Trophic ecology and ecomorphology of fish assemblages in coastal lakes of Benin, West Africa[1]

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Abstract: The feeding ecology and morphological diversification of fish assemblages of two coastal lakes in southern Benin (West Africa) were examined to compare patterns of community organization. Though located only 18 km apart, the two fish assemblages had dissimilar species composition, and this is largely derived from differences in connectivity to the Gulf of Guinea, salinity and pH. Among the 35 and 20 species sampled from Lake Nokoue (connected with a sea) and Lagoon Toho-Todougba (no sea connection), respectively, only a few species dominated each system. Lake Nokoue was dominated by the perciform *Gerres melanopterus* and the clupeiform *Ethmalosa fimbriata*, and Lagoon Toho-Todougba was dominated by the characiform *Brycinus longipinnis*. In Lake Nokoue, the akadja habitat (dense stands of woody debris installed by humans to attract fishes) had high species richness compared to the other lake habitats. Multivariate procedures were used to examine trophic guilds and the relationship between morphology and diet. Overall, thirteen trophic guilds were identified, with detritivore and piscivore guilds having the most species. Lagoon Toho-Todougba was dominated by detritivorous and insectivorous species and Lake Nokoue, a larger lake with a connection to the sea, was dominated by piscivores. In Lagoon Toho-Todougba, consumption of vegetation and insects was common, but these items were very rare in Lake Nokoue fish diets, possibly because the destruction of its fringing mangroves has reduced their availability for fishes. Despite major differences in taxonomic composition, the two fish assemblages had similar mean values for most morphological traits and morphological-based centroids from multivariate analyses were remarkably similar. Because members of the same feeding guild tended to have similar morphologies, some degree of diet specialization has accompanied morphological diversification in the taxa comprising these communities.

Keywords: Africa, diet specialization, ecological diversification, feeding guild, morphology, multivariate analysis.

Résumé: L'écologie trophique ainsi que la diversification morphologique ont été étudiées dans les communautés de poissons de deux lacs côtiers situés dans le sud du Bénin (Afrique de l'ouest), afin d'en comparer le patron d'organisation. Bien qu'ils ne soient distants que de 18 km, les deux communautés présentent une composition spécifique différente, en grande partie attribuable aux différences de communication avec le Golfe de Guinée, de la salinité et du pH. Seulement quelques-unes des 35 et 20 espèces échantillonnées respectivement dans le lac Nokoue (relié à la mer) et le lagon Toho-Todougba (non relié à la mer) prédominent dans chaque système. L'assemblage du lac Nokoue est dominé par le poisson perciforme *Gerres melanopterus* et le poisson clupéiforme *Ethmalosa fimbriata*, et celui du lagon Toho-Todougba, par le poisson characiforme *Brycinus longipinnis*. Dans le lac Nokoue, l'habitat que constitue l'akadja (sites où des débris ligneux sont accumulés par l'homme pour attirer les poissons) affiche une grande richesse en espèces par comparaison aux autres habitats du lac. Une analyse multivariée a été utilisée pour étudier les guildes alimentaires et la relation entre la morphologie et la diète. Dans l'ensemble, 13 guildes trophiques ont été identifiées, les guildes détritivores et piscivores comportant le plus grand nombre d'espèces. Les espèces détritivores et insectivores prédominent dans le lagon Toho-Todougba, et les espèces piscivores dans le Lac Nokoue, un lac de plus grande taille, en lien avec la mer. Dans le lagon Toho-Todougba, la consommation de plantes et d'insectes est fréquente mais ces éléments se trouvent rarement dans la diète des poissons du lac Nokoue, parce que la destruction des mangroves a peut-être contribué à faire diminuer leur disponibilité pour les poissons. En dépit de différences importantes dans la composition taxonomique, les deux communautés de poissons ont des valeurs moyennes similaires pour la plupart des caractères morphologiques, et les centroïdes basés sur la morphologie et issu des analyses multivariées sont très similaires. Comme les membres d'une même guilde ont tendance à avoir une forme similaire, un certain niveau de spécialisation au plan de la diète s'est effectuée en même temps que la diversification morphologique chez les taxons formant ces communautés.

Mots-clés: Afrique, spécialisation alimentaire, diversification écologique, guilde alimentaire, morphologie, analyse multivariée.

Introduction

Two major goals of community ecology are to identify patterns of community organization that are consistent across geographical locations and divergent taxa and to formulate causal mechanisms for these patterns. The comparative approach using data collected from natural systems is particularly valuable for addressing the first goal and experimental manipulations in field and laboratory settings

can test ideas about mechanisms (Schoener, 1987). Because all organisms interact with other species (*e.g.*, prey, competitors, predators) in the process of acquiring resources, patterns of resource use provide a valuable metric for community organization. The similarity in resource use (*i.e.*, niche overlap) within species assemblages can be viewed in terms of species niche segregation (Inger & Colwell, 1977; Winemiller & Pianka, 1990) and guild structure (Pianka, 1976; Simberloff & Dayan, 1991). This report examines ecological and morphological patterns in

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coastal fish assemblages in tropical West Africa in order to compare guild structure and ecological diversification.

The relationship between form and ecological function is well documented for a variety of morphological attributes of fishes (Gosline, 1971; Gatz, 1979; 1981; Webb, 1984; Wainwright & Richard, 1995). Keast & Webb (1966) were among the first to discuss the ecological correlates of morphological variation in fishes at the faunal level. The feeding ecology, swimming mode and even habitat use of a fish often can be inferred by examining its morphology (Keast & Webb, 1966; Gatz, 1979; 1981; Page & Swofford, 1984; Winemiller, 1991; Motta et al., 1995). The shape of a fish's body and fins can be used to predict its swimming behavior and habitat preferences (Keast & Webb, 1966; Gatz, 1979; Webb, 1984). The functional properties of a number of fish morphological features have been revealed by laboratory studies of the functional morphology of feeding (Alexander, 1970; Liem, 1974; Wainwright, 1988) and locomotion (Webb, 1984).

Ecomorphology operates under the premise that ecological relationships can be inferred from an appropriate set of morphological features (Hespenheide, 1973). Hutchinson's (1959) research on body size ratios was one of the first quantitative attempts at ecological inference based on morphology and later studies have applied this research at a variety of resolution scales for several animal taxa (Fenton, 1972; Findley, 1973; Karr & James, 1975; Ricklefs & Travis, 1980; Moyle & Senanayake, 1984; Pianka, 1986; Motta, 1988; Wikramanayake, 1990). Several studies have shown higher levels of ecomorphological diversification (Findley, 1973; Ricklefs & Travis, 1980; Ricklefs, Cochran & Pianka, 1981; Winemiller, 1991) and species packing (Watson & Balon, 1984) in more species-rich assemblages. Following the concept of limiting similarity (MacArthur & Levins, 1967), these trends suggest an historical effect of interspecific resource competition. Theoretically, as new species are added to a saturated community, they could reduce interspecific competition during periods of resource limitation by using new methods to acquire alternative resources. Or, competition for core resources could remain constant with the addition of species if ecological specialization were to result in a more fine-scaled use of core resources (i.e., species packing). The study of community organization via analysis of morphological features assumes that 1) in the short term, local species assemblages interactively exclude certain regional elements, or 2) in the long term, the evolution of phenotypes is influenced by the presence of sympatric species.

This paper reports findings from an ecological and morphological analysis of fish assemblages from two coastal lagoons in West Africa. Relative to other regions of the world, scant ecological information is available for fishes and aquatic ecosystems in Africa. A major issue is whether or not fishes are more similar or less similar to each other in a species-rich assemblage compared with those from a species-poor assemblage. This study also identifies major feeding guilds, the taxonomic composition of guilds, and differences in resource use by fish assemblages of the two lakes. Two major factors influence the taxonomic differences between the two lakes: 1) differences in area, and 2) presence or absence of a direct connection with the sea.

Study sites

LAKE NOKOUE

Located in the south of the Republic of Benin (West Africa), Lake Nokoue (6° 27' N, 2° 26' E) covers 14 000 ha and connects both with the Atlantic Ocean in the south and the Oueme and Sô Rivers in the southeast and north, respectively (Figure 1). During the rainy season, these rivers increase their discharges into Lake Nokoue (Texier et al., 1980) and cause a gradual decrease in salinity. Lake Nokoue is also connected to the lagoon of Porto-Novo, which in turn is connected to the lagoon of Lagos in the Republic of Nigeria. Average annual rainfall is approximately 1150 mm, and the maximum rainfall usually occurs during June. Monthly mean temperature ranges from 29.3°C to 33.6°C, and the monthly mean evaporation varies between 59.2 and 145 mm.
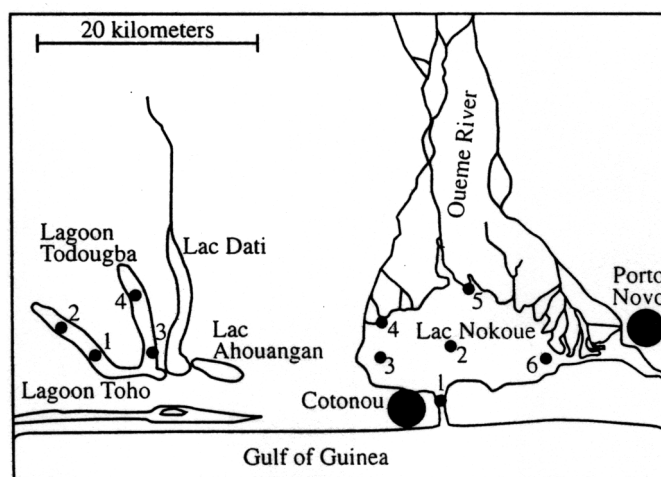

FIGURE 1. Map illustrating the location of Lake Nokoue and Lagoon Toho-Todougba in the coastal region of southern Benin.

Until a few years ago, Lake Nokoue was bordered by dense mangroves, mainly Avicennia and Rhizophora, that provided the lake with nutrient enrichment from decomposition. The mangroves also served as spawning substrate for fishes and reduced shoreline erosion. These mangroves were gradually destroyed by the increasing population of fishermen surrounding this lake, and this has resulted in a variety of ecological problems. The lake has also been invaded by the floating water hyacinth, Eichhornia crassipes, which now covers a considerable part of the lake. Because of its large area and the resources it provides, Lake Nokoue is the most important brackish water ecosystem in Benin.

LAGOON TOHO-TODOUGBA

Lagoon Toho-Todougba is located in the south of Benin between 6° 23' and 6° 27' N and 2° 07' and 2° 13' E (Figure 1). This 995 ha lagoon is completely isolated from other aquatic ecosystems and local precipitation runoff is its only source of water. Because of the proximity of this lagoon to Lake Nokoue, the two systems have virtually the same climate. In fact, Lagoon Toho-Todougba was once connected with Lake Nokoue, but because of the construction of the bridge between Cotonou (city to the south) and

Benin's central region, this lake has become isolated. Monthly mean temperature ranges from 29.3 to 33.6°C, and the monthly mean evaporation varies between 59.2 and 145.0 mm. Average annual rainfall is 982.6 mm (based on data from 1970 to 1987, unpubl.), and the highest precipitation is recorded during June or July. This lake contains rooted plants such as *Alchornea cordifolia, Jussiaea stenoraphe, Fimbristylis aphylla, Rhyncospora corymbosa, Thalea welwichii, Cyclosorus striatus, Panicum maximum, Paspalum vaginatum, Anthocleista vogelii, Ficus congensis, Cyrtosperma senegalensis, Cyperus articulatus, Cyperus compressus,* and *Typha australis* (Adite & Van Thielen, 1995). The withdrawal of water for the irrigation of palm tree plantations influences the lake's volume.

