Seasonal dynamics in the trophic status of **Papyrocranus afer** *(Günther, 1868) (Notopteridae) in a Nigerian rainforest stream*

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ABSTRACT

The stomach contents of Papyrocranus afer *comprised primarily midwater invertebrates, allochthonous macrophyte debris, allochthonous invertebrates and preyfish. Epiphytic algae, benthic invertebrates, neustonic invertebrates and miscellaneous insects were secondary components while zooplankton was of incidental importance. The fish thus utilized food from the three major spatial levels of the stream surface, midwater and bottom. The diet was dominated by occasional food-types which were consumed during less than 3 months of the year. It was closely linked to the distributional ecology of the fish in the vegetated marginal water biotope where most of the dietaries abound. There was considerable seasonal plasticity in the specific food-types utilized and this resulted in high year-round trophic diversity. A wide trophic spectrum and attendant expanded diet breadth were considered as attributes of high foraging success of* P. afer.

KEYWORDS: *Papyrocranus afer* — Nigeria — Seasonality — Dietary habit — Fish.

RÉSUMÉ

L'ÉVOLUTION SAISONNIÈRE DU RÉGIME ALIMENTAIRE DE *PAPYROCRANUS AFER* (GÜNTHER, 1868) (NOTOPTERIDAE) DANS UNE RIVIÈRE FORESTIÈRE DU NIGERIA

Le contenu stomacal de Papyrocranus afer *est constitué d'invertébrés de pleine eau, de débris de plantes et d'insectes allochtones, et de poissons. Les algues épiphytes, les invertébrés benthiques et divers insectes sont des composantes secondaires tandis que le zooplancton n'est qu'occasionnel. Il apparaît ainsi que ce poisson utilise les trois principales zones de son milieu : la surface, la pleine eau et le fond. Le régime est principalement opportuniste avec des proies qui sont consommées durant moins de trois mois par an. Il est également en relation étroite avec la répartition du poisson dans les zones herbeuses de bordure. On a observé une grande plasticité du régime qui se traduit par une diversité importante sur un cycle annuel. Ce large spectre trophique est considéré comme caractéristique de l'espèce.*

MOTS CLÉS : *Papyrocranus afer* — Rivières — Nigeria — Régime alimentaire — Poissons.

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INTRODUCTION

The quality and quantity of available natural food resources influence aspects of the life history of fishes including inter alia, growth rate, longevity, reproductive investment, sexual maturity and fecundity. Diet diversity is a measure of the degree of complexity or specialization in items consumed. Some fish species are oligophagous, utilizing a limited number of food resources while others are polyphagous, subsisting on wider spectra of items.

The adaptative significance of a broad trophic spectrum (high diet diversity) is that it ensures a constant energy source, facilitates adequate utilization of available food resources and enables the fish to easily switch from one food source to another in response to natural pulses in their relative abundances and availability (KING, 1993). Conversely, oligophagous fishes (low diet diversity) would be adversely affected should there be a dwindle or collapse in the food resource-base.

Tropical riverine fishes inhabit dynamic aquatic environments and are thus exposed to seasonal pulses in hydrometeorological attributes. Seasonality in habitat conditions influences fishes mainly through qualitative and quantitative changes in available food resources (LOWE-MCCONNELL, 1987). Seasonal variations in dietary status and diversity of fishes presumably stem from the inherent dynamics in food resources availability / abundance and/or intrinsic changes in foraging ethology e.g. active predilection for specific food-types. In any aquatic ecosystem, the evolutionary adaptations should therefore favour fishes that have evolved trophic strategies that ensure optimum foraging under a seasonally available food resource condition.

The present study was aimed at documenting the overall food composition and extent of temporal plasticity (monthly and seasonal patterns) in dietary status and diversity of *Papyrocranus afer* in a Nigerian rainforest stream. It centers on the influence of the tropical dry-wet season cycle on the seasonality regimes of these trophic attributes. Very little has been published on the general biology and ecology of *P. afer*. Brief and fragmentary accounts of aspects of its reproductive and food habits are contained in ALBARET (1982) and TEUGELS *et al.* (1992) respectively.

STUDY AREA

The present study was conducted in Ikpa River, a small perennial rainforest tributary stream located West of the lower reaches of the Cross River in southeastern Nigeria (Fig. 1). The stream has a main-channel total length of 53.5 km between its source in Ikono Local Government Area and where it discharges into the Cross River, close to Nwaniba.

Ikpa River has a watershed area of 516 km^2, of which 76 km^2 (14.8 %) of the lower reaches is liable to annual flooding of the fringing low land riparian zone during the rainy season. The nonflood zone of the upper reaches has a basin area of 440 km^2 (85.2 %) and mean depth and width of 2.0 m and 12.5 m respectively.

The entire length of the main channel of the stream lies at the interface of two different geological deposits: tertiary sedimentary rocks and cretaceous deposits (see geological map of Nigeria in CLAUSEN, 1964). The stream is considerably shaded by overhanging canopy of riparian vegetation (mostly *Elaeis guineensis*, *Raphia hookeri*, *Raphia vinifera* and other tropical forest trees). The aquatic macrophytes are mainly *Nymphaea*, *Vossia* and *Crinium* species. The seasonal variation in stream surface temperature is 23.3 - 28.0 °C, Secchi disc transparency 12.5 - 101 cm and pH 6.6 - 7.7. Conductivity varies between 13.0 and 69.2 μS cm^{-1}. The stream current velocity is 3.5 - 6.9 cm s^{-1}.

