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SOME OBSERVATIONS ON FISH MIGRATIONS IN CAPRIVI, NAMIBIA

B.C.W. van der Waal University of Venda, P/Bag 5050, Thohoyandou, 0950, South Africa.

Summary

Longitudinal and lateral migrations of freshwater fish were observed in 63 (83%) of the fish of the Upper Zambezi in the Caprivi region, Namibia. The results of 20 surveys showed that longitudinal upstream migrations were undertaken by most small cyprinids, mormyrids, distichodontids, characids, schilbeids, clariids and mochokids but by only a few of the larger cichlids. Similarly, lateral migrations out of permanent waters were common for young mormyrids, some smaller barbs, small characids, Schilbe, a few mochokids, cyprinodonts, most cichlid species and both anabantids. Breeding migrations were observed only in Clarias spp and some barbs. All other fish movements seem to be connected with invasions into newly inundated habitat, escape from desiccation, movement back to permanent water or else an upstream or downstream movement away from areas with temporary high densities in an effort to escape predation or seek new feeding ground. An unexpected large number of fish species (34) were collected in isolated pools at the edge of the floodplain after the floods had receded.

Introduction

Fresh water is becoming one of the strategic commodities in Southern Africa and can be regarded as the most limiting natural resource available (Ashton et al 1986). In an effort to provide enough water for consumers, almost all major rivers in South Africa have been altered through construction of weirs, impoundments and recently, water carriers and canals linking major river systems (Jackson 1989). impact of these structures on indigenous fish populations is not well documented (Jubb 1967, Bok et al 1989, Skelton 1990). One of the impacts of weirs and walls in rivers is the prevention of migrations or even absence of species in upper portions of rivers (Clay 1976). Only a handful of fish ladders have been built in southern Africa to facilitate the movement of fish (Jubb 1953, Meyer 1974, Cambray 1990, Skelton 1990). There appears to be a general absence of scientific motivation for the need for fish ladders for southern African indigenous fishes. This was borne out during a workshop in 1990 on fish ladders where it became apparent that little is known of the migratory biology of our South African

species (Bowmaker 1973, Cambray 1990, Skelton 1990). Recent workshops on the Kruger National Park Rivers Research Programme and on Fishways have underlined the need for basic information on migratory habits of our fish species. These considerations motivated the presentation of observations made in Caprivi during 1974-1977 during a fisheries research programme (Van der Waal 1976, 1980, 1985, 1990, Van der Waal and Skelton 1984).

Methods

Observations on actual fish migrations require intensive monitoring at selected sites (Bell-Cross 1960, Meyer 1974). The present data were collected during routine surveys of fish communities in Lake Liambezi and in the area where opportunities arose.

Where fish migrations were observed, attempts were made to collect samples. Data on earlier migrations could be inferred where water bodies were sampled at the end of the high water season in floodplains or temporary water courses that were known to have been completely dry during the previous dry season.

The following collecting apparatus was employed to collect fish samples:

- * Bagged seine nets of 20 by 2 m with 10 mm mesh and 40 by 3 m with 25 mm stretched meshes respectively.
- * D-frame hand net of 70 by 50 cm with a deep bag and 2.5 mm mesh netting.
- * Electroshocker delivering 300W at 250V AC fitted to a forked adjustable electrode holder, used in conjunction with scoop nets.
- * Fleet of gillnets consisting of ten stretched mesh sizes from 25 to 190 mm.

- Inspection of catches of valved fish traps (lukuko) and fish funnels (lifula) of local fishermen.
- * Experimental valved trap and fish fence constructed from 2.5 mm mesh material set across a small stream draining a pool.

Voucher specimens of fish collections were submitted to the Albany Museum and JLB Smith Institute of Ichthyology for confirmation of preliminary field identifications and permanent reference purposes.

Table 1. Fish species recorded during migrations in the Zambezi River in Namibia.

Scientific name		Standard name
Mormyridae	·	
Hippopotamyrus discorhynchus	(Peters, 1852)	Zambezi parrotfish
Marcusenius macrolepidotus	(Peters, 1852)	bulldog
Mormyrus lacerda	Castelnau, 1861	western bottlenose
Petrocephalus catostoma	(Günther, 1866)	churchill
Pollimyrus castelnaui	(Boulenger, 1911)	dwarf stonebasher
Cyprinidae	· · ·	
Barbus afrovernayi	Nichols and Boulton, 1927	spottail barb
Barbus barnardi	Jubb, 1965	blackback barb
Barbus barotseensis	Pellegrin, 1920	Barotse barb
Barbus bifrenatus	Fowler, 1935	hyphen barb
Barbus eutaenia	Boulenger, 1904	orangefin barb
Barbus fasciolatus	Günther, 1868	red barb
Barbus haasianus	David, 1936	sicklefin barb
Barbus lineomaculatus	Boulenger, 1903	line-spotted barb
Barbus multilineatus	Worthington, 1933	copperstripe barb
Barbus paludinosus	Peters, 1852	straightfin barb
Barbus poechii	Steindachner, 1911	dashtail barb
Barbus radiatus	Peters, 1853	Beira barb
Barbus thamalakanensis	Fowler, 1935	Thamalakanane barb
Barbus unitaeniatus	Günther, 1866	longbeard barb
Coptostomabarbus wittei	David and Poll, 1937	upjaw barb
Labeo cylindricus	Peters, 1853	redeye labeo
Labeo lunatus	Jubb, 1963	Upper Zambezi labed
Opsaridium zambezense	(Peters, 1852)	barred minnow
Distichodontidae		
Hemigrammocharax machadoi	Poll, 1967	dwarf citharine
Hemigrammocharax multifasciatus	Boulenger, 1923	multibar citharine
Nannocharax macropterus	Pellegrin, 1925	broadbarred citharine

