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AN HYDROBIOLOGICAL STUDY OF THE MWENDA RIVER AND ITS MOUTH, LAKE KARIBA

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Salisbury, Rhodesia 1973

DECLARATION

The following thesis, apart from help and services which are acknowledged herein, is the result of my own work. No part of it has been submitted in part or is being or is to be submitted for a degree in any university apart from the University of the Witwatersrand. The information used in this thesis was obtained while I was a Research Fellow of the Nuffield Lake Kariba Research Station. During the later analysis I was employed both as a temporary lecturer of the University of the Witwatersrand and lecturer at the University of Rhodesia.

Corrigendum: At the time sections involving Salvinia were prepared, the plant was known as Salvinia auriculata Aublet. Subsequently it has been renamed Salvinia molesta D.S. Mitchell (Mitchell, 1973).

ABSTRACT

This thesis reports on an hydrobiological survey of an area associated with the mouth of a small (280 km^2 catchment) seasonally flowing river entering the tropical man-made Lake Kariba. It was conducted approximately a decade after the dam's closure.

The study was holistic in approach and incorporated sampling of most ecological aspects, including physico-chemical hydrology, plankton, benthic animals associated with a variety of substrates, and fishes. The particular aims of the study were: to assess the composition and seasonal variations of the fauna of various habitats, providing a basis for comparison by future workers and indicating productive avenues of research for more limited and intensive studies in the area; to investigate faunal feeding relationships; to determine biotic and abiotic effects of a permanent floating mat of Salvinia molesta in the study area; and to investigate the breeding accumulations and migrations of the potamodromous fish species. The inherent variability of the fauna was such as to place limitations on the reliability of results.

Physico-chemical characteristics of the water were profoundly affected by the inflowing river during the rainy season and were affected to a lesser extent by depth, physical enclosure, and the Salvinia mat at other times of the year.

The Salvinia mat decreased in extent during the study, whereas the littoral hydrophytes increased following their invasion of the area. The effects of these changes on the fauna were investigated.

The standing crop of plankton collected in daylight and retained by a 112µ mesh was relatively low, highest densities occurring in the winter and in association with the Salvinia mat. Circumstantial evidence indicated that a main source of food to zooplankton was dead particulate organic matter. As judged by size composition of the "herbivorous" elements of the zooplankton, only moderate predator pressure was being exerted by fishes.

The results of benthic sampling are presented and discussed in depth. It was found that although the faunal standing crop was suppressed by the Salvinia mat away from the shoreline, overall faunal standing crop was enhanced by the presence of the mat in the absence of rooted hydrophytes, which themselves caused a more profound increase in faunal density. The importance of the drowned trees as a productive substrate is emphasized.

Fish were found to accumulate at the river mouth before and during the rainy season and moved upstream with a variation in behaviour between species not previously recorded. The Salvinia mat was found not to have any deleterious effect on the fishes. The development of a telemetric tracking device is described. The fish found in dry season pools of the river are discussed in relation to different pool types and the size composition of populations in these is considered.

Fish breeding data are considered in terms of seasonality, maturation sizes, sexual proportions and fecundity. Modal sizes of ova taken from ripe gonads are used in an attempt to assess frequency of breeding. The early development of two species is described.

The food and feeding behaviour of the fish population are described and discussed in relation to the faunal food webs. Relatively few feeding niches were filled due to lack of variety of the fish fauna. The importance of two benthic components is emphasised: the Oligochaeta, which were not utilised as food even though they formed one of the main benthic components; and the Chaoborinae which played an important role in recycling energy away from the moderately utilised zooplankton and into the well-represented benthic feeding fishes.

Future avenues for research are listed and obvious changes which have occurred subsequent to the field investigation are described.

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TABLE OF CONTENTS

			PAGE
CHAPTER 1		INTRODUCTION	1
CHAPTER 2		LAKE KARIBA	9
	1	General information	9
	2	The limnological development of Lake Kariba	15
	3	Present limnological characteristics of Lake Kariba	17
		3.1 Temperature	17
		3.2 Water quality	18
	4	The dynamics of *Salvinia molesta* D.S. Mitchell	19
CHAPTER 3		THE MWENDA RIVER AND BAY	21
	1	The river	21
	2	The pools	26
	3	The "estuary" and bay	33
	4	The study area	36
CHAPTER 4		THE VASCULAR HYDROPHYTES	39
	1	Free floating forms	39
		1.1 *Salvinia*	39
		1.1.1 The forms of *Salvinia*	39
		1.1.2 Secondary growth	40
		1.1.3 Floating "sudd" islands	44
		1.1.4 The dynamics of the mat in the Mwenda River "estuary"	46
		1.1.5 Factors affecting the *Salvinia* mat dynamics	47
		1.1.5.1 Factors contributing to mat accumulation	49
		1.1.5.2 Wind action	49
		1.1.5.3 Factors contributing to mat dissemination	51
	2	The emergent littoral hydrophytes	52
	3	The submerged littoral hydrophytes	55
CHAPTER 5		THE PHYSICO-CHEMICAL LIMNOLOGY	62
	1	Methods	62
		1.1 Rainfall	62
		1.2 Flow	63
		1.3 Lake level	63
		1.4 Temperature	64
		1.5 Dissolved oxygen	64
		1.6 Turbidity	65
		1.7 Water samples	65
		1.8 Specific conductivity	66
		1.9 Total alkalinity and carbon dioxide	65
		1.10 The hydrogen ion concentration (pH)	66
		1.11 Laboratory analyses	66

2 Results 68
2.1 Rainfall 69
2.2 Flow 70
2.3 Lake level 70
2.4 Seasonal temperature changes 71
2.4.1 Seasonal temperature changes of the water column 71
2.4.2 Seasonal temperature changes from bay to river mouth 75
2.4.2.1 Waters free of Salvinia 75
2.4.2.2 The effects of the Salvinia mat .. 76
2.5 Seasonal changes in dissolved oxygen 76
2.6 Thermal and oxygen stratification 78
2.7 Flow effects 86
2.8 Other physico-chemical data 91
2.8.1 The characteristics of flowing river water 96
2.8.2 Enclosed "estuarine" waters free of Salvinia 96
2.8.3 Open "bay" waters 98
2.8.4 Enclosed "estuarine" waters covered by Salvinia 99
2.8.5 The change in water quality from river mouth to bay 105
2.8.6 The effects of the river on water quality 107
2.8.7 The effects of the Salvinia mat on water quality 107
2.8.8 Seasonal changes in static river waters 110
2.8.9 The water quality of different pools . 116
3 Discussion 118

CHAPTER 6 THE PLANKTON 128
1 Method 128
1.1 Problems in plankton sampling 129
1.2 Qualitative analysis 132
2 Results 135
2.1 Variations in plankton density 135
2.2 Spatial distribution of components 140
2.3 "Seasonal" distribution of components 142
2.4 Density centres 146
2.5 Important species not significant in samples 146
3 Discussion 148
3.1 Feeding relationships 148
3.2 The food of "herbivores" 151
3.3 Plankton density and flow 152
3.4 Plankton distribution in relation to the thermocline and dissolved oxygen 153
3.5 Plankton density and water quality 154
3.6 The level of plankton production 155
4 Conclusions 156

CHAPTER 7 THE BENTHOS OF LAKE WATERS 158

1 Introduction 158

2 The substrates 159

2.1 Methods 159

2.2 Results 160

3 The fauna 165

3.1 Methods 165

3.2 Results and discussion 170

3.2.1 The main station survey (February 1967 - February 1968) 171

3.2.1.1 Spatial differences in composition 171

3.2.1.2 Spatial differences in abundance . 177

3.2.1.3 "Seasonal" differences in abundance 181

3.2.1.4 "Seasonal" and spatial distribution of the numerically important species in each depth zone 182

3.2.1.5 The spatial distribution of all species 185

3.2.2 The drowned river bed transect (February 1967 - November 1968) 191

3.2.2.1 The major differences in "seasonal" and spatial abundance . 191

3.2.2.2 Faunal composition 195

3.2.2.3 The effect of Salvinia on the benthos of the drowned river bed . 201

4 General discussion 205

4.1 The effect of Salvinia on the benthos 205

4.2 The effect of lake level fluctuations in the marginal benthos 208

4.3 The effect of substrate on the benthic standing crop of the drowned river bed ... 215

4.4 The effect of depth and associated factors on the benthos 215

4.5 Distribution of the benthos in relation to water quality 214

4.6 The categorisation of the benthos 216

4.7 Faunal stability 216

4.8 Chaoborus in relation to zooplankton density 219

4.9 Standing crop 220

4.10 The bottom fauna food web 221

5 Conclusions 226

CHAPTER 8 THE FAUNA OF SUBSTRATES OTHER THAN THE BOTTOM MUDS 232

1 Introduction 232

2 The fauna of the drowned trees 232

2.1 Methods 233

2.2 Results 234

2.3 Discussion 235

3 The fauna of the Salvinia mat 237

3.1 Methods 237

3.2 Results 243

3.2.1 Salvinia compaction 243

3.2.2 Faunal composition 244

3.2.3 Variations in faunal density 249

3.2.4 Flow effect 262

3.2.5 The effect of compaction on faunal density 264

3.2.6 Biomass 264

4 The fauna of vascular hydrophytes 268
4.1 Introduction 268
4.2 Methods 268
4.3 Results 272
4.3.1 Faunal density and "seasonal" change . 273
4.3.2 Faunal composition 274
5 The variety and abundance of animals on the different substrates 277
6 Trophic representation 292
7 Observations on fish associated with the hydrophytes 296
8 Observations on the Odonata 297
8.1 The emergence of Odonata from breeding aquaria 297
8.1.1 Substrate suitability 300
8.1.2 Species importance and distribution .. 302
8.1.3 "Seasonal" variation 305
8.1.4 Discussion 307
8.2 Adult collections and their significance . 309

CHAPTER 9 THE FISHES: DISTRIBUTION IN LAKE AND RIVER ... 313
1 Methods of sampling 315
1.1 Mesh selectivity 320
2 Results from the quarterly gillnet programme (1967/68) 322
2.1 Species composition as reflected by gillnets 322
2.2 Variations in gillnet catches 322
2.3 Vertical distribution of species 326
2.4 Spatial differences in species composition 328
2.5 "Seasonal" differences in species composition 330
2.6 "Seasonal" changes in spatial distribution of species 332
2.7 The effects of unseasonal flooding 335
3 Discussion of the quarterly gillnet programme . 337
4 Results of the fortnightly gillnet programme (1968/69) 345
5 Discussion of all gillnetting results 355
6 Results and discussion of river catches 359
6.1 The trammel net and trap 359
6.2 Headlines 367
7 Telemetric tracking 368
7.1 The transmitter 368
7.2 The receiver 369
7.3 Encapsulation of the transmitter 369
7.4 Trials 371

CHAPTER 10 THE FISH: POPULATION OF THE DRY SEASON POOLS . 379
1 Introduction 379
2 Methods 379
3 The species 384
4 Annual differences in composition 385
4.1 Faunal density 385
4.2 Faunal composition 387
5 Distribution in relation to pool type 388
6 Size composition of pools fish 390
7 Juvenile habitat preference 393
8 Effects of pool attenuation 401
9 The tagging experiment 405
10 Discussion 407

CHAPTER 11 THE FISH: BREEDING 410
1 "Seasonal" changes in sexual activity 410
2 The sexual composition of species populations . 412
2.1 Maturation 412
2.2 The effect of size on sexual composition . 412
2.3 "Seasonal" changes in sexual proportions . 415
2.4 Sex ratios 416
3 Fecundity 416
4 The size of ova 418
5 Gonad stirfication in Hydrocynus 426
6 Early development 428
6.1 Hydrocynus vittatus 428
6.1.1 The perivitelline space 437
6.1.2 Preserved material 437
6.1.3 Yolk sac 438
6.1.4 Hatching time 438
6.1.5 Larval behaviour 438
6.1.6 Pigmentation 439
6.1.7 Growth rate 439
6.1.8 Teeth 440
6.2 The clariid (Heterobranchus longifilis) .. 441
7 Potamodromesis in the Mwenda River 447
7.1 Previous work on potamodromesis in Africa 447
7.2 Fish migration 449
7.3 Variations in migrational behaviour 455

CHAPTER 12 THE FISH: FOOD AND FEEDING 460
1 Introduction 460
2 Results and observations 462
2.1 Mormyridae 462
2.1.1 Mormyrops deliciosus 468
2.1.2 Cyphomyrus discorhynchus 465
2.1.3 Mormyrus longirostris 468
2.2 Characidae 473
2.2.1 Hydrocynus vittatus 473
2.2.2 Alestes imberi 476
2.2.3 Micralestes acutidens 478
2.3 Distichodontidae 479
2.3.1 Distichodus schenga 479
2.4 Cyprinidae 479
2.4.1 The Barbus species 479
2.4.2 The Labeo species 480
2.5 Schilbeidae 480
2.5.1 Eutropius depressirostris 480
2.6 Clariidae 482
2.6.1 Clarias gariepinus 482
2.7 Mochokidae 488
2.7.1 Synodontis zambezensis 488
2.8 Cichlidae 490
2.8.1 Tilapia mortimeri 490
2.9 Feeding activity 491
3 Discussion 495
3.1 A feeding categorisation of the fish fauna 495
3.1.1 Planktivorous species 495
3.1.2 Periphytic algal eaters 497

	3.1.3 Grazers	498
	3.1.4 Detritus feeders	498
	3.1.5 Invertebrate feeding	498
	3.1.5.1 Oligochaeta	498
	3.1.5.2 Crustacea	498
	3.1.5.3 Odonata	498
	3.1.5.4 Hemiptera	499
	3.1.5.5 Ephemeroptera	499
	3.1.5.6 Lepidoptera	499
	3.1.5.7 Trichoptera	499
	3.1.5.8 Culicidae	500
	3.1.5.9 Chironomidae	500
	3.1.5.10 Ceratopogonidae	500
	3.1.5.11 Terrestrial insects	500
	3.1.6 Molluscivorous fishes	500
	3.1.7 Fish predators	501
	3.1.8 Fish debris eaters	503
	3.2 Substrate utilisation	504
	3.3 Feeding and food availability	506
CHAPTER 15	GENERAL DISCUSSION	510
	REFERENCES	515
	APPENDICES	525

LIST OF TABLES

		PAGE
1.1	Some physical characteristics of man-made lakes.	2
1.2	Field periods spent at Sinamwenda and work carried out.	9
2.1	Main features of the morphology of Lake Kariba.	11
2.2	Lake Kariba water level fluctuations in metres - December, 1956, to December, 1969.	14
2.3	Water quality of the Mlibizi and Binga (I and II) and Central and Sanyati (III and IV) basins.	18
2.4	Total area of Salvinia on Lake Kariba (A) and percentage of lake surface covered by the plant (B).	19
5.1	Proportions of tributaries of Zambezi River drowned by flooding. Grouped according to length.	22
5.2	The pools of the lower reaches of the Mwenda River.	26
5.1	The analysis of kept samples.	67
5.2	Floods of the Mwenda River. July, 1966, to June, 1969.	70a
5.3	Water quality differences between the river and bay and the effects of the Salvinia mat.	96
5.4	The effects of enclosure and the Salvinia mat on lake water.	108
5.5	"Seasonal" changes in the water quality of the river.	111
6.1	Plankton counting trials on the basis of at least 100 plankters being counted.	133
6.2	Plankton density in mg/m^3, dry weight.	136
6.3	"Seasonal" variations in density of the main plankton species.	144
7.1	Description of the substrate types found at all stations.	161a
7.2	Bottom mud sample areas.	168
7.3	Approximate conversion values from numbers to wet weight for benthic organisms.	172
7.4	The total numbers/m^2 of each faunal taxon collected over five "seasons".	173
7.5	The percentage composition of faunal taxon by numbers.	174
7.6	The relationship between the number of numerically important species and the depth zones.	186
7.7	The total numbers of animals collected "seasonally" and the mean numbers per station.	192
7.8	"Seasonal" changes in the percentage composition of the fauna of the drowned river bed.	198
7.9	"Seasonal" variation in marginal populations.	210
7.10	Benthic sampling periods in relation to flow.	215
7.11	A comparison of the density of Chaoborus in benthos and plankton concentrations.	219
7.12	The mean standing crop in mg wet wt/m^2 of the "seasonal" survey, 1967/1968.	220
8.1	A comparison of the fauna of closely associated drowned trees within and away from the Salvinia mat.	255
8.2	The size, distribution and frequency of sampling of the Salvinia mat.	259

8.4	Mean "seasonal" differences (in numbers/m^2) of the major taxa collected from Salvinia throughout the study area.	245
8.5	The important constituents of the Salvinia fauna.	247
8.6	Total numbers of animals sampled in relation to area and live weight of Salvinia.	250
8.7	The relative importance of major taxa in relation to situation in the study area and occurrence at the edge or within the Salvinia mat.	258
8.8	Results (as nos/m^2) of the important constituents of the permanent mat transect, November, 1967, and February, 1968.	260
8.9	Mean standing crop of Salvinia fauna.	266
8.10	Faunal components of Salvinia in terms of percentage number and percentage weight.	267
8.11	The mean faunal collection of the aquatic macrophytes by "seasons".	273
8.12	The percentage, based on numbers, of faunal composition of rooted macrophytes by major taxa.	274
8.13	The percentage composition (based on numbers) of important species on rooted aquatic macrophytes.	275
8.14	The biomass of faunal components of the aquatic macrophytes.	278
8.15	The percentage composition by biomass of the fauna on various substrates.	279
8.16	The proportions of Chironomidae collected on different substrates.	284
8.17	The distribution and importance of the various species on the different substrates.	288
8.18	Proportions of population biomass of the different substrates separated as trophic levels.	294
8.19	Species emerged from all substrates and their relative importance based on numbers emerged.	300
8.20	The relative production and number of species found on each substrate.	302
8.21	The species composition of the different substrates.	303
8.22	The Odonata emergence data.	308
8.23	List of species present at Lake Kariba whose nymphal habitat is known.	310
9.1	The fish species taken by gillnet and their overall percentage composition by weight from April, 1967, to February, 1968.	323
9.2	The mean "seasonal" gillnet catch at different stations.	324
9.3	The "seasonal" mean abundance of fish species at all stations in g/8.2m/12 hours.	332
9.4	The effects of unseasonal flooding on the fishes at Station 3.	336
9.5	The importance of fish susceptible to gillnets relative to their own distribution and that of other fish species.	339
9.6	Population composition at 10 m as reflected by gillnets.	346
9.7	Catch by meshes.	347
9.8	Catch data from the flowing river.	350
9.9	Percentage composition of trammel net catches by numbers on different sampling periods.	361

10.1	Pools and dates these were sampled.	385
10.2	Annual differences in composition of the fish fauna of Surprise Pool.	386
10.3	The percentage composition by weight of pools with few rocks and those predominantly rocky. November, 1966.	389
10.4	Habitat preference of adult pools fish.	391
10.5	Estimate of growth of potamodromous species in the first nine months following spawning.	395
10.6	Mark recapture data. Deep Pool, 1967.	407
11.1	The size of sexual maturity of some species and the maximum length of these taken by gillnets.	414
11.2	The mean egg production per cm and regression coefficient "b" of some fishes.	418
11.3	The modal diameters of ova.	424
11.4	The numbers and percentage of specimens of each species containing ova with uni- or bimodal diameter frequency distributions.	424
11.5	Summarization of fish breeding data.	427
11.7	The development of the early stages of Hydrocynus vittatus at 24° - 26°C.	435
11.8	Approximate ageing criteria for Hydrocynus kept between 24° and 26°C up to 30 days and 28° thereafter.	441
11.9	The development of the early stages of a clariid at 22° - 25°C.	
12.1	Food items found in the stomach of Marcusenius deliciosus in the lake.	455
12.2	Food items found in the stomach of Marcusenius deliciosus from the flowing river.	455
12.3	The stomach contents of Cyphomyrus discorhynchus.	466
12.4	The stomach contents of Marcusenius longirostris.	470
12.5	The stomach contents of juvenile Marcusenius longirostris captured in the river pools.	473
12.6	The stomach contents of adult Hydrocynus vittatus.	474
12.7	The food of Alestes imberi from the lake.	477
12.8	The food of Alestes imberi from 11 to 13.1 cm in the pools.	478
12.9	The food of Petrocephalus deprezsirostris from the lake.	481
12.10	The food of Clarias gariepinus separated by station and "season".	485
12.11	The food of Synodontis zambezensis.	487
12.12	The proportions of larval and pupal chironomids in three fish species.	490
12.13	The proportions of larval and pupal Pinnaeodopsis gonagasis in three fish species.	490
12.14	Feeding activity of adult fish expressed as percentage of fish feeding.	492
12.15	The percentage frequency of occurrence of major food categories in adults of the different fish species of the lake.	496
12.16	A summarization of adult fish feeding categories.	505
12.17	The percentage frequency of occurrence of fish food separated according to source.	506

LIST OF FIGURES

		PAGE
2.1	Kariba.	10
3.1	Elevation gradient of the Mwenda River.	23
3.2	Typical stretch of the lower reaches of the Mwenda River. The rock barrier above Crocodile Bend Pool. January, 1968.	24
3.3	Typical stretch of the lower reaches of the Mwenda River. The rapid and fall above Deep Pool. December, 1966.	24
3.4	Typical stretch of the lower reaches of the Mwenda River. The downstream end of the Champs Elysees. January, 1968.	25
3.5	Typical stretch of the lower reaches of the Mwenda River. The downstream end of the Champs Elysees. October, 1968.	25
3.6	Deep Pool towards the end of the dry season (24.10.67) looking downstream.	29
3.7	Deep Pool in January, 1968. Flow approximately 200 cusecs.	29
3.8	Pool at the head of the Champs Elysees in August, 1967, looking downstream four months after the last rains.	30
3.9	The same, shortly before drying up completely two months later (24.10.67).	30
3.10	Diagrammatic plans and sections of three pool types (a) Champs Pool, (b) Surprise Pool, (c) Deep Pool, as interpreted from surface indications.	31
3.11	Cross sections of the drowned river bed.	35
3.12	The stretch between the Elbow and Jacana Bend.	37
3.13	The stretch between Winterthorn and Jacana Bend.	37
4.1	Salvinia auriculata. The "mat" form.	41
4.2	Salvinia auriculata. The "open-water" form, with some "mat" form plants from which they developed.	42
4.3	The Mwenda "estuary" in April, 1967.	43
4.4	The Mwenda "estuary" in October, 1968.	43
4.5	The ruderal and semi-aquatic colonisers of a block of floating dead Salvinia eleven months old.	45
4.6	The blockage at Eagles Nest in August, 1967, showing the main colonisers of the live Salvinia substrate.	45
4.7	Variation in area covered by Salvinia. May, 1965, to January, 1969.	48
4.8	The shoreline of Ceratophyllum Bay.	53
4.9	A stand of Panicum repens on the shoreline of Klipspringer Bay, Marker Island (November, 1968).	53
4.10	Potamogeton pusillus in an invasive stage.	56
4.11	Ceratophyllum demersum growing in 3 m of water.	56
5.1	Rainfall in fortnightly periods at the Nuffield Kariba Research Station showing flow and flooding periods in the Mwenda River.	69
5.2	Water level fluctuations of Lake Kariba, 1966 - 1968.	72
5.3	1°C isotherms at Station 5.	74
5.4	"Seasonal" transect of surface and bottom temperature.	75
5.5	"Seasonal" changes of dissolved oxygen at stations.	74
5.6	"Seasonal" changes of isotherms and dissolved oxygen isopleths of the water column overlying the drowned river bed, 25th April, 1967.	81

5.7	22nd July, 1967.	82
5.8	9th November, 1967.	83
5.9	20th January, 1968.	84
5.10	The effects of flow on the structure of static waters as described by isotherms and dissolved oxygen isopleths, 8th February, 1968.	89
5.11	2nd May, 1967.	90
5.12	A diagrammatic summarisation of flow effects on static waters near the river mouth.	93
5.13	"Seasonal" changes in the depth of visibility of a 30 cm Secchi disc. Transect results.	94
5.14	"Seasonal" changes in the depth of visibility of a 30 cm Secchi disc at the different stations.	94
5.15	"Seasonal" changes on selected chemical characteristics at the various stations. Station 5.	101
5.16	Station 1.	102
5.17	Station 4.	103
5.18	Station 6.	104
5.19	The "seasonal" changes in water quality of the static river.	113
5.20	Untreated water samples from the different pools.	115
5.21	Water quality of the different pools at the end of the dry season.	117
5.22	The range in estimates of nitrate, phosphate and total hardness from open lake to river.	125
6.1	The density isopleths of plankton over the drowned river bed in mg/m^3, dry weight.	157
6.2	The mean "seasonal" density changes.	158
6.3	The overall mean density of plankton components at the different stations.	159
6.4	The mean "seasonal" changes in density of the more important planktors.	145
6.5	The plankton food web showing relative sizes of planktors and their proportionate importance in the sampled population by weight.	150
7.1	Substrate of the drowned river bed.	162
7.2	A typical van Veen grab sample from the river bed.	164
7.3	The faunal composition at different stations and depths. January, 1967 - January, 1968.	175
7.4	Spatial differences in faunal abundance. January, 1967 - January, 1968.	178
7.5	"Seasonal" changes by depth and by station.	180
7.6	"Seasonal" differences in numbers of bottom fauna on the drowned river bed transect.	195
7.7	The "seasonal" distribution and abundance of the more important species of the river bed transect (1967 - 1968)	198
7.8	Temporal changes in abundance of some important species of the drowned river bed.	218
7.9	The gradation of mandible, labial plate and lingua in the larvae of the main chironomid genera of the Mwenda River south (1 - 8). Mandible of the larvae of *Dimesodiamesa zambesiana* and "Orthocladius" sp. 19 (9 and 10).	225
7.10	Food web of the bottom fauna from all depths showing relative abundance by numbers of constituents, fish excluded. January, 1967 - January, 1968.	227

7.11	Food web of the bottom fauna of the river bed showing the relative abundance by numbers of constituents, fish excluded. January, 1967 - November, 1968.	228
8.1	Test washings for faunal extraction from different vegetation substrates.	241
8.2	The Salvinia fauna (nos/m²) April and July, 1967.	251
8.3	The Salvinia fauna (nos/m²) November, 1967.	252
8.4	The Salvinia fauna (nos/m²) February, 1968.	253
8.5	The Salvinia fauna (nos/kg wet weight).	255
8.6	Typical samples of Ceratophyllum demersum and Potamogeton pusillus for faunal extraction.	271
8.7	Data of the emergence of Odonata from plant substrates.	301
9.1	Typical gillnet catches.	316
9.2	Total catches of various meshes by species.	321
9.3	The distribution and abundance of fish as reflected by gillnets.	325
9.4	The overall mean catch of different fish species separated according to vertical distribution.	327
9.5	The species composition in the open lake (1), the Salvinia-free waters of the "estuary", (3) and the Salvinia-covered portion of the "estuary" (5) at surface and bottom.	329
9.6	"Seasonal" changes in important species in surface and bottom nettings at the various stations.	333
9.7	Lake level and surface water temperatures of Sinazwenda Bay. July, 1968 - April, 1969.	345
9.8	Fluctuations of the mean total catch in Kg/91.8m/12 hrs showing flooding and flow periods.	349
9.9	Temporal fluctuations in density of the more important species as reflected by gillnets.	350
9.10	The transmitter circuit of Dr. A.E. Rogers.	369
9.11	The aerial and receiver.	370
9.12	The encapsulated transmitter.	372
9.13	Clarias and the first type of transmitter.	373
9.14	The transmitter in dissected stomach.	374
9.15	The effects of the second type of transmitter in the stomach of Hydrocynus after one week.	377
10.1	The 15 mm seine net operating in Surprise Pool, November, 1968.	380
10.2	A typical catch of the 15 mm seine net.	380
10.3	The sequential catch of a 15 mm seine net before and after application of rotenone.	381
10.4	The collection of juvenile and small adult fishes after the application of rotenone.	382
10.5	Part of a typical collection of juvenils and adult fish following the application of rotenone.	382
10.6	The size composition of the entire fish population of Hammerkop and Surprise Pools. November, 1968.	393
10.7	Size composition of fish in Champe and Hammerkop Pools. November, 1967.	394
10.8	The length frequencies of Labeo and Tilapia in Surprise and Rocky Pools, November, 1968.	398
10.9	Length frequencies of fish in Champe Pool.	402
10.10	Weight differences in individual tagged Hydrocynus in Deep Pool between August and November, 1967.	404
10.11	Photograph to illustrate condition of 100, 500 and 1000 g fish. Deep Pool. November, 1967.	404

10.12	A comparison of condition of Hydrocynus relative to size in the lake and in Surprise Pool.	406
11.1	"Seasonal" changes in sexual activity of male and female fishes.	411
11.2	The sexual composition of different species populations in relation to length.	415
11.3	"Seasonal" changes in the proportion of male fish.	417
11.4	Egg production of ten species in relation to length.	419
11.5	Ova diameter frequency of "ripe" specimens of 15 species.	422
11.6	The early development of Hydrocynus vittatus.	430
11.7	The early development of a clariid, probably Heterobranchus longifilis.	445

A map of the study area is bound with the end fly-leaf.

