exclude the other (Giller, 1984). Consequently it is the coexistence of closely related and morphologically similar species that is the most difficult to explain. Most studies on food partitioning among neotropical freshwater fishes explore patterns of food exploitation among a relatively large number of species that are more often than not only distantly related with each other, and also morphologically very distinct. Yet, if food partitioning is important in preventing competitive exclusion, differences in food utilization must exist not only at the generic level, but also, and more importantly, between closely related and morphologically similar species.

The present study examines diet composition and diet overlap among three closely related and morphologically similar armoured catfishes of the subfamily Callichthyinae (Hoedeman, 1952; Burgess, 1989), *Hoplosternum littorale* (Hancock, 1828), *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), and *Callichthys callichthys* L., 1758. All three species are widely distributed throughout (sub)tropical South America, and often occur together in the same waterbody (i.e. they are syntopic) (Mol, 1994). In Suriname, they are among the most common bottom dwelling fish of coastal plain swamps (Ouboter & Mol, 1993). Floating bubble nests of the callichthyids appear in the newly flooded swamps at the onset of the rainy season (Mol, 1993a). Reproduction continues with few interruptions until swamp water levels drop and the fish move back to their dry season habitat of pools, canals and creeks. The following questions are essential to this study: (1) Do these closely related catfishes partition available food resources? (2) Do seasonal trends of resource availability affect diet composition and diet overlap among the three species? (3) What is the relationship between ontogeny and food resource partitioning?

MATERIAL AND METHODS

STUDY SITE

In the period December 1989–December 1992 *H. littorale*, *H. thoracatum*, and *C. callichthys* were collected in swamps and swamp forests in the coastal plain of Suriname (5–6° N). Most fish (89%, $n=681$) were collected at two localities; a *Typha* dominated swamp at Weg Naar Zee, 5 km north of the capital Paramaribo; and a mixed

swamp and swamp forest area at Lelydorp, 20 km south of Paramaribo. The coastal plain experiences extensive sheet flooding during the two rainy seasons each year (December–January and April–July; Snow, 1976). In the main dry season of August–November the water retreats into small pools, canals and creeks. The chemistry of the coastal plain water bodies changes considerably during the seasonal cycle, mainly as a result of dilution by electrolyte-poor rainwater, and the influence of penetrating sea water in the dry season (Mol, 1993b). Fish and aquatic invertebrates also react to the regular flooding of the swamps (Mol, 1993a, b). As rainfall in December–January was relatively heavy during the period of investigations and the swamps remained flooded in February and March, the annual cycle was divided in a rainy season, or high water period from 15 December to 15 August, and a dry season, or low water period from 15 August to 15 December.

SAMPLING

In the rainy season, larvae (terminology of Balon, 1985), juveniles and adults were collected in the swamps. In the dry season adults and a few juveniles were collected in pools, canals and creeks. There was no success in attempting to catch larvae at the breeding grounds and eggs were therefore collected on the point of hatching from floating bubble nests (Mol, 1993a), and the newborn free embryos (yolk-sac larvae) reared for 4 days at the exact location of the nest in mosquito mesh enclosures of $(1.0 \times 0.5 \times 0.5\text{ m}; 1.7\text{ mm unstretched mesh})$. The mesh size of the enclosures was larger than the width of the mouth gape of the larvae ($0.73 \pm 0.04\text{ mm}$, mean \pm S.E., $n=60$; age 4 days). One or two days after hatching the yolk sac was consumed, and at approximately 7 mm total length the larvae started feeding on exogenous food. The stomach fullness of the larvae (Appendices 1–3) did not indicate a negative effect of the enclosures on the feeding activity of the fish. Larvae of *H. littorale* were identified by the nest from which they were taken (Mol, 1993a); larvae of *H. thoracatum* and *C. callichthys* were identified by their pigmentation pattern (Mol, in preparation) after rearing a few fish of each nest for 10 days in the laboratory with *Artemia nauplii*. Juveniles were collected by seines at the spawning grounds at various intervals during the rainy season. They were identified by their pigmentation pattern and morphological characteristics. Adults were collected by gillnet in the rainy season, and by seine and cast net in the dry season. Larvae and juveniles were preserved in 4% formalin. Adults were preserved in 10% formalin or frozen at -15°C .

PREPARATION AND ANALYSIS OF STOMACH CONTENTS

All specimens were measured for standard length to the nearest 0.1 mm; fresh weight was determined to the nearest 0.1 mg for larvae and juveniles, and to the nearest 0.1 g for adults. The width of the mouth gape was measured to the nearest 0.1 mm as the maximum horizontal distance across the inner side of the open mouth. Unpublished data from a laboratory culture were also used to determine the relationship between the standard length and the width of the mouth gape. In order to establish morphological similarity between the three callichthyids 25 adult specimens of each species were examined following methods developed by Keast (1966) and Nijssen (1970).

The alimentary canal of the larvae and juveniles was removed, and opened under a dissecting microscope. Stomach fullness was estimated as 0, 5, 25, 50, 75 or 100% of a fully extended stomach. The stomach contents of each individual were spread out on a $5 \times 5\text{ cm}$ glass slide and examined systematically under a light microscope (100 and $400\times$). Food items were identified, counted, and their volume was estimated as a percentage of total stomach contents by determining the amount of surface of the glass slide covered for each item. Estimated volume percentages were adjusted for stomach fullness in all further calculations (Hyslop, 1980). Frequency of occurrence was based on examined, including empty stomachs. Calculations of the mean number of food items also included empty stomachs.

Adult specimens often showed large visceral fat deposits in the coelomic cavity. These fat deposits were removed and weighed to the nearest 0.1 g. The length of the intestine was measured to the nearest 1 mm. The contents of the stomach were spread out on a Petri dish and examined under a dissecting microscope following procedures described above for larvae and juveniles. Samples of the stomach contents of each fish were examined under a light microscope for presence of small food items and setae of Oligochaeta.

Initially 46 categories of food items were recognized, but for analyses of diet breadth and diet overlap, food items were grouped into 16 categories: algae, Testacea (dipflugidae), Rotifera, Nematoda and Oligochaeta, microcrustacea (Cladocera, Copepoda, Ostracoda and Conchostraca), aquatic larvae and nymphs of insects, aquatic adult insects, Gastropoda, terrestrial Arthropoda (including insects), fish scales, invertebrate cysts, seeds/spores, detritus, chitinous remains, vegetative plant matter, and a miscellaneous group. Detritus was defined as dead organic matter that has been altered in some way that renders it unlike its original form (Bowen, 1983).

For analysis of ontogenetic diet shifts, dissected specimens were grouped into 10-mm intervals. The average volumetric proportion of the major food items, Rotifera, microcrustacea, aquatic insects (including larvae and nymphs) and detritus, was determined for each interval.

