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FISH RESPONSE TO THE ANNUAL FLOODING REGIME IN THE KAVANGO RIVER ALONG THE ANGOLA/NAMIBIA BORDER

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The results of the first seasonal survey of the fish of the Kavango River floodplain along the Angola/Namibia border are reported. The river experiences peak flooding from February through June, with the 375-km long floodplain extending up to 5 km across. The floodplain was sampled five times in 1992 by seine, fish traps and rotenone. The data indicated a pronounced structural and functional response of the fish community in relation to the alternating flood and drought conditions in the river. Catch per unit effort and diversity were highest during months of peak flooding (May and June), and lowest during the month of least flow (November). The reproductive strategies of K-selected piscivorous cichlids and tigerfish were in advance of flooding. Many r-selected invertivores, especially cyprinids, were in relative synchrony with flooding and the stimulation of littoral zone plant growth, while other invertivores lagged the cyprinids. Herbivores had lowest relative abundance during peak flooding; this seemingly inverse relationship with the invertivores should not be interpreted as replacement, but rather the swamping of the system with young-of-the-year r-selected invertivores. The data support the Flood Pulse Concept, which hypothesizes that flooding is the major "driver" of productivity in lowland or floodplain rivers.

Key words: behaviour, floodplain fishery, migration, Okavango Delta, r-/K-selection, subsistence fishery

A seasonal survey of the fish of the Kavango River floodplain along the Angola/Namibia border was conducted during 1992 and 1993, as a cooperative effort between the University of Namibia, the Namibian Ministry of Fisheries and Marine Resources (MFMR) and the University System of Maryland. The Kavango (also known as the Cubango) flows south from its origin in the highlands of central Angola, and then turns east to form the 415-km long border between Namibia and Angola (Fig. 1); approximately 375 km of this reach has the lowest gradient in the drainage, with extensive floodplains (Hocutt *et al*. 1994), and is the study area for this manuscript (Fig. 2). The river then flows southeast through Namibia for another 35 km before it reaches Botswana and terminates in the 15 000 km^2 Okavango Delta.

The Kavango River remains a pristine catchment in the context of the definition used in the western world, with minor human impact along the Namibia/Angola border other than through organic enrichment and riparian zone mismanagement. Development in the basin has to date been retarded; however, with political normalization of the region, various regional schemes for water resource utilization are being considered for the catchment (Baldwin 1991). For this reason, Hocutt *et al*. (1994) and Hay (1995) developed the rationale for a routine monitoring protocol based on the Index of Biotic Integrity (IBI) as a measure of long-term shifts in the structural and functional components of the fish community. However, a fundamental requirement of utilizing any measure of environmental alteration of an aquatic system is the need to understand natural variability, both spatially and temporally (Bruton and Jackson 1983). This manuscript addresses that need, at least in part.

Knowledge of the seasonal structure and functioning of the floodplain fishery is largely anecdotal, despite laudable efforts made by the MFMR. As the MFMR seeks solutions to manage the fishery in light of increasing demand, it is critical to understand the relationship between seasonal flooding and productivity, particularly given the current regional plans to change or interrupt the natural processes of this important floodplain river system (Breen *et al*. 1984).

The survey described here differs from historical efforts of the MFMR, which for a variety of reasons has been restricted to surveying the Kavango once only per year, thus not including a cycle that can be correlated to the annual flooding regime. The database here is taken from Hocutt *et al*. (1994), whose data hinted (their Fig. 6) that a seasonal trend might be discernible if interpreted further.

Jubb's (1967) and Skelton's (1993) works on the freshwater fish of southern Africa and Poll's (1967) tome on the fish of Angola were hallmark contributions to regional ichthyology. Castelnau (1861) described

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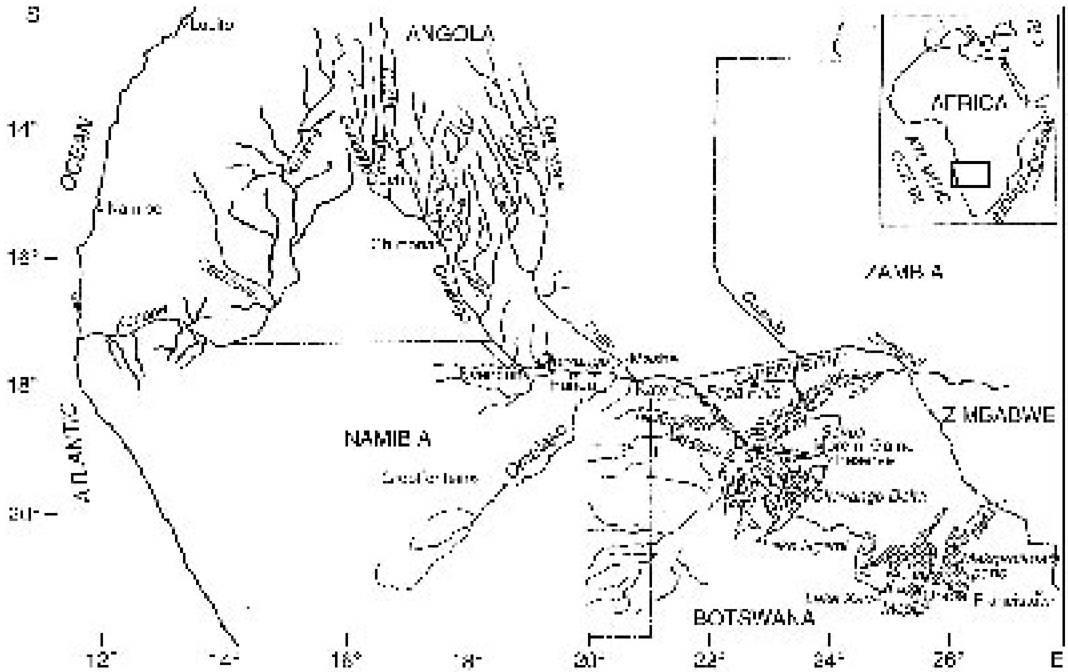

Fig. 1: Map of the Kavango (Cubango) River basin (after Skelton *et al.* 1995)

the first specimens from the Okavango Swamp region of Lake Ngami, based on specimens collected by Daviaud (Jubb and Gaigher 1971). The first account of the upper Cubango River fish fauna in Angola was given by Pellegrin (1936), and three years later the first collection of fish from the Kavango River in Namibia (then called South West Africa) was obtained by Eedes (Jubb and Gaigher 1971).

The ichthyofauna of the Namibia and Botswana portion of the Kavango drainage is well documented (Jubb and Gaigher 1971, Skelton *et al.* 1983, 1985, Skelton and Merron 1984, 1985, 1987, Minshull 1985, van der Waal 1987, 1991, Merron 1991, 1993, van Zyl 1992, Hay *et al.* 1999), but the Angolan portion of the catchment is only modestly known, primarily through the works of Poll (1967). Merron and Bruton (1985, 1989, 1995) considered the fishery of the Delta in Botswana. The latter work, particularly, parallels the research reported here in that seasonal shifts in abundance and diversity of the Delta's fish community are discussed.