APPENDICES

		PAGE
1.1	Preliminary observations on some aspects of the biology of the Sinazwenda estuary, Lake Kariba.	525
5.1	The use of the word "estuary" in a freshwater context.	532
5.1	Hydrological sampling: January/February, 1967.	537
5.2	Hydrological sampling: April, 1967 (Prior to flooding).	538
5.3	Hydrological sampling: May, 1967 (after flooding).	539
5.4	Hydrolobical sampling: July/August, 1967.	540
5.5	Hydrological sampling: October/November, 1967.	541
5.6	Hydrological sampling: January/February, 1968.	542
6.1	Species density of plankton in mg/m^3 dry weight on different sampling dates.	543
7.1	A list of invertebrate species collected.	545
7.2	Benthic marginal sampling.	555
7.3	Benthic animals at 5 m.	556
7.4	Benthic animals from 10 m.	557
7.5	Benthic animals of the river bed: January, 1967, to January, 1968.	558
7.6	The constitution of the benthic fauna by taxa at the various depths (January, 1967, to January, 1968).	559
7.7	The constitution of the benthic fauna by taxa at the various stations (January, 1967, to January, 1968).	560
7.8	The river bed transect. January, 1967.	561
7.9	The river bed transect. April/May, 1967.	562
7.10	The river bed transect. July, 1967.	563
7.11	The river bed transect. October, 1967.	564
7.12	The river bed transect. January, 1968.	565
7.13	The river bed transect. May, 1968.	566
7.14	The river bed transect. July, 1968.	567
7.15	The river bed transect. October, 1968.	568
8.1	General collections from submerged trees.	569
8.2	Results of sampling of the *Salvinia* mat: April, 1967.	570
8.3	Results of sampling of the *Salvinia* mat: July, 1967.	571
8.4	Results of sampling of the *Salvinia* mat: November, 1967.	572
8.5	Results of sampling of the *Salvinia* mat: February, 1968.	573
8.6	The fauna collected from *Ceratophyllum demersum*.	574
8.7	The fauna collected from *Potamogeton pusillus*.	575
8.8	The fauna collected from *Lagarosiphon ilicifolius*.	576

CHAPTER 1

INTRODUCTION

The last decade has been one of active construction of major dams and the formation of man-made lakes throughout Africa. Present indications are that this trend will continue. Many of these dams (Table 1.1) have been built primarily as reservoirs for hydro-electric power generation, but their creation provides the opportunity for other uses, such as irrigation, fisheries, transport and recreation. If account is taken of the human population explosion at present taking place in Africa, it is foreseeable that in the future the relative importance of the alternative uses of these lakes will change, perhaps, to production of food, and especially animal protein, rather than the generation of hydro-electricity.

Lake Kariba was unique, in that at the time of its closure, little experience had been gained of the types of physical, chemical and biological changes that could be expected during the formation and maturation of a tropical man-made lake. This inexperience can be gauged by reactions which were, for example, generated by the unexpected invasion by the water fern, Salvinia auriculata Aublet. Various attempts had been made to anticipate possible changes; by clearing bush at great expense to make fishing grounds; by introductions of Tilapia macrochir (Boulenger) to fill the open water microphytophagous niche which, it was thought, would not be filled by any of the lotic fish populations endemic to the Zambesi River. In view of subsequent experience,

TABLE 1.1 SOME PHYSICAL CHARACTERISTICS OF MAN-MADE AFRICAN LAKES

Partly after Worthington (1966)

Lake/Reservoir	Area when full (km^2)	Maximum depth (m)	Maximum drawdown (m)	Ratio of annual outflow to volume
Kariba	5,250	120	9	0.26
Volta	8,500	70	3	0.25
Nasser	5,000	97	na	0.50
Kainji	1,280	55	10	4.00
Kafue Gorge	c. 3,090	58	c. 7	2.00 (after White, 1965)
*Teshi Teshi	c. 310	34	26	2.00 (after White, 1969)
Jebel Auliya	600	12	c. 6	8.00
Sennar	140	16	c. 17	70.00
Roseires	200	na	c. 42	14.00
*Cabora-Bassa	2,739	157	na	na
*J.C. Strydom	133	70	34	0.43
Hendrik Verwoerd	364	70	41	0.47
*P.K. Le Roux	97	76	47	

*Projects incomplete na: not available

some of the preparatory action which took place before the formation of Lake Kariba is open to question. Retrospective criticism is of value only when used pragmatically and in this respect, the experience gained from the formation and maturation patterns of Lake Kariba could be particularly valuable if applied to subsequent schemes in tropical Africa.

As soon as it was decided, in March 1955, that the Kariba dam was to be built, the desirability of research in the area to be flooded was widely appreciated. In the limnological field, however, research on the middle Zambezi prior to closure was limited to some taxonomic data pertaining to fish species present in the middle Zambezi by R.A. Jubb, and to four research trips by the Joint Fisheries Research Organisation in 1956 and 1957 (Jackson 1961a). Work undertaken by this Organisation was severely limited owing to its commitments elsewhere in Northern Rhodesia but nevertheless is valuable as the only limnological research carried out at the time. The J.F.R.O. continued research in the area on closure of the dam (Bowmaker 1960) as well as after closure (Harding 1961, 1962, 1964a and b, 1965, 1966). Following closure the situation improved in that several organisations participated in limnological research on the infant lake. One of these was the Zoology Department of the University of the Witwatersrand which organised expeditions to the Binga area of the lake in 1959 and 1960 (Balinsky and James 1960) to record some of the first biotic changes caused by the formation of a lotic environment. Notwithstanding the participation of many different Government and quasi-governmental organisations, in 1959 it was recognised by both the University of the Witwatersrand and the University College of

Rhodesia that the creation of a focus for research on a long term basis was necessary. Representations made by these two Institutions to this end resulted in an area of 150km^2 of the Chete Game Reserve, between the Lusikulu and Mwenda Rivers, being set aside in 1960 as a Research Reserve by the Southern Rhodesian Government, and grants amounting to £74,000 were subsequently donated by the Nuffield Foundation for the establishment of a field station. In 1968 the financial responsibility for the Nuffield Lake Kariba Research Station was assumed jointly by the two Universities concerned.

The terms of reference of the Research Station are, broadly, to study both the short and long term effects of the inundation of the Zambezi valley in all its scientific and social aspects. The aims of the present project are:

1. To investigate the hydrobiology of the Mwenda river and its mouth with especial reference to (a) the seasonal abiotic changes, (b) the spatial and seasonal changes in the distribution and abundance of the biota, and (c) the feeding relationships of the aquatic fauna, culminating in fish.
2. To investigate the effects of a permanent mat of floating vegetation on the hydrobiology of the area in the immediate vicinity of the river mouth.
3. To investigate the potamodromous behaviour of the fish species of Lake Kariba in the Mwenda river.

It was considered, in planning this work, that the rivers entering Lake Kariba and particularly the areas associated with their mouths, were likely to be of critical biological importance

for several reasons. Firstly, it was not known whether or not the biota in the "estuarine" areas of the lake were distributed in such a way as to imply the existence of an ecotone between river and lake. Secondly, the rivers were known to be a major source of fresh nutrient, and little or nothing was known of the method of entry of their waters into the lake. Thirdly, the distribution and abundance of species could give some indication of the sources of the lake fauna, although findings would inevitably be confusing. Would, for example, species found to be present in the lake have arisen directly from the present lotic fauna, or would its presence in both indicate colonisation in the opposite direction? Namely, lentic foothold might have been necessary prior to lotic colonisation, and the present lotic fauna could have been modified by the lake's formation. This interesting problem could only be solved partially at this stage of Lake Kariba's maturation and a comparative knowledge of the original situation can now only be derived from a study of similarly sized rivers downstream of the dam wall. Investigation of a similarly sized tributary to be flooded by the Cabora-bassa dam, before and after flooding, would be particularly interesting in this context. The fourth reason for the biological importance of river mouths arises from the potamodromous breeding behaviour of a significant portion of the fish population of Lake Kariba. This is emphasised by the fact that, perhaps because of their lotic origin, the fish population would appear to be largely confined to the margins of the lake.

The somewhat formidable scope generated by the holistic approach of this project was intentionally chosen for two main

reasons and arose from the terms of reference for the Research Station imposed by the Trustees of the Nuffield Foundation. The first involved the necessity for an understanding of the overall ecological circumstances of an important part of the research reserve so as to form a basis for the design of future more intensive projects of limited scope. Secondly, it was and is anticipated that the project, or parts of it, will be repeated at intervals of ten or fifteen years so that a reasonably exhaustive and accurate picture of the sequence of maturation of the Mwenda river and bay may be ascertained. A further intention was that the results of this project would contribute towards an eventually comprehensive picture of the hydrobiology of the Sinamwenda area as one step in a succession of projects, started by those of my colleagues, Balinsky, James, Douglas, Mitchell, McLachlan, A., McLachlan, S., Hancock, Thomas, Jarman and Magadza. (See Anon. 1969).

The planning of this project was directed towards obtaining as accurate, statistically verifiable data as possible on a seasonal basis. Any approach on a shorter term basis or the use of a larger area for a project of this scope, however desirable, was impracticable. It was found that during the course of the project efficiency in data collection improved considerably and the volume of unprocessed data accrued alarmingly. It was therefore considered that, apart from the limit on time, a continuation of routine data collection would preclude any exploratory lines of research. Furthermore, the degree of correlation in any two years must, it was considered, be limited and to increase annual

correlations would have required a continuous routine for five, or perhaps even ten years. In addition to this, the situation being monitored was essentially one of change and maturation. For these reasons the full routine of seasonal data collection was continued for five seasons only. A limited routine was instituted thereafter which left sufficient time for other research within the scope of aims of the project, which included the feeding requirements of Hydrocynus vittatus (Cast.), and the development of bioteleometric tracking devices on two species of potamodromous fishes. A more detailed description of work carried out while at Sinamwenda is given in Table 1.2.

The first chapters which follow concern the limnological history of Lake Kariba, followed by a description of the study area. Thereafter, the approach adopted separates the different chapters according to the ecological grouping of the communities studied. The methods used to collect information, and the data obtained, is presented and discussed. Later chapters consider various aspects of fish biology. Full results are presented as appendices, for the benefit of future workers in the area. Relevant data are extracted for presentation within the text.

TABLE 1.2 FIELD PERIODS SPENT AT SINAMWENDA AND WORK CARRIED OUT

Date		Nature of work undertaken
4/8-7/8	1966	Exploratory examination of study area.
20/10-17/11	1966	Manufacture of weir, gillnets, plankton sampling gear and other equipment. Breeding of larval and pupal forms. Intensive study of Surprise Pool. Exploratory sampling of study area.
5/1-11/2	1967	First full sampling routine of hydrology, plankton, benthos, aquatic plant fauna and fish population started. (1)
12/4-9/5	1967	Full sampling routine. Benthic transect initiated. (2)
23/5-25/5	1967	Visit with supervisor.
8/5	1967	Flight over Kariba shoreline.
13/7-12/8	1967	Full sampling routine. Pools biocoenoses examined. (3)
18/10-17/11	1967	Full sampling routine. Pools biocoenoses examined. (4)
19/1-13/2	1968	Final full sampling routine. Concentration of effort, when routine complete, on potamodromous fish. (5)
6/5-10/5	1968	Benthic transect. Tanks for feeding experiments set up, exploratory fish introduced. Seining in river.
28/6-30/7	1968	Feeding experiment I. Benthic transect. Netting programme at Station 3 initiated. Champs Pool exclusion experiment started. Some pools biocoenoses examined.
1/9-8/9	1968	Student field trip. Champs Pool experiment, stage 2.
19/10-25/11	1968	Feeding experiment II. Benthic transect. Champs Pool experiment final stage. Biotelemetric tracking device trials. Pools Biocoenoses sampled.
9/12-18/12	1968	Biotelemetric tracking device trials.
12/2-23/2	1969	Biotelemetric tracking device trials. Final benthic transect.
4/4	1969	Termination of Station 3 gillnetting programme.
August	1969	Initiation of deep water gillnetting programme.

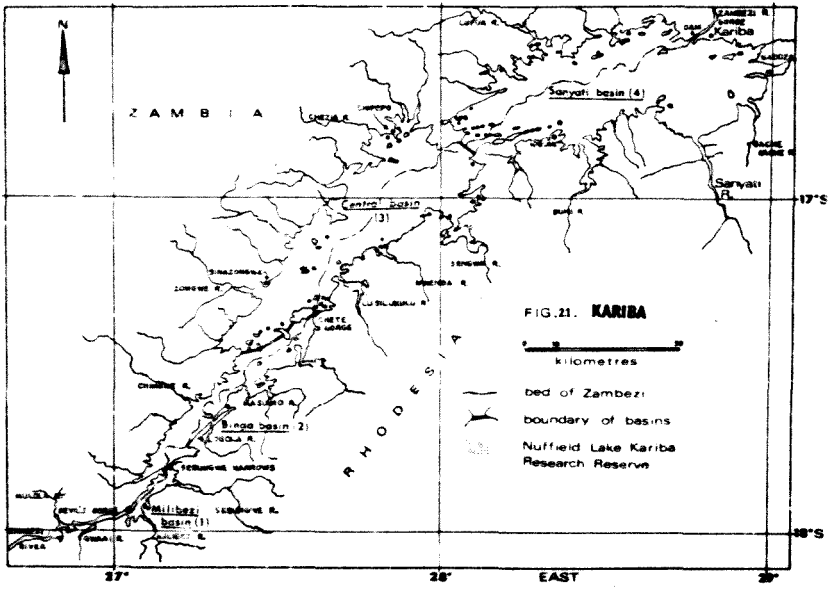
CHAPTER 2

LAKE KARIBA

1. GENERAL INFORMATION

In December 1958, closure of the dam across the Kariba Gorge resulted in the creation of one of the largest man-made lakes in the world. This impoundment is shared by Zambia and Rhodesia; the boundary between these countries follows the submerged bed of the Zambesi River, which more or less bisects the lake longitudinally.

Lake Kariba is naturally divided into four connected basins, classified by Bond (1965) along the North-East to South-West axis as the large Sanyati basin, the Central basin and the smaller Binga and Sebungwe-Milibisi basins (Fig. 2.1). Bond's estimates show that much of the present lakeshore consists of Karroo sedimentary deposits of the Maltano series, though gneisses occur on the southern shoreline of the Sanyati basin in the vicinity of the Matusadona fault. Bond also describes the flooded valley of Zambesi as being a relatively flat peneplain. Apart from one section of the Sanyati basin shoreline the peneplain has been submerged and the shoreline consists of steep slopes which bounded this erosional feature. The steepness of slope is modified in places by local irregularities and is also affected by the background topography of the region. This is of a dipslope-scarpslope type and the structural grain runs parallel to the axis of the lake. Thus the north-facing scarpslopes emphasize slope steepness on the southern, Rhodesia, side of the lake and south-facing dipslopes


N
ZAMBIA
Kariba
Sanyati basin (4)
Sanyati R.
17°S
Centre basin (3)
RHODESIA
Binga basin (2)
Mlibizi basin (1)
18°S
27°
28°
29°
EAST
FIG.21. KARIBA
kilometres
bed of Zambezi
boundary of basins
Nuffield Lake Kariba Research Reserve

moderate the steepness of the northern shoreline. As the lake is subjected to greater, more abrupt fluctuations than those normally experienced by natural lakes, this variation in shoreline slope is a feature of importance to the littoral biota of Lake Kariba. The flooding of the old peneplain has had a marked effect on the characteristics of the Zambezi tributaries as these now flow directly into the lake with characteristics of headwaters. Using the classification suggested by Illies (1961) and followed by Harrison (1965), the rithronic parts of these rivers, with steep elevation gradients, enter directly into the lake, and the potamonic sections, once present in the old peneplain, have been obliterated. This factor will be considered later in the light of biological effects.

Lake Kariba lies at an altitude of 484 m above mean sea level (at operational level) and between latitudes 16° 28'S and 18° 6'S and longitudes 26° 40'E and 28° 03'E. The longitudinal axis of the lake is orientated along a line from South-West to North-East. The main features of the lake's morphology are given in Table 2.1

TABLE 2.1 MAIN FEATURES OF THE MORPHOLOGY OF LAKE KARIBA (after Coche 1968)

Length	300–320 km
Width (mean)	20 km
Width (maximum)	40 km
Depth (mean)	29.5 m
Depth (maximum)	120 m
Area (484 m a.m.s.l.)	5,250 km^2
% Area between 0–15 m	28%
% Area between 15–30 m	28%
% Area between 30–60 m	38%
% Area between 60–116 m	6%
Volume	155 x 10^9 m^3

The meteorological year in the vicinity of Lake Kariba is divided into seasons based on temperature and rainfall. The warm season lasts from October to March, during which period the monthly mean air temperature range is between 22°C and 29°C. The cooler period lasts from April to September and the lowest air temperatures (15°C) occur in June and July, although frost did occur in the vicinity of Kariba Township in 1968. The rainy season begins in November and usually extends to March. Annual rainfall varies from approximately 700 mm on the Zambian shoreline to between 400 and 600 mm on the Rhodesian side of the lake. Only exceptionally does rain fall in the dry season between April and October. Strong south-easterly winds occur between April and August, and for the rest of the year prevailing winds are lighter and northerly. Potential evaporation has been estimated by Cochè (1968) to range between 2,500 and 3,600 mm annually. The seasons can be roughly separated as follows:

Cold/dry season	June-August	(Winter)
Hot/dry season	September-November	(Spring ?)
Hot/wet season	November-March	(Summer ?)
Cool/dry season	March-May	(Autumn ?)

It can be seen that temperate seasonal nomenclature is unsuitable.

After the dam's closure in December 1958, peak level was reached four and a half years later in July 1963 (487.81 m a.m.s.l.). The lake level was then dropped to "normal operating level" (about 484 m) around which point it fluctuated gently until the abnormal rains experienced in early 1969, when the level again rose rapidly to over 487 m a.m.s.l. During the period 1964-1969, following

the filling period, minimum levels normally occurred during January, February and March, and maximum levels in July or August, following the inflow of the main Zambezi floods from the Barotse flood plains. The normal maximum operating level for hydro-electric purposes has been set at 484 m above mean sea level. The lowest drawdown level is 475 m and the maximum flood storage level 489 m. The annual fluctuation was planned to average 3.5 m. Actual levels reached and fluctuations experienced up until May 1969, are given in Table 2.2.

2. THE LIMNOLOGICAL DEVELOPMENT OF LAKE KARIBA

Limnological data pertaining to Lake Kariba stem from the works of Harding (1962, 1964a and b, 1965, 1966) who covered the period from closure in December 1958, up to December 1963; Coche (1968) whose work covered the period from April 1965, to January 1966; and Begg (1969) who reported on results obtained during 1967 and 1968. The pattern of maturation which seems to emerge from these works, as illustrated by the findings of these workers at the "Boom Station" in the Kariba gorge, is as follows: Initially, stratification was established quickly during the hot season, but the metalimnion was pushed deeper as the hot season progressed and was eventually broken down during the cold season by the action of wind and lowering surface temperatures, when complete mixing occurred. The hypolimnion became anoxic within weeks of closure and hydrogen sulphide was generated from the decomposition of the large accumulation of organic matter resulting from the inundation and subsequent death of terrestrial vegetation. This anoxic period persisted for seven months, until July 1960, when turnover

TABLE 2.2 LAKE KARIBA WATER LEVEL FLUCTUATIONS IN METRES - December 1958 to December 1969
(Data from the Central African Power Corporation)

	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Maximum	411.20	449.93	461.55	472.38	480.39	487.84	483.05	485.49	486.17	484.07	485.01	487.62
Minimum	391.43	418.73	450.37	461.31	472.04	481.53	480.71	482.61	481.79	482.54	482.83	482.13
Difference	19.77	31.20	11.16	11.07	8.35	6.31	2.34	2.88	4.38	1.53	2.18	5.50

——————— Filling Period ———————

resulted in aerobic conditions in the deeper waters. The thermocline was reconstituted by October 1961, at a depth of 4 m, but by early January, when anoxic conditions again prevailed in the hypolimnion, it moved deeper to 15 m. Anoxic conditions and H_2S generation in the hypolimnion was again found to persist for seven months until the July overturn. In 1962, the anoxic period lasted for eight months, but H_2S only appeared in the hypolimnion for the latter six months and by 1963 the respective periods were eight months and three months. No data were collected on H_2S generation in 1964. In 1965 Coche found that this decrease persisted, but for the first time dissolved oxygen was found to occur for three months prior to overturn in the upper waters of the hypolimnion. Oxygen was again found in the upper waters of the hypolimnion in 1966, but occurred here six months after thermocline formation and persisted for three months after the water associated with the bottom had become anoxic.

The pattern established immediately upon closure was thus repeated annually, with the basic difference that both the anoxic and the hydrogen sulphide period became progressively shorter, suggesting that nutrients leached from decomposing vegetation and newly flooded soils of the peneplain were becoming depleted. Harding's (1964) chemical analyses support this supposition, in that dissolved salines declined from 69 ppm in 1958 to 48 ppm in December 1961, and 42 ppm in December 1964. By 1965, Coche, whose research involved the entire lake and not just the "Boom Station" at the dam wall used by Harding, found that H_2S was confined to some deep valleys within the hypolimnion and then only towards the end of the stagnation period. Coche also found differences between the four basins.

In the Milibisi/Sebungwe basin (I), nearest the inflowing Zambesi River, he found that there was always at least 5 ppm dissolved oxygen present at all times. In the other three basins, the rate at which oxygen depletion occurred increased progressively towards the lower, Kariba, end of the lake. During 1967 Begg found that the H_2S period at the "Boom Station" increased to seven months. During 1968 no H_2S was detected at the "Boom Station" at all. It did occur, however, in bottom debris associated with permanent Salvinia mats. Begg's findings indicate that the presence of H_2S and anoxic conditions in the hypolimnion of the Kariba gorge area (the "Boom Station" on which the maturation picture is based) results from a complex flow pattern associated with the flushing of the Sanyati basin by river water. He believed that the lack of H_2S in the gorge area in 1968 was a result of the poor flow conditions of the Sanyati River during the 1967/68 rains. The divergence of the 1967 and 1968 conditions from the trend traceable prior to these years would suggest that these two years are atypical and until such time as this new trend, if it be so, is established by future findings, should perhaps be regarded as such. Some reservations should also apply to considerations of data collected at the "Boom Station", which are typical of only one small part of the lake. On the other hand, this is the only published sequential data available since the closure of the dam and consequently must be used.

With these reservations and except for what may have been atypical results during 1967, the general pattern of stabilisation of Lake Kariba has followed a sequence which could be expected after consideration of the events experienced in temperate climates explained by Stroud (1966) as follows: "for three or five years

(after closure) there characteristically is an extinction of dissolved oxygen in the hypolimnion and distinct chemical as well as thermal stratification. These conditions become modified favourably to a greater or lesser extent in the following years". Beckmann (discussion in Rzoska 1966) quotes the more specific phasing of maturation by I.I. Lapitsky as follows, (1) a sudden increase in the standing crop, (2) a depression which lasts some time, (3) a gradual increase in productivity. He considered that the second stage may last six to ten years in southern reservoirs (less than 50° latitude) and twenty to thirty years in high latitudes.

The high temperature regime of Lake Kariba and the findings of Harding, Cochet and Begg indicate, on consideration of Lapitsky's phasing, that the third stage of maturation has, or has nearly, been reached. A gradual increase in productivity should therefore be expected.

3. PRESENT LIMNOLOGICAL CHARACTERISTICS OF LAKE KARIBA

3.1 Temperature

The established thermal regime of Lake Kariba follows a regular annual cycle, where the water mass overturns and reaches homothermy at between 21.4 and 23.4°C between March and July. Restratification normally starts in September and the metalimnion thereafter moves progressively towards the bottom. In the majority of cases the top of the metalimnion reaches 20 m by February of each year.

Coche (1968) classifies Lake Kariba, on the basis of the thermal properties of the water masses and in analogy with the classification proposed for lakes by Hutchinson (1957), as a warm monomictic

reservoir.

5.2 Water Quality

Table 2.3 gives the ranges of values found by Cocke (1968) for waters of the two upper and two lower basins, which he separates on the basis of the influence of the inflowing Zambezi River. Basins III and IV were found to be richer than basins I and II.

TABLE 2.3 WATER QUALITY OF THE MILIBIZI AND BINGA (I & II) AND CENTRAL AND SANYATI (III & IV) BASINS. (Data from Cocke (1968))

		BASINS I & II	BASINS III & IV
pH		7.7–8.4	7.5–8.6
Specific conductivity (μmhos)		50–100	86–116
Calcium	ppm	2–10	7–13
Magnesium	ppm	0.5–3.0	0.5–3.0
Sodium	ppm	1.–3.6	3.2–4.7
Potassium	ppm	TR–1.8	0.6–1.6
Nitrites	ppm	0–0.002	0–0.004
Nitrates	ppm	0.003–0.040	0.010–0.050
Phosphates	ppm	0–0.05	0.01–0.05

Cocke (1968) found that at overturn there was a drop in total hardness, while concentrations of magnesium, nitrites and phosphates increased in surface waters. A sharp increase in nitrates and a synchronous decrease in nitrites was observed to occur several weeks later. As the thermocline established, nitrates and phosphates were found in ever increasing quantities in the hypolimnion, and decreasing quantities in the epilimnion. Nitrites progressively appeared in deeper waters. He defines Lake Kariba on the basis of water quality as being chemically mesotrophic.

4. THE DYNAMICS OF SALVINIA AURICULATA AUBLET

Perhaps one of the most obvious indicators of changing conditions in Lake Kariba is the population fluctuations experienced by the Kariba "weed", Salvinia auriculata Aublet, and associated plants, which form dense, sometimes impenetrable mats of vegetation on the lake's surface. This vegetation has been reported on quite extensively, by Schelpe (1961), Hattingh (1961) and Boughey (1963). The most valuable contribution has been that of Mitchell (1960, 1965, 1967, 1969, 1970) in his study of the autecology of this water fern.

TABLE 2.4 TOTAL AREA OF SALVINIA ON LAKE KARIBA (A) AND PERCENTAGE OF LAKE SURFACE COVERED BY THE PLANT (B) (FROM MITCHELL 1969). COVERAGE FIGURES OBTAINED BY AERIAL SURVEY

Date	(A) km^2	(B) Percentage
April 1960	286	12
August 1960	421	14
March 1961	580	18
August 1961	724	18
May 1962	1003	22
April 1965	795	15
March 1964	529	11
May 1965	651	12
June 1967	823	16

Salvinia auriculata appears to have been introduced to the Zambezi River before 1949, when it was first collected above the Victoria Falls. The species made spectacular use of excessive nutrient and calm conditions during the formation of the lake, and from 1959 to 1962 expanded rapidly (Table 2.4) until 22% of the lake surface was covered by Salvinia. These mats of vegetation offered a stable substrate for the development of secondary invaders, studied by

Boughey (1963) who lists a total of forty species. One of the principal species which colonised the Salvinia mat was the sedge Scirpus cubensis Poepp. and Kunth , whose prostrate habit had the effect of binding and consolidating blocks of Salvinia. At the time of very high level reached in 1963, however, Mitchell (1965) proposed that fewer sheltered areas suitable for the growth of this plant were available. This factor, coupled with the increased fetch of waves, resulted in the extensive destruction of the mats, which were cast onshore. Mitchell (1965) points out that the further decrease in 1964 resulted from a rapid drop in water level. This stranded large blocks of mat, which as a result died. Although by 1967 the mat had increased to cover 16% of the lake surface, Mitchell (1969) points out that since 1963 the plant has been largely confined to sheltered bays and inlets; even here if results presented later in this work are broadly applicable, there are fluctuations resulting from river floods.

The picture which emerges from consideration of research findings on Lake Kariba is, therefore, one of comparative rapid change in what was still, ten years after closure, an early phase of maturation. Other biotic changes which have occurred will be presented for discussion in later relevant chapters.

CHAPTER 3

THE MWENDA RIVER AND BAY

1. THE RIVER

The Mwenda River is one of the smaller rivers flowing into Lake Kariba and is perhaps typical of most of the drowned Zambezi tributaries both in size and physical conformation, as partly demonstrated in Table 3.1. The catchment of the Mwenda River is relatively local being below the upper edge of the Zambezi escarpment, and is small, extending over an area of 270 km^2, with the source 22.5 km inland by the shortest distance, at a level 800 m a.m.s.l., about 123 m above normal operating level of the lake. The length of the river bed is approximately 40 km, so that the mean elevation gradient is 1 : 125. The lower gradient (1 : 320) of the flooded portion of the river reflects the levelling effect of the valley peneplain. Variations in gradient are shown in Fig. 3.1. The river arises from and descends through the very broken country of the Zambezi escarpment, in this area composed of Karroo sedimentary sandstones and shales of the Molteno series, so that it is characterised by frequent small waterfalls and some long boulder stream rapids, interspersed with broad flat stretches of mud, sand and gravel, or mixtures of each (Figs. 3.2 - 3.5).

No hydrophytes were found in the river bed during the period of study, other than for the occurrence of a species of Chara in some of the pools during the dry season. This is a reflection of the rigorous environment imposed by the extreme changes

TABLE 2.1 PROPORTIONS OF TRIBUTARIES OF ZAMBEZI RIVER DROWNED BY FLOODING (partly after Begg, 1970) GROUPED ACCORDING TO LENGTH.