Material and methods

FISH SAMPLES

During the tropical wet period (June-September) of 1994, fishes were captured from six sites in Lake Nokoue and four sites in Lagoon Toho-Todougba (Figure 1). The first Nokoue site (chenal de Cotonou) is in the south near the channel that connects the lake and the ocean. This site has mostly open water with fast current compared to the other sites. This site is deep (5.12 m) with high salinity (35.6 ppt), an alkaline pH (8.05), relatively high dissolved oxygen (9 mg/L), and low transparency (0.82 m Secchi depth). This low transparency is the result of the combined effect of the rapid water movement and the proximity of this site to an open public market, 'Dantokpa', from which large quantities of organic material are introduced. The second Nokoue site (centre lac) is also characterized by relatively fast water movement, lower depth (1.43 m), relatively low salinity (10.3 ppt), neutral pH (7.1), high dissolved oxygen (11 mg/L), and high transparency (1.29 m). The third Nokoue site is located in the west within the 'akadja' zone. Akadja is a traditional fisheries/aquaculture method that uses plots of tree branches to attract fishes into shallow areas of the lake (see Welcomme, 1972 for descriptions). This site is shallow (depth = 1.39 m) with a high salinity (26.0 ppt), pH = 7.5, dissolved oxygen = 8.75 mg/L, and low transparency (0.75 m). The fourth Nokoue site (Onatho) is a shallow area (depth = 0.6 m) in a zone of natural vegetation (mainly *Paspalum vaginatum*) in the southwest of the lake. The salinity was 12.3 ppt, pH = 7, dissolved oxygen = 9 mg/L, and transparency = 0.6 m. The fifth Nokoue site (Ouedogbadji) is located in the north of the lake in a shallow (depth = 1.63 m), naturally vegetated area where pH was neutral (pH = 7), dissolved oxygen was high (9 mg/L), salinity was low (0.05 ppt) and transparency was high (1.38 m). The last Nokoue site is located in the southeast near the canal of Totche that connects Lake Nokoue and the lagoon of Porto-Novo. This site was shallow (1.42 m, but can become deeper depending on the tides), with low salinity (0.04 ppt) and high turbidity (transparency = 0.4 m) from water movement. Except for the center lake site (sandy bottom), all of the sites have a mixture of mud and sand substrates.

Four sites in Lagoon Toho-Todougba were surveyed (Figure 1). Site 1 (village Dossinou) is shallow (mean depth = 1.95 m) with vegetation. Site 2 (village Daguetome) is shallow (1.93 m) but with less vegetation than site 1. Site 3 (village Tchiakpecodji) is shallow (depth = 1.61 m) with a moderate water current. Site 4 (in front of village Fandji Adebohoue) is deep (depth = 2.8 m) with fast water current. At the four Toho-Todougba survey sites, pH ranged from 6.2 to 6.6, dissolved oxygen ranged between 10.5-12.5 mg/L, salinity was nearly 0 ppt and turbidity was high.

Because population structure varies in relation to season for many species in both lakes, our data are only representative of assemblage structure during the rainy season. Lake Nokoue is a particularly dynamic ecosystem, and its habitats and fish assemblages probably change on a multi-year basis as well. Two to four collections were made at each survey site, and a variety of gears and fishing methods were used in an attempt to obtain maximum information on species diversity within a short period of time. Based on earlier research on Lake Nokoue (Welcomme, 1972; Van Thielen *et al.*, 1987; Adite & Van Thielen, 1995), the common species were well represented in our samples. Furthermore, the use of various sampling gears helped to increase the probability of capturing rare species. Fishes were captured with a nylon seine (5.6 m; 7 mm mesh) and a 46.2 m nylon monofilament gill net with panels of different mesh sizes (20-75 mm mesh). Stationary fish traps and longlines were also used, especially in shallow areas fringing the lakes. During every outing at each site, total fishing effort ranged from 5 to 12 hours during the daylight period. Each captured specimen was tentatively identified to genus or species level, recorded, preserved in 10-20% formalin, and stored in the Fishery Department laboratory in Benin prior to shipment to Texas A&M University for further lab examinations.

In the lab, specimens were removed from the formalin solution and transferred to 70% ethanol. Holden & Reed (1972), Van Thielen *et al.* (1987), and Lévêque, Paugy & Teugels (1990a,b) were referenced for taxonomy. After confirmation of species identification, each specimen was measured (standard length) and weighed on an electronic balance (nearest 0.1 g). Since shrinkage is expected to be fairly minimal after a few months at our formalin concentrations (Parker, 1963), measurements were not corrected for shrinkage. Reference fish samples were deposited in the Texas Cooperative Wildlife Collection (TCWC) of Texas A&M University.

Species abundances and species relative abundances were computed for each of the 10 sites and both lakes based on the number of individuals in samples, and computed again based on sample biomass. Species richness and species diversity (Shannon & Weaver, 1963) was determined for each survey site and both lakes. To compare faunal similarity of the two lakes, the coefficient of biogeographic resemblance (Duellman, 1990) was calculated as

$$CBR = 2C/(N_1 + N_2) \qquad [1]$$

where C is the number of species common to the two biotas, and N_1 and N_2 are the species richnesses in the first and second biotas, respectively. This index measures the similarity in species composition between two samples and ranges from 0 (no species in common) to 1.0 (share the same relative numbers and kinds of species).

MORPHOLOGICAL MEASUREMENTS

Morphological measurements were made for 51 species, 35 from Lake Nokoue and 20 from Lagoon Toho-Todougba (with 4 species in common). Measurements were made on a sample of three individuals of average adult size per species (except for uncommon species for which only 1-2 individuals were measured: *Caranx hippos, Trachinotus teraia, Pegusa triopthalma, Gerres nigri, Progobius schlegelii, Liza grandisquamis, Lutjanus agennes, Monodactylus sebae, Polydactilus quadrifilis, Sphyraena afra, Strongylura senegalensis, Clarias agboyiensis, Gymnarchus niloticus, Parachana obscura, Pellonula sp.,* and *Protopterus annectens*). Only the largest individuals were used in order to minimize potential allometric effects of ontogeny in the morphological analysis (Gatz, 1979). Morphological attributes were measured to the nearest 0.1 mm using vernier calipers or a clear plastic ruler. Twenty-eight characters were chosen based on information presented in Gatz (1979), Watson & Balon (1984) and Winemiller (1991). Following the criteria and descriptions in Winemiller (1991), these ecomorphological traits were as follows: 1. standard length (SL), 2. maximum body depth (MBD), 3. body depth below mid-line (BDBL), 4. maximum body width (BODW), 5. caudal peduncle length (PEDL), 6. caudal peduncle depth (PEDD), 7. head length (HEAL), 8. head depth (HEAD), 9. head width (HEAW), 10. eye position (EYEP), 11. eye diameter (EYED), 12. mouth position (MOUO) as the angle formed by lines passing through the corner of the mouth and the tips of the upper and lower jaws, 13. mouth width (MOUW), 14. mouth height (MOUH), 15. snout length (SNLS), 16. dorsal fin length (DORL), 17. dorsal fin height (DORH), 18. pectoral fin length (PECL), 19. caudal fin length (CAUL), 20. caudal fin height (CAUH), 21. pelvic fin length (PELVL), 22. anal fin length (ANAL), 23. anal fin height (ANAH), 24. maximum tooth length, 25. number of gill rakers (GRAK), 26. maximum gill raker length (GRL), 27. gut length (GUTL), 28. swim bladder length (SWBL).

DIETARY ANALYSIS

Preserved specimens were dissected and all food contained in the stomach or anterior half of the gut (the latter for those species not having a defined stomach) were removed and spread on a glass slide for identification under a dissecting microscope. Water was sometimes added to facilitate the examination. Whenever the digestive tract was packed with a mixture of macroscopic and microscopic particles (*i.e.*, detritivores and algivores), a small sample was taken from the anterior-most gut segment for identification (Grossman, 1986; Winemiller, 1990). References on aquatic invertebrates (Needham & Needham, 1962; Pennak, 1978), terrestrial arthropods (Borror, Delong & Triplehorn, 1976) and fishes (Hoese & Moore, 1977; Van Thielen *et al.*, 1987; Lévêque, Paugy & Teugels, 1990a, b) were consulted for prey identification. The length of each prey item was measured to the nearest 1 mm with vernier calipers then classified by 1 cm intervals. A volumetric method was used to quantify stomach contents. The food items or samples were blotted dry on a paper towel then measured by water displacement using an appropriately-sized graduated cylinder. For detritivores and algivores, a wet mount sample

was viewed under a compound microscope and the relative proportions of each major food category were visually estimated. These proportions were later multiplied by the total volume of the specimen's gut and contents (Winemiller, 1990). For small stomach contents (< 0.002 mL), the material was spread on a glass slide and the volume was visually estimated based on comparison with a small sample of known volume (Winemiller, 1990).

DATA ANALYSIS

MORPHOLOGY

The grand mean standard length (SL) was calculated for the combined-lake dataset based on common species. Linear measures for individual fish were multiplied by a conversion factor (grand mean/individual fish SL) to standardize to a uniform body size, then all linear measures were $\log_{10}$ (value + 1) transformed to normalize distributions for statistical analyses. Angles were adjusted by (value + 90) to make their log transformations positive. The faunal mean and the standard deviation were calculated for each morphological feature.

DIET

Volumes of individual diet items were summed across all specimens of a given species, and volumetric proportions were calculated based on the total volume of food consumed by the species in our sample. Because many fishes undergo ontogenetic diet shifts, this method biases species consumption estimates in favor of larger individuals. In most cases, our samples contained mostly adult size classes; notable exceptions being the detritivores *Sarotherodon galilaeus* and *S. melanotheron* with abundant immature and adult size classes. This method was also desirable from the standpoint of our examination of diet-morphology relationships which stressed adult size classes. To facilitate between-fauna comparisons, the diet items then were aggregated into the following 16 broad food categories: detritus, algae, protozoa/rotifers, vegetation, seeds, microcrustacea, worms/coelenterata, molluscs, macrocrustacea, aquatic insects, terrestrial arthropods, unidentified fishes, perciforms, clupeiforms, mugiliforms, and cypriniforms. Only our directly documented dietary data were used for this study and those species for which all specimens had empty stomachs were omitted from the dietary analysis. Levin's index (1968) of niche breadth (also called niche width or niche size) was calculated from the formula:

$$B = 1 \Big/ \sum_{i=1}^{n} p_i^2 \qquad [2]$$

where B is niche breadth, p_i is the volumetric proportion of food item i in the diet and n is the total number of food items in the diet. B ranges from 1, when only one resource is used, to n, when all resources are used equally by the consumer. The maximum value for diet breadth is obtained when all resources are equally available and the consumer shows no discrimination (Krebs, 1989). We calculated the standardized niche breadth (B_a) following Hurlbert (1978):

$$B_a = (B-1)/(n-1) \qquad [3]$$

B_a ranges from 0, when only one resource is used, to 1 when all resources are used equally.