From a zoogeographic perspective, the ichthyofauna of the Kavango has affinities with the adjacent Cuveili, Cuando (Mashi) and upper Zambezi drainages (Jubb 1964, 1967, Gabie 1965, Jubb and Farquharson 1965, Bell-Cross 1968, 1972, 1976, Hay *et al.* 1999), although the historical relationships remain unresolved (Gaigher and Pott 1973, Greenwood 1983). Bell-Cross (1968, 1972, 1976), Bowmaker *et al.* (1978) and Bell-Cross and Minshull (1988) reviewed the fish of the upper Zambezi River system, and their checklists of fish included the Okavango drainage. Explanation of current distributions may be the presence of obstacles or barriers during periods of former drainage connections (Gaigher and Pott 1973), such barriers being physical (Crass 1962), ecological (Jackson 1962), climatic (Stuckenburg 1969, Gaigher and Pott 1973), behavioural (Bell-Cross and Minshull 1988), or the result of competitive interactions. Gaigher and Pott (1973) list other influences on current distribution patterns: extermination by predation, retreat due to competition, and catastrophic destruction of fish life in intermediate areas.

The river continuum concept (Vannote *et al.* 1980) is a widely accepted model of longitudinal structure and functioning of lotic systems, although it is challenged in some circles (e.g. Statzner and Higler 1985, Davies *et al.* 1993). Junk *et al.* (1989) outlined the flood pulse concept, and hypothesized that flooding is the major "driver" of lowland or floodplain rivers.

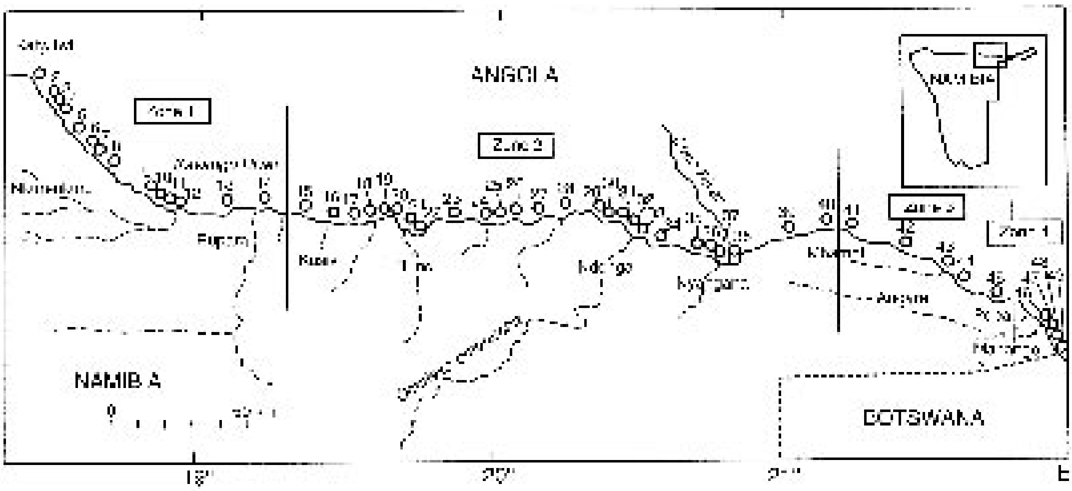

Fig. 2: Zones of the lower Kavango River and the study area (Zone 2) along the Namibia/Angola border (after Hocutt *et al.* 1994)

The concept implies that the frequency, magnitude and rates of rise and fall of flooding will be reflected in the ecological character of the associated biota (Davies *et al.* 1993). Junk *et al.* (1989) defined the floodplain as an aquatic-terrestrial transition zone that excludes permanent lotic and lentic habitats within the zone of inundation, so emphasizing the floodplain as an area of alternation of wetting and drying phases (Davies *et al.* 1993).

The Kavango River floods seasonally, normally from December to July, with a general maximum 6 m above low flow conditions and an average discharge of 10 500×10^6 m^3 per year at the Botswana border (Baldwin 1991). Flooding peaks from February through June, i.e. some 3–4 months later than peak rainfall in Angola. The floodplain can extend more than 2 km away from the stream bed during flooding. Local rainfall is usually ineffectual in the flooding pattern itself, other than perhaps assisting the saturation of the water table.

According to the definition of Welcomme (1979a), the Kavango River floodplain is a fringing floodplain lying between river valley walls (v. internal, e.g. the Okavango Delta). Typically the alluvial plain of the river can be divided into two major zones: levees, which are higher ground more or less following the channel of the river and its former beds, and the flats, which extend away from the levees toward the terraces. Levees are submerged for a shorter time than the flats, and often appear as islands. The flats are the areas of highest productivity. In the Kavango floodplain, the flats may have standing trees, or appear as a savannah, depending upon location. Smith (1976) and Bethune (1991) discussed the vegetation along the Kavango floodplain.

Hocutt *et al.* (1994) subdivided the Kavango channel into four latitudinal zones along the Namibia/Angola border, based on the occurrence of extended floodplain and associated habitats (Fig. 2): Zone 1, from Katwitwi to Kasivi, has little floodplain development and mostly shallow-water environments with sand and/or rock substrata. Small rapids are scattered throughout, with prevalent submerged vegetation and aquatic weed beds in a rather well defined river bed. In Zone 2 from Kasivi to Mbambi, the primary study area discussed here, the floodplain is well developed, extending at times to >5 km in breadth (Sandlund and Tvedten 1992). The river valley is wider, with the main channel seasonally broadening into innumerable inferior back channels, bays and oxbow ponds forming over submerged pasture-land during flooding, and connected by faster-flowing anastomosed channels; these features usually dry out as the river retreats. The substratum in the main river is predominantly sand, but with rock outcroppings. Zone 3, from Mbambi to Popa Falls, has a greatly reduced floodplain valley. Large boulders, rubble and gravel substrata associated with rapids are common. Zone 4 below Popa Falls is considered as the uppermost "panhandle" portion of the Okavango Delta proper (van der Waal 1987), and it has well established reed and papyrus beds that are permanently inundated.

Table I: Relative monthly abundance of all fish species collected along the Kavango River floodplain in 1992, with a notation of their trophic level (adapted from Hocutt *et al.* 1994)