DIET BREADTH AND DIET OVERLAP

Only specimens caught at Lelydorp in the 1991/1992 breeding season were used for the determination of diet breadth and diet overlap ($n=374$, Table II). Estimated percentage volumes adjusted for stomach fullness were used in the calculations. Diet breadth was calculated by Levins' measure (Krebs, 1989). Levins' standardized measure was also used because the number of resource categories in the diet differed among developmental stages.

$$B = 1/(\sum p_i^2) \text{ and } B_A = (B - 1)/(n - 1)$$

where: B =Levins' measure of niche breadth; p_i =proportional contribution of resource i to the total diet ($\sum p_i = 1.0$); B_A =Levins' standardized niche breadth; n =number of possible resource categories.

Diet overlap was calculated by Horn's information index (Krebs, 1989). Horn's index was chosen because it is commonly used, the bias for number of resource categories, sample size and resource unevenness is relatively low compared to other indices (Smith & Zaret, 1982), and the index can be evaluated statistically by χ^2 (Zaret & Smith, 1984). Horn's index (R_0) varies from 0, when diets are completely distinct (containing no food categories in common), to 1 when diets are identical with respect to proportional food category composition.

$$R_0 = [\sum (p_{ij} + p_{ik}) \cdot \log(p_{ij} + p_{ik}) - \sum p_{ij} \cdot \log p_{ij} - \sum p_{ik} \cdot \log p_{ik}] / 2 \cdot \log 2$$

where: R_0 =Horn's index of overlap for species j and k ; p_{ij} =proportional contribution of resource i to the total resources utilized by species j ; p_{ik} =proportional contribution of resource i to the total resources utilized by species k .

Statistical evaluation by χ^2 of the null-hypothesis of complete overlap follows Zaret & Smith (1984):

$$\chi^2_R = 4 \cdot n \cdot (\ln 2) \cdot (1 - R_0) \text{ with } r - 1 \text{ degrees of freedom}$$

where χ^2_R =chi-square statistic; $n=2 \cdot N_j \cdot N_k / (N_j + N_k)$; N_j =sample size species j ; N_k =sample size species k ; R_0 =Horn's index of diet overlap for species j and k ; r =number of food items used by both species.

Principal component analysis based on volume percentages of food items grouped into 16 categories was used to summarize the results. Computation was done using STATGRAPHICS produced by Statistical Graphics Corporation.

TABLE I. Morphological data for adults of three armoured catfish, *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* in the coastal plain of Suriname (mean \pm S.E., n=25)

	<i>H. littorale</i>	<i>H. thoracatum</i>	<i>C. callichthys</i>	ANOVA	
				<i>F</i>	<i>P</i>
Total length T.L. (mm)	165.8 \pm 3.5	157.0 \pm 1.6	164.3 \pm 3.6	N.S.	0.0958
Standard length s.l. (mm)	128.4 \pm 3.0	125.4 \pm 1.3	133.8 \pm 2.7	N.S.	0.0573
Fresh weight (g)	89.9 \pm 6.7	78.7 \pm 3.5	77.1 \pm 4.6	N.S.	0.1641
Mouth width/s.l.	9.7 \pm 0.2	9.5 \pm 0.2	10.3 \pm 0.2	5.5	0.0061
Eye diameter/s.l.	4.8 \pm 0.1	4.1 \pm 0.1	2.7 \pm 0.1	113.5	<0.0001
Head length/s.l.	28.3 \pm 0.2	25.9 \pm 0.2	22.3 \pm 0.0	122.9	<0.0001
Body width/s.l.	26.9 \pm 0.5	27.0 \pm 0.4	26.4 \pm 0.4	N.S.	0.6423
Body depth/s.l.	31.7 \pm 0.3	29.5 \pm 0.4	21.5 \pm 0.3	282.7	<0.0001
Body depth/body width	1.19 \pm 0.02	1.09 \pm 0.01	0.82 \pm 0.01	161.6	<0.0001
Intestine length/s.l.	1.36 \pm 0.04*	1.02 \pm 0.04**	1.56 \pm 0.04*	37.2	<0.0001
Length barbel upper lip/s.l.	29.4 \pm 0.6	28.9 \pm 0.7	23.3 \pm 0.7	27.2	<0.0001
Length barbel lower lip/s.l.	46.3 \pm 1.9	49.7 \pm 1.0	32.0 \pm 0.8	49.6	<0.0001
Number of lateral scutes					
Ventral row	23	23	26		
Dorsal row	25	25	28		
Mouth position	Terminal	Terminal	Terminal		
Form of caudal fin	Forked	Rectangular	Rounded		
Form of body	Fusiform, laterally compressed	Fusiform, laterally compressed	Fusiform, dorsoventrally compressed		

RESULTS

Although adult *H. littorale*, *H. thoracatum* and *C. callichthys* look very similar, small but significant differences in body form, width of the mouth gape, length of the barbels, eye diameter, and form of the caudal fin were found (Table I).

ONTOGENETIC DIET SHIFTS

Dominant food items in the diet of *H. littorale*, *H. thoracatum* and *C. callichthys* were rotifers, microcrustacea, aquatic insects and detritus (Appendices 1, 2 and 3 respectively). All three species experienced ontogenetic shifts in the consumption of these four major food items (Fig. 1).

Four days after hatching and approximately 2 days after they start feeding, the diet of the larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* was dominated by Rotifera (e.g. *Lecane*, *Monostyla*, *Platyas*, *Cephalodella*) and microcrustacea (mainly Cladocera). Algae, difflugiids (e.g. *Arcella*, *Difflugia*, *Centropyxis*) and Oligochaeta were present in small quantities (Appendices 1-3). Larvae of *C. callichthys* seemed to be able to handle slightly larger food items like small chironomid larvae and Oligochaeta (Appendix 3).