The climate of the area is typical of tropical rainforests; it comprises dry (November - February) and wet (March - October) seasons. Meteorological data from the University of Uyo meteorological station sited within Ikpa River basin (Fig. 2) indicate the precipitation and ambient temperature regimes during this study. The dry season was characterized by prevalence of dry tropical continental winds from the Sahara desert and low mean monthly precipitation; peak dry season occurred in January - February. The wet season was typified by prevalence of moist tropical maritime winds from the Atlantic Ocean and high mean monthly rainfall. Annual rainfall was 255.8 cm. The cyclic hydrological regime is typified by high water level and flow rate during the rains and vice-versa in the dry season.

More descriptive information on the Ikpa River basin is provided by KING (1989) and TEUGELS *et al.* (1992).

MATERIALS AND METHODS

Monthly samples of *Papyrocranus afer* were obtained from each of eight stations in Ikpa River (Fig. 1) for 5 days during mid-month (November, 1988-October, 1989 inclusive). Fishing was conducted by the use of 3 gill-nets with 30 mm, 50 mm and 80 mm stretched mesh respectively and 50 single-hook (size No. 2) set-lines baited with earth

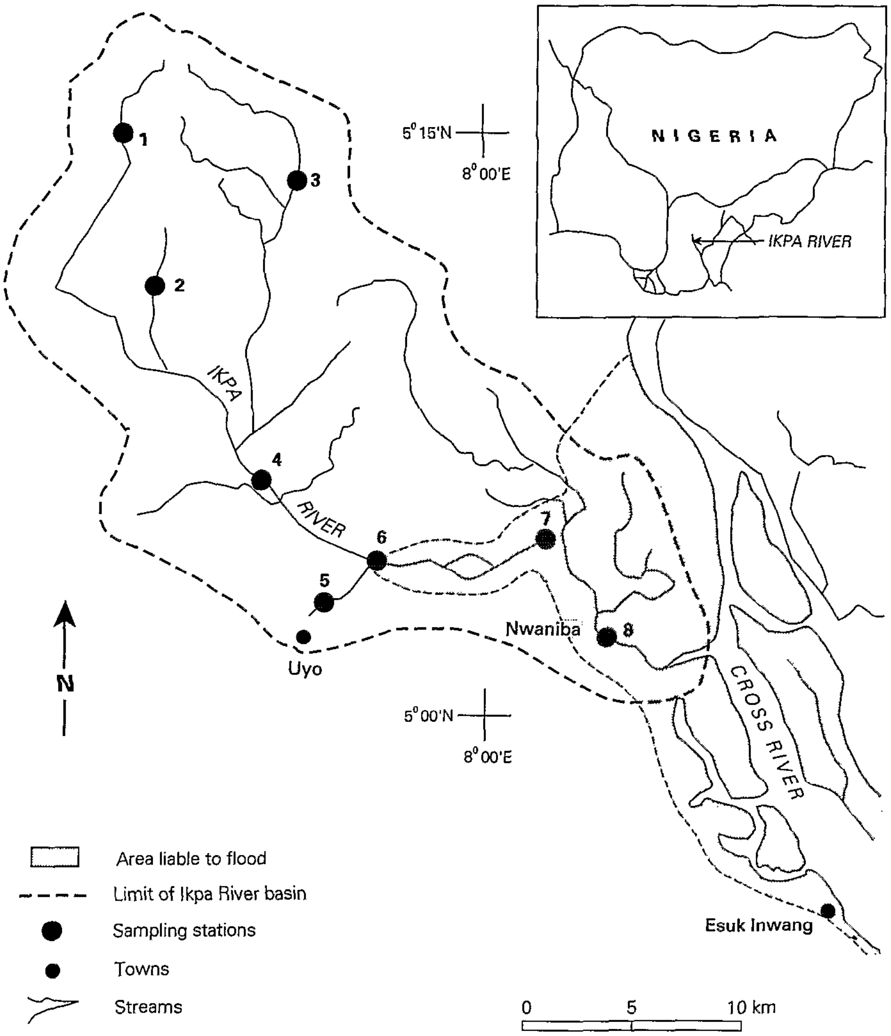

FIG. 1. — Map of Ikap River, showing the sampling stations. Inset : map of Nigeria showing the location of Ikpa River.
Carte de situation de la rivière Ikpa et des stations de pêche, avec les zones inondables (hachurées).

worms. Attemps to capture *P. afer* with the valued basket traps were unsuccessful. Day and night fishing were conducted in the open water, littoral zone and fringing swamps.

The specimens were transported to the laboratory where they were measured to the nearest 0.1 cm total length (TL). They were eviscerated and the stomachs slit open. The stomach contents of each specimen were placed in a Petri dish and aggregates dispersed with a few drops of water prior to macroscopic and microscopic (with variable magnifications up to × 40) examinations. The contents were sorted, identified and categorized according to taxonomic and microhabitat (i.e. where an item occurred most commonly) criteria based on author's field notes on the potentially available food resources to stream fishes. This is similar to WHYTE's (1975) taxonomic/ecological groupings of the diets of the fishes of Lake Bosumtwi, Ghana. The merits of this system of categorization of food in fish dietary studies are discussed by BERG (1979).