To directly estimate diet similarity between species, dietary overlap was calculated using Pianka's (1976) niche overlap index, also called percentage overlap (Krebs, 1989). This index is calculated as:

$$\emptyset_{jk} = \sum_{i=1}^{n} p_{ij} p_{ik} \Big/ \left(\sum p^2_{ij} \bullet \sum p^2_{ik} \right)^{1/2} \qquad [4]$$

where $\emptyset_{jk}$ is the symmetrical niche overlap between species j and species k, p_{ij} is the proportion of resource i used by species j, p_{ik} is the proportion of resource i used by species k, and n is the total number of resource states. Dietary proportions were $\log_{10}$ (value + 1)-transformed for use in statistical analyses.

PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis (PCA) was performed on both the dietary and standardized morphological datasets. PCA is a multivariate method used to examine the correlation structure among variables and to lessen the influence of the variables that contribute relatively little information to the overall patterns (Jeffers, 1978). The eigenvalue, eigenvectors (loadings of the dietary or morphological attributes on the gradient axes), and percentage contribution of each attribute to total variation was calculated for each PC axis. Species scores on the major PC axes were used to compare dietary or morphological distances between assemblages. Statistical computations were performed with SAS (SAS, 1989).

EUCLIDEAN DISTANCE AND CLUSTER ANALYSIS

The average Euclidean distance between species (ED_{ss}), an expression of the ecological similarity or packing of species (Gatz, 1979; Watson & Balon, 1984) was computed for each assemblage. The average distance between each species and its assemblage centroid or hypothetical average species, (ED_{sc}) was computed. According to Gatz (1979), ED_{sc} indicates the total niche space occupied by the assemblage. Species scores for the first ten and first five PCA axes for the dietary and morphology data, respectively, were used to determine species pairwise Euclidean distances with the formula:

$$ED = \left[\sum (x_1 - x_2)^2 \right]^{1/2} \qquad [5]$$

The inverse of Euclidean distance was used as the measure of similarity for cluster analysis. We used sequential, agglomerative, hierarchical, nested clustering algorithm (SAHN) to produce dendrograms based on similarity. Both Euclidean distances and cluster analyses were generated using the Numerical Taxonomy and Multivariate Analysis System (NTSYS) (Rohlf, 1993).

Results

SPECIES RICHNESS AND FAUNAL COMPOSITION

Species richness and composition of the two ecosystems differs greatly. Thirty-five species belonging to 20 families were collected from Lake Nokoue. The Mugilidae was the most important family with six species: *Liza falcipinnis*, *L. dumerili*, *L. grandisquamis*, *Mugil bananensis*, *M. cephalus* and *M. curema* (Table I). The Cichlidae followed with four species: *Hemichromis fasciatus*, *Sarotherodon melanoth-*

TABLE I. Abundances, relative abundances, mean lengths, size ranges and mean weights of the 35 fish species (20 families) from Lake Nokoue samples. SA = sample abundance, RA = relative abundance, ML = mean length (mm), SR = size range (mm), MW = mean weight (g)

Species	SA	RA	ML	SR	MW
FAMILY BAGRIDAE					
Chrysichthys nigrodigitatus	7	0.006	154	150-207	73
FAMILY BELONIDAE					
Strongylura senegalensis	2	0.002	302	256-348	49
FAMILY BOTHIDAE					
Citharichthys stampflii	20	0.017	97	61-120	15
FAMILY CARANGIDAE					
Caranx hippos	2	0.002	96	85-107	27
Trachinotus teraia	2	0.002	110	110	46
FAMILY CICHLIDAE					
Hemichromis fasciatus	11	0.009	98	90-120	36
Sarotherodon melanotheron	100	0.086	98	63-160	49
Tilapia guineensis	36	0.031	54	6-145	29
Tilapia zillii	2	0.002	153	140-165	170
FAMILY CLUPEIDAE					
Ethmalosa fimbriata	458	0.39	95	55-118	16
FAMILY CYNOGLOSSIDAE					
Cynoglossus senegalensis	4	0.003	301	261-325	129
FAMILY ELEOTRIDAE					
Eleotris senegalensis	7	0.006	139	90-190	80
Kribia nana	3	0.003	84	74-93	21
FAMILY ELOPIDAE					
Elops lacerta	53	0.046	174	90-225	71
FAMILY GERREIDAE					
Gerres melanopterus	259	0.22	94	67-119	21
Gerres nigri	1	0.001	80	80	16
FAMILY GOBIIDAE					
Gobionellus occidentalis	9	0.008	125	108-133	22
Porogobius schlegelii	2	0.002	89	88-90	12
FAMILY LUTJANIDAE					
Lutjanus goriensis	29	0.025	101	52-190	51
Lutjanus agennes	2	0.002	128	100-155	79
FAMILY MONODACTILIDAE					
Monodactylus sebae	2	0.002	77	67-87	35
FAMILY MUGILIDAE					
Liza dumerili	3	0.003	167	162-170	74
Liza falcipinnis	82	0.070	141	90-220	54
Liza sp.	2	0.002	117	117	24
Liza grandisquamis	1	0.001	103	103	20
Mugil bananensis	3	0.003	179	132-226	119
Mugil cephalus	2	0.002	189	188-190	128
Mugil curema	11	0.009	145	120-168	61
Mugil sp.	1	0.001	120	120	30
FAMILY OPHICHTHYIDAE					
Myrophys plumbeus	4	0.003	410	358-455	47
FAMILY POLYNEMIDAE					
Polydactilus quadrifilis	3	0.003	249	160-356	387
FAMILY POMADASYIDAE					
Pomadasys jubelini	14	0.012	121	70-168	46
Pomadasys peroteti	9	0.008	131	93-145	67
FAMILY SERRANIDAE					
Epinephelus aeneus	6	0.005	100	79-125	27
FAMILY SPHYRAENIDAE					
Sphyraena afra	1	0.001	190	190	42
FAMILY SOLEIDAE					
Synaptura lusitanica	9	0.008	158	111-190	41
Pegusa triopthalma	2	0.002	115	114-115	23
Total number	1164				

eron, Tilapia guineensis and *T. zillii*. Each of the remaining families contained only one or two species. Lagoon Toho-Todougba samples contained only 20 species belonging to 13 mostly freshwater families (Table II). The most speciose family was the Cichlidae with seven species: *Sarotherodon galilaeus, Tilapia guineensis, T. mariae, T. zillii, Chromidotilapia guntheri, Hemichromis fasciatus* and *H. bimaculatus* accounting for 35% of the total species collected in this lake.

TABLE II. Abundances, relative abundances, mean lengths, size ranges and mean weights of the 20 fish species (13 families) from Lagoon Toho-Todougba samples. SA = sample abundance, RA = relative abundance, ML = mean length (mm), SR = size range (mm), MW = mean weight (g)

Species	SA	RA	ML	SR	MW
FAMILY BAGRIDAE					
Chrysichthys auratus	7	0.018	179	140-210	117
Chrysichthys nigrodigitatus	2	0.005	170	125-215	112
FAMILY CHARACIDAE					
Brycinus longipinnis	239	0.600	71	60-82	9
FAMILY CICHLIDAE					
Chromidotilapia guntheri	13	0.033	83	13-105	27
Hemichromis bimaculatus	10	0.025	49	32-63	5
Hemichromis fasciatus	8	0.020	69	5-113	13
Sarotherodon galilaeus	11	0.028	182	110-350	187
Tilapia guineensis	1	0.002	125	125	70
Tilapia mariae	11	0.028	45	22-125	18
Tilapia zillii	1	0.002	108	108	60
FAMILY CLARIIDAE					
Clarias agboyiensis	1	0.002	235	235	103
FAMILY CLUPEIDAE					
Pellonula sp.	2	0.005	21	20-22	0.1
FAMILY CYPRINIDAE					
Barbus callipterus	30	0.075	36	31-46	1
FAMILY CYPRINODONTIDAE					
Aplocheilichthys pfaffi	4	0.010	22	20-22	0.1
FAMILY GYMNARCHIDAE					
Gymnarchus niloticus	1	0.002	530	530	485
FAMILY HEPSETIDAE					
Hepsetus odoe	27	0.067	168	50.4-320	85
FAMILY NOTOPTERIDAE					
Xenomystus nigri	6	0.015	148	142-157	21
FAMILY OPHIOCEPHALIDAE					
Parachanna obscura	2	0.005	209	201-216	118
FAMILY POLYPTERIDAE					
Polypterus senegalus s.	20	0.050	195	177-220	5
FAMILY PROTOPTERIDAE					
Protopterus annectens	2	0.005	408	360-456	323
Total number	408				

The coefficient of biogeographic resemblance (*CBR*) between the two ecosystems was 0.14, indicating low inter-assemblage faunal similarity. Low similarity was also indicated by the low *CBR*s between individual sites from the two lakes, which ranged from 0 to 0.18. Only two families (*i.e.*, Cichlidae with *Tilapia guineensis, T. zillii* and *Hemichromis fasciatus*; Bagridae with *Chrysichthys nigrodigitatus*) are shared by the two systems. Unlike the inter-assemblage faunal pattern, local biotas within lakes had relatively high faunal similarities. In Lake Nokoue and Lagoon Toho-

Todougba, *CBR* ranged from 0.32 to 0.67 and from 0.33 to 0.63, respectively. Also, there was no significant difference in the mean *CBR*s of the two lake assemblages ($F_{1,49}$ = 0.10, p = 0.75), an indication that the degree of between-site faunal similarity was similar in each lake.

In Lake Nokoue, the five most abundant species were *Ethmalosa fimbriata* (39%), *Gerres melanopterus* (22%), *Sarotherodon melanotheron* (8.6%), *Liza falcipinnis* (7%), and *Elops lacerta* (4.6%), which together comprised 81.2% of the total fish sample. Percent composition based on biomass showed a similar trend (Table I). Lagoon Toho-Todougba also had five dominant species (*Brycinus longipinnis, Hepsetus odoe, Barbus callipterus, Polypterus senegalus senegalus* and *Chromidotilapia guntheri*) that comprised 80% of our overall fish sample. Fish biomass was dominated by five species (*Brycinus longipinnis, Hepsetus odoe, Sarotherodon galilaeus, Polypterus senegalus* and *Chrysichthys auratus*) that together accounted for about 75.3% of the total sample biomass (Table II).

In both lakes, most species were captured from shallow areas (< 2 m) either with or without aquatic macrophytes (10-30 species per site). The percentage of species captured from deep habitats (> 2 m) was very similar in the two lakes (Nokoue = 29%, Toho-Todougba = 30%). In Lake Nokoue, the akadja habitat yielded 30 species out of the total of 35 that were sampled from the whole lake. Welcomme (1972) reported only 19 species from akadja samples from Lake Nokoue, but his sample included five species that we did not encounter (*Clarias lazera*, 2 *Synodontis spp.*, *Parachanna [Parophiocephalus] obscura, Labeo senegalensis*). A high species diversity of 1.28 was recorded for the akadja, compared with values < 1.0 for the other sites.