Characidae		
Brycinus lateralis	(Boulenger), 1900	striped robber
Hydrocynus vittatus	Castelnau, 1861	tigerfish
Micralestes acutidens	(Peters, 1852)	silver robber
Rhabdalestes maunensis	(Fowler, 1935)	slender robber
Hepsetidae		
Hepsetus odoe	(Bloch, 1794)	African pike
Claroteidae	,	r ·
Parauchenoglanis ngamensis	(Boulenger, 1911)	Zambezi grunter
Schilbeidae	(= 1B11,	Samoth Brance.
Schilbe intermedius	Rüppel, 1832	silver catfish
Amphiliidae	Kappen, 1002	Sirver Catrisii
Amphilius uranoscopus	(Pfeffer, 1889)	starrager (mountain cathda)
Clariidae	(1101101, 1007)	stargazer (mountain catfish)
	(Durahall 1922)	-1AAbAC1
Clarias gariepinus Clarias ngamensis	(Burchell, 1822)	sharptooth catfish
Clarias ngamensis Clarias stappersii	Castelnau, 1861	blunttooth catfish
Clarias stappersti Clarias theodorae	Boulenger, 1915 Weber, 1897	blotched catfish
	W CUCI, 107/	snake catfish
Mochokidae	Davis and 1011	
Chiloglanis neumanni	Boulenger, 1911	prickleback suckermouth
Synodontis leopardinus	Pellegrin, 1914	leopard squeaker
Synodontis macrostigma	Boulenger, 1911	largespot squeaker
Synodontis nigromaculatus Synodontis woosnami	Boulenger, 1905	spotted squeaker
•	Boulenger, 1911	Upper Zambezi squeaker
Cyprinodontidae	(B. 1. 1010)	
Aplocheilichthyshutereaui	(Boulenger, 1913)	meshscaled topminnow
Aplocheilichthysjohnstoni	(Gunther, 1893)	slender topminnow
Aplocheilichthyskatangae	(Boulenger, 1912)	striped topminnow
Mastacembelidae		
Aethiomastacembelus frenatus	(Boulenger, 1901)	longtail spinyeel
Cichlidae		
Hemichromis elongatus	(Guichenot, 1859)	banded jewelfish
Oreochromis andersonii	(Castelnau, 1861)	threespot tilapia
Oreochromis macrochir	(Boulenger, 1912)	greenhead tilapia
Pharyngochromis acuticeps	(Steindachner, 1866)	Zambezi happy
Pseudocrenilabrus philander	(Weber, 1897)	southern mouthbrooder
Sargochromis carlottae	(Boulenger, 1905)	rainbow bream
Sargochromis codringtonii	(Boulenger, 1908)	green bream
Sargochromis giardi	(Pellegrin, 1903)	pink bream
Serranochromis altus	Winemiller and	
	Kelso-Winemiller, 1991	humpback largemouth
Serranochromis angusticeps	(Boulenger, 1907)	thinface largemouth
Serranochromis macrocephalus	(Boulenger, 1899)	purpleface largemouth
Serranochromis robustus jallae	(Boulenger, 1896)	nembwe
Serranochromis thumbergi	(Castelnau, 1861)	brownspot largemouth
Tilapia rendalli	(Boulenger, 1896)	redbreast tilapia
Tilapia ruweti	(Poll and Thys van den	
Tilania snarrmanii	Audenaerde, 1965)	Okavango tilapia
Tilapia sparrmanii	Smith, 1840	banded tilapia
Anabantidae	(D. H 1000)	
Ctenopoma intermedium	(Pellegrin, 1920)	blackspot climbing perch
Ctenopoma multispine	Peters, 1844	manyspined climbing perch

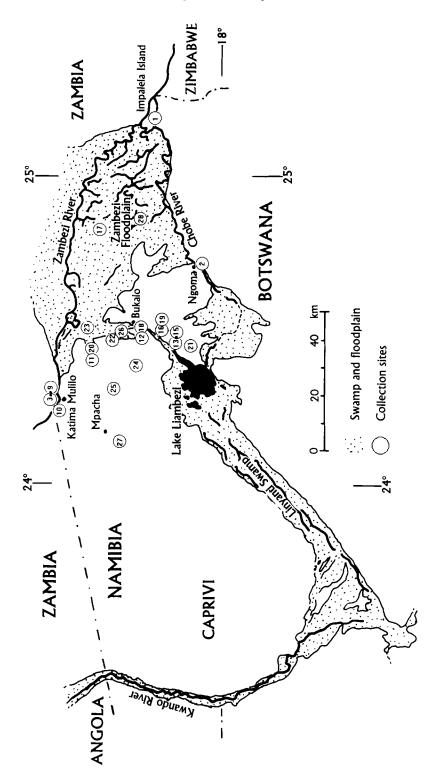


Figure 1. Map of Caprivi region, north eastern Namibia, indicating collection sites.

Table 2. Fish species collected in four migration types in Caprivi.