The frequency occurrence of each item as dominant (by volume) (d_i) and non-dominant (f_i) stomach contents were noted. The integrated importance of each item was then expressed by the food ponderal index (FPI) (KING, 1991):

$$FPI = \frac{(f_i + d_i)}{\sum_{i=1}^{n} (f_i + d_i)} \times 100 \qquad (1)$$

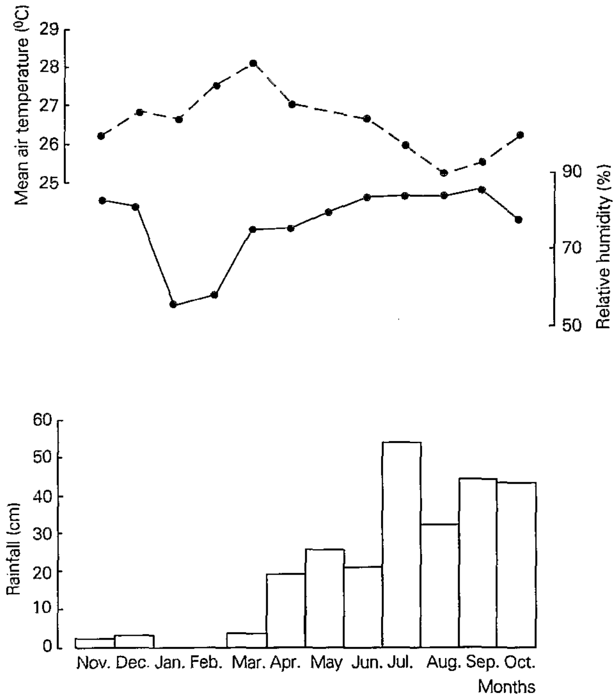

FIG. 2. — Seasonal variation in some meteorological parameters of Ikpa River basin at Uyo.
Variations climatiques à Uyo, dans le bassin de la rivière Ikpa.

This index has a range of 0-100 %; items with FPI ≥ 10 % were arbitrarily considered as primary dietaries, those with FPI = 1.0 — 9.9 % as secondary and those with FPI < 1.0 % as incidental. The percent compositions were used to describe the overall diet and temporal changes in food habit.

The regularity with which each food-type was consumed on a monthly basis was evaluated by a percentage constancy index (CI):

$$CL = \frac{m_i\,100}{M} \qquad (2)$$

where m_i = number of months in which food-type i was consumed; M = total number of months in the study period (here 12 months). This index is scaled from 0 (for absence throughout the year) to 100 % (for occurrence in every month of the year). The KOCH's (1957) composite index of biotal dispersity (IBD) was used to assess how widely dispersed the dietaries were between months and seasons:

$$IBD = \frac{(T-S)\,100}{S(n-1)} \qquad (3)$$

where T = arithmetical sum of dietaries in each of n compared months/seasons; S = total list of dietaries in n compared months/seasons. The IBD ranges from 0 (for completely different set of dietaries in each month/season) to 100 % (for identical sets of dietaries in each month/season).

An index of diet diversity (F) was computed from the % FPI data using the formula (see ALATALO, 1981; GRUNDEL, 1990):

$$F = \left(\sum_{i=1}^{n} P_i^2\right)^{-1} - \left[\exp\left(-\sum_{i=1}^{n} ln\ P_i\right) - 1\right]^{-1} \qquad (4)$$

where P_i = proportion of the diet comprised by resource type i and n = number of food categories in the diet. This index is sensitive to changes in two attributes *viz* food richness and equitability (= the degree to which all items are equally represented); it increases as food richness and its equitability increase and declines when few items dominate the diet. The F is scaled such that 1.0 represents an even distribution and zero, a strongly skewed distribution.

To evaluate short-term (i.e. month-to-month) and long-term (i.e. seasonal) changes in diet composition, the percentage similarity coefficient S was used (MOSS and EATON, 1966):

$$S = \sum_{i=1}^{n} min\ (X_i, Y_i) \qquad (5)$$

where X_i and Y_i = proportions of the components of the series of n^{th} comprising the diets of X and Y. This index ranges from zero, for totally disimilar dietary compositions, to 100 % for identical diets.

The significance of the deviations of calculated values of S and IBD from maximum possible values (i.e. S_{max} = 100 % and IBD_{max} = 100 % respectively) were evaluated by X^2-test (BAILEY, 1959). The magnitude of variation in F was assessed by the coefficient of variation (LOWETIN, 1966), regarding values above 30 % as high.

RESULTS

Papyrocranus afer was available all year-round in catches from the eight sampling stations, thus indicating that it is a resident species in the stream. It was found to be a solitary limnophilic fish that was most commonly caught in quiet and gently-flowing vegetated littoral zone and fringing swamps of the stream. It tended to evade swift open water stretches of the stream. There was no preference for any particular substrate-type as it was caught over both muddy and sandy bottoms; there were also no temporal and ontogenetic regimes in habitat preference.

TABLE I

Monthly numbers and sizes of *P. afer* from Ikpa River examined for food (November 1988 - October 1989)
Nombre et taille des spécimens de P. afer *capturés et examinés (novembre 1988 - octobre 1989)*

Months	Number of specimens examined	Total length (cm)
November	34	19.4 - 39.8
December	24	15.1 - 34.0
January	14	15.5 - 36.8
February	7	19.3 - 36.0
March	10	14.2 - 38.7
April	3	18.5 - 35.6
May	12	18.0 - 42.0
June	30	21.7 - 38.0
July	20	19.6 - 41.0
August	16	17.5 - 36.9
September	32	18.7 - 37.5
October	17	13.9 - 37.6

Altogether, 219 specimens of *Papyrocranus afer* were examined for trophic attributes. The number of specimens examined per month and their size limits are presented in Table I. Although relatively few specimens were available during February - April, the results indicate that these did not overly influence the values of the trophic parameters.

Diet composition

The overall food composition of *Papyrocranus afer* (Table II) shows the utilization of a wide assortment of food resources which were assigned to ten major ecological categories: epiphytic algae, allochthnous macrophyte debris, benthic invertebrates, midwater invertebrates, neustonic invertebrates, allochthonous invertebrates, miscellaneous insects, zooplankton, preyfish and sand grains. The food habit was overwhelmingly carnivorous, with 71.5 % of the diet comprising faunal food-types while items of plant origin encompassed 20.7 %. Abiogenic materials (sand grains) constituted a small proportion of the stomach contents. The carnivorous habit of *P. afer* centered predominantly on arthropods which accounted for 59.1 % of the diet. The arthropod prey comprised various developmental stages, including imagoes (adults), subadults, nymphs, deutonymphs and larvae.