Taxon	Monthly catch						Total (%)
	Feb.	May	Jun.	Sep.	Nov.	All months	
Mormyridae (1.95% total annual catch)							
Hippopotamyrus ansorgii[I]	0	0	0	1	1	2	0.02
H. discorhynchus[I]	0	4	0	6	0	10	0.13
Marcusenius macrolepidotus[I]	0	11	1	38*	7	57	0.74
Mormyrus lacerda[I]	4	0	1	1	0	6	0.08
Petrocephalus catostoma[I]	0	1	20	11	4	36	0.47
Pollimyrus castelnaui[I]	0	9	13	16	1	39	0.51
Characidae (4.8% total annual catch)							
Brycinus lateralis[I]	1	12	32	6	75*	126	1.64
Hydrocynus vittatus[P]	9	24	0	6	30	69	0.90
Micralestes acutidens[I]	14	125	16	2	13	170	2.21
Rhabdalestes maunensis[I]	0	1	0	0	0	1	0.01
Hepsetidae (0.03% total annual catch)							
Hepsetus odoe[P]	1	1	0	0	0	2	0.02
Distichodontidae (1.69% total annual catch)							
Hemigrammocharax machadoi[I]	0	3	5	9	0	17	0.22
H. multifasciatus[I]	3	76	27	5	1	112	1.46
Nannocharax macropterus[I]	0	1	0	0	0	1	0.01
Cyprinidae (28.9% total annual catch)							
Barbus afrovernayi[I]	1	9	8	13	1	32	0.42
B. annectens[I]	1	0	2	0	0	3	0.04
B. barnardi[I]	1	0	11	2	0	14	0.18
B. barotseensis[I]	17	10	10	0	0	37	0.48
B. bifrenatus[I]	9	28	33	22*	0	92	1.20
B. codringtonii[I]	0	0	1	0	0	1	0.01
B. eutaenia[I]	32	0	3	3	0	38	0.50
B. fasciolatus[I]	0	69	6	6	0	81	1.06
B. haasianus[I]	0	0	0	5	0	5	0.07
B. lineomaculatus[I]	0	11	26	0	0	37	0.48
B. paludinosus[I]	1	449*	32	6	23	511*	6.66*
B. poechii[I]	120*	134	104*	38*	143*	539*	7.02*
B. radiatus[I]	42	111	242*	12	3	410*	5.34*
B. thamalakanensis[I]	82*	123	38*	1	0	244	3.18
B. unitaeniatus[I]	14	64	1	0	0	79	1.03
Labeo cylindricus[H]	24	0	2	12	15	53	0.69
Opsaridium zambezense[I]	23	0	0	1	2	26	0.34
Amphiliidae (0.026% total annual catch)							
Leptoglanis dorae[I]	0	0	0	1	0	1	0.01
L. rotundiceps[I]	0	1	0	0	0	1	0.01
Claroteidae (0.026% total annual catch)							
Parauchenoglanis ngamensis[O]	0	2	0	0	0	2	0.02
Clariidae (0.57% total annual catch)							
Clarias gariepinus[O]	6	7	0	1	4	18	0.23
C. ngamensis[O]	7	2	2	3	2	17	0.22
C. theodorae[I]	0	5	0	1	3	9	0.12
Mochokidae (0.91% total annual catch)							
Chiloglanis fasciatus[I]	0	0	0	3	0	3	0.04
Synodontis spp.[O]	4	21	7	19	16	67	0.87
Schilbeidae (1.63% total annual catch)							
Schilbe intermedius[O]	8	27	27	8	55*	125	1.63
Cyprinodontidae (6.2% total annual catch)							
Aplocheilichthys hutereaui[I]	6	5	11	0	35	57	0.74
A. johnstoni[I]	75	143*	92*	52*	47	409*	5.33*
A. katangae[I]	1	7	0	0	1	9	0.12

(continued)

Table I *(continued)*

Taxon	Monthly catch						Total (%)
	Feb.	May	Jun.	Sep.	Nov.	All months	
Cichlidae (53% total annual catch)							
Oreochromis andersonii[H]	22	186*	0	2	0	242	3.15
O. macrochir[H]	0	0	0	0	1	1	0.01
Pharyngochromis acuticeps[I]	111*	90	4	11	118*	334	4.35
Pseudocrenilabrus philander[I]	264*	574*	119*	131*	59*	1 147*	14.94*
Sargochromis codringtonii[I]	0	0	1	18	4	23	0.30
S. giardi[I]	0	0	2	0	1	3	0.04
Serranochromis angusticeps[P]	2	1	9	2	0	14	0.18
S. macrocephalus[P]	10	15	23	10	165*	223	2.91
S. robustus[P]	47	26	10	4	5	92	1.20
Tilapia rendalli[H]	536*	168*	39*	19*	134*	896*	11.67*
T. ruweti[H]	92*	247*	0	0	3	342	4.46
T. sparrmanii[H]	102*	389*	151*	111*	17	770*	10.03*
Anabantidae (0.26% total annual catch)							
Ctenopoma multispine[I]	2	17	1	0	0	20	0.26
Mastacembelidae (0.04% total annual catch)							
Aethiomastacembelus vanderwaali[I]	0	0	0	3	0	3	0.04
Number of species	36	42	39	40	32	57	
Number of specimens	1 694	3 209	1 132	621	1 021	7 677	
Number of collections	9	11	5	5	8	38	
Number of specimens per collection	188	292	226	124	127	202	

* The seven most abundant species by sampling period
[H] = herbivore
[I] = invertivore
[P] = piscivore
[O] = omnivorous scavenger

The Kavango River fishery was addressed by van der Waal (1991), Sandlund and Tvedten (1992), van Zyl (1992), Yaron *et al*. (1992), Hocutt and Johnson (1993) and Hay *et al*. (2000). These works included discussions of fishing methods used along the river and their selectivity, and of intensity of fishing activities, and estimates of total production. Data indicate that the complete fish biodiversity of the Kavango River constitutes the subsistence fishery. Clear signs of overexploitation are not evident, but lower frequencies of larger individuals in experimental and commercial catches may indicate otherwise (Skelton and Merron 1984, 1985, 1987, van der Waal 1991). Recently, escalation of the civil war in Angola and associated border activities in Namibia, while unfortunate for those involved, is expected to be beneficial to the fisheries.

MATERIAL AND METHODS

Hocutt *et al*. (1994) made 80 collections along the Kavango River in 1992, including 38 samples in the floodplain, corresponding to rising flood conditions (February), peak flooding (May and June), decreasing flow (September), and low flow conditions (November). The latter collections are analysed here, with the data repeated for 1991 (before) and 1993 (after) to create computer-generated graphics of annual trends (see Figs 4–7 later). Locations were determined with a Magellan 1000-Plus Global Positioning Satellite (GPS) unit. It must be emphasized that the remoteness of the region, the distance from the base in Windhoek (more than 1 000 km in some instances), the small size of the research team (2 persons), the high temperature (seasonally near 40°C), the state of flooding and the general lack of facilities were all mitigating circumstances to sampling. Supplemental information regarding the survey is provided in Hocutt *et al*. (1994).

Fish collections were primarily obtained using a small seine 1.5 m high and 3.2 m long, with 5 mm mesh. This gear was used in much the same manner that the Kavango people use traditional methods for fish capture, such as the *shikuku, tambi* and *sididi*. In other words, fish are herded into the seine by disturbing the vegetation or substratum that might provide refuge. Additionally, wire mesh fish traps, conceptually similar to a *sintunga*, and rotenone were occasionally used. All

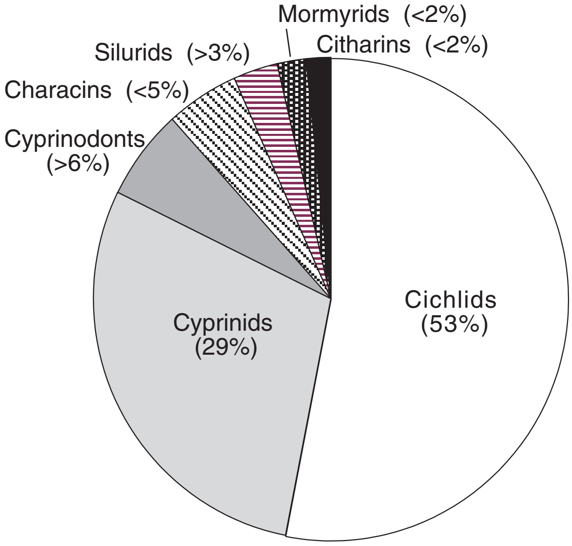

Fig. 3: Dominant fish by family along the Kavango River floodplain in 1992

these techniques bias the catch (Hocutt 1978, 1981) towards smaller species that dominate bio-diversity or early life stages of larger species that, in combination, mimic catch in the local subsistence fishery.