										ion	of fi													
	D	ow	nst	ream								To	fl	000	dpla	ain				Ba	ick	to	riv	er
Collection site no.	. 1	2	3	freq	4	5	6	7	8	9	freq	10	11	12	! 13	14	15	16	freq	17	18	19	20	frec
Mormyridae																								
H. discorhynchus	+			1															-					
M. macrolepidotus	+	+		2							-							+	1	+				l
M. lacerda	+			1							-								-		+	+		2
P. catostoma	+	+	+	3							-							+	1	+	+			2
P. castelnaui	+		+	2							-							,	-	+				1
Cyprinidae																								
B. afrovernayi				_			+	+			2	+							1					_
B. barnardi				-	Ċ	+		+		Ċ	2							,	-		+			1
B. barotseensis		·		_	+	+	+	+	+	•	5	+	•	+		•	•	•	2				•	-
B. bifrenatus	+			1		+	+	+	+		4			+		+			2	+	+		•	2
B. eutaenia	+	Ċ		1	Ċ	+		+	+		3				•				-	,	Ċ		•	-
B. fasciolatus		·		_							-								_	+				1
B. lineomaculatus				-	+						1				•	•			_	Ċ		•	•	
B. multilineatus	+			1		Ċ		-			-	+	•		+	+		•	3		•		•	_
B. paludinosus	+	+	+		+	+	+			Ċ	3	+			·	+			2	+	+	•	+	3
B. poechii	+			1	+	+	+		+	+	5	+				Ċ		+	2	+	+			2
B. radiatus				-	+	+		+			3						,		-		+		•	1
B. thamalakanensis		,				+					ī			+		•			1				•	•
B. unitaeniatus				-					+		i	+					Ċ		i	•		•	•	
C. wittei											-			+			Ť		i	•		•	+	1
L. cylindricus	+			i		+	+		+		3				Ċ				-		•	•	•	•
L. lunatus				-	+						1			+					1					_
O. zambezense	+			1			,				_				Ċ		•			•	•	•	•	_
Distichodontidae																					•		•	
H. multifasciatus				_	+	_	_				3													
N. macropterus				_	+	+	+				4	•	•	•	•				-				•	-
Characidae	•	•					•		,	•	7				•		•		-		•	•	•	•
B. lateralis				1							-													
H. vittatus	+		+	-		+	+			٠	2			+					1		+			1
M. acutidens			+	1 1	1			٠			-								1		+			ì
R. maunensis	٠		7	1	•	_	+	•	+	+	5 -	+		+					2					-
	•	•		-	•	•	٠	•	٠	٠	-	•		+					1					-
Hepsetidae																								
H. odoe	+	,		1	٠		٠			٠	-							+	1		+			l
Clarotidae																								
P. ngamensis		,		-					+		ì								-					-
Schilbeidae																								
S. intermedius	+	+		2		+	+				2			+			,	+	2	+	+			2
Amphiliidae																								_
A. uranoscopus	+			ı							_								_					
Clariidae							-	•				•	•			•	•	•			•		•	-
C. gariepinus		+		i								+					t	,	2		,			2
C. ngamensis	•	+		i	٠		•	•	*	•	-	-				•	+	+	3	٠,	+	+	•	2
C. stappersii		,			•			•	•		-		•		•	٠		~	1		+	+		3
C. theodorae	•	•		_	•	٠	+		•		1		•	•	•				-	+	•		٠	1
	,				•		,		•		•		•		•				-	+		•		l
Mochokidae																								
C. neumanni				-					+	٠	1								-					-
S. leopardinus	+			l	+		٠		+		2							+	l					-
S. macrostigma	+			1		٠					!								-					-
S. nigromaculatus		+		1	4		+				1							+	1		+			l
S. woosnami	+	+		2	+	+	+		+		4							+	1		+			1

Cyprinodontidae																								
A. hutereaui				-							_			+					1				+	1
A. johnstonii				-						+	2								2		Ċ			2
Cichlidae																								
H. elongatus	+			i	+	+					2								_					_
O. andersonii				-							_							+	1		+	+	Ċ	2
O. macrochir				-							-								2	Ċ	+	+		2
P. acuticeps				-		+	+		+		3	+							1		+		,	1
P. philander				-	+	+	+		+		4	+							2	Ċ	+			2
S. carlottae				-							-							+	1				Ċ	-
S. codringtoni				-							-							+	1			Ċ		1
S. giardi				-							-							+	1					-
S. angusticeps/altus				-							-								-		+			1
S. macrocephalus				-							-								_	+	+			2
S. robustus				,-							-				,			+	1	+	+			2
S. thumbergi				-							-							+	1		+	+		2
T. rendalli	+	+		2		+					1	+		+		+		+	4		+	+		2
T. ruweti				-							-	+				+			2					-
T. sparrmanii	+			1		+	+				2	+				+		+	3		+	+		2
Anabantidae																								
C. intermedium				-							-		+						1	+				1
C. multispine				-							-		+	+		+		+	4	+	+		Ċ	3
Species total	22	9	5	27	13	20	17	6	1.5	3	31	14	2	12	1	10	1	21	39	15	27	11	1	36
Water level	F	F	F		н	Н	Н	F	F	F	-	R	Н		-	R	_		37	F		F	F	50
Season	w	S	w			Α		-	_	_		M		A						w	-	A	-	
Collecting gear	••		••		1 1	1.		′ •	′ 1	1		141	А	л	141	141	IVI	A		vv	А	A	А	
Traps	1	1																		,				
Seine net						٠								•								٠.		
		٠				•								1				1				1		
Scoop net		٠	•			/						1	/		1	1					/		1	
Electric shocker	٠		٠				٠		1															
Gill nets		٠					•								•			1			✓			

H = highwater; R = rising level; F = falling level.

M = midsummer; A = autumn; W = winter; S = spring.

Results

No less than 63 of the 76 fish species recorded from Caprivi by Van der Waal and Skelton (1984) were collected during surveys of migrating fish in waters of Caprivi or found in isolated pools directly after the flood season (Table 1). Some of the fish species that were described after this survey was undertaken (such as *Synodontis* spp. and *Serranochromis altus* (Skelton 1993a, 1993b) may have been present in samples but were not recognised. This implies that the total number of fish recorded in migrations in the Caprivi section of the Zambezi may exceed 63 species.

Fish migrations were intercepted and collections made at the following localities. Collection numbers refer to Tables 2 and 3 and the respective sites are indicated in Figure 1.

To simplify interpretation, the data have been grouped according to habitat and observed direction of migration. All observations could be grouped into five categories, based on the direction of fish movement:

- 1. Longitudinally in the Zambezi and Chobe rivers:
 - a. Downstream
 - b. Upstream
- Laterally, from permanent rivers and lakes into previously dry floodplains and forests:
 - Into floodplains
 - b. Back to permanent waters
- Remaining behind in isolated temporary pools on floodplains (after having moved onto the floodplains).

1. Longitudinal migrations in rivers

a. Downstream migrations

Site 1. Rapids in Chobe River at Impalela Island, 3 km upstream of the Zambezi/Chobe confluence, 26.6.73. Catches of the efficient 3-4 m long traditional funnel traps (lifula) contained 22 fish species, dominated by P. catostoma and H. discorhynchus. important seasonal fishery during the receding phase of the flood cycle of the Zambezi River is based on this downstream migration at Impalela Island. Fish from the 100 km long floodplain move downstream and away from the floodplain. The lifula were left overnight when considerable greater catches were made than during daytime. The catch of fishermen is sundried and sold as far away as markets in Zambia and in Botswana (Van der Waal 1990).