Of the 45 items that formed the diet, 14 (31 %) were of allochthonous origin while 31 (69 %) were of autochthonous sources. Primary dietaries were midwater invertebrates (35.8 %), allochthonous macrophyte debris (16.0 %), allochthonous invertebrates (14.2 %) and preyfish (12.5 %); sand grains (7.8 %), epiphytic algae (4.6 %), miscellaneous insects (3.5 %), benthic invertebrates (3.4 %) and neustonic invertebrates (1.5 %) were secondary dietaries while zooplankton (0.7 %) was of incidental importance. Of the epiphytic algae browsed, filamentous forms *(Spirogyra, Ulothrix, Oscillatoria, Lyngbya)* were most important while only small proportions of unicellular desmids *(Closterium, Cosmarium, Docidium, Penium, Euastrum, Plurotaenium, Scenedesmus)* and diatoms *(Amphora, Surirella, Pinnularia, Gomphonema, Eunotia, Nitzchia)* were represented. Coarse detritus dominated the allochthonous macrophyte debris dietary components as a primary item whereas fine detritus were of secondary importance. The detrital particles were derived largely from decaying shed leaves of overhanging riparian macrophytes. Other components of allochthonous macrophyte debris included floating seeds, fruits, flowers, leaf fragments and other vascular plant matter of riparian vegetation.

Although a variety of benthic invertebrates were utilized (10 categories), each category was of incidental status and constituted less than 0.8 % of the diet. It is however noteworthy that crabs *(Potamonautes paecilei)* and shrimps *(Caridina africana, Macrobrachium dux, Macrobrachium vollenhoveni)* in this diet category are fairly large-sized items when compared with the sizes of other benthic invertebrates such as ostracods, arachnids and insects. The 9 dietary components of midwater invertebrates were dominated by anisopteran (dragon fly) nymphs as the single most important constituent (20.9 %); this was followed by adult naucorids *(Pelocoris)* (9.8 %), zygopteran (damsel fly) nymphs (1.3 %) and hydrophilid imagoes (1.4 %) as secondary dietaries whereas each of the remaining midwater invertebrates, with less than 1.0 % contribution to food composition, was of incidental importance. Field observations revealed that most of the midwater invertebrates were closely associated with submergent marginal aquatic vegetation; they were either periphytic and/or nektonic among the macrophytes.

The two insect taxa constituting the neustonic fauna were coleopterans, with gyrinids (whirligig beatles) as secondary items while the velliids (broad-shouldered water striders) were incidentally consumed. Allochthonous fauna in the diet comprised invertebrates that dropped into the water from the emergent littoral and overhanging riparian macrophytes as well as those washed into the stream by surface runoff. The 11 categories of allochthonous invertebrate dietaries were dominated by adult formicids (black ants) (4.2 %) and coleopterans (4.7 %).

TABLE II

Overall and seasonal trophic spectra, and constancy indices of the dietaries of *P. afer* in Ikpa River.
Spectre trophique global et saisonnier, et indice de constance (CI) du régime alimentaire de P. afer *dans la rivière Ikpa.*

Food items	% Food Ponderal Index (FPI)			% Constancy index (CI)
	Overall composition	Dry season	Wet season	
Epiphytic algae				
Filamentous algae	2.3	2.2	2.4	58.3
Unicellular algae - Desmidiaceae	1.6	1.6	1.7	50.0
Baccillanophyceae	0.7	0.7	0.7	33.3
Allochthonous macrophyte debris				
Coarse detritus	10.5	14.2	8.9	91.7
Fine detritus	4.6	4.0	4.8	71.0
Other debris	0.9	1.5	0.7	33.3
Benthic invertebrates				
Nematoda (free living)	0.1	0.4	-	8.3
Ephemeroptera nymphs	0.4	0.7	0.2	16.7
Diptera - Chironomid larvae	0.2	0.4	0.2	16.7
Trichoptera larvae	0.4	1.1	-	16.7
Crustacea - Ostracoda	0.1	-	0.2	8.3
Potamidae : *Potamonautes paecilei*	0.2	-	0.3	8.3
Atyidae *Caridina africana*	0.2	0.4	0.2	16.7
Palaemonidae : *Macrobrachium dux*	0.5	0.7	0.3	16.7
Macrobrachium vollenhoveni	0.6	1.1	0.3	16.7
Arachnida	0.7	0.4	0.9	41.7
Midwater invertebrates				
Odonata - Anisoptera nymphs	20.8	20.4	20.9	91.7
Zygoptera nymphs	1.3	0.7	1.6	41.7
Coleoptera - Hydrophilidae adults	1.4	2.9	0.7	50.0
Dytiscid : Adults	0.7	-	1.0	16.7
larvae	0.4	-	0.5	16.7
Hemiptera - Naucorid adults	9.8	7.6	10.9	100.0
Nepidae : *Nepa* adults	0.9	2.2	0.3	33.3
Notonectidae : *Notonecta* adults	0.2	0.4	-	8.3
Unidentified Heteroptera adults	0.3	0.7	-	8.3
Neustonic invertebrates				
Coleoptera - Gyrinidae	1.3	3.3	0.3	25.0
Velliidae	0.2	-	0.3	8.3
Allochthonous invertebrates				
Orthoptera - Gryllidae adults	0.2	-	0.3	8.3
Acrididae adults	1.3	0.4	1.7	33.3
Hymenoptera : Formicidae adults	4.2	1.5	5.5	75.0
Isoptera : adult termites (winged reproductives)	0.1	-	0.2	8.3
Lepidoptera larvae	0.5	1.5	-	8.3
Copeoptera : Adults	4.7	5.4	4.3	66.7
Larvae	0.7	1.5	0.3	25.0
Anisoptera adults	0.1	-	0.2	8.3
Unidentified terrestrial adult insects	1.8	2.6	1.4	50.0
Arachnida - Aranae (adult spiders)	0.1	0.4	-	8.3
Diplopoda - Juliformia	0.5	-	0.7	16.7
Miscellaneous insects	3.5	4.7	2.9	66.7
Zooplankton				
Crustacea - Cladocera	0.4	-	0.5	16.7
Copepoda	0.1	-	0.2	8.3
Rotifera	0.2	-	0.3	8.3
Preyfish				
Whole fish	3.6	4.0	3.4	66.7
Fish scales	8.9	5.8	10.4	91.7
Sand grains	7.8	4.7	9.4	100.0