Fish were preserved in 10% formalin immediately after collection and stored for 10 or more days to ensure proper hardening. They were then rinsed with freshwater before being transferred to 70% ethyl alcohol. All specimens were donated to the State Museum of Windhoek for cataloguing. Specimens were identified using Jubb (1967), Poll (1967), Jubb and Gaigher (1971), Skelton *et al*. (1985) and Bell-Cross and Minshull (1988). Similar to Merron and Bruton (1995), the taxonomically difficult genus *Synodontis* was treated as a single species for the purpose of this manuscript.

RESULTS AND ANNOTATED DISCUSSION OF INDIGENOUS FISH

A total of 7 677 specimens representing 14 families, 29 genera and 57 species was collected along the Kavango River floodplain during the five seasonal sampling periods in 1992 (Table I). The total number of species collected along the floodplain was fewer than encountered in the drainage during the same period

Table II: Relative abundance of the dominant fish families by season from the Kavango River floodplain during 1992

Fish family/ group	Relative monthly abundance (%)					Relative annual abundance (%)
	Feb.	May	Jun.	Sep.	Nov.	
Cichlidae	70	53	32	50	50	53.3
Cyprinidae	22	31	46	19	18	28.9
Cyprinodontidae	4.8	4.8	9.0	8.3	8.1	6.2
Characidae	1.5	5.0	4.0	2.2	12.0	4.8
Siluriforms	1.5	2.0	3.0	5.6	7.8	4.3
Mormyridae	0.2	0.8	3.0	11.8	1.3	2.0

(14 families, 33 genera, 62 species), or reported by others in the literature, but is reflective of their relative importance to the floodplain fishery. By comparison, Merron and Bruton (1995) recorded 65 species from the Okavango Delta, Botswana, over a period of three years. The following annotated discussion is structured such that each family of fish (or group) is addressed in descending order of total relative abundance. Total annual catch was dominated by the family Cichlidae (53.3%), and to a lesser extent by the Cyprinidae (28.7%, Table II, Fig. 3).

Cichlidae

The cichlids dominated the catch in 1992. The shallow floodplain refugia harboured an abundance of these fish, as members of this family made up more than half the total number collected. Seasonally, this group was most abundant during February and May as juveniles, and during November as young of year. As many cichlids migrate to and utilize floodplains for either spawning, nursery, refugia or ranging movements (Bell-Cross and Minshull 1988), it is not surprising to find such a preponderance of these fish during periods of relatively high flood.

Five genera and 13 species of cichlids were collected from the Kavango River. The southern mouthbrooder *Pseudocrenilabrus philander* was the most common species of the entire biota, accounting for nearly 15% of the total catch for the year. The redbreast tilapia *Tilapia rendalli* and the banded tilapia *T. sparrmanii* were the two next most abundant species, 11.67 and 10.03% of the total catch respectively. *Pseudocrenilabrus philander* was found during each sampling period, with greatest abundance during the February and May flood conditions, and least abundance during the reduced water levels of November. It thrived in the flooded, vegetated, shallow-water habitats of the Kavango River. *Tilapia rendalli* and *T. sparrmanii* were found in 80% of the samples, and were represented during all sampling periods. The fewest individuals of both the redbreast and banded tilapia were taken during the June, September and November sampling periods, as floodwaters receded and habitats of choice became less available. Although predation and subsistence fishing may contribute to declining numbers, populations of both species rebounded with flooding.

The Okavango tilapia *T. ruweti* was much less common and more restricted in its distribution than *T. rendalli* and *T. sparrmanii*, representing less than 5.0% of the total yearly catch. Bell-Cross and Minshull (1988) observed that the Okavango tilapia is generally rare, but locally or seasonally common.

The Zambezi happy *Pharyngochromis acuticeps* was found in 75% of all samples and constituted some 4.35% of the total yearly catch. It was most abundant during the flood transition period from November through February.

The genus *Oreochromis* is represented in the study area by the threespot tilapia *O. andersonii* and the greenhead tilapia *O. macrochir*. Of the two, *O. andersonii* was more common, although virtually absent from June through November. *O. macrochir* was rare, only a single specimen being collected along the floodplain during this survey. This scarcity may be related to an annual shift or to gear selectivity. Hay *et al*. (2000) reported a much higher relative abundance of the species, although B. C. W. van der Waal (University of Venda, pers. comm.) noted the absence of these two species in traditional funnel trap catches. *Oreochromis* species appear to be replaced in importance in the upper Kavango River by *Tilapia* spp.

Three cichlids of the genus *Serranochromis* were collected along the floodplain, the piscivorous purpleface largemouth *S. macrocephalus* and nembwe *S. robustus* being somewhat prominent in the fish community. Both these species were found in more than half the samples taken and constituted 1.2–2.9% of the total yearly catch. The thinface largemouth *S. angusticeps* was uncommon in the Kavango River, most individuals being collected during June. Hay *et al*. (2000) collected all three species by gillnet.

Three *Sargochromis* species were collected during the 1992 survey. The green happy *S. codringtonii* and the pink happy *S. giardi* were encountered rarely. Only a single specimen of the rainbow happy *S. carlottae* was collected elsewhere in the drainage, but other workers have collected them with gillnets, so their relative abundance might be related to gear selectivity (Hay *et al*. 2000). Bell-Cross and Minshull (1988) state that all three species are important to the commercial gillnet fishery of the upper Zambezi system.

Two additional *Serranochromis* (*S. altus* and *S. thumbergi*) and one *Sargochromis* (*S. greenwoodi*) species are known from the Kavango River, Namibia/Angola (Skelton *et al*. 1985, Skelton and Merron 1987, Bell-Cross and Minshull 1988, van der Waal 1991, Hay *et al*. 2000), but were not found during this study. *Serranochromis altus* was described from the upper Zambezi River (Winemiller and Kelso-Winemiller 1991). *Serranochromis thumbergi* is common throughout the Okavango Delta (Merron and Bruton 1995), and *S. greenwoodi* is found in the upper river in Angola.

The banded jewelfish *Hemichromis elongatus* is the only other cichlid encountered in the Kavango. Similar to the upper Zambezi (Bell-Cross and Minshull 1988), *H. elongatus* tends to prefer rocky habitats, and it was absent in these samples of the Kavango floodplain.

Cyprinidae

The Cyprinidae, represented by three genera and 17 species, was the most speciose family along the floodplain, and it constituted 28.7% of the total yearly catch. The June sample yielded the highest proportion (45.8%) and diversity (15 of 17 species). November, the driest month, yielded only 187 specimens (18.3%) and 6 (of 17) species from the entire survey area.