Site 2. Chobe River, Ngoma Bridge, 4.9.74. A small migration down the swampy and choked upper section of the Chobe River was monitored in September, when the last flood water was running out of a swampy area upstream of Ngoma. This water was deoxygenated and smelled strongly of hydrogen sulphide. Catches of valved traps set in the running water caught mainly M. macrolepidotus, S. intermedius and B. paludinosus.

Site 3. Zambezi River, Katima Mulilo, July 1975. A small downstream migration of predominantly P. catostoma, P. castelnaui and B. paludinosus was observed along open beaches at Katima Mulilo after a major upstream migration at the same sites had terminated. It took place during receding flood levels and a D-frame net was used to make collections.

b. Upstream migrations

Sites 4 to 9. Zambezi River, Katima Mulilo. Separate collections were made on 2 and 9 April and 22 and 27 May 1975. An

uninterrupted migration started on 26 March with the movement of large numbers of M. acutidens, followed by barbs and young labeos, and lasted day and night till the end of May. This spanned the period of maximum water level of the Zambezi, which reached 7.05 m in mid March 1975. continuous stream of small fish, 2-8 cm long, and consisting of 30 fish species was observed on the edge of the river and could be intercepted at rocky promontories or along open beaches with the D-frame handnet. The fish were moving inshore in a band of about one metre wide and swimming upstream at a speed of between 0.5 and 1 metre per second in densities of about 100 per square metre. They kept one half to two metres from the bank and near the substratum in an effort to escape the continuous predation especially by small tigerfish, small catfish and largemouths.

These migrations were characterised by small riverine species but with the prominent absence of Mormyrids and also larger Cichlids and Clariids. Dominant species included: *M. acutidens, B. barotseensis, B. poechii* and *L. cylindricus* (Table 2). Collections were made during daytime only.

This migration pattern was repeated in 1976 but then it started later in May and lasted till July; it was characterised by *B. lateralis* and *R. maunensis* together with barbs and juvenile cichlids.

2. Lateral migrations from river or lake into floodplain

a. From river to floodplain

Site 10. Rainfed molapo next to Zambezi River, 1.6 km north of Katima Mulilo, 7.1.74. A variety of 14 species, dominated by small barbs in ripe running condition, was collected in January while the flood water level was still in the early rising phase. The fish species colonising the newly uninhabited molapo included juvenile H. vittatus of < 50 mm.

Site 11. Culvert near Namalubi, between Katima Mulilo and Bukalo, 11.4.75. At the edge of the floodplain large numbers of C. intermedium and B. wittei were collected with the handnet while moving with rising water level into freshly inundated areas at a culvert. It was significant that no other fish species were collected together with these colonising species. After a few days, various barbs, juvenile Clarias spp., C. wittei and then later S. intermedius, O. macrochir, T. sparrmanii and T. rendalli juveniles followed. Only when the water at the culvert had reached a depth of more than were larger H. odoe Serranochromis spp. caught on artificial lures.

Site 12. Bukalo Mulapo, 8.4.75, 12.4.75 and 8.5.75. A temporary link was established during which fish from the Zambezi floodplain moved through the temporary connection at Bukalo towards Lake Liambezi. This included fish species not previously collected in the Lake such as B. barotseensis, C. wittei and L. lunatus.

Site 13. Small forest stream entering Lake Liambezi, 28.2.75. During the rainy season, B. multilineatus were collected with a handnet as they were moving upstream into a small temporary stream entering Lake Liambezi from the east.

Site 14. Temporary forest entering Lake Liambezi at Kalengwe, 24.1.75 and 25.2.75. Very young individuals (10-20 mm TL) of larger fish species took part in these migrations. Active migration from the lake into the freshly formed rainwater pans in the mopane forest was observed of specimens of 10-50 mm total length of the following species, listed in order of dominance: O. macrochir, T rendalli, T. sparrmanii, T. ruweti, B. paludinosus, B. bifrenatus, C. multispine, A. johnstonii, P. philander, B. multilineatus. These fish migrated up to

8 km away from the lake into small shallow pans of 10-30 cm depth with afternoon water temperatures reaching 40°C.

Site 15. Temporary forest stream entering Lake Liambezi, 20.12.74 and 24.1.75. Adult C. gariepinus were observed during massive spawning runs into the shallow pans during the nights of 20.12.74 and 24.1.75 after considerable rainfall had been recorded the day before resulting in a rise of lake water level. Ten score individuals in ripe-running condition were speared by local fishermen in the very early morning. In both cases fertilised eggs were collected the next day on flooded grass blades in the shallow pans and young were later collected when moving back to the lake.

Site 16. Bukalo molapo and Kalengwe channel north of Lake Liambezi, 9.4.75. An important migration of all large and commercial fish species from the lake into the rainwater flooded grassy Bukalo Mulapo took place when the floodwaters started feeding the lake from the Kalengwe Channel. Two weeks later, large numbers of adult cichlids and clariids were caught in commercial gillnets of fishermen who all moved from the lake to Bukalo to participate in the temporary lucrative fishery.

Before the water had stopped flowing towards the lake, fishing success abruptly dropped as all these fish had already migrated back to the lake with the exception of a large number of large *C. gariepinus* in a deep pool.

b. From floodplain back to permanent waters.

Site 17. Stream at Nsundwa, east of Schuckmannsburg, 20.6.73 and 21.6.73. At the end of the draw-down phase, a stream 10 m wide and 50 cm deep draining a large swampy molapo was barred by a traditional reed fence (siyandi) with four valved traps with 5 mm slits (lukuko). The catches from the traps were monitored for two days and

nights. Catches were dominated by *M. macrolepidotus* and *S. intermedius*. The fish collected was used by the single owner of the *siyandi* for consumption but surplus fish was daily dried for later sale in Zambia.

Site 18. Molapo at Bukalo draining to Lake Liambezi, 13.3.74. Rainfed floodwater was flowing strongly towards the lake at the bridge at Bukalo. Twenty-six fish species were observed in seine catches, including all major cichlids found in the lake with the exception of S. longimanus, S. giardi, S. carlottae, and T. ruweti. Smaller fish species were collected with seine nets and the D-frame net.

