Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, South West Africa

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ABSTRACT

Aspects of the biology of 27 fish species inhabiting the shallow Lake Liambezi are discussed. Gill and seine nets were used to collect fish over an eighteen month period from five stations in the lake. Length distribution, growth rates, reproduction and food habits are briefly discussed. Variation is found both in breeding strategy (spawning sites, period and behaviour) and also in the wide range of food items utilised, lessening competitive pressure amongst species.

KEY WORDS:

Freshwater fish biology, Zambezi River System, age and growth, reproduction, food habits.

CONTENTS

1 INTRODUCTION

Lake Liambezi lies in the Kwando Linyanti-Chobe River system which flows into the Zambezi River and forms a focus of fishing activities in Caprivi (Figure 1a). The fish life and fisheries of this lake were studied from 1973 to 1976 in order to draw up a management plan for the lake. The limnological characteristics of Lake Liambezi have been described briefly by Seaman, *et al.* (1978) and Van der Waal (1980) described the fisheries and experimental catches of Lake Liambezi.

The present data were collected for background knowledge and are presented here because the general biology of many fish species in the lake is unknown. The results are to a large extent superficial as the study was aimed at providing a broad picture of the ecology of Lake Liambezi rather than detailed information on the biology of the individual species.

2 METHODS

Fish were collected over a period of 18 months using the following seine and gill nets:

Seine nets: 40m long, 3m deep, 25mm stretched mesh and 50m long, 3m deep, 50mm stretched mesh, both with a bag of 3m deep.

GILL NETS:

Mesh size, stretched	Twine thickness	No.	Net length m	No. of nights set
25mm	210/3	1	10,0	60
50mm	210/4	1	21,4	69
60mm	210/4	1	27,3	67
80mm	210/4	1	14,3	56
96mm	210/6	1	32,0	56
100mm	210/6	2	30,5 27,2	56
127mm	210/6	3	43,0 42,0 26,7	176
140mm	210/6	1	80,7	14
160mm	210/9	2	88,3 90,3	35
190mm	210/9	1	87,0	5

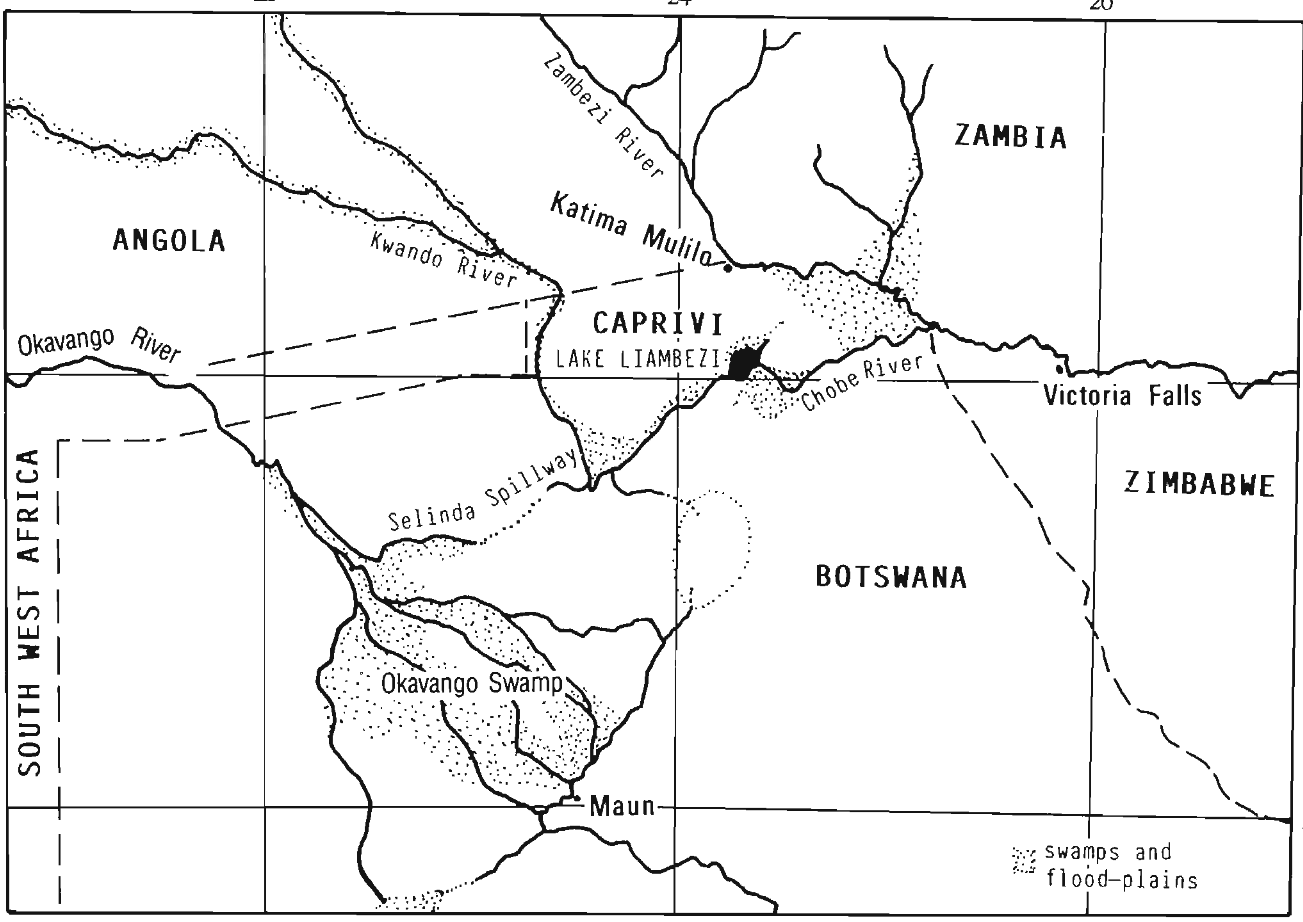
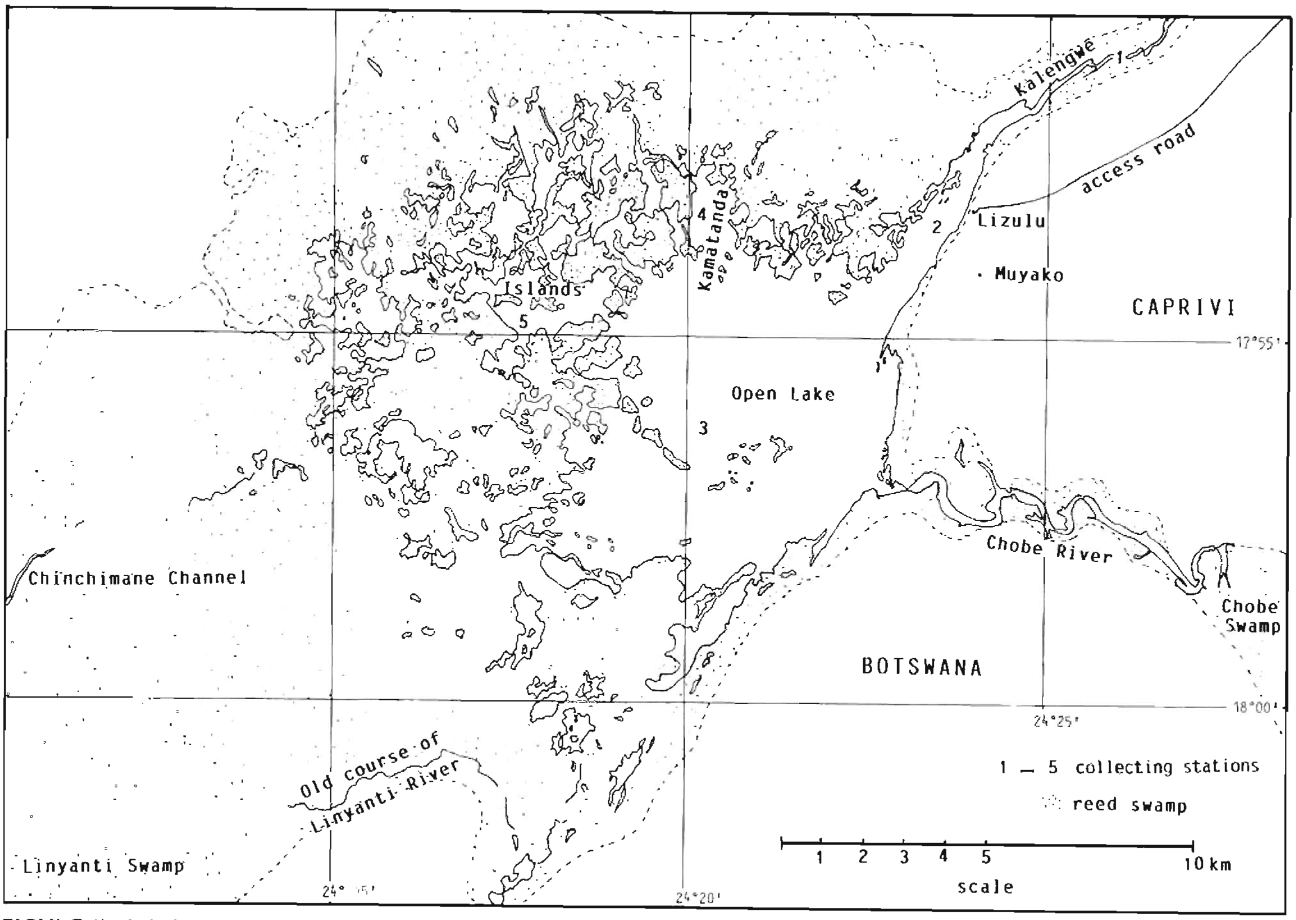


FIGURE 1a: Map of Lake Liambezi, Caprivi.



FIGUKE 1b: Relation of Lake Liambezi to major river systems in Botswana and Zambia.

Gill nets are hung on the half and are 2,0 to 2,5m deep when hung. Gill nets were set in series at 16h00 and lifted at 08h00 at five localities in Lake Liambezi, representing the five main habitat types as indicated in figure 1b. Seine nets could only be used at four sites near the camp at Lizulu where beaches had to be specially prepared for seining. Nets were set out up to 70m from the shore, where the water was up to 3m deep.

Fish were collected every six weeks and the following data collected from each fish: fork or total length (clariids and cichlids) to the nearest mm, mass (g), sex and gonad developmental stage (after Nikolsky, 1963). Stomach contents and ripe ovaries were preserved in 4% formalin. Scales from the dorsal region below the dorsal fin or pectoral spines (scaleless species) were stored in envelopes. A modified projector was used to read scales and an ordinary dissecting microscope to interpret rings on cross-sections of pectoral spines. Sections of 0,2—0,5mm thickness were cut with a hand held 25mm diameter carborundum disk fitted to a dentist drill from the proximal end of the spine,

List of 43 fish species collected in Lake Liambezi.		COLLECTED IN GILL NETS
Mormyridae		
Petrocephalus catostoma (Günther, 1866)	churchill	X
Marcusenius macrolepidotus (Peters, 1852)	bulldog	X
Mormyrus lacerda Castelnau, 1861	western bottlenose	X
Characidae		
Hydrocynus vittatus (Castelnau, 1861)	tigerfish	X
Alestes lateralis Boulenger, 1900	striped robber	X
Rhabdalestes maunensis (Fowler, 1935)	Okavango robber	
Hepsetidae		
Hepsetus odoë (Bloch, 1794)	African pike	X
Cyprinidae		
Barbus poechii Steindachner, 1911	dashtail barb	X
Barbus paludinosus Peters, 1852	straightfin barb	
Barbus multilineatus Worthington, 1933	copperstripe barb	
Barbus unitaeniatus Günther, 1866	longbeard barb	
Barbus bifrenatus Fowler, 1935	hyphen barb	
Barbus barotseensis Pellegrin, 1920	Barotse barb	
Barbus barnardi Jubb, 1965	blackback barb	
Barbus radiatus Peters 1853	Beira barb	
Coptostomabarbus wittei David & Poll, 1937	upjaw barb	
Labeo lunatus Jubb, 1963	Upper Zambezi labeo	
Clariidae		
Clarias gariepinus (Burchell, 1822)	sharptooth catfish	X
Clarias ngamensis Castelnau, 1861	blunttooth catfish	X
Clarias theodorae Weber, 1897	snake catfish	
Schilbeidae		
Schilbe mystus (Linnaeus, 1762)	silver catfish	X
Mochokidae		
Synodontis nigromaculatus Boulenger, 1905	spotted squeaker	X
Synodontis woosnami Boulenger, 1911	Upper Zambezi squeaker	X
Synodontis macrostigma Boulenger, 1911	largespot squeaker	X
Synodontis leopardinus Pellegrin, 1914	leopard squeaker	X
Cyprinodontidae		
Aplocheilichthys johnstonii (Günther, 1893)	Johnston's topminnow	
Aplocheilichthys hutereaui (Boulenger, 1913)	trellised topminnow	
Cichlidae		
Oreochromis macrochir (Boulenger, 1912)	greenhead tilapia	X
Oreochromis andersonii (Castelnau, 1861)	threespot tilapia	X
Tilapia sparrmanii Smith, 1840	banded tilapia	X
Tilapia rendalli rendalli (Boulenger, 1896)	northern redbreast tilapia	X
Tilapia ruweti (Poll & Thys, 1965)	Okavango tilapia	
Serranochromis (Sargochromis) giardi (Pellegrin, 1904)	pink happy	X
Serranochromis (Sargochromis) codringtoni (Boulenger, 1908)	green happy	X
Serranochromis (Sargochromis) carlottae (Boulenger, 1905)	rainbow happy	X
Pharyngochromis darlingi (Boulenger, 1911)	Zambezi happy	X
Serranochromis (Serranochromis) robustus jallae (Boulenger, 1896)	nembwe	X
Serranochromis (Serranochromis) macrocephalus (Boulenger, 1899)	purpleface largemouth	X
Serranochromis (Serranochromis) longimanus (Boulenger, 1911)	longfin largemouth	X
Serranochromis (Serranochromis) angusticeps (Boulenger, 1907)	thinface largemouth	X
Serranochromis (Serranochromis) thumbergi (Castelnau, 1861)	brownspot largemouth	X
Pseudocrenilabrus philander (Weber, 1897)	southern mouthbrooder	X
Anabantidae		
Ctenopoma multispinis Peters, 1844	manyspined climbing perch	X

where the lumen starts becoming closed. Glycerine and indirect light helped to obtain contrast (Gaigher, 1969). A scale or section was read at least three times and discarded if readings did not agree.

Stomach contents were sorted into components in a petri dish and a rank value given to each item according to relative volume and frequency of occurrence.

3 RESULTS

3.1 Species analysed

The following 43 fish species were collected in Lake Liambezi of which 27 grow large enough to be caught in the experimental gill nets (25—190mm stretched mesh) and for which biological data were collected. The smaller fish species are also of economic importance and are widely caught by traps and baskets on the flood plains of the Zambezi, Chobe and Linyanti Rivers where they are used for consumption or dried for barter on the cash market at Katima Mulilo.

3.2 Length frequency distribution

The length frequency distributions of all fish that were collected with gill nets are represented in figure 2. As the nets used were of different lengths, all the results are expressed per 50m of hung net length (100m stretched). Apart from the small fish species, *P. catostoma, A. lateralis, B. poechii* and *P. darlingi*, the

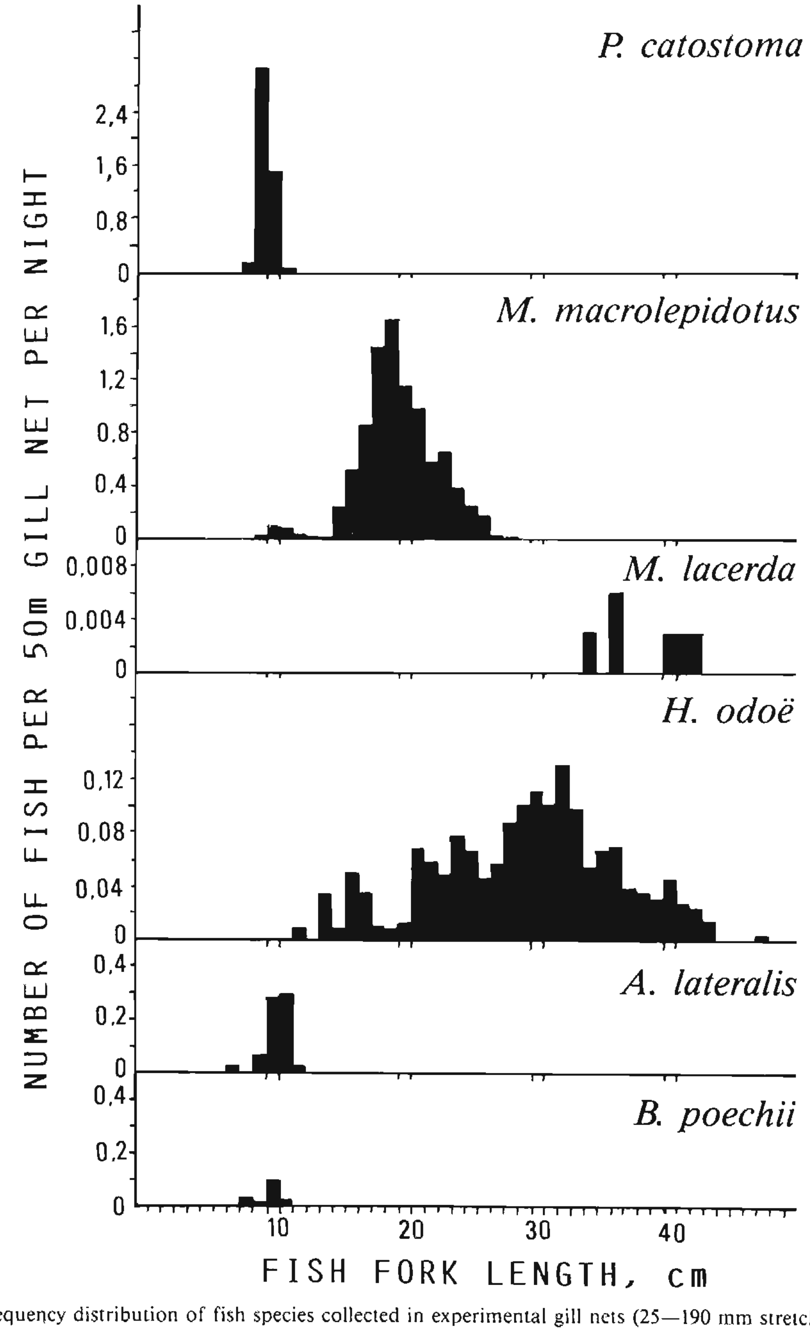


FIGURE 2: Length frequency distribution of fish species collected in experimental gill nets (25—190 mm stretched mesh) in Lake Liambezi.

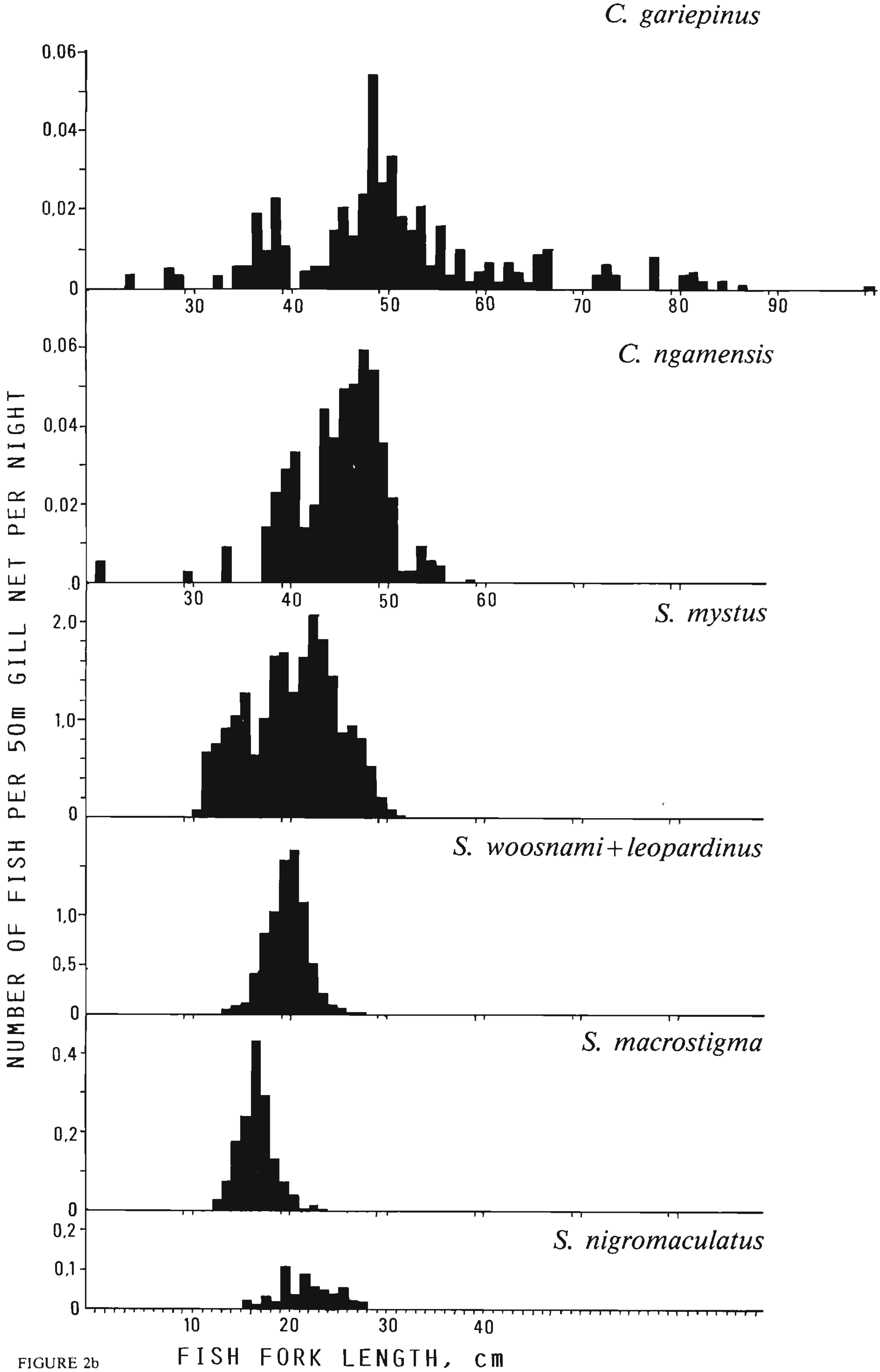

C. gariepinus
0,06
0,04
0,02
0
30
40
50
60
70
80
90
C. ngamensis
0,06
0,04
0,02
0
30
40
50
60
S. mystus
2,0
1,0
0
S. woosnami+leopardinus
1,0
0,5
0
S. macrostigma
0,4
0,2
0
S. nigromaculatus
0,2
0,1
0
10
20
30
40
NUMBER OF FISH PER 50m GILL NET PER NIGHT
FISH FORK LENGTH, cm