The genus *Barbus* was represented by 15 species. The dashtail barb *B. poechii* was the most common cyprinid, found in more than half the samples and making up >7% of the total annual catch. It was the fourth most abundant species for the entire survey, and was represented in all sampling periods. It is perhaps more widely distributed in the Kavango River than the upper Zambezi, where it is considered only fairly common (Bell-Cross and Minshull 1988).

The straightfin barb *B. paludinosus* and the Beira barb *B. radiatus* were the two next most abundant and commonly collected cyprinids, each being in the top seven species collected during this floodplain survey. The Thamalakane barb *B. thamalakanensis* is another prominent cyprinid. Each species was relatively uncommon during months when the river was dropping (September and November), but increased in abundance at peak flood (May and June).

The spottail barb *B. afrovernayi* and hyphen barb *B. bifrenatus* were less common, although they were present during most seasons. The blackback barb *B. barnardi*, Barotse barb *B. barotseensis*, orangefin barb *B. eutaenia*, red barb *B. fasciolatus* and longbeard barb *B. unitaeniatus* were each collected on three of the five surveys, each in highest numbers during flood conditions (February through June), as was the linespotted barb *B. lineomaculatus*.

Three *Barbus* species were collected infrequently and in such low numbers that they can be considered scarce: this group included what the authors identified as the broadstriped barb *B. annectens*, although this species was not recognized from the drainage by Skelton (1993); a single specimen of the upper Zambezi yellowfish *B. codringtonii*, collected by gillnet; and sicklefin barb *B. haasianus*. The copperstripe barb *B. multilineatus* and the upjaw barb *Coptostomabarbus wittei* were collected elsewhere in the Kavango River during this study, but not along the floodplain.

Two other cyprinids were collected along the Kavango River floodplain in the faster flowing rivulets: redeye labeo *Labeo cylindricus* and barred minnow *Opsaridium zambezense*. Numbers of *L. cylindricus* were lowest during the peak-flood months of May and June, and *O. zambezense* was most abundant during the rising flood of February. The upper Zambezi labeo *L. lunatus* was not collected along the floodplain, although it is considered rare in the study area (Hay *et al*. 2000); Merron and Bruton (1995) thought it preferred the perennial floodplain habitats of the Okavango Delta.

Cyprinodontidae

Ranked third as a group in relative abundance, with more than 6% of the total annual catch, this family is currently represented in the Kavango drainage by three species from the genus *Aplocheilichthys*: the meshscaled topminnow *A. hutereaui*, Johnston's topminnow *A. johnstoni* and the striped topminnow *A. katangae*. *A. johnstoni* was the most ubiquitous and abundant of the topminnows, ranked seventh in total relative abundance of all species collected and found in >80% of the collections. For each species, numbers peaked in May, the height of the flood. *A. hutereaui* and *A. katangae* were common and scarce respectively.

Characidae

Four species, each representing monotypic genera, constitute the characin family in the Kavango River: the striped robber *Brycinus lateralis*, the tigerfish *Hydrocynus vittatus*, the silver robber *Micralestes acutidens* and the slender robber *Rhabdalestes maunensis*. As a group these fish made up <5.0% of total annual catch by number. Seasonally, the characins peaked in May and November, representing 5 and 12% of the total catch during those months (Table II). The most common species of the family was *M. acutidens*. Bell-Cross and Minshull (1988) maintain the silver robber to be probably the most common species anywhere it occurs in Zimbabwe. It is considered locally abundant in the Kavango River. *Brycinus lateralis* was rather common also, peaking during the low flow conditions of November. *Rhabdalestes maunensis* was rare, only a single specimen being captured along the floodplain of the Kavango, but it is more common in the Delta. Tigerfish are open-water carnivores, and were assuredly more common than the samples indicate owing to gear selectivity. Juvenile tigerfish (<15 cm total length *TL*) were particularly noticeable in November in small flooded inlets and around vegetation beds. Merron and Bruton (1995) noted that the species was restricted to the riverine floodplain and perennial swamp environs of the Okavango Delta.

Siluriformes

There are five families of catfish in the Kavango River, three of which are represented by several species (Amphiliidae, Clariidae, Mochokidae) and two that are monotypic in Namibia (Claroteidae, Schilbeidae). The most common and abundant catfish are the mochokids, primarily of the genus *Synodontis*. Presumably, there are seven species of *Synodontis* in the Kavango River: leopard squeaker *S. leopardinus*, largespot squeaker *S. macrostigma*, largemouth squeaker *S. macrostoma*, spotted squeaker *S. nigromaculatus*, *S. thamalakanensis*, *S. vanderwaali* and the upper Zambezi squeaker *S. woosnami* (Skelton and White 1990). Collectively, *Synodontis* spp. were found at more than half the sample localities and were collected during all sampling periods. The final mochokid collected during the study was the Okavango suckermouth catlet *Chiloglanis fasciatus*, which was considered rare along the floodplain.

The silver catfish *Schilbe intermedius* is the only member of the family Schilbeidae in Namibia. It was common spatially and seasonally, with its highest relative abundance during the low-flow conditions of September and November. Bell-Cross and Minshull (1988) suggested that predation pressure could dictate its relative abundance.

The family Clariidae was represented by three species of the genus *Clarias*: the sharptooth catfish *C. gariepinus*, the blunttooth catfish *C. ngamensis* and the snake catfish *C. theodorae*. Collectively, the clariids were taken with regularity during the study, with highest numbers during flooding conditions. Their abundance was likely related to gear selectivity. Bell-

Cross and Minshull (1988) found each species to be numerous in Zimbabwe, with *C. gariepinus* the most common. Merron (1993) described the unusual pack-hunting behaviour of *C. gariepinus* and *C. ngamensis* in relation to seasonal flooding in the Delta. Three additional clariid catfish are known from the Kavango River in Namibia (Skelton *et al*. 1985, Bell-Cross and Minshull 1988, Hay *et al*. 2000) but were not collected during this study. They are the smoothhead catfish *Clarias liocephalus*, the broadhead catfish *Clariallabes platyprosopos* and the blotched catfish *C. stappersii*.

The family Amphiliidae is represented in the Kavango River by three cryptic species: the stargazer mountain catfish *Amphilius uranoscopus*, the Chobe sand catlet *Leptoglanis dorae* and the spotted sand catlet *L. rotundiceps* (Skelton 1993). The amphiliids were along the floodplain, *L. dorae* and *L. rotundiceps* each being represented by a single specimen. No *A. uranoscopus* were caught.

The Zambezi grunter *Parauchenoglanis ngamensis* has recently been placed in the family Claroteidae (Skelton 1993). The species is locally common in the Kavango River, but not along the floodplain, only two specimens being collected during this study.

Mormyridae

This family is represented in the Kavango River by six species in five genera: the slender stonebasher *Hippopotamyrus ansorgii*, the Zambezi parrotfish *H. discorhynchus*, the bulldog *Marcusenius macrolepidotus*, the western bottlenose *Mormyrus lacerda*, the churchill *Petrocephalus catostoma* and the dwarf stonebasher *Pollimyrus castelnaui*. Collectively, the mormyrids constituted some 2% of the total number of fish collected. The bulldog was the most abundant mormyrid along the floodplain, followed by the dwarf stonebasher and the churchill. The Zambezi parrotfish and the western bottlenose were less common, and the slender stonebasher was rare. Mormyrid numbers were at their least during the low flows of November through the increasingly flooded conditions of February, but they peaked during September, when they represented 8.5% of all fish collected. It can therefore be concluded that the floodplain vegetation is critical to their life history.