Site 19. Temporary forest stream to Lake Liambezi at Kalengwe, 21.3.74 and 25.3.75. A small rainfed stream into Lake Liambezi started to dry up when summer rains ended abruptly in the first week of March 1974. Masses of juvenile cichlids, especially O. macrochir, T. rendalli. T. sparrmanii, and O. andersonii, together with C. multispine and also M. macrolepidotus, A. johnstonii, P. philander, S. thumbergii and young and larger C. gariepinus and C. ngamensis returned through a 60 cm wide and 5 cm deep stream draining rainflooded areas of the low lying mopane forest as far as 8 km away Heavy mortalities were from the lake. observed over a period of four days as many piscivorous birds including marabou storks (Leptopilos crumeniferus) actively preyed on the easily accessible fish. Most cichlids measured between 5 and 10 cm but some T. rendalli of 14 and 15 cm were measured. indicating a phenomenal growth rate for fish only three months old (see Site 14).

Site 20. Culvert at edge of floodplain, at Namalubi, 30.4.75. When the floods began to recede at the edge of the floodplain, movements through a culvert were dominated by C. wittei. Other fish included B. paludinosus, A. hutereaui and A. johnstonii. No larger fish species (Site 11) were collected as these had already moved to deeper water (Bell-Cross 1974).

Table 3. Fish species collected in isolated pools on the floodplains.

Collection site no.	21	22	22	24	25	26	27	20	freq
Conection site no.	21	22	23	24	23	20	21	28	rreq
Mormyridae									
M. macrolepidotus		+	+			+		+	4
M. lacerda		•				+			ļ
P. catostoma		+	•						ļ
P. castelnaui			+						i
Cyprinidae									
B. barnardi		+							1
B. barotseensis	٠			+		+		•	2
B. bifrenatus B. haasianus		+	•	+	+	•			2
B. multilineatus			•	+	т.			•	i
B. paludinosus	+	+		+	+	+	· +	•	7
B. poechii		+		+		+	•		3
B. radiatus	•		•		•	+			í
B. thamalakanensis				+					i
C. wittei					+		+		2
L. cylindricus	+								1
Distichodontidae									
H. machadoi			_	+					1
Characidae									•
B. lateralis		+				+	+		3
				•		•	,	•	5
Hepsetidae H. odoe		_				_			2
	٠	*	•			Τ.		*	2
Schilbeidae									_
S. intermedius		+	+	+		+	•	+	5
Clariidae									_
C. gariepinus	+	+	+			+		+	5
C. ngamensis	+	+	+			+			4
Mochokidae									
S. woosnami						+			1
Cyprinodontidae									
A. hutereaui					+				1
A. johnstonii	+	+		+	+	+			5
Cichlidae									
O. andersonii		+	,			+		+	3
O. macrochir	+	+	+			+	+	+	6
P. acuticeps		+				+			2
P. philander	+	+			+		+		4
S. codringtoni						+			1
S. giardi	*					+			1
S. robustus T. rendalli	+	+			٠	+	+	+	3
T. ruweti	+	-		+	+	+	+	+	6 4
T. sparrmanii	,	+	+	-	-	+	+		4
· · · · · · · · · · · · · · · · · · ·	•	•	,	•		,	•		7
Anabantidae	+	+		_	_				4
C. multispine		τ-	+	+	+	+	٠	•	6
Species total	10	20	9	13	9	23	8	6	
Water level	F	F	L	L	L	L	L	l.	
Season	M	Α	W	W	W	W	W	S	
Gear used:									
Seine net		,				,	,	,	
	٠,	•	٠.	٠.	٠.	•	٧.	•	
Scoop net	/		1	/	/		/		
Fish shocker					1		1		

H = highwater; L = low water; R = rising level; F = falling level; M = midsummer; A = autumn; W = winter; S = spring.

3. Fish remaining in depressions in floodplains at the end of the flood period.

Site 21. Small depressions in mopane forest at Chaka's shop, 6 km east of Lake Liambezi, 21.3.74. Fish trapped in small pools were scooped with hands and scoopnets. Nine species were collected. The only way they could have found access to this area is by a temporary rainwater connection during the previous month.

Site 22. Pool in molapo on edge of floodplain 10 km north of Bukalo, 11.5.74. Twenty fish species were collected with a seine in a pool of 130 cm depth, dominated by B. paludinosus, S. intermedius, C. gariepinus and T. rendalli. A total of 200 kg of fish was collected from an area of 0.05 ha.

Site 23. Shallow weedy pool at Lisikili, remnant of larger molapo, 7.6.75. Nine fish species were collected by a group of children collecting with fish spears (muwayo), traditional scoop nets (lishino) and push baskets (singunde). Catches included adult M. macrolepidotus, P. castelnaui. B. paludinosus and juveniles of S. intermedius, Clarias spp. and Oreochromis spp.

Site 24. Isolated pools in drying out molapo, 40 km south of Katima Mulilo, 26.6.75. Thirteen species were collected with a D-frame net, dominated by seven Barbus species.

Site 25. Floodplain at Moambezi, Mambala, 1.7.75. A series of seasonal rainfed grass covered molapos were connected to the floodplains of the Zambezi only during high flood levels when they contained some fish species. Nine small fish species were collected with a seine and handnets.

Site 26. Abandoned gravel pit in mulapo near Bukalo, 30.7.75. A seine was used to collect more than 200 kg of fish from this 3 m deep gravel pit of only 0.045 ha. The catch consisted predominantly of S. intermedius, C. gariepinus and

O. andersonii and 23 species were collected from this single site.

Site 27. Water holes at Kasheshe, near Mpacha, 10.8.75. A series of molapos in the northern forest area of Caprivi lie west of the Zambezi floodplain. Only during exceptionally good rainfall or high floods is there any connection with the Zambezi floodplain, some 30 km away. Nine fish species were collected with seines and explosives in thick aquatic vegetation in depressions of the drying out molapos.