River	Present Length (km)	Drowned Portion (km)	Percentage of Original River Drowned (%)
Senyati	451	45	10
Sengwa	229	45	16
Bumi	150	45	25
Mlibizi	101	10	10
Nacdza	92	59	30
Setungwe	80	11	12
Charara	60	30	54
Lusilukulu	58	16	22
Mwenda	42	18	30
Semkwe	32	19	38
Lagala	32	8	20
Gache Gache	27	55	86
Sibilobilo	13	16	86
Masumo	13	28	67

FIG. 3 ELEVATION GRADIENT OF THE KENYENDA RIVER

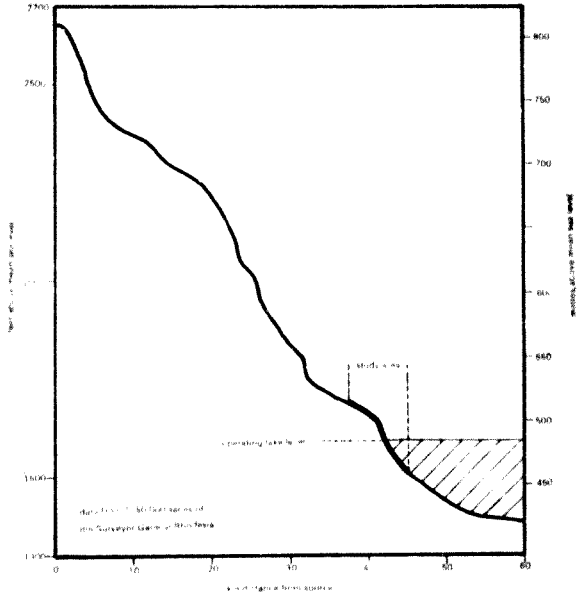




Fig. 4. Typical stretch of the lower reaches of the Mwaru River, on route Murrier-Aucru Bridge-Mwaru Falls. January, 196 .



Fig. 5. Typical stretch of the lower reaches of the Mwaru River. The rapid and fall above last fall. November, 196 .



Fig. 7.4. Typical stretch of the lower reaches of the Mwanja River. The downstream end of the Lake Chilwa. January, 1965.



Fig. 7.5 Typical stretch of the lower reaches of the Mwanja river. The lowstream end of the Chezza Plateau. October, 1964. The thin layer of sand deposited over the sand has been disturbed by the passage of game animals.

in seasonal water availability. The vegetation described by Jarman (1938) as "riverine" was found in a narrow band up to 30 m wide along the river bank, wherever level areas allowed its development, but the only macrophytic vegetation which actually contacts the water, and this only in as much as its branches trail in the water during the rainy season, is the shrub Combretum obovatum, which was found with some frequency directly along the margins of the river and was usually growing abundantly wherever steeply cut banks occurred; perhaps as a result of interaction between high water requirement and the necessity for protection from flooding.

At the beginning of the rains, normally in December, the river starts flowing and its main characteristic thereafter is one of intermittent, violent, flash flooding, which could cause a rise of up to 3 metres within 30 minutes, when flow has been roughly calculated and approximates to 57 cubic metres/second, and is followed by an equally abrupt decrease of lesser magnitude. Thereafter there is a gradual decrease to a trickle of 0.1 to 0.3 cubic metres/second within a week to ten days, and it may actually cease. For most of the rainy season the river is characterised by long post-flood periods when small, slowly decreasing quantities of water flow downstream. The Mwenda River finally stops flowing in April or May with the end of the rains and quickly dries up into a series of pools several hundreds of metres apart (see map against end cover), which largely persist until the onset of the following rains.

8. THE POOLS

The pools of the Mwenda River within the study area, and their environmental characteristics, are tabulated in geographical

sequence in Table 3.2. Typical pools are illustrated in Figures 3.6 to 3.9. The basic difference between pools physically unaffected by the lake is related to their permanence. Some are persistent throughout the dry season, others are ephemeral in nature and dry before the river starts to flow again. Another basic environmental difference is associated with the degree of cover, provided by broken rock, to the faunal constituents. Pools fall into two clear cut categories in this respect; namely, they either have extensive rock coverage (30 - 60%), or very little (0 - 10%).

Research was largely concentrated on four pools (see map against end cover) as examples of the three main environmental types present in the study area. Surprise Pool was chosen as being representative of conditions in a pool which was persistent with minimal cover (2% estimated rock coverage); the pool at the head of Champs Elysees (Champs Pool Figs. 3.5, 3.9) is representative of an ephemeral pool (1%); and Hammerkop and Deep Pools (Figs. 3.6, 3.7) as being persistent with a maximum rock cover of 50% and 60% respectively. These three environmental types are illustrated diagrammatically in idealised versions in Fig. 3.10. A further environmental difference, in this case in their attenuation characteristics, existed between persistent pools with and without cover. These pools without cover were up to 3 times larger at the beginning of the dry season than at the end, so that during the course of the dry season the population captured by pool formation was subjected to a progressive presumably deteriorating environment and a decrease in "lebensraum". This was not the case in the deeper pools associated with cover, where

TABLE 3.2 THE POOLS OF THE LOWER REACHES OF THE HAENDA RIVER

POOL	FORMATION	BLACKFLOODING BY LAKE	ATTENUATION CHARACTERISTICS*	ESTIMATE OF PERCENTAGE ROCK COVER	ROCK BARRIERS
Whirlpool	Secured on outside bend of river	Never occurs	20%	2%	Upstream
Surprise	Secured on outside bend of river	Never occurs	70%	2%	Downstream
Hammerkop	Secured on outside bend of river	Never occurs	30%	50%	Above and below
Champs Pool	Secured below rapid	Never occurs	100%	1%	Upstream
Crocodile Bend	Secured on outside bend of river below rapid	Never occurs	30%	30%	Above and below
Bypass Pool	Secured on outside bend of river	Never occurs	50%	40%	Downstream
Deep Pool	Secured on outside bend of river below rapid	When lake level above ca 486.2 m a.s.l.	30%	60%	Above and below
Weir Pool	Secured below steep rapid	When lake level above ca 483.4 m a.s.l.	0 - 60%	10%	Upstream
Long	Secured below rapid	When lake level above ca 483.4 m a.s.l.	0 - 90%	10%	Upstream
Gauge Pool	Secured below rapid	When lake level above ca 483.4 m a.s.l.	0 - 20%	40%	Above and below
Elbow Pool	Secured on outside bend of river above rock barrier	When lake level above ca 483.4 m a.s.l.	0 - 20%	10%	Downstream

*Percentage surface area of water lost between the beginning and end of dry season



Fig. 3.6 Downstream across the mouth of the dry channel (Km.16.2), looking eastwards. Note the degree of bank erosion by the river and the undercut bank and fallen boulders against the inner bend. Swartkloof Dam, Natal, Mgeni woodland, Tongati.



Fig. 3.7 Same scene in January, 1974. Flow approximately 200 cusecs.



Fig. 4. Pool at the head of the Chuna Elyeuna in August, 1971, looking downstream, four months after the last rains.



Fig. 5. The same, shortly before drying up completely two months later (24.10.72). Note the lack of water in the water, leaving exposed sloping banks at the top of the bank and the green riparian fringe.

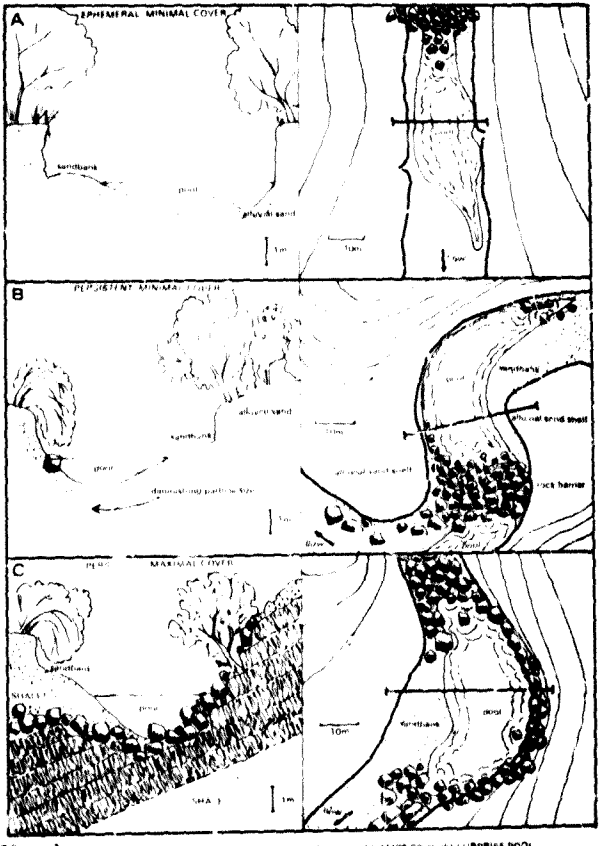


Fig.3.16. DIAGRAMMATIC PLANS AND SECTIONS OF THREE POOL TYPES (a) CHAMPS POOL (b) SURPRISE POOL (c) DEEP POOL AS INTERPRETED FROM SURFACE INDICATIONS

the effect of drying out was largely confined to the vertical dimension only. Accurate depths of the various pools were not readily obtainable as most pools contained up to four large crocodiles. Approximate depths were measured by angle wire in the sample pools during May, 1966, and were found to be, at their deepest, as follows; Deep Pool 2.3 m, Champs Pool 0.9 m, Surprise Pool 1.2 m. The sizes of the pools may be gauged in Fig. 3.10.

Depth changes at Surprise Pool were measured, apart from June and August, from May to December, 1968. These showed an initial relatively slow loss of 3 mm/day, which increased during the period July to October to 5 mm/day. During November, an abrupt increase to 10 mm/day was measured. It is considered probable that this abrupt increase in evaporation cannot be attributed to a sudden increase in relative humidity, as in the previous year Magadza (1969) found that the r.h. increased during November. Some other factor must therefore be responsible for this abrupt drop in level in November. Cocha (1968) estimated the evaporation rate of Lake Kariba to vary between 2,500 and 3,600 mm per annum, about 7 to 10 mm per day, thus higher than the observed rate of fall of Surprise Pool. The intense heat of the Mwenda valley and the isolation of the pools can only result in a lower relative humidity and higher evaporation rate than experienced by the lake but would have appeared in fact, to have been lower, except after the abrupt increase in rate during November. The only factor so far not taken into account which could affect pool levels is sub-surface water. Should ground water in fact flow into the pools, this would explain the

apparent discrepancy between recorded fall in pool level prior to November, and Cooke's (1968) estimates of evaporation rate of the lake. The fact that during November the level of the pool started to drop rapidly appears to support the ground water augmentation supposition, in that ground water supplies above pool level could by this time have become exhausted. If Cooke's (1968) evaporation estimates are correct, augmentation from ground water must apparently be at a rate of at least 2 to 4 mm/day from May to October. The ground conformation adjoining pools would also seem to support the supposition that ground water maintains pool level to some degree. On the one hand, tailrace pools similar to Champs [illegible] (Figs. 3.8, 3.9) are without any apparent "reservoir" and are by nature ephemeral. On the other hand, sand is laid down by the river on the inside of a meander and pools secured on a bend in the river are thus associated with this deposition (Fig. 3.10b). This deposition could act as a reservoir of ground water which is not subject to evaporation and which retains and slowly releases water to the pool. Apart from this, the river may also cut into sloping strata of Karri sandstone (Figs. 3.6, 3.7, 3.10c) which has the same effect. Available evidence suggests, therefore, that pool levels are quite likely to be maintained by ground water, but further more definite data derived from a project, specifically aimed at solving this problem, are necessary.

3. THE "ESTUARY" AND BAY

The use of the term "estuary" to describe the area where a river enters a static body of fresh water could lead to confusion. There is, however, no suitable limnological term to describe such

an area. The question has been discussed (Bowaker 1968) and is appended (Appendix II). On the basis of the opinion of Professor G. Kay of the Geography Department of the University of Rhodesia, the term is being used in this work, as its "ambiguity . . . . . is abrogated by the context in which they (it) are (is) used." (op. cit.). Thus the term "estuary", as used in this work, refers to an area of static freshwater associated with an inflow of fresh water, and will be used in parenthesis.

The map (against the end cover) was compiled by myself for this study from aerial photographs and depth transects, using a plumb line and Mimco offshore echosounder, and was edited and produced by Messrs. M.C. Collins (Pvt.) Ltd., of Salisbury. It may be seen on this map, that the point of entry of the river is given as below Elbow Rapid. This is only true when lake level is below 485.4 m a.m.s.l., as above this height the river was backflooded by the lake, during the period of study, as far as the weir site above Elbow Pool. Since field work was terminated, the exceptional level reached during March 1969, backflooded Deep Pool at a level of 486.2 m a.m.s.l. The drowned river bed remains narrow (100 - 200 m) and steep-sided some 1400 m from the Elbow and gradually deepens to ca. ten metres at Parrot Bend. Thereafter, the bay gradually broadens and deepens, so that by 2000 m further along the drowned river bed it is approximately 22 m deep and 900 m wide.

Cross sections of the "estuary" and bay (Fig. 5.11), the positions of which are marked on the map, show more clearly this gradual deepening and broadening of the bay. It is not possible to define quite where the "estuary" ceases and the bay begins, but for the

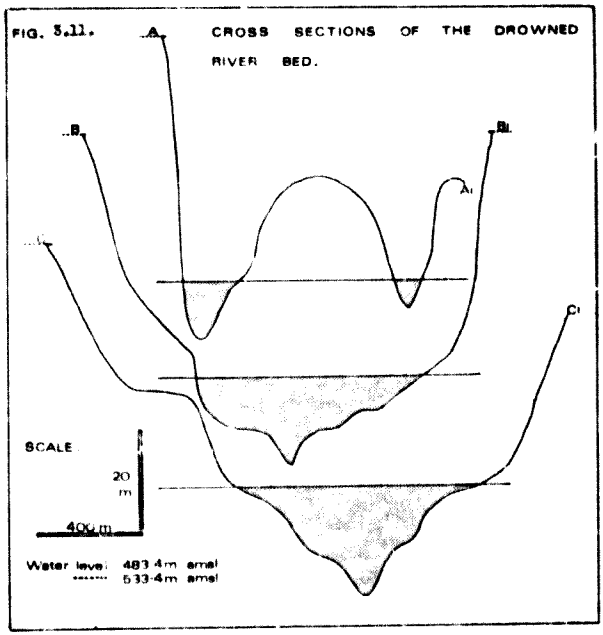


FIG. 3.11. CROSS SECTIONS OF THE DROWNED RIVER BED.

purposes of this work the narrow area, from the Elbow to Parrot Bend on the drowned river bed, which is considerably affected by inflowing river water, is considered as being the "estuary", whereas the area beyond this has been termed "bay". The separation is somewhat arbitrary and has been introduced for convenience. The "estuarine" area is essentially, therefore, steep-sided, narrow and shallow (Figs. 3.12, 3.13) and obviously affected by the river when it is flowing; the bay, on the other hand, is wider, broadly shelving, deeper and, by its situation, affected by open lake conditions to a greater extent.

4. THE STUDY AREA

The area chosen for study included 7 km of river bed. 3,540 m of this was always covered by the lake, a further 675 m was covered for some months and 2,820 m was never physically affected by lake water during the course of the study. The main stations of the survey were established arbitrarily as shown on the map, with Station 1 being the outermost and Station 5 the innermost. These five stations were permanently lacustrine in character. At these stations sampling was carried out quarterly, for five seasons, to assess the chemical and physical hydrology, plankton, benthos and fish fauna of the study area. At Stations 3, 4 and 5, sampling of the fauna of the Salvinia mat was also undertaken. Class II stations were established above the drowned river bed to sample the changes in the benthic fauna more precisely, particularly in their association with the varying degree of cover by the Salvinia mat during the course of study. Class II stations were also established in the river. These were sampled with varying intensity during the course of the study to assess the hydrology,



Fig. 7.1. The marsh between the Elbow and Jacana canal. The Elbow is in the far background, Station 4 is central and Jacana canal is bottom right.



Fig. 7.2 The stretch between Winterbourn and Jacana canal. Jacana canal is in the central distance.

benthos, nekton and fish of the lotic and pool populations. Class III stations were established to sample shallower water benthic populations and the populations associated with the various hydrophytes which developed during the course of the study.

Details of actual sampling undertaken are submitted in their relevant chapters. A planned sampling routine was normally followed, but the scope of this work, and unexpected environmental changes and developments which occurred, enforced at times an opportunistic rather than rigid approach.

CHAPTER 4

THE VASCULAR HYDROPHYTES

Mitchell (1970a) has separated the vascular hydrophytes of Lake Kariba into two main groups; the free-floating, represented by Salvinia auriculata Aubl., and Pistia stratiotes L., and those attached to the submerged soils. The latter he subdivides into a further three groups; "emergents", those growing on constantly submerged or wet exposed soils of the marginal "sedge-zone"; "floating leaved", growing on submerged soils up to about 3 m depth; and "submerged", growing on submerged soils up to about 10 m depth. All groups except the "floating leaved" forms were found and studied in the Mwenda area, from August 1966, to January 1968, more from the viewpoint of a dynamic substrate than as vegetation per se.

1. FREE FLOATING FORMS

No Pistia was found in the area during 1967 and 1968, although this plant has been frequently reported from Lake Kariba (Mitchell 1970a).

1.1 Salvinia

1.1.1. The forms of Salvinia

Mitchell (1970b) discussed taxonomic problems arising from the species of Salvinia colonising Lake Kariba and concluded that it was not possible to be certain of its identification, and at the time suggested continuation of the use of the name Salvinia auriculata Aublet. Subsequently (Mitchell et al, 1972) the species has been given the name Salvinia molesta.

The proportion of the study area covered by Salvinia mat, and the type of mat encountered, varied considerably during the survey period. Three morphological forms of the plant have been described by Mitchell (1960); a "mat" form (Fig. 4.1) an "open water" form (Fig. 4.2) and a "primary" form. These forms result from interaction between nutrient and space availability. The "primary" form normally occurs in newly colonised areas, where both space and nutrient are readily available. The "mat" form is found in mature mats when space is minimal. The intermediate "open water" form occurs normally at the edge of a mature mat, where space is readily available.

During the initial period of filling, the development of stable Salvinia mats provided the opportunity for colonisation by many species of plants which otherwise would apparently have not established themselves on the lake shore. The association of these plants studied by Beaghey (1963) have been termed "sudd" by him and Mitchell (1970) and the "Salvinia complex" by Donnelly (1970).

1.1.2 Secondary growth

In the Mwenda estuary the mat was colonised by relatively few species. An almost pure stand of Scirpus cubensis Peopp. and Kunth existed in association with Salvinia (Figs. 4.3, 4.4). Occasional isolated clumps of Typha latifolia subspecies australis Rohr, Phragmites mauritianus Kunth, Polygonum spp. and Ludwigia stolonifera (Guill. and Perr.) Raven occurred, but the only species found regularly to exist floating out of association with Salvinia was T. latifolia; previously, this has only been reported for Ludwigia stolonifera (Mitchell 1970).



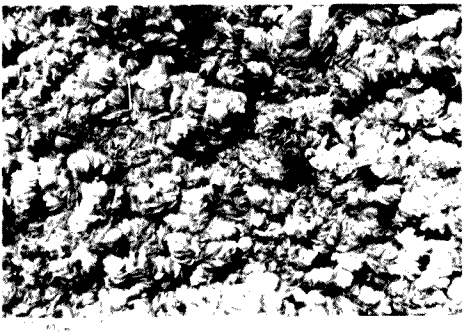




Fig. 4. *Salvinia auriculata*. The "open-water" form, with some "mat" form plants from which they developed. The leaves are smaller and the lower surface of the leaf is mostly in contact with the water surface, but the leaves are still slightly keeled, whereas on the primary form, leaves are smaller and lie flat on the water surface. In the open water forms illustrated the internodes are long and delicate. Station 7, October, 1961.



Fig. [illegible] [illegible] in April, 19[illegible], [illegible] [illegible] *[illegible]* [illegible] [illegible] *[illegible]*. [illegible] the [illegible] in the *[illegible]* [illegible] the [illegible] [illegible] the [illegible].

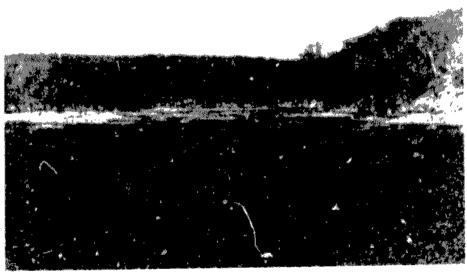


Fig. [illegible] [illegible] in [illegible], 19[illegible], [illegible] [illegible] *[illegible]* [illegible] [illegible].

1.1.3 Floating "mudd" islands

Floating islands of dead Salvinia, up to sixty square metres in extent and two metres deep, were found to occur in the Salvinia mat. Upon these developed the ruderal and semi-aquatic species mentioned by Boughey (1963). These included species of Sonchus, Conyza, Pavonia, Eclipta, Polygonum, Cyperus, Typha and Ludwigia. Little apparent competition occurred between these plants and Scirpus. Figure 4.5 shows the initial colonisation of one of these islands by this type of vegetation. The island illustrated was nearly a year old at the time. A much older island, estimated to be in the region of four to five years old, is illustrated in the left of Fig. 4.3, where the Ludwigia adscendens stood approximately three metres above the water surface.

These islands were formed in two different ways. At the end of 1966 the stretch of river bed between the Elbow and the weir site, which had been previously backflooded and later colonised by Salvinia, dried out as a result of a rapid drop in water level. Extensive sheets of Salvinia were left stranded by the receding water and died. During December, when the river flooded, these sheets were compacted and floated into the then permanent mat where they formed two large floating islands. During 1968, the river was again backflooded during July and was colonised by Salvinia as far as the weir site. In this case, however, the river flooded at the same time as the lake level receded below the Elbow and the live Salvinia was actually observed to be compacted and built up at rapids to form heaps two to three metres in height which were then washed into the permanent mat, died, and again formed floating islands.

The somewhat exclusive colonisation of these islands by ruder-





als on the one hand, and the preponderance of Typha and, particularly, Scirpus on the live Salvinia mat on the other (unless typical only of the Mwenda River), tends to indicate a situation which has changed since Boughey's (1963) observations prior to 1961. He does not differentiate between the live and dead Salvinia substrate and it is quite likely that the circumstances conducive to the latter's formation had not arisen as yet, yet Boughey's (1963) list of 40 species includes many ruderals and semi-aquatics now not found on the live Salvinia substrate in the Mwenda River. It was thought that this apparently recent success of Scirpus cubensis could have been due to the lessening nutrient level of the lake as a whole favouring this plant, but Mitchell (1970) has shown that nutrient availability within Salvinia mats has not changed.

1.1.4 The dynamics of the mat in the Mwenda River "estuary"

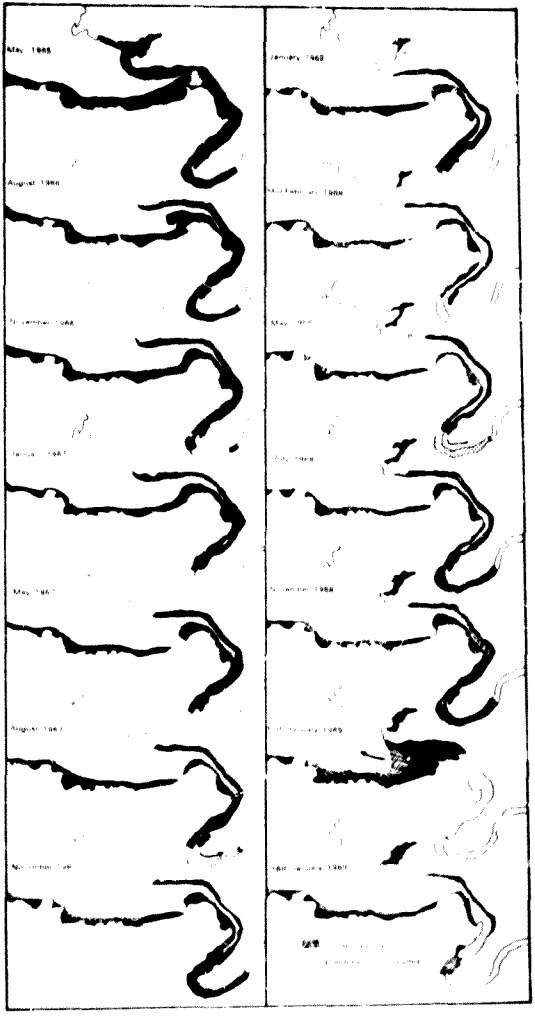
During the course of study the Mwenda "estuary" was freed from Salvinia mat for the first time since initially colonised in 1961. Aerial photographs taken in May 1965, show that the entire "estuary" from Station 3 as far as the weir site, was covered. A large part of this area, particularly along the river bed, was covered by secondary growth sufficiently heavy to be recognizable from a height of 40,000 feet. When the area was first visited, in August of the following year, a section from Station 3 to as far as Winterthorn had moved out of the estuary. The main secondary growth, concentrated from here to Jacana Bend, consisted of Typha latifolia, whereas from this point to the Elbow, Scirpus cubensis grew in an almost pure stand on the Salvinia, as in Figure 4.3. This situation persisted until, following heavy flooding in early May, the

centre of the "estuary" was cleared as far as Eagles Nest, where a compaction of Typha and floating islands against the corner formed a blockage (Fig. 4.6) stopping any further outward movement. In November 1967, this blockage was found to have been moved out of the "estuary", apparently by wind action, and the central channel was cleared as far as Station 4. During the previous June, the lake had backflooded the section of the river from the Elbow to the weir site, and by August the action of wind and a slight back-flow had resulted in this stretch being colonised by Salvinia. The flow of the river then cleared this section by January 1968, and a further small section of the channel was cleared. Heavy rains which fell in early February 1968, resulted in the complete elimination of Salvinia from the "estuary", except for marginal bands outside the main force of the flood. Thereafter, once flow had ceased, Salvinia, either originating from the margins, or blown into and trapped by the "estuary", covered a small area below Elbow Rapid. During May backflooding again occurred and the river was colonised as far as the weir site, as had happened in the previous June. By November 1968, Salvinia again covered the "estuary" as far as Jacana Bend, and further small windblown blocks of Salvinia were continuously being introduced into and being trapped by the "estuary". On the 10th January 1969, exceptionally high floods completely cleared the "estuary" of Salvinia, but within six days some plants had been blown back into the "estuary" as illustrated in Figure 4.7.

4.1.5 Factors affecting the Salvinia mat dynamics

The dynamics of the Salvinia mat in the Mwenda "estuary" are controlled by a number of factors. Some contribute towards the

Fig. 4.7. VARIATION IN AREA COVERED BY SALVINIA FROM MAY 1965 TO JANUARY 1969



formation of the mat, others towards its destruction. Wind action would appear to contribute to both.

1.1.5.1 Factors contributing to mat accumulation

(a) The nature of the estuary. The three corners of the estuary are such as to trap any plants which have been blown into it and have an accumulative blocking and retentive effect during minor flooding. The gradual broadening of the "estuary" into the bay helps considerably towards the accumulation of Salvinia.

(b) Exponential growth. Mitchell (1970) has demonstrated that the growth of a Salvinia mat is exponential. This characteristic, coupled with the trap-like nature of the "estuary" results in a very quick recovery following expulsion (Fig. 4.7; February to November 1968).

(c) Secondary growth. A mat with secondary growth is far less susceptible to breaking up than one without. Once bound by the rhizomes of Scirpus the whole unit is cohesive and requires a great deal of disturbance to dislodge it. Mats are therefore vulnerable in an early stage of colonisation. On the other hand, at this stage, expelled Salvinia may easily re-enter, whereas once a mat with secondary growth has been dislodged and expelled, it would seem to be invariably destroyed by wave action.

1.1.5.2 Wind action

Wind effect varies considerably according to the nature of the mat. Pure stands of Salvinia, or individual plants, are easily moved by wind. Once Scirpus is established in the mat, however, the binding effect results in a stage of development least susceptible to movement by wind. More mature communities, similar

to that shown in Fig. 4a6, are once again, with their increased windage, susceptible to wind action. The mature mat has, however, to be previously disturbed by other agents and broken up before wind can have any effect. Reference to the dynamics of the mat in the Mwenda "estuary" shows that the effect of wind is basically to accumulate Salvinia within the estuary. A study of seasonal windroses, prepared by the Rhodesian Department of Meteorological Services from data collected during daylight hours show the dominating winds to be northerly throughout the year. As has been previously stated, there is also a strong south-easterly component from April to August. Furthermore, it is in my own experience at Sinamwenda that strongest winds occur at night and from the south-east at this time of the year, particularly in July. Mitchell (1963) and Scudder (1962) have both recorded high winds to have occurred at night in their experience on Lake Kariba, and in the Zambezi valley prior to inundation. Local topographic conditions undoubtedly have a marked effect on wind direction and velocity in the "estuary". The valley of the Mwenda River lies from south-east to north-west, across the axis of the gentle structural grain (SW/NE). Thus when these strong south-easterly winds occur, the river valley has a funnelling effect which tends to strengthen the air flow down the valley and gives rise to local, short-lived, gale force winds in the Mwenda Bay and "estuary". Reference to the topography of the study area (see map) demonstrates the steep 100 m hillside above the northern shoreline of the "estuary" from Jacana Bend to beyond Parrot Bend. This slope tends to veer these strong southerly winds to follow the "estuary". This factor, coupled with the lie of this section of the flooded river, results

in a susceptibility of the mat outside Jacana Bend to wind induced outward movement, whereas within this bend the lie of the estuary and protection by Mwaluma Fold cancels wind effect.