FIGURE 2b

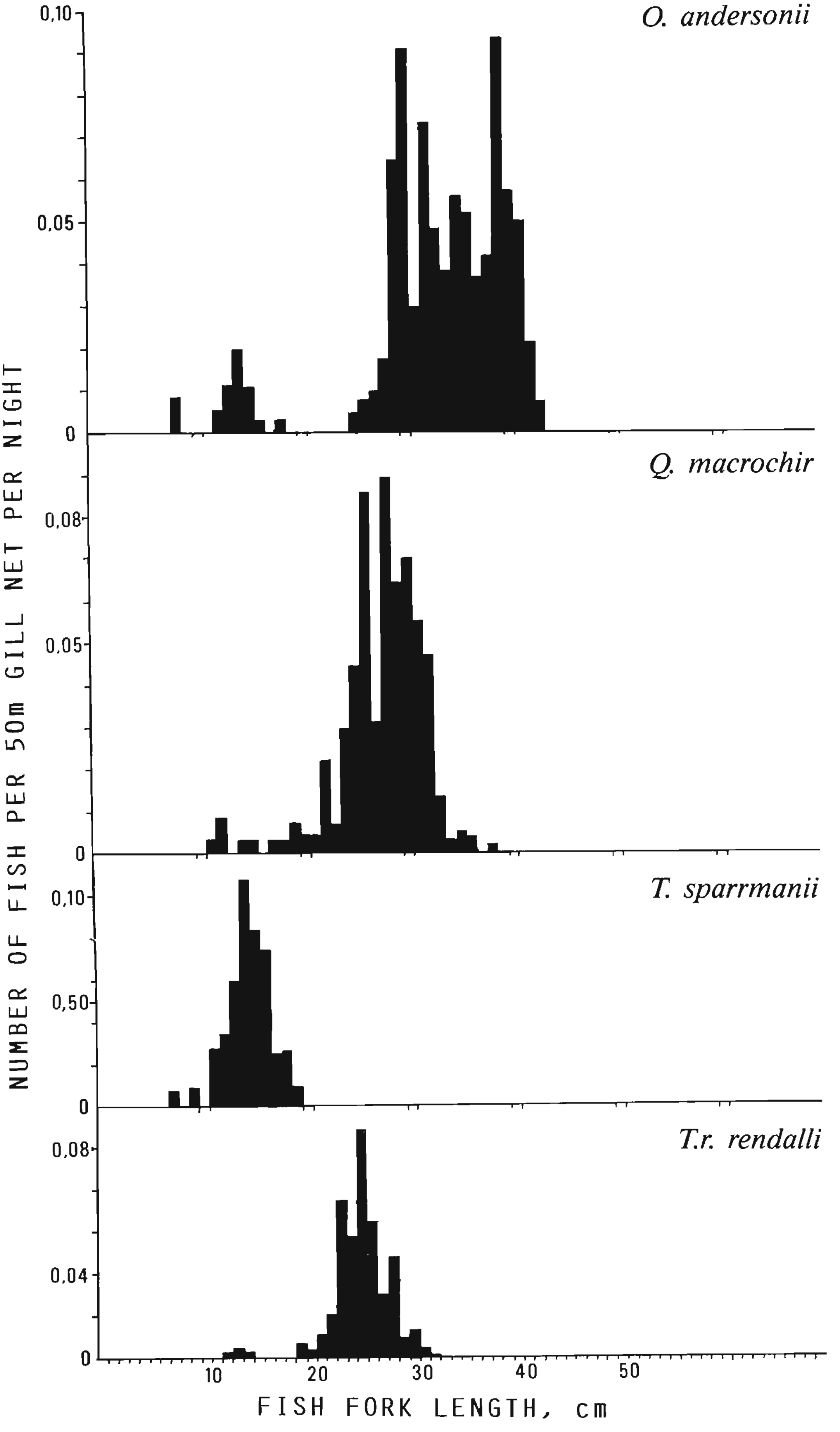

O. andersonii
Q. macrochir
T. sparrmanii
T.r. rendalli
0,10
0,05
0
0,08
0,05
0
0,10
0,50
0
0,08
0,04
0
NUMBER OF FISH PER 50m GILL NET PER NIGHT
10
20
30
40
50
FISH FORK LENGTH, cm

FIGURE 2c

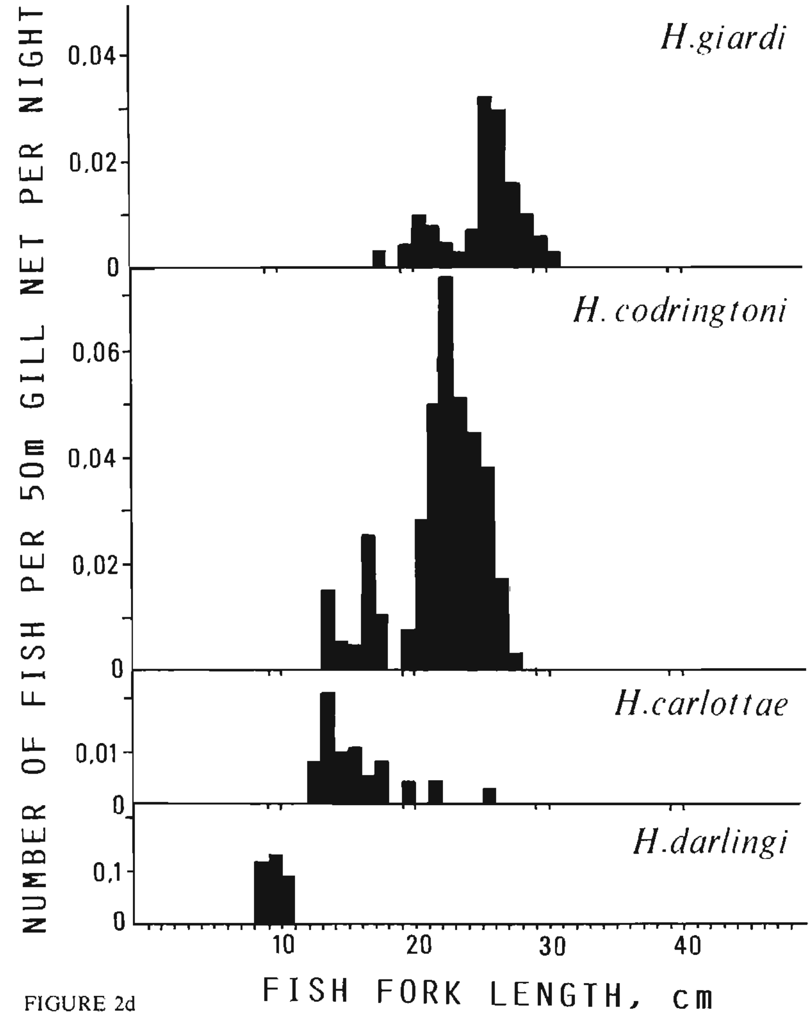


FIGURE 2d

series of gill nets covered the whole size range of most fish species and nets do also overlap sufficiently in their catching ability and size selectivity to be able to catch a representative sample of the fish populations, provided there are no other factors affecting efficiency of gill nets (of which there are many, unfortunately) (Hamman, 1981).

It was found in Lake Liambezi that gill nets might indeed offer a more representative sample than seine net results, as many of the dominant smaller fish species in gill net catches were just not collected in the seine net catches (Table 1), possibly as result of the behaviour of these fish species and the limited area that could be sampled by seine nets (Van der Waal, 1980).

Figure 2 shows that most fish species have a normal length frequency distribution but with a prominent lack in numbers of smaller size groups, that cannot be attributed to small effort by smaller mesh gill nets as all gill nets were treated per unit length. This phenomenon will be further commented on under growth and reproduction.

3.3 Age and growth

Caprivi lies well within the tropics but there are marked differences between summer and winter temperatures. The mean winter water temperature of Lake Liambezi (based on daily readings) during July 1973 and 1974 was 17,25°C and 18,3°C respectively. The hottest month in 1973 was November with a mean water temperature of 26,2°C and February 1975 with a mean water temperature of 27,4°C. The seasonal difference is thus nearly 10°C. In all fish species studied, clear checks could be identified on scales with typical overcutting and wider spaces between circuli on the outside annuli indicating a faster growth rate. On sections of pectoral spines clear rings could be identified. These checks and rings are accepted to represent annuli (Ricker, 1968; FAO, 1969; Batchelor, 1974; Bruton and Allanson, 1974; Potgieter, 1974; Hecht, 1980) and the age of fish is indicated as 0+, 1+, 2+ etc. where an annulus or check indicates one winter. A fish of 1+ year group can thus be one or two growth seasons old. Table 2 and figure 3 show that the growth rates in length of most fish species are higher during the young stages, and then decrease in older age groups. In almost all fish species the growth rate decreases at maturity length as is shown in Table 3.

As soon as the fish reach sexual maturity, growth slows down as energy is then also spent on the production of ova and sperm as well as sexual behaviour. The rapid growth of juveniles could also be attributed to

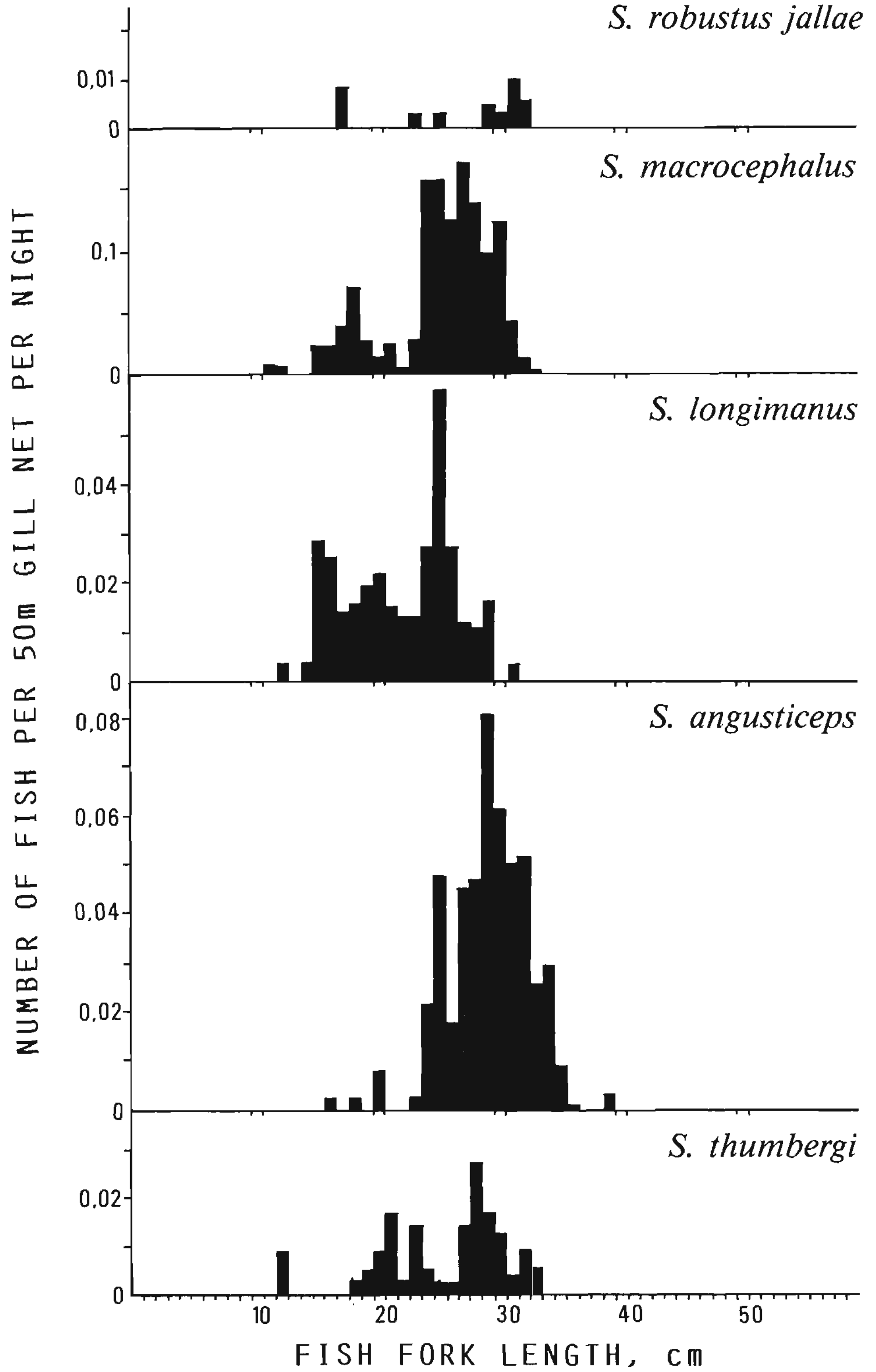


FIGURE 2e

a response to predation pressure of *H. vittatus* as has been shown by Jackson (1961). It should also be noted that very few immature fish were collected with the experimental series of gill nets (Figure 2), reflecting different behaviour patterns in immature fish which prefer vegetated areas and seem to avoid open water where nets were set and where adult fish were caught.

The only species where a relatively high growth rate is maintained in older age groups, are *H. odoë*, *C. gariepinus* and *S. robustus jallae*. These fish species also grow to a great length (see Figure 3). *O. andersonii* and *O. macrochir* reach lengths comparable to that of *H. odoë* but take much longer. Based on maximum age reached the fish species studied can be divided into groups: fish with a relatively high growth rate but short life span: *H. odoë*; fish with a high growth rate and long life span: *C. gariepinus*. Another group of fish have relatively slower growth but long life-span:

TABLE 1: Percentage composition of seine and gill net catches in Lake Liambezi from Nov. 1973 to May 1975.

Fish species	Collection gear used		
	Seine net 25 mm mesh	Seine net 50 mm mesh	Mean of gill net catches 25-190 mm mesh
	n = 2157	n = 6725	n = 15014
P. catostoma	—	—	11,6
M. macrolepidotus	—	0,01	19,3
M. lacerda	—	—	0,02
H. vittatus	—	0,02	0,02
H. odoë	1,4	3,6	2,9
A. lateralis	7,3	0,1	2,1
B. poechii	1,8	0,1	0,9
C. gariepinus	0,1	0,1	0,7
C. ngamensis	0,1	0,2	0,8
S. mystus	—	0,1	32,9
S. woosnami +	—	0,1	13,9
S. leopardinus			
S. macrostigma	—	0,04	2,6
S. nigromaculatus	—	—	1,1
D. macrochir	16,6	60,6	1,1
O. andersonii	3,9	6,6	1,3
T. sparrmanii	5,9	1,6	0,9
T. r. rendalli	15,3	7,1	0,8
S. giardi	0,6	0,3	0,3
S. codringtoni	2,2	3,4	0,9
S. carlottae	2,4	1,1	0,1
P. darlingi	35,2	4,8	2,2
S. robustus jallae	0,1	0,2	0,02
S. macrocephalus	3,1	3,5	2,7
S. longimanus	1,5	2,9	0,6
S. angusticeps	1,3	1,8	0,9
S. thumbergi	1,1	2,2	0,3
P. philander	0,1	—	—

TABLE 2: Length frequency distribution of year groups of fish species collected from Lake Liambezi.

M. macrolepidotus

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11										
12										
13	1									
14	3									
15	17	2								
16	14	7	1							
17	8	3	4							
18	2	13	6	1						
19		18	22	2						
20		5	29	7	3					
21		2	35	19	1					
22		1	20	22	4	1				
23			13	34	16	1				
24		1	5	16	11	2				
25			1	5	4	2				
26				2	7	1	1			
27					1	1				
28							1			

M. lacerda

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
35										
36					1					
37										
38					1					
39					1					
40							1			
41						1				
42						1	1			
43										
44										
45										

C. gariepinus

Length group cm \ No. of rings	0	1	2	3	4	5	6	7	8	9
20										
22	1	1								
24										
26										
28										
30										
32	1									
34										
36	1									
38	1	3								
40		2		1						
42			2							
44	1	1								
46		1	1							
48		4	1	2						
50		4	3	1	1					
52		1	2	1						
54		4	1	1						
56			2	3						
58			4	3		1				
60				7	2					
62		1		1						
64				1						
66				1	1					
68					1	1				
70										
72					1	3				
74					1			1		
76						1				
80							1			
82					1	2				
84										
86					1	3				
88						1				
90							2			
92							2		1	
94									1	
96										
98										
100										
102								1		
104										
106										
108									1	
110										

TABLE 2 continued

C. ngamensis

Length group cm \ No. of rings	0	1	2	3	4	5	6	7	8	9
40		2								
41		1	1							
42			4							
43										
44				5	1					
45			1	2	1					
46				4	1					
47				4						
48				3	2					
49			1	4	3					
50				2		1	1			
51										
52										
53										
54					1					
55					1					
56										
57										
58										
59					1					
60										

O. macrochir

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
8	1									
9	3									
10	9									
11	5	2								
12	10	2								
13	10	4								
14	7	8	1	1						
15	3	9								
16	2	10	1	3						
17	1	22	2	3						
18		11	4							
19		4	4	1						
20		1								
21			2							
22										
23										
24				3						
25			1	9						
26			3	14	3					
27		1	1	27	1					
28				28	7					
29				31	9					
30				28	20	1				
31				9	12	1				
32				10	27	4				
33					10	5				
34					17	12	2	1		
35					5	16	6			
36					2	22	11			
37						2	8	2		
38							9	8	1	
39								2	4	

S. mystus

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
19		1								
20		1								
21			1	1						
22			4	2						
23			4	5	3	1				
24			4	8	2	2				
25			4	13	5	1				
26			2	15	5	1				
27			1	9	4	1				
28			2	12	11	3				
29				4	3	1				
30				2	3	1				

TABLE 2 continued

O. andersonii

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10	1									
11	3									
12	4	1								
13	12	1								
14	4									
15	5	1								
16	2	1								
17										
18		1								
19										
20		1								
21										
22										
23										
24										
25										
26										
27										
28		1	1	1						
29		2	2							
30			13	4						
31		1	20	6	1					
32			17	13						
33			12	18	5					
34			2	16	10					
35				14	14	1				
36				9	9	2				
37				3	10	5				
38			1		8	6	1			
39				1	5	12	3			
40				1	2	8	4	1		
41					1	16	8			
42							3	2		
43						2	3	1	1	
44								1		
45							1			

S. codringtoni

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11		1								
12	2									
13	1	1								
14		1								
15			1							
16			1	1						
17				1						
18			1	1						
19				1						
20				4	2					
21			2	1						
22				3		1				
23				2	5	2				
24					4	1				
25					7	8				
26					6	7	2			
27						5	1			
28								2		
29								1		
30										

T. sparrmanii

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
5										
6										
7										
8		1								
9	1	2								
10	1	1	2							
11		1	3							
12		2	3							
13			3	3						
14			1	6						
15			1	7	6					
16				4	6					
17				1	6	1				
18					1	4				

T.r. rendalli

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10	3									
11	4									
12	7	1								
13	6	3	1							
14	4	6	1							
15		7	3							
16		3	4	1						
17		1	3							
18			2							
19			1	1						
20			1	3						
21				3	2					
22			2	5	3					
23				8	9	1				
24			1	11	10	2	1			
25				7	16	4	1			
26				8	14	3				
27				2	9	7	1			
28					6	6				
29					5	5	4			
30							3			
31					1	2	3	3		
32								1		
33										
34								1		

TABLE 2 continued

S. giardi

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
18			1	2						
19					1					
20										
21				1	1					
22					2					
23					1	1				
24					1					
25					1	3				
26				1		3	2			
27					2			1		
28						2		1		
29						1				
30										
31										
32										
33								1		
34										

S. carlottae

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11		1								
12		6		1						
13			6							
14		3	4	2						
15			2	2						
16			1	1						
17				2	2					
18										
19				1	1	3				
20							1			
21					1					
22						2	1			
23										
24						1				
25										
26							1			
27										
28										
29										
30										

S. robustus jallae

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11										
12										
13										
14	1									
15	1									
16										
17		1								
18										
19										
20										
21										
22										
23										
24										
25										
26										
27					1					
28										
29										
30					1	1				
31										
32						1				
33										
34										
35							1			

S. macrocephalus

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
5										
6										
7										
8										
9	1									
10										
11										
12										
13	1									
14	2									
15	1	1								
16	3									
17	1	3								
18		5								
19				1						
20			2							
21		4	2							
22		1	4	2						
23				4	1					
24		1	2	8	3					
25			1	17	2					
26			1	11	6					
27				6	18					
28				3	18	6				
29				4	10	10	1			
30					6	16	3			
31						4	2			
32						1	1		1	
33										
34										
35										

TABLE 2 continued

S. angusticeps

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11										
12										
13										
14		1								
15	2	1								
16		1								
17		1								
18		1								
19										
20			1							
21			1							
22		1								
23			1							
24		1	1							
25				5						
26			3	2	1					
27			1		1					
28				4	4					
29				2	4					
30				3	7	2				
31				1	7	2				
32				2	8	6				
33					4	3	1			
34					2	1	2	1		
35					1	1	1	1		
36						1		1		
37										
38										
39										
40										
41									1	
42										

S. thumbergi

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11										
12										
13										
14	2									
15	2									
16	5	2								
17	1	6	1							
18		6	3							
19	1	6	1							
20			4							
21		2	4							
22		1	9							
23			5	1						
24				4						
25			1	2						
26			1	4						
27				4	1					
28				4	1					
29					3	1				
30					4	3				
31					6					
32					3	2	1			
33					1	2				
34										
35										

S. longimanus

Length group cm \ Year group	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
10										
11										
12										
13										
14		2								
15		1								
16		2	4							
17		3	2							
18		3	1	2						
19		2	7	2						
20			11	9	2					
21	1		7	3	2					
22			2	4						
23			1	3	2					
24				1	4					
25					6	4				
26					5	2				
27				1	1	3				
28							1			
29						1				
30								1		

TABLE 3: Lengths at which fish species of Lake Liambezi reach maturity.