DIET

Fish assemblages of both lakes consumed a wide variety of food resources, ranging from detritus and algae to molluscs and fishes (Tables III and IV). Vegetation and aquatic insects were common in the diets of several Toho-Todougba fishes but were extremely rare in the diets of Lake Nokoue fishes. Todo-Todougba fishes consumed fruits, flowers, duckweeds and seeds; the aquatic insects were mostly immature Ephemeroptera, Odonata nymphs, Hemiptera, Coleoptera, and chironomids and other aquatic Diptera. Two resource groups that were found in the diets of Lake Nokoue fishes were absent in Lagoon Toho-Todougba fish diets: (1) rotifers, protozoa, coelenterata, oligochaete worms, and amphipods; and (2) crabs, unidentified Crustacea, eubranchiopods and crustacean nauplii. *Polypterus senegalus* was the only Lagoon Toho-Todougba fish documented to feed on shrimp (Decapoda).

In Lagoon Toho-Todougba, diet breadth (*B*) varied from 1 (B_a = 0) to 3.76 (B_a = 0.25) (Figure 2). *Barbus callipterus* had broadest diet (3.76) with 7 food categories (detritus, vegetation, seeds, microcrustacea, molluscs, aquatic insects, terrestrial arthropods), whereas *Hemichromis fasciatus* and *Parachanna obscura*, piscivorous species, had the lowest diet breadths. Diet breadths tended to be lower in Lake Nokoue (Figure 3) than in Lagoon Toho-Todougba (Figure 2), and ranged from 1 (B_a = 0) to 3.16 (B_a = 0.20), but overall, there was no significant difference ($F_{1,50}$ = 2.42, p = 0.13)

TABLE IV. Volumetric proportions of diet items of 19 fish species from Lagoon Toho-Todougba. Proportions are based on 16 food categories in Table 1

| Species	Number examined	Detri	Algae	Prot/rotif	Veget	Seeds	Micro-crust	Worm/coele	Mollu	Macro-crust	Aqua insect	Terr arth	Unid fish	Perci	Clupe	Mugi	Cypri
Aplocheilichthys pfaffi	2	0	0	0	0	0	0		0	0	0.49			0			
Barbus callipterus	24	0.37	0	0	0.06	0.02	0.01		0.01	0	0.25			0			
Brycinus longipinnis	188	0.01	0	0	0.01	0.06	0		0.01	0	0.39			0.01			
Chromidotilapia guntheri	20	0.58	0	0	0.01	0.12	0.03		0.01	0	0.10			0			
Chrysichthys auratus	7	0.60	0	0	0	0.01	0.01		0.09	0	0.30			0			
Chrysichthys nigrodigitatus	3	0.24	0.02	0	0	0	0.01		0	0	0.73	0		0			
Clarias agboyiensis	1	0.49	0	0	0	0	0		0	0	0.51	0		0			
Hemichromis bimaculatus	10	0.01	0	0	0	0	0		0	0	0.44	0		0			
Hemichromis fasciatus	5	0	0	0	0	0	0		0	0	0			0			
Hepsetus odoe	21	0	0	0	0	0	0		0	0	0			0			
Parachanna obscura	2	0	0	0	0	0	0		0	0	0			0			
Pellonula sp.	2	0.40	0	0	0	0	0.60		0	0	0			0			
Polypterus senegalus s.	31	0.08	0	0	0	0.01	0.06		0.51	0.02	0.68	0.01		0			
Protopterus annectens	2	0.48	0	0	0	0	0		0	0	0.01			0			
Sarotherodon galilaeus g.	3	0.86	0.13	0	0	0	0		0	0	0.01			0			
Tilapia guineensis	1	0.76	0.24	0	0	0	0		0	0	0			0			
Tilapia mariae	11	0.81	0.16	0	0	0	0		0	0	0.03			0			
Tilapia zillii	1	0.91	0.09	0	0	0	0		0	0	0			0			
Xenomystus nigri	7	0	0	0	0	0	0.09	0	0	0	0.91			0			
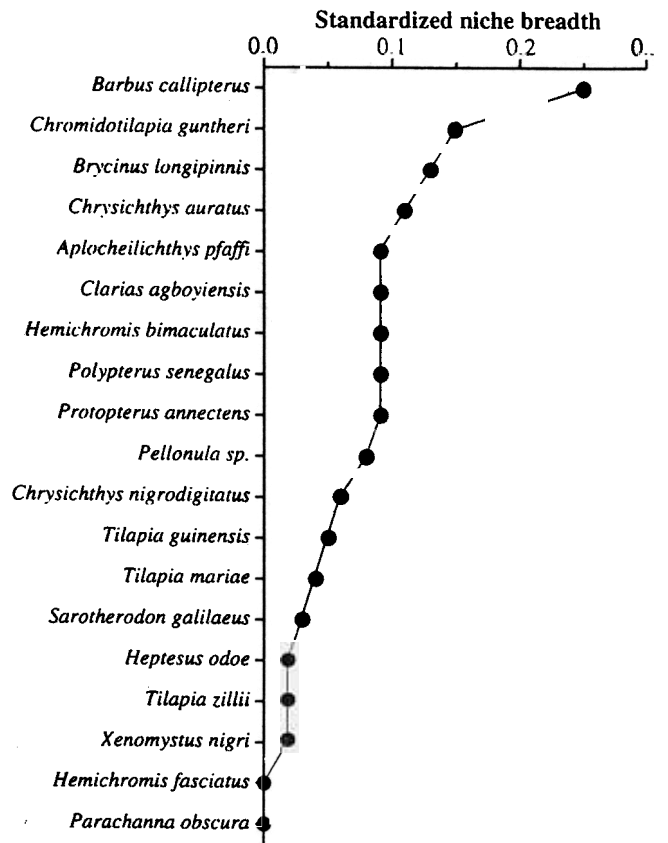
FIGURE 2. Standardized dietary niche breadths estimated for 19 species from Lagoon Toho-Todougba.

between the diet breadths of the two lake fish assemblages (Toho-Todougba mean = 1.78; Lake Nokoue mean = 1.50). In Lake Nokoue, *Elops lacerta* had the greatest diet breadth with five diet categories (detritus, macrocrustacea, unidentified fish, clupeids, mullet). Unlike Lagoon Toho-Todougba, Lake Nokoue contained a high proportion of species (44%) that used a single resource ($B = 1$), and most of these species were piscivores ($N = 6$) or invertebrate (*e.g.*, polychaete worm) feeders (*e.g.*, 5 mugilid spp).

Based on the 16 broad diet categories, pairwise diet overlaps were computed among the 13 and 11 most abundant species from Lake Nokoue and Lagoon Toho-Todougba, respectively. The overall mean overlap was 0.38 (± 0.35) and 0.29 (± 0.39) for Lake Nokoue and Lagoon Toho-Todougba, respectively (Table V and VI). However, the difference in means cannot be evaluated with statistics due to the interdependence of pairwise overlaps. In Lake Nokoue (Table V), three major groups were detected based on the diet overlap patterns among the 13 most common species. The largest group had species that fed mostly on detritus with overlaps ranging from 0.92 to 1.00 (*e.g.*, *Chrysichthys nigrodigitatus, Ethmalosa fimbriata, Liza falcipinnis, Sarotherodon melanotheron, Synaptura lusitanica,* and *Tilapia guineensis*). The second group had niche overlaps between 0.88 and 0.95 and was comprised of species that were largely piscivorous (*Eleotris senegalensis, Hemichromis fasciatus* and *Lutjanus goriensis*). The remaining species had low overlaps with all other species
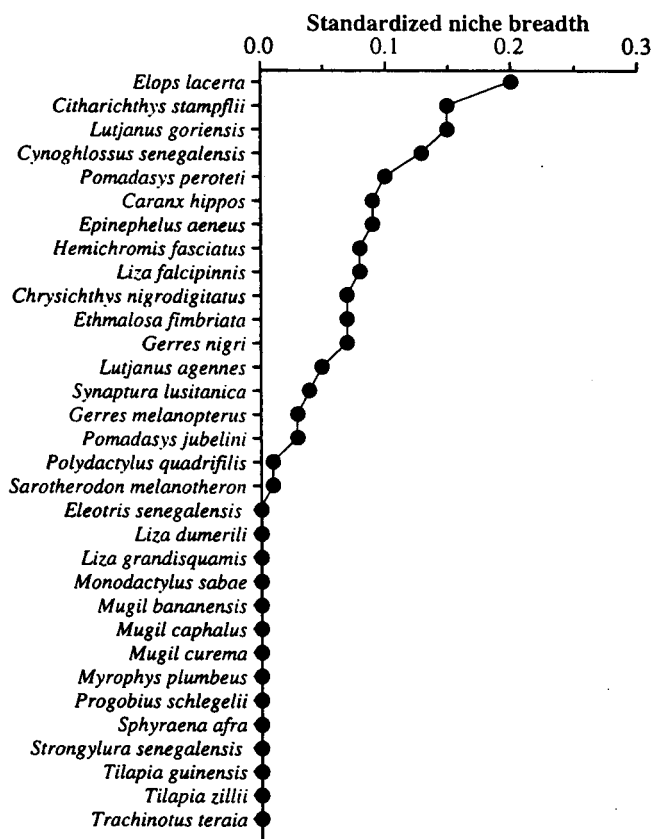
FIGURE 3. Standardized dietary niche breadths estimated for 32 species from Lake Nokoue.

(overlaps < 0.4) and fed on zooplankton (*Gerres melanopterus*), invertebrates (*Pomadasys jubelini*), and fishes (*Citharichthys stampflii, Elops lacerta*). In Lagoon Toho-Todougba (Table VI), three major feeding groups were recognized based on diet overlaps: (1) species that fed on detritus and had diet overlaps ranging from 0.72 to 1.00 (*e.g., Barbus callipterus, Chrysichthys auratus, Chromidotilapia guntheri, Sarotherodon galilaeus, Tilapia mariae*), (2) species with overlaps ranging from 0.61 to 0.97 that fed mostly on insects (*Xenomystus nigri, Polypterus senegalus, Brycinus longipinnis*), and (3) piscivores with overlaps ranging from 0.77 to 0.99 (*Hemichromis fasciatus, Hemichromis bimaculatus, Hepsetus odoe*).