On the one hand, therefore, persistent light northerly winds occur throughout the year in daylight hours. These tend to gather and accumulate Salvinia plants within the "estuary". On the other, short-lived, sometimes gale force winds occur from the south-east, mainly at night, and exert considerable pressure on the mat, particularly when Typha has developed. The effect of these winds is to move the mat in the stretch between Jacana and Parrot Bends out of the estuary. It is demonstrable (Fig. 4.7) that the persistent northerly winds have a greater overall effect by continuously re-colonising the "estuary" with Salvinia. The interaction between these winds, taking into consideration the fact that any mature mat which is moved from the shelter of the estuary is destroyed, thus encourages the dispersal of mature sudd and the accumulation of Salvinia without secondary growth.

1.1.5.3 Factors contributing to mat dissemination

(a) The action of launches. A 14 m launch was the only means of entry into the mature mat for sampling purposes. Once having cut a path through the Cairnus rhizomes, the same path was used and kept open thereafter (Fig. 4.3) and must have made the mat more susceptible to the action of winds and flooding.

(b) Flooding. During the study period, exceptional floods occurred on 5th May 1967, when the "plunge point" occurred at Jacana Bend; on 11th February 1968, when the plunge point occurred between Eagles Nest and Winterthorn, and on 10th to 12th January

1969, (S.A. Mitchell, personal communication) when the plunge point occurred at Station 3. Prior to May 1967, minor changes in the mat were attributable to wind and boat action, but after this all major changes which occurred resulted from flooding.

About seven years after its formation, therefore, the mat of the Mwenda River mouth started to break up, which it did over a period of two flood seasons through the combined actions of wind, flooding and, to a lesser extent, the disturbance resulting from the regular entry of a launch.

2. THE EMERGENT LITTORAL HYDROPHYTES

At the stage of development of Lake Kariba reached in 1966 and 1967, the paucity and sometimes complete lack of emergent littoral hydrophytes along considerable stretches of the coast was perhaps the single most outstanding characteristic of the shoreline (Fig. 4.8). Several factors, apart from the considerable distance between the Zambezi River and the present shoreline, have been suggested as being the cause of this. Firstly, where exposed, the shoreline is rendered somewhat sterile by wave action, resulting in boulder armoured coastlines where sandstone is met and clean sand where the more easily eroded shales are encountered. The finer particles of these substrates are washed out and deposited offshore (Bond 1965). Thus marginal hydrophytes can only develop satisfactorily in sheltered inlets. Here, however, dry stranded mats of Salvinia tend to be most frequent, and are reported (Magadza, in press; Mitchell, pers. comm.) as having an inhibitory effect on the germination of other plants. Secondly, the considerable and sometimes rapid annual fluctuations of lake level,



Fig. ..



Fig. ..

as a concomitant of lake management for power generation, result in stranding or drowning of the primary colonisers. As Mitchell (1969) has pointed out, only species able to withstand these two actions are likely to survive. Three species of plant seem to a varying degree to be able to exist under these conditions; the grass Panicum repens (Bowmaker 1968; Mitchell 1969; Donnelly 1969; Magadza in press); the herb, Ludwigia stolonifera (Mitchell 1969) and the sedge, Cyperus articulatus (Bowmaker 1969).

There are cases, however, where Magadza's and Mitchell's observation on the inhibitory effects stranded Salvinia mat has on germination, have not held true. In fact a mulch of Salvinia flotsam above the wave line can improve sterile coastal conditions and generate the growth of marginal plants, particularly Panicum repens (Fig. 4.9). The discrepancy between my own and Magadza's and Mitchell's observations probably arises from the source or age of stranded Salvinia. Mitchell (pers. comm.) has said that all cases of inhibition which he has observed were associated with stranded stable mat, whereas my own observation involves an old accumulation of single Salvinia plants. The indications were that recently dead Salvinia accumulated in this way does inhibit the growth of Panicum, whereas an older accumulation did not, and in fact stimulates growth (Fig. 4.9).

Cyperus articulatus was first recorded in the Mwanda Bay in January 1968 when a small stand was found on Saiche Tower Island. This particular stand withstood a water level drop of 0.8 m and a rise thereafter of 2.18 m to the high August 1968 level. It was thought that the exceptional height of the lake in May 1969 (487.6 m

a.s.l.), some 4.4 m higher than when the plant was first seen, would obliterate the species from the margins of Nyanda Bay, but this was not the case. Part of the original stand withstood this fluctuation, but smaller stands which had, subsequent to the initial colonisation, developed elsewhere in the bay, have disappeared. It would seem therefore, that where Cyperus articulatus has had the opportunity of establishing itself in appreciable stands, it will be able to resist exceptional lake level fluctuations, which is not true for the other two marginal species mentioned above (Panicum repens and Ludwigia stolonifera). At this time (1967, 1968) these two species appeared to maintain themselves relatively precariously, as stands of these plants did not persist in any one situation, but appeared haphazardly and seemed to survive, under the lake level fluctuation regime, by reseeding. Magadza (1970) feels, however, that "it is possible that it (Panicum repens) would lead to a stabilisation of this (marginal) habitat". The marginal vegetation was found so infrequently during the course of study that it did not warrant sampling.

3. THE SUBMERGED LITTORAL HYDROPHYTES

For the purposes of this study this section includes both truly submerged plants and plants which are rooted to the bottom but with floating leaves, as opposed to the marginal aquatic hydrophytes considered above, which are predominantly emergent. McLachlan (1968) has reported the occurrence of Nymphoides and Nymphaea in ephemeral pools on the lake margin, but once inundated, these plants did not persist. Potamogeton schweinfurthii has been reported from the Sinamwenda area and the Sanyati Basin by Mitchell (1970).

The role played by submerged littoral hydrophytes, as primary producers, as a substrate for the development of aufwuchs algae and as a means of protection for juvenile and small fish species from predation, is most important. The poor development of this type of vegetation can only retard the productivity in any body of static fresh water. In Mwenda Bay, the lack of littoral hydrophytes was manifest at the end of 1966, and has been discussed in the context of deleterious effect on fisheries productivity by Bowmaker (1968) (Appendix 1). Subsequently McLachlan (1968) has demonstrated the importance of establishment of littoral hydrophytes on the benthos of Lake Kariba, and Donnelly (1970) has clearly shown its value with regard to the successful breeding of Tilapia petrinari in the littoral zone of gently shelving shorelines of the cleared areas of Lake Kariba. He emphasises that this is particularly true for Lake Kariba where juvenile and small fish species are subjected to considerable predator pressure by the tiger fish, Hydrocynus vittatus, as was first propounded by Jackson (1961c).

Mitchell (1970) records the occurrence of the various submerged rooted littoral hydrophytes during the formation of Lake Kariba. Ceratophyllum demersum has always been present in the lake, particularly associated with river mouths and has at times grown in very dense stands. McLachlan (1968) records this species as growing to a depth of 10 m and Donnelly (1970) to 7 m. Potamogeton nodosus was not, however, recorded prior to 1964, when McLachlan (1968) found it occurring sparsely in the Sengwa West cleared area. Within a few months this species occupied the entire cleared area up to a depth of 4 m. Donnelly (1970)

records this species as growing in a band from approximately 1.5 m to 3 m depth. Lagarosiphon ilicifolius was first recorded in the lake at its western, Zambezi, end at the end of 1966 in "fairly deep sheltered areas" (Mitchell 1970) and various other species have recently been recorded by Donnelly and Begg (Mitchell 1970, Donnelly 1970) in the Sanyati River region of the lake, perhaps as a result of this area being studied intensively for the first time. These include species of Vallisneria, Ottelia, Utricularia, Potamogeton schweinfurthii and the alga, Chara.

During the course of this project, there were considerable changes in the populations of the three species found in the Mwenda Bay, i.e., Ceratophyllum demersum, Potamogeton pusillus and Lagarosiphon ilicifolius. In August and November of 1966, isolated occurrences of single plants of Ceratophyllum and Potamogeton were noted. These were most frequent in the harbour of the Research Station and could, perhaps, have been introduced to the Mwenda Bay by boats from areas elsewhere in the lake, where these two plants were already established. This supposition is lent some support by the fact that by May 1967, isolated large stands of these two species had already developed around the Bay and Potamogeton was actively invading shallow waters (Fig. 4.10). Differences in distribution of the two species were found that could apparently be related to substrate and wave action. Potamogeton was generally found on sheltered wave-washed rock and sand points, whereas Ceratophyllum occurred in inlets free of Salvinia (Fig. 4.11), normally amongst trees in quiet waters. The two species were infrequently found together and only where a gradation between tur-



Fig. 4.10 Lobophora variegata in an invasive stage. C.2 m depth of water. Mauritius, May, 1967.

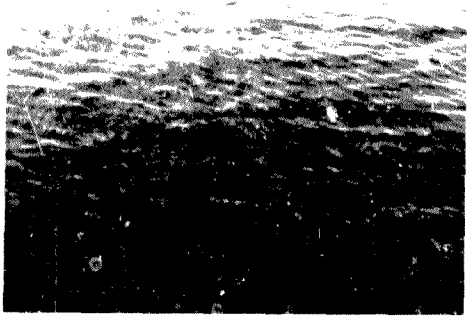


Fig. 4.11 Cymatothallum formosum, growing in 5 m of water. Mauritius, May, 1967.

bulent and still waters occurred. It was considered at the time that wave action was probably the most important factor limiting distribution. This was partly borne out by the fact that Potamogeton kept in aquaria quickly developed a thick coating of periphyton and died, whereas Ceratophyllum, under the same conditions, persisted for several weeks. Perhaps Potamogeton offers a more favourable substrate for development of periphyton and can only survive under turbulent water conditions, which keep the leaf surfaces clean and photosynthesising, whereas under calm conditions periphytic growth is so successful that light is largely taken up before reaching the leaf surface. Certainly, further research in this problem could yield interesting and valuable results.

The isolation between these two species resulted in a situation markedly different from that found by Donnelly (1970) on semi-sheltered gently sloping shorelines, where abrupt zonation occurred. He found Potamogeton occupying an inner band at depths of 1.5 m to 3 m and Ceratophyllum outside this, from 3 m to about 7 m. Potamogeton, in Mwanda Bay, was found from 0.2 m to ca. 3.5 m and Ceratophyllum 1 m to ca. 6 m. Depth distribution of these plants was not examined exhaustively, however, so that the outer depth ranges must be regarded as estimates.

By July 1967, the situation remained unchanged with regard to these two species but Lagarosiphon was found for the first time in the bay, growing in a single dense stand in one situation. Gradually, during the course of the next year, Ceratophyllum, and particularly Potamogeton, were replaced by the invading Lagarosiphon so that by November 1968, very few stands of Pota-

Aponeton were recorded. The entire coastline, except where particularly steeply shelving or unprotected, or covered by a permanent Salvinia mat, was occupied by Lagarosiphon in a bar . at depths ranging between 2 and 4 m. Where protection from wave action was most effective, beds of Ceratophyllum were found to occur outside the Lagarosiphon between 4 m to 6 m. This situation persisted until January 1969, when recording was discontinued.

These rooted littoral hydrophytes never occurred underneath permanent Salvinia mat along the shoreline or further inside the "estuary" than Chris' beach.

The reasons for the slow development of this important association and the basic productivity of Lake Kariba have been discussed at some length by Bowmaker (1968), Mitchell (1970), and Donnelly (1970). It is now generally believed that the two main causes for this tardy development are the fluctuations of lake level and the presence of light-excluding permanent mats of Salvinia. In this context, it is significant that development of littoral plants occurred during a period when fluctuations were at their lowest since the dam was closed (Fig. 5.2).

It is unwise to try to predict the future development of the littoral submerged hydrophytes. Lagarosiphon ilicifolius has, however, shown a pattern of colonisation starting in the Mlibezi/Sebungwe Basin and gradually moving down the lake to the Sanyati Basin. Wherever this plant has become established it has persisted, so that it would probably not be going too far to suggest that this species appears to be well suited to Lake Kariba in its present stage of development and could quite easily remain a

successful constituent for some time to come.

The three species discussed above, and the non-vascular plant Chara sp. which occurs in the river pools, were sampled quite extensively to assess their faunas.

(Note: Changes which have occurred subsequently to 1970, when this chapter was written, are included in the final chapter).

CHAPTER 5

THE PHYSICO-CHEMICAL LIMNOLOGY

The collection of physico-chemical data was undertaken to ascertain the hydrological background of the study area, its nutrient status and the seasonal changes experienced, with the possibility in mind that correlations could exist between physico-chemical and biotic changes. The information was also necessary in order to ascertain the abiotic status of the arbitrary stations in relation to each other. A further aim was to assess the effect of the Salvinia mat on the abiotic part of the ecosystem being studied.

1. METHODS

1.1 Rainfall

Rainfall figures were taken from the Research Station records where rain was measured by gauge, daily at 08.00 hours. These figures cannot represent the daily rainfall in the catchment of the Mwenda River as most rain was received from storms which were characteristically local in nature. Individual storms have been observed to be recorded by the gauge but not to have delivered rain within the catchment of the river and vice versa. Rainfall in the area is, however, governed by the position of the Inter-Tropical Convergence Zone, which occurs between moist northerly and dry south-easterly winds. This results in intermittent rain periods of from two to ten days during which rainfall, taken over the period, is of a general nature. Hence gauge measurements considered as fortnightly quotas are considered to approximate quite closely to the rainfall experienced by the catchment of the Mwenda River.

1.2 Flow

Owing to the seasonal nature of this project it was not possible to obtain accurate flow data for the Mwenda River. The crucial nature of the effects of flow on the ecosystem being studied was appreciated at the outset of this study. An arrangement for accurate continuous flow measurement, bearing in mind the seasonal nature of visits and the commitments of the Research Station staff, was not possible under the conditions then prevailing at the Research Station. Neither was it financially practical, at the time, to build a weir on the river so that a constant level recorder could be installed. A gauging weir has now (1972) been built in the river and continuous flow recording has been started.

It was possible, however, to ascertain the actual start and cessation of flow in the river and when major floods occurred. The volume of flow for non-flood periods was determined from fortnightly rainfall figures as observations of flow during field periods bore a close relationship to fortnightly summations of station rainfall records.

In December 1967, when greater emphasis was placed on the study of potamodromosis, a gauge was installed in the river, graduated at 0.1 m intervals. Steel "snagging" pegs were placed at each graduation with the intention that unobserved floods would leave flotsam suspended on these at the highest water level reached. This device was successful.

1.3 Lake level

Lake levels were taken from data supplied by the Central African Power Corporation and converted to metres above mean sea level. The gauge mentioned above was placed arbitrarily

and gauge levels were later correlated to lake levels after the lake had backflooded sufficiently to allow comparison by simultaneous readings of both. The gauge zero was found to be at 483.2 m a.m.s.l. The top of Elbow Rapid, at which level the lake backflooded some 675 m of the river, was measured in relation to gauge zero by Abney level and found to be 483.4 (±0.1) m a.m.s.l.

1.4 Temperature

Temperatures were measured to the nearest 0.05°C by thermistor. The circuit was constructed by the writer to the design of Mortimer and Moore (1953), and was calibrated before and after each seasonal visit. Spot checks were made on surface temperatures using a mercury thermometer during the course of the field work. Temperatures were measured at one metre depth intervals at both Class I and Class II stations in the lake. Measurements from surface to bottom were also taken against the mat edge, at 10 m, and 50 m inside the edge of the mat. Pool and river temperatures were measured by mercury thermometer.

1.5 Dissolved Oxygen

Until May 1967, dissolved oxygen concentrations were measured at 5 m depth intervals using a Friedinger sampling bottle, and the unmodified Winkler method described by Mackereth (1963). Subsamples were fixed immediately and titrated within three days of being collected. After May 1967, an E.I.L. biological oxygen meter, designed by F.J.H. Mackereth, was used and dissolved oxygen values determined at meter depth intervals simultaneously with temperature readings. This meter was regularly calibrated and spot checks by Winkler titration were carried out, at least once every field trip, through the range of values found. Meter readings

never varied more than 3% from the values given by titration results. When marked changes in the flow of the river occurred during a field period, the temperature and oxygen characteristics of the water body were re-measured.

1.6 Turbidity

The depth of visibility was measured using a 30 cm diameter Secchi Disc with black and white quadrants.

1.7 Water Samples

The dissolved oxygen isopleths and isotherms plotted from the data collected clearly showed where water characteristics differed in the study area. Selective sampling of the different water bodies was then undertaken using a Friedinger sampling bottle, to ascertain their chemical characteristics. Samples were split three ways. pH and conductivity were measured immediately and alkalinity was measured within twenty-four hours from the first sample; the second sample was kept, unpoisoned, in a polythene bottle; the third sample was immediately poisoned by the addition of approximately 1 ml/l of saturated mercuric chloride solution, and kept in a polythene bottle. Care was taken to see that samples contained no air.

1.8 The Specific Conductivity

Conductivity was measured in micromhos or reciprocal megohms per cm (µmhos) using a Dionic Water Tester, corrected to 20°C.

1.9 Total Alkalinity and Carbon Dioxide

Total alkalinity was determined by titration, using 4.5 indicator as described by Mackereth (1965). Carbon dioxide values were derived from these readings and pH values of the sample,

using Mackereth's (1963) nomogram.

1.10 The Hydrogen Ion Concentration (pH)

pH values were determined colorimetrically, using a Lovibond Comparator.

1.11 Laboratory Analyses

Kept samples were analysed in Salisbury by the Government Analyst's Laboratory within a month of collection. The methods used and degree of accuracy of these are tabulated (Table 5.1). Whenever results were obtained which diverged markedly, the analysis was checked and sometimes re-checked.

The method of preservation of samples, by poisoning with $HgCl_2$, was chosen as neither sophisticated analytical nor freezing facilities existed at the Research Station at the time. Hellwig (1964) has shown poisoning with $HgCl_2$ to be effective for polluted samples up to two weeks after collection. In these, biological activity can be expected to be far higher (and thus effect determinations more) than in water samples from Lake Kariba. The method is ignored by more recent workers (Golterman, 1969) and would therefore seem to have limitations, even though most convenient. Present opinion favours immediate analysis of samples, particularly for nitrogen and phosphorus. The estimations of water chemistry presented in this thesis, particularly in the case of N and P, must therefore be regarded with some reservation and can only be compared with similarly treated samples. The inaccuracy inherent in some of the sampling methods and analyses used in this study are manifest after consideration of Golterman's (1969) discussion of the chemical analysis of fresh waters. They are, however, at least equivalent in accuracy to previous analyses of fresh waters,

TABLE 5.1 THE ANALYSIS OF KEPT SAMPLES

ANALYSIS	METHOD	ACCURACY (p.p.m.) *
Calcium and magnesium hardness	Versenate	1
Sodium and potassium	Flame photometer	0.1
Phosphate (PO_4^{---})	Shake-out into butanol, stannous chloride/molybdate colour (Analyst 1965 p.29)	0.005
Nitrate nitrogen	Shake-out with 2-6 xylenol (Analyst 1964 p.730)	0.05
Nitrite nitrogen	Hallige standard disc after diazotisation	0.02
Ammoniacal nitrogen	Distillation and nessleri-sation	0.01
Albuminoid nitrogen	Distillation after addition of $KMnO_4$ and nesslerisation	0.01

*1. Accuracy refers to the establishod accuracy of the method used and not to the actual values in the water body sampled, as analysis took place between 14 and 30 days after collection.

2. Analysis of Ca^{++}, Mg^{++}, Na^{+} and K^{+}, were carried out on un-poisoned samples.

3. Phosphate and nitrogen estimations were carried out on samples poisoned by the addition of saturated $HgCl_2$ solution.

particularly in Africa. It will undoubtedly take some time for local facilities to become sufficiently developed to allow the achievement of higher degrees of accuracy.

Laboratory analysis was limited to suspended solids, dried solid residue, ignited solid residue, loss on ignition, chloride, nitrate, nitrite, ammoniacal and albuminoid nitrogen, calcium, magnesium, potassium, sodium and phosphate; emphasis was thus placed on suspended matter, organic load and the nutrient content of waters sampled.

2. RESULTS

2.1 Rainfall

Rainfall data in fortnightly periods are presented in Figure 5.1. It is clear that both the amount and seasonality of rainfall varied considerably during the study period. More or less "normal" rainfall was experienced in 1966/67 (544.06 mm) and was concentrated in December and January. The rains had apparently ceased by the end of April, but the third heaviest single fall (38.6 mm) of the season was subsequently experienced following a storm on 2nd May, 1967.

During the 1967/68 season, only 350.01 mm of rainfall was recorded. On three occasions more than 25 mm fell in a single twenty-four hour period, compared to eight occasions in the previous season.

In the following season a total of 781.55 mm of rain fell, more than twice as much as in the previous year. Another feature of 1968/69 season was the very low rainfall of the latter half of January and February, totalling 42 mm over six weeks, follow ' by the exceptional March rains of 455 mm. Falls of greater than 25 mm were recorded on eleven separate twenty-four hour periods.

Fig. 5.1 RAINFALL IN FORTNIGHTLY PERIODS AT THE NUFFIELD KARIBA RESEARCH STATION SHOWING FLOW AND FLOODING PERIODS IN THE MWENDA RIVER

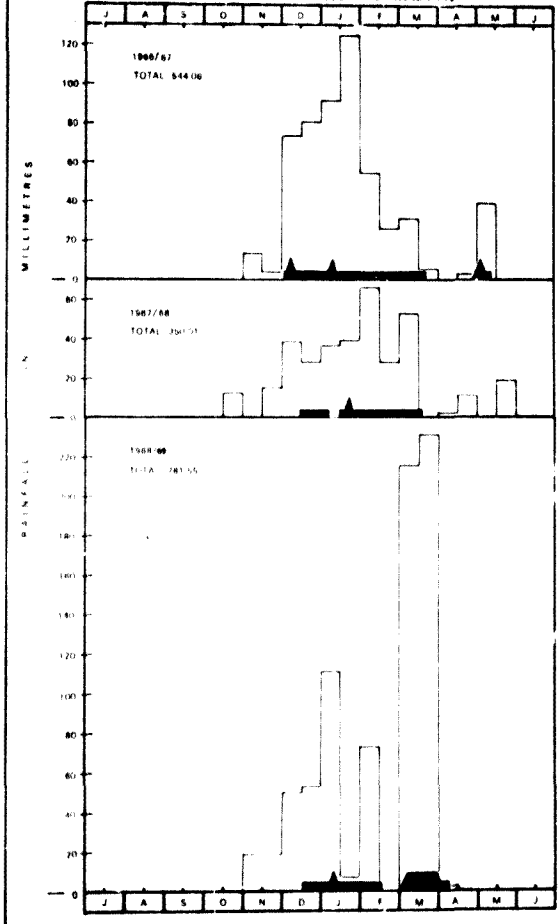


TABLE 5.2 FLOODS OF THE MAENDA RIVER. JULY 1966 TO JUNE 1969

DATE	APPROXIMATE FLOW (m^3/s)	PLUNGE POINT	GAUGE READING (m)
10/12/66	28	-	-
8/1/67	23	Station 4	-
2/5/67	61	Eagles Nest	-
25/1/68	15	Station 5	1.7
8/2/68	6	Elbow Rapid	0.9
10/1/69	100	Station 3	2.7
March 1969	350	Station 3/2	4.0

2.2 Flow

Figure 5.1 also shows the flow and flooding periods of the Mupata River. The relative volumes of flow can be gauged roughly from the amount of rain received in fortnightly periods for the reasons given above (Section 1.2).

During the 1966/67 rains, the river started to flow in early December and flooded on the 10th December. It continued to flow until late March, flooding again on 8th January. No flow was experienced between late March and the beginning of May, when an exceptional storm resulted in the largest single flood of the season. Flow finally ceased within a few days of this and did not start again until mid-December 1967. As can be expected from the low rainfall experienced in the 1967/68 rains only one minor flood occurred on 25th January, and flow ceased finally in mid-March. A ten-day period without flow also occurred in mid-January 1968. The river started flowing again in mid-December, flooding violently on the 10th January 1969. Flow ceased during the low rainfall period in the second half of February, but recommenced as exceptional floods which continued throughout March 1969. The river finally ceased to flow in mid April. Data regarding floods are shown in Table 5.2.

2.3 Lake Level

The temporal pattern of lake level fluctuations was normal between 1966 and 1969, with high levels resulting after the Barotse floods, between June and September, and lowest levels occurring between February and April. During 1967 and 1968, fluctuations remained at a low level (Table 2.2), not having been much more than two metres. During 1966 and 1969 these fluctuations were more than double the two intermediate years.

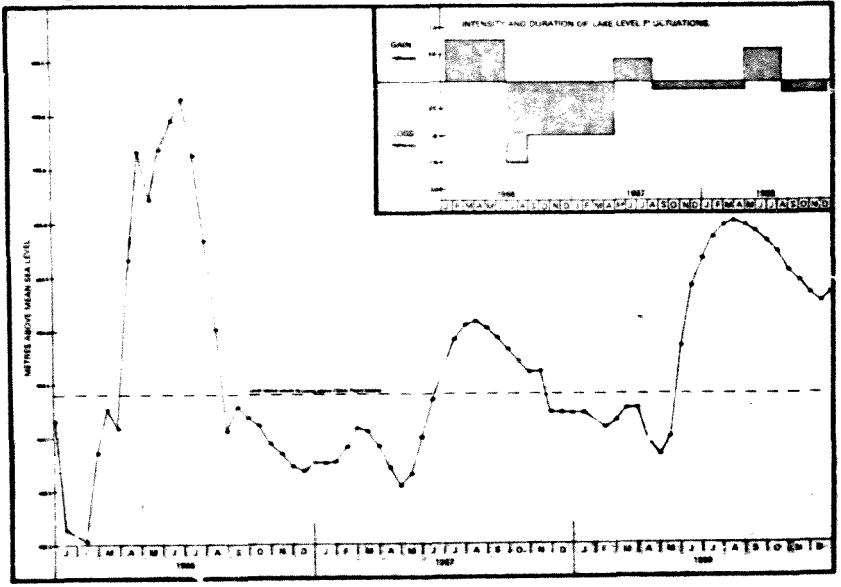
Lake levels have been plotted in Fig. 5.2 and the intensity and duration of fluctuations during the study period are also shown as metres rise or fall per month. This figure demonstrates the relatively stable conditions experienced between May 1967, and December 1968. The main physical effect of fluctuations in the study area is related to the back-flooding of the lower reaches of the river up to the weir site. This back-flooding occurred between April and September 1966; June and November 1967, and May 1968 to January 1969. The steepness of the shoreline in the Mwenda Bay generally (Fig. 5.11) results in relatively small horizontal movements during water level changes, the ratio ranging from no unit of horizontal movement to one unit of vertical movement to approximately 10 : 1. Effects of water level fluctuations are therefore considerably less than the Sengwa West cleared area, which McLachlan (1968) found to be about 400 : 1.

2.4 Seasonal Temperature Variations

2.4.1 Seasonal temperature changes of the water column

Figure 5.3 shows the seasonal distribution of 1°C isotherms at Station 3, and indicates four phases within the annual cycle. Initially, surface water temperatures dropped 4°C between January and the end of May 1967, indicating a slow cooling phase of less than 1°C/month. The second phase from late May until mid-July, was one of rapid decrease (of 7°C in two months) to 20°C. The third phase consisted of rapid increase to 27°C in two months and the fourth phase, one of slow increase at the rate of 1°C/month, took place between October and January. Thus for eight months over the hot season, temperature changes were gradual in surface waters (8°C), and for four months over the cold period, changes were relatively

Fig. 5.2 WATER LEVEL FLUCTUATIONS OF LAKE KARIBA 1956-1968



abrupt (14°C).

Bottom temperature changes related normally to those of the surface, occurring up to two months prior to them during the cooling phase, and lagging as much as four months behind during the heating phase. The rapid change apparent at the beginning of May was due to heavy flooding which occurred at this time.

The situation at Station 3 reflects the pattern found at all stations with water deeper than 6 m. Other stations differed only in the relationship of change between surface and bottom water, which varied as a function of their depth.

2.4.2 Seasonal temperature changes from bay to river mouth

Figure 5.4 shows the results of seasonal transects of surface and bottom temperatures.