Fish species	50 per cent of fish collected	Min. length males	Min. length females	Max. immature length
M. macrolepidotus	14	13	15	15
H. odoë	27	18	20	27
C. gariepinus	37	27	30	37
C. ngamensis	39	35	30	38
S. mystus	16	12	14	18
S. woosnami	—	< 14	< 14	—
S. macrostigma	—	< 13	< 13	—
S. nigromaculatus	—	< 16	< 16	—
O. macrochir	20	14	15	20
O. andersonii	26	16	26	21
T. sparrmanii	10	7	8	15
T. r. rendalli	14	11	13	17
S. giardi	17	15	18	18
S. codringtoni	16	13	14	22
S. carlottae	12	12	10	16
P. darlingi	8	8	7	10
S. macrocephalus	15	13	14	20
S. angusticeps	18	17	18	22
S. longimanus	15	14	14	20
S. thumbergi	17	14	15	21

TABLE 4: Maximum lengths of fish species collected in Lake Liambezi compared with those of the Barotse Flood Plain, FAO (1968, 1969).

Fish species	Lake Liambezi Max. length, cm	Barotse Flood Plain Max. length, cm
P. catostoma	12	—
M. macrolepidotus	29	26
M. lacerda	42	41
H. vittatus	64	66
H. odoë	47	40
A. lateralis	12	—
B. poechii	11	—
C. gariepinus	120	100
C. ngamensis	59	74
S. mystus	33	29
S. woosnami + *S. leopardinus*	28	25
S. macrostigma	24	—
S. nigromaculatus	28	31
O. macrochir	39	48
O. andersonii	43	50
T. sparrmanii	19	22
T. r. rendalli	32	40
S. giardi	31	48
S. codringtoni	28	32
S. carlottae	26	34
P. darlingi	11	—
S. robustus jallae	32	45
S. macrocephalus	33	43
S. longimanus	31	—
S. angusticeps	41	48
S. thumbergi	33	—

M. macrolepidotus, and most cichlids with life-spans of up to 9+ years. Fish with a shorter life-span and slow growth, include: *C. ngamensis, S. mystus* and *T. sparrmanii.* Due to insufficient data no conclusions can be reached on the other species in this respect.

Table 4 compares maximum lengths of fish species collected in Lake Liambezi to those of the same species collected from the Barotse Flood Plain, Zambia, 150km north west of Caprivi, using a fleet of 37—150mm stretched mesh gill nets (FAO, 1968, 1969). There is agreement for most species with the exception of *C. ngamensis, O. macrochir, O. andersonii, T.r. rendalli, S. giardi* and *Serranochromis (Sargochromis)* spp. which grow to a larger size on the Barotse Flood Plain. Observations on these species collected in the Zambezi River and its flood plains in Caprivi, sub-

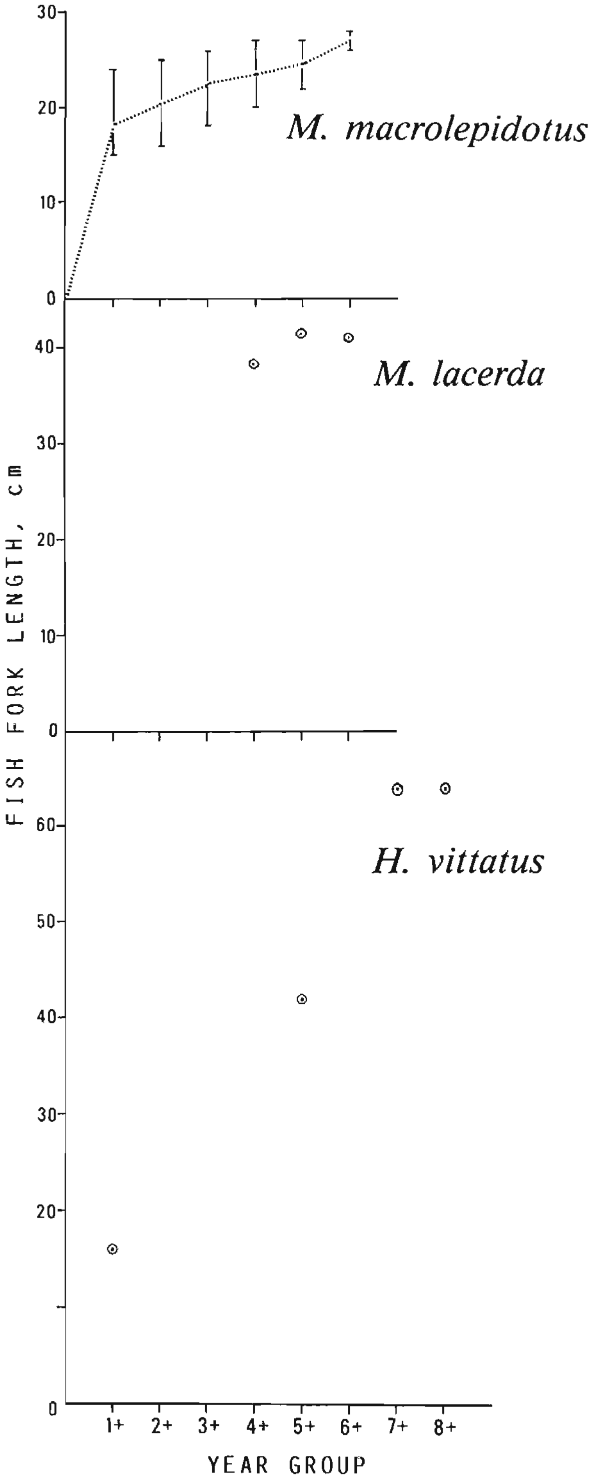


FIGURE 3: Empirical growth curves of fish species (with span indicated) based on age determinations.

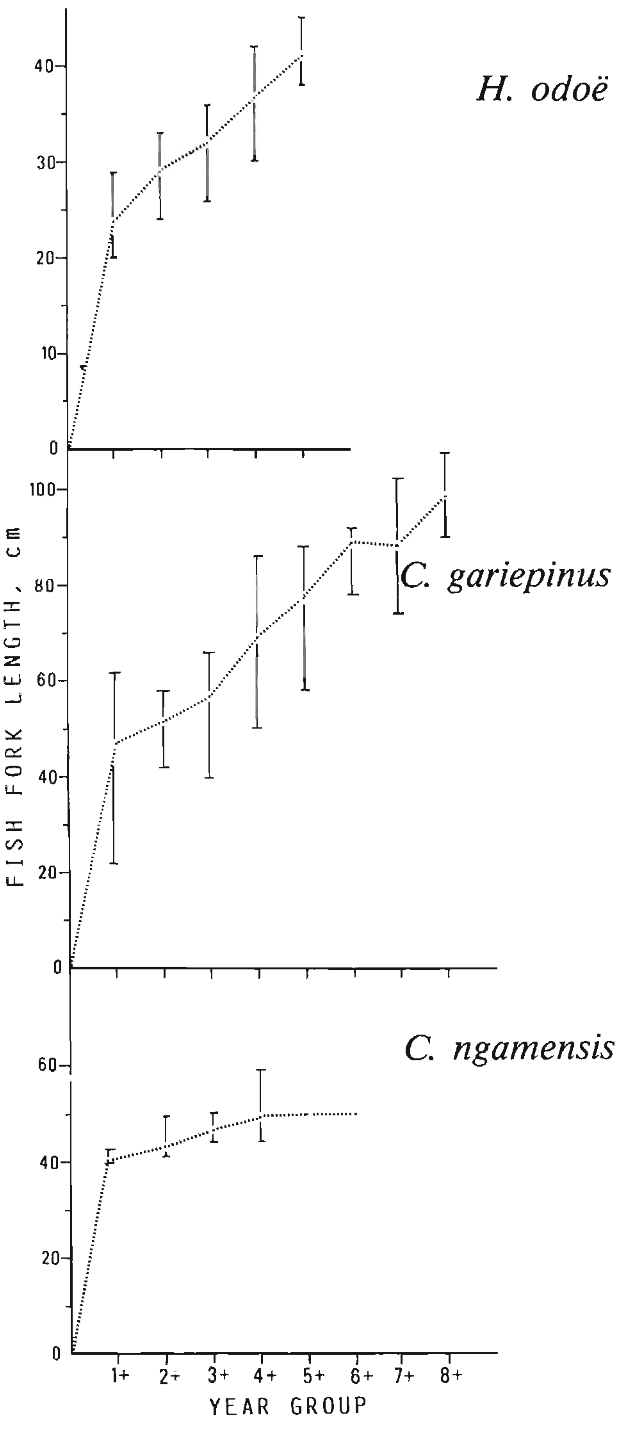


FIGURE 3b

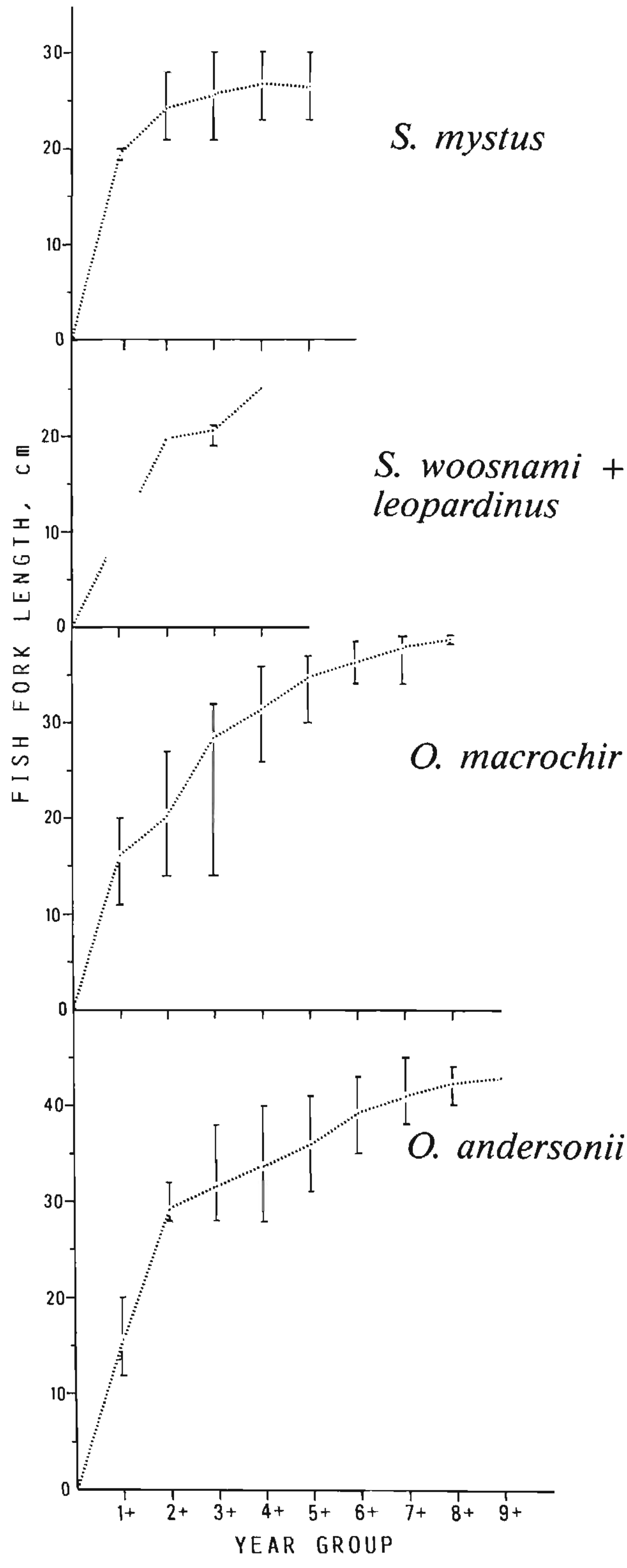


FIGURE 3c

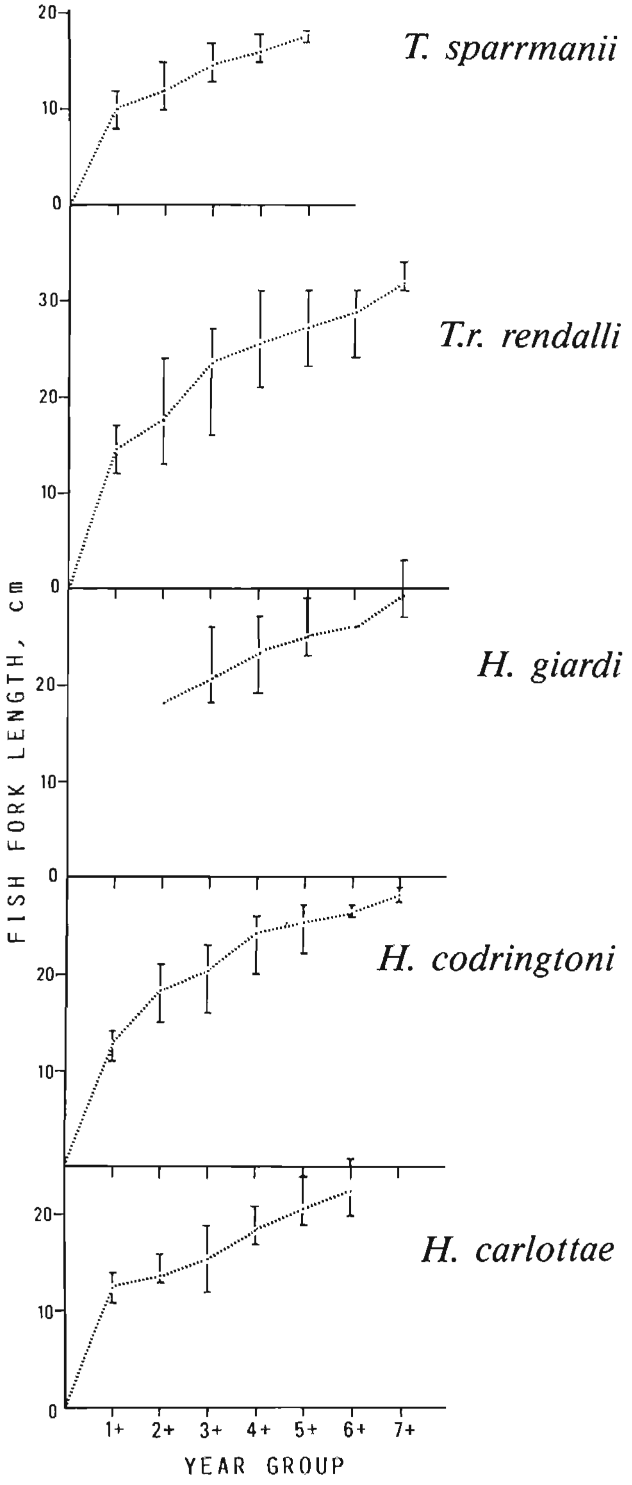


FIGURE 3d

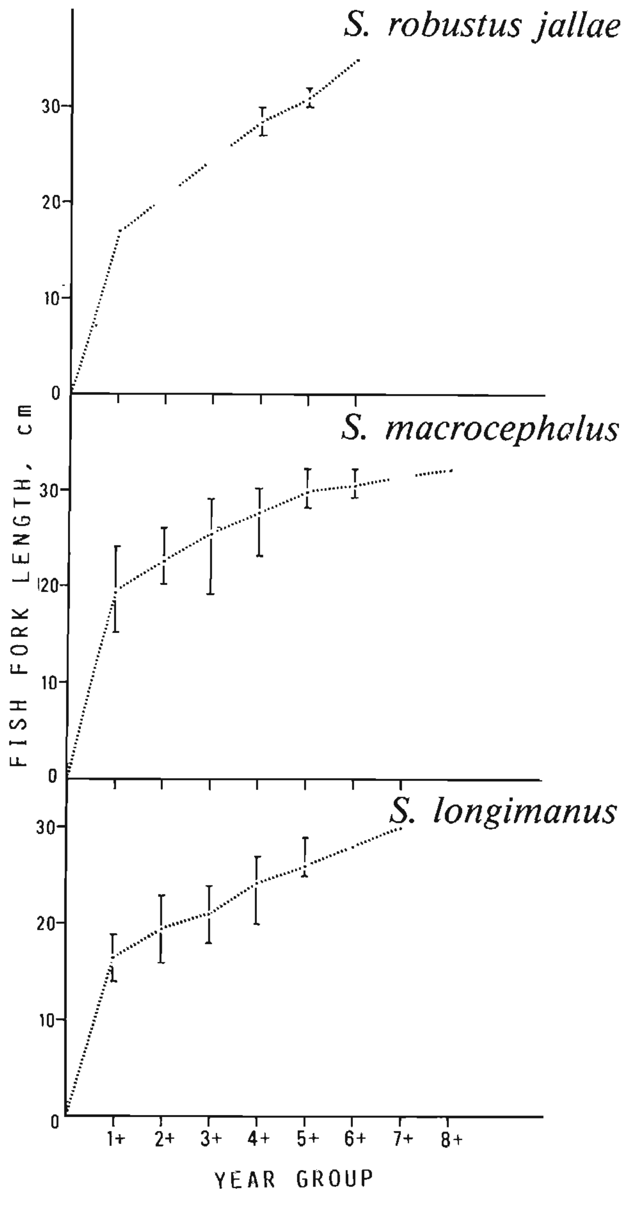


FIGURE 3e

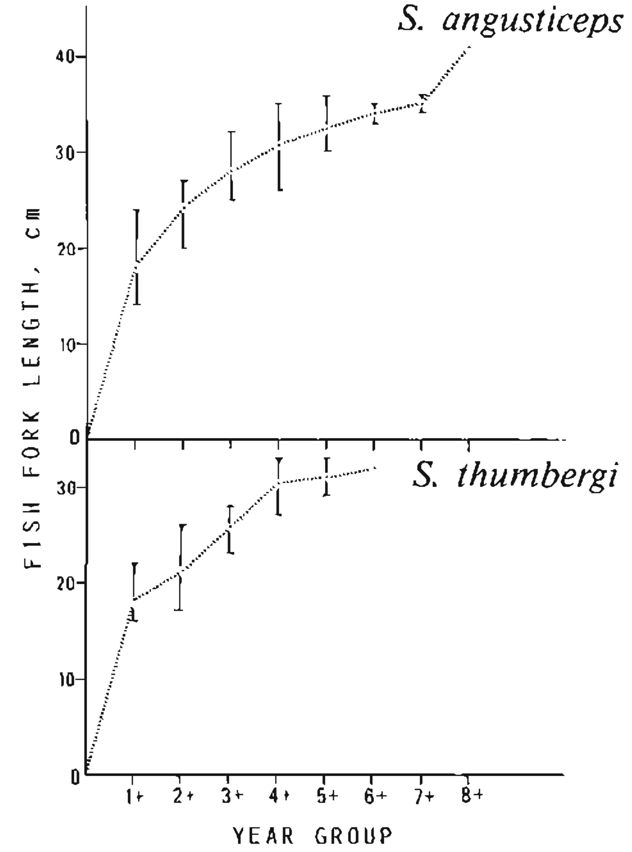


FIGURE 3f

stantiate these findings. Environmental conditions in the lake may therefore not be optimal for these species.

Where enough material was available, growth of males and females is presented separately in Table 5.

The fish species of Lake Liambezi may conveniently be divided into groups, according to the relative growth rate of males and females. *M. macrolepidotus, C. ngamensis, O. andersonii, S. macrocephalus* and *S. angusticeps* are species where males show a higher growth rate than females. The opposite situation is found with *H. odoë* and *S. mystus* while no clear trends can be deducted from the growth curves of *Clarias gariepinus, O. macrochir, Tilapia* spp., *S. codringtoni, S. carlottae, S. longimanus* and *S. thumbergi.*

When the length frequency distribution of sexes (Figure 4) and maximum age are compared, a picture on differential growth is obtained. The following fish species have more males than females of larger lengths: *M. macrolepidotus, C. ngamensis, O. macrochir, O. andersonii, T. sparrmanii, T.r. rendalli, S. giardi, S. codringtoni, S. carlottae* and also all *Serranochromis (Serranochromis)* spp.. The opposite situation is found in *H. odoë, S. mystus, S. woosnami/leopardinus, S. macrostigma* and *S. nigromaculatus.* Apart from growing faster and being

TABLE 5: Mean lengths of age groups of males and females of fish species collected in Lake Liambezi.

Age Group	Sex	Fish species									
		M. macrolepidotus	Number	*H. odoe*	Number	*C. gariepinus*	Number	*C. ngamensis*	Number	*S. mystus*	Number
0+	M	16,00	24	—	—	—	-	—	—	—	—
	F	16,36	11	—	—	—	—	—	—	—	—
1+	M	18,20	19	23,29	7	47,00	4	40,50	2	—	—
	F	18,71	31	24,60	5	49,63	16	40,00	1	19,50	2
2+	M	21,27	55	29,25	28	51,50	8	44,33	3	23,00	9
	F	20,21	82	29,71	17	51,71	7	42,50	4	24,90	14
3+	M	23,07	60	30,62	26	57,27	11	47,33	15	24,80	20
	F	21,65	49	32,56	72	55,66	10	46,00	8	26,38	52
4+	M	24,00	33	30,50	2	68,67	6	49,13	8	25,13	8
	F	22,44	12	37,18	34	68,67	3	47,00	2	27,17	29
5+	M	24,83	6	—	—	73,50	4	50,00	1	24,40	5
	F	23,50	2	41,25	12	78,86	7	—	—	28,33	6
6+	M	27,00	2	—	—	91,00	2	—	—	—	—
	F	—	—	—	—	87,33	3	50,00	1	—	—
7+	M	—	—	—	—	87,00	2	—	—	—	—
	F	—	—	—	—	—	—	—	—	—	—
8+	M	—	—	—	—	93,00	2	—	—	—	—
	F	—	—	—	—	108,00	1	—	—	—	—

TABLE 5 cont.