The first three axes from PCA based on 16 diet categories consumed by fishes from the two regions explained 34% of the total variation in diet space (Figure 4, Table VII). The first PCA axis (eigenvalue = 2.2) was mainly influenced by consumption of seeds (eigenvector = 0.58), vegetation (eigenvector = 0.57), aquatic insects (eigenvector = 0.29), terrestrial arthropods (eigenvector = 0.27), unidentified fish (eigenvector = -0.26), detritus (eigenvector = 0.18), and decapods (eigenvector = -0.18) (Table VII). The second PC axis (eigenvalue = 1.91) was influenced by consumption of detritus (eigenvector = -0.61), algae (eigenvector = -0.51), unidentified fish (eigenvector = 0.39), terrestrial arthropods (eigenvector = 0.18), and cypriniforms (eigenvector = 0.17); whereas the third PC axis (eigenvalue = 1.41) was associated with consumption of perciforms (eigenvector = 0.50), clupeiforms (eigenvector = 0.52), decapods (eigenvector = 0.19), molluscs (eigenvector = 0.25), and terrestrial arthropods

TABLE V. Matrix of diet overlaps among the 13 most abundant species from Lake Nokoue. Overlap indices were computed following Pianka's (1976) index using 16 diet categories

Species	CN	CS	ES	EL	EF	GM	HF	LF	LG	PJ	SM	SL	TG
Chrysichthys nigrodigitatus	1	0.13	0.06	0.05	0.93	0.05	0.05	0.90	0.07	0.11	0.95	0.92	0.95
Citharichthys stampflii	1	0.08	0.24	0.13	0.12	0.08	0.13	0.28	0.02	0.14	0.13	0.14	
Eleotris senegalensis			1	0.44	0	0	0.88	0	0.91	0	0	0	0
Elops lacerta				1	0.07	0	0.60	0.03	0.73	0.02	0.03	0.03	0.03
Ethmalosa fimbriata					1	0.01	0.04	0.95	0.04	0.12	0.98	0.95	0.98
Gerres melanopterus						1	0	0.01	0	0	0	0	0
Hemichromis fasciatus							1	0.01	0.95	0.03	0	0	0
Liza falcipinnis								1	0.01	0.15	0.95	0.92	0.94
Lutjanus goriensis									1	0.02	0.01	0.01	0.01
Pomadasys jubelini										1	0.12	0.36	0.12
Sarotherodon melanotheron											1	0.97	1
Synaptura lusitanica												1	0.97
Tilapia guineensis													1

TABLE VI. Matrix of diet overlaps among the 11 most abundant species from Lagoon Toho-Todougba. Overlap indices were computed following Pianka's (1976) index using 16 diet categories

| Species	BC	BL	CG	CA	HB	HF	HO	PS	SG	TM	XN
Barbus callipterus	1	0.42	0.85	0.87	0.31	0	0	0.56	0.72	0.73	0.48
Brycinus longipinnis		1	0.14	0.29	0.39	0.01	0.01	0.61	0.03	0.05	0.61
Chromidotilapia guntheri			1	0.91	0.31	0.25	0.25	0.32	0.92	0.92	0.17
Chrysichthys auratus				1	0.29	0	0	0.53	0.88	0.89	0.44
Hemichromis bimaculatus					1	0.78	0.77	0.77	0.02	0.04	0.62
Hemichromis fasciatus						1	0.99	0.21	0	0	0
Hepsetus odoe							1	0.21	0	0	0
Polypterus senegalus s.								1	0.12	0.15	0.97
Sarotherodon galilaeus g.									1	1	0.08
Tilapia mariae										1	0.04
Xenomystus nigri											1
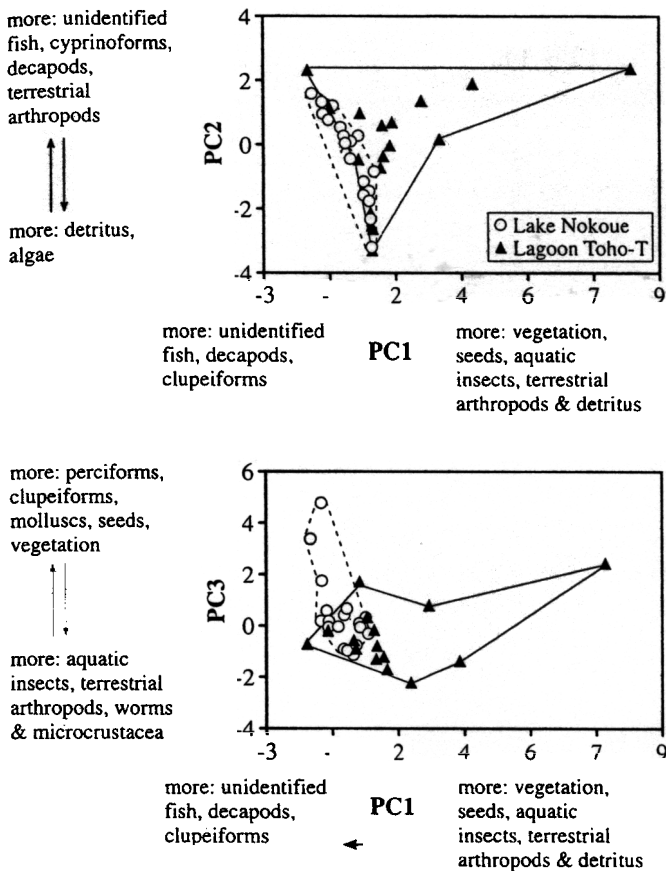
FIGURE 4. Plots of the first three principal components axes based on 16 diet categories from 32 species in Lake Nokoue and 20 in Lagoon Toho-Todougba.

(eigenvector = -0.25). The Lagoon Toho-Todougba fish assemblage was associated with a broader dietary space than the Lake Nokoue fish assemblage (Figure 4). However,

TABLE VII. Results from principal components analysis based on 16 food categories from 52 brackish and freshwater fish species: 32 from Lake Nokoue and 20 from Lagoon Toho-Todougba. Eigenvectors listed are those > 0.10 or < -0.10

	PCA axis		
	---	2	---
Eigenvalue	2.20	1.91	1.41
Proportion of variation	0.14	0.12	0.09
Cumulative variation	0.14	0.26	0.34
Detritus	0.18	-0.61	0.14
Algae		-0.51	
Protozoa/rotifers			
Vegetation	0.57	0.20	0.22
Seed	0.58	0.19	0.22
Microcrustacea			-0.14
Worm/coelenterata			-0.22
Molluscs		-0.10	0.25
Decapods	-0.18	0.15	0.19
Aquatic insects	0.29	0.13	-0.34
Terrestrial arthropods	0.27	0.18	-0.25
Unidentified fish	-0.26	0.39	-0.002
Perciformes			0.50
Clupeiformes	-0.14	0.16	0.52
Mugiliformes			
Cypriniformes	-0.11	0.17	

the two fish assemblages showed an extensive region of overlap in diet space. Lagoon Toho-Todougba had a higher proportion of species that ate vegetation, seeds, aquatic insects, terrestrial arthropods, and detritus. Species, such as *Barbus callipterus*, *Brycinus longipinnis*, *Aplocheilichthys pfaffi*, *Chromidotilapia guntheri*, *Chrysichthys nigrodigitatus* and *Xenomystus nigri*, had high positive scores on axis 1 and intermediate scores on PC axes 2 and 3 (Table VIII). Conversely, Lake Nokoue had a higher proportion of species eating decapods, microcrustacea, worms and fishes, and this group included *Elops lacerta*, *Lutjanus goriensis*, *Citharichthys stampflii*, *Myrophys plumbeus, and Gerres melanopterus*. Piscivores, such as *Hepsetus odoe*, occupied the region of low scores on PC axis 1 and high scores on axes 2 and 3 (Table VIII). These trends are visible in the diet based-dendrogram (depicting diet similarity) in which the detritivores and the piscivores form two fairly distinct clusters (Figure 5).

FEEDING GUILDS

Trophic guilds were determined using diet volumetric proportions, PCA scores, and the dendrograms generated from the derived cluster analysis (Tables III, IV and VIII; Figures 4 and 5). Using a similarity criterion of Euclidean distance < 5.0 with all 51 species, 8 feeding guilds were identified and five species did not cluster. Among the five species with divergent diets, two were piscivores, two were omnivores, and one was a molluscivore (Figure 5). Detritivores formed a large group of 14 species (27% of the total number of species) with relatively narrow niche breadths. Though this feeding group contained about an equal number of species from the two assemblages, relative to assemblage species richness, Lagoon Toho-Todougba was more dominated by detritivores. Species present in both lakes, such as *Tilapia guineensis* and *T. zillii*, fed on similar foods in both ecosystems and were classified in the same feeding guilds. The second largest feeding guild, the piscivores (10 species), was dominated by species from Lake Nokoue. Like the detritivores, most of these piscivores had relatively narrow niche breadths. A third feeding guild contained five species, all from Lagoon Toho-Todougba that fed mostly on aquatic insects. The five Lake Nokoue fishes in the fourth largest feeding guild fed on polychaete worms and coelenterates and had relatively narrow diet breadths (as discussed below, most of the mugilids probably feed heavily on detritus also). A fifth feeding guild contained three piscivorous species that also fed on decapods/crustacea and were exclusively from Lake Nokoue. Most species in this group had broad diets. A sixth guild had three species that fed mostly on planktonic microcrustacea and rotifers. Insectivorous *Aplocheilichthys* and *Brycinus* from Toho-Todougba formed a two-species cluster.

In Lagoon Toho-Todougba, terrestrial vegetation, algae and detritus were the sources of primary production used by fishes, whereas in Lake Nokoue, algae and detritus were the major components of primary production consumed. In Lagoon Toho-Todougba, the major secondary producers consumed by fishes were terrestrial insects, aquatic insects and zooplankton, whereas in Lake Nokoue decapod crusctacea and zooplankton dominated. Lake Nokoue had
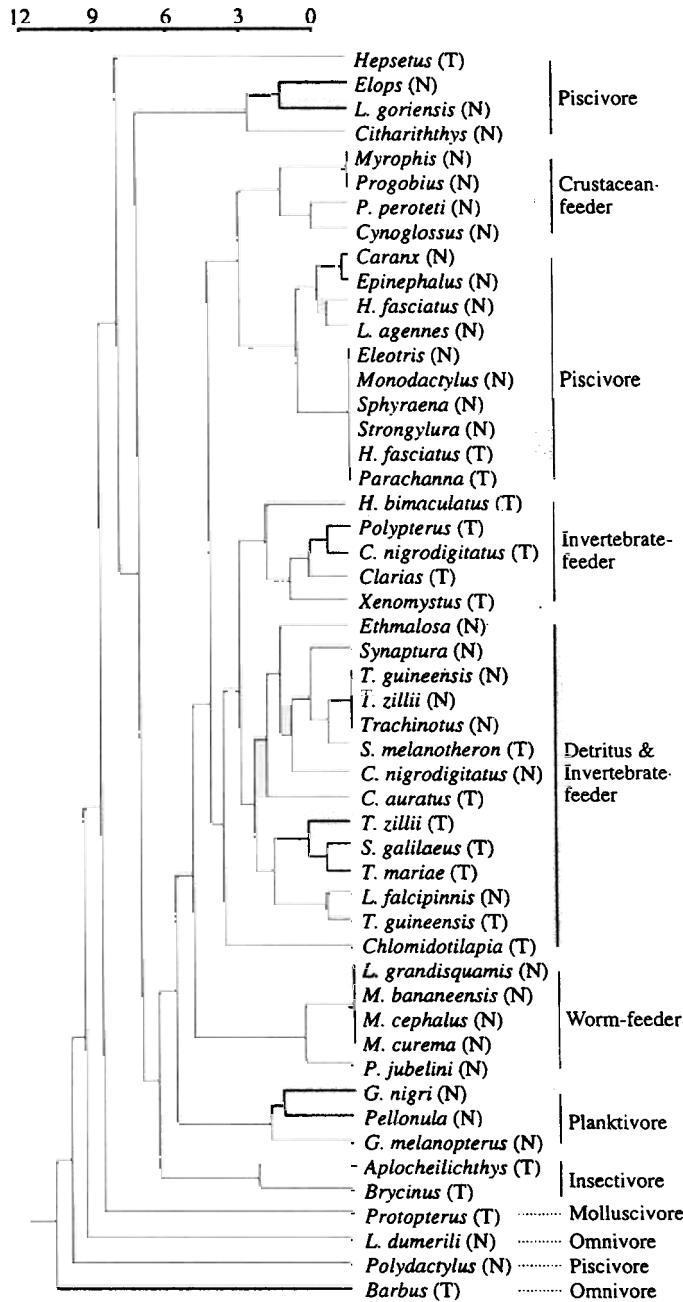
FIGURE 5. Dendrogram from cluster analysis (SAHN) showing dietary similarities between the two lagoon fish assemblages. Euclidean distances based on species' first 10 PCA scores were used for the similarity measures. The letter N designates Nokoue populations and the letter T designates the Toho populations.

more piscivores than Lagoon Toho-Todougba. Nokoue had a complex food web with more species, trophic levels, and trophic links than Lagoon Toho-Todougba.