Site 28. Pool in floodplain, Mutualwize, Lusese, 1.10.73. A large remnant overgrown pool in the floodplain was sampled with a seine and contained six larger fish species, dominated by T. rendalli.

Data of collections made at the end of the flood season in natural and man-made depressions in the floodplains (sites 21 to 28), are summarised in Table 3. Many of the fish species remaining in the pools are also common in collections of fish returning to the river. Two small fish species were collected in remaining pools on the floodplain although not recorded in migrations: Hemigrammocharax machadoi and Barbus haasianus. They are assumed also to have migrated onto the floodplain.

The results of the fish collections made in the molapo, next to the Zambezi, that was artificially connected to the river and drained, are summarised in Table 4. No less than 39 fish species were observed to make the migration back to the Zambezi. Some of the species that were prominent in migrations into floodplains were notably absent in this collection: B. barnardi, B. fasciolatus, B. multilineatus, B. unitaeniatus, C. wittei, L. lunatus, H. vittatus, M. acutidens, S. nigromaculatus, S. codringtoni, S. angusticeps and S. thumbergi. The fact that this molapo was never filled to a great depth may have prevented the immigration of the larger fish species that prefer deeper water (Bell-Cross and Minshull 1988). Two fish species not collected previously in any

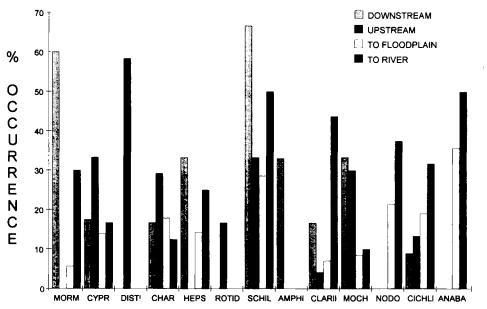


Figure 2. Participation in migration types by fish families in Caprivi, expressed as percentage occurrence in observed migrations.

(MORM = Mormyridae; CYPR = Cyprinidae; DISTI = Distichodontidae; CHAR = Characidae; HEPS = Hepsetidae; ROTID = Claroteidae; SCHIL = Schilbeidae; AMPHI = Amphiliidae; CLARII = Clariidae; MOCH = Mochokidae; NODO = Cyprinidontodae; CICHLI = Cichlidae; ANABA = Anabantidae).

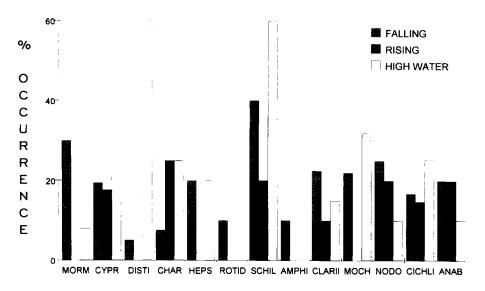


Figure 3. Participation in migration during different phases of the hydrological cycle of the Zambezi River by fish families, expressed as percentage occurrence.

Table 4. Composition of 12 trap collections from a flooded mulapo draining back to the Zambezi River from 21 August to 5 September 1975.

	No. collected	contribution as %	% frequency				
Mormyridae							
M. macrolepidotus	1 057	4.2	66.7				
M. lacerda	8	0.03	16.7				
P. catostoma	214	0.9	66.7				
P. castelnaui	411	1.6	58.3				
Cyprinidae	711	1.0	30.3				
B. afrovernayi	1 030	4.1	50.0				
B. barotseensis	16	0.06	16.7				
B. bifrenatus	1 233	4.9	83.3				
B. multilineatus	18	0.07	33.3				
B. paludinosus	13 520	54.2	83.3				
B. poechii	276	1.1	41.7				
B. radiatus	2	0.01	16.7				
B. thamalakanensis	$\overline{1}$	0.01	8.3				
Distichodontidae							
H. multifasciatus	10	0.04	33.3				
Characidae		3.3 .	22.2				
B. lateralis	2	0.01	16.7				
R. maunensis	14	0.06	25.0				
Hepsetidae	11	0.00	25.0				
H. odoe	25	0.1	16.7				
Claroteidae	23	0.1	10.7				
P. ngamensis	4	0.02	25.0				
Ç	4	0.02	23.0				
Schilbeidae	1.160	4.7	75.0				
S. intermedius	1 169	4.7	75.0				
Clariidae	26	0.4					
C. gariepinus	26	0.1	33.3				
C. ngamensis	128	0.5	50.0				
C. stappersii C. theodorae	6	0.02	25.0				
	107	0.4	50.0				
Mochokidae	124	0.5					
S. woosnami	124	0.5	41.7				
Cyprinodontidae	•	0.01					
A. hutereaui	1	0.01	8.3				
A. johnstonii	60	0.2	33.3				
A. katangae	12	0.05	8.3				
Mastacembelidae	10	0.04	14.				
A. frenatus	10	0.04	16.7				
Cichlidae	_						
H. elongatus	1	0.01	8.3				
O. andersonii	68	0.3	25.0				
O. macrochir	56	0.2	25.0				
P. acuticeps	2 205	0.01	8.3				
P. philander	3 395	13.6	83.3				
S. macrocephalus S. robustus jallae	1 14	0.01	8.3				
T. rendalli	165	0.06	33.3				
T. renaditi T. ruweti	149	0.7 0.6	50.0				
T. sparrmanii	1 347	5.4	33.3 83.3				
Anabantidae	1 347	J. +	83.3				
Anabantidae C. intermedium	9	0.4	25.0				
C. multispine	257	0.4 1.0	25.0 66.7				
o. munispine	431	1.0	66.7				
Total	24 948	100.22	12				

other sampled migration were collected in the trap draining this molapo:

Aplocheilichthys katangae and Aethiomastacembelus frenatus.

The frequencies of occurrence in the migration types differ amongst fish species, with some families or species showing a clear pattern (Figures 2 and 3, Tables 2, 3 and 4).