Arachnida = (Leimnohalacarid mites) : Hydrachnella adults and deutonymphs.

These were accompanied by unidentified insects (1.8 %) and acridids (short-horned grasshoppers — *Zonocerus*) (1.3 %) while each of the other taxa constituted less than 0.6 % of the diet. Imagoes of gryllids (crickets) and isopterans (termites) consumed were represented by the genera, *Acheta* and *Macrotermes* respectively, both of which are known to exhibit high nocturnal activity. The allochthonous lepidopterans (butterfly larvae), coleopterans (adults and larvae), anisopterans (adults), araneids (spiders) and juliform millipeds could not be identified below the operational levels presented in Table II.

The 3 components of zooplankton were minor dietaries and formed 0.1-0.4 % of the diet. Preyfishes consisted of cyprinodonts *(Epiplatys sexfasciatus, Aphyosemion gardneri, Aphyosemion splendopleure, Aphyosemion bivittatum)*, juvenile tilapiine *(Tilapia mariae)* and chromidotilapine *(Chromidotilapia guntheri)* cichlids. The fish scales consumed closely resembled those of adult *T. mariae* and *C. guntheri*. Several stomachs of *Papyrocranus afer* were found filled with fish scales and no other fish remnants of whole fish, thus suggesting that the scales were probably resped from the bodies of live fishes.

Diet stability

The monthly dynamics in the food components of *Papyrocranus afer* revealed that they can be arbitrarily arranged in three groups:

(a) constant elements: 14 (31 % of total number of food-types ingested) items which appeared in the stomachs during 6-12 months of the year (i.e. CI ≥ 50 %),

(b) accessory elements: 8 (17.8 %) items which occurred in the stomachs for a period of 3-5 months (CI = 25 - 40 %),

(c) occasional elements: 23 (51.1 %) food-types wich were consumed during less than 3 months of the year (CI < 25 %).

It is thus apparent that the diet of *Papyrocranus afer* was dominated by occasional elements, comprising items which were opportunistically consumed. The low index of biotal dispersity (IBD = 29.1 %) indicated considerable month-to-month changes in qualitative food composition. Filamentous algae, desmids, coarse detritus, fine detritus, anisopteran nymphs, adult hydrophilids, naucorids, formicids, unidentified terrestrial insects, whole preyfish and fish scales constituted important food sources for 6-12 months of the year while all other food-types played accessory or occasional roles in the annual food habit of the fish since they featured in the stomachs during only 1-5 months of the year.

There was considerable monthly variation in the relative importance of the food-types which alternated about the primary, secondary and incidental scales (Table III). Epiphytic algae formed secondary dietaries during June - December. A marked decrease in the relative consumption of this item occurred as

TABLE III

Monthly variations in the % food ponderal index (FPI) of *P. afer* in Ikpa River.
Évolution mensuelle de l'indice pondéral (FPI) de P. afer.

Food items	Months											
	N	D	J	F	M	A	M	J	J	A	S	O
Epiphytic algae	6.8	4.5	-	-	-	-	-	8.0	6.8	3.6	4.4	5.3
Allochthonous macrophyte debris	20.5	15.3	17.4	33.3	5.3	30.7	7.9	15.8	11.0	15.6	11.1	24.1
Benthic invertebrates	3.9	7.5	7.7	-	5.3	7.7	2.6	4.0	5.5	1.2	0.7	-
Midwater invertebrates	32.5	33.7	40.2	41.7	23.7	7.7	44.9	41.3	37.0	42.1	34.0	30.7
Neustonic invertebrates	5.3	3.0	-	-	-	-	5.3	1.6	-	-	-	-
Allochthonous invertebrates	12.1	13.6	19.3	4.2	44.7	23.1	13.2	8.8	12.3	-	18.6	20.1
Miscellaneous insects	1.5	9.1	3.9	12.5	-	-	5.3	3.9	5.5	7.2	-	-
Zooplancton	-	-	-	-	-	-	5.3	-	-	2.4	1.5	-
Preyfish	11.3	10.6	9.6	-	15.7	23.1	15.8	10.3	12.3	12.1	18.6	10.6
Sand grains	6.1	3.0	1.9	8.3	5.3	7.7	2.6	6.3	9.6	15.8	11.1	9.2

the months progressed from June to September but increased slightly between October and November. Allochthonous macrophyte debris was of primary dietary status throughout the year, except in March when it was of secondary importance; peaks occurred in February, April, June, August and October - November.