MORPHOLOGY

Overall, the two assemblages had relatively high morphological similarity. The mean values for individual morphological features that characterized the average fish (faunal means derived from unweighted mean attribute

values of each species), or faunal centroid, were similar for the two lakes assemblages (Table IX). Most of the morphological features failed to show a mean difference between the two assemblages (e.g., standard length: $F_{1,126} = 0.06$, $p = 0.80$; eye position: $F_{1,126} = 0.12$, $p = 0.73$; eye diameter: $F_{1,126} = 3.60$, p = 0.06; head width: $F_{1,126} = 0.01$, $p = 0.91$; head length: $F_{1,126} = 0.71$, p = 0.40; head depth $F_{1,126} = 0.01$, $p = 0.96$).

The first three PC axes based on 27 morphological features of fishes from both regions explained 72% of the total variation in morphological space (Figure 6, Table X). The first PC axis (eigenvalue = 14.96) was most influenced by maximum body width, caudal peduncle depth, head length, head depth, eye position, eye diameter, dorsal fin height, caudal fin height and anal fin height (eigenvectors = 0.23). The second axis (eigenvalue = 0.55) was most influenced by body depth (eigenvector = 0.32), body depth below midline (eigenvector = 0.30), head width (eigenvector = 0.35), mouth orientation (eigenvector = -0.35), dorsal fin (eigenvector = 0.26), anal fin length (eigenvector = 0.39), and swim bladder length (eigenvector = -0.35). Species such as Monodactylus sebae, Chromidotilapia guntheri, Tilapia mariae, T. guineensis, T. zillii, S. galilaeus, S. melanotheron, Lutjanus goriensis, L. agennes, Hemichromis bimaculatus
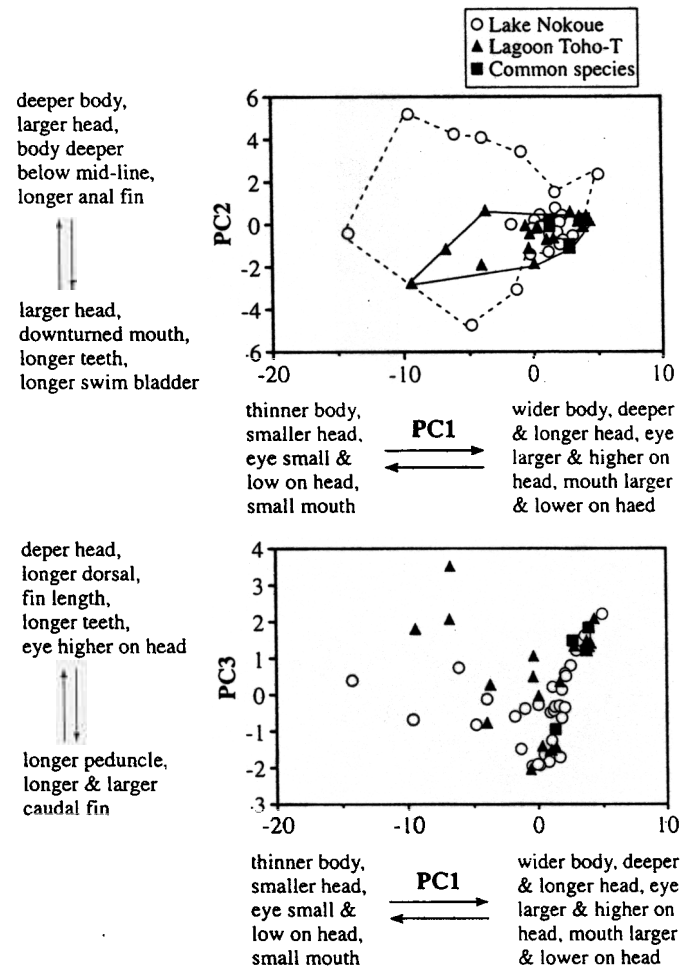

FIGURE 6. Plots of the first three principal components axes based on 27 morphological features of 32 species in Lake Nokoue and 18 in Lagoon Toho-Todougba.

TABLE VIII. Species scores on the first three PC axes based on dietary and morphological data

Species	Diet			Morphology		
	PC1	PC2	PC3	PC1	PC2	PC3
LAGOON TOHO-TODOUGBA						
Hepsetus odoe	-1.66	2.34	-0.71	0.14	-0.18	0.01
Hemichromis fasciatus	-0.96	1.20	-0.20	2.85	-1.08	1.47
Parachanna obscura	-0.96	1.20	-0.20	-0.28	-1.11	1.08
Pellonula sp.	-0.10	-0.48	-0.54	-0.49	-0.08	-2.02
Hemichromis bimaculatus	-0.05	0.97	-0.89	2.93	0.53	1.37
Tilapia zillii	0.26	-2.17	0.24	3.62	0.19	1.24
Sarotherodon galilaeus g.	0.29	-2.50	0.26	3.57	0.34	1.47
Protopterus annectens	0.08	-1.31	1.69	-6.75	-1.15	3.52
Tilapia mariae	0.32	-2.62	0.23	4.30	0.23	2.04
Tilapia guineensis	0.32	-3.31	0.35	3.89	0.25	1.84
Chrysichthys auratus	0.60	-0.73	-0.10	1.52	0.00	-1.42
Polypterus senegalus s.	0.61	0.61	-1.28	-3.93	-1.91	-0.75
Clarias agboyiensis	0.66	-0.36	-0.82	-3.63	0.65	0.28
Chrysichthys nigrodigitatus	0.85	-0.03	-1.24	1.46	0.19	-0.92
Xenomystus nigri	0.95	0.69	-1.71	-6.82	-1.23	2.09
Aplocheilichthys pfaffi	1.79	1.38	-2.23	0.37	-0.14	-1.40
Chromidotilapia guntheri	2.34	0.17	0.75	3.91	-0.11	1.37
Brycinus longipinnis	3.36	1.89	-1.39	1.83	-0.62	0.35
Barbus callipterus	8.14	2.38	2.45	1.12	-0.68	-1.47
LAKE NOKOUE						
Elops lacerta	-1.55	1.60	3.42	-0.22	-1.43	-1.95
Lutjanus goriensis	-1.22	1.32	1.73	2.99	-0.56	1.24
Citharichthys stampflii	-1.19	0.97	4.79	-0.96	3.41	-0.38
Myrophys plumbeus	-1.03	0.78	0.62	14.21	-0.44	0.38
Progobius schleglii	-1.19	0.99	0.21	1.38	-0.42	-0.35
Caranx hippos	-0.99	0.99	0.21	2.19	0.47	0.61
Epinephalus aeneus	-0.99	1.00	0.20	2.24	-0.95	0.53
Hemichromis fasciatus	-0.99	1.05	0.15	2.85	-1.08	1.47
Lutjanus agennes	-0.98	1.11	-0.02	2.67	-0.66	0.81
Eleotris senegalensis	-0.96	1.20	-0.20	1.23	-1.25	0.23
Monodactylus sebae	-0.96	1.20	-0.20	5.01	2.39	2.22
Sphyraena afra	-0.96	1.20	-0.20	-1.35	-3.08	-1.45
Strongylura senegalensis	-0.96	1.20	-0.20	-4.76	-4.72	-0.81
Polydactylus quadrifilis	-0.64	0.51	-0.07	0.80	0.27	-1.76
Liza grandisquamis	-0.52	0.19	-0.96	1.18	0.04	-1.25
Mugil bananensis	-0.52	0.19	-0.96	0.95	0.21	-1.80
Mugil cephalus	-0.52	0.19	-0.96	1.08	0.25	-1.62
Mugil curema	-0.52	0.19	-0.96	1.13	0.34	-1.40
Liza dumerili	-0.49	-0.01	-0.86	0.04	-0.23	-1.93
Pomadasys jubelini	-0.47	0.04	-0.78	1.95	-0.28	0.17
Pomadasys peroteti	-0.43	-0.29	0.38	2.11	0.12	-0.37
Cynoglossus senegalensis	-0.36	-0.45	0.70	-9.62	5.17	-0.66
Gerres nigri	-0.34	0.11	-0.95	1.29	0.14	-0.43
Gerres melanopterus	-0.14	0.27	-1.12	3.74	-0.01	1.54
Ethmalosa fimbriata	0.07	-1.55	0.09	1.70	0.78	-1.72
Synaptura lusitanica	0.08	-1.15	-0.05	-6.07	4.23	0.73
Tilapia guineensis	0.23	-1.49	0.17	3.89	0.25	1.84
Tilapia zillii	0.23	-1.49	0.17	3.62	0.19	1.24
Trachinotes teraia	0.23	-1.49	0.17	1.77	1.57	-0.31
Sarotherondon melanotheron	0.24	-1.77	0.20	3.74	-0.01	1.54
Liza falcipinnis	0.29	-3.23	0.28	0.58	0.48	-1.65
Chrysichthys nigrodigitatus	0.37	-0.83	-0.31	1.46	0.19	-0.92

and *H. fasciatus* had high positive scores on PC1 and possessed wider bodies, deeper and longer heads, larger eyes higher on the head and larger mouths (Table VIII). *Myrophis plumbeus, Gymnarchus niloticus, Xenomystus nigri, Protopterus annectens, Strongylura senegalensis, Polydactilus quadrifilis, Clarias lazera, Sphyraena afra, Cynoglossus senegalensis, Synaptura lusitanica* and *Pegusa triophtalma* had high negative scores for PC1 and had thinner bodies (except for the three flat fishes which are actually laterally compressed), smaller heads, smaller eyes lower on the head and smaller mouths (Table VIII). In general, the Lake Nokoue fish assemblage encompassed a larger morphological space compared to the Lagoon Todougba assemblage, but the two did have a large region of overlap (Figure 6).