2.4.2.1 Waters free of Salvinia

Higher surface temperatures occurred within the "estuary" than elsewhere during the hot season in January 1967, which can be attributed to the smaller volume of the enclosed waters, and invasions of hot (up to 35.5°C) water from the river during lesser flow periods. Bottom waters showed a gradual increase inversely proportional to depth. By April, when the cooling process was rapid, temperatures were similar throughout the length of the drowned river bed, and showed little difference between surface and bottom. By July, when the greater temperature gradient between surface and bottom indicated a start of the warming phase, water outside the "estuary" appeared to be warming faster than within, and temperatures along the bottom followed surface temperature differences closely. The warming process was at a height when next sampled in November, and temperatures within the "estuary" were up to 1°C lower than open water. The

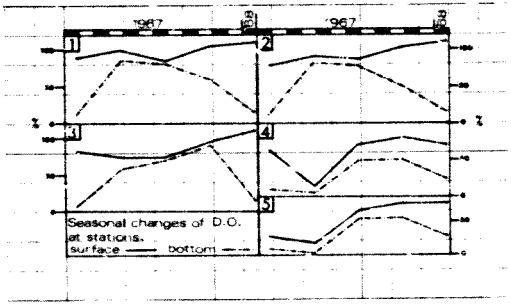


Fig. 5.5

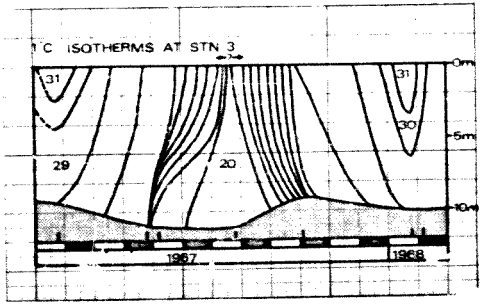


Fig. 5.3
Vertical bars indicate sampling dates

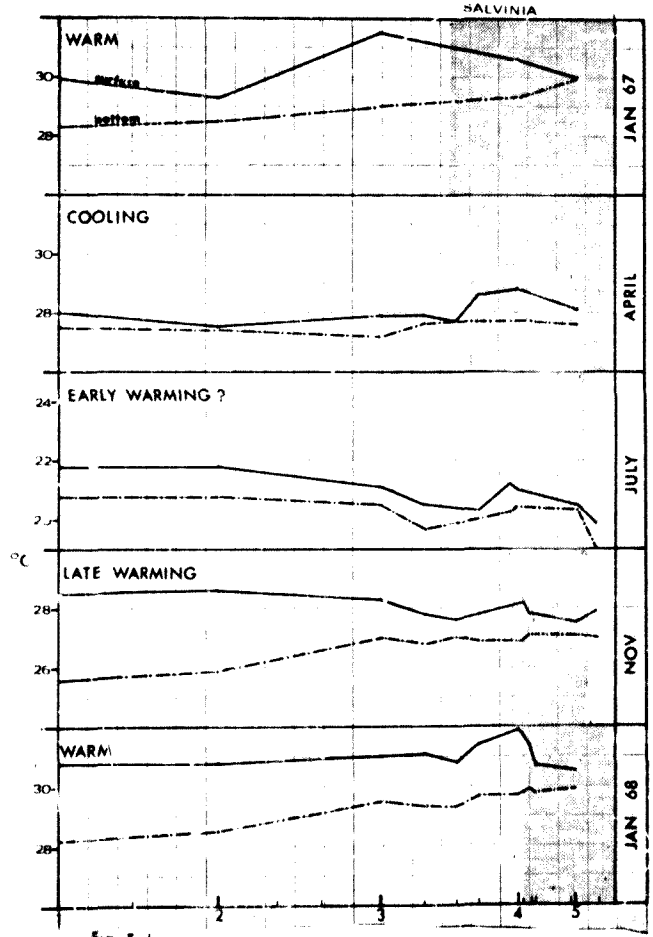


Fig. 8.4
Seasonal transect of surface and bottom temperature
Stippling indicates water covered by Salvinia

slope of bottom temperature outside the "estuary", in conjunction with the gradient between surface and bottom temperatures would appear to have been associated with the development of stratification, which will be discussed below.

Greater annual fluctuation therefore occurred in enclosed waters than in the open bay area and the data indicate that changes within these waters occurred after changes in the bay and must therefore have continued to rise or fall after open waters had stabilised at highest or lowest temperatures. When the magnitude of these changes are compared to annual variation in temperature, however, the biological effects of these differences cannot have been great.

2.4.2.2 The effects of the Salvinia mat

As could be expected, the effect of the Salvinia mat was basically insulatory. Thus during the hot and warming periods, "estuarine" water was cooler under the mat; during cooling and the cold season, waters under the mat were found to be warmer, clearly demonstrated by the abrupt fall in temperature of a block of open shallow water which happened to occur near the river mouth in July. The Salvinia mat therefore had the effect of reducing the differences between open waters and enclosed "estuarine" waters.

2.5 Seasonal Changes in Dissolved Oxygen

Figure 5.5 shows the seasonal changes in oxygen content of surface and bottom waters at the five main stations. The situation found at Stations 1 and 2 would appear to be identical. Surface saturations at these outer stations remained very high throughout the year. Bottom waters, on the other hand, varied considerably, being low in January (10 - 20%) and increasing to a peak in April (80 - 90%), thereafter tensions decreased slowly until the January low level was

experienced again in 1968. Thus, in waters associated with the bottom at about 22 m, oxygen conditions appeared not to be limiting, as far as is known, except possibly in mid-summer. ~~The reasons for this~~ The situation at this time of year could be caused by two factors. Firstly, the development of stratification, and secondly, the decomposition of fresh organic matter laid down during recent flooding.

Surface waters at Station 3 showed a similar pattern to the open surface waters, but conditions in waters associated with the bottom were different in that highest values were found in November, with an abrupt decrease to a January low. The reasons for this difference are associated with the development of de stratification at the outer stations, not present at this station. (See below).

Stations 4 and 5, underneath the Salvinia mat, generally showed lower oxygen concentrations throughout. Similar trends were observable in both surface and bottom waters, with higher values at the surface. Seasonal changes also differed in that low January concentrations persisted until April. From July to November the indications were that oxygen tensions ranged between 50 and 80% throughout waters underneath the Salvinia. Values dropped again by January 1968, in bottom waters, to 20% saturation, in keeping with the low concentrations experienced in January and April 1967. Surface concentrations in January 1967, did not follow the pattern outlined above. This is considered to be for the same reason as the high values found in January of the following year, namely, surface waters in both cases were of direct riverine origin. The 1967 concentrations were sampled when the river had virtually ceased to flow, whereas sampling in 1968 was undertaken when the river was flowing lightly. This could explain the apparent discrepancy between Stations 4 and 5 in 1967, where the

block of warm, oxygenated river water is thought to have passed beyond Station 5, but not Station 4, hence the higher oxygen tensions at the latter. It will be seen, below, that when the river flows weakly, river water remains at the surface in the "estuary", a characteristic which allows this explanation.

2.8 Thermal and Oxygen Stratification

Theoretically, the more enclosed a body of water and the higher the ratio between depth and surface area, the more abrupt should temperature changes occur with depth, and the shallower these changes should occur. These characteristics should be emphasised if the enclosed body of water is experiencing greater temperature fluctuation. Thus, the exposed outer stations, (1 and 2) with their large surface area, lower ratio of depth to surface area, and lower range of annual temperature fluctuations, stratification could theoretically be expected to be deeper and less abrupt than at the inner stations (3 to 5). This pattern was followed only in part, as follows.

During April 1967 (Fig. 5.6) stratification was generally weak (0.6°C/m at 28°C), and sloped from 6 - 7 m in depth at Station 1 to 4.5 m at Station 2, with no apparent stratification inside this, except the abrupt changes which occurred in surface waters inside the Salvinia mat. Dissolved oxygen values sloped inwards, independently of the thermal stratification, with highest values at the surface at outer stations, and lowest values underneath the mat. The pattern of isotherms and dissolved oxygen values indicated considerable mixing to have been taking place in the vicinity of the mat edge, probably associated with wind induced surface currents being activated along the mat edge, but not under the mat, and the associated compensation from the bottom waters. This results in a "tilt" in the opposite

direction to that experienced in outer waters.

The following July showed a duplication of this pattern (Fig.5.7), but stratification was deeper and far more abrupt (1.2°C/m at 21°C), sloping from 10 m at Station 1 to 5 m at Station 2, and 2.5 m at Station 3. Oxygen values showed a sharper gradient in association with temperature stratification in open water, but thereafter characteristically "sloped" independently of temperature, with a rapid reduction between surface and bottom within the "estuary" and particularly against the edge of the Salvinia mat, though values did not drop below 50% saturation. More highly oxygenated water intruded at Elbow Rapid as a result of back-flooding which occurred at this time.

By November (Fig.5.8), double stratification was established. The strong upper stratification layer (1.4°C/m at 28°C) sloped characteristically, but more shallowly than previously, having risen to 6 m at Station 1, 5 m at Station 2 and 5 m at Station 3. Deep stratification (0.7°C/m at 27°C) was established horizontally at 14.5 m. Oxygen values were found to vary independently of the upper thermocline, but a marked "oxycline" (100 - 80%/m) occurred in association with the deeper thermocline and oxygen values fell rapidly underneath this, though values remained above 50% saturation throughout the area of study during this month.

The double thermocline persisted until January 1968, (Fig.5.9) but the shallower was found now to be horizontal and stronger at outer stations (1.5°C/m at 30°C) where it occurred between 4 and 5 m depth. The deeper thermocline was found to be both less abrupt and deeper than in November, occurring at 20 m. Two sloped and marked "oxyclines" occurred, the shallower running from 12 m at Station 1

Figures 5.6 to 5.9

Seasonal changes of isotherms and dissolved oxygen isopleths of the water column overlying the old river bed. Sampling points indicated by dots; stations by numerals. Salvinia is indicated on the water surface.

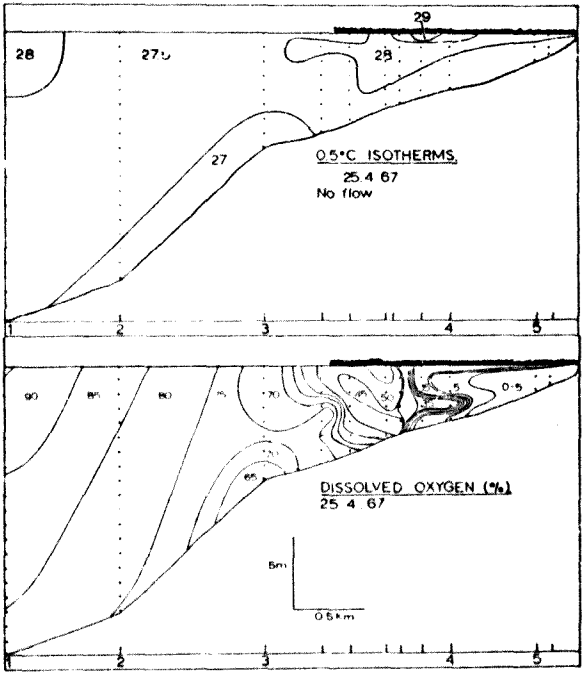


Fig. 5.6 25th April, 1967

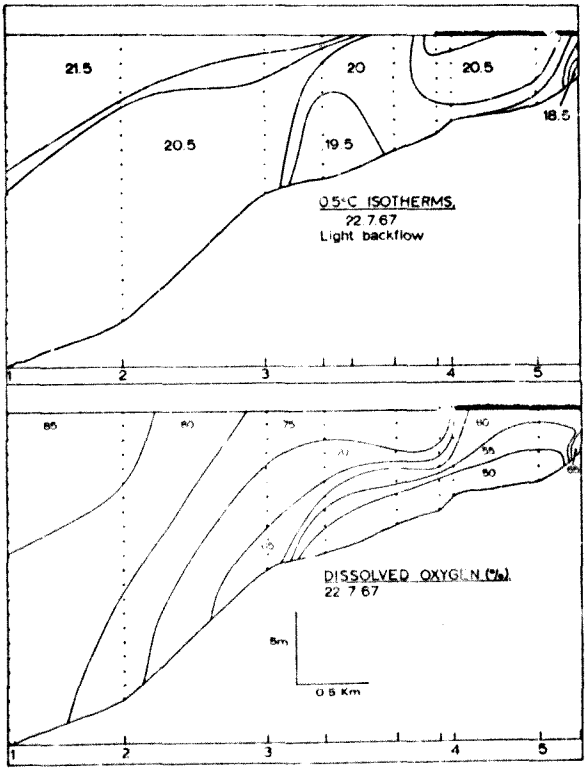


Fig. 5.7 22nd July, 1967

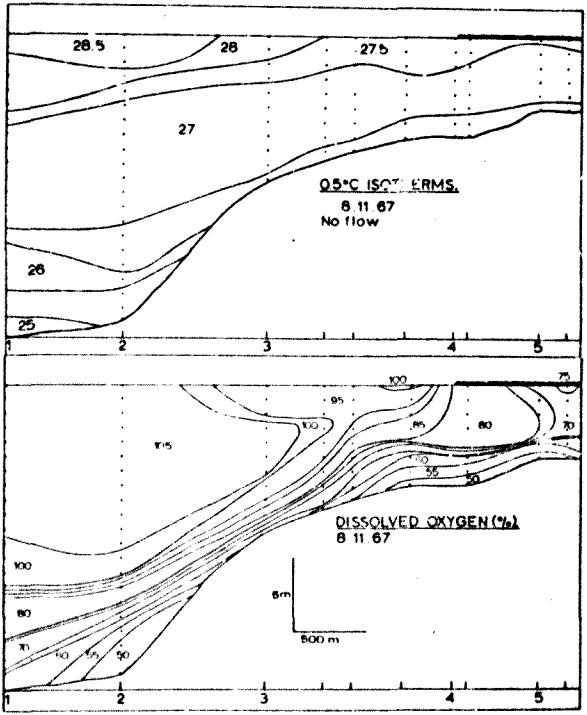


Fig. 5.8 8th November, 1967

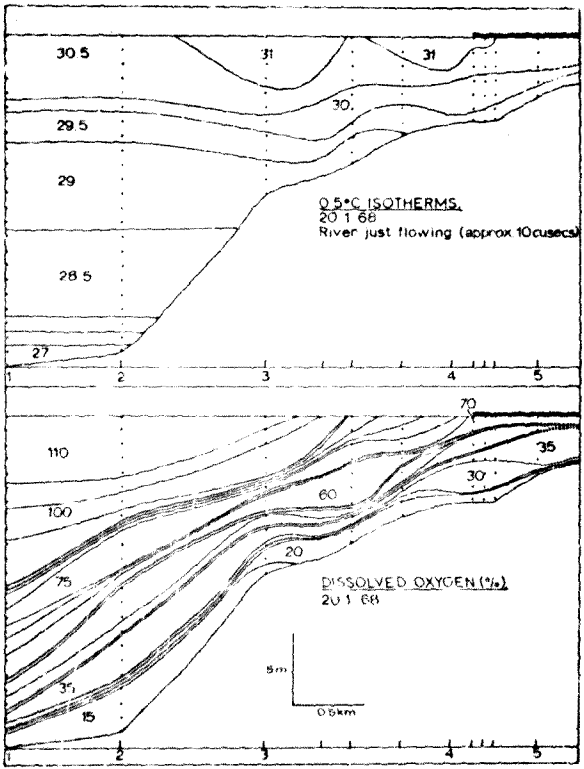


Fig. 1.9 20th January, 1968

to 7 m at Station 2 and 4 m at Station 3. The lower oxycline (36 - 15%/m) occurred within 2 to 3 m of the bottom and extended well into the estuary, thus both occurred independently of thermal stratification.

It is considered that the deeper thermocline, which became apparent in November and which was closely associated with an abrupt decrease in oxygen was probably, judging by its depth, the outer edge of the overall lake thermocline, which moved deeper by the following January, in keeping with findings by other workers (Coche, 1968 Begg, 1969). The fact that the oxycline was independent of this stratification by January indicates effects other than stratification and it is suggested that this could be caused by flooding of the river. Initially, this would cause an increase in oxygen, but considerable organic matter would also be deposited. Once flooding had ceased and relative stabilisation achieved, the effects of fresh organic matter being deposited on the river bed could persist and result in de-oxygenation of water associated with it, hence the "oxycline" which closely follows the bottom contour, and the sloped layering of the dissolved oxygen isopleths (Fig.5.9).

The fact that a shallow thermocline is persistent in the Mwenda Bay and has not been reported from open waters of the lake indicates that this is local, and characteristic perhaps of "bayed" areas of the lake.

Thus the theoretical characteristics of stratification would appear to be borne out in part by the findings, in that there is a progressive shallowing of the "bay" thermocline as exposure decreases. On the other hand, temperature gradients in outer waters were generally more abrupt, contrary to theory. Perhaps this is due to the

external characteristics of the Waranda "estuary", in that the steep and high hillside against the greater part of the north-eastern shoreline funnels winds on to the water surface and generates mixing currents.

Thus the shallower "bay" thermocline appeared to be present throughout the year, having been weak in April and going deeper and becoming more definite by July. By November it had become very definite and had moved towards the surface in deeper waters, until becoming more or less horizontal by January at 5 m beneath the surface. The deeper "lake" thermocline had appeared by November when it had a definite effect on oxygen distribution to deeper layers, and although persistent until January this effect had, it is suggested, been disrupted by inflowing river water so that it no longer had any apparent effect on oxygen distribution.

2.7 Flow Effects.

The temperature and oxygen characteristics of the transect, sampled while the river was flowing at a low level, estimated as approximately 0.3 m^3/s, are illustrated in Figure 5.9. The characteristics of the river at this time were extremely high temperature (35.6°C) associated with its sluggish flow, high oxygen content (98%) and although turbid, the silt load was low. Turbidity extended to between Stations 3 and 4, but no marked convergence zone was present. As may be seen from the figure, the effects of river water appear to be limited to surface waters, in that high oxygen values and temperatures were found directly underneath the mat, lying over a very abrupt oxycline (70 - 30%/m). It would seem that the excessive temperature of the river water overcame any density associated with silt load and that this water flowed along the surface and was quickly

assimilated by estuarine water. Under these conditions the passage of a boat over apparently turbid waters was observed to result in a wake of deeper clear water where turbid surface waters had been displaced.

Figure 5.10 illustrates a light flood, estimated as a flow of 8 m^3/s, which took place in February 1968. River water temperature at the time of sampling was found to be 27°C, considerably cooler than lake water. At the same time the silt load was quite high. This resulted in the river water being considerably denser than lake water, and flow along the bottom resulted. The temperature gradient away from the river mouth was rapid, indicating considerable early mixing. Oxygen concentrations indicated a displacement upward and "downstream" of bottom water underneath the mat, and the formation of an interflow between 3 m and 7 m at Station 3, which dissipated rapidly as a result of peripheral mixing and the broadening of the flooded river basin, so that little effect on the water column was discernable at Station 2. The turbid water and clear lake water convergence was seen on the surface between these two stations.

On the 2nd May 1967, the river flooded violently after approximately 50 mm of rain had fallen in the previous twelve hours. Flow was estimated at 61 m^3/s. The river water was cold (21.5°C) and carried a heavy silt load. The force of flow was sufficient to dislodge the Salvinia mat and compact it against Jacana Bend. A strong counter current was set up on the surface in the region of Station 3, and a definite flow convergence occurred underneath the compressed mat. Figure 5.11 illustrates the effect of flooding. The river clearly stayed within its bed. A strong thermocline was established 2 m above the bottom at the outermost station and this overlay flowing

Figures 5.10 and 5.11

The effects of flow on the structure of static waters as described by isotherms and dissolved oxygen isoplothe.

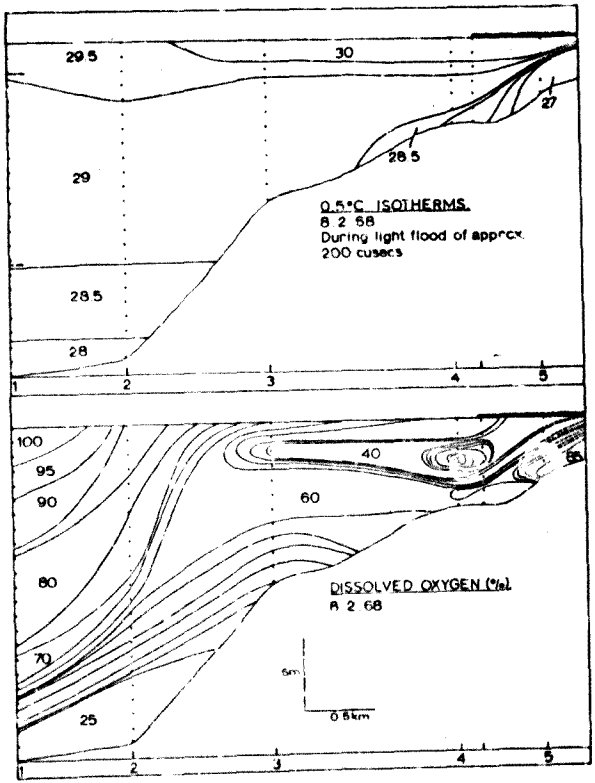


Fig. 5.10 8th February, 1968

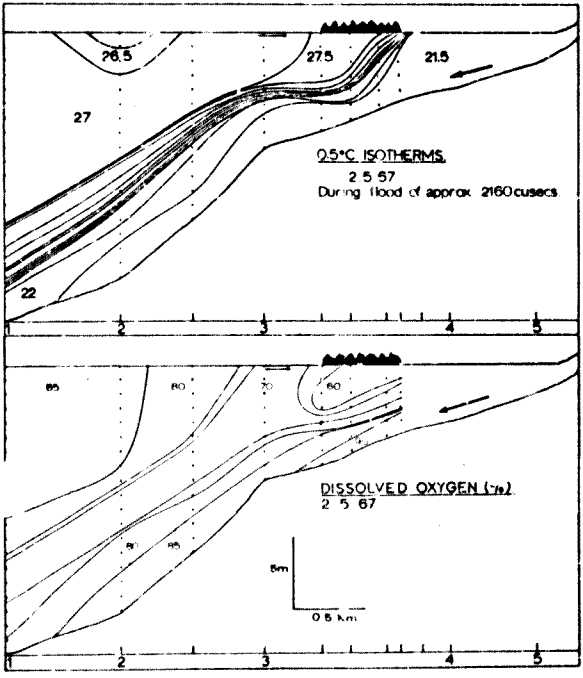


Fig. 5.11 2nd May, 1967

water. The wire of the Friedinger sampling bottle used to sample these waters started vibrating when the bottle was lowered into the last two metres, some 20 m from the water surface. Bottom waters were displaced to a degree that lowest oxygen tensions were found 5 m off the bottom, above a strong temperature gradient. A further sloped thermocline was established 5 m above this. The effects of various grades of flooding are summarised in Figure 5.12.

2.8 Other Physico-Chemical Data

The seasonal relationship of the physico-chemical characteristics of the waters in the study area are complex and in order to facilitate their analysis, arbitrary types of water are considered separately. These are patently artificial, as horisontal changes in water quality are more likely to be gradual than abrupt, as may be seen in Figure 5.15. The separations are:

(a) open "bay" waters (Stations 1 and 2),

(b) enclosed "estuarine" waters free of Salvinia (Station 3),

(c) enclosed "estuarine" waters covered by Salvinia (Stations 4 and 5),

(d) flowing river water.

Static river waters do not directly affect the characteristics of the lake and are therefore considered separately. The seasonal characteristics of these water types will be considered first and thereafter their relationships will receive attention. All physico-chemical estimations which were undertaken are appended (Appendix 5.1 - 5.5) and the range of quality values for different water types have been tabulated, for easier reference, in Table 5.5 .

Figure 5.12

A diagrammatic summarisation of flow effects on static waters near the river mouth.

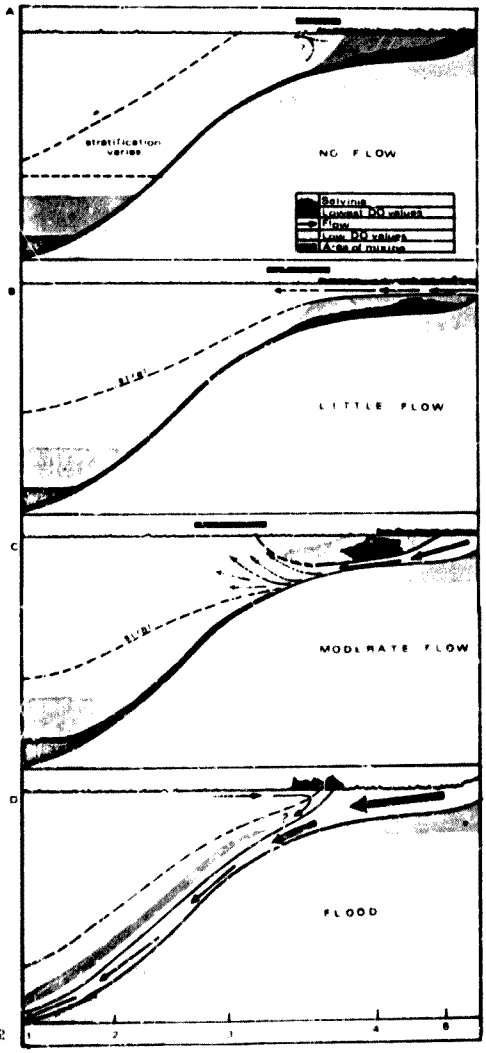

A
stratification varies
NO FLOW
Salinity
Lowest DO values
Flow
Low DO values
Axis of maxima
B
LITTLE FLOW
C
MODERATE FLOW
D
FLOOD
1
2
3
4
5

Fig. 5.32

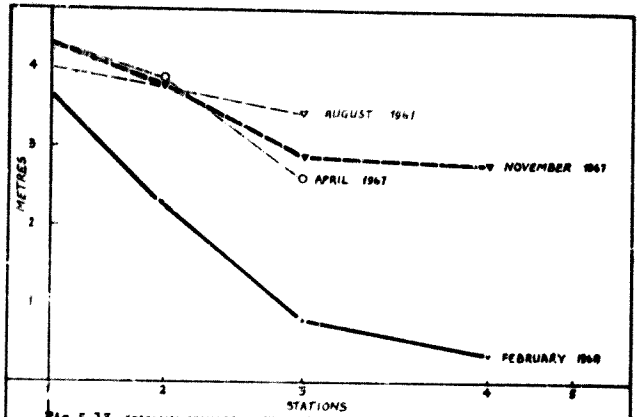


Fig.5.13 SEASONAL CHANGES IN THE DEPTH OF VISIBILITY OF A 30cm SECCHI DISC. TRANSECT RESULTS

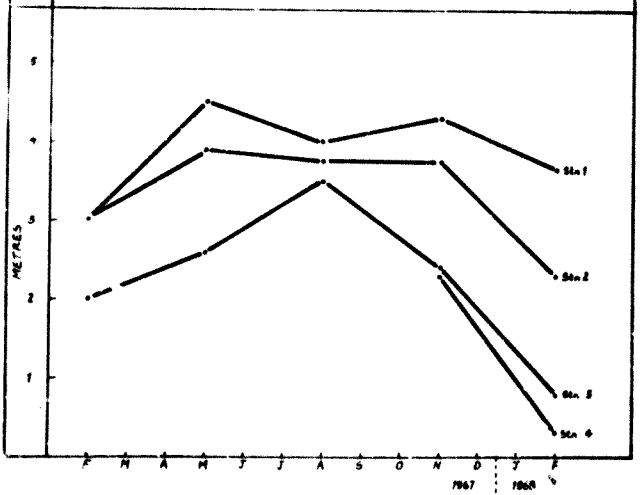


Fig.5.14 SEASONAL CHANGES IN THE DEPTH OF VISIBILITY OF A 30cm SECCHI DISC AT THE DIFFERENT STATIONS.

TABLE 3.1 [illegible]

Values in mg/l unless otherwise stated
( ) Bracket: samples not taken during full flood
Blank line: values not taken due to [illegible], or lack of sufficient depth

	[illegible] (Stations 1 and 2)		[illegible] (Station 3)		[illegible] (Stations [illegible])		[illegible]	[illegible]		[illegible]	[illegible]
	Surface	Bottom	Surface	Bottom	[illegible]		Surface	[illegible]	[illegible]	[illegible]	Surface
Conductivity (umhos/cm)	72 - 86	64 - 84	74 - 33	33 - 85	([illegible]) - 64	([illegible]) - 24	74	33	47 - 57	74 - [illegible]	31
Visibility (m)	3.0 - 4.5	-	2.1 - 3.9	0.8 - 2.5	Very clear / very turbid	-	Very clear	Very turbid	turbid	turbid	turbid
pH	7.4 - 7.9	6.4 - 7.8	7.0 - 7.6	6.6 - 7.6	(6.5) - 6.9	(6.5) - 7.5	7.2	6.8	7.0 - 7.5	7.0 - 7.5	7.0
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]-(7.48)	[illegible]-(2.46)	5.40	[illegible]	6.4 - [illegible]	[illegible]-1.50	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible] - (77.9)	[illegible] - ([illegible])	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	([illegible])	([illegible])	[illegible]	[illegible]	[illegible]	[illegible]	-
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	-
Suspended solids	[illegible]	[illegible]	[illegible]	[illegible]	[illegible] - ([illegible])	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Solid residue [illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible] - 112	[illegible]
Loss on ignition	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	30	[illegible]	4 - 41	18
Total hardness ($CaCO_3$)	[illegible]	[illegible]	[illegible] - 40	[illegible]	([illegible]) - [illegible]	[illegible]	[illegible]	18	[illegible]	31 - [illegible]	[illegible]
Nitrate NO_3	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	0.14
Nitrite NO_2	0	0	0	0	[illegible]	[illegible]	[illegible]	[illegible]	0	[illegible]	0
Ammoniacal nitrogen	0.01 - 0.08	[illegible]	0.01 - 0.05	0.01-0.16	[illegible] - (0.06)	0.38 - (0.17)	0.05	0.12	0.16 - 0.15	0.07 - 0.13	0.04
Albuminoid nitrogen	[illegible] - 0.20	[illegible] - 1.90	0.16 - 0.26	0.05-0.87	0.06 - (0.49)	0.08 - (0.40)	0.07	[illegible]	0.27 - 0.37	0.15 - 0.35	0.15
Calcium (as $CaCO_3$)	[illegible] - 95	27 - 76	75 - 32	8 - 34	(24) - 35	(20) - [illegible]	75	10	14 - 17	17 - 36	27
Calcium (as Ca^{++})	9 - 12	6 - 30	9 - 13	3 - 14	(10) - 15	(8) - [illegible]	9	4	6 - 7	7 - 20	11
Magnesium (as $MgCO_3$)	5 - 13	1 - 12	4 - 11	3 - 13	1 - [illegible]	1 - 15	10	9	5 - 12	11 - 30	17
Magnesium (as Mg^{++})	1 - 4	1 - 5	1 - 4	1 - 4	2 - 4	[illegible] - 4	4	5	2 - 5	4 - 11	5
Potassium (as K^+)	[illegible] - [illegible]	1.4 - 4.5	1.4 - 1.8	1.4 - 4.8	1.4 - (4.1)	[illegible] - (4.5)	1.3	1.4	1.0 - [illegible]	0.6 - 6.7	0.4
Sodium (as Na^+)	3.8 - 4.6	2.5 - 4.8	1.9 - 4.7	1.9 - 4.4	(3.[illegible]) - 4.5	([illegible]) - 4.5	4.0	1.9	1.6 - 7.4	1.7 - 8.1	3.7
Phosphate (as PO_4)	0.036-0.177	0.080-0.250	0.050-0.215	0.040-0.519	[illegible]	[illegible]-0.777	[illegible]	0.104	0.213-0.617	0.106-0.279	0.089

2.8.1 The characteristics of flowing river water

When flooding, the electrolytic load of the river was low (33 μmhos/cm) which would indicate an inverse relationship between salt load and flow volume. This was also reflected in the cation estimations (except potassium) even though the water is particularly turbid. This turbidity must therefore result from immediately insoluble particles in suspension. The river waters were particularly well oxygenated, slightly acid (pH 6.6) and had a low alkalinity and hardness and therefore a relatively high carbon dioxide content (22.5 mg/l). Matter in suspension (94 ppm) and the organic content was high, which is reflected by both loss on ignition (38 mg/l) and albuminoid ammonia (0.88 mg/l) estimations. The most important feature, biologically speaking, was the nutrient, particularly nitrate, load (NO_3 : 0.40 mg/l; NH_4 : 0.12 mg/l). Phosphate is also present in quite high concentrations.

2.8.2 Enclosed "estuarine" waters free of Salvinia

Seasonal changes in selected physico-chemical characteristics are demonstrated in Figure 5.15. The specific conductivities of these waters ranged between 67 and 83 μmhos. Generally conductivities were slightly higher on the surface and there was little seasonal change except when flooding occurred. The cation concentrations behaved similarly to conductivity, although calcium showed a decrease between January and April 1967, and magnesium a gradual increase, so that the Ca/Mg ratio dropped from 14 to 3 around which latter point it remained for the rest of the year. The pH in surface waters remained about 7.5 through the year, except when flooding occurred. The bottom waters were less alkaline and fluctuated around 7.2, except when affected by floodwaters, and during November when the pH

rose sharply to 7.8. Alkalinity was similar at surface and bottom and remained between 40 and 42 mg/l $CaCO_3$ through the year. Dissolved carbon dioxide concentrations were low, particularly in surface waters, but a slight increase in both surface and bottom waters was measurable during the rainy season. Surface waters were almost free of suspended solids throughout the year. At the bottom suspended solid values were much higher during the rains, but from August until the rains started, conditions on the bottom were similar to those on the surface. Surface and bottom waters showed a marked similarity with regard to seasonal fluctuations of dissolved (residual) solids, although bottom concentrations were slightly higher. Concentrations were higher in January 1967 than at any other time (ca 85 mg/l), decreased to ca 55 mg/l in July, increased in November and surprisingly showed a decrease in January 1968. No seasonal change in dissolved organic matter was apparent (loss on ignition) and surface and bottom waters carried similar amounts (ca 12 mg/l).

No nitrites were found in the enclosed waters free of Salvinia. In surface waters more free ammonical nitrogen was present between May and August than from November to February, whereas, apart from January 1967, nitrates tended towards the opposite, even though the dissolved oxygen content of these waters remained high throughout the year. In waters associated with the bottom, ammonical nitrogen content was generally from 0.025 mg/l to 0.1 mg/l higher than found at the surface and tended to be in higher concentrations during the rainy season. Nitrates were also higher at this time being absent in winter in both surface and bottom waters.

Phosphates throughout the water column remained at approximately 0.06 mg/l through the year, except in November, when there was an

inexplicable increase to 0.215 mg/l. Phosphates would therefore seem to have been readily available at all times, whereas the non-availability of nitrate could have been biologically limiting in winter (July) and in surface waters during January 1967.

2.0.3 Open "bay" waters

Whereas the depth of water at Station 3, chosen as typical of enclosed estuarine waters free of Salvinia, ranged around 10 metres, the depth at outer stations ranged between 17 and 22 metres, approximately twice this amount. The water characteristics of Stations 1 and 2 were so similar that it is not considered necessary to present them separately. Figure 5.16 demonstrates seasonal changes of selected characteristics. The specific conductivity of open waters indicates, apart from slightly lower winter concentrations, a remarkable similarity in having low concentrations through the water column throughout the year. The pH of the somewhat alkaline surface waters (7.5 - 7.9) indicates slightly greater alkalinity during the rains than in winter, when surface and bottom pH's were the same. In waters associated with the bottom, conditions were less alkaline and an increase occurred in winter. During November, however, bottom waters became slightly acid. As alkalinities (as $CaCO_3$) were found to be quite stable, dissolved carbon dioxide showed an increase at this time. Slightly greater concentrations of carbon dioxide existed in the bottom through most of the year. The analyses of solids showed little seasonal change and little difference in the water column except early in 1967 when larger quantities of suspended solids were found in bottom waters.

Nitrates were never found to be present. Nitrites were always present except on the bottom at Station 2 in January 1967. Generally they were found to be in slightly higher concentrations on the surface

and during the rains. Ammoniacal nitrogen in surface waters decreased during the course of sampling, but showed an increase on the bottom in November and during the rains. The phosphate content of surface waters remained approximately constant except for a sharp four-fold increase in November to 0.53 mg/l, thereafter decreasing to previous levels by the following January. In bottom waters the concentration of phosphate in January 1967 was high (0.24 mg/l) but dropped by April to the surface content and thereafter fluctuated in the same way as found at the surface.

2.0.4 Enclosed "estuarine" waters covered by Salvinia

As the "estuary" shallows and becomes narrower, the effects of enclosure and of the river must become more pronounced. These effects are partially obscured, however, by the presence of the Salvinia mat which will be discussed in greater detail below (2.0.7). The seasonal changes in water quality are shown in Figures 5.17 and 5.18. As has been described, Station 4 (Fig. 5.17) became free of Salvinia by November 1967, so that what may seem to have been seasonal changes after August 1967, must to some extent have been affected by this. Samples were not taken at Station 5 (Fig. 5.18) in July 1967, but further inland, where a perceptible (upstream) flow as a result of backflooding resulted in a patch of water free of Salvinia which must have passed underneath the whole length of the Salvinia mat.

The electrolytic content of surface waters were generally slightly higher than at the bottom and a slight decrease occurred both in winter and during the rains, with highest values being recorded in April and November. Greater discrepancy between surface and bottom occurred during the rains. The pH indicated conditions at Station 5 to be relatively acid (6.5) prior to July 1967, more so than at Station 4.

Figs. 5.15 to 5.18

Seasonal changes in selected chemical characteristics at the various stations. The effects of flooding in May 1967, can be seen in Figs. 5.15 and 5.16.

Surface o——o

Bottom •——•

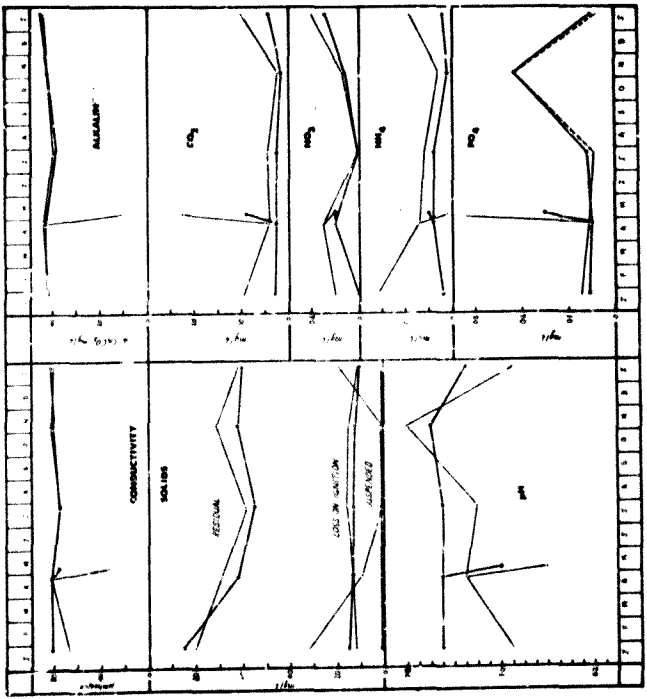


Fig. 5.15 Station 5

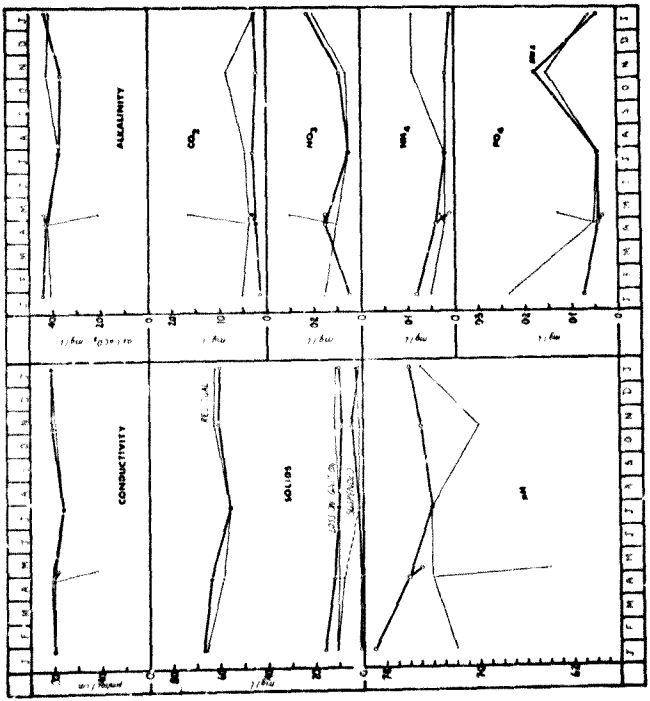


Fig. 5.16 Station 1

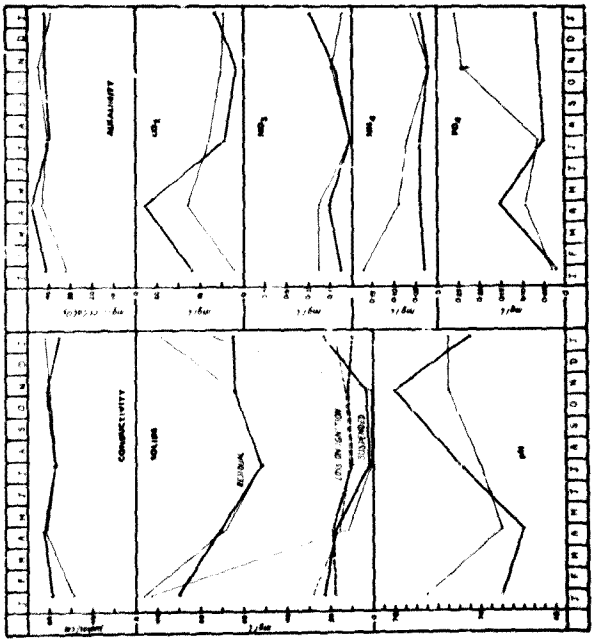


Fig. 5.17 Station 4

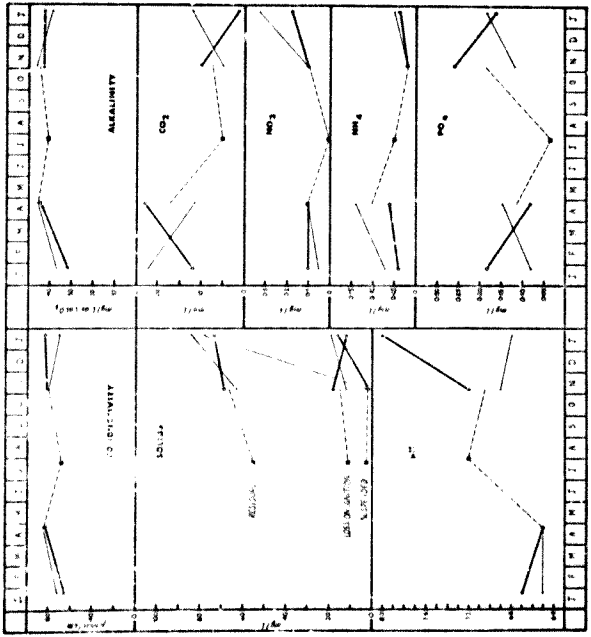


Fig. 5.18 Station 5

A general rise in pH occurred during the course of the work, particularly in surface waters, so that by January 1969 conditions were definitely alkaline (8.0) at Station 5. Alkalinity remained relatively constant, but the seasonal fluctuations in the carbon dioxide content were rather abrupt and the differences between the surface and bottom content were relatively large. Suspended solids are particularly high during the rains but decrease to low levels from April to November. Little change could be seen in the organic matter content of the water and residual solids followed the same pattern as suspended solids. Nitrate was present throughout the year, except winter, and a gradual decrease in ammoniacal nitrogen through 1967 was found which occurred synchronously with an increase in nitrate at Station 5. Phosphate showed a marked increase in the bottom waters at Station 4 during the study period, but was relatively stable at the surface. At Station 5 the phosphate content was generally higher than at Station 4, except in winter when it dropped to less than 0.05 mg/l.

2.3.5 The change in water quality from river mouth to bay

The effect of flood waters will be considered below. Other effects on water quality must stem from the spatial relationship of the water "types", water depth, enclosure (inasmuch as the water body becomes progressively smaller) and the Salvinia mat. The effects of the mat will also be considered separately so that the present consideration only involves spatial relationships, water depths, and the effects of enclosure as defined above. The gradation of characteristics from river mouth to bay can be seen in the turbidity readings in Figure 5.15, where the clarity of the water progressively increased from the edge of the Salvinia mat to the bay. Much of the data indicate a similar trend in other quality characteristics. pH and alka-

linity (as $CaCO_3$), for example, also showed an increase. Waters became more alkaline the further they were from the river mouth and more markedly so at the surface (the tilt of dissolved oxygen is repeated). Conductivities changed very little and, if anything, showed a slight decrease away from the river mouth, as did albuminoid ammonia, ammoniacal nitrogen, nitrate, phosphate, potassium and dissolved carbon dioxide. On the other hand, there appeared to be no discernable difference in the quantities of sodium, magnesium and calcium ions in solution.

2.0.6 The effects of the river on water quality

The degree to which the river affected the static waters has been shown to be dependent on the volume of flow. Not only do flood waters completely replace the waters of the narrow part of the system and disrupt conditions, particularly in deep water, of the bay, but throughout the rains areas nearer the river mouth are subjected to almost continuous intrusions of slowly flowing river water, very different in quality from flood waters.

The effects of flooding on the water chemistry of static waters can be clearly seen in Figures 5.15 and 5.16. Conductivity, pH, alkalinity and ammoniacal nitrogen all show a radical decrease, as do sodium, magnesium and calcium. On the other hand, the solids load is increased greatly (Appendix 5.5) and carbon dioxide content, albuminoid ammonia, nitrate and phosphate also increase. Thus the quality of river water is impressed upon the static waters it invades and even has an immediate, small, effect on surface waters some 20 m above it.

The river was therefore an extremely important source of nutrient, both nitrogen and phosphorus, the former having been introduced mainly

in the albuminoid form and was thus not immediately available. However, the stirring action of flow on the alluvium of the drowned river bed and oxidation of this by flood water would also seem to have an important effect. For ammoniacal nitrogen, derived from albuminoid nitrogen and which decreases, appears to have been oxidised and to have caused an increase of nitrate. This matter is discussed further below (5).

Introduction of phosphate cannot be as important in the short term as there would appear to have been an excess at the time of study.

2.8.7 The effects of the Salvinia mat on water quality

As the lake level rises and backflooding of the lower reaches of the Mwenda River occurs, a very gradual flow from the lake into the river takes place. By monitoring the characteristics of waters which had passed underneath the Salvinia, but which had not mixed with waters of the pools, and by comparing these, firstly with the trend of change in characteristics from the bay to the outer mat edge, and secondly, with the characteristics of the outer mat edge, it should be possible to differentiate between "enclosure" effects and the effects of the Salvinia mat at that time.

During July 1967, this situation occurred and a patch of Salvinia free water was found below Elbow Rapid. This water was exceptionally clear. As Kariba waters are somewhat turbid the effect was dramatic, thus the term Salvinia "distillate" was coined to describe it. The physico-chemical data collected have been extracted in Table 5.4 and by comparison, as described above, few characteristics seem to have been affected by the Salvinia mat only. Apart from dissolved oxygen and temperature, which have already been considered,

TABLE 5.4 THE EFFECTS OF ENCLOSURE AND THE SALVINIA MAT ON LAKE WATER

		STATION 1 Open	STATION 5 Enclosed	STATION 4a Mat edge	BLACK RAPID Salvinia "distillate"
Specific conductivity mhos/cm at 20°C		72	74	74	74
Temperature °C		21.7	21.1	21.1	19.1
Turbidity (m)		4.0	3.5	2.5 m	very clear
pH		7.4	7.5	7.2	7.5
Dissolved oxygen	(mg/l)	5.80	4.36	4.22	5.20
Dissolved oxygen corrected % sat.		87.3	77.9	69.2	60.2
Alkalinity as $CaCO_3$	(mg/l)	37.5	38.7	39.7	40.5
Dissolved carbon dioxide	(mg/l)	3.0	2.5	4.5	5.0
Suspended solids dried at 100°C	(mg/l)	1.5	0.5	1.5	1.5
Total solid residue dried at 180°C	(mg/l)	56	55	55	55
Total dissolved solids	(mg/l)	37.5	55.5	55.5	5 .5
Loss on ignition	(mg/l)	10	15	14	11
Total hardness as $CaCO_3$	(mg/l)	36	36	36	36
Nitrate NO_3^-	(mg/l)	0.05	Nil	Nil	Tr
Nitrite NO_2^-	(mg/l)	Nil	Nil	Nil	Nil
Ammoniacal nitrogen	(mg/l)	0.02	0.04	0.04	0.02
Albuminoid nitrogen	(mg/l)	0.08	0.08	0.10	
Calcium as Ca^{++}	(mg/l)	9	9	10	
Magnesium as Mg^{++}	(mg/l)	3	4	4	4
Potassium as K^+	(mg/l)	1.4	1.4	1.4	1.3
Sodium as Na^+	(mg/l)	3.7	3.8	3.9	4.0
Phosphate as PO_4^{---}	(mg/l)	0.048	0.081	0.080	0.084
TIME:		1015	1100	1200	1230

these include pH and turbidity, which were decreased, and carbon dioxide and suspended solids, which were increased. Certain other characteristics seem to have been affected by both enclosure of the water body and the Salvinia mat. These were alkalinity and ammoniacal nitrogen which showed an increase. The sodium content of the water seems only to have been affected by enclosure, as the increase found was progressive and was not affected by the mat.

The Salvinia mat had the effect, on some characteristics, of reverting the effects of enclosure to conditions more similar to those found in open water. These were total solids and phosphate. Apart from nitrate, the other characteristics tabulated showed little or no change between open waters, enclosed waters, and waters which had passed under the mat.

The increase of carbon dioxide and decrease of dissolved oxygen probably resulted from the respiration of subsurface elements of the Salvinia plants, coupled with the physical barrier a dense mat imposed on gaseous interchange at the surface. Photosynthetic activity and oxygen generation is limited to the chlorophyllous aerial parts.

The decrease in phosphate indicated a higher level of utilisation by the Salvinia mat than by the phytoplankton in open waters at that time of year, but the content present was still in excess of requirements. Nitrates, on the other hand, showed considerable decrease on enclosure, but a slight increase in the "distillate" which could be explained by the release of nitrate in excess of requirement following decomposition of dead Salvinia, as found by Mitchell (1970). The lack of nitrate could therefore have been limiting at this time of year in enclosed Salvinia free waters.

A possible solution to the increase in suspended solids in the "distillate", in the light of the exceptional clarity of the water, was that this increase was due to the presence of the ubiquitous trichomes of the submerged parts of Salvinia (the Salvinia root hairs), which by their nature would have tended to give high suspended solid readings without impairing the clarity of the water relative to other types of solids in suspension, such as phytoplankton or soil particles.

The extreme clarity of the Salvinia distillate probably resulted from the suppression of both turbulence and phytoplankton development by the Salvinia mat, in that it protected the water from wind action and suppressed the entry of light into the water.

The lack of nitrate and the low level of phosphate at the time of sampling could be attributable to the fact that the winter months are the most favourable growth period for Salvinia. This is, however, contrary to Mitchell's (1970) findings and the synchronous decrease of nutrient in Salvinia free pools of the river at this time of year suggests the involvement of some other factor or factors.

2.8.0 Seasonal changes in static river waters

The change that can be seen in the physico-chemical conditions in the river and, subsequently, pools, following the cessation of flow are given in Table 5.5 and figured in Fig. 5.19. The specific conductivity, which was relatively low (57 µmhos) in the static river during the rains becomes even lower (46 µmhos) by May, but thereafter increased to as much as 222 µmhos in the pools by the end of the dry season. Calcium is the most important cation and followed, with magnesium and potassium, the initial decrease shown by the specific conductivity, whereas sodium increased from a low January figure (1.6 mg/l) to an October high (8.1 mg/l).

TABLE 5.5 SEASONAL CHANGES IN THE QUALITY OF RIVER WATER

		STATIC RIVER		SWAMP POOL		RAPIDS POOL		DEEP POOL	
		January	May	July	October	8.8.67	24.10.67 (no fish)	24.10.67 (with fish)	
Specific conductivity mhos/cm at 20°C		97	48	97	222	98	126	132	
Temperature °C		26.5	21.0	19.0	28.0	16.4-20.0	28.5	27.5	
pH		6.5	6.8	7.5	7.5	7.0	7.5	7.5	
Dissolved O_2	(mg/l)	6.4	6.1	1.20	5.42	5.40	5.44	5.82	
Dissolved oxygen corrected 5 ppt.		90	90	54.0	62.0	54.0	80.0	90.0	
Alkalinity (as $CaCO_3$)	(mg/l)	55	18.0	48.4	90	33.2	56	-	
CO_2	(mg/l)	21.5	8.0	5.0	5.1	6.0	5.5	-	
Suspended solids (dried at 105°C)	(mg/l)	180	9[illegible]	7.5	19	24	5.0	80	
Total solid residue (dried at 180°C)	(mg/l)	128	124	68	182	80	98	98	
Loss on ignition	(mg/l)	57	38	4	41	18	80	21	
Total hardness (as $CaCO_3$)	(mg/l)	50	21	48	102	21	71	44	
Nitrate nitrogen NO_3^-	(mg/l)	0.26	0.45	0.1	0.09	0.10	0.10	0.14	
Nitrite nitrogen NO_2^-	(mg/l)	011	011	011	011	011	011	011	
Ammoniacal nitrogen	(mg/l)	0.08	0.12	0.3[illegible]	0.10	0.04	0.09	0.07	
Albuminoid nitrogen	(mg/l)	0.27	0.26	0.18	0.44	0.28	0.29	0.28	
Calcium (as Ca^{++})	(mg/l)	8	4	10	22	7	11	10	
Magnesium (as Mg^{++})	(mg/l)	5	1	7	11	1	6	8	
Potassium (as K^+)	(mg/l)	6.8	3.4	4.4	5.8	3.8	7.8	6.8	
Sodium (as Na^+)	(mg/l)	1.8	3.5	5.8	011	3.8	5.8	5.1	
Phosphate (as PO_4^{---})	(mg/l)	0.227	0.104	0.008	0.217	0.018	0.106	0.138	

The highest temperature was recorded in January (35.5°C). This had fallen nearly 14°C by May and a further 2°C by July to 19°C. By October the temperature rose again to 26°C but was still considerably lower than the previous January.

Dissolved oxygen showed a gradual decrease from high levels in the first part of the year (6 - 8 mg/l) to low levels by July (3.2 mg/l) which persisted until October (3.4 mg/l). The carbon dioxide content of the water behaved similarly, except that the decrease occurred between January and May, when concentrations fell from 21.5 mg/l to 5 mg/l.

Suspended solids also showed a gradual decrease from high January levels (159 mg/l) to low July levels (7.6 mg/l), prior to showing an increase again in October to 19 mg/l. In contrast, residual solids, and their organic content, remained at a high level from January to May, decreased sharply in July and increased to their highest levels in October.

The content of nitrates and phosphates behaved similarly, being present at high concentrations in January and showing a sharp decrease to very low levels in July and thereafter increasing again by October. Ammoniacal nitrogen, on the other hand, was at its lowest concentrations in January and highest concentrations from May to July.

The fluctuation patterns of the various analyses can be grouped. In the first instance, certain of these showed a progressive accumulation or increase through the year, namely, specific conductivity, pH and alkalinity, the latter going to very high levels. Secondly, others showed a loss to a winter low and then a marked increase in October. These included temperature, residual solids, organic matter, albuminoid ammonia and phosphate. Thirdly, some showed a loss until

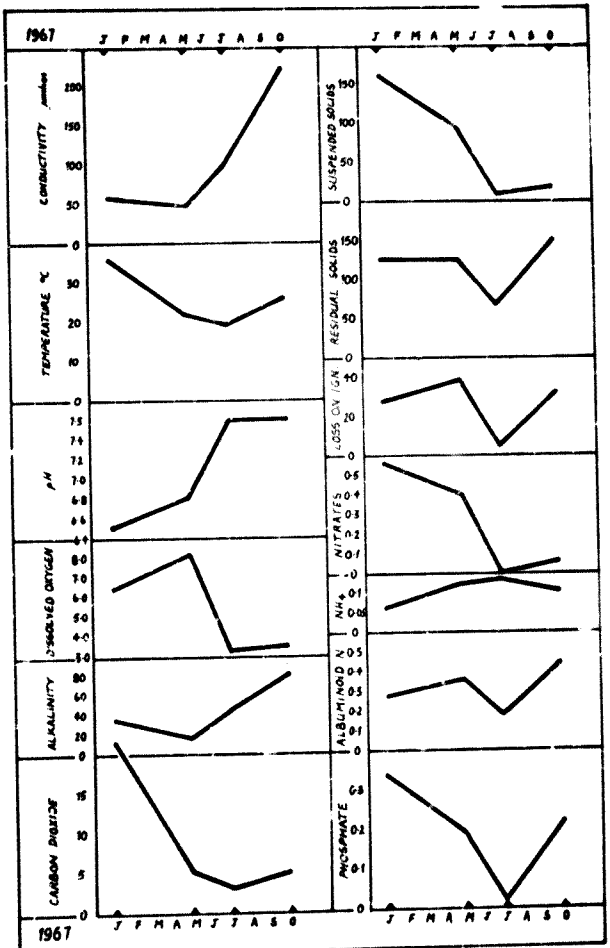


Fig.5.10 THE SEASONAL CHANGES IN WATER QUALITY OF THE ATIC RIVER.
Readings in mg/l unless otherwise stated.

the winter and then increased slightly in October, namely dissolved oxygen and carbon dioxide, suspended solids and nitrate.

Thus a steady increase in ionic concentration occurred as the pools dried out, apparently a purely physical effect. A gradual settling of suspended material also occurred, although a slight increase was apparent in October, perhaps as a result of the activity of fishes (Fig. 3.20) and game animals which used the pools as a source of drinking water. The fact that nutrient levels were at their lowest in winter would suggest that at this time biological activity was at its highest which is anomalous in the light of the temperature regime. High winter activity would be confirmed, bearing in mind the possible effect of concentration of the fish population, if at the same time the suspended solid content of the water was high, which it was not. The inexplicable increase following low winter levels could have been the result of defaecation and disturbance of the bottom muds by game animals and fish eating birds for, during winter, water was still widely available in the small ephemeral pools in the river bed which were not sampled. It was noticed that a preference was shown for these small pools by game animals, perhaps as a result of either the likelihood of attack by crocodiles in the larger pools or the preference for the more saline waters in highly attenuated pools, or a combination of both. Fish eating birds also preferred the attenuated pools as their prey were more easily captured in these. By October, however, all the minor pools had dried out and the animals were forced to use the larger pools which yielded these results. This could have had the effect of raising the nutrient level to such a degree that a slight excess was available, even though the biological demand was high, perhaps higher than in winter. Thus the conclusion that the highest

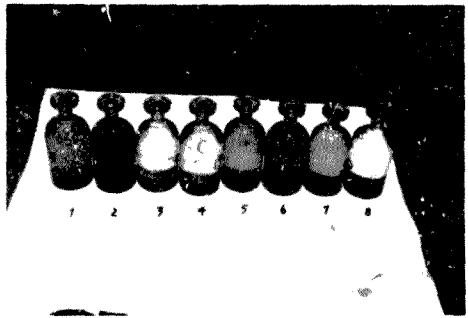


Fig. 5.20 Untreated water samples from the different pools taken within two hours of each other on 24th October 1967, showing differences in water colour. Pools 3 and 4 had been virtually cleared of fish two months previously. Pool 8 had been recently backflooded by the lake.

Samples Nos. 1: Whirlpool
2: Surprise Pool
3: Hammerkop Pool
4: Champs Pool
5: Crocodile Bend
6: Bypass Pool
7: Deep Pool
8: Weir Pool

demand occurred in winter, on the basis of these figures alone, are likely to be erroneous.

In comparison with lake waters, the pools exhibited much higher conductivities. Calcium, potassium and, particularly, sodium were found in considerably higher concentrations, whereas the magnesium content was much the same. Alkalinities were also of a much higher order. Nitrate concentrations rose as high as the Salvinia covered bottom waters and the flowing river, and phosphates fluctuated between the lowest concentration recorded and the highest found in static waters. Other properties exhibited much the same range as the static waters of the lake.

2.3.9 The water quality of different pools

Pools were sampled almost simultaneously on 24th October, towards the end of the dry season when attenuation effects were at their highest, in order that a comparison of the chemical characteristics could be made. Fish had been removed from two of the pools (Hammerkop, Champs) in the previous August, however, so that only a few Clarias gariepinus remained in Hammerkop Pool and a small proportion of the smaller fish of the original population occurred in Champs Pool. This would seem to have had some effect on water quality (Fig. 5.20). The results are given in Appendix 5.5 and illustrated in Fig. 5.21.

No convenient separation can be applied to these data, for each pool would appear to have been somewhat unique. However, several factors are worth noting. The effects of backflooding by the lake and the resultant dilution can be clearly seen in the relative characteristics of Elbow Pool. Although the conductivities and dissolved organic matter concentrations in the attenuated Champs Pool were high, nitrate concentrations were low. Surprise Pool was characterised

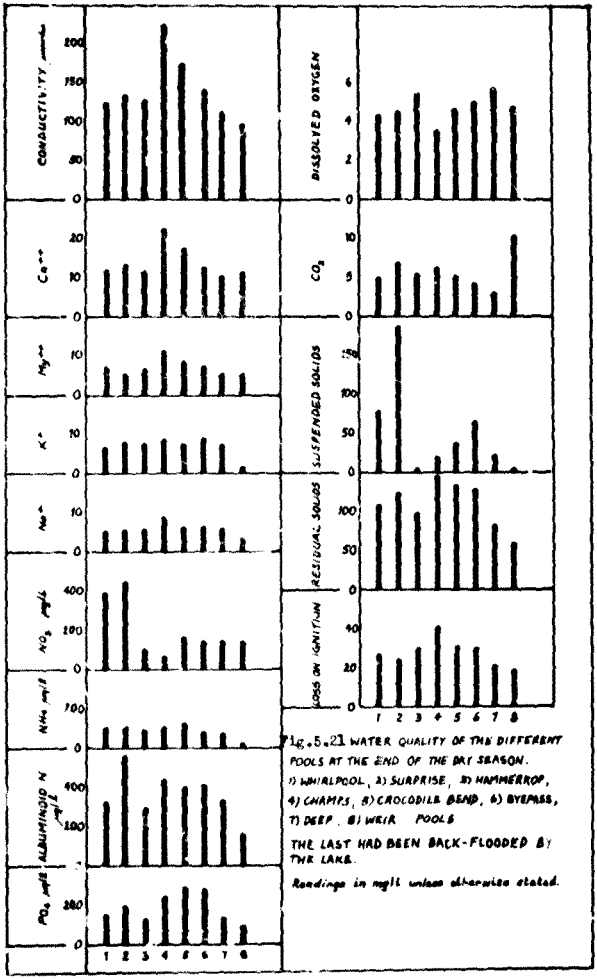


Fig.5.21 WATER QUALITY OF THE DIFFERENT POOLS AT THE END OF THE DRY SEASON.
1) WHIRLPOOL, 2) SURPRISE, 3) HAMMERROP, 4) CHAMPS, 5) CROCODILE BEND, 6) BYEPASS, 7) DEEP, 8) WEIR POOLS
THE LAST HAD BEEN BACK-FLOODED BY THE LAKE.
Readings in mg/l unless otherwise stated.

by a relatively low ion content, yet suspended solids and albuminoid ammonia were very high relative to the other pools. Those pools from which fish had been removed showed very little matter in suspension.

5. DISCUSSION

Birge's rule that temperature changes of at least 1°C per metre were necessary to constitute a true thermocline was strictly adhered to by Welch (1952). He objected to the use of the term in a tropical context where changes which apparently constituted thermoclines were not as great. Use of the term was defended by Hutchinson (1957) and others, following Damas (1951) who demonstrated that density differences between epi- and hypolimnion were the same in tropical as in temperate regions, even though the temperature differences were not as great. It is for this reason that the strength of the thermocline has been indicated in this work, namely, the rate of change with depth at a given temperature (e.g. 1.2°C/m at 20°C).

The works of Worthington and Beadle (1932), Jenkin (1932), Fish (1951), Newell (1960), Talling (1965 and 1964), Beauchamp (1940 and 1964), Coulter (1963 and 1963) and Wood, Prosser and Baxter (1960 and 1969) have shown that a wide variety of types of thermal stratification occur in African lakes, ranging from polymictic to monomictic to meromictic.

The difference between natural and man-made lakes which has the greatest effect in the context of stratification is basically due to differences in inflow and outflow budget. Munro (1966) has shown, for example, that Lake McIlwaine, a quite substantial impoundment on the Rhodesian Highveld which is usually monomictic in character and typically overturns in winter, can be affected by summer rain inflow

to the extent that complete mixing takes place. Thomas (1966) showed that a small water body in East Africa showed no set pattern and mixed or stratified intermittently. Summer rain storms have also been shown (Allanson and Gieskes, 1961) to disrupt the stratification of Hartebeespoort dam, another highveld dam considerably colder in winter than Lake McIlwaine, and results in a complex double stratification.

In the larger tropical man-made lakes the effects of inflowing water are not as obvious. Initial development of stratification also varies considerably. In direct contrast to the situation at Lake Kariba, where a definite thermocline was found by Harding (1961) within months of closure, Lake Volta (Ewer, 1966) did not stratify within the first year and subsequently Biswas (1966) showed that there was usually a marked temperature gradient within the first few metres and that the temperature gradually decreased until no further change occurred at between 20 - 30 m depth. Viner (1969) believed that at a later stage a "slight but definite thermocline develops at about 20 m" (Lawson et al, 1969) in this lake, similar to the situation in Lake Kariba. Lake Volta is dimictic, overturning during floods between June and September and, as a result of the Harmattan winds, in December/January. (Lawson et al, 1969).

The results presented in this work suggest an upward tilting of the thermocline at the shoreline of Lake Kariba, in much the same way that Cooke (1960) and Mitchell (1970) have shown that along the longitudinal axis of the lake, stratification tilts to become shallowed towards the dam wall. The relationship between the shallow thermocline and the deeper thermocline, which is taken to be that of the lake, is obscure on present data and requires further research. It

is considered, however, due to the horizontal nature of the shallower stratification when what is taken to be the overall lake thermocline is present near the river mouth in summer, and the considerable depth of water separating these two, that the two sets of stratification are distinct and do not merge further away from the river mouth.

In Lake Kariba, the fact that rivers, and particularly the Zambesi River, flow along their old courses as a natural function of their higher density has been appreciated and mentioned since Harding's first observation in 1959, though the phenomenon had not been clearly demonstrated and discussed as such, with reference to the Zambesi River, until Cocho (1968) and Mitchell's (1970) work. Begg's (1969) observations on the Sanyati River gorge also indicate a displacement of anoxic bottom waters upwards by river waters flowing into the lake. As long ago as the 1920's the phenomenon of inter and under-flow were appreciated. Wasmund (1927) and Elster (1937 and 1939) studied the interflow of the Rhine in Lake Constance. More recently, Bell's (1942a, b) experimental work on density currents has greatly clarified their characteristics and Benedict et al (1965) have discussed them in relation to the mechanics of sediment transportation.

The results obtained in this study, summarised in Figure 5.12, indicate, perhaps, a more complex situation than Cocho (1968) and Mitchell (1970) suppose. River water entering the lake behaves in accordance with its density characteristics, based primarily on temperature and silt load, relative to the density of the lake water it enters. These characteristics vary proportionately to the speed and volume at which rain water is introduced from the catchment into the lake. Under conditions of minimal flow, the temperature of river water rises considerably, and silt load drops, hence density decreases. As flow increases, density increases as a result of increased silt load and de-

creased temperatures. Thus the greater the flow experienced, the deeper into the lake the river water must penetrate to find its own density layer. Furthermore, peripheral mixing takes place as soon as the lake is entered, so that the smaller the volume of inflowing water, the more quickly it is affected by the static water body it enters. Thus a large volume of inflowing water not markedly different in character from the water of the lake may retain its original characteristics longer than a small volume of markedly different inflowing water. Smaller volumes of inflowing water therefore tend to be influenced by lake water to a degree that interflow and dissipation take place quickly (Fig. 5.12c). The question relevant to these considerations is whether or not, when the Mwenda River, and rivers like it, flood to the degree shown in Figure 5.12d, they reach the old Zambesi course still retaining a large proportion of their original characteristics, or whether their density is influenced to the degree that interflow takes place at depths not much greater than those sampled, further away from the river mouth.

For it has been shown and is discussed further below, that the river is an important source of nitrogen, phosphate and potassium. Under circumstances of early mixing these would immediately become available. This would not be the case if cycled as an inter- or underflow beneath the thermocline, when they would be made available several months later, after turnover had occurred, from open water.

The nutrient load of the river has been shown to vary inversely to flow, thus with accurate flow assessment, regular sampling of river water and monitoring of mixing characteristics associated with different flows, a nutrient "budget" could be worked out which would help considerably in problems such as whether or not Salvinia has a significantly limiting effect on other aquatic plant production by the

extraction of nutrients directly from inflowing rivers (which it can only do on the basis of these findings under minimal flow conditions) and raises a further question, namely: How much of the total nutrient budget does enter the lake under these conditions?

Further consideration of the effects of underflow in relation to the introduction and release of nitrogen on the bottom of the lake are necessary. It has been suggested that the main cause for nitrate availability on the bottom during heavy flooding is the result of physical disturbance and oxidation of bottom deposits rich in ammonia which results in a release of nitrate, rather than the introduction of fresh nitrate as such. The incoming river water is seen to carry low ammoniacal nitrogen concentrations, yet the albuminoid nitrogen content is very high and is, presumably, deposited on the old river bed. Although in its albuminoid form nitrogen is not readily released, during the quiescent period of the year the mineralization of albuminoid nitrogen to ammonia must take place, in the bottom deposits, so that during flooding, in following years, further nitrate is released on oxidation of the ammonia arising from the decomposition of proteinaceous material. The scouring, oxidising and depositional role of underflows could therefore be equally as important to the nutrient level in lake waters as the direct introduction of readily available nitrogen in the form of nitrate.

Most of the rivers now enter Kariba through steep sided narrow gorges which have been backflooded by the lake. These gorges now offer the most suitable habitat for colonisation by Salvinia, and all hydrological findings in them have been related to the presence of weed mats. The effects of enclosure have been ignored, largely, it is thought, because mat-free gorges have not been available for comparative purposes. Yet these findings in the Mweni River suggest

that there is a definite enclosure effect, quite separate from the effects of the Salvinia mat. The Salvinia mat certainly causes a drop in dissolved oxygen tensions and increases the carbon dioxide content. But enclosure alone can affect other characteristics. Apart from a slight decrease in dissolved oxygen, and a more marked decrease in nitrate, alkalinity and ammonia both show an increase. Certain effects of enclosure seem to be reverted by the Salvinia mat, namely, temperature, dissolved solids and phosphate. With regard to temperature, the more marked fluctuations of enclosed, Salvinia-free, waters were rendered more equable, apparently as a result of the insulatory properties of the mat. The solids content of the water also increased under Salvinia, having dropped between open and enclosed waters and, conversely, phosphates which were low in open waters and showed an increase in enclosed waters, usually decreased again under the mat. Apart from these characteristics, all other analyses which were carried out showed no trends of increase or decrease. Thus the conclusions drawn following physico-chemical analysis of enclosed, Salvinia-covered, waters which have attributed changes to the Salvinia mat alone, would appear to require reconsideration.

Cooke (1963) made measurements of relative light intensity, expressed as a percentage of surface light, simultaneously with depth of visibility readings, using an identical Secchi Disc to that used in this work. He found that normally, about 50% of light was absorbed in the first two metres of water and that the depth of 1% relative light intensity (R.L.I.), as the classical level at which the cessation of general photosynthetic activity takes place, related to depth of Secchi disc visibility in a ratio of about 3 : 1. If this rather variable ratio can be applied to the depth of visibility data of this work, 1% R.L.I. levels in the bay (Station 1) varied between about 9 and

14 metres, and in enclosed waters (Station 3) between 5 and 10 metres, considerably lower than Cooke's figures for the open lake, which ranged around 15 metres, with one reading at 24.6 metres.

Cooke (1960) concluded from his data that "Lake Kariba exhibits basin individuality, chemically as well as thermally" with basins nearer the Zambesi River being poorer in nutrient than basins towards the dam wall. He gives one of the reasons for this as being "the increased fertility of the river tributaries from the Zambesi River northeastward, up to the Sibilobilo Narrows" (the lower limit of the Central basin). Cooke's station 3332 was at the confluence of the Mwenda and Zambesi Rivers in the centre of the Central basin. He gives estimates for nitrate, phosphate and total hardness from this station during 1964/65 and his range of values have been compared with my own in Figure 5.22.

Surface nitrates clearly increased from open water to river. However, a higher range of values occurred in the bay than within the "estuary", which is inexplicable unless it can be related to a physical concentration of phytoplankton within the "estuary", or as a result of an excess in what may be the optimal depositional zone (the area around the outer bay station).

Surface phosphates also show a marked increase from lake to river, both in their concentration and range. Although the nitrate concentration in pools can get considerably higher than in any other water types, phosphate concentrations were considerably lower than in the flowing river and were similar to those found in water associated with the Salvinia mat.

Bottom phosphates behaved similarly to bottom nitrates but were always present.

Total hardness estimations were similar in both value and range

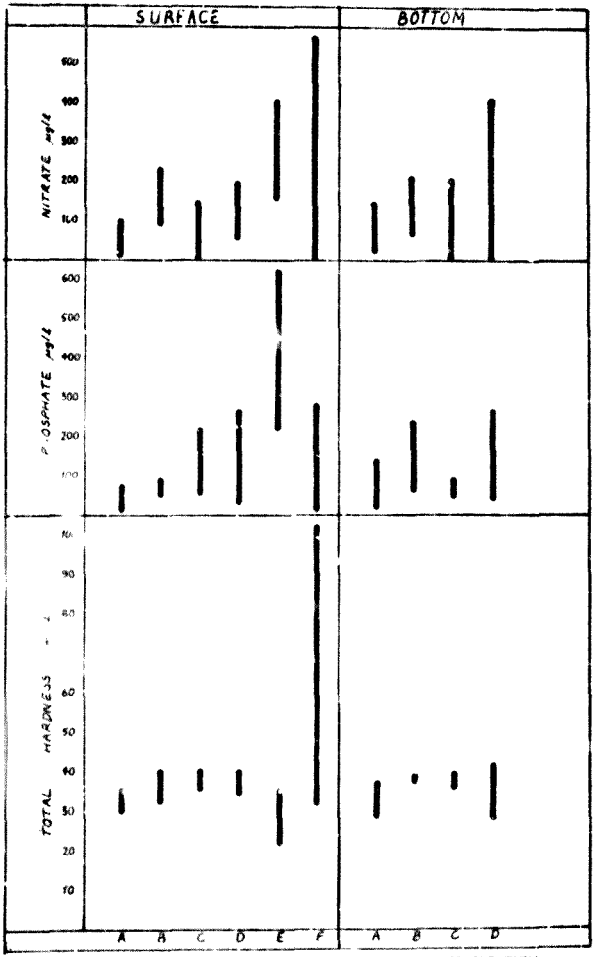


Fig. 8.22 THE RANGE IN ESTIMATES OF NITRATE, PHOSPHATE AND TOTAL HARDNESS FROM OPEN LAKE (SOCHE) TO RIVER.

A: Mwenda/Zambesi confluence (Coche 5332)
B: Stations 1 and 2 (open bay)
C: Station 3 ("estuary")
D: Stations 4 and 5 (Salvinia covered)
E: The river
F: The pools

between open lake and static estuarine waters at the surface and at the bottom. Estimations on the flowing river, due to dilution, showed lower values and, conversely, the pools showed much higher values and wider range.

Thus it would seem that in the light of Cooke's data also, the Mwenda River is an important source of nutrient to the lake. Furthermore, the annual range of nitrate levels were usually slightly higher in enclosed waters (Station 5) than Cooke found in the lake. Yet in the intermediate bay waters a higher range of values was found. Phosphates, on the other hand, increased progressively from open lake to river.

There is now a general belief that "inorganic N (is) a possible widespread limiting nutrient"(Talling 1969) to phytoplankton production in African lakes. That nitrate is limiting to phytoplankton growth has been shown by Prowse and Talling (1958) in the White Nile, Talling (1965 and 1966) in Lake Victoria and Moss and Mose (1969) in Lake Chilwa, Malawi. Mitchell (1970) has given evidence that nitrate was limiting the growth of Salvinia in Lake Kariba in 1962. In the vicinity of the Mwenda River mouth, inorganic nitrogen appeared to have been definitely limiting only within enclosed water in the winter months and at the surface in enclosed Salvinia-free waters in January 1967, a situation which was not repeated in 1969. As turnover had occurred, during 1967, shortly prior to sampling, the opposite would have been expected to occur. It can only be supposed that sampling took place at the climax of the phytoplankton growth period and that all available nitrogen was being or had been taken up. More closely spaced sampling periods are necessary to clarify the point.

Nitrate concentration in the Mwenda "estuary" was consistently higher than Cooke's (1963) estimates elsewhere in Lake Kariba

(0.005 mg/l to 0.2525 mg/l), the latter value being found in the Sanyati River in December 1964. Results achieved by Marshall (1971) give the range of nitrate in Lake McIlwaine, generally accepted as being eutrophic, to range between a trace and 0.47 mg/l ($\bar{x}$: 0.05 mg/l). This makes the level of nitrate estimation presented here so high that it must be suspect. Nevertheless, some support as to their accuracy is given by Cooke's (1960, Table 7) nitrate values taken at his Station 5352, the Zambezi/Mwenda confluence in Basin III, which were also higher than he found elsewhere in the lake, though this is not mentioned in the text. If, as it therefore appears, the estimates made here are accurate, the Mwenda River could be of some importance as a nitrate contributor to Lake Kariba.

CHAPTER 6

THE PLANKTON

The plankton was sampled at Stations 1 to 4 during the course of a single day in each field period, starting in February 1967, and ending in February 1968. It was not possible to reach Station 5 in February 1967, but samples were taken here subsequently. On the whole, therefore, five seasonal samples were taken at each station. Samples were collected from each station from between the water surface and 1 metre depth, from midwater at Stations 1 to 3 (at 10 m at Stations 1 and 2 and 5 m at Station 3) and from water 1 m above the bottom.

1. METHOD

A 1½ h.p. open impeller motor pump, drawing water through a 76 mm diameter reinforced plastic hose at a rate of 15,600 l/hour was used to sample plankton. The intake nozzle was designed to draw water as horizontally as possible and was protected by heavy mesh to exclude debris. A 0.2 m^3 (44 gallon) sample was taken once the pipe had been cleared of extraneous water. The sample was then decanted via a 51 mm (2") valve through a splitting funnel, consisting of a series of four grit-gauze meshes of decreasing size (1000 µ, 265 µ, 150 µ and 112 µ) and plankton collected by those meshes were preserved separately in 4% formaldehyde. The first, coarse mesh, usually retained allochtonous debris only and as the washing process was thorough during decanting no planktonic organisms were retained by the debris. It was found that the volume of water involved and the speed that this was introduced to the splitting funnel, resulted in a relatively efficient separation of plankton by size.

The four resulting sub samples which constituted all plankton from the 0.2 m^3 sample were individually centrifuged (in the laboratory) at 4000 rpm for ten minutes and the volume noted. The mean conversion of volume in ml to dry weight in mg was found to be 0.04275 (± 0.0026). Dry weight of samples in mg/m^3 were obtained using this conversion x5. This method was advantageous in that samples were still available for qualitative analysis.

1.1 Problems in Plankton Sampling

Quantitative methods for the sampling of zooplankton have always been open to error. Ricker (1938) maintained that results obtained by the use of the Kemmerer water sampler were open to error as a result of avoidance by certain plankters. The same could hold true for the Friedinger bottle used for water sampling in this study, although Welch (1940) considers the error in the use of sampling bottles as "minimal". Trials with the Friedinger bottle showed this method to be unsuitable, however, due to the small numbers of plankters taken per sample. Similarly nets have also resulted in error, due primarily to changing filtering efficiency during the course of a single haul and the inability to sample accurately discrete depths of water using closing nets and the vertical haul method. This applies to shallow waters particularly. Welch (1940) considered that only a fraction of the total plankton population could be sampled by net, hence the term "net plankton" when referring to a sample obtained in this way. Welch (1940) also considered the "pump and hose" method of sampling to be inaccurate, due to rheotactic reaction of plankters near the intake nozzle and at the time he wrote stated that the method had been largely abandoned in quantitative work. He considered that further disadvantages arose from, firstly, the inability of the method to take

a discrete depth sample and, secondly, fragmentation of plankton which resulted from the action of the pump.

Nevertheless, this method was chosen as being the best available for this particular study, due to the relative shallowness of the water and the necessity to sample under the Salvinia mat. Care was taken to pump at high speed so that rheotactic avoidance was reduced to a minimum. The nature of the impeller in the pump used, which was open, seemed suitable as it was thought that minimum fragmentation would result. This appeared to be the case, for although some of the Cladocera in the samples were found to have had damaged valves, actual fragmentation of zooplankton was not found to occur in the samples collected. The method was, however, unreliable with regard to depth accuracy. Tests in a laboratory aquarium using dyes and a venturi pump showed a current set up around the nozzle not unlike the pattern given by a magnetic field. The greater the sample volume therefore, the less discrete the sample depth. In order to overcome this weakness, samples were only taken at a minimum of 5 m horizontal intervals (unless station depth dictated otherwise) and as soon as extraneous "pipe water" had been cleared. The sometimes startling differences in samples taken only two metres apart at Station 5 suggest that the method as used gave a reasonably representative sample of the population at a particular depth.

Quantitative sampling of sparse plankton populations, which require large samples, would appear to be incompatible with their statistical evaluation, for field replication is not possible. The reason for this involves the spatial distribution of plankton and the disturbance which results from the removal of a large sample; thus the required movement away from the original sample to relatively undis-

turbed water could result in sampling a different population density and an erroneous impression of inefficiency would emerge. An analysis of the results achieved do show, moreover, a distribution of plankton which seems to be peculiarly clumped and localised. In order to overcome this problem to some unknown degree, a large sample was taken in one position at high speed in an attempt firstly, to apply the formula derived by Mundie (1957) to test for accuracy, and secondly, to overcome rheotactic avoidance. Mundie's formula is, however, dependent on the data having either random or poisson distribution, so that the mean equals the variance and the standard deviation = $\sqrt{\bar{x}}$. On this basis he derived that $n = \frac{400}{\bar{m}}$ (where n = number of samples necessary for 10% limits of accuracy, $\bar{m}$ population mean). This is similar to the formula given by Southwood (1966) to test for number of samples necessary to be within a given level of accuracy:

$$\text{Number of samples required} = \frac{ts}{D\bar{x}}^2$$

where s is standard error, D the required level of accuracy (normally 0.1 = 10%) and t is quantity, depending on number of samples and obtained from tables. As firstly the data were analysed by weight and not numbers, secondly, the distribution when tested was found to be contagious (Taylor's power law factor $p = 0.152$) and thirdly, Southwood (1966) clearly states that data must be derived from within an ecologically homogenous habitat to apply his formula (which has a similar derivation to that used by Mundie). As the river mouth is essentially heterogeneous the formula cannot be applied. No within sample test is known to be available in order to find the accuracy of the samples.

Even though the accuracy of the method is still open to conjecture,

it is considered the size of sample and the speed with which it was taken (0.4 m^3 in 1 minute) should have resulted in a better sample than could have been obtained by nets. A further problem detracts from the value of data collected. The nature of the project mitigated against more frequent daylight sampling and more importantly perhaps, the assessment of diurnal variations. Changes in plankton populations can be particularly rapid, even on an hourly basis (Raceska, 1960), so that generally speaking, results cannot be considered as being representative of seasonal variations. Conclusions based on the data can only, therefore, be derived either from substantial variation or consistent trends.

1.2 Qualitative Analysis

Mesh sub-samples were made up or down to exactly 10 ml without affecting plankton numbers, were thoroughly shaken and a 1 ml sample removed. In thicker samples, the 1 ml sample was diluted to 5 ml and a 1 ml sample taken off this. Thus two dilutions were used to obtain material for counting, 1 : 10 and 1 : 50, depending on the number of plankters present. These samples of the mesh sub-samples were placed in a perspex counting trough, made for the purpose, and the different species counted. The percentage composition of each species in the mesh sub-sample was derived from these counts. In order to test for accuracy of the 1/10th and 1/50th samples, three random samples of different density were entirely counted: a "thin" sample (105 plankters), a "medium" sample (4,952) and "thick" sample (11,276). A comparison of the percentage composition as reflected by sampling against actual percentage composition of the mesh sub-samples are shown in Table 6.1. An arbitrary decision was made, based largely on "cost / value" considerations, to count in mesh

TABLE 6.1 PLANKTON COUNTING TRIALS ON THE BASIS OF AT LEAST 100 PLANKTERS BEING COUNTED

	"THIN" SAMPLE	"MEDIUM" SAMPLE	"THICK" SAMPLE
Sample size	1/10	1/50	1/50
Number samples required to count at least 100	10	1	1
Total number planktors	105	4932	11,276

SPECIES	SAMPLE %	ACTUAL %	SAMPLE %	ACTUAL %	SAMPLE %	ACTUAL %
Diaptomus I	6.7	6.7	9.0	5.4	12.0	10.9
Diaptomus II	3.8	3.8	1.4	0.3	4.5	1.8
Cyclopoids	10.5	10.5	26.2	27.1	2.6	4.1
Copepod nauplii	7.6	7.6	0.7	0.6	0	1.0
Bosmina I			4.1	4.2	5.2	6.5
Bosmina II			12.4	14.3		
Ceriodaphnia	67.6	67.6	22.8	24.4	62.0	61.8
Diaphanosoma	3.8	3.8	13.1	11.3	1.9	2.6
Daphnia I			1.4	1.1	0.4	0.7
Chydcris I					0.8	0.6
Chydoris II					0	0.1
Trichocerca			2.3	0.7	0	0.1
Rotifer II			0	0.1		
Rotifer V			1.4	1.4		
Anuraytis			2.3	0.8	4.1	1.0
Volvox			3.5	7.4	6.4	1.2

sub-sample units so that at least 100 animals were counted. Thus two mesh sub-samples were entirely counted if the first held less than 100 plankters. It can be seen in this table that the "thin" samples required complete counting to fulfil this stipulation. In the "medium" samples, nine species were within 1% of their true proportion, two were within 2% and two within 4%. In the "thick" sample, eight were within 1%, two within 2% and one within 4%. Some of the most infrequent species were not found by this method, although present, and it is recognised that the tabled results could be due to chance but this is considered unlikely in the light of their similarity. In view of the general nature of this part of the survey and the unknown inaccuracy of the sampling method, it was decided to use the following method: entire 1 ml samples of the mesh sub-samples were counted qualitatively until 100 plankters or more had been processed. From these percentage composition figures, densities in mg/m^3 dry weight for each mesh sub-sample were calculated and then added to give the total plankton density for the station/depth sample. This means of calculating plankton density was greatly aided by splitting the sample through the decreasing meshes, for if the station/depth samples had not been split, the smaller, more numerous species would have been disproportionately enlarged and the larger species reduced. As a result of splitting this problem was overcome and species of more or less the same size made up each mesh sample. Thus truer values of proportionate weight were obtained. In the same way, the *anaoystis* colonies in the different meshes were similarly sized and could therefore be counted.

The methods used to sample and assess both species composition and plankton density were therefore essentially gross and any conclusions based on these data must be regarded as tentative.

2. RESULTS

2.1 Variations in Plankton Density

The variations in plankton density as found at the different depths of the stations on the various sampling dates are given in Table 6.2, and are figured (Fig. 6.1). On the basis of these methods and results, the density of plankton varied considerably ranging between 0 and 979 mg/m^3. The overall mean was found to be 220 mg/m^3 (SD = 214). Although it is somewhat speculative to assume, on the basis of a series of single day, seasonally spaced samples that the results are representative of seasonal changes, the substantial discrepancy between the sampling days indicate lowest densities during and after the rains and highest densities during the winter (Fig. 6.2). This pattern was followed in Stations 1, 2 and 4. At Station 3, however, densities were more or less static after May and at Station 5 which was permanently covered by Salvinia on sampling dates, a decrease in plankton occurred over the course of the project. It is also clear that densities of plankton were at their highest near the river mouth and decreased progressively away from the "estuary" (Fig. 6.3). In terms of depth distribution, at the "bay" Stations 1 and 2 there seemed to be little difference between the overall mean densities of plankton on the surface, in midwaters and on the bottom. Within the "estuary", however, a definite increase was found associated with waters of at least 5 metres depth and at Station 5, where the depth was never greater than 3 m, little difference between surface and bottom is apparent when mean densities are considered.

Distributional peculiarities of plankton are apparent when the sampling dates are considered separately as density isopleths (Fig. 6.1). Two centres of higher density were found at times. The one, associated with waters inside the "estuary" was usually

TABLE 6.2 PLANKTON DENSITY IN MG/M^3, DRY WEIGHT

STATION	DEPTH (m)	5/2/67	5/5/67	31/7/67	10/11/67	5/2/68	TOTAL	MEAN
1	1	53	17	305	160	48	583	117
	9	5	118	393	99	143	761	152
	20	13	78	258	109	170	628	126
2	1	-	15	357	357	84	813	203
	9	-	38	508	189	38	773	193
	15-18	-	25	212	209	279	725	181
3	1	13	242	145	244	218	862	172
	5	34	372	300	305	183	1194	239
	9	74	212	462	260	237	1245	249
4	1	61*	63*	916	113*	74*	1227	225
	on 5	73*	200	588	979*	47*	1887	377
5	1	-	617	461*	203*	69*	1350	338
	on 3	-	-	316	782*	328*	1426	475
	TOTAL	329	1997	5221	4009	1918	13474	
	MEAN	41	166	402	308	148		226

- : No sample taken

* : Density back-calculated from numbers, due to presence of *Salvinia* debris

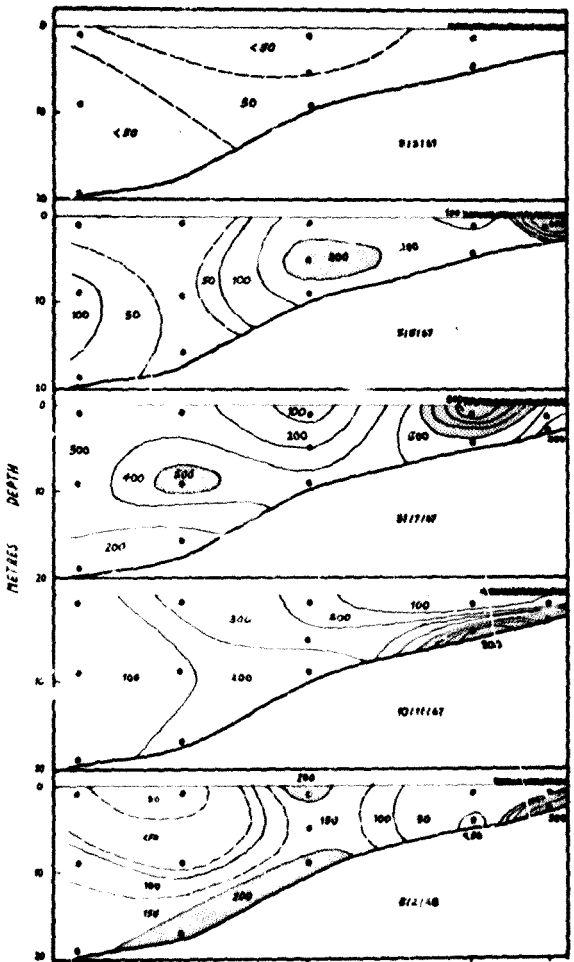


FIG. 61 THE DENSITY ISOPLETHS OF PLANKTON OVER THE DROWNED AFRICA BED IN mg/m³ DRY WEIGHT
D = SAMPLING POINTS, ■ = SALVINIA, 'DENSITY CENTRES'

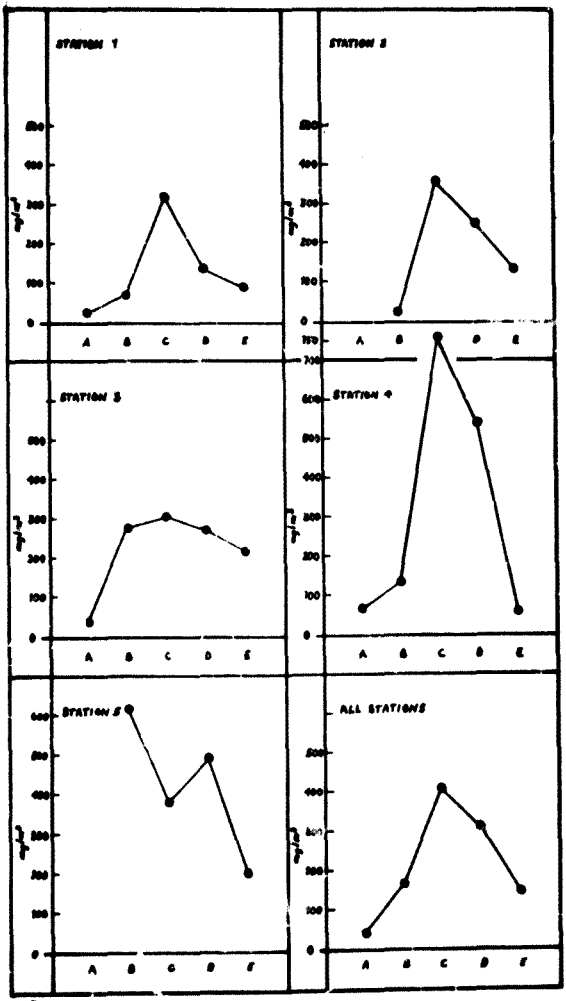


FIG. 6.2

THE MEAN 'SEASONAL' DENSITY CHANGES

A: 5/8/67. B: 5/9/67. C: 30/11/67. D: 10/1/68. E: 5/3/68.

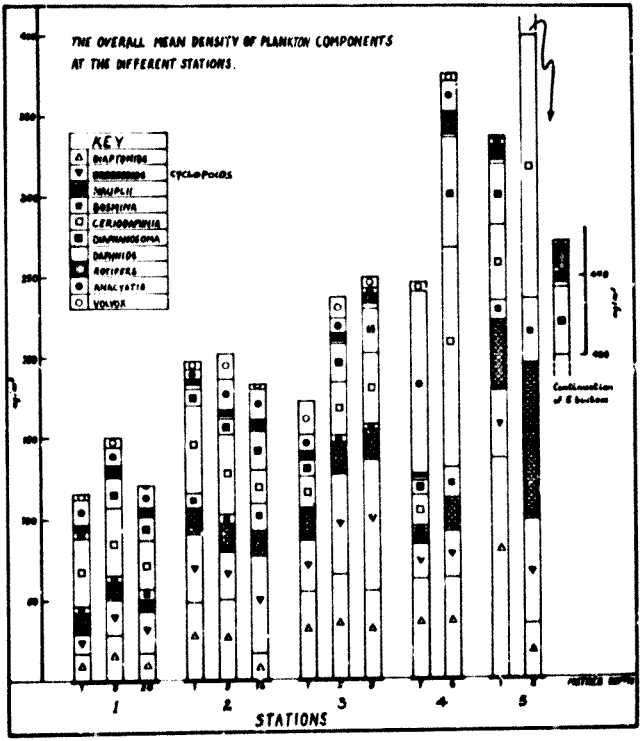

THE OVERALL MEAN DENSITY OF PLANKTON COMPONENTS
AT THE DIFFERENT STATIONS.
KEY
DIAPTOMUS
CYCLOPOIDS
NAUPLII
BOSMINA
CERIODAPHNIA
DIAPHANOSOMA
DAPHNIDS
ROTIFERS
ANACYATIS
VOLVOX
Continuation of 5 bottom
STATIONS
1
2
3
4
5

Fig. 6.3

present, sometimes in surface waters associated with Salvinia and at other times associated with the bottom.

The other was found at 5 m depth at Station 5 on 9th May 1967, at 10 m at Station 2 on 31st July 1967, and on the bottom, between Stations 2 and 5 on 5th February 1968. These centres will be analysed further below.

2.2 Spatial Distribution of Components

A reference collection of plankton species was made. Specimens have been kept as duplicate sets both in alcohol and as permanent mounts, stained in borax carmine and mounted in Swann's modification of Berlese's medium. One of the sets is at present being named and until this is completed, a species list cannot be included here. Twenty-seven "species" of zooplankton and two species of phytoplankton were found. Densities of most of these species found by station, date and depth have been tabled and are appended (App. 6.1). The proportions of all collected zooplankton, by weight, constituted 84% Copepoda, 4% Cladocera and 3% Rotifera. The copepods were dominated by the diaptomids (24% of total) and the cyclopoids (19%). Copepod nauplii constituted 11%. The most important cladoceran was Ceriodaphnia (26%); Diaphanosoma (12%) and Bosmina (8%) were also significant constituents.

The mean density of the different species of plankton found during the survey are figured by stations and depths and shown in Figure 6.5.

The diaptomids showed a tendency to increase into the estuary and appeared to favour water of less than 10 m depth. The density of the diaptomid component of the plankton in association with Salvinia in the surface waters of Station 5 was almost twice that found else-

where. Coriodaphnia, the single most important zooplankter, showed little difference, in open water, in its distribution between 10 m and the surface, but decreased in waters deeper than this. In enclosed waters shallower than 10 m this tendency was reversed and greater concentrations were found associated with the bottom, especially under the Salvinia.

The cyclopoid copepods showed a definite tendency towards greater density near the bottom throughout the area. Unlike any of the other species, they were found in largest concentrations at Station 3, decreasing both towards open water and towards the river mouth.

Copepod nauplii were ubiquitous in fair concentration, showing no apparent depth preference. A five-fold increase was found at the station nearest the river mouth, underneath the Salvinia mat, and in association with the bottom.

Bosmina, one of the minor zooplankton constituents, showed a progressive increase into the river mouth, particularly in association with the bottom.

Diaphanosoma also showed a preference for bottom waters. Densities of this species were more or less constant in open and enclosed waters, except underneath the Salvinia where a marked increase was found.

The rotifers were ubiquitous in small concentrations showing no definite trends of preference associated either with depth or nearness to the river mouth. The apparent increase at Station 5 was due largely to a single tively enormous concentration of a species of Keratella (Rotifer II) which occurred in February 1960, and which could be attributable to an accumulation arising from the flowing

river (see below).

The daphnids occurred only sparsely and were in more or less constant concentration through the study area.

Although the small quantities of the blue green alga *Anacystis cyanea* collected, relative to the larger quantities of zooplankton taken simultaneously, strongly suggest that the method used is unsuitable for the quantitative sampling of this species (in that the action of the pump largely disintegrates the colonies to a size smaller than the smallest mesh used, 112μ) the data should be accurate on a relative basis, as the technique used was consistent. *Anacystis* was found at all depths of all stations at more or less the same concentrations, but was particularly abundant on 31st July 1967, on the surface at Station 4. This is considered to be as a result of dead, floating colonies having been collected here on the edge of the *Salvinia* mat by wind action and could therefore give an erroneous impression of spatial distribution.

The comparatively tough consistency and size of *Volvox* colonies, on the other hand, were better suited to the pumping method. In the open bay, greatest concentrations were found at 10 m. At Station 3 *Volvox* was apparently a more important phytoplankton constituent than *Anacystis* and was densest at the surface, showing a constant decrease towards the bottom. Although quite high concentrations were found equally distributed between surface and bottom at Station 4, very few colonies were found further into the *Salvinia* mat at Station 5, and then only at the surface.

2.3 "Seasonal" Distribution of Components

Bearing in mind the reservations imposed by the potentially inadequate sampling, consideration of the temporal fluctuations of indivi-

dual species at each depth point would be unrealistic. An attempt has been made to overcome this, at least partly, by grouping temporal results for each species throughout the study area and regarding each sampling point as a "seasonal" subsample. This should result in more reliable information on the possible seasonal fluctuations of each species, as the resulting sample is considerable, representing plankton collected from 2.6 m^3 (572 gallons) of water. The data for the more important species treated in this way are given in Table 6.3 and figured (*Fig.* 6.4).

Major changes which are apparent are as follows:

Cyclopoid copepods were at their greatest density in November 1967, being relatively sparse at other times.

Calanoid nauplii showed a similar pattern to the cyclopoids, with some indication of a decrease in July 1967, which was not found in the cyclopoids.

Diaptomids maintained a high density between May and August 1967, and fell off considerably at other times of the year.

Cladocera: Bianhanosoma and Bosmina showed little change throughout the sampling period, but Ceriodaphnia showed a considerable increase in July 1967.

Rotifers: the rotifer population showed a decrease in July. 1967, but increased considerably by the following November. A further increase the following February was attributable mainly to Kerratella (Rotifer II). Trichocerus, the only other rotifer species to appear consistently in most samples, remained relatively constant, apart from the possibility of a decrease in July 1967.

Phytoplankton: Both Volvox and Anacystis were present on all sampling periods, normally in low concentrations. Both also showed

TABLE 6.3 "SEASONAL" VARIATIONS IN DENSITY OF THE MAIN PLANKTON SPECIES (MEAN DENSITY IN MG/M³ FROM ALL STATIONS AND DEPTHS ON THE DIFFERENT SAMPLING DATES)

	5/2/67	5/5/67	31/7/67	10/11/67	5/2/68
COPEPODA					
Diaptomid I	3.8	65.6	77.3	36.2	11.4
Cyclopoids	13.0	14.6	75.9	78.6	41.8
Nauplii	4.9	24.1	14.6	41.6	16.9
CLADOCERA					
Bosmina spp.	2.6	4.5	12.8	19.4	3.9
Ceriodaphnia	5.4	6.2	134.3	68.1	21.9
Diaphanosoma	5.6	26.7	12.8	40.0	27.3
ROTIFERS					
Keratella	0.7	1.5	0.3	2.2	9.1
Trichocerca	0.4	2.5	0.2	1.1	1.0
TOTAL	1.9	4.2	0.9	7.8	12.4
ALGAE					
Anacystis	1.7	5.5	77.9	3.2	6.2
Volvox	0.6	2.3	25.6	3.5	1.9

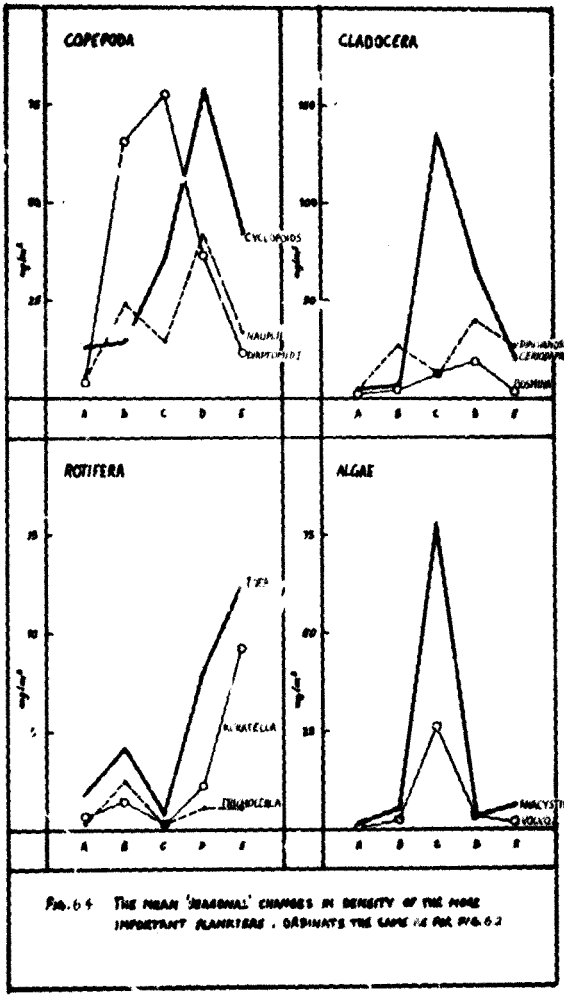


FIG. 6.4 THE MEAN 'SEASONAL' CHANGES IN DENSITY OF THE MORE IMPORTANT PLANKTERS. ORDINATE THE SAME AS FOR FIG. 6.2

a considerable increase in July 1967.

On these tentative findings the main plankton species can be separated into 4 categories as below. Those which, on the basis of the magnitude of change are more reliable, are not followed by the bracketed question mark, which indicates unreliability.

1. Those which showed an increase in July: Anaevatis, Volvox and Ceriodaphnia.
2. Those which increased in May through to July; diaptomids.
3. Those which increased in November; cyclopoids, rotifers, copepod nauplii, Bosmina (?) and Diaphanosoma (?).
4. Those which decreased during July; rotifers (?), copepod nauplii (?), Diaphanosoma (?).

All three groups which showed a possible July decrease showed an increase in the following November.

The mean "seasonal" figures for total plankton collected shown in Table 6.2 indicate lowest production in February 1967; in May 1967 and February 1968 production was found to be about four times greater than this; a further approximate three fold increase to highest production was found in July 1967, followed by a small decrease to a high November production.

2.4 Density Centres

The presence of "density centres" mentioned above, which are apparent in Figure 6.1 suggest, on quantitative data alone, the presence of separate populations, which, if on qualitative analysis show a different species composition, would be verified. If, however, the density centres are constituted of the same components, it is more likely that the population would be the same.

On 5th May 1967, the concentration in midwater at Station 5

was mainly due to the diaptomid I which constituted 44% of the sample. The same species constituted 45% at Station 5, though in this case 20% of the sample was Diaphanosoma.

Diaptomid I was also an important component of the "density centres" on 31st July constituting 27% at 9 m at Station 2 and 23% on the surface at Station 4. At this time the more important constituent at the outer centre was Ceriodaphnia, however (30%) and at the inner, Anacystis (60%) thought to be mainly dead, floating, allochtonous, material.

The density centre on the bottom at Station 4 on 10th November was due to an extreme concentration of equal proportions of Ceriodaphnia and Diaphanosoma which together constituted 73% of the sample.

On 5th February 1968 a departure from what had been previously experienced occurred. Instead of the outer "density centre" being in mid water, it appeared along the bottom and at an isolated point on the surface at Station 5. As in the previous November, the inner "density centre" was on the bottom, underneath the Salvinia mat, but much nearer the point of entry of the river. Along the bottom at Stations 2 and 3 the population was dominated by the cyclopoid copepods (40%) and, to a lesser extent, Diaphanosoma (15%). On the surface at Station 2 the high cyclopoid component (33%) was also apparent, but Diaphanosoma had been replaced by diaptomid I (22%). Underneath the Salvinia mat, on the other hand, the main component was Ceriodaphnia (50%).

On consideration of the three sampling days which showed both an inner and outer "density centre", the indications are that, on the basis of species distribution, on 5th M[illegible]967, the two centres were essentially of the same population; on 31st July 1967, the populations

were also similar, though the importance of Corixidae/Notonecta under the Salvinia suggested some difference; and on 5th February 1960, the indications are that the populations were entirely different. No general rule regarding these centres is therefore applicable, but it is interesting to note that the findings resultent upon consideration of the species composition are also suggested by the conformation of the density isoplethe in Figure 6.1.

2.5 Important Species not Significant in Samples

During the post turnover period of each year, from June to August, a bloom of Anaspretis cyanea was observed to occur. Concurrently, the presence of sometimes large concentrations of the fresh water jellyfish Limnocnida was found, in concentrations estimated to be up to 20 individuals/m^3. Greater concentrations seemed to occur within the "estuary".

Another species which judging by their numbers in benthic samples (Chapter 7) must have constituted an important component of plankton at night, was the predatory larva of the phantom midge Chaoborus, which is known to be benthic during daylight and planktonic at night (S.A. Mitchell, personal communication).

3. DISCUSSION

3.1 Feeding Relationships

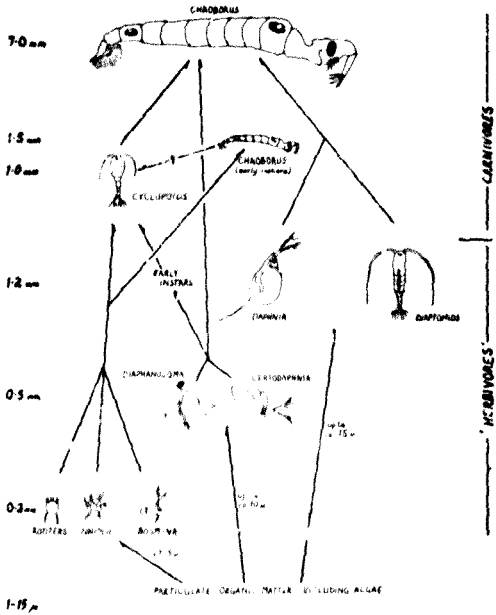
Brooks (1969) has reviewed knowledge regarding feeding behaviour of plankton and the effects of predation on plankton composition. His findings with reference to planktonic "herbivores" (those which eat particulate matter) may be summarised as follows:

1. They all compete for fine particulate matter (1 to 15 u).
2. Larger species have a marked advantage over smaller species both in terms of filtering efficiencies, which increase with

at least the square of body length and in their ability to assimilate larger food particles.

3. When predator pressure from fish is low, larger herbivores predominate and when high, smaller species are allowed to, for fish select the larger species.
4. Moderate predation prevents the elimination, both as a result of feeding competition and with population predation, of the smaller species by the larger.

In order to apply Brooks' (1969) findings, the gut of main zooplankton species found during the survey were studied microscopically to ascertain food preferences. Particulate organic matter showed up clearly where present in the gut so that on the basis of presence or absence the species was deemed herbivore or predator. These findings were supplemented by an examination of mouthparts, the relative sizes of the different species and Brooks' (1969) statement that cyclopoid copepods are generally predatory whereas the calanoids, with few exceptions, are not. A within-plankton food web has been prepared from these findings (Fig. 6.5) showing the proportionate sizes of the main components. The relative importance of these expressed as percentage by weight of all plankton collected, is also figured. Brooks and Dodson (1965) showed that in Crystal Lake before predation, the mode of the plankton population length was about 0.8 mm with crustacean components below 0.4 mm being absent, whereas after introduction of the plankton eating fish Alosa aestivalis, the mode dropped to 0.3 mm. The preponderance of the group composed of Cariodaphnia and Bianhanocama, balanced by the more or less equal proportions made up by the 0.4 mm and 1.2 mm groups suggests that only moderate predation pressure was being exerted on the plankton population during 1967. This aspect of



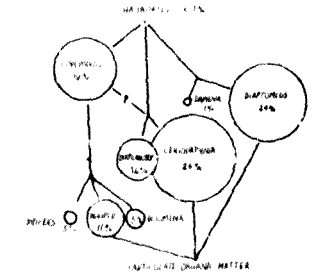


FIG. 6.5 THE PLANKTON FOOD WEB, SHOWING RELATIVE SIZES OF PLANKTERS AND THEIR PROPORTIONATE IMPORTANCE IN THE SAMPLED POPULATION BY WEIGHT

plankton will be expanded further when discussing the feeding of the planktivorous Clarias gariepinus.

3.2 The Food of "Herbivores"

Although it has been stated above, that the sampling method was inadequate for the purposes of estimation of the phytoplankton population, the fact that there is a definite increase of all herbivorous elements of the plankton population within the estuary (which could be due to the presence of Salvinia), yet that the predatory cyclopoid copepods do not show this, suggests that the main source of food for the "herbivores" is not phytoplankton, which is sparse in association with Salvinia, but particulate organic matter in suspension in the water.

On the other hand, an increase was seen in some of the "herbivores" in July, indicating utilisation of phytoplankton at this time of the year. The most startling increases were recorded for the diaptomids and Ceriodaphnia, from the top and middle "size tiers" of the herbivores. The opposite reaction which possibly took place in the nauplii and the rotifers, both of the lowest herbivorous tier, is perhaps explicable in similar terms to Hrbacek's (1964) suggestions regarding zoo/phytoplankton interaction in the River Elbe of Czechoslovakia. Namely, that the development of the Anacystis in July initiated by nutrient release following overturn results in a lowering of production in the plant nannoplankton, the source of food for the smallest zooplankters. This premise, which arises from the contradictory fluctuation of two of the tiers of the in-plankton food web, is lent some support by the low nitrate and phosphate levels found (Chapter 5) at a time when highest levels could be expected; in that the available nutrient is taken up by a peak Anacystis population,

which is stimulated by post-turnover nutrient availability to the precarious level where nutrients released on decay are almost immediately recycled within the Anacystis population. Thus the nannoplanktonic food of the smallest zooplankters could have been suppressed in July 1967, by the overwhelming bloom of Anacystis. A further implication which arises from this is that the plant nannoplankton formed an essential constituent to the lowest tier herbivores at other times of the year.

5.3 Plankton Density and Flow

On two occasions plankton were sampled within two weeks following flooding: on 5th May 1967, following a flood of 61 m^3/s on 2nd May and on 5th February 1968, following a flood of 15 m^3/s on 25th January 1968.

Theoretically, on these two occasions, the inner density centres were of riverine origin and the outer density centres were either of displaced lacustrine origin, or a concentration at a suitable feeding site. With reference to Fig. 6.1, the inner density centre on 5th May 1967, must be purely of riverine origin (unless a nucleus was retained in the Salvinia "rocks" and released following flooding) following displacement by the considerable flood which occurred (see Fig. 5.11). Although plankton associated with the head of the "estuary" prior to flooding could have been displaced upwards and outwards by the nature of the underflow and therefore caused to concentrate in the middle layers at Station 5. It was found that on the occasion qualitative analysis of density centres showed a similar species composition, which would indicate a distribution that has recovered from flooding. On consideration of the amount of space which has been colonised, recovery of the plankton following flooding

seems to be surprisingly rapid and suggests that Salvinia may act as a source for recolonisation as mentioned above.

The distribution of plankton found on 5th February 1968, lends itself to easier explanation in terms of delayed flooding effect on the plankton distribution. The outer density centre may have been associated either with the pattern of nitrate release along the bottom, or with the presence of concentrations of particulate organic matter, following flooding. The inner density centre would theoretically have been a concentration of lotic origin. The qualitative differences found between the density centres at this time suggest that these somewhat theoretical suppositions could be true; provided the main components were herbivorous. This was not the case, however, for the dominating component of the outer density centre were the predatory cyclopoid copepods. First conclusions regarding immediate and delayed effects of flooding, based only on quantitative analysis, would therefore seem to be misleading. The effects of flow on the plankton population of the "estuary" cannot therefore be classified on present data. More closely spaced sampling is necessary before, during and after flooding occurs.

5.4 Plankton Distribution in Relation to the Thermocline and Dissolved Oxygen

A comparison of plankton distribution (Fig. 6.1) and the double thermocline formations which occurred (Chapter 5) showed that temperature stratification seemed to have little effect on plankton distribution.

On the other hand, highest plankton concentrations were frequently associated with low dissolved oxygen tensions, as follows: Inner density centre, 5/5/67, D.O. 15%; Inner density centre 31/7/67, D.O. nearly lowest found at time, 60%; Inner density centre 10/11/67,

D.O. lowest found at time, 8%; Along the bottom 5/2/68, inner and outer density centres, D.O. lowest found at the time, 15 - 2%. This association between high plankton density and lowest available oxygen concentrations suggest that the zooplankton can resist low oxygen concentrations in order to utilise the particulate organic matter causing deoxygenation. It follows that they must be able to do so to be able to utilise this food where it is most abundant. Although an attempt was made to correlate this negative relationship mathematically, the probability of the resultant regression had little significance (n = 36, t with two degrees of freedom : 0.47). This is considered to be the result of selection by the plankton for the lowest oxygen content available (and therefore the highest food concentration) which could be as high as 5% to 6%.

3.5 Plankton Density and Water Quality

In order to see if any correlations existed between plankton density and the individual physico-chemical characteristics of the water, linear regressions between individual physico-chemical characteristics and density of different plankton species, where the two types of sampling coincided in relatively stable conditions, were computed and figured. Results obtained in May 1967, were omitted due to the possibility of instability following flooding and phytoplankton densities were only considered in surface waters. The independent variables considered were conductivity, temperature, pH, dissolved oxygen, total hardness (as $CaCO_3$), nitrate, ammonia and phosphate. These were individually computed against the dependent variables: total plankton, diaptomid *f*, cyclopoid copepods, copepod nauplii, Bosmina, Ceriodaphnia, Diaphanosoma, the rotifers, Anuraeis and Volvox. In four cases a definite linear relationship was found to

occur, namely:

temperature against total plankton ($y = 1104.3 - 51.9x$, $p > 0.005$);

temperature against Cericlarbnia ($y = 399.2 - 12.4x$, $p > 0.