Distichodontidae

The citharines in the Kavango River are represented by three species in two genera: the dwarf citharine *Hemigrammocharax machadoi*, the multibar citharine *H. multifasciatus* and the broadbarred citharine *Nannocharax macropterus*. Of the three, the multibar citharine was the commonest along the floodplain, concurring with Bell-Cross and Minshull's (1988) findings in Zimbabwe; it was locally abundant in the Kavango, with highest abundance during the peak of flood, May and June. The dwarf citharine is considered uncommon, although Bell-Cross and Minshull (1988) found it to be as numerous as the multibar citharine, and fairly well distributed where swampy conditions prevail in Zimbabwe river systems. It was prevalent during the peak flood conditions of May through dropping water levels of September. *Nannocharax macropterus* is known in this study from a single individual collected during May.

Anabantidae

The manyspined climbing perch *Ctenopoma multispine* was the only member of this family collected during the survey; it was most prevalent during May. A second species in this family (the blackspot climbing perch *Microctenopoma intermedium*) is known from the Kavango and Okavango Delta (Skelton *et al*. 1985, Skelton 1988, Merron and Bruton 1995), but it was not collected during this study.

Mastacembelidae

Two species of spiny eels are known from the Kavango River, both in the genus *Aethiomastacembelus*: the shorttail spiny eel *A. frenatus* and the ocellated spiny eel *A. vanderwaali*; the two species prefer vegetated and rocky habitats respectively (C. Hay, MFMR, pers. comm.). The former was taken only outside the floodplain study area, but the latter is considered rare along the floodplain, based on frequency of occurrence.

Hepsetidae

The single member of this family, the Kafue pike *Hepsetus odoe*, was rare during this study, but this is probably a reflection of gear selectivity based on its increased occurrence in recreational angling efforts (P. and L. Kibble, Rundu, pers. comm.). Bell-Cross and Minshull (1988) found *H. odoe* to be uncommon in Zimbabwe when coexisting with tigerfish, but extremely numerous in areas devoid of *H. vittatus*. Rather than a reflection of competition, the presence

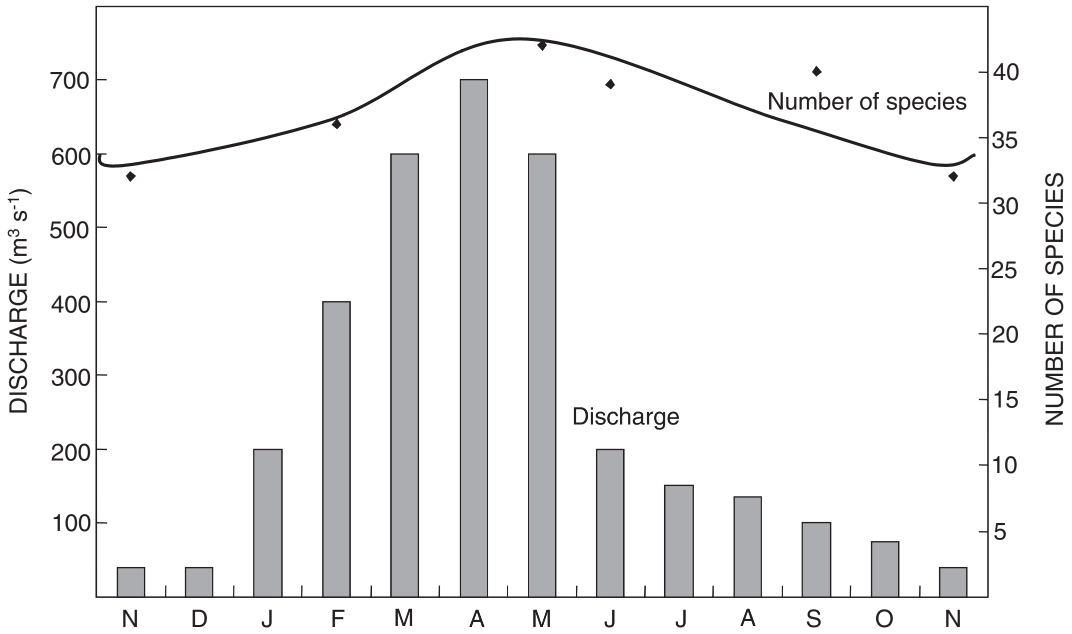

Fig. 4: Seasonal trends in biodiversity v. flood stage in the Kavango River floodplain in 1992

of pike in the absence of tigerfish is more likely explained by their preference for well-vegetated systems and seasonal floodplains (Merron and Bruton 1995).

DISCUSSION

Despite the fact that floodplain rivers constitute the basis for up to 45% of Africa's inland fisheries (Welcomme 1979a) and that Africa's floodplain fisheries are subsistence or artisanal in nature, hardly any data exist on cause/effect relationships. This statement is further underscored by the paucity of recent information on African riverine ecology outside South Africa, which itself generally lacks floodplain systems similar to that described here. Works that do exist are typically scholarly overviews (e.g. Welcomme 1979 a, b, Lowe-McConnell 1987), dated or written in popularized fashion (Merron and Bruton 1989). Davies *et al.* (1993) stated that there had been little research "...to establish the importance of fish populations in the functioning of river ecosystems" in Africa. Ecologically based research is needed to gain further understanding of the species and community level processes that regulate fish community dynamics (Welcomme 1979b, Yamaoka 1991).

Six terrestrial communities and three aquatic plant communities have been identified with the Pongola River floodplain, serving respectively as allochthonous and autochthonous inputs into the system (Heeg and Breen 1982). Grasses around the pans were highly productive, yielding up to 23 kg ha^{-1} day^{-1} of dry mass, much of it transformed by grazing cattle and hippopotamus, permitting its re-entry into the system. This situation is akin to that of the Kavango floodplain, where herds of cattle (replacing natural herbivores) seasonally graze the vegetation and transform it, making it available for the next seasonal rains. The Kavango drainage has had hardly any impact on it other than localized deforestation, some overgrazing and organic enrichment.