Age Group	Sex	Fish species																			
		O. macrochir	number	*O. andersonii*	number	*T. sparrmanii*	number	*T. r. rendalli*	number	*S. codringtoni*	number	*S. carlottae*	number	*S. macrocephalus*	number	*S. longimanus*	number	*S. angusticeps*	number	*S. thumbergi*	number
0+	M	—	—	—	—	—	—	13,75	4	—	—	—	—	—	—	—	—	—	—	—	—
	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1+	M	19,78	9	—	—	12,00	1	15,20	10	—	—	12,20	5	18,40	5	17,50	4	20,25	4	18,33	15
	F	18,00	2	—	—	8,87	3	15,00	1	14,00	2	13,50	2	21,00	4	17,17	6	—	—	18,80	5
2+	M	22,00	3	—	—	13,00	4	16,50	10	18,00	3	13,86	7	23,00	7	19,14	7	25,00	5	21,25	16
	F	26,00	3	29,67	3	12,17	6	22,00	3	18,00	5	13,75	4	22,00	3	19,17	24	22,67	3	21,80	10
3+	M	28,75	62	32,22	18	14,88	16	23,00	21	20,00	7	16,00	5	26,24	25	21,20	10	28,20	5	25,20	5
	F	28,15	94	31,13	46	14,50	4	24,11	27	21,06	16	14,00	3	24,68	31	20,77	13	27,77	13	26,25	12
4+	M	31,89	82	34,29	48	16,30	10	25,75	36	24,43	23	17,00	2	27,96	45	24,30	10	31,60	15	30,62	13
	F	30,21	28	32,79	38	15,86	7	25,05	38	24,00	30	21,00	1	26,33	18	24,00	12	30,21	24	29,83	6
5+	M	34,84	56	36,58	40	17,75	4	27,43	21	26,05	20	20,20	5	29,69	29	25,86	7	32,00	7	31,75	3
	F	33,86	7	35,08	25	18,00	1	26,33	9	25,23	26	—	—	29,29	7	27,00	3	32,67	9	30,50	4
6+	M	36,44	34	39,54	46	—	—	29,43	7	26,75	4	22,67	3	30,43	7	28,00	1	34,50	2	32,00	1
	F	36,50	2	38,33	6	—	—	28,17	6	27,25	4	—	—	—	—	—	—	33,50	2	—	—
7+	M	37,69	13	41,00	22	—	—	32,00	4	28,50	2	—	—	—	—	30,00	1	—	—	—	—
	F	—	—	41,00	1	—	—	31,00	1	28,00	1	—	—	—	—	—	—	35,00	3	—	—
8+	M	38,80	5	42,20	5	—	—	—	—	—	—	—	—	32,00	1	—	—	41,00	1	—	—
	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9+	M	—	—	43,00	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

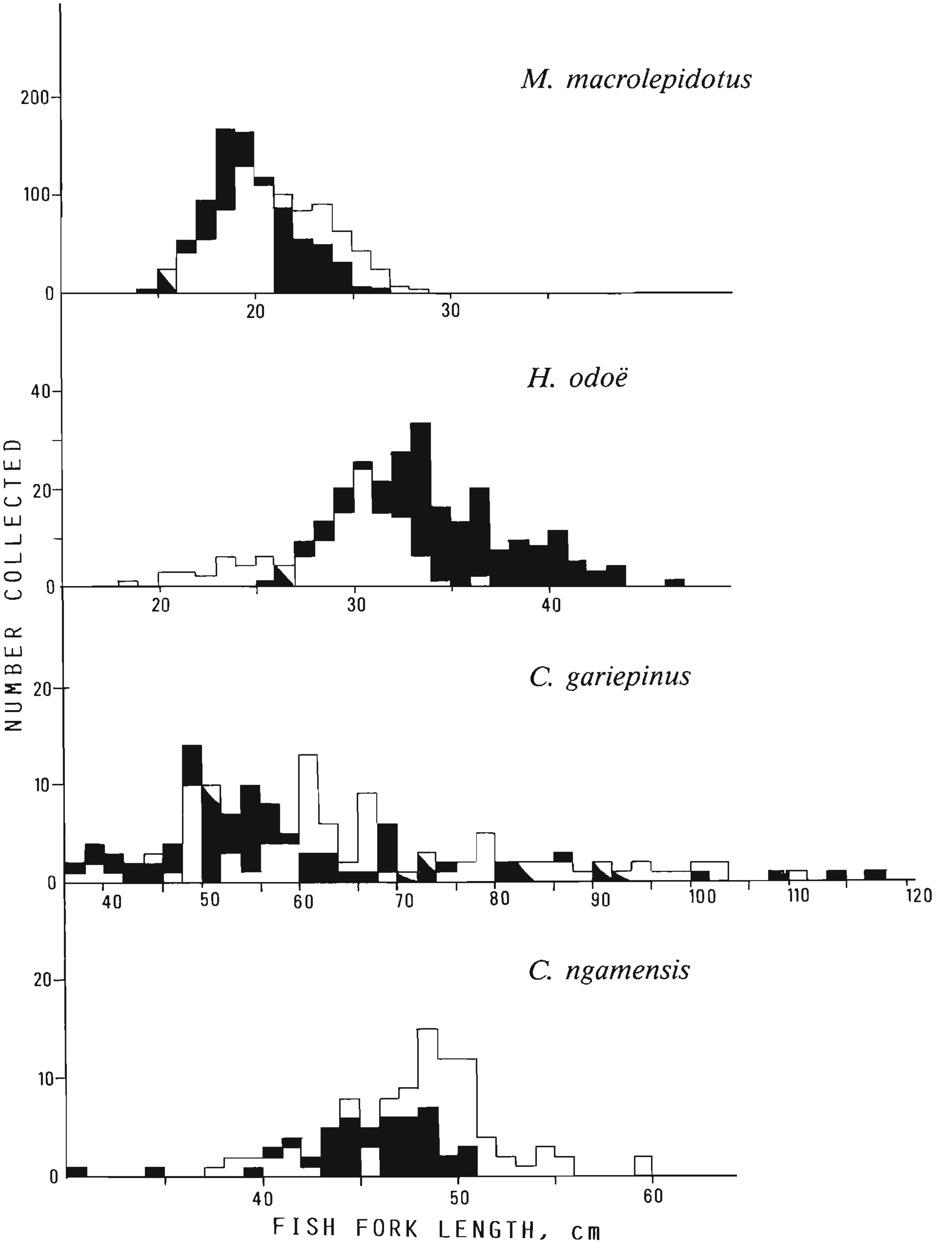


FIGURE 4: Length frequency distribution for males and females of fish species collected with gill and seine nets in Lake Liambezi.

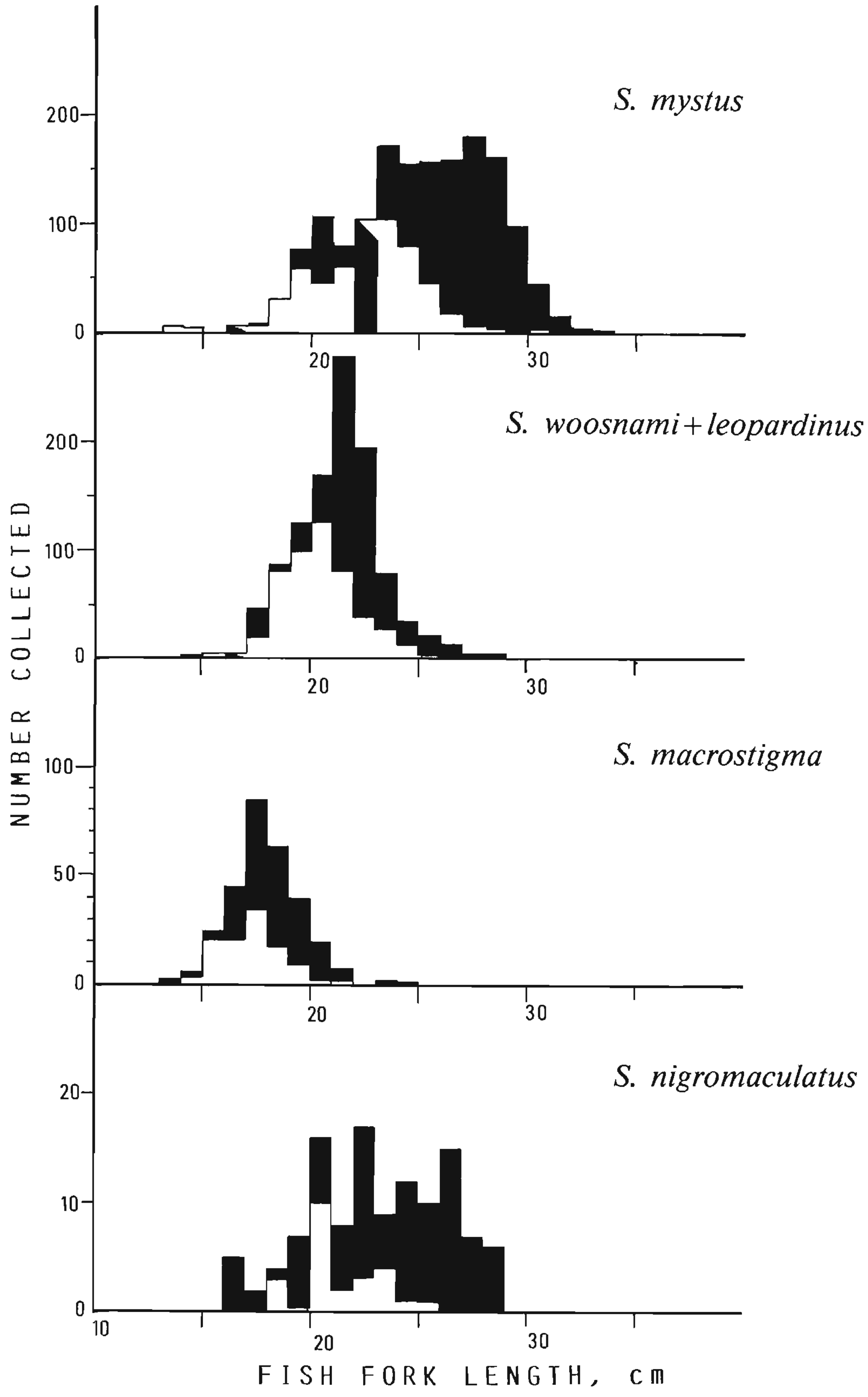
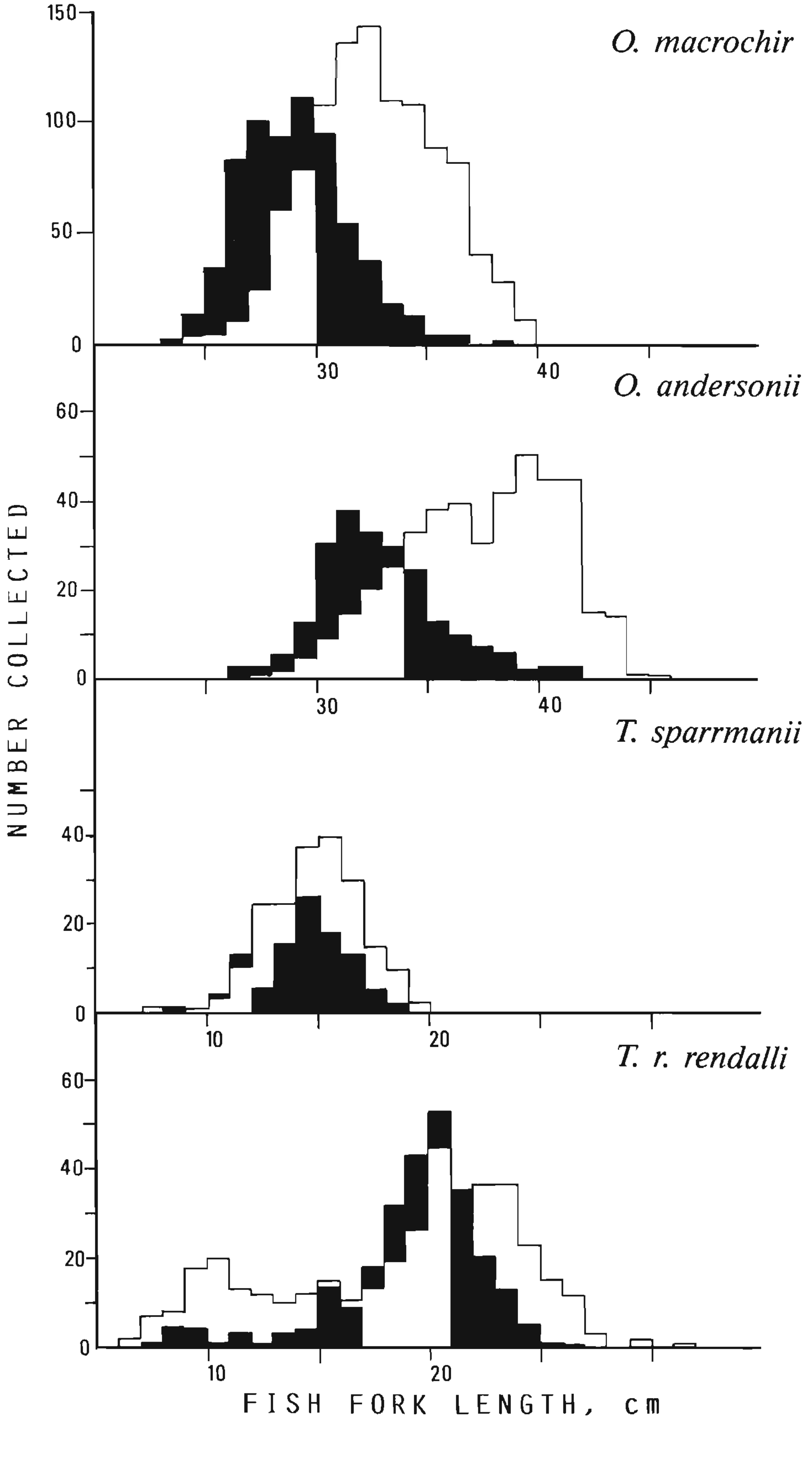

S. mystus
S. woosnami+leopardinus
S. macrostigma
S. nigromaculatus
NUMBER COLLECTED
200
100
50
20
10
0
10
20
30
FISH FORK LENGTH, cm

FIGURE 4b



O. macrochir
150
100
50
0
30
40
O. andersonii
60
40
20
0
30
40
T. sparrmanii
40
20
0
10
20
T. r. rendalli
60
40
20
0
10
20
NUMBER COLLECTED
FISH FORK LENGTH, cm

FIGURE 4c

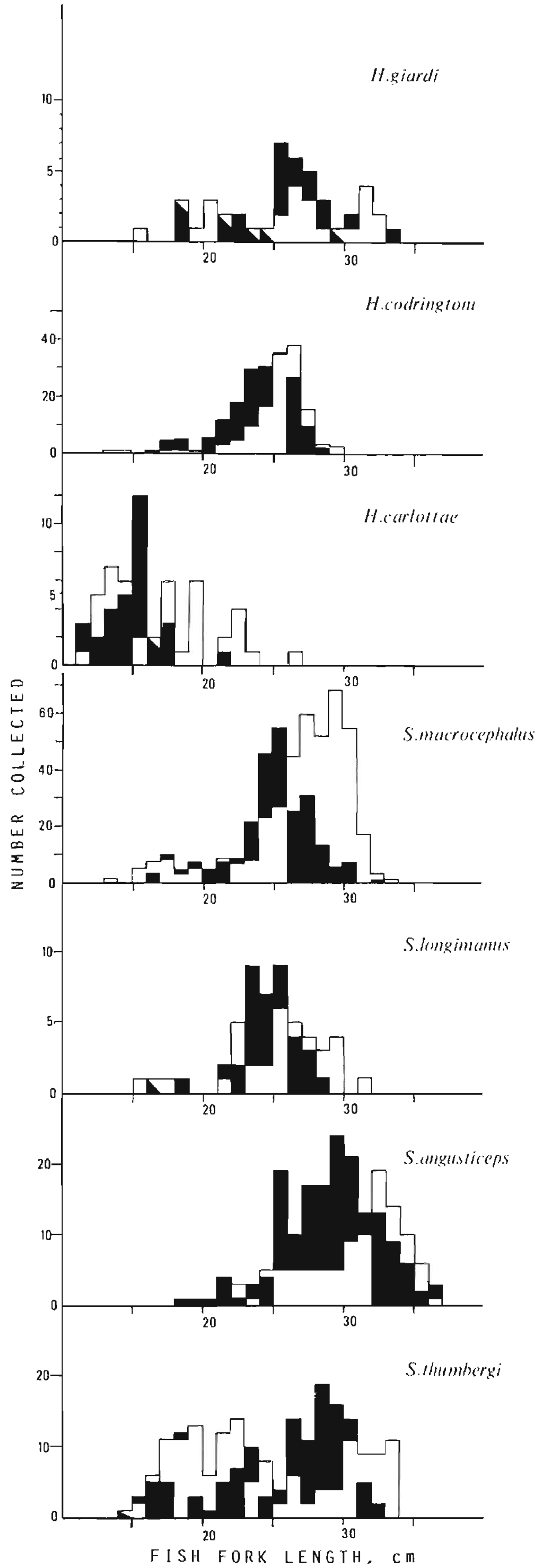


FIGURE 4d

more abundant in larger length groups of a population, the faster growing sex also lives to a higher age, for instance *H. odoë, O. macrochir, O. andersonii, S. carlottae, S. macrocephalus* and *S. longimanus* (figure 3 and Table 5).

3.4 Reproduction

3.4.1 Sex ratio

Table 6 shows that species in which mature fish of one sex grow faster and/or reach a higher age, generally reflect a sex ratio in favour of that sex e.g. *H. odoë, S. mystus, Synodontis* spp., *Oreochromis* spp. and *S. carlottae*. In general these findings agree with those of Carey and Bell-Cross (1967) on the same fish species on the Kafue Flood Plain. Exceptions as with *C. gariepinus* may be the result of the small samples available. The sex ratio for *M. macrolepidotus* in both Lake Liambezi and Kafue Flood Plain does not follow the expected trend where males show a slightly higher growth rate (Table 5) and form the majority of larger fish of the population (Figure 4).

3.4.2 Size at maturity

The lengths at which 50 per cent maturity is reached, are summarised in Table 3. It is known that different populations of the same fish species exhibit varying growth rates and linked with this, lengths at which maturity is reached. For instance, the following minimum lengths are quoted for *O. macrochir* : 14 cm (Charpy, 1954, in ponds), 18 cm (Anon, 1965, Lake Mweru) and 23 cm (Huet, 1936, Katanga).

Lake Liambezi fish of this species start maturing only at 23cm.

Some published minimum lengths for female *C. gariepinus* are as follows (in cm): 20 (Lake Sibaya (Bruton, 1979), 28 (Lake McIlwaine (Clay, 1977), 30 (Elands River (Van der Waal, 1972)), 38 (Mazoe Dam, (Van der Lingen, 1965)), 39 (Lake McIlwaine, (Munro, 1965)), 44 (Lake Kariba, (Bowmaker, 1973)), 45 (Vaal River, (Mulder, 1971)) and 65 (Hardap Dam, (Gaigher, 1977)). As Gaigher (1977) states, the length reached when sexual maturity is reached, may reflect the favourability of environmental conditions and could possibly be used as a management tool in fisheries.

3.4.3 Spawning season and sites

Mormyrids

All have a short breeding season commencing at the beginning of the rainy season and may thus be stimulated to spawn by floods. Spent *P. catostoma* were collected in April and *M. macrolepidotus* in March to July (figure 5).

No signs of a spawning migration as observed in the Kafue Gorge (Anon, 1965), were observed in Lake Liambezi. The very limited information on *M. lacerda* indicates a spawning season in midsummer. Ripe fish have been collected in Barotseland as early as November (FAO, 1968).

Characids

Only a few *H. vittatus* were collected of which some were ripe in December. The scarcity of this fish in Lake Liambezi (0,02 per cent of experimental catches) is ascribed to unsuitable breeding conditions (Kenmuir, 1973) as the lake starts rising only late in the rainy season. The collection of two specimens of 17cm in Lake Liambezi four years after the last possible immigration of tiger fish from the Zambezi Flood Plain into Lake Liambezi, indicates that some successful breeding might however take place in the lake. *A. lateralis* breeds in November and December and spent females were collected in December and February. It does not seem dependent on floods for spawning as is also illustrated by the hepsetid, *H. odoë*.

H. odoë has a long breeding season extending from September to January — February with a peak in November — December. This fish may not be dependent on floods for spawning and is a multiple spawner as eggs of different sizes were found in ripe females.

Clariids

The spawning season is closely correlated to the rainy season in both species. *C. gariepinus* spawns mainly in January and March and *C. ngamensis* in November — December. Spawning migrations of both species into temporary rain-water drainage channels were observed. *C. gariepinus* migrated out of the lake as far as 3 km into shallow grassy vleis. Migrations were observed after heavy downpours on 13 December 1973, 20 December 1974 and 24 January 1975.

These fish may spawn more than once per season as ripe ovaries often contained eggs of different size classes (Bruton, 1980).

Schilbeïds

S. mystus obviously spawns from November to April with ripe running females being most abundant in January and February. Fingerlings of 30 mm length were collected in the Zambezi River in March. There seems to be one spawning per year and eggs in ripe ovaries were of uniform size.

Mochokids

All four species occurring in Lake Liambezi breed late in summer. Ripe running females were collected from February to April and spent females from April to August. Young *S. woosnami* of 20 mm length were collected in the Zambezi River in April. No difference could be found between spawning seasons of the four *Synodontis* species. Ripe ovaries contained eggs of similar size.