Apart from the percentage frequency of presence of the recorded species for each fish family presented in Figure 2, the percentage frequency in three recorded hydrological phases of the floods (rising, high water and falling) is shown in Figure 3. As no observations were ever made of fish migrating during the low water phase, it was omitted from Figure 3.

mormyrids were collected in downstream and in one instance in floodplain migrations. Figure 3 implies that movement was recorded mainly during falling water levels. The barbs of the family Cyprinidae were prominent in upstream migrations and well represented in all other types of migrations. They took part in migrations during the rising, high and falling phases. Attention is drawn to the complete absence B. eutaenia, B. lineomaculatus O. zambezense in any lateral movements towards or away from the floodplains. C. wittei, on the other hand, was never collected in any riverine migration and was collected only on the very edge of the floodplain. Labeo spp. took part in especially upstream migrations.

The small distichedontids were well represented in upstream migrations during high water conditions. The characids took part in all types of movement, with A. acutidens prominent in upstream migrations. H. odoe showed migratory movement only downstream and towards the floodplain during the high and falling phases. P. ngamensis of the Claroteidae was collected only in upstream migrations when

the water level was falling.

S. intermedius was common in all types migrations, with the highest representation during downstream migration under highwater conditions. The single amphiliid representative was recorded in downstream migrations only with falling water level. Clariids showed a low frequency in all migrations movements from floodplains back to the river. However, migrations were observed during all stages of water C. stappersii was collected in floodplain migrations only. Of the mochokids, longitudinal migrations were prominent in Synodontis spp., with some lateral activity as well. They were only collected when water levels were either high or falling, rising never in the phase. The cyprinodontids took part movements. A. hutereaui was collected floodplain movements A. johnstonii also showed longitudinal migrations during all phases of water level. Of the cichlids. T. rendalli and T. sparrmanni were the most migratory fish, followed by the smaller P. philander and P. acuticeps. Of the other larger cichlids, only movements from and back to permanent waters were recorded. H. elongatus is an exception and seems to be limited to the rivers as they were only collected in the Zambezi where they took part in longitudinal movements. T. ruweti and both anabantids were collected only floodplain The migrations. movements did however take place during rising, high and falling water levels.

On the basis of the collected data the migrating fish species could be divided into three groups:

- 1. Fish species staying in the river,
- 2. Fish species staying on the floodplain,
- Fish species moving in the river and laterally onto the floodplain.

Lists of fish species are presented in Table 5.

Table 5. Fish species grouped according to migration area.

Group A	Group C						
Fish species staying in the river	Fish species moving in rivers						
H. discorhynchus	and onto floodplains						
B. eutaenia	M. macrolepidotus						
B. lineomaculatus	M. lacerda						
L. cylindricus	P. catostoma						
O. zambezense	P. castelnaui						
H. multifasciatus	B. afrovernayi						
N. macropterus	B. barnardi						
P. ngamensis	B. barotseensis						
A. uranoscopus	B. bifrenatus						
C. neumanni	B. multilineatus						
S. macrostigma	B. paludinosus						
H. elongatus	B. poechii						
	B. radiatus						
Group B	B. thamalakanensis						
Fish species staying on the floodplain	B. unitaeniatus						
B. fasciolatus	L. lunatus						
C. wittei	B. lateralis						
R. maunensis	H. vittatus						
C. stappersi	M. acutidens						
A. hutereaui	H. odoe						
O. andersonii	S. intermedius						
O. macrochir	C. gariepinus						
S. carlottae	C. ngamensis						
S. codringtoni	C. theodorae						
S. giardi	S. leopardinus						
S. angusticeps	S. nigromaculatus						
S. macrocephalus	S. woosnami						
S. robustus	A. johnstonii						
S. thumbergi	P. acuticeps						
T. ruweti	P. philander						
C. intermedium	T. rendalli						
C. multispine	T. sparrmanii						

Discussion and conclusions

Migrations of South African freshwater fish species have been recorded by many authors (Jubb 1953, Bell-Cross 1960, Jackson 1961, Jubb 1967, Pott 1969, Meyer 1974, Pienaar 1979, Bell-Cross and Minshull 1988, Bok 1990, Coke 1990, Merron 1993), but relatively little detailed information is available. Some form of migration amongst our freshwater fishes seems to be quite common; Meyer (1974) reported on the upstream and downstream migration of 28

out of a possible 30 fish species in the Elands River, Central Transvaal as well as 20 out of 33 fish species present in the Letaba River in the Kruger National Park that used the fish ladder at the Engelhardt Dam. Coke (1990) lists breeding migrations of 22 of the 49 freshwater fish species of Natal. In southern Africa, specific fish migrations have been reported for mormyrids (Zambia, Game & Fisheries Dept. 1965b), Labeo species (Bowmaker 1973), H. vittatus

(Bowmaker 1973), *C. gariepinus* (Spinage 1971, Merron 1993) and *O. macrochir* (Zambia, Game & Fisheries Dept. 1965a).

Of the 76 fish species recorded in Caprivi (Van der Waal and Skelton 1990), 63 species took part in some form of migration. The fish species of which no migrating data were collected, can be divided into those that specialists include habitat such H. ansorgii, B. kerstenii (tangandensis), L. dorae, L. rotundiceps, C. platyprosopos, Nothobranchius sp. and A. vanderwaali and a second group of fish species that seem to be present in Caprivi waters in very low B. brevidorsalis (puellus), S. longimanus and S. greenwoodii. All of these mentioned species were collected in low numbers and may also be found to display migratory behaviour.

Larger fish species and especially the commercially important cichlids are underrepresented in the data. This is the result of inefficient collection in deeper moving water of rivers and deeper water bodies where gill nets and seines could not be used effectively (see bottom of Table 2). The presented data should thus be interpreted with care and with due consideration of the selectiveness of gear (Table 2).

Welcomme (1979) divided the fishes of floodplain rivers into:

- Species that migrate upstream to breed and then migrate laterally into the floodplains and later move back with receding flood waters to permanent waters and sometimes show an additional downstream migration;
- species that never move out of the main channel;
- a group of species that stays on the floodplain and breeds there.

This model is not applicable to the Phongolo floodplain in South Africa (White et al 1984) but can be applied to the Upper Zambezi in Caprivi (Table 5). The distinction between floodplain residents and

migrating species is however not so clear as most parts of the floodplains dry out annually and then the surviving fish are all forced into permanent waters on the floodplains. The information in Table 5 is tentative and has to be refined. Special care should be taken in the interpretation of data on larger cichlids as their movements could not be sampled representatively in the deeper rivers.