During the first 3 weeks after hatching larvae of the three callichthyids show considerable changes in form of the head, body and fins (Mol, in preparation). Approximately 2 weeks after hatching, at a standard length of 8-9 mm, positive

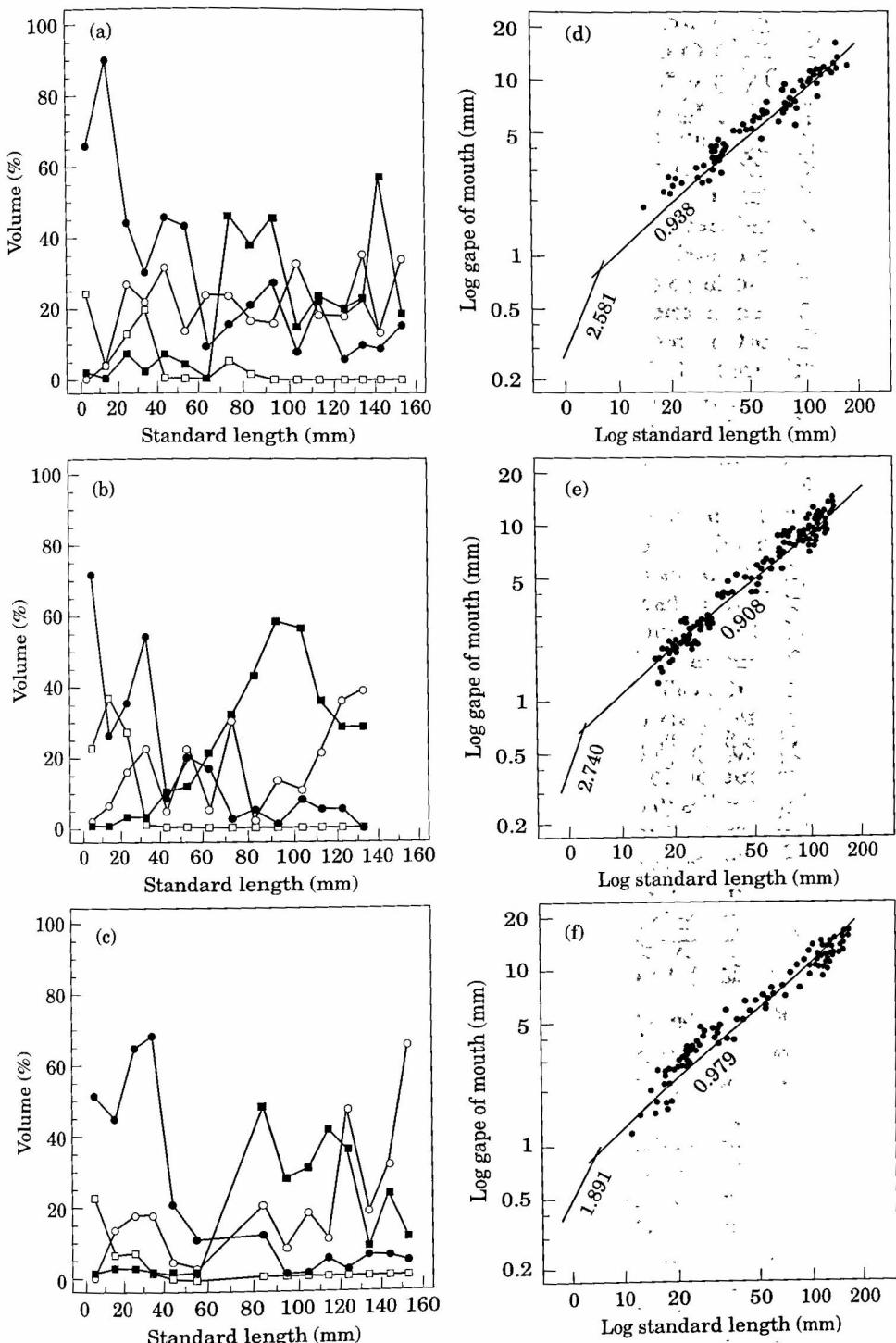


FIG. 1. Average volume percentages of Rotifera (□), microcrustacea (●), aquatic insects, including larva (○) and detritus (■) in the stomach of *H. littorale* (a), *H. thoracatum* (b) and *C. callichthys* (c) grouped by length interval. Growth of the mouth gape with respect to body length of (d) *H. littorale*, (e) *H. thoracatum* and (f) based on tank culture data (solid lines) and field data (●).

allometric growth of the mouth gape changed into isometric growth (Fig. 1). Transformation to a juvenile fish was completed in the third week. Juveniles shifted to a mixed diet comprised primarily of aquatic insects (mainly chironomid larvae) and microcrustacea, with Rotifera still important to the smallest size classes, and detritus to the larger size classes (Fig. 1).

At a standard length of 70–75 mm (*H. thoracatum*), 80–85 mm (*H. littorale*) and 85–90 mm (*C. callichthys*), the fully developed armour of bony plates and mature gonads revealed that juveniles had reached maturity. The diet of adult fish was dominated by aquatic insects and detritus (Fig. 1). Chironomid larvae were found in large numbers in the stomach of all three species. Oligochaeta were not often detected probably due to their fast digestion (Kennedy, 1969), but setae were often present in the stomachs (compare frequency of occurrence of setae with that of Oligochaeta in Appendices 1–3). Oligochaeta are quite abundant in coastal plain zoobenthos samples (Mol, 1993b). Two specimens of *C. callichthys* had consumed a small characoid fish. The width of the mouth gape of *C. callichthys* is larger than that of both *Hoplosternum* species (Table I; Fig. 1).

The relative intestine length (intestinal ratio), defined as the length of the intestine divided by the standard length of the fish, is relatively short in adult *H. littorale*, *H. thoracatum* and *C. callichthys* (1·0–1·6; Table I) compared to that of known detritivores like *Labeo*, *Oreochromis mossambicus* Peters and *Prochilodus* (Bowen, 1983). A muscular grinding stomach, pyloric caeca and extensive mucosal folding of the intestine wall characteristic of *Prochilodus* (Bowen, 1983) are absent in the callichthyids. The intestine is often filled with air.

Diet breadth in larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* was low (Table II). Levins' standardized index is well below 0·1, and only two or three food items out of 16 categories were consumed frequently (Table II). Diet breadth in juveniles (0·096–0·287) showed no large differences with that in adults in the rainy season (0·165–0·354) (Table II). Although Levins' index for juveniles and adults indicates a varied diet for the population as a whole, individual fish often feed on only a few food items. With 44% of the juvenile fish only one or two food items made up 90 volume per cent of the diet. In both rainy and dry seasons 68% of the adult fish had one or two food items making up 90% of their diet.

SEASONALITY IN DIET COMPOSITION

In the dry season mainly adults were collected. Most specimens showed large visceral fat deposits in the coelomic cavity during the first months of the dry season (Table III). These fat stores made up approximately 1% of the body weight in the dry season and 0·3% in the rainy season, the difference being significant (Mann–Whitney test; *H. littorale*, $P=0\cdot026$; *H. thoracatum*, $P<0\cdot001$; *C. callichthys*, $P<0\cdot001$).