TABLE 6: Sex ratios of fish species collected with gill and seine nets in Lake Liambezi and on Kafue Flood Plains*

Fish species	Lake Liambezi					Kafue Flood Plains*	
	Males		Females		Sex ratio	Sex ratio	n
	n	%	n	%	m:f	m:f	
M. macrolepidotus	819	49	848	51	1:1,0	1:1,5	824
M. lacerda	2	40	5	60	1:2,5	—	—
H. odoë	121	29	303	71	1:2,5	1:1,4	1853
A. lateralis	—	—	—	—	—	1:6,4	2395
C. gariepinus	107	48	118	52	1:1,1	1:0,5	36
C. ngamensis	108	65	59	35	1:0,6	1:0,6	21
S. mystus	595	27	1579	73	1:2,7	1:1,2	1607
S. woosnami + *S. leopardinus*	521	34	1029	66	1:2,0	—	—
S. macrostigma	111	26	312	74	1:2,8	1:3,0	1068
S. nigromaculatus	23	16	118	84	1:5,1	—	—
O. macrochir	1120	61	707	39	1:0,6	—	—
O. andersonii	350	61	223	39	1:0,6	—	—
T. sparrmanii	194	64	109	36	1:0,6	1:0,9	1260
T. r. rendalli	375	59	266	41	1:0,7	—	—
S. giardi	34	43	45	57	1:1,3	—	—
S. codringtoni	157	45	190	55	1:1,2	—	—
S. carlottae	46	58	34	42	1:0,7	—	—
S. robustus jallae	14	74	5	26	1:0,4	—	—
S. macrocephalus	393	61	255	39	1:0,7	1:0,6	33
S. longimanus	120	43	158	57	1:1,3	—	—
S. angusticeps	105	37	178	63	1:1,7	1:0,8	281
S. thumbergi	91	52	84	48	1:0,9	—	—

* From Carey and Bell-Cross, 1967.

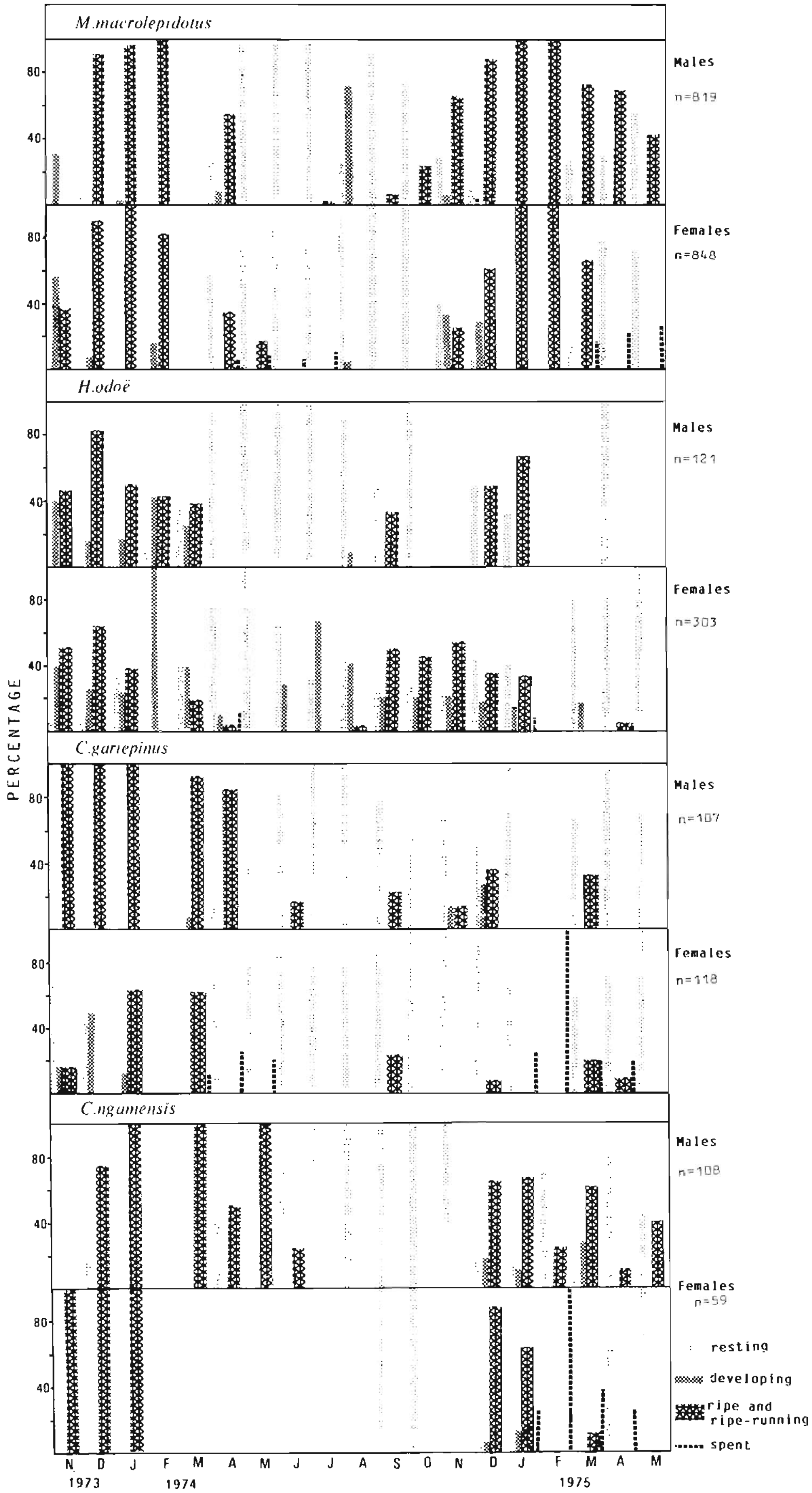


FIGURE 5: Gonad development of fish species in Lake Liambezi.

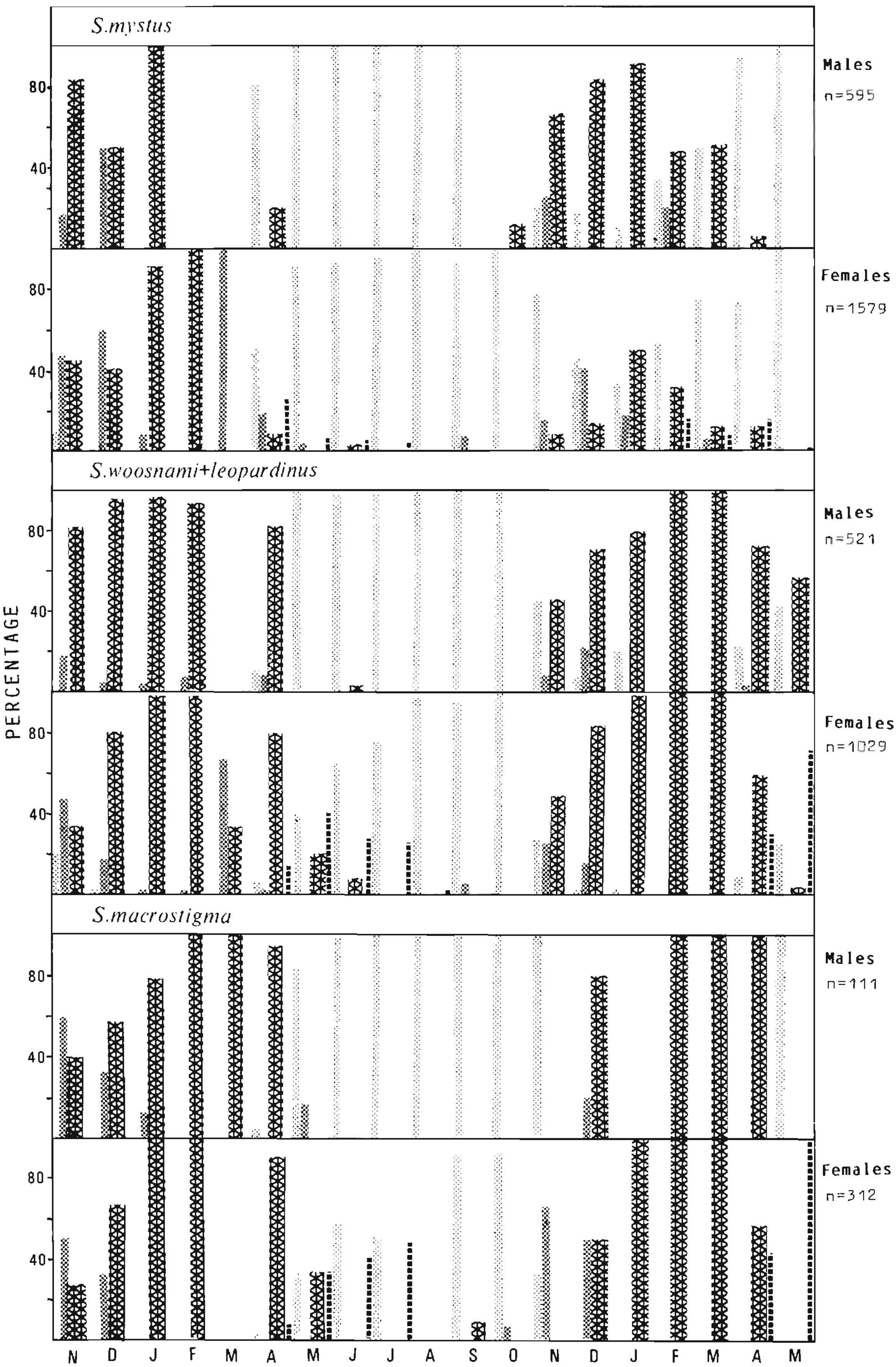

S.mystus
Males
n=595
Females
n=1579
S.woosnami+leopardinus
Males
n=521
Females
n=1029
S.macrostigma
Males
n=111
Females
n=312
PERCENTAGE
80
40
N D J F M A M J J A S O N D J F M A M

FIGURE 5b

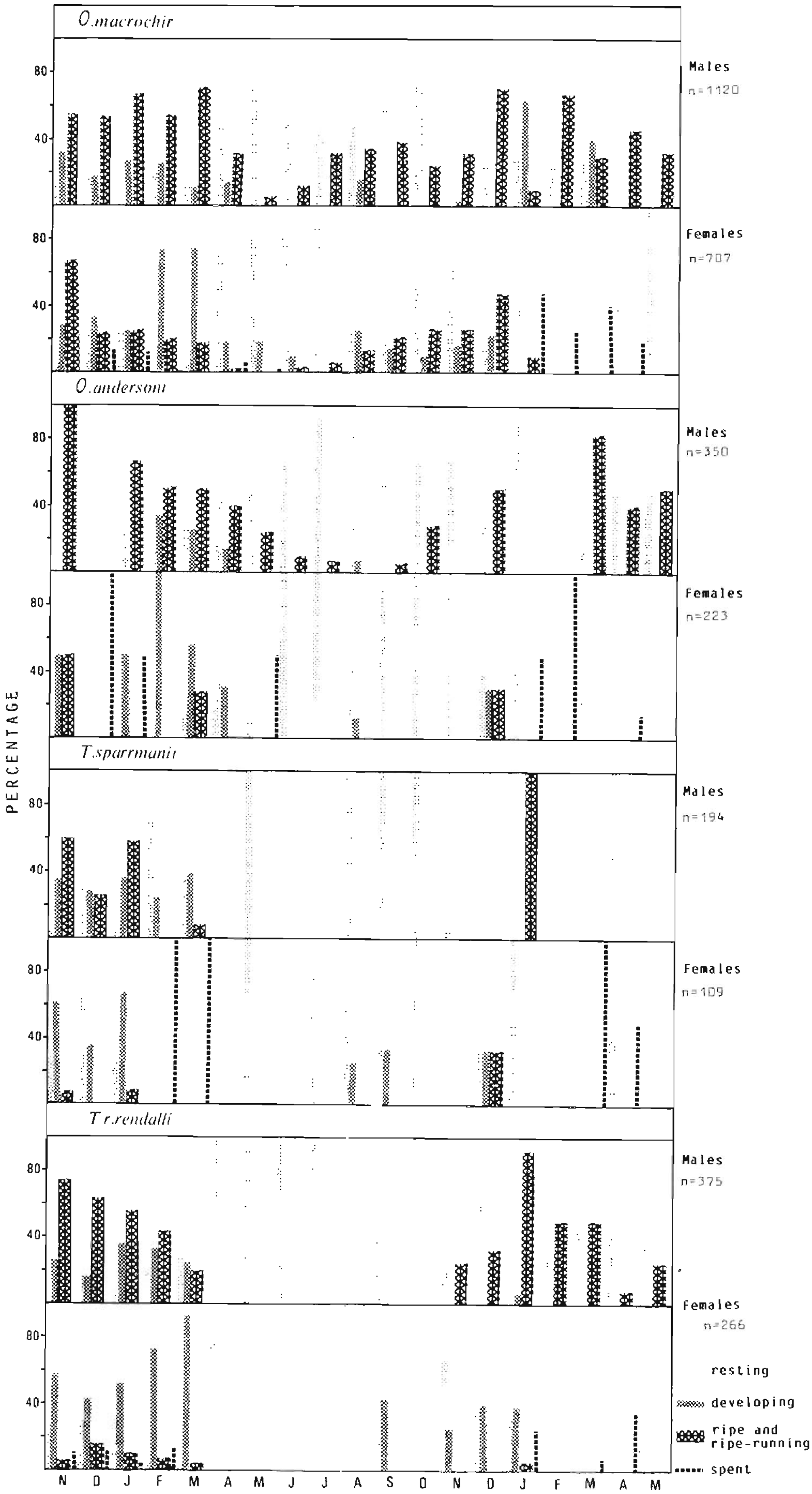

O.macrochir
Males
n=1120
Females
n=707
O.andersoni
Males
n=350
Females
n=223
T.sparrmanii
Males
n=194
Females
n=109
T.r.rendalli
Males
n=375
Females
n=266
PERCENTAGE
80
40
resting
developing
ripe and ripe-running
spent
N D J F M A M J J A S O N D J F M A M

FIGURE 5c

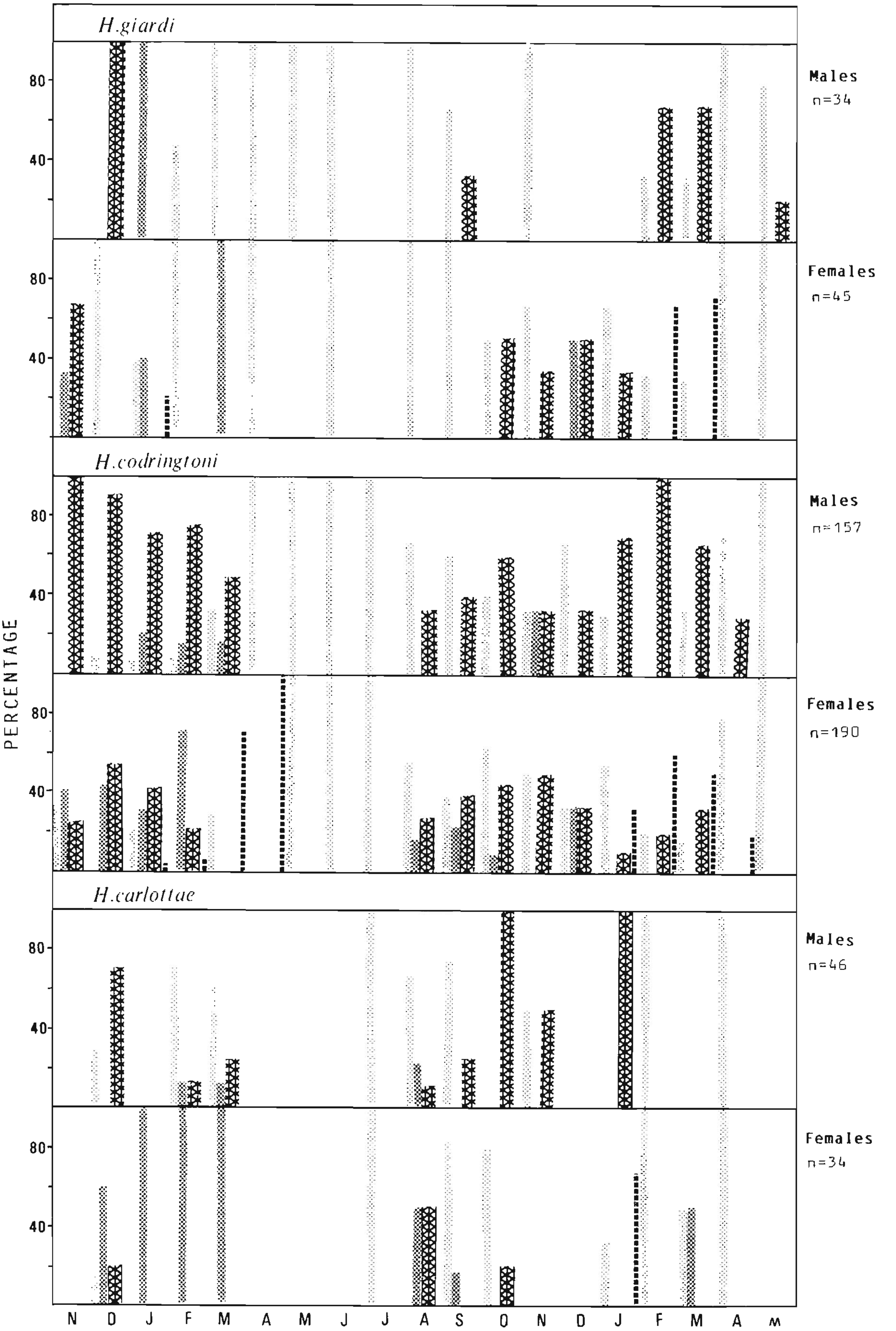

H.giardi
Males
n=34
Females
n=45
H.codringtoni
Males
n=157
Females
n=190
H.carlottae
Males
n=46
Females
n=34
PERCENTAGE
80
40
N D J F M A M J J A S O N D J F M A M

FIGURE 5d

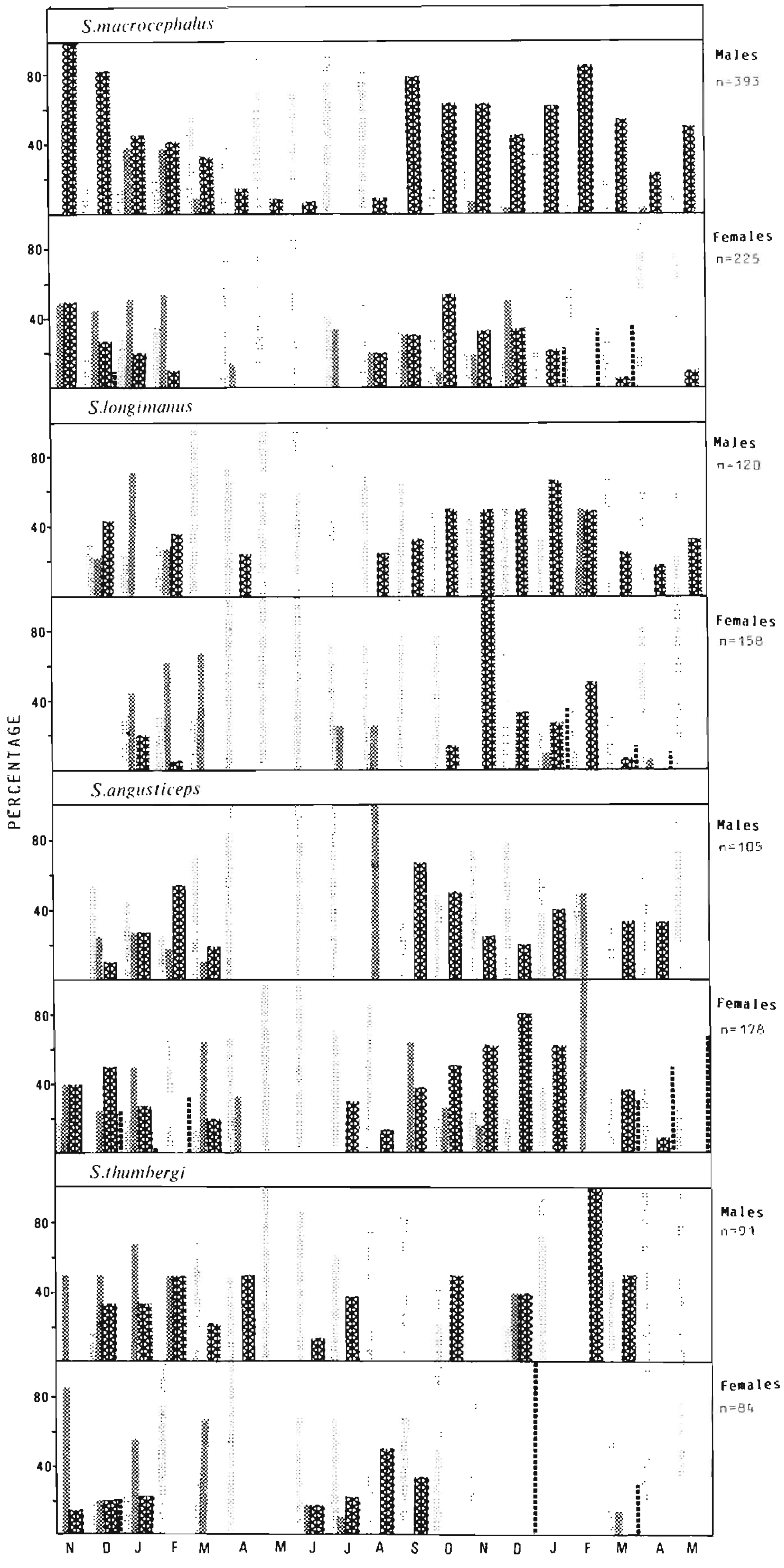

S.macrocephalus
Males
n=393
Females
n=225
S.longimanus
Males
n=120
Females
n=158
S.angusticeps
Males
n=105
Females
n=178
S.thunbergi
Males
n=91
Females
n=84
PERCENTAGE
80
40
N D J F M A M J J A S O N D J F M A M

FIGURE 5e

Cichlids

Members of this family, renowned for its progressive breeding habits, are not dependent on stimuli like flooding or rain-water, but other factors such as water temperature and day length (Mortimer, 1960; Fryer and Iles, 1972). In Lake Liambezi this is borne out in many species where spawning takes place before and after the rainy season. *O. macrochir* shows a very long breeding season with ripe females found from August to March but with a clear peak in November — December.