The clustering dendrogram generated from morphological features tended to group species based on taxonomic affiliations and secondarily according to feeding niches (Figure 7). For example, 7 cichlids clustered at a distance approximately ≤ 1.4. The exception was *Hemichromis fasciatus*, which was grouped closer to *Lutjanus* species than to its congener, *H. bimaculatus* (Figure 7). In general, the relatively deep-bodied

TABLE IX. Mean values and standard deviations (SD) of 27 morphological features from 52 fish species: 34 from Lake Nokoue (brackish water) and 18 from Lagoon Toho-Todougba (freshwater). Individual fish features were standardized by a conversion factor (grand mean SL / specimen SL), then $\log_{10}$(value + 1)-transformed to generate the final value to be used in the analysis. Angles were adjusted by $(x + 90)$ to make all values positive

Morphological feature	Lake Nokoue		Lagoon Toho-Todougba	
	Mean	SD	Mean	SD
Maximum body depth	1.64	0.26	1.57	0.20
Body depth below mid-line	1.39	0.24	1.36	0.21
Maximum body width	1.31	0.17	1.37	0.13
Peduncle length	1.24	0.42	1.06	0.52
Peduncle depth	1.19	0.40	1.08	0.51
Head length	1.66	0.13	1.63	0.13
Head depth	1.40	0.27	1.39	0.24
Head width	1.39	0.19	1.41	0.17
Eye position	1.17	0.22	1.15	0.26
Eye diameter	0.99	0.21	0.95	0.30
Mouth orientation	1.90	0.19	1.89	0.14
Mouth width	1.08	0.19	1.16	0.13
Mouth height	1.14	0.22	1.10	0.16
Snout length shut	1.26	0.19	1.26	0.20
Dorsal fin height	1.40	0.29	1.33	0.46
Dorsal fin length	1.81	0.25	1.61	0.53
Pectoral fin length	1.48	0.36	1.50	0.21
Caudal fin length	1.58	0.31	1.35	0.64
Caudal fin height	1.49	0.35	1.32	0.64
Pelvic fin length	1.36	0.36	1.37	0.45
Anal fin length	1.56	0.28	1.40	0.46
Anal fin height	1.37	0.26	1.27	0.42
Maximum tooth length	0.21	0.17	0.33	0.15
Number of gill raker	1.28	0.44	1.17	0.18
Maximum gill raker length	0.54	0.29	0.43	0.19
Gut length	2.25	0.33	2.23	0.42
Swim bladder length	1.47	0.62	1.48	0.58

TABLE X. Results from principal components analysis based on 27 morphological attributes from 52 brackishwater and freshwater fish species: 34 from Lake Nokoue, 18 from Lagoon Toho-Todougba. Centroids from fish assemblages are incorporated in the analysis. Eigenvectors listed are those > 0.10 or < -0.10

	PCA axis		
	1	2	3
Eigenvalue	14.96	2.70	1.76
Proportion of variation	0.55	0.10	0.07
Cumulative variation	0.55	0.65	0.72
Maximum body depth	0.18	0.32	0.17
Body depth below mid-line	0.20	0.30	0.20
Maximum body width	0.23		
Peduncle length	0.21	-0.13	-0.34
Peduncle depth	0.23		-0.19
Head length	0.23	-0.12	
Head depth	0.23		0.22
Head width	0.15	0.35	
Eye position	0.23		0.18
Eye diameter	0.23		
Mouth orientation	0.11	-0.35	0.14
Mouth width	0.21	-0.11	0.14
Mouth height	0.22		
Snout length shut	0.21	-0.14	
Dorsal fin height	0.23		-0.14
Dorsal fin length		0.26	0.26
Pectoral fin length	0.22	-0.14	0.13
Caudal fin length	0.21	0.13	-0.31
Caudal fin height	0.23		-0.25
Pelvic fin length	0.22		
Anal fin length		0.39	0.16
Anal fin height	0.23		
Maximum tooth length		-0.23	0.50
Number of gill raker	0.10	0.15	-0.18
Maximum gill raker length	0.18	0.10	-0.15
Gut length	0.15	0.11	0.15
Swim bladder length	0.13	-0.35	0.10

percamorph fishes formed larger and tighter clusters compared with elongate fishes from a variety of orders and families. The two faunal centroids were nearest neighbors in morphological space and clustered with the fusiform fishes *Parachanna*, *Hepsetus* and *Eleotris*.

To examine the linear relationships between diet and morphology, correlations were computed for pairwise combinations of 27 morphological features and 16 food categories. Correlations between morphological traits and diet categories were weak, with coefficients of correlation varying from 0 to 0.58. There was a moderate, positive correlation between gut length and detritus ($r = 0.55$), and gut length and algae ($r = 0.47$). Also, there was a positive correlation between the volume of fish eaten and mouth orientation ($r = 0.58$), and tooth length ($r = 0.51$); that is, fishes with upturned mouths and longer teeth tended to eat more fish.

Discussion

ASSEMBLAGE PATTERNS

Fish assemblages of Lake Nokoue and Lagoon Toho-Todougba differ in both species richness and composition. Of the 55 species (35 from Lake Nokoue and 20 from Toho-Todougba), only four species from two families (Cichlidae with *Hemichromis fasciatus*, *Tilapia guineensis*, *T. zillii*,

and Bagridae with *Chrysichthys nigrodigitatus*) were shared by the two lakes. Though faunal similarity frequently increases with the geographic proximity (Jackson & Harvey, 1989; Hugueny & Lévêque, 1994), other parameters such as physicochemical attributes (Minns, 1989; Baran, 1995), habitat complexity and area effects (Hugueny, 1989; Oberdorff, Guégan & Hugueny, 1995) may influence faunal similarity and species richness. Lake Nokoue has great habitat heterogeneity influenced by rivers (Oueme, Sô) and tides (Atlantic Ocean) that affects species richness. The greater salinity of Lake Nokoue probably is another major factor that influences this low inter-assemblage faunal similarity. A long history of frequent residence in inland locations undoubtedly has selected for some typical salt or brackishwater fishes to become adapted to freshwater habitats. For instance, salt and brackishwater species, such as *Citharichthys stampflii*, *Pomadasys jubelini*, *Eleotris senegalensis*, *Kribia nana* and *Ethmalosa fimbriata*, were found in the Totche channel (Lake Nokoue) where salinity was nearly 0 ppt.

Baran (1995) summarized data for fish species richness in west African coastal lagoons and reported values ranging from 52 (Gambia) to 153 (Cote d'Ivoire) species. In Lake Nokoue, 62 species were reported by Van Thielen *et al.* (1987), a number greater than our finding (35 species). However, some species recorded in our survey, such as
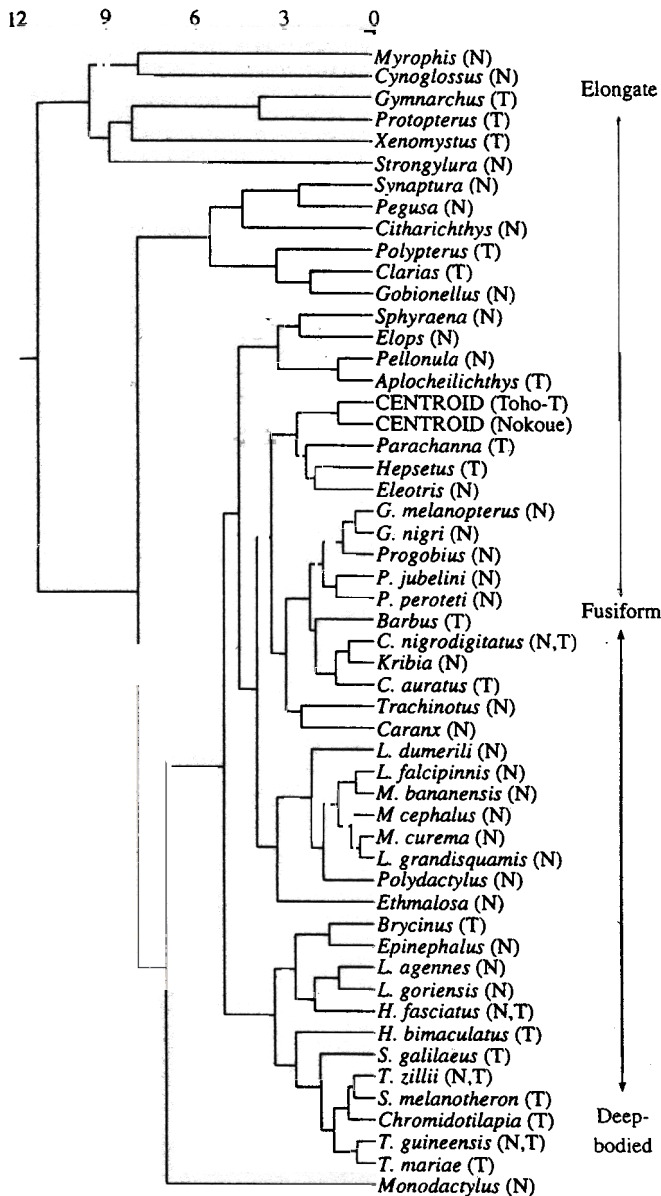
FIGURE 7. Dendrogram from cluster analysis (SAHN) showing morphological similarities between the two fish assemblages. Euclidean distances based on species' first 5 PCA scores were used for the similarity measures.

Synaptura lusitanica, *Pegusa triopthalma* and *Sphyraena afra*, were not recorded in that study. Although, Van Thielen *et al.*'s study encompassed more stations and a greater period than our survey, the dominant species were essentially the same in both studies. Though seasonal changes in physical factors may affect species distributions, spatial variation in physicochemical parameters was probably the primary factor influencing these reported differences in species richness.

In Lake Nokoue, high species packing (spatial concentration) occurred in the akadja habitat (of the 35 species recorded from the whole lake, 30 were present in the akadja). The akadja is a nutrient-rich habitat that serves as a refuge, feeding, and breeding habitat for the fishes (Welcomme,

1972). Species uncommon in the rest of the lake were found in the akadja. According to the local fishermen, some species, such as *Polydactilus quadrifilis*, that had been absent from trap net, gill net and cast net catches for about six years, were found in the akadja. As a consequence, this habitat alone might be used to indicate temporal changes in fish biodiversity for the entire lake. In addition to structural complexity and high productivity, high salinity may explain the high incidence of brackish and marine fish in the akadja habitat. Though the akadja practice is widespread in the lake, it is more common in the southwestern sector, an area that seems to function as a reservoir for saline water. Marine water moving up from the south is driven to the southwest by the water current from the Oueme River in the east and the Sô River in the north in such a way that this part of the lake is almost always brackish (7ppt-32 ppt) even during floods (Texier *et al.*, 1980; Adite & Van Thielen, unpubl.).