There is disagreement in the literature as to what factors most influence fish living in seasonably varying environments. For instance, temperature is generally considered as a controlling factor of activity in poikilotherms (Fry 1947), particularly in terms of reproductive or migratory behaviour. Temperature, however, is relatively more consistent in tropical streams and is therefore considered to be less a governing factor of fish behaviour than in temperate catchments (Lowe-McConnell 1987), although streams at higher elevation

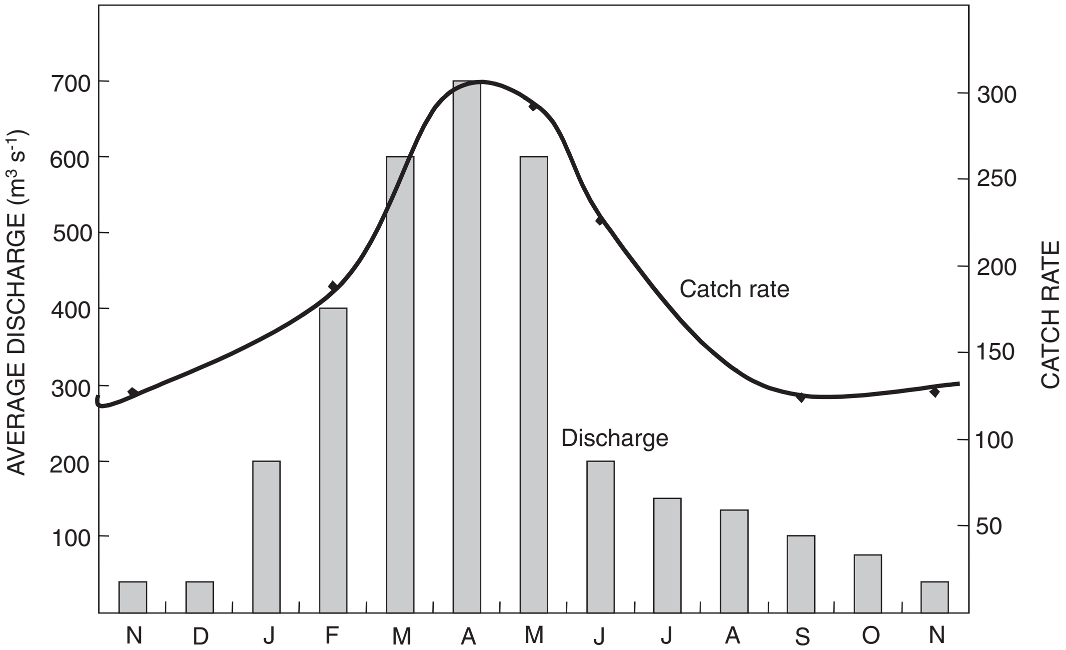

Fig. 5: Seasonal trends in catch rate v. flood stage in the Kavango River floodplain in 1992

can experience substantial seasonal shifts. Longitudinal migrations of tropical fish and their reproductive cycles in Africa may well be timed in relation to seasonal flooding (Bruton and Jackson 1983). For instance, Merron and Bruton (1989) noted pre-flooding migration "runs" of sharptooth catfish and tigerfish in the Okavango Delta, whereas Jackson and Coetzee (1982) reported post-flooding spawning runs of the mud mullet *Labeo umbratus*. Mormyrids such as the Zambezi parrotfish and the bulldog *M. macrolepidotus* migrate up streams in schools during the flood season (Bell-Cross and Minshull 1988, Bowmaker 1973). In floodplain environments, it is thought that a lateral migration of fish will accompany inundation of newly flooded areas, which then act as sites of feeding, reproduction, nurseries, shelter or refugia (Bruton and Jackson 1983).

Figures 4–7 indicate a pronounced structural and functional response of the Kavango fish community to the alternating flood and drought conditions in the river, with lowest diversity and fewest specimens during the low flow months, October–December, but increasing thereafter through May, the month of peak flooding.

The reproductive strategies of some Kavango fish were in advance of flooding in January/February. For instance, young K-selected piscivorous *Serranochromis* spp. and tigerfish appeared in November during low flows, growing to juveniles by February (Figs 6, 7). Among the herbivores, *T. rendalli* bred earlier than *T. sparrmanii*, young occurring in November and February respectively. Numbers of redbreast tilapia peaked during February, whereas numbers of *T. sparrmanii* did so in May.

The ubiquitous r-selected invertivores, dominated by the cyprinids, were in relative synchrony with flooding and the stimulation of littoral zone plant growth (Figs 6, 7). In terms of relative abundance, they peaked in May (65%), June (77%) and September (68%), during the height of flooding, and were available as prey to young piscivores (Fig. 7). Other r-selected invertivores, such as the mormyrids, appeared to lag slightly behind the cyprinids in their use of the floodplain for reproduction and nursery areas, with highest relative abundance in June (3%) and September (11%; Table II). The r-selected *P. philander* was a major component of the catch during the whole year.

Hocutt *et al*. (1994) provided the criteria for subdividing the fish community into trophic levels as a preliminary step to calculating an Index of Biotic

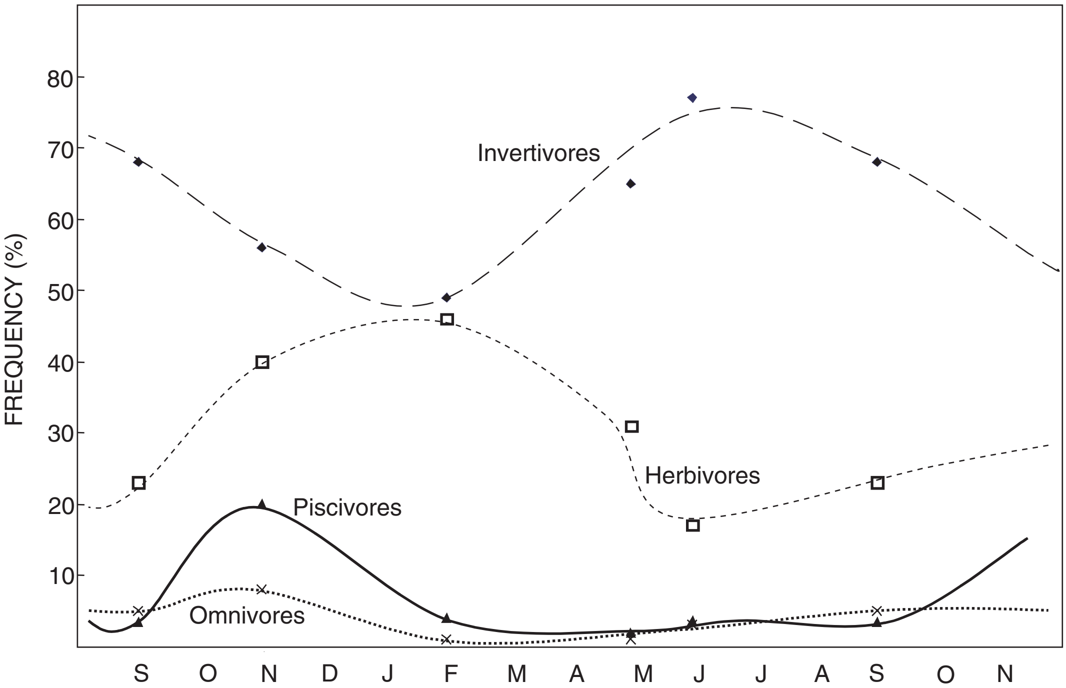

Fig. 6: Seasonal trends in trophic levels of fish along the Kavango River floodplain in 1992 (piscivores × 10)

Integrity (IBI). They noted that relative abundance of herbivores was highest from November through February, but was lower from May through June, increasing in September (their Fig. 6). This inferred an inverse relationship with the invertivores, which peaked in importance during May and June, decreasing in September. This led Hocutt *et al.* (1994) to suggest that invertivores and herbivores might spatially and temporally replace one another. However, in retrospect, it is better to interpret the data as indicating the seasonal swamping of the system with young-of-the-year, r-selected, (largely) ephemeral invertivores, especially cyprinids, rather than their straight replacement of herbivores.