Upstream fish movement in Caprivi is dominated by non-cichlid species. Jackson (1961, 1989) and Welcomme (1979) maintain that this migration is related to a requirement to spawn in freshly inundated shallow vegetation. The young stay on the floodplain until water levels drop and the fish have to move back to permanent waters. In the Caprivi, observed upstream migrations were distributional rather than breeding migrations. They were recorded during receding water levels only and the fish taking part were mainly non-breeding juveniles.

Bell-Cross (1974, 1976) and Bell-Cross and Minshull (1988) observed juveniles and adult small species moving back to the river with falling water level and then shoaling upriver along the shallow water close to the banks for several weeks until this was terminated by a loss of stimulus to migrate, due to decrease in water velocity or intense predation by predators. In the Zambezi River the observed migration started only days after the highest flood level had been reached in 1975. No massive exodus back to the river had at that time begun. The site of this migration may explain some aspects: Katima Mulilo lies upstream of the 100 km long Caprivi Floodplain (Figure 1) and 180 km downstream of the Central Barotseland Floodplain (Bell-Cross 1974). This upstream fish migration may be a distributional migration relieving temporary high fish population in the floodplain section of the river. A similar downstream fish migration occurs at the lower end of the same Caprivi Floodplain (see Site 1). Cambray (1990) proposed that overcrowding of especially the young fish in the lower, more permanent parts of the river leads to food shortages and that this triggers the juvenile upstream movement. This concept could help to explain both observed upstream and downstream migrations. Escape from intense predation may also play a role (Jackson 1961).

In the Zimbabwean tributaries of the Zambezi, upstream migrations during high water level were observed of small *Barbus* spp, *Labeo* spp, *Clarias* spp., large *Barbus*, and also young *O. mossambicus*, adult *P. acuticeps*, *P. philander* and *T. sparrmanii* (Jubb 1953).

The presented data on movement back to the main channels support the notion that the larger species, including H. vittatus and large Oreochromis and Serranochromis, start moving back when the water levels are still high (Bell-Cross 1974, Sydenham 1977, Bell-Cross and Minshull 1988). These fish species seem to have a high "depth dependency" factor (Bell-Cross 1974) and this partly explains their low frequencies in collections that were mostly made when water levels were generally lower (See Figure 3 and Table 2).

When dividing the observed migrations into the four phases of the hydrological cycle (Figure 3), it was realised that no obvious fish migrations were ever observed during low water conditions.

It is difficult to explain why so many species became stranded in isolated pools in The three fish species the floodplains. singled out by Jackson (1989) as the last to survive in stagnant pools in drying out floodplains or pans, viz. B. paludinosus, C. gariepinus and an Oreochromis species, well represented in the list of remainers (Table 3), but the unexpectedly long, including at least 34 species (Welcomme 1979).

The observations made on young fish colonising temporary pans in flooded mopane forest is comparable to the invasion of immature fish in the Phongolo floodplains that had been dry previously (Merron et al 1985). Similar cichlid fry colonisation of grassed temporary rainpools and timeous return to permanent water has been described from Sudd swamps in Sudan (Hickley and Bailey 1987).

Extensive breeding migrations of O. macrochir as is the case in Lake Mweru (Zambia, Game & Fisheries Dept. 1965a) or large scale migration in cichlids (Williams 1971), were not observed in Lake Liambezi or the Zambezi River. This may be due to the inability to sample large fish movement during high water conditions. Gregarious nesting of S. thumbergi in protected sandy coves of the western part of Lake Liambezi may indicate a local breeding migration by this fish species (Van der Waal 1976).

Substratum selection as described by Holden (1963) in Welcomme (1979) and Welcomme (1986) has not been observed and during longitudinal migrations mixtures of floodplain and strictly riverine fish were evident.

Prominent prebreeding upstream migration with a rising water level, as found in the Niger (Welcomme 1986), was never observed in the Zambezi River, but a similar prebreeding migration has been documented in Lake Kariba where fish congregated at river mouths before the rainy season (Bowmaker 1973). Dry season upstream non-breeding migrations were not recorded in the Caprivi. No large scale feeding migration of predatory fish as the Clarias run in the Okavango Swamps (Merron 1993) was recorded. However, concentrations of predatory fish in the Zambezi River were observed at the end of the flood season and early spring at outlets of drainage channels from the floodplains. This then implies local migrations of H. vittatus, C. gariepinus and S. robustus and S. angusticeps/S. altus.

Migrations of fish species in Caprivi play an important role in the functioning of the floodplain system. Every year the more than 50 km wide floodplain is populated anew from the rivers and isolated inocula in permanent ancient channels (kasaya). Not only do extensive lateral migrations to and from the temporary floodplains take place, but longitudinal movements in rivers play an important role in distribution of fish populations to newly formed habitats on the floodplains (Bell-Cross 1974, Welcomme 1974, 1979). These migrations also form the basis of a traditional fishery on the floodplains (van der Waal 1990). changes to the flood regime caused by factors such as water abstraction. impoundment, canalization and construction of roads on the floodplains can have a serious negative effect on the functioning of this river and floodplain system. Even an increase in the silt load as result of erosion or increase in nutrient load, affecting aquatic vegetation growth and thus water movement, impacts on the migrational patterns of fish. Eventually, fishermen will have to bear the negative effects of such actions. The Upper Zambezi is presently still in a relatively pristine condition. For that reason alone, this system should be better studied to provide a baseline for future manipulations. Extreme care should be taken in the planning of any major development projects, be it intensive agriculture, abstraction of water for the thirsty South or major impoundment. With increasing population pressure in the Zambezi catchment, agricultural projects and increased fishing pressure, it is imperative that further studies of fish migration in this region are undertaken. Fish are a valuable natural resource of this water-rich peninsula of Namibia that can only be managed properly for the benefit of the local fishing people if present and future development is based on sound understanding of the functioning of the system.

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