Adite & Van Thielen (1995) reported 16 species in Lagoon Toho-Todougba *versus* 20 in the present study. Six species (*Xenomystus nigri*, *Barbus callipterus*, *Pellonula* sp., *Hemichromis bimaculatus*, *Chrysichthys nigrodigitatus* and *Brycinus longipinnis*) mentioned in this study were not found in the previous investigation. This is probably because the previous fish surveys were based on commercial catches. Three species, *Parachana africana*, *Heterotis niloticus* and *Clarias agboyiensis* reported in the previous study were absent in the present study, possibly resulting from stock reductions, seasonal effects or both. The relatively large number of cichlids recorded in Lake Nokoue (4 species) and Lagoon Toho-Todougba (7 species) is typical of many African aquatic ecosystems. In Lagoon Porto-Novo, Lagoon Toho-Todougba, and the Oueme River of southern Benin, the Cichlidae are the most diverse family with 6-7 species (Van Thielen *et al.*, 1987).

DIETARY PATTERNS

Lake Nokoue and Lagoon Toho-Todougba fish assemblages revealed some major differences in patterns of food resource use. The vegetation categories (flowers, duckweeds, seeds) used by Toho-Todougba species, such as *Chromidotilapia guntheri* (12.6% of diet), *Barbus callipterus* (8.8%) and *Brycinus longipinnis* (7%), were completely absent in diets of Lake Nokoue fishes. Forty eight percent of the Lagoon Toho-Todougba species fed consistently on aquatic or terrestrial insects, whereas only 2% of the Lake Nokoue fishes (*Chrysichthys nigrodigitatus*, *Gerres melanopterus*) fed only partially on insects. Though this might result from a low number of species capable of exploiting these resources, a very low availability of these resources in Lake Nokoue also could produce this pattern. Habitat heterogeneity can strongly influence resource utilization and ecological interactions (Crowder, 1982; Polis *et al.*, 1996). The total destruction of mangroves bordering Lake Nokoue has greatly reduced the vegetated shoreline. Though the relatively high salinity of Lake Nokoue (0.04-35.6 ppt) may account for reduced insect diversity, the recent loss of shoreline vegetation probably contributes to the low availability of insects, because aquatic insects are frequently associated with submerged vegetation and terrestrial insects with emergent vegetation. Insects comprised 23.8% of diet

of the bagrid, *Chrysichthys nigrodigitatus*, in Lake Nokoue, compared with 73.1% for conspecifics in Lagoon Toho-Todougba. Based on frequency of occurrence and a larger sample, Laleye, Baras & Philippart (1995) also found that insects were a minor component in the diet of *C. nigrodigitatus* from Lake Nokoue and Lagoon Porto-Novo (microcrustacea, decapods, and molluscs were more important in their sample, and detritus was more important in our sample), and they noted that more insects were consumed from flooded marginal areas during wet season spates. In contrast to insects, the resource category "polychaete worms and coelenterata" was heavily utilized by 17% of the fishes from Nokoue but entirely absent in Toho-Todougba diets. A similar trend was seen for the diet group "macrocrustacea and molluscs", eaten by 28.5% of the fishes from Lake Nokoue *versus* 9.5% of the Lagoon Toho-Todougba fishes. Because crabs (*Callinectes sp.*), shrimp (*Penaeus sp.*), and polychaete worms are usually associated with brackish water, these diet trends probably reflect differences in resource availability rather than prey selection.

Among the Cichlidae, the tilapiines (*Tilapia guineensis, T. zillii, T. mariae, Chromidotilapia guntheri, Sarotherodon galilaeus, S. melanotheron*) had a high affinity for detritus and algae (filamentous algae, blue-green algae, desmids, diatoms) and to some extent microcrustacea. Similar results were reported by Winemiller, Kelso-Winemiller & Brenkert (1995) for *Oreochromis andersonii, Oreochromis macrochir, Tilapia sparrmanii, T. rendalli* and *T. ruweti*, and by Munro (1967) for *Tilapia zilli, Oreochromis mossambica* and *Oreochromis macrochir*. With the exception of *Chromidotilapia guntheri*, which showed a more omnivorous feeding strategy (niche breadth = 2.62), the cichlids had narrow niche breadths between 1.04 and 1.58. Our sample sizes for some of these species were relatively large (*N* = 10-52), so this apparent trophic specialization could result from interspecific morphological diversification, as observed in African lake cichlids (Fryer, 1972; Hori, 1983; 1991; Hori, Yamaoka & Takamura, 1983; Greenwood, 1984; Ribbink, 1984; Yamoaka, Michio & Kuratani, 1986).

The trophic ecology of the mullets (Mugilidae) in Lake Nokoue was comparable to that discussed by Albaret & Legendre (1986) in Lagoon Ebrie (Côte d'Ivoire, west Africa). *Liza falcipinnis* fed primarily on desmids, diatoms, blue-green algae, green algae, copepods, detritus, and perhaps incidentally, worms. Very similar diets were reported by Fagade & Olanyan (1973) and Payne (1976; 1978, cited by Albaret & Legendre, 1986). In Lake Nokoue, only polychaete worms were found in the stomachs of *Mugil cephalus* and *M. curema*, whereas in Lagoon Ebrie, these species exhibited the same trophic strategy as *Liza falcipinnis*. Mugil species are known to feed heavily on detritus in other regions, and this difference was caused by small sample sizes (*N* = 2, 5) for these two species in our study. The detritivorous food habit of *Ethmalosa fimbriata* (Clupeiformes) in Lagoon Ebrie, was described by Albaret & Legendre (1986), and this was corroborated by our data from Lake Nokoue.

The piscivorous feeding habit of the characiform *Hepsetus odoe* in Lagoon Toho-Todougba was similar to Winemiller & Kelso-Winemiller's (1994) findings, from the Zambezi River. Because the sample was small for Toho-Todougba fish, cypriniforms (*Barbus sp.*) were the only identifiable taxon in stomach contents and comprised about 10.5% by volume. Winemiller & Kelso-Winemiller (1994) reported ontogenetic diet shifts in *Hepsetus* and low diet overlap between small, medium and large size classes. As noted for other members of the family, Lake Nokoue eleotrids were carnivorous, and some, such as *Eleotris senegalensis*, were completely piscivorous (100% fish in diet).

One of the most abundant species in Toho-Todougba, the characiform *Brycinus longipinnis*, fed primarily on ants (Hymenoptera) at all sampling locations. Two factors could explain this finding. *Brycinus* might not have been highly selective for ants, but ants may have been extremely abundant in the lake during the period when we sampled. Because our surveys were made during the early high-water period, ant nests, which are common on the lagoon shore, may have been inundated. We have no data to indicate whether or not ants are a major diet component during the low-water period. Omnivorous midwater characids have been shown to increase their consumption of terrestrial arthropods during the annual high-water period in other tropical regions (Zaret & Rand, 1971; Esteves, 1996). A second hypothesis is that *Brycinus longipinnis* may have actively selected ants, perhaps even sensing the ants' chemical secretions used for defense or communication. Additional spatial and temporal diet and prey availability data are needed to determine the selectivity of *Brycinus* for ants. The polypteriform, *Polypterus senegalus*, an insectivore found at most of the same sites in Toho-Todougba where *Brycinus longipinnis* was present, did not feed on ants. The gerreids of Lake Nokoue (*Gerres melanopterus, G. nigri*), with their protudable jaws effective for suctorial particle feeding, were the only fishes that consumed large percentages of zooplankton.

ECOMORPHOLOGICAL RELATIONSHIPS

Though Lagoon Toho-Todougba and Lake Nokoue have low faunal similarity (*CBR* = 0.18), their assemblages had remarkably similar means for most morphological traits (Table IX), as indicated by the short distance between faunal centroids (*i.e.*, "average fish") in morphospace. Winemiller (1991) reported similar trends among fish assemblages from five biotic regions (Alaska, Texas, Costa Rica, Venezuela, Zambia). The Lake Nokoue fauna showed greater morphological variation than Toho-Todougba, which, following the ecomorphological assumption, indicates greater ecological diversification in this more species-rich assemblage. From this result, one would predict a larger assemblage-wide diet space for Lake Nokoue compared with Lagoon Toho-Todougba, but this was not the case. PCA results for diet data indicated a greater diet space for Lagoon Toho-Todougba than Lake Nokoue. A factor that may contribute to this discrepancy is the recent destruction of the mangroves in Nokoue which has reduced littoral microhabitats and, in turn, has reduced invertebrate densities, especially those of insects. Another factor that could have influenced our patterns of assemblage divergence is the scale of resolution for diet categories. Most of our categories were fairly broad, and the Lake Nokoue assemblage might have shown greater interspecific resource partitioning than Toho-Todougba

fishes within categories such as microcrustacea, worm/coelenterata, and molluscs. Whereas it is important to consider these and other factors, such as diet sample sizes and seasonal diet shifts that potentially can influence comparisons, we conclude that dietary diversity actually was larger for the Toho-Todougba assemblage during the interval of our field survey.

Fishes with comparable morphological traits should use similar resources (Gatz, 1979; Winemiller, 1990). In this regard, feeding guilds were compared with the morphology-based dendrogram to detect the proportion species that were grouped together by diet and morphology. The percentage match was moderate to high (range = 30-80%), indicating a varying degrees of association between morphology and diet specialization. For example, among the 12 species in the detritivore guild, six species (*Tilapia guineensis, T. mariae, T. zillii, Sarotherodon galilaeus* and *S. melanotheron*) were clustered together (Euclidean distance < 3.0) in the morphology-based dendrogram. Likewise, three (*Epinephelus aeneus, Lutjanus agennes, Hemichromis fasciatus*) of ten species from the largest piscivore guild were clustered in the morphology-based dendrogram (plus some of the fishes from the two different piscivore guilds clustered morphologically; *e.g., Elops* and *Sphyraena*), four (three *Mugil* species and *Liza grandisquamis*) of five species from the worm-feeder guild, and two (2 *Gerres* species) of three species from the planktivore guild (Figures 5 and 7). In many instances, phylogenetic distance was related to morphological distance (*e.g.,* congeners tended to cluster in the morphological dendrogram in Figure 7). In very few cases, species grouped closely together by overall morphological similarity were not closely related and also had divergent diets. For example, *Brycinus* (insectivore) was similar morphologically to *Epinephalus* (piscivore).

The association between morphology and feeding also was explored by regressing the volumetric consumption of diet items with morphological traits. Though not statistically significant, a greater proportion of detritus in the diet was associated with greater gut length. Consistent with previous studies (Winemiller, 1990; Motta, 1995; Winemiller, Kelso-Winemiller & Brenkert, 1995), greater piscivory was associated with a larger gape, longer teeth, and an upturned mouth. Again, small diet samples for some species and seasonality would likely influence these bivariate analyses. A multivariate approach, such as canonical correspondance analysis (CCA), that simultaneously models relationships between both the complete diet and morphology datasets, could eliminate redundancies and reveal major associations. We performed CCA on this dataset, but the results are not reported here because the number of variables was too small relative to the number of common species.

Further research, especially field surveys conducted over several years that encompass more life stages, is needed to better document spatiotemporal variation in patterns of resource use by fishes of these and other African freshwater systems. In this regard, the present study provides evidence that a more diverse fish assemblage with coastal marine elements contains greater morphological diversity without greater diet diversity relative to an isolated freshwater lake located just 20 km away. Nonetheless, a relatively large fraction of the species formed similar clusters based on dietary and morphological similarity, a result consistent with earlier comparative research on fish ecomorphology.

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