The trend of omnivorous scavengers represented by the silurid catfish was counter to that of other fish, i.e. they were minor components of the fish community on a rising flood, February through May (Table II). However, they increased in number during decreasing flow, rising to 8% of November's catch. The data support the contention that scavengers lag herbivores and invertivores in the annual flood cycle. Oddly, hardly any young-of-the-year silurids were collected.

Serafy (1992) reviewed much of the literature relative to fish distributions in seasonally fluctuating environments of the northern hemisphere. He surmised that there might not be a direct dependence of fish biomass on aquatic vegetation, i.e. that fish might simply concentrate in these areas. He gave a number of examples indicating that fish populations are not necessarily adversely affected by the reduction or disappearance of macrophytes. However, none of his examples considered a tropical floodplain river environment such as the Kavango, with its characteristic shifting sand substratum between two well defined banks that collectively contribute to a rather sterile mid-channel condition that continues until the floodplain floods laterally (Welcomme 1979a). This in turn stimulates plant growth and enhances the success of fish populations through a number of direct and indirect pathways.

The high macrophyte growth in the Kavango River littoral zone serves as nesting areas, feeding zones and refugia for most fish species, few having a true affinity for the more open and structureless mid-channel. The vegetation itself acts as a mineral and nutrient sink, Kavango water having minimal levels of conductivity (e.g. <40 μmS cm^{-1} and nutrients during

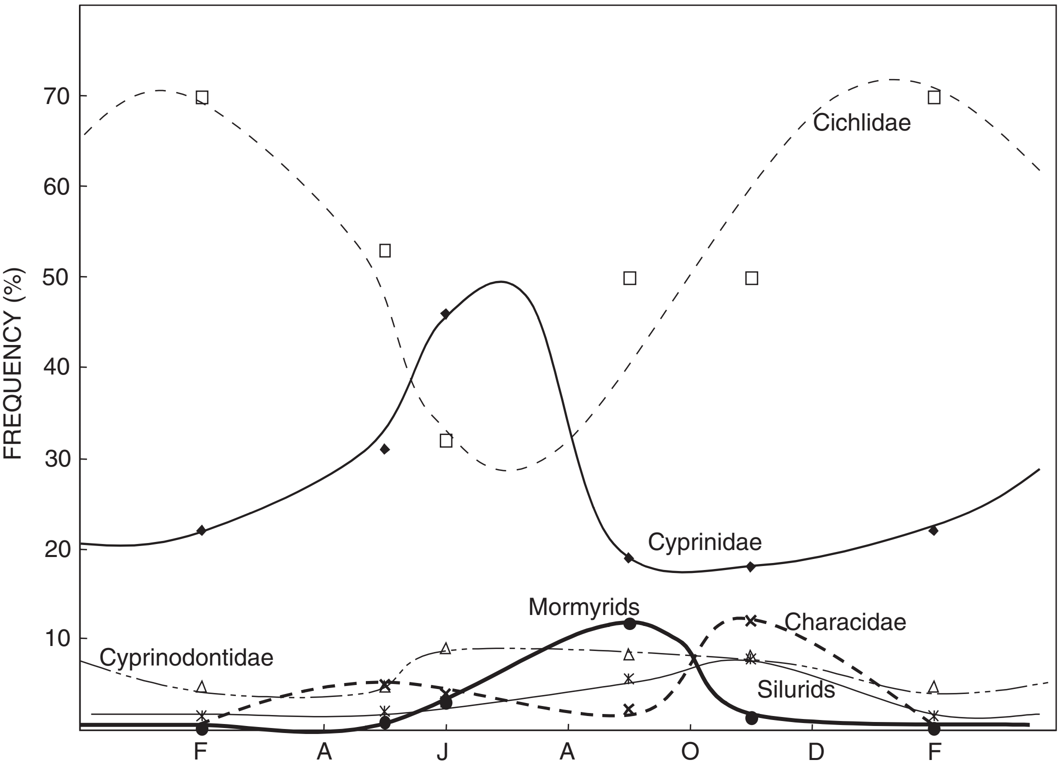

Fig. 7: Seasonal trends by family of fish along the Kavango River floodplain in 1992

flooding conditions; Hay *et al*. 2000). Phytoplankton productivity is considered negligible, but its true significance requires assessment.

Pertinent questions are where does the fish community go during low flow conditions, and from where is it derived during the rising flood? The results presented here do not adequately depict the virtual vanishing of species and overall numbers during conditions of low flow; e.g. a relatively large number of species (32) was taken from the Kavango during November, but that total comes from combining all the species taken from all stations sampled that month, with each station contributing few fish to sampling effort. In peak flow conditions the same number of species could occur at each station.

The synthesis of Lowe-McConnell (1987) predicts that many floodplain fish will exhibit (a) greatly fluctuating populations, (b) short life cycles with early maturation and rapid growth, and (c) seasonal reproductive cycles, with predominant r-type selection. These characteristics of the Kavango invertivore fauna, combined with the magnitude of the subsistence fishery, dictates that high productivity on the rising flood will be followed by high total mortality (natural plus fishing) during the flood subsidence. Downstream drift of fish during flooding has been considered the primary inoculum for fish breeding and productivity in the Kavango floodplain, especially for small r-selected species. However, shoreline vegetation, including root systems, undercut banks and oxbow lagoons/pools might be refugia that also make significant contributions. This phenomenon needs to be explored.

SUMMARY

This single year of information for the Kavango River is unique and provides the first, albeit cursory, examination of fish community dynamics and cause:effect relationships in this floodplain system above the

Okavango Delta. The data, in combination with the historical literature base and the recent publications of Hocutt *et al*. (1994), Hay (1995) and Merron and Bruton (1995), give new insight to the functioning of this important transboundary river.

The major trends of the fish community in relation to the flood cycle and emergence of littoral zone vegetation were (a) the timing of peak diversity and productivity; (b) seasonality of the piscivores, herbivores, invertivores and omnivores; and (c) the overall dominance (and importance) of cichlids and cyprinids. It is thought that, despite the overall richness of other families, cichlids dominate annual catch because they occupy (a) three different trophic levels (piscivore, herbivore and invertivore) and (b) the full spectrum of reproductive strategies, from r- through K-selection.

If it can be assumed that flooding is the primary driver of floodplain (fisheries) productivity as indicated here, then it should be considered that the degree and timing of the annual flooding cycle is variable. Therefore, the answer to a fundamental question remains obscure: is productivity dependent upon the annual flood or the magnitude of flooding from the previous year(s)? Intuitively, it is both.

As stated here in support of the flood pulse concept (Junk *et al*. 1989), it is likely that the success of fish in a given year is reliant upon the annual magnitude of littoral zone flooding that stimulates primary production, which in turn serves for food, shelter, etc. However, the success of annual aquatic macrophyte production is dependent not only upon the height and duration of the current flood stage, but the availability of detritus and nutrients through decomposition from the previous year(s) of flooding as well.

Finally, once these data are interpreted in terms of (1) the local Kavango population and their ever-increasing subsistence/nutritional needs, and (2) the prospects of various schemes of water resource utilization, it is clear that nothing short of a sound basin-wide management agenda is required.

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