Nests of *O. macrochir* were observed in shallower parts (1-2m) of Lake Liambezi both on sandy and muddy substrates. Underwater observations in one of the channels leading into the lake, Chinchimane Channel, showed that its nest consists of a conically shaped heap with a diameter of up to more than 1m at the bottom and 50cm high with a saucer-shaped cleaned depression of 20cm diameter on top. A circular canal is formed around the nest by the removal of material for construction. This pattern of nest building differs from the star-shaped pattern found in Lake Mweru (Congo System (Anon, 1965a)) but is similar to that found in populations from the Kafue River (Mortimer, 1960). However, populations of the Zaïre (Congo) River and Upper Zambezi — Kafue Rivers may be different on subspecies or even species level (Fryer and Iles, 1972). Throughout the breeding season females with eggs in two or three size classes were collected; females incubating eggs often had completely developed eggs in their ovaries. De Bont (1949) in Mortimer (1960) and Mortimer (1960) state that *O. macrochir* spawns up to six times per year if water temperatures stay above 21°C. In Lake Liambezi minimum water temperatures were above 21°C from September to March — April (Seaman *et al.,* 1978).

In contrast with *O. macrochir, O. andersonii* females contained ripe ovaries only in November, December and March and spent females were collected in December — February and in April — May. It may thus have a main spawning season early in the summer (as on the Barotse Flood Plain (FAO, 1969)) with a smaller second spawning in the end of the summer. Ovaries did not contain eggs of varying sizes as with *O. macrochir.* Mortimer (1960) found that it spawns once or twice per year in Zambian fish-ponds.

Few *T. sparrmanii* with ripe ovaries were collected but data point to a spawning season in early summer. The absence of ripe male and female fish in samples may be due to the breeding habits of this fish species. According to Bruton (1979a) both parents incubate and protect eggs and young at the nesting site in shallow water amongst aquatic vegetation for up to six weeks and were thus not vulnerable to gill nets set in open water.

The same trends were observed for *T.r. rendalli* where ripe females were collected in very low frequencies from November to March. Ovaries of *T.r. rendalli* contained eggs in varying stages of development. Nests in use were observed on the edge of the Zambezi Flood Plain in March-April and as early as in August on the flood plain of the Kwando River, showing remarkable adaptation to utilise advantageous conditions.

Nests of *T.r. rendalli* were observed in the Chinchimane Channel, western bays of the lake and on flood plains of the Kwando and Zambezi. They consisted of a cleaned area of 50 to 120cm diameter, usually between *Phragmites* stolons, water plants or inundated grass tufts in water 50—300cm deep, usually on stabilised sandy soil. In the centre of the nest from seven up to 20 holes often 10cm in diameter and five to 50cm deep are made (blown). It was observed several times that both parents participate in protecting and cleaning eggs and larvae which are regularly transferred from one hole to the other (especially when disturbed) (Fryer and Iles, 1972).

Ripe running females of *S. giardi* were collected from October to December — January and males were active till March. Nests observed in the Chinchimane Channel consisted of round or oval level cleaned areas of 20 to 30cm diameter amongst thick submerged vegetation *(Ottellia, Ceratophyllum, Najas)* in water 3m deep, and were guarded by territorial males.

S. codringtoni has a long spawning season from September to March. It is also a mouth brooder and constructs a simple nest similar to that of *S. giardi.* Eggs of varying size were found in ripe ovaries and it may thus spawn more than once per year. No ripe running females of *S. carlottae* were collected during the survey. Ovaries start to develop in August and spent females were collected in January. Underwater observations in the Chinchimane Channel showed that *S. carlottae* males are territorial, as are other *Serranochromis,* and make a small saucer-shaped nest amongst water-plants.

Few specimens of *S. robustus* were collected. Ripe females were collected in January and March and ripe males in November to January and April.

Males in the typical bottle green spawning dress with bright orange-yellow dorsal fins and egg dummy marks were collected with artificial lures in Lake Liambezi as early as August. Nests guarded by territorial males were observed amongst dense submerged vegetation and *Phragmites* in shallow water of only 40cm. The nest is a simple cleaned saucer-shaped area of 30cm on sandy substrate. As with *Serranochromis (Sargochromis)* species, all *Serranochromis* males show clear spots or "egg dummies" on the anal fins during the spawning season, varying in size and colour from species to species, those of *S. robustus* and *S. angusticeps* being bright yellow, of *S. giardi* pink, *S. macrocephalus* bright red and *S. longimanus* orange. It was observed by Pott and Le Roux (1968) that the female *S. meridianus* actually nibbles at the anal fin of the male after she has taken up eggs in her mouth, thereby probably stimulating the male to fertilise the eggs in the female's buccal cavity. *S. macrocephalus* breeds from October to March. Spent females were collected in March and April and ripe males as early as August up to as late as June. As with most Cichlids studied in Lake Liambezi, all mature females are never simultaneously in a ripe running condition as was the case in eg. *M. macrolepidotus, C. ngamensis* and *Synodontis* spp. The closely related *S. longimanus* (Jubb, 1967) breeds from November to March and ovaries of ripe females contained eggs of varying sizes.

S. angusticeps has an extremely long breeding season in Lake Liambezi with females in ripe condition collected from July to April and spent females from March to May.

In both seasons that were studied, no ripe females were collected in February. Territorial males were observed in the Chinchimane Channel, defending nests consisting of small sandy open spaces in submerged hydrophyte beds at depths of 1—3m.

Ripe females of *S. thumbergi* were collected in November to January and also from June to January during the two seasons studied, whilst ripe males were collected more or less throughout the year. Territorial males in breeding colours were collected with artificial lures in midwinter in sandy bays where the water is 1—2m

TABLE 7: Egg counts of ripe females of fish species from Lake Liambezi, Kafue River (Carey and Bell-Cross, 1967) and Bangweulu (Anon, 1964).

Fish species Length (cm)	Lake Liambezi	Kafue River and Flood Plain		Lake Bangweulu	
		n	Average count	n	Average count
M. macrolepidotus		10	5336	4	3040
19	2 800				
23	8 176				
25	6 300 6 800				
M. lacerda					
39	4 149				
40	3 788				
41	3 063				
42	7 236				
H. odoë		2	6041	3	5832
32	175				
33	1 378 1 599				
38	1 086				
C. gariepinus	—			9	83423
C. ngamensis				1	134811
41	67 208				
43	17 427				
45	87 663				
S. mystus		3	11522		
24	38 500				
26	42 500				
27	67 500				
29	1 600 27 500				
30	102 000				
S. woosnami and *leopardinus*					
21	25 500 29 500 32 000				
22	26 000 46 000 46 500 46 500 55 000				
23	12 000 24 500 25 500 35 500 47 000				
26	87 000				
28	66 500				
S. macrostigma		8	13909		
14	45 000				
S. nigromaculatus				9	21983
21	15 500				
22	62 500				
26	16 000				

TABLE 7 continued

Fish species Length (cm)	Lake Liambezi	Kafue River and Flood Plain		Lake Bangweulu	
		n	Average count	n	Average count
S. macrochir		1	469	2	518
25	522 545				
26	656 669				
27	187 398 681 514 1 223				
28	398 440 490 599				
29	297 301 418 435 527 589				
31	411 549 695 764 856 1 010				
32	492				
33	785				
S. andersonii		2	2375	1	567
31	976		all eggs?		(Mortimer 1960)
T. r. rendalli	—	3	12613 all eggs?		
T. sparrmanii	—	2	1486 all eggs?		
S. codringtoni					
23	369				
24	209 347 434 470 500				
25	479				
26	314				
27	253 590				
S. robustus		3	398	3	330
31	579				
S. macrocephalus		3	334		
25	291				
27	1 839				
S. angusticeps		10	575	8	286
27	471				
28	536				
29	488				
30	995				
31	907				
32	398 984				
33	653				
34	615 711				
S. thumbergi		2	775		
28	407				
30	329 601				
S. longimanus					
24	311 492				

TABLE 8: Food habits of *P. catostoma, M. macrolepidotus* and *M. lacerda* in Lake Liambezi.

Food item	*P. catostoma*		*M. macrolepidotus*		*M. lacerda*	
	Rank in relative % volume	Percentage frequency	Rank in relative % volume	Percentage frequency	Rank in relative % volume	Percentage frequency
Fish material	—	—	11	0,5	—	—
Terrestrial insects	—	—	7	2,5	—	—
Odonate nymphs	3	43	5	6,0	3	50
Ephemeropteran nymphs	1	71	2	64,8	2	50
Chirononomid larvae	4	14	1	80,5	1	100
Chaoborus larvae	2	57	3	20,2	—	—
Other water insects	5	14	8	5,3	—	—
Hydracarina	—	—	11	0,5	—	—
Caridina nilotica	—	—	10	0,7	—	—
Ostracods	—	—	4	19,3	—	—
Plant tissue	—	—	6	9,8	—	—
Detritus	—	—	9	2,5	—	—
Number of stomachs inspected		7		156		2

deep. Gregarious nesting takes place at these sites and from 20 to 50 nests, spaced 50—150cm apart, were observed in bays. The nests are simple circular saucer-shaped depressions of 20cm diameter. Ripe ovaries contain eggs in varying stages of development and this species, like the other *Serranochromis*, is thus a multiple spawner.

3.4.4 Fecundity

Egg counts of those species yielding sufficient ripe ovaries are presented in Table 7. For comparative purposes, information by Carey and Bell-Cross (1967) from the Kafue River and Flood Plain and from Lake Bangweulu (Anon, 1964) is presented. The mormyrids both have relative low fecundities which increase in larger fish. Compared to *H. vittatus* (Kenmuir, 1973) the egg counts of *H. odoë* are particularly low. In the present study only ripe eggs of more than 2mm diameter were counted whereas the two references may have included all immature eggs as well. No counts were made on *C. gariepinus*. The mature eggs of *C. ngamensis* are smaller (1,2mm) than those of *C. gariepinus*. *S. mystus* also has small eggs and a high fecundity with a strong indication of increased numbers with greater length. *Synodontis* spp. are also very fecund but no clear trend in increasing lengths was apparent from the small samples available.

It is interesting that *O. andersonii* with a relatively short breeding season and *T.r. rendalli* and *T. sparrmanii* (both non-mouth brooders) as reported by Carey and Bell-Cross (1967), show higher egg counts than the other cichlid species in Lake Liambezi which have an extended breeding season (multiple spawning) as well as more intensive parental care.

3.5 Food habits

Occurrence and relative volume were used as indices of relative importance of food items. Results are discussed by families.

Mormyrids

Table 8 shows that mormyrids feed on aquatic insect larvae, as has been found elsewhere in Africa (Petr, 1968; Okedi, 1971). *P. catostoma* prefers ephemeropterans and *M. macrolepidotus* eats more chironomids but a wide range of food items was found in its stomach. *M. macrolepidotus* is a successful fish in Lake Liambezi with a high growth rate (see figure 3) and its main food, chironomids, is plentiful, especially on *Phragmites* stems and in the bottom substrate (Seaman *et al.*, 1978). Ephemeropteran larvae were not found in bottom substrate samples in any large numbers, but underwater observations indicate dense populations on the stems of *Phragmites*, an abundant food source for the commonly occurring *P. catostoma*. The morphological differences of mouth parts of species of this family may be special adaptations to collect food items from different substrates. *M. lacerda*, with its bottle-shaped terminal mouth, also feeds on insects, but specimens collected in the Zambezi River when floods receded contained numerous small fishes, similar to those that were migrating back from the flood plain into the river.

Table 9 shows an increase in relative importance of ephemeropterans in the stomach contents of *M. macrolepidotus* and a concurrent decrease in chironomids and *Chaoborus* over the 1,3-year study period. This can possibly be connected to the steady rise in lake level over this period, (figure 6) making conditions more favourable for ephemeropterans. During the rainy sea-

TABLE 9: Seasonal variation in food habits of *M. macrolepidotus*.

Season / Food item	Rank in relative % volume							Percentage frequency of occurrence						
	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Jan., rainy season	Average	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Jan., rainy season	Average
Fish material	—	—	—	9	—	—	11	—	—	—	3	—	—	0,5
Caridina nilotica	—	—	8	—	—	—	10	—	—	4	—	—	—	0,7
Terrestrial insects	—	4	7	—	—	—	7	—	11	4	—	—	—	2,5
Odonate nymphs		6	6	3	3	—	5	—	5	12	12	7	—	6,0
Ephemeropteran nymphs	3	3	2	2	1	1	2	27	22	64	88	88	100	64,8
Chironomid larvae	1	1	1	1	1	2	1	100	95	60	97	81	50	80,5
Chaoborus larvae	2	2	4	8	—	—	3	47	51	20	3	—	—	20,2
Other water insects	5	6	5	7	—	—	8	13	5	8	6	—	—	5,3
Hydracarina	—	9	—	—	—	—	11	—	3	—	—	—	—	0,5
Ostracods	6	5	3	4	5	3	4	7	5	40	9	5	50	19,3
Plant material	4	8	—	5	4	4	6	20	3	—	6	5	25	9,8
Detritus	7	—	—	6	6	—	9	7	—	—	6	2	—	2,5
Number of stomachs inspected								15	37	25	33	42	4	

son terrestrial insects are utilised when they are also more plentiful. The fish material consisted of cichlid fish scales.

Characids and hepsetids

Only two tiger-fish with stomach contents consisting of fish material and a piece of *Phragmites* were collected. As Jackson (1961) proposes, *H. vittatus* has a strong effect on the behaviour of fish species living in the same habitat as a result of its active feeding behaviour in open water. The size and extremely good condition of specimens collected by the local fishermen and sport anglers in Lake Liambezi (up to 10 kg), is a reflection of optimal environmental and feeding conditions as a result of an abundance of suitable prey.

Table 10 shows that *H. odoë* is also an active predator, but not with the same hunting behaviour, being more restricted to vegetated environments. *H. odoë* was for instance never collected in the Zambezi River proper but was abundant in some of its side channels and vegetated bays where *H. vittatus* adults were absent. On the other hand *H. odoë* was collected over the whole of Lake Liambezi and also in the strongly flowing channels of the Linyanti Swamp in Caprivi, where *H. vittatus* occurs in very low numbers (Lake Liambezi) or is totally absent (Linyanti Swamp). Immature cichlids form the bulk of food items found in stomachs but adult *P. darlingi* as well as *A. lateralis* and *Barbus* spp. were also consumed. As *H. odoë* forms 2,9 per cent of experimental gill net catches in Lake Liambezi (Van der Waal, 1980), it probably has a regulating effect on small fish species and especially on the prolific cichlids.

Most prey consumed by *H. odoë* ranged in length from 5—10cm although prey fish of 14, 17 and even 18 cm were also consumed, representing a prey/predator size ratio of up to 40 per cent, very similar to that of *H. vittatus* (Gaigher, 1967; Kenmuir, 1973). In a study in the Kafue River, Carey (1971) also found a ratio for *H. odoë* of 30—40 per cent. Here the percentage of cichlids in the diet was only 19 per cent, the rest consisting of *M. macrolepidotus, A. lateralis* and *S. macrostigma* — all three actively migrating species.

Clariids

The stomach content composition of *C. gariepinus* and *C. ngamensis* is summarised in Table 11. Both species feed predominantly on fish but *C. gariepinus* feeds also on a wide variety of food items, including zooplankton, roots and leaves of grasses, terrestrial insects, molluscs and *Otomys* sp.. *C. ngamensis* feeds to a lesser extent on fish and here molluscs (gastropods and pelecypods — *i.a. Mutela), Nymphaea* seeds and water insects form important food items. The tooth structure of *C. ngamensis* is well-adapted by its large strong bony vomerine and mandibular tooth plates to crush these food items. Many pelecypods and most gastropods were found in a crushed condition in stomachs of *C. ngamensis* ; this was never the case with *C. gariepinus*. Pack hunting of both species was observed in Lake Liambezi similar to that described by Donnelly (1966), Tait (1967), and Bruton (1979b). In 1973 this took place in a bay in the western portion of Lake Liambezi. Flocks of reed cormorants *Phalacrocorax africanus* Gmelin, numbering a few hundred, hunted a small silvery fish species, presuma-

TABLE 10: Food habits of 82 *H. odoë* in Lake Liambezi.

Food item	Rank as % volume	% occurrence
* Fish material	1	98
Insectivora-fam. Soricidae	3	1
Plant tissue	2	5
No of stomachs inspected		82
* Analysis of fish material		
Fish species		
Non-cichlid total		15
A. lateralis		9
B. poechii		1
Barbus sp.		1
C. multispinis		4
Cichlid total		74
O. macrochir		13
T. rendalli		1
Tilapia spp.		5
S. giardi		1
S. codringtoni		1
P. darlingi		11
S. angusticeps		4
S. macrocephalus		6
S. longimanus		1
S. thumbergi		1
Cichlid indet.		30
Digested		10

TABLE 11: Food habits of *C. gariepinus* and *C. ngamensis* in Lake Liambezi.

Fish species	*C. gariepinus*		*C. ngamensis*	
Food item	Rank as % volume	Percentage occurrence	Rank as % volume	Percentage occurrence
* Fish material	1	63	1	41
Rodentia — Murids	7	3	—	—
Molluscs	10	7	2	28
Terrestrial insects	4	10	4	28
Odonate nymphs	8	7	5	28
Ephemeropteran nymphs	—	—	13	3
Chironomid larvae	11	3	8	13
Chaoborus larvae	—	—	9	9
Caridina nilotica	9	9	6	19
Potamon sp.	—	—	9	3
Ostracods and Copepods	2	23	9	3
Unicellular and filamentous algae	4	13	12	6
Nymphaea seeds	—	—	3	24
Plant tissue	3	20	—	—
Detritus	6	13	7	6
No. of stomachs inspected		30		32
* Analysis of fish material				
Fish species				
Non-cichlid total		10		16
B. poechii		—		8
H. odoë		—		8
S. mystus		5		—
Indet.		5		—
Cichlid total		80		50
O. macrochir		16		—
T. r. rendalli		11		—
Tilapia spp.		5		17
S. codringtoni		5		—
P. darlingi		11		25
Serranochromis spp.		—		8
Indet.		32		—
Digested		10		34

TABLE 12: Food habits of 371 adult *S. mystus* during seasons in Lake Liambezi.

	Rank as % volume								Percentage occurrence							
Food item \ Season	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average
Fish material	1	1	1	1	1	1	1	1	57	46	39	81	57	75	86	63,0
Vertebrates	—	—	11	6	6	8	—	8	—	—	2	2	5	4	—	1,9
Molluscs	—	—	12	—	10	9	—	10	—	—	2	—	1	2	—	0,7
Terrestrial insects	—	2	2	4	2	5	2	3	—	69	34	12	36	17	14	26,6
Odonate nymphs and hemipterans	4	4	7	5	5	3	—	5	14	8	20	9	10	19	—	11,4
Ephemeropteran nymphs	2	3	5	6	4	4	—	4	50	15	22	5	17	15	—	17,7
Chironomid larvae	6	6	3	—	9	9	—	7	14	8	18	—	2	2	—	6,3
Chaoborus larvae	—	—	10	6	—	—	—	12	—	—	4	2	—	—	—	0,9
Caridina nilotica	3	4	4	2	3	2	3	2	50	8	27	16	22	35	8	23,7
Ostracods	—	—	12	—	10	—	—	13	—	—	2	—	1	—	—	0,4
Algae	—	—	—	—	10	—	4	11	—	—	—	—	1	—	3	0,6
Plant tissue	5	—	8	3	7	7	4	6	14	—	8	16	6	8	3	7,9
Detritus	—	—	9	9	8	6	—	9	—	—	5	2	4	6	—	2,4
No. of stomachs inspected									14	13	108	43	108	48	37	

bly *A. lateralis* in conjunction with a shoal of very active *C. ngamensis* which were slowly moving in one direction whilst the birds stayed in front of them amongst the prey fish, only surfacing to swallow their prey.

The prey-predator size ratio was found to vary from 10 to 30 per cent in *C. gariepinus.* A whole specimen of *S. macrochir* with a total length of 30cm was found in a *C. gariepinus* of 100cm. Prey fish of 14, 16 and 18cm in length were also found but most fish ingested were 8—12cm long. Small cichlids form the majority of fish prey eaten by *C. gariepinus* and *C. ngamensis.*

Schilbeids

Results of stomach content analyses are presented in Table 12. Adult *S. mystus* feed predominantly on fish, *Caridina nilotica,* terrestrial insects and larger aquatic insects but are opportunistic predators as is shown by the large variety of food items consumed. Vertebrate remains found in *S. mystus* stomachs include *Rana,* snake skin and bird skin and feathers. Terrestrial arthropods include members of Orthoptera, Lepidoptera, Hemiptera, Coleoptera, Isoptera, Hymenoptera and also some arachnids. No clear seasonal change in feeding habits is evident. The composition of prey fish is represented in Table 13. About half of identifiable fish remains consisted of small cichlids. Smaller fish species such as *Barbus* spp., *A. lateralis* and *P. darlingi* of 4—10cm length form the main fish prey but prey of up to 13cm was collected in stomach contents, with a prey-predator length ratio of up to 30 per cent, which is lower than the 40 per cent mentioned by Carey (1971) of *S. mystus* from the Kafue River where *M. macrolepidotus, A. lateralis, L. cylindricus, C. gariepinus* and *S. macrostigma* form the main prey species.

TABLE 13: Composition of prey fish ingested by 221 adult *S. mystus* in Lake Liambezi.