Benthic invertebrates were secondary dietaries in all months except in February/October when they were not consumed and September when they formed incidental components. Midwater invertebrates dominated the diet of *Papyrocranus afer* in all months except during the onset of the rains in March and April when they were replaced by allochthonous invertebrates and allochthonous macrophyte debris respectively. Midwater invertebrates were primary dietaries throughout the year except in April when they played a secondary role. Neustonic invertebrates were secondary dietaries in November - December and May - June. Allochthonous invertebrates constituted primary dietaries in November - January, March - May, July and September-October and secondary dietaries in February and June. Miscellaneous insects were of primary and secondary dietary value in February and May - August/November - January respectively. Zooplankton was a secondary dietary in each of the three months (May, August, September) that it was consumed. Preyfish was of primary dietary status in March-December and of secondary importance in January. Sand grains were encountered in the stomachs year-round and formed primary contents in August - September and secondary contents in October - July.

Overall, the results established considerable month-to-month plasticity in diet composition, with overlap values (S) ranging between 26.9 % (February - March) and 75.4 % (July - August) (Table IV). Moderately high diet overlaps ($S \geq 68$ %) occurred in June - July, July - August and September - October whereas other pairwise monthly diet similarities revealed lower overlaps ($S < 60$ % in each case). The magnitude of variability in food composition is further attested by the low average month-to-month overlap coefficient ($S = 53$ %).

The composite diet data for the dry and wet seasons are presented in Table II. Ostracods, *Potamonautes paecillei*, adult and larval dytiscids, adult veliids, isopterans and anisopterans, juliform millipeds, cladocerans, copepods and rotifers were not consumed during the dry season whereas free living nematodes, trichopteran larvae, adult notonectids and unidentified heteropterans, larval lepidopterans and aranae were excluded from the wet season diet.

Papyrocranus afer fed to a larger extent on allochthonous macrophyte debris, benthic invertebrates, neustonic invertebrates and miscellaneous insects in

TABLE IV

Mean diet diversity between adjacent months and month-to-month food overlap of *P. afer* in Ikpa River.
Diversité moyenne et recouvrement entre mois de la nourriture de P. afer.

Months	Mean diet diversity (F)	Food overlap (% S)
November - December	0.699	56.6
December - January	0.738	58.8
January - February	0.780	42.7
February - March	0.832	26.9
March - April	0.871	46.9
April - May	0.769	25.9
May - June	0.670	57.3
June - July	0.661	68.9
July - August	0.635	75.4
August - September	0.669	55.4
September - October	0.802	68.1

the dry season than during the rains. Conversely, the relative importance of midwater invertebrates, allochthonous invertebrates, zooplankton and prey-fish were slightly higher during the rains than in the dry season. Approximately equal proportions of epiphytic algae are consumed in both seasons.

The low biotal dispersity and mean monthly overlap indices for the dry ($IBD = 37.4$ %; $S = 52.7$ %) and wet ($IBD = 30.9$ %; $S = 56.8$ %) seasons depicted low intraseasonal diet stability. Similarly, the significant deviations from maximum possible values, of interseasonal biotal dispersity ($IBD = 60.0$ %: $X^2 = 10.00$, df = 1, $P < 0.01$) and diet overlap ($S = 73.6$ %: $X^2 = 4.015$, df = 1, $P < 0.05$) indices portrayed low interseasonal diet stability.

Diet diversity

The magnitude of the composite trophic diversity ($F = 0.614$) represented 61.4 % of maximum possible diversity (i.e. $F_{max} = 1.000$); intra-annual variability was low ($CV = 13.1$ %). Minimum and maximum trophic diversity were attained in September ($F = 0.576$) and March ($F = 0.917$) respectively. It increased from October to March and declined from April to September. Diet diversity index was not markedly different in the dry and wet seasons (Fig. 3) but intraseasonal variability was higher in the dry ($CV = 18.4$ %) than wet ($CV = 13.4$ %) season.

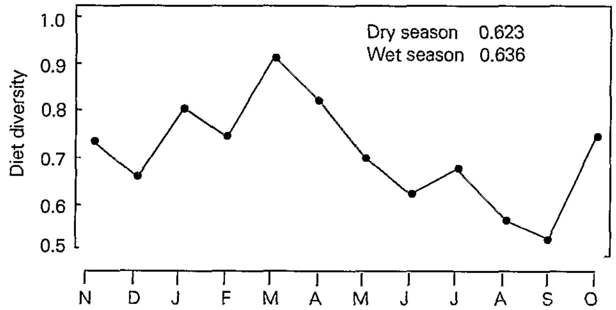

FIG. 3. — Seasonal variation in diet diversity of *P. afer* in Ikpa River.
Diversité du régime alimentaire de P. afer *dans la rivière Ikpa au cours de l'année.*

Mean diet diversity index of successive months and diet overlap coefficients between these months (Table IV) were inversely correlated ($r = -0.611$, $df = 9$, $P < 0.02$) according to the linear function:

$$F = 0.895 - 0.0035 \quad (6)$$

This relationship indicates that diet diversity decreased as food overlap increased and *vice-versa*.

DISCUSSION

The overall stomach contents of *Papyrocranus afer* from Ikpa River depicted a high dietary complexity, associated with the exploitation of autochthonous and allochthonous food resources (Table II).

The trophic status of the fish can be primarily assigned to the pelagic (midwater) foraging "generalized invertivore guild" since invertebrates comprised 58.9 % of the diet. The fish can be considered as a "primary consumer" due to the ingestion of algae, detritus and macrophytes; a "secondary consumer" due to the consumption of invertebrates and a "top consumer" because of Ris piscivorous habit. *P. afer* is thus capable of exploiting the primary, secondary and tertiary trophic levels of the stream. The principal food items can be ranked in the following order of decreasing importance: midwater invertebrates < allochthonous macrophyte debris < allochthonous invertebrates < preyfish < epiphytic algae < miscellaneous insects < benthic invertebrates < neustonic invertebrates < zooplankton.