Adults showed no significant seasonal differences in the proportion of empty stomachs and in mean stomach fullness (Appendices 1–3). Dietary diversity was also little affected by season (Table II). When the consumption of major food items was compared between seasons, only minor differences were found. *H. thoracatum* consumed more microcrustacea (t -test, $P=0\cdot051$) and less Rotifera (t -test, $P=0\cdot051$) in the rainy season. Rotifera, however, were not

TABLE II. Dietary diversity (diet breadth) as expressed by Levins' index (B), Levins' standardized index (B_A) and the number of frequently consumed food items (volume >5%) for larvae, juveniles and adults of *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* at Lelydorp, Suriname (1991/92)

	<i>n</i>	B	95% confidence interval for B	B_A	Number of food items with volume >5%
Larvae					
<i>H. littorale</i>	52	1.81	± 0.452	0.054	2
<i>H. thoracatum</i>	50	1.57	± 0.367	0.038	2
<i>C. callichthys</i>	78	2.21	± 0.544	0.081	3
Juveniles					
<i>H. littorale</i>	29	3.05	± 1.428	0.137	5
<i>H. thoracatum</i>	25	5.31	± 2.208	0.287	6
<i>C. callichthys</i>	41	2.44	± 0.887	0.096	4
Adults, rainy season					
<i>H. littorale</i>	11	3.47	± 2.003	0.165	4
<i>H. thoracatum</i>	14	4.33	± 8.260	0.222	4
<i>C. callichthys</i>	15	6.31	± 3.422	0.354	6
Adults, dry season					
<i>H. littorale</i>	18	3.74	± 2.079	0.183	4
<i>H. thoracatum</i>	27	4.08	± 1.977	0.205	6
<i>C. callichthys</i>	14	3.94	± 1.904	0.196	4

TABLE III. Visceral fat deposits of *H. littorale*, *H. thoracatum* and *C. callichthys* in the dry season and rainy season expressed as percentage of body weight (mean ± S.E.)

Species	Body weight (g)	Fat deposits (%)
Dry season		
<i>H. littorale</i>	79.9 ± 5.3 (39)	1.15 ± 0.26 (39)
<i>H. thoracatum</i>	54.3 ± 3.0 (48)	1.19 ± 0.14 (48)
<i>C. callichthys</i>	62.3 ± 6.2 (35)	1.11 ± 0.18 (35)
Rainy season		
<i>H. littorale</i>	83.8 ± 8.4 (15)	0.27 ± 0.06 (15)
<i>H. thoracatum</i>	59.0 ± 2.3 (74)	0.19 ± 0.03 (74)
<i>C. callichthys</i>	75.7 ± 4.0 (42)	0.45 ± 0.28 (42)

Number of observations in parentheses.

important in the diet of adult *H. thoracatum* (Appendix 2). Differences in consumption of aquatic insects, aquatic insect larvae and detritus were not significant. In the rainy season Gastropoda were of some importance in the diet of *H. littorale* and, to a lesser extent, *C. callichthys* (Appendices 1, 3). Fish scales were found in dry season stomachs of *H. littorale*, *C. callichthys* and both juveniles and adults of *H. thoracatum* (Appendices 1–3). Juveniles of *H. thoracatum* and *H. littorale* fed on unicellular algae (mainly Euglenophyta) in the dry season. On 20 October 1992 six juvenile *H. thoracatum* were collected in a

TABLE IV. Comparison of diets of larvae, juveniles and adults of *Hoplosternum littorale* (*Hl*), *Hoplosternum thoracatum* (*Ht*) and *Callichthys callichthys* (*Cc*) at Lelydorp (1991/92) using Horn's index of diet overlap

	Larvae			Juveniles			Adults					
			<i>Ht</i>	<i>Hl</i>	<i>Cc</i>	Rainy season			Dry season			
	<i>Ht</i>	<i>Cc</i>				<i>Hl</i>	<i>Ht</i>	<i>Cc</i>	<i>Hl</i>	<i>Ht</i>	<i>Cc</i>	
Larvae												
<i>H. littorale</i>	0.976*	0.964*	0.709	0.596	0.833	0.575*	0.444	0.302	0.506	0.162	0.071	
<i>H. thoracatum</i>		0.952*	0.697	0.551	0.838	0.577*	0.437	0.280	0.459	0.108	0.026	
<i>C. callichthys</i>			0.733	0.590	0.871*	0.592*	0.460	0.349	0.545	0.210	0.104	
Juveniles												
<i>H. littorale</i>				0.791*	0.837*	0.850*	0.774*	0.764*	0.877*	0.549	0.636*	
<i>H. thoracatum</i>					0.681	0.666*	0.582*	0.528	0.687*	0.534	0.330	
<i>C. callichthys</i>						0.830*	0.713*	0.573	0.661*	0.327	0.188	
Adults, rainy season												
<i>H. littorale</i>							0.895*	0.819*	0.771*	0.494	0.403	
<i>H. thoracatum</i>								0.857*	0.777*	0.633*	0.557*	
<i>C. callichthys</i>									0.798*	0.720*	0.717*	
Adults, dry season												
<i>H. littorale</i>										0.806*	0.660*	
<i>H. thoracatum</i>											0.676*	
<i>C. callichthys</i>												

Values marked with an asterisk did not differ significantly from 1 (complete overlap) ($\chi^2_{df,0.05}$).

dry season mud pool with fully extended stomachs filled with the euglenids *Phacus*, *Trachelomonas*, *Lepocinclus* and *Euglena*.

INTRA- AND INTERSPECIFIC DIET OVERLAP

Average diet overlap among *H. littorale*, *H. thoracatum* and *C. callichthys* was high for larvae (0.964), juveniles (0.770) and adults, both in the rainy season (0.857) and dry season (0.715) (Table IV). Most of the pairwise interspecific diet overlaps within one developmental stage were not significantly different from 1 (Table IV), which means that these diets showed complete overlap. Interspecific diet overlap within one developmental stage was larger than intraspecific overlap between two developmental stages. Diet overlap was relatively low between larvae and adults (0.349–0.575, Table IV).

Overlap between the diets of the adults of a species in the rainy and dry season averaged 0.707. They were not significantly different from 1 (Table IV).

Principal component analysis was used to summarize the results of the diet analyses (Fig. 2). Diets of larvae, juveniles and adults of *H. littorale*, *H. thoracatum* and *C. callichthys* were grouped into clusters which reflected primarily the three developmental stages of the callichthyids, and not the species themselves. Clusters were most clearly differentiated by proportional consumption of Rotifera, microcrustacea, insect larvae and detritus (Fig. 2). The rainy season diet of adult *H. littorale* was not assigned to a cluster due to the large Gastropoda component (Appendix 1).

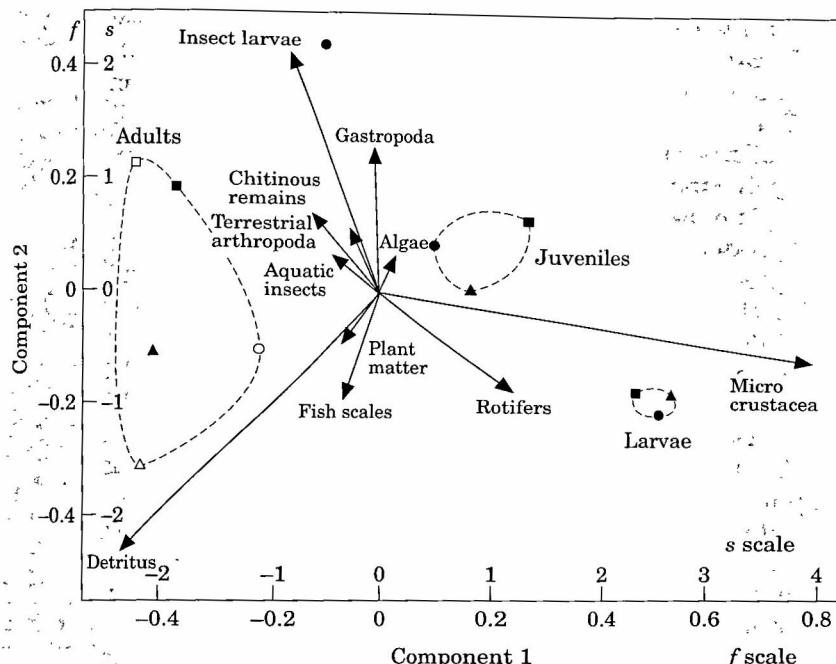


FIG. 2. Principal component analysis ordination diagram of the stomach contents of larvae, juveniles and adults of *H. littorale* (●, ○), *H. thoracatum* (▲, △) and *C. callichthys* (■, □) in covariance biplot scaling (Jongman *et al.*, 1987) with the food items represented by arrows. Closed symbols represent diets in the rainy season and open symbols represent diets of adults in the dry season. The *f* scale applies to food items, the *s* scale to species and their developmental stages. Food items not represented in the diagram lie close to the origin (0, 0). The first component axis accounts for 83.4% of the variance and the second axis explains 5.7%. ---, Grouping of stomach contents derived from average linking cluster analysis of the same data.

DISCUSSION

DIET COMPOSITION

Larvae of *H. littorale*, *H. thoracatum* and *C. callichthys*, fed almost exclusively on microcrustacea and rotifers. Although he did not provide quantitative data, Machado-Allison (1986) stated that in the Venezuelan Llanos 3-day-old larvae of *H. littorale* consumed mainly zooplankton. Zooplanktivorous feeding in larvae of temperate freshwater fish (Keast, 1980; Hartmann, 1983; Mark *et al.*, 1987), and marine fish (Hunter, 1980) is well documented.

Associated with the transformation of the larvae into juveniles, *H. littorale*, *H. thoracatum* and *C. callichthys* started feeding on a more diverse diet of microcrustacea, aquatic insects, Oligochaeta, Nematoda and detritus. The growth of the mouth gape seems to be of special importance, improving prey catch success (Drost, 1987), and allowing feeding on larger, alternative food items (Hartmann, 1983; Osse, 1990). Dietary change with age appears to be the rule in fishes where growth is indeterminate (Helfman, 1978; Werner & Gilliam, 1984), and is also reported for neotropical freshwater fish (Angermeier & Karr, 1983; Winemiller, 1989).

The diet of juvenile *H. littorale* in the coastal plain of Suriname corresponds well with quantitative data on stomach contents of juvenile *H. littorale* in the

Venezuelan Llanos (Winemiller, 1987). In the Surinamese swamps, diets of juvenile *C. callichthys* and *H. thoracatum* resembled that of *H. littorale*. Knöppel (1970) found mainly larvae of Ephemeroptera and Trichoptera in the stomach of juvenile *C. callichthys* from Amazonian rainforest streams. This different diet probably reflects differences in habitat between the shaded rainforest stream (studied by Knöppel, 1970) with very low autochthonous production, and an open floodplain swamp or savanna with more nutrient-rich water and autochthonous production (Lowe-McConnell, 1987). In Suriname, larvae of Ephemeroptera and Trichoptera are characteristic of small rainforest streams in the interior (Leentvaar, 1975).

Adult *H. littorale*, *H. thoracatum* and *C. callichthys* showed a diet comprised mainly of benthic invertebrates (primarily chironomids) and detritus, although microcrustacea were also taken. In Venezuela, Winemiller (1987) also found large volumes of chironomid larvae and detritus in the stomach of adult *H. littorale*. In contrast, detritus (82 volume %) and microcrustacea were the most important food items in adult *H. littorale* in Trinidad (Singh, 1978; unpublished thesis, University of the West Indies). The two isolated findings of piscivory in *C. callichthys* in Suriname are probably no coincidence as this species was found to feed occasionally on fish in Amazonian rainforest streams as well (Knöppel, 1970).

The intestine of adult callichthyids (Table I) is short compared to that of detritivores (Bowen, 1983). Knöppel (1970) even found an intestinal ratio of 0.8 in young adults of *C. callichthys*. The anterior digestive portion of the alimentary tract of *Hoplosternum* is relatively short compared to other teleosts (Huebner & Chee, 1978), and the transparent wall of the larger posterior part is structurally adapted to a respiratory function (Carter & Beadle, 1931; Huebner & Chee, 1978). The same conclusion probably holds for *C. callichthys*. The short intestine and absence of a grinding stomach, pyloric caeca and extensive mucosal folding, indicate that these fish probably are not able to assimilate detrital nonprotein amino acids [as demonstrated in *O. mossambicus* by Bowen (1980, 1981)]. The composition of the detritus in the stomach of the three callichthyids differed from detritus found in *O. mossambicus*. Callichthyid detritus consisted of partially decomposed but easily recognizable plant matter originating from both trees and macrophytes, mixed with small quantities of animal remains. Inorganic mud was never observed in the stomach and sand was not frequent (Appendices 1-3). Detritus in the stomach was very similar to detritus in the posterior part of the intestine, indicating that little digestion had occurred. Detritus in the stomach of *O. mossambicus* consists of a complex aggregate of very fine, flocculant organic matter of uncertain origin, and substantial amounts of inorganic mud (unpublished observations, $n=23$; also see Bowen, 1981, 1983). I think it probable that the three callichthyids accidentally ingested large amounts of detritus when they foraged on benthic invertebrates. On the other hand the callichthyids may actively forage on detritus, and utilize the associated microflora of fungi and bacteria as suggested by Singh (1978).

SEASONALITY AND DIET

Seasonal fluctuation of the water-level was probably the single most important factor affecting the life of fishes in the coastal plain of Suriname. Zooplankton

densities in the flooded swamps (rainy season) were higher than in dry season pools, canals and creeks (Mol, 1993b). Competition theory predicts less dietary overlap between similar species during the lean season when resources are scarce (Schoener, 1982).

Goulding (1980) pointed out that large fish react in a different way to the reduced food availability in the dry season than small species. Large fishes, having a greater volume per surface area, are able to store sufficient fat reserves during the high water period to survive their 'physiological winter' (dry season) (Goulding, 1980; Junk, 1985). A large proportion of empty stomachs and low stomach fullness reveal that large fish almost cease to feed in the dry season. It is during the high water season that they most clearly show their feeding adaptations and partition food resources (Goulding, 1980). Small species, limited by their size in fat storage potential, do not cease to feed in the dry season. Intense competition of large numbers of fish for shrinking food supplies may force these species to specialize in the dry season as was found by Zaret & Rand (1971).

Medium-sized *H. littorale*, *H. thoracatum* and *C. callichthys* did show large fat stores in the first months of the dry season (Table III). This was reported for *H. littorale* in Trinidad (Singh, 1978: unpublished thesis) and Venezuela (Winemiller, 1987). On the other hand mean stomach fullness and the number of empty stomachs in the dry season indicated that adult callichthyids did not cease to feed when confined to low-water habitats (Appendices 1-3). Diet breadth was also little affected by season (Table II). Only minor differences in the diet between seasons, e.g. the presence of fish scales in dry season stomachs were detected. Overcrowding in a shrinking aquatic habitat and deterioration of the water quality cause the death of many fish in the dry season. The callichthyids are hardy fish adapted to low oxygen levels by their air-breathing habit (Carter & Beadle, 1931) and to desiccation by their armour of bony plates. In the dry season they probably feed partly on the accumulating remains of dead fish. It is not likely they are true scale-eating fish (Sazima, 1983) because they are morphologically not well equipped for fast attacks on living fish and lack specialized teeth (Table I; Burgess, 1989).

A possible explanation for the lack of seasonality in the diet of these bottom-dwelling catfishes is that their major food source, benthic invertebrates, is less affected by season than other food items like zooplankton and allochthonous food (Bonetto, 1975; Mol, 1993b).

DIET OVERLAP

Interspecific diet overlaps among *H. littorale*, *H. thoracatum* and *C. callichthys* were typically high (approximately 0.8; Table IV). In fact, most pairwise overlaps among larvae, juveniles and adults did not differ significantly from 1.

In temperate lakes interspecific diet overlap values are typically low (<0.3), except for congeneric species, where values may be moderate (Keast, 1978), and larvae/juveniles which often show high similarity in diet composition (Mark *et al.*, 1987; but see Keast, 1980).

Within a tropical river system Lowe-McConnell (1987) showed high dietary overlap correlated with shaded Amazonian headwater streams, where fishes are mostly polyphagous, and important feeding specializations and low overlap with

a greater diversity of niches provided by the floodplain habitat downstream. In Panamanian rainforest streams Angermeier & Karr (1983) found large diet overlaps (>0.9) within feeding guilds. However, only six food categories were distinguished by these authors. In another study of Panamanian stream-fish, Zaret & Rand (1971) reported low diet overlap in the dry season and moderately high overlap (>0.6) in the rainy season. Although diet overlap was not calculated by Knöppel (1970) and Saul (1975), stomach content analyses indicated that most fishes in small Amazonian streams ate the same food whatever was available.

In floodplains of the Venezuelan Llanos, Winemiller (1989) found low dietary overlaps (<0.3) among nine piscivores. However, Winemiller's calculations were based on 118 food categories, making bias of his values probably high (Smith & Zaret, 1982). Furthermore, if search images of fishes are rather roughcasted (Hartmann, 1983), the question whether the 118 food categories distinguished by Winemiller are really relevant to the fishes he studied, must also be considered. Goulding (1980) reported important feeding specializations (low dietary similarity) in large Amazonian floodplain fishes.

Thus, compared with other studies on food partitioning in neotropical freshwater fish, interspecific diet overlap among *H. littorale*, *H. thoracatum* and *C. callichthys* was high. The high overlap is most probably due to a similar morphology of these catfishes (Table I). Food overlap values of a comparable high magnitude (>0.9) were found among juveniles and adults of two morphologically similar *Astyanax* species in Brazil (Arcifa *et al.*, 1991). Goulding (1980) also found little food resource partitioning between large, congeneric floodplain species.

Intraspecific diet overlap in the callichthyids was distinctly lower than interspecific overlap, stressing the importance of the effects of indeterminate growth on fish interactions (Helfman, 1978; Keast, 1978; Werner & Gilliam, 1984). Keast (1978) argued that some fish species simultaneously occupy several niches. Size (age) classes may function as 'ecological species' by showing the same differences in morphology and resource use as exists between biological species (Polis, 1984).

Given this large diet overlap among three callichthyids, what prevents competitive exclusion from occurring? First, it is not clear to what extent food availability is really limiting. High predation pressure and stranding at the end of the rainy season probably result in high mortalities (Lowe-McConnell, 1987), and population densities may not reach levels at which competition becomes important (Connell, 1975; Roughgarden & Feldman, 1975). In the wet season (reproductive season) densities of zooplankton, the most important food item of larvae and juveniles, are relatively high (Mol, 1993b) while dispersal of the fishes is extensive. Second, the three catfishes might separate out on time of activity or habitat use. Segregation in time of activity on a daily or a yearly basis does not seem probable. *H. littorale* is active at dusk and in the night (Boujard *et al.*, 1990), and the same diel pattern of activity probably holds for *H. thoracatum* and *C. callichthys* (personal observations in tanks and experience with angling). Reproduction is strongly correlated with seasonality in rainfall in all three species. Onset and duration of the spawning season do not differ much (Mol, in preparation), and larvae and juveniles grow up in the same period of the year.

Habitat differentiation among the callichthyids seems not important as all spend most of their time in the same bottom habitat. However, I have observed that in the rainy season nest (micro)habitats of the three species differ with respect to vegetation type and water depth (Mol, in preparation). Whereas the reproductive season lasts as long as the swamps are flooded and individual fish remain reproductively active during this period (Pascal *et al.*, 1994), the three species (reproducing adults, larvae and possibly juveniles) are separated spatially when population sizes are largest and most of the feeding takes place. Werner (1977) pointed out that where considerable intraspecific size (age) class segregation of food resources exists, habitat separation of closely related species is far more effective than food separation in preventing species overlap. After comparing primary and secondary production in a temperate and a tropical lake, Burgis & Dunn (1978) concluded that the size of fish populations in a tropical lake might well be limited by lack of suitable nursery and breeding areas or predation on juveniles and not by food shortage. Habitat segregation among congeneric tropical freshwater fishes with similar feeding habits is reported for two *Astyanax* species in Brazil (Arcifa *et al.*, 1991) and three *Barbus* species in Sri Lanka (De Silva & Kortmulder, 1977).

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APPENDIX 1. Composition of the diet of *Hoplosternum littorale* in the coastal plain of Suriname

Food items	Larvae						Juveniles						Adults						
	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.	
Filamentous algae	11.5	0.19	0.10	30.8	4.75	0.50	19.0	20.71	0.07	7.8	4.61	0.43	4.61	—	—	—	—	—	
Chlorophyta	55.8	1.62	1.98	50.0	9.50	1.98	—	—	—	2.0	0.59	0.00	0.59	—	—	—	—	—	
Bacillariophyceae	3.8	0.06	0.02	26.9	17.96	1.16	—	—	—	11.8	158.80	0.17	158.80	—	—	—	—	—	
Euglenophyta	—	—	—	19.2	2.54	0.23	9.5	11.90	0.00	2.0	98.00	0.38	98.00	—	—	—	—	—	
Rhizopoda (Testacea)	44.2	0.98	1.19	48.1	11.40	1.29	—	—	—	7.8	3.90	0.17	3.90	—	—	—	—	—	
Rotifera	94.2	10.15	21.16	67.3	43.40	8.02	4.8	4.76	0.00	13.7	25.10	0.47	25.10	—	—	—	—	—	
Nematoda	9.6	0.10	0.78	44.2	4.27	2.30	47.6	5.33	0.81	35.3	3.50	2.67	3.50	—	—	—	—	—	
Oligochaeta	9.6	0.12	1.75	23.1	0.88	1.42	14.3	0.14	0.14	17.6	0.80	0.96	17.6	—	—	—	—	—	
Oligochaeta, seta	13.5	—	—	59.6	—	—	38.1	—	—	41.2	—	—	41.2	—	—	—	—	—	
Hydracarina	—	—	—	7.7	0.12	0.06	9.5	0.48	0.27	2.0	0.04	—	0.04	—	—	—	—	—	
Cladocera	96.2	13.33	68.89	84.6	252.30	33.59	57.1	980.40	22.04	37.2	769.70	12.59	12.59	769.70	—	—	—	—	
Copepoda	15.4	0.47	2.26	75.0	13.01	5.72	42.8	7.76	0.77	37.2	156.20	6.36	156.20	—	—	—	—	—	
Ostracoda	—	—	—	11.5	38.81	2.06	47.6	75.95	7.74	19.6	40.60	4.73	40.60	—	—	—	—	—	
Palaemonetes carteri	—	—	—	—	—	—	—	4.8	0.14	0.02	2.0	0.02	0.02	0.02	—	—	—	—	
Diptera larvae	—	—	—	78.8	10.33	11.96	71.4	15.33	19.70	45.1	30.60	13.57	30.60	—	—	—	—	—	
Coleoptera larvae	—	—	—	30.8	0.52	2.88	28.6	1.38	5.38	9.8	0.50	1.29	0.50	—	—	—	—	—	
Odonata nymphs	—	—	—	5.8	0.08	0.11	4.8	0.05	0.23	3.9	0.20	0.38	3.9	—	—	—	—	—	
Aquatic adult Coleoptera	—	—	—	—	—	—	9.5	0.10	0.09	29.4	0.70	2.36	29.4	—	—	—	—	—	
Hemiptera	—	—	—	—	—	—	14.3	0.14	0.59	5.9	0.10	0.11	5.9	—	—	—	—	—	
Gastropoda	—	—	—	7.7	0.27	0.05	47.6	11.28	16.02	13.7	0.40	0.82	13.7	—	—	—	—	—	
Terrestrial Arthropoda	—	—	—	23.1	0.29	0.92	19.0	0.19	1.36	21.6	0.40	1.24	21.6	—	—	—	—	—	
Fish scales	—	—	—	19.2	0.62	0.36	4.8	0.10	0.00	27.4	3.00	3.02	27.4	—	—	—	—	—	
Invertebrate cysts	1.9	0.04	0.05	36.5	9.15	3.21	4.8	0.05	0.09	7.8	0.60	0.00	0.60	—	—	—	—	—	
Seeds/spores	1.9	0.02	0.03	13.5	0.98	0.20	33.3	0.57	0.63	29.4	4.40	1.90	29.4	—	—	—	—	—	
Detritus	1.9	—	1.75	42.3	—	11.54	71.4	—	15.54	54.9	—	35.03	54.9	—	—	—	—	—	
Chitinous remains	—	—	—	32.7	—	5.41	52.4	—	5.88	45.1	—	3.58	45.1	—	—	—	—	—	
Vegetative plant matter	—	—	—	—	—	—	42.8	—	2.26	39.2	—	4.22	39.2	—	—	—	—	—	
Sand	—	—	—	17.3	—	4.46	23.8	—	0.11	21.6	—	2.53	21.6	—	—	—	—	—	
Other items	—	—	—	3.8	0.82	0.56	—	—	—	2.0	0.24	0.36	2.0	—	—	—	—	—	
Total	27.08	99.96	422.00	99.99	—	—	1136.76	99.74	—	—	1303.00	99.98	—	—	—	—	—	—	
No. of stomachs examined	52	—	—	—	—	—	21	—	—	—	—	—	—	—	—	—	—	—	
No. empty stomachs	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	
Mean stomach fullness (%)	3.44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Standard length range (mm)	77	70	13.5-81.4	56-70	53	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152	86-152

Frequency of occurrence (%), mean numerical composition and mean volume (%) of stomach contents of larvae, juveniles and adults in the rainy and dry season.

APPENDIX 2. Composition of the diet of *Hoplosternum thoracatum* in the coastal plain of Suriname

Food items	Larvae			Juveniles			Adults		
	Freq.	n	Vol.	Freq.	n	Vol.	Rainy season		Dry season
							Freq.	n	Vol.
Filamentous algae	6.0	0.06	0.05	50.0	6.02	1.23	1.2	1.16	0.08
Chlorophyta	36.0	0.50	0.45	73.1	29.10	4.23	—	—	0.00
Bacillariophyceae	32.0	0.64	0.07	62.8	7.50	0.78	9.3	4.13	—
Euglenophyta	2.0	0.02	0.00	14.1	0.33	8.94	3.5	0.04	0.08
Rhizopoda (Testacea)	82.0	3.20	2.33	71.8	30.78	5.02	59.77	0.26	1.6
Rotifera	98.0	12.80	17.40	80.8	100.80	16.38	—	—	3.91
Nematoda	—	—	—	47.4	1.27	1.36	2.3	1.45	3.30
Oligochaeta	6.0	0.06	0.79	26.9	0.54	1.30	20.9	0.88	14.1
Oligochaeta, seta	20.0	—	—	59.0	—	—	31.2	0.29	12.60
Hydracarina	—	—	—	5.1	0.05	0.18	47.7	—	15.6
Cladocera	100.0	15.88	69.20	71.8	85.15	22.79	23.2	0.07	35.9
Copepoda	46.0	2.18	5.13	73.1	184.55	7.87	12.8	0.00	4.7
Ostracoda	28.0	0.42	3.44	7.7	0.27	0.24	17.4	614.90	20.3
<i>Palaemonetes carteri</i>	—	—	—	1.3	0.01	0.12	4.7	0.07	20.3
Diptera larvae	2.0	0.02	0.55	57.7	3.69	8.77	47.7	14.08	3.40
Coleoptera larvae	—	—	—	25.6	0.37	1.69	23.2	1.28	46.9
Odonata nymphs	—	—	—	—	—	—	4.7	0.05	12.19
Aquatic adult Coleoptera	—	—	—	—	—	—	4.7	0.05	0.71
Hemiptera	—	—	—	—	—	—	7.4	1.02	20.3
Gastropoda	—	—	—	—	—	—	5.94	15.6	26.80
Terrestrial Arthropoda	—	—	—	15.4	0.01	0.12	4.7	0.06	2.30
Fish scales	—	—	—	15.4	0.28	1.95	11.6	0.17	3.1
Invertebrate cysts	4.0	0.32	0.22	14.1	1.51	2.69	10.5	0.29	12.19
Seeds/spores	2.0	0.02	0.04	12.8	3.08	6.49	17.4	4.23	0.22
Detritus	—	—	—	47.4	—	5.99	73.2	—	7.8
Chitinous remains	—	—	—	30.8	—	1.28	54.6	0.45	2.18
Vegetative plant matter	—	—	—	—	—	39.5	—	43.8	4.7
Sand	—	—	—	—	—	—	6.68	0.45	0.10
Other items	—	—	—	3.8	0.68	0.23	7.0	0.36	9.4
Total	36.12	99.67	457.80	100.00	723.20	100.00	723.20	99.98	313.55
No. of stomachs examined	50	—	—	78	—	—	86	—	64
No. of empty stomachs	0	—	—	0	—	—	23	—	19
Mean stomach fullness (%)	73	—	—	0	—	—	57	—	62
Standard length range (mm)	6.2-7.4	—	—	15.2-69.3	—	—	85.136	—	70-150

APPENDIX 3. Composition of the diet of *Callichthys callichthys* in the coastal plain of Suriname

Food items	Larvae			Juveniles			Adults			Dry season		
	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.	Freq.	n	Vol.
Filamentous algae	1.3	0.02	0.02	17.9	0.73	0.21	—	—	—	—	—	—
Chlorophyta	12.8	0.20	0.56	22.4	0.79	0.12	—	—	—	—	—	—
Bacillariophyceae	6.4	0.06	0.01	61.2	5.70	0.46	4.2	15.62	0.04	2.9	14.70	0.08
Euglenophyta	—	—	—	4.5	0.10	0.03	—	—	—	—	—	—
Rhizopoda (Testacea)	82.0	2.54	3.81	68.6	20.51	1.71	—	—	—	—	—	—
Rotifera	88.5	7.01	19.38	73.1	66.06	5.32	2.1	10.42	0.04	—	—	—
Nemaloda	5.1	0.05	0.66	31.3	0.52	0.31	12.5	0.46	0.23	20.6	0.60	0.47
Oligochaeta	17.9	0.19	7.17	34.3	3.73	8.28	8.3	0.33	0.68	2.9	0.10	0.17
Oligochaeta, seta	35.9	—	—	73.1	—	—	27.1	—	—	14.7	—	—
Hydracarina	3.8	0.04	0.41	3.0	0.03	0.02	8.3	0.08	0.04	5.9	0.10	0.00
Cladocera	80.8	4.95	57.10	76.1	511.10	55.43	31.2	304.40	8.52	2.9	22.00	5.15
Copepoda	23.1	0.83	6.64	65.7	10.67	1.94	25.0	77.69	1.56	—	—	—
Ostracoda	—	—	—	13.4	0.24	0.32	18.8	2.00	0.38	—	—	—
<i>Palaeomonetes carteri</i>	—	—	—	1.5	0.01	1.92	—	—	—	—	—	—
Diptera larvae	2.6	0.02	1.12	68.6	5.92	12.09	35.4	4.56	4.62	17.6	1.60	0.52
Coleoptera larvae	—	—	—	38.8	0.86	5.05	35.4	2.75	12.95	11.8	0.40	2.45
Odonata nymphs	—	—	—	1.5	0.07	0.46	4.2	0.06	0.43	8.8	0.90	11.59
Aquatic adult Coleoptera	—	—	—	—	—	—	43.8	1.64	8.47	29.4	1.20	13.07
Hemiptera	—	—	—	—	—	—	10.4	0.12	0.34	5.9	0.10	0.62
Gastropoda	—	—	—	4.5	0.09	0.30	16.7	0.35	3.58	2.9	0.03	0.00
Terrestrial Arthropoda	—	—	—	10.4	0.18	1.80	27.1	1.00	5.12	23.5	0.70	10.77
Fish scales	—	—	—	3.0	0.18	0.01	—	—	—	8.8	1.40	2.58
Invertebrate cysts	2.6	0.42	0.59	6.0	0.15	0.05	8.3	1.60	0.43	2.9	0.20	0.00
Seeds/spores	1.3	0.01	0.01	17.9	0.85	1.15	10.4	0.46	0.23	8.8	0.40	0.13
Detritus	7.7	—	1.36	25.4	—	2.68	58.3	—	29.04	38.2	—	27.53
Chitinous remains	—	—	—	6.0	—	0.33	45.8	—	12.74	29.4	—	18.46
Vegetative plant matter	—	—	—	—	—	—	29.2	—	4.96	11.8	—	1.84
Sand	—	—	—	—	—	—	4.2	—	0.16	14.7	—	0.11
Other items	3.8	0.01	0.39	3.0	0.01	0.01	10.4	3.66	5.39	2.9	3.63	1.70
Total	16.35	99.23	628.50	100.00	427.20	99.95	48.16	99.99	—	—	—	—
No. of stomachs examined	78	—	—	67	48	—	—	—	—	—	—	—
No. of empty stomachs	4	—	—	12	16	—	—	—	—	—	—	—
Mean stomach fullness (%)	52	—	—	74	48	—	—	—	—	—	—	—
Standard length range (mm)	5.6-8.4	—	—	11.1-8.2	101-161	92-160	—	—	—	—	—	—

Frequency of occurrence (%), mean numerical composition and mean volume (%) of stomach contents of larvae, juveniles and adults in the rainy and dry season.