Fish species	Percentage occurrence
A. lateralis	8,6
B. poechii	1,0
Barbus sp.	3,5
C. gariepinus	1,0
C. theodorae	0,5
Synodontis spp.	0,5
Indet.	5,1
Non-cichlid total	20,2
O. macrochir	0,5
T. sparrmanii	0,5
Tilapia indet.	5,6
P. darlingi	8,6
S. thumbergi	0,5
Serranochromis spp.	0,5
Indet	15,2
Cichlid total	31,4
Digested	48,5

TABLE 14: Food habits of 10 — 14 cm long *S. mystus* in Lake Liambezi.

Food item	Rank as % volume	Percentage occurrence
Fish material	4	17
Terrestrial insects	1	58
Hemipterans and odonates	6	6
Ephemeropteran nymphs	3	30
Chironomid larvae	2	38
Chaoborus larvae	7	9
Caridina nilotica	5	11
Plant tissue	8	2
No. of stomachs inspected		53

Table 14 shows that terrestrial insects and smaller aquatic insects are the main food items utilised by immature *S. mystus.* This coincides with the results of Olatunde (1979).

The food habits of *S. mystus* in Lake Liambezi are similar to those of the closely related *Eutropius depressirostris* which feeds on fish, insects, plant material and crustaceans in the Transvaal (Gaigher, 1968; Potgieter, 1974).

Mochokids

The stomach content composition of *S. woosnami/S. leopardinus* and *S. macrostigma* (Table 15) showed considerable similarities. These fish feed mainly on ephemeropteran nymphs, chironomid larvae, ostracods and plant tissue, whilst *S. nigromaculatus* stomachs contained predominantly fish material, chironomids, *Chaoborus,* odonate nymphs, terrestrial insects and plant tissue.

Fish material found in stomachs of *S. woosnami/S. leopardinus* and *S. macrostigma* consisted of one *A. lateralis,* fish scales and also pieces of fish flesh. *S. nigromaculatus* stomachs contained fish scales (45%), larvae and eggs of cichlids (33%), *C. multispinis* (11%) and digested fish material (11%). It is not known how cichlid eggs and larvae (up to 1000 in one stomach!) were collected as cichlids incubate orally or guard eggs and larvae in nests (the fish were collected in a gill net). *S. nigromaculatus* is more omnivorous in feeding habits and shows a tendency to utilise larger food items than the other *Synodontis,* like odonate nymphs and the active *Chaoborus* larvae.

The food habits of *S. nigromaculatus* differ from the other three species, where very little variation was found. Morphologically it is also separated from the other species (Jubb, 1967), which are so closely related that *S. leopardinus* and *S. woosnami* had to be lumped together in the field.

On the Barotse Flood Plain *S. woosnami* was found to live on plants, detritus, snails, insects and algae (FAO, 1968) which differs from the present results in that aquatic insects and ostracods did not form important food items. Environmental differences and availability of food items may play a role here. The same phenomenon was found for *M. macrolepidotus.*

TABLE 15: Food habits of *Synodontis* species in Lake Liambezi.

Fish species	*S. woosnami* and *leopardinus*		*S. macrostigma*		*S. nigromaculatus*	
Food item	Rank as % volume	% occurrence	Rank as % volume	% occurrence	Rank as % volume	% occurrence
Fish material	8	6,3	8	7	1	53
Molluscs	7	3,7	—	—	8	12
Terrestrial insects	13	3,3	10	4	6	24
Odonate nymphs	9	5,8	7	15	4	35
Ephemeropteran nymphs	1	51,5	2	70	5	29
Chironomid larvae	2	70,8	1	89	2	47
Chaoborus larvae	6	13,0	8	7	3	41
Other water insects	12	0,8	—	—	—	—
Caridina nilotica	12	1,0	11	4	10	6
Ostracods and Cladocerans	3	30,3	3	37	8	6
Filamentous algae	4	27,0	5	7	—	—
Plant tissue	—	—	4	19	7	24
Plant seeds	5	25,0	—	—	—	—
Detritus	11	7,7	6	11	—	—
No. of stomachs inspected		136		27		17

TABLE 16: Food composition of 136 *S. woosnami* and *leopardinus* during seasons.

Season / Food item	Rank as % volume: Jan.—Feb., '74 rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr., autumn	Average	% occurrence: Jan.—Feb., '74 rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr., autumn	Average
Fish material	4	—	—	10	—	4	8	16	—	—	2	—	20	6,3
Molluscs	—	—	6	5	—	—	7	—	—	14	8	—	—	3,7
Terrestrial insects	5	8	—	10	—	—	10	11	7	—	2	—	—	3,3
Odonate nymphs	7	—	—	8	4	—	9	5	—	—	5	25	—	5,8
Ephemeropteran nymphs	3	3	1	1	1	4	1	37	33	72	72	75	20	51,5
Chironomid larvae	1	1	2	2	2	6	2	84	87	69	70	75	40	70,8
Chaoborus larvae	2	7	7	—	—	—	6	58	13	7	—	—	—	13,0
Other water insects	7	—	—	—	—	—	12	5	—	—	—	—	—	0,8
Caridina nilotica	—	—	—	7	—	—	12	—	—	—	6	—	—	1,0
Ostracods	—	4	4	3	—	3	3	—	53	38	31	—	60	30,3
Filamentous algae	—	2	3	6	3	1	4	—	47	24	6	25	60	27,0
Plant seeds	5	5	5	4	5	2	5	11	40	17	17	25	40	25,0
Detritus	7	6	—	9	5	—	11	5	13	—	3	25	—	7,7
No. of stomachs inspected								19	15	29	64	4	5	

Table 16 shows seasonal variation in the stomach content of *S. woosnami* and *leopardinus*. As with *M. macrolepidotus*, a decline in the importance of chironomids together with an increase in the intake of ephemeropterans occurred over the study period, which can again be linked to raised water levels (figure 6).

Cichlids

Representatives of this family show a wide range of feeders, including herbivores, filter feeders and predators, although not as specialised as cichlids from Lakes Victoria and Malawi (Fryer and Iles, 1972).

O. macrochir

The stomach contents of *O. macrochir* consist mainly of small and unrecognisable items and are difficult to sort or analyse under an ordinary stereo-microscope. Detritus or finely divided organic material (with bacteria, protozoans, etc.) forms the main food item of adult and young *O. macrochir*, followed closely by blue-greens, diatoms and other algae (Table 17). Plant material, consisting of dead material and roots, is also ingested throughout the year. Cladocerans and aquatic insects are utilised to a lesser extent and a partly digested small cichlid and fish scales were also found in *O. macrochir* stomachs. Young (9—14cm) fish food habits are basically similar to those of adults. Very young fish do however feed on zooplankton (see also Le Roux, 1956). The feeding habits of *O. macrochir* are comparable to those on the Barotse Plains (FAO, 1969) and in Lake Mweru (Anon, 1965a) where it was found that food particle size increases with fish size.

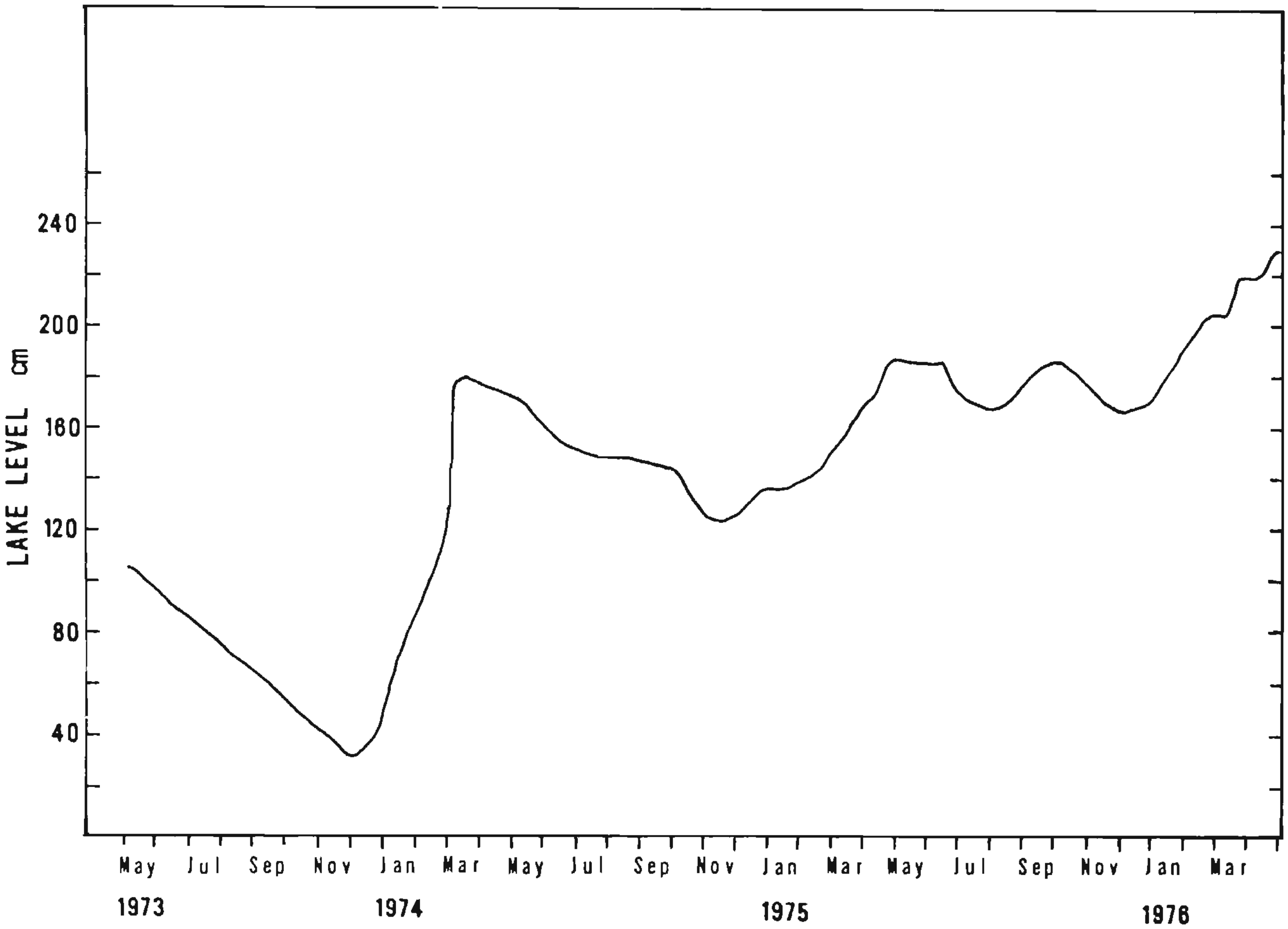


FIGURE 6: Water levels of Lake Liambezi during study period.

TABLE 17: Food habits of 287 large and 74 small *O. machrochir* in Lake Liambezi.

Large fish, 23 — 39 cm	Rank as % volume								% occurrence							
Food item / Season	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average
Fish material	3	—	5	—	—	—	—	5	13	—	2	—	—	—	—	2,1
Insect eggs	—	—	—	4	—	—	—	7	—	—	—	3	—	—	—	0,4
Chironomid larvae	—	—	—	—	5	4	—	6	—	—	—	—	2	5	—	1,0
Chaoborus larvae	—	—	6	—	—	—	—	8	—	—	1	—	—	—	—	0,1
Cladocerans	—	4	4	5	4	—	—	4	—	5	20	3	12	—	—	5,7
Blue-green algae and diatoms	1	2	1	2	2	1	2	2	100	100	99	100	100	100	100	100,0
Plant material	3	3	3	3	3	3	3	3	13	17	41	39	34	64	88	42,3
Detritus	2	1	2	1	1	2	1	1	50	100	96	97	100	100	100	91,9
Number of stomachs inspected									8	64	99	36	50	22	8	

Small fish, 9 — 14 cm	Rank as % volume	% occurrence
Chironomid larvae	5	1
Zooplankton	4	8
Algae	2	100
Plant material	3	30
Detritus	1	97
No. of stomachs inspected		74

TABLE 18: Food habits of 176 adult and 18 young *S. andersonii* in Lake Liambezi.

Large fish, 26 — 45 cm	Rank as % volume								% occurrence							
Season / Food item	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average	Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average
Fish eggs and larvae	—	4	—	—	—	—	—	5	—	3	—	—	—	—	—	0,4
Terrestrial insects	—	—	—	4	—	—	—	5	—	—	—	4	—	—	—	0,6
Odonate nymphs	—	5	—	—	—	—	—	7	—	6	—	—	—	—	—	0,9
Ephemeropteran nymphs	—	—	5	—	—	—	—	7	—	—	2	—	—	—	—	0,3
Cladocerans and copepods	—	2	1	2	2	2	3	2	—	68	94	89	95	88	52	69,4
Blue-green algae, diatoms and filamentous algae	1	1	2	1	1	1	1	1	100	100	100	100	97	100	100	99,6
Plant material	—	6	4	—	4	—	4	4	—	3	10	—	3	—	43	8,4
Detritus	—	3	3	3	3	3	2	3	—	21	71	21	33	25	57	32,6
No. of stomachs inspected									2	34	48	28	39	16	9	

TABLE 18 continued

Small fish 13 — 15 cm	Rank as % volume	% occurrence
Ephemeropteran nymphs	5	6
Cladocerans and copepods	4	17
Blue green algae and diatoms	2	100
Plant material	3	44
Detritus	1	100
No. of stomachs inspected		18

Food items were generally of similar size, reflecting a bottom filter feeding behaviour. Moriarty (1973) was able to demonstrate that the common belief that tilapia cannot digest especially blue-green algae (Fish, 1952) is not true for *O. niloticus*. Lysis of cell walls occurred in the stomach when pH values of 1,4 were recorded. Faeces had a brown colour when chlorophyll was converted into phaeophytin through the action of the acid medium. In Lake Liambezi the typical change of the green-grey stomach contents to brown, especially adjacent to the stomach wall, was observed regularly, indicating that the dominant algae, *Microcystis*, is partly utilised by *O. macrochir*.

O. andersonii

Results of stomach content analyses of juvenile and mature *O. andersonii* are represented in Table 18.

Blue-green algae, diatoms and filamentous algae form the dominant food items together with zooplankton and detritus. The food habits differ from those of *O. macrochir* in that zooplankton is more important and possibly reflects an open water filter feeding rather than a bottom feeding habit. Young (13—15cm) *O. andersonii* show a difference by ingesting more detritus and less zooplankton. In the Barotse Flood Plain this species lives on periphyton, plant tissue and zooplankton (FAO 1968, 1969), reflecting different feeding habits under different environmental conditions. Mortimer (1960) established that all length classes feed on algae as well as detritus and mud, and that it has a filter feeding as well as bottom feeding habit. Large *O. andersonii* were observed feeding at night off the surface film in Lake Liambezi. As with *O. macrochir*, faeces were usually brown, indicating digestion of blue-green algae.

T. sparrmanii

Table 19 summarises results of stomach content analyses on *T. sparrmanii*. This species inhabits vegetated inshore areas and feeds on periphyton, and diatoms scraped from water-plants, organic material, aquatic insects and also fish, zooplankton and terrestrial insects. In the Barotse Flood Plain *T. sparrmanii* was found to have similar feeding habits with periphyton, detritus, fish and insects as main food items (FAO, 1968).

TABLE 19: Food habits of *T. sparrmanii* in Lake Liambezi.

Food item	Rank as % volume	% occurrence
Fish material	5	7
Terrestrial insects	8	7
Odonate and ephemeropteran nymphs	5	7
Chironomid larvae	4	20
Zooplankton	7	13
Diatoms	1	100
Plant material	3	33
Detritus	2	93
No. of stomachs inspected		15

T. r. rendalli

T. r. rendalli feeds on aquatic plants, detritus, algae, filamentous algae, aquatic insects, larvae, zooplankton and fish as shown in Table 20. A wide spectrum of

TABLE 20: Food habits of 120 *T. r. rendalli* in Lake Liambezi.

Food item \ Season	Rank as % volume: Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average	% occurrence: Nov. 1973, spring	Dec.—Mar., rainy season	Apr.—May, autumn	June—July, winter	Aug.—Nov., spring	Dec.—Mar., rainy season	Apr.—May, autumn	Average
Fish material	—	5	—	—	—	—	—	7	—	7	—	—	—	—	—	1,0
Terrestrial insects	—	10	—	—	—	—	—	10	—	1	—	—	—	—	—	0,1
Odonate nymphs	—	9	2	—	4	—	—	5	—	6	25	—	1	—	—	4,6
Ephemeropteran nymphs	—	5	—	—	—	—	—	7	—	3	—	—	—	—	—	0,4
Chironomid larvae	3	3	—	2	—	—	—	4	14	26	—	7	—	—	—	6,7
Chaoborus larvae	5	7	—	—	—	—	—	6	29	1	—	—	—	—	—	4,3
Zooplankton	—	8	—	—	—	—	—	9	—	10	—	—	—	—	—	1,4
Filamentous algae	2	4	—	2	2	2	3	3	29	23	—	7	39	40	100	34,0
Plant material	1	1	1	1	1	1	1	1	100	93	100	100	94	100	100	98,1
Detritus	4	2	2	2	3	2	2	2	43	33	25	7	33	40	100	40,1
No. of stomachs inspected									7	70	4	15	18	5	1	

food items is utilised but plants form by far the major food. The following hydrophytes could be identified from stomach content analyses:

	% occurrence
Lagarosiphon major	63
Leaves of grass spp.	14
Stems and roots of *Phragmites*	11
Leaves of *Phragmites*	4
Najas pectinata	4
Nymphaea seeds	4

With the exception of seeds and roots all vegetable matter was fresh, green and macerated. It was often observed how *Phragmites* leaves were pulled into the water and torn to pieces.

On the Barotse Flood Plain *T.r. rendalli* lives on green plant material, detritus and insects (FAO, 1969) and Potgieter (1974) and Batchelor (1974) found that in the Transvaal *T.r. swierstrae* feeds on plant material as main food item together with algae, detritus, zooplankton, insects and fish. Under certain conditions this fish species may become over-populated, even in large dams, destroying all plant life (Junor, 1969; Wager, 1968). This apparently only applies where it is imported. In these waters it also tends to become predacious.

In spite of an abundance of a variety of water-plants in Lake Liambezi, *T. r. rendalli* is not abundant (Table 1; Van der Waal, 1980) and also does not show a rapid growth rate (figure 3).

S. giardi

Stomach content composition is summarised in Table 21. Molluscs form by far the most important food item. The following molluscs could be identified from stomach contents:

Gastropods:	% occurrence
Melanoides sp.	52
Lanistes sp.	16
Pila sp.	16
Pelecypods:	
Corbicula sp.	8
Aspatharia sp.	8

TABLE 21: Food habits of *S. giardi* in Lake Liambezi.

Food item	Rank as % volume	% occurrence
Fish scales	4	18
Molluscs	1	100
Odonate nymphs	2	18
Chironomid larvae	5	9
Plant seeds	2	9
No. of stomachs inspected		11

Other food items ingested include odonate nymphs, fish scales, chironomids and seeds. Bell-Cross (1975) shows that *S. giardi* lies at the end of a line of feeding specialisation found in the larger *Serranochromis (Sargochromis)* species from *S. frederici* (=*S. greenwoodi*) — *S. carlottae* — *S. codringtoni* — *S. giardi* where *S. frederici* has a narrow pharyncheal plate with curved sharp teeth and *S. giardi* a strong wide pharyncheal plate with large molariform teeth, adapted for crushing molluscs.

S. codringtoni

Table 22 shows that *S. codringtoni* feeds on *Nymphaea* seeds which are rich in carbohydrates, as well as water insects, molluscs and fish material, (scales of large cichlids). Only gastropods were identified in stomach contents. Bell-Cross (1975) found that this species lives on water insect larvae, molluscs, fish scales and terres-

TABLE 22: Food habits of *S. codringtoni* in Lake Liambezi.

Food item	Rank as % volume	% occurrence
Fish material	3	20
Molluscs	4	10
Odonate nymphs	6	10
Ephemeropteran nymphs	4	10
Chironomid larvae	2	60
Nymphaea seeds and other plant material	1	80
No. of stomachs inspected		10

trial insects in the Kafue and Middle Zambezi Rivers. On the Barotse Flood Plain it eats plant material, filamentous algae, snails and seeds (FAO, 1968). No stomachs of *S. carlottae* were collected but Bell-Cross (1975) mentions that it feeds on insect larvae, snails and plant material.

P. darlingi

Stomach content analyses are summarised in Table 23. It feeds on cladocerans, chironomid larvae and also on plant tissue and detritus. The presence of fish scales in the stomachs of many fish species is not in my opinion necessarily an indication of a predatory habit, especially where large scales of large fish species are found in small and small-mounthed fish species eg. *S. nigromaculatus* and *M. macrolepidotus*. These scales may have been scraped off dead fish in the gill net fleet or commercial gill nets.

TABLE 23: Food habits of *P. darlingi* in Lake Liambezi.

Food item	Rank as % volume	% occurrence
Fish scales	4	14
Chironomid larvae	2	57
Cladocerans	1	57
Plant material	3	29
Detritus	4	14
No. of stomachs inspected		7

Serranochromis (Serranochromis) spp.

The food composition of the five species is summarised in Table 24. All species are predators but a degree of specialisation and selectivity is evident.

S. robustus collected in the Zambezi River and in channels of the Linyanti Swamp contained *Potamon* as the major food item and in the Barotse Flood Plain apart from fish, also gastropods, pelecypods and insects (FAO, 1969).

S. macrocephalus, S. longimanus and *S. thumbergi* all ingested small quantities of aquatic insects, terrestrial insects, plant material and detritus. On the Barotse Food Plain *S. macrocephalus* is recorded ingesting small quantities of aquatic insects (FAO, 1969). All five species can thus be regarded as predators. Table 24 gives a breakdown of prey species identified in stomach contents. *S. longimanus* and *S. thumbergi* eat more cichlid young than non-cichlids, while *S. angusticeps* seems to prefer *A. lateralis* as prey. *S.*

TABLE 24: Food habits of 5 *Sarranochromis (Serranochromis)* species in Lake Liambezi and percentage composition of fish prey.