The selective advantage of a euryphagic trophic strategy (heterotrophy) involving different aquatic ecosystem energy levels is that it facilitates the effective utilization of available food resources and the associated ability of the fish to easily switch from one food resource to another. Availability and abundance were not determined in this study; however, if the diet composition is a reflection of food availability and abundance in the habitat, the proportions of the various dietaries in the stomachs can be considered as surrogate measures. Thus, the "occasional status" of the diet constancy index for over 50 % of the food-types (Table II) and the low index of biotal dispersity may be advanced as evidences of diet switching in *P. afer*.

A wide feeding spectrum also ensures the reduction of competition for food between conspecifics and congeners occupying the same marginal water biotope. The inverse function between diet diversity and diet overlap coefficients (eqn. 6) provides evidence that diversification of diet may reduce intraspecific competition for food. In aquatic systems where the supply of specific components of food-base is unstable or unreliable, the evolution of opportunistic foraging habit as in *Papyrocranus afer* would facilitate greater success of the fish than the specialized foragers. The abundance of *P. afer* may therefore not be limited by food resources but by other ecological factors.

Papyrocranus afer is a slow-moving fish that preferentially inhabits the vegetated littoral zone of Ikpa River. Personal non-quantitative field observations indicated that this biotope supported large populations of diverse taxa of aquatic invertebrate fauna as also noted by WELCOMME (1979) and LOWE-MCCONNELL (1987) for other tropical aquatic systems. The preferred biotope of *P. afer* thus attunes with the high dietary importance of the midwater invertebrate assemblage associated with submerged macrophytes of marginal waters. Although the epiphytic algae in the diet were probably inadvertently engulfed along with the aufwuchs fauna, they are of nutritional significance, having a high caloric content (ODUM, 1971). WELCOMME (1979) has pointed to the abundance of epiphytic algae as food source on submerged marginal vegetation in tropical waters. Other plant food resources of allochthonous origin enter the stream largely through the marginal water inhabited by *P. afer*.

Since the presence of submerged vegetation encourages the concentration of benthic invertebrates, the secondary dietary role played by benthic invertebrates for *Papyrocranus afer* is not astonishing. The neuston, a dietary component of *P. afer*, is usually abundant in sheltered vegetated areas (WELCOMME, 1979), this corresponding with the biotope preference of the fish. In stream ecosystems, the input of allochthonous materials (an important food source for *P. afer*) is highest in marginal waters from the overhanging macrophytes of the riparian zone (KARR *et al.*, 1981). The cyprinodonts and juvenile cichlids consumed by *P. afer* are known to inhabit the quiet marginal waters (Reed *et al.*, 1967; Holden and Reed, 1971).

From the foregoing evidences, it is apparent that the vegetated marginal water represents a natural "food concentrate". *Papyrocranus afer* thus inhabits a biotope in which it is in close proximity to its abundant food resources. The trophic bioenergetic significance of this food-consumer relationship is that *P. afer* prefers a biotope from where its food resources are easily accessible and readily obtained with limited effort and expenditure of the energy cost of foraging; consequently, it maximizes the net energy intake and hence, the maintenance of the fish population.

The food habit of *Papyrocranus afer* in Ikpa River is broadly in accord with the preliminary findings of Teugels *et al.* (1992) and closely parallels the food habit of the allied *Xenomystus nigri* in Oueme River, Benin Zaire (Welcomme, 1979) and in equatorial forest waters of Central Zaire (Welcomme, 1979; Lowe-McConnell, 1987). The predominance of coarse detritus over fine detritus parallels the dietary habit of *Brienomyrus brachyistius* in Ikpa River and is a reflection of the abundance of this item in the stream (King, 1989). The ecological significance of this item as principal energy source in headwater streams has been discussed by Welcomme (1979, 1985). The overall food composition of *P. afer* comprised 20.6 % plant materials which also featured in the diet year-round. Although the assimilation efficiency of plant matter by fish is generally lower than that of animal prey, its consumption provides satiation by virtue of mere filling of the stomach as well as increasing gastric evacuation rates and hence ration size, both of which compensate for the low nutritional quality (Magalhaes, 1992).

Most of the stomach contents of *Papyrocranus afer* were indicative of vigorous reliance on surface, pelagic and benthic foraging. Surface foraging was evidenced by the ingestion of surface-dwelling cyprinodont preyfish, neuston and allochthonous foods that landed on the water surface. The role of terrestrial food resources in the trophic ecology of tropical stream fishes has been noted by several authors, including Welcomme (1979), Angermeier and Karr (1983) and Lowe-McConnell (1987).

Pelagic foraging was indexed by the consumption of midwater fauna (mainly insects and juvenile cichlids) and epiphytic algae while the benthic invertebrates, sedimented detritus and sand grains in the stomachs attested to benthophagy. Although each component of "benthic invertebrates" was of incidental importance, they could be of much nutritional value by virtue of the large sizes of some of them e.g. potamid, atyid and palaemonid crustaceans. It is energetically more profitable to consume large items than small ones (Angermeier, 1985). Sand grains may have been inadvertently ingested during benthic foraging, this assertion being supported by the fact that no stomach was found exclusively with sand. The presence of associated fine particulate organic matter (i.e. organic matter adhering to sand particles) in stomachs indicates that some nutritional benefit may accrue from the ingestion of sand, although this is not anologous to that derived by deposite feeders subsisting predominantly on mud/sand with associated organic matter, epipelic/episammic algae and microzoobenthos (Welcomme, 1979, 1985, 1986). Moreover, the sand grains ingested by *Papyrocranus afer* may assist in the mechanical maceration of food in its muscularized stomach eventhough its stomach walls are not as muscularized as those of mugilids (Bond, 1979).