Food item	Fish species									
	S. robustus		*S. macrocephalus*		*S. angusticeps*		*S. longimanus*		*S. thumbergi*	
	Rank as % volume	% occurrence	Rank as % volume	% occurrence	Rank as % volume	% occurrence	Rank as % volume	% occurrence	Rank as % volume	% occurrence
Fish material*	1	100	1	100	1	100	1	94	1	100
Odonate nymphs	—	—	2	8	—	—	2	12	—	—
Chironomid larvae	—	—	—	—	—	—	—	—	2	4
Terrestrial insects	—	—	3	—	—	—	—	—	—	—
Plant material	2	25	4	3	—	—	3	6	3	2
Detritus	—	—	—	—	2	4	—	—	3	2
No. of stomachs inspected	4		37		27		17		52	
*Prey species	%		%		%		%		%	
A. lateralis	—		14		33		—		6	
B. paludinosus	—		—		—		—		2	
B. poechii	—		3		—		—		—	
B. bifrenatus	—		—		4		—		4	
Barbus sp.	—		8		4		—		15	
Aplocheilichtys sp.	—		3		—		—		—	
C. ngamensis	25		—		—		—		—	
C. multispinis	25		—		—		—		—	
Indet.	—		14		7		13		—	
Non cichlid total	50		42		48		13		27	
O. macrochir	25		—		—		—		6	
P. darlingi	—		—		—		—		9	
Tilapia sp.	—		16		15		13		15	
Indet.	25		22		11		44		25	
Cichlid total	50		38		26		57		55	
Digested	—		20		26		31		18	

robustus jallae and *S. macrocephalus* do not show clear preferences.

It should be noted, however, that not one prey fish in the stomach contents of any of the 52 *S. thumbergi* collected was longer than 50mm. Up to 74 very young *S. macrochir* were collected from one stomach. On the other hand, prey fish of up to 110mm in length were found in *S. macrocephalus* and in *S. angusticeps*. Here only one to three prey fish were present per stomach.

In the Barotse Flood Plain, *Serranochromis* species eat mainly mormyrids, *Barbus* and cichlids as is the case with *H. odoë* and *Clarias* (FAO, 1969). No mormyrids were observed in any stomach contents although they are well represented in Lake Liambezi.

4 DISCUSSION AND CONCLUSIONS

Lake Liambezi has a varied fish fauna dominated by cichlid species. In both feeding and breeding habits a tendency towards specialisation can be illustrated. Figure 7 summarises breeding cycles of the larger fish species showing that breeding of different fish species is virtually scattered over the whole year. Amongst the cichlids, which are nesting species, differences in actual spawning seasons are observed. Suitable sandy nesting sites, which are very localised in Lake Liambezi, may thus be utilised by different cichlid species in sequence through the year.

No large difference in breeding pattern could however be found amongst the four *Synodontis* species, but *S. nigromaculatus* showed a longer period of ripeness

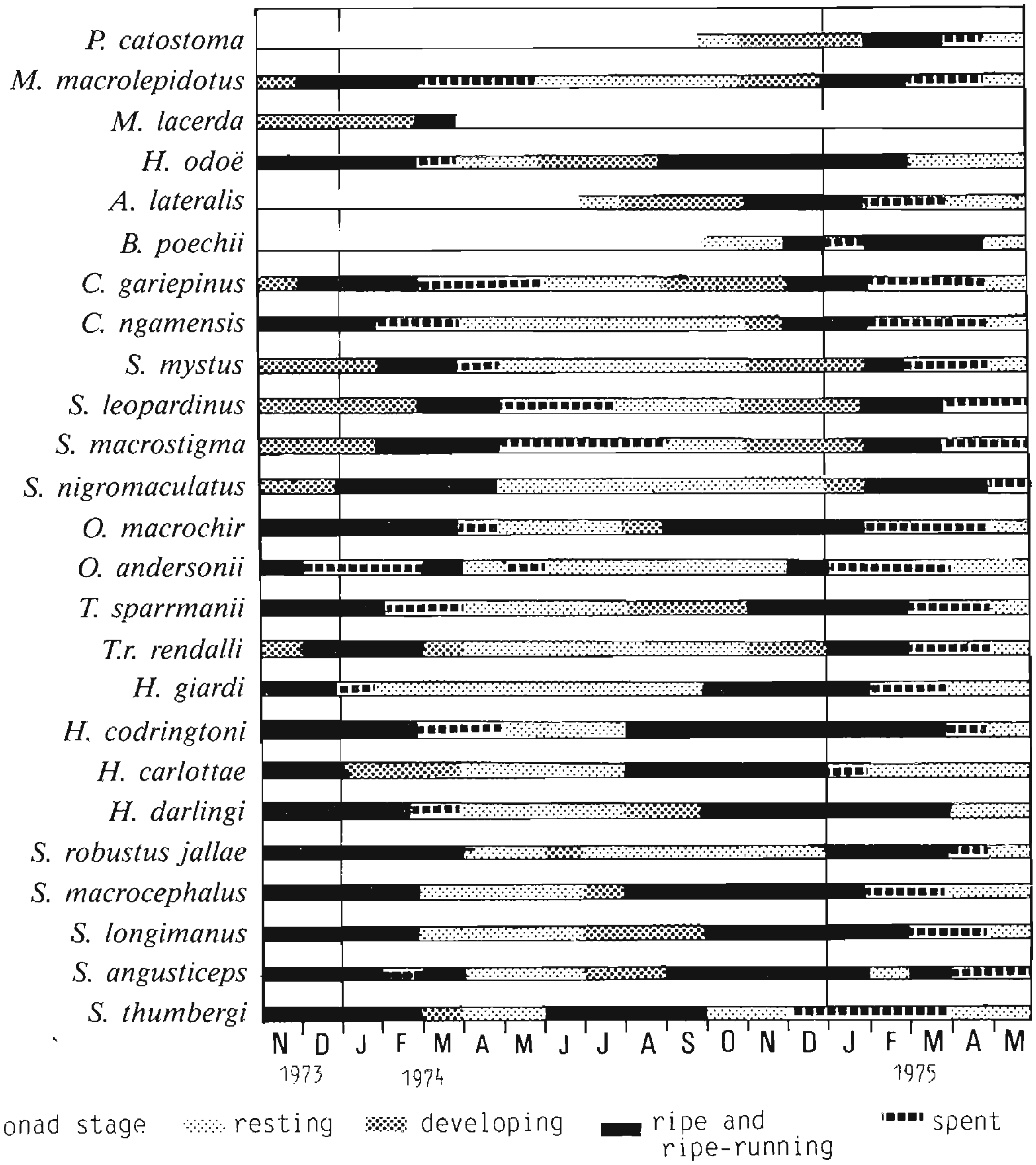


FIGURE 7: Breeding seasons of fish species in Lake Liambezi.

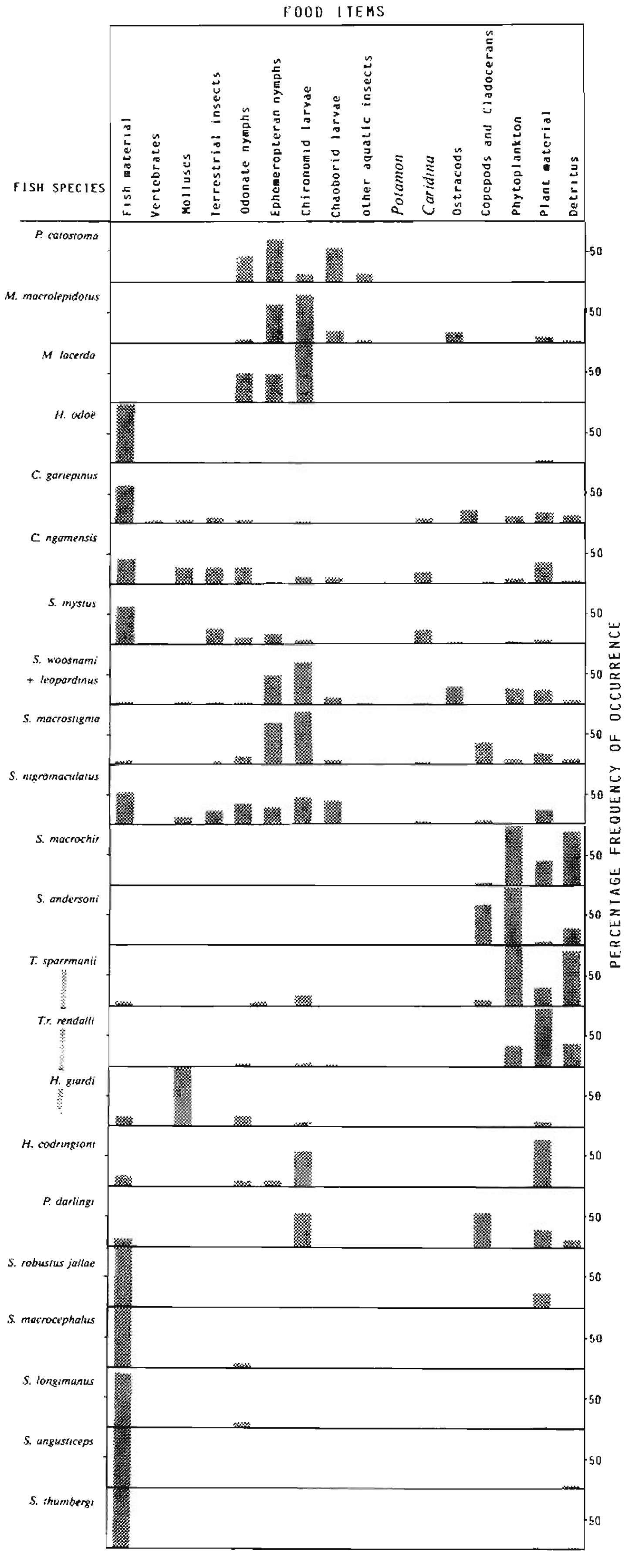


FIGURE 8: Food habits of fish species in Lake Liambezi, based on observed occurrence of food items in stomach contents.

than the other three species. The location of spawning also differs amongst fish species, once again as adaptation to utilise all possible habitats and lessen any direct competition. The *Clarias* species spawn outside the lake in temporary streams and many *Serranochromis* species in very shallow water, with *Oreochromis* in bays and even in the main lake. A difference in the breeding season of some species can also be noticed between 1973/74 and 1974/75 which again shows the adaptability of these fish species to utilise favourable conditions.

Feeding habits of fish species are represented schematically in Figure 8. A wide spectrum of the available food items is utilised in Lake Liambezi with some indication of specialisation in feeding habits amongst species:

a) Predators	*H. vittatus, H. odoë, C. gariepinus* and all five species of *Serranochromis (Serranochromis). C. ngamensis, S. mystus* and *S. nigromaculatus* can also be regarded as predators.
b) Insectivores	All three representatives of mormyrids, *S. woosnami, S. leopardinus, S. macrostigma* and to some extent also *S. nigromaculatus, S. codringtoni* and P. darlingi.
c) Molluscivores	*S. giardi* and *C. ngamensis*
d) Zooplanktivores	*O. andersonii* and *P. darlingi*
e) Phytoplanktivores	*O. macrochir, O. andersonii* and *T. sparrmanii*
f) Herbivores	*T.r. rendalli, H. codringtoni* and *C. ngamensis*
g) Detritivores	*O. macrochir* and *T. sparrmanii*

Some species show interspecific specialisation in order to avoid competition as found amongst mormyrids, *Synodontis* spp. and well-illustrated in the case of *Serranochromis (Serranochromis)* spp. and *S. codringtoni* and *S. giardi.* Other species again can be regarded as omnivores utilising a wide range of food items for example *C. ngamensis* and *Synodontis* spp. although specialisation here is also evident.

It has been shown (Seaman *et al.,* 1978) that Lake Liambezi can be regarded as partly eutrophic but with low algal growth potential, with most nutrients derived from detritus. The lake is dominated by insectivorous fish species such as the mormyrids, mochokids and schilbeids, all living on organisms that live partly on detritus, produced by the wide fringe of *Phragmites* swamp around the lake. The most important commercial fish species, the two *Oreochromis,* also ingest detritus directly, whereas the numerous predacious fish species illustrate the stability of the whole food web.

Primary producers in Lake Liambezi consist mainly of higher plants and very little nutrients are available to phytoplankton (Seaman *et al.,* 1978). This is illustrated by the fact that primary consumers are relatively rare in the fish community — only *T.r. rendalli* (with a poor growth rate) and partly *O. macrochir.* Secondary consumers, living on detritivorous zoobenthos, form the bulk of the fish community and the production rate of this lake is thus more closely linked to the availability of detritivores than primary consumers.

5 SUMMARY

Lake Liambezi is inhabited by 43 fish species of which 27 are large enough to be captured by a fleet of experimental gill nets, and also have an economic value. Aspects of their biology were studied. In spite of the use of small mesh (25, 50 and 60mm stretched mesh) gill nets, very few immatures of the larger fish species were collected. Data are presented on length frequency distribution of catches, age determinations on the basis of interpretation of annuli on scales or sections of pectoral spines, gonad condition over the study period, sex ratios, fecundity, spawning sites and food habits based on stomach content analyses. The lake is inhabited by fish species adapted to the swampy conditions that live mainly on aquatic insect larvae, detritus, or are predacious. The whole system is based on the gradual decomposition of the vast amounts of organic material of the surrounding reed swamp and fish play an important role in the recycling of nutrients.

6 ACKNOWLEDGEMENTS

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REFERENCES

ANON.
1964: Research results, Lake Bangweulu III. Fecundity of some Bangweulu fishes. *Rep. jt Fish. Res. Org. Nth. Rhod.,* **11**:23.

1965a: Breeding behaviour of *Tilapia macrochir. Fish. Res. Bull. Zambia,* Govt. Printer, Lusaka: 12—13.

1965b: A note on the Gnathonemus fishery, Kafue Gorge. *Fish. Res. Bull. Zambia,* Govt. Printer, Lusaka: 28.

BALON, E.K.
1971: Replacement of *Alestes imberi* Peters, 1852 by *A. lateralis* Boulenger, 1900 in Lake Kariba, with ecological notes. *Fish. Res. Bull. Zambia,* **5**: 119—162.

BATCHELOR, G.R.
1974: An ecological investigation of the Doorndraai Dam, Sterk River, Transvaal with special reference to fish management. Transvaal Provincial Administration Report, roneod, 131p.

BELL-CROSS, G.
1975: A revision of certain *Haplochromis* species (Pisces: Cichlidae) of Central Africa. *Occ. Pap. natn. Mus. Rhod.,* B5(7): 405—467.

BRUTON, M.N.
1979a: The breeding biology and early development of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias (Clarias). Trans. zool. Soc. Lond.,* **35**: 1—45.

1979b: The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of Cichlids. *Trans. zool. Soc. Lond.,* **35**: 47—114.

BRUTON, M.N. and ALLANSON, B.R.
1974: The growth of *Tilapia mossambica* Peters (Pisces: Cichlidae) in Lake Sibaya, South Africa. *J. Fish Biol.,* **6**: 701—715.

CAREY, T.G.
1971: Hydrobiological survey of the Kafue Flood Plain. *Fish. Res. Bull. Zambia,* **5**: 245—295.

CAREY, T.G. and BELL-CROSS, G.
1967: Breeding seasons and gonad data. Kafue River and Floodplain Research. *Fish. Res. Bull. Zambia,* **3**: 12—21.

CHARPY, B.
1954: Premier rapport sur les études effectuees par la station piscicole de la Djouma. Jan 1953 — Juin 1954 (Duplicated, quoted by Mortimer, 1960).

CLAY, D.
1977: Biology of the Tropical Catfish (Family: Clariidae) with special emphasis on its suitability for culture (including a bibliography of the Clariidae and related topics. *Fish. Mar. Serv. M.S. Rep.,* 1458. 68p.

DONNELLY, B.G.
1966: Shoaling, communication and social hunting in the catfish *Clarias ngamensis. Piscator,* **20** (6/7): 54—55.

F.A.O.
1968: Report to the Government of Zambia on fishery development in the Central Barotse Flood Plain. Based on the work of D.W. Kelley, FAO/TA Inland Fishery Biologist Rept. FAO/UNDP (TA) (2554). 83p.

1969: Report to the Government of Zambia on fishery development in the Central Barotse Flood Plain. (Second Phase). Based on the work of D.C. Duerre, FAO/TA Inland Fishery Biologist Rept. FAO/UNDP(TA) (2638). 80p.

FISH, G.R.
1952: Digestion in *Tilapia esculenta. Nature,* Lond., **167**: 900.

FRYER, G. and ILES, T.D.
1972: *The Cichlid fishes of the Great Lakes of Africa.* Oliver & Boyd, Edinburgh, 641p.

GAIGHER, I.G.
1967: 'n Opname van die visserybronne van die Incomatisisteem met spesiale verwysing na die ekologie van tiervis. Second Report., Transvaal Provincial Administration, roneod. 97p.

1968: 'n Opname van die visserybronne van die Incomatisisteem met spesiale verwysing na die ekologie van die tiervis. Final report, Transvaal Provincial Administration, roneod. 106p.

1969: A technique for age determination in the Silver barbel *(Eutropius depressirostris). News lett. Limnol. Soc. sth. Afr.,* **13**: 72—75.

1977: Reproduction of the catfish *Clarias gariepinus* in the Hardap Dam, South West Africa. *Madoqua,* **10**(1): 55—59.

HAMMAN, K.C.D.
1981: Aspekte van die bevolkingsdinamika van die Hendrik Verwoerddam met verwysing na die ontwikkeling van 'n visserybestuursplan. Ph.D. thesis, Rand Afrikaans University, 209p.

HECHT, T.
1980: A comparison of the otolith and scale methods of ageing, and the growth of *Sarotherodon mossambicus* (Pisces: Cichlidae) in a Venda impoundment (Southern Africa) *S. Afr. J. Zool.,* **15**(4): 222—228.

HUET, M.
1956: *Traite de Pisciculture,* Brussels, Belgium (Quoted by Mortimer, 1960).

JACKSON, P.B.N.
1961a: *Ichthyology. Kariba Studies.* The fish of the Middle Zambezi. Trustees of the National Museums of Southern Rhodesia. Manchester University Press. 36p.

1961b: The impact of predation, especially by the tiger fish (*Hydrocyon vittatus* Cast.) on African freshwater fishes. *Proc. zool. Soc. Lond.,* **136**(4): 603—622.

JUBB, R.A.
1967: *Freshwater fishes of Southern Africa.* A.A. Balkema, Cape Town. 248p.

JUNOR, F.J.R.
1969: *Tilapia melanopleura* Dum. in artificial lakes and dams in Rhodesia with special reference to its undesirable effects. *Rhod. J. Agric. Res.,* **7**: 61—69.

KENMUIR, D.H.S.
1973: The ecology of the tigerfish *Hydrocynus vittatus* Castlenau *(sic)* in Lake Kariba. *Occ. Pap. natn. Mus. Rhod.,* **B5**(3): 115—170.

LE ROUX, P.J.
1956: Feeding habits of the young of four species of Tilapia. *South Afr. J. Sci.,* **53**(2): 33—37.

MORIARTY, D.J.W.
1973: The physiology of digestion of blue-green algae in the cichlid fish, *Tilapia nilotica. J. Zool., Lond.,* **171**: 25—29.

MORTIMER, M.A.E.
1960: Observations on the biology of *Tilapia andersonii* (Castelnau) (Pisces, Cichlidae), in Northern Rhodesia. *Rep. jt Fish. Res. Org. Nth. Rhod.,* **9**: 42—67.

MULDER, P.F.S.
1971: 'n Ekologiese studie van die hengelvisfauna in die Vaalriviersisteem met spesiale verwysing na *Barbus kimberleyensis* Gilchrist en Thompson. Ph.D. thesis, Rand Afrikaans University, 118p.

MUNRO, J.L.
1967: The food of a community of East African Freshwater Fishes. *J. Zool., Lond.,* **151**: 389—415.

NIKOLSKY, G.V.
1963: *The ecology of fishes.* Academic Press, London. 352p.

OKEDI, J.
1971: The food and feeding habits of the small Mormyrids of Lake Victoria, East Africa. *Afr. J. Trop. Hydrobiol. Fish.,* **1**(1): 1—12.

OLATUNDE, A.A.
1979: The food and feeding habits of *Physailia pellucida* and *Schilbe mystus* with notes on the diets of *S. uranoscopus* and *Siluranodon auritus,* family Schilbeidae (Osteichthyes: Siluriformes) in Lake Kainji, Nigeria. *Freshwat. Biol.,* **9**(3): 183—190.

PETR, T.
1975: On some factors associated with the initial high fish catches in new African man-made lakes. *Arch. Hydrobiol.,* **75**(1): 32—49.

POTGIETER, F.J.
1974: 'n Ekologiese studie van die rooiborskurper *Tilapia rendalli* Gilchrist & Thompson, 1917 (Pisces: Cichlidae) in Transvaal, met verwysing na geassosieerde varswatervissoorte. Transvaal Provincial Administration Report, roneod. 52p.

POTT, R. McC. and LE ROUX, P.J.
1968: Breeding behaviour of *Serranochromis meridianus* Jubb, 1967. *News lett. Limnol. Soc. sth. Afr.,* **10**: 13—16.

SEAMAN, M.T., SCOTT, W.E., WALMSLEY, R.D., VAN DER WAAL, B.C.W. and TOERIEN, D.F.
1978: A Limnological survey of Lake Liambezi, Caprivi. *J. Limnol. Soc. sth. Afr.,* **4**(2): 129—144.

TAIT, C.C.
1967: Pelican and Clarias predation and a note on cormorant predation. *Fish. Res. Bull. Zambia,* **3**: 31—32.

VAN DER LINGEN, M.I.
1965: Some problems of breeding biology of fish in impounded waters. Kariba Research Symposium, 8—9 June 1965, Rhodesia: 97—103.

VAN DER WAAL, B.C.W.
1972: 'n Ondersoek na aspekte van die ekologie, teel en produksie van *Clarias gariepinus* (Burchell) 1822. M.Sc. thesis, Rand Afrikaans University, 119p.

1980: Aspects of the fisheries of Lake Liambezi, Caprivi. *J. Limnol. Soc. sth. Afr.,* **6**(1): 19—31.

WAGER, V.A.
1968: Destruction by Tilapia. *African Wild Life,* **22**(4): 328—339.