The ability of *Papyrocranus afer* to exploit the surface, midwater and bottom water spatio-trophic niches for allochthonous and autochthonous foods is a spectacular ecological feature which may account in part for the wide variety of items consumed, since the fish is capable of encountering and hence, making full use of available food resources in the entire water column. This phenomenon also ensures constant encounters with food resources regardless of the vetical level at which the fish finds itself in the stream.

The diet constancy index portrayed that the food of *Papyrocranus afer* was dominated by occasional elements. This points to the high degree opportunistic foraging strategy of the fish. Allochthonous foods such as coarse detritus, fine detritus, macrophyte debris, acridids, formicids, coleopteran imagoes and larvae and unidentified insect taxa were of constant or accessory statuses. This type of trophic reliance on allochthonously produced food resources would profitably persist only in stream ecosystems with thick and stable riparian vegetation that ensure the regularity in the supply of specific food items and suggests that large/small scale anthropogenic alteration in the riparian forest composition and structure may impose adverse impacts on the trophic status of *P. afer*.

The overall euryphagy, low index of biotal dispersity and diet constancy index (for most dietaries) of *Papyrocranus afer* may be relevant in illustrating the selective pressures that lead to the evolution of this trophic pattern (cf. Lowe-McConnell, 1987). High trophic specialization is expected of fishes that live in equilibrium habitats and whose dietary habits are regulated by deterministic (stable) processes of food supply; alternatively, trophic generalization is an expected attribute of fishes inhabiting non-equilibrium or stochastic habitats and whose dietary habits are regulated by the differential responses of the fish to unpredictable or unstable processes of food supply. Specialization in dietary habits can be deterministically regulated in fishes subsisting largely on autochthonous foods whereas generalized food habits are stochastically regulated in fishes with heavy reliance on allochthonous foods. This agrees with the notion of THOMAS (1964) that the availability of allochthonous fauna as fish food is uncertain, being determined largely by extrinsic factors such as rainfall, wind, air temperature and the occurrence of marginal vegetation.

In the light of available diet data for *Papyrocranus afer*, it can be inferred that the interplay of deterministic and stochastic processes are likely to be critical elements in regulating the trophic strategy of the fish. The relative importance of either ecological factor can be discerned from the composite of food preponderance of autochthonous (66.3 %) and allochthonous (30.2 %) foods which portrayes deterministic pressures as assuming much greater significance than stochastic pressures in structuring the dietary strategy of *P. afer* in Ikpa River.

The low values of the overall index of biotal dispersity and month-to-month diet overlap coefficients (Table IV) suggest that the euryphagy of *Papyrocranus afer* and high degree plasticity in food preference was maintained throughout the year. These are further buttressed by the high diet diversity index in most months of the year. Given the supposition that foraging activity of *P. afer* remained constant throughout the year, the seasonality in the relative importance of the dietaries can be interpreted as a crude index of the pulses in food resources availability and abundance (cf. KING, 1989; MAGALHAES, 1992). Thus the dry season increase in the relative importance of allochthonous macrophyte débris corresponds with the period when many forest trees shed their leaves.

Papyrocranus afer consumed more benthic invertebrates in the dry season than during the rains in contrast to the regime in abundance of this food category in tropical streams (ANGERMEIER and KARR, 1983). A number of reasons can be advanced for the observed trend: STOUT (1982) has reported a reduction in invertebrate abundances in tropical streams, resulting from the impacts of scoring discharge and HYNES (1975) has cited studies showing that the down-stream drift of invertebrates in rivers positively correlates with flow rate while WELOMME (1979) reviewed works suggesting wider dispersion and higher rate of dislodgement and downstream transport of benthic fauna during floods. Reduction in the abundance and availability of benthic invertebrates in Ikpa River by one or more of the above mechanisms, probably accounted for the decline in their importance during the rains in *P. afer* (cf. KING, 1989).

With the onset of the dry season and accompanying reduction in stream level and flow rate, the dietary importance of benthic invertebrates increased, perhaps as a consequence of greater abundance and availability; this increase in the dietary importance of benthic invertebrates is reflected in the increased ingestion of sand grains.

The dietary importance of midwater invertebrates in the wet season slightly exceeded that of the dry season but that of neustonic forms was higher during the dry season contrary to LOWE-MCCONNELL's (1975) anecdotal report that the abundance of neustonic fauna increased during the rains. The wet season increase in the dietary importance of allochthonous invertebrates (cf. LOISELLE, 1971; KING, 1989) was particularly pronounced in the gryllids, acridids, formicids, isopterans, anisopterans and juliform millipeds. The reports of ZARET and RAND (1971), LOWE-MCCONNELL (1975), WELCOMME (1979) and ANGERMEIER and KARR (1983) lend support to the regime observed here (i.e. hightened dietary importance of allochthonous fauna during the rains and lower status in the dry season).

Availability of allochthonous invertebrates to tropical stream fishes may increase during the rains due to higher productivity, expanded stream area *vis-à-vis* the dry season, and the mechanical dislodgement and transfer of the fauna from the normal substrates into the stream through the actions of wind, rain and surface runoff (cf. ANGERMEIER and KARR, 1983; Pers. observ.). In Ikpa River, the stormy early rains of the March-April seasonal transition appeared to be the period of maximum input of allochthonous invertebrates as indexed by the considerable increase in their dietary importance in *Papyrocranus afer* during these months (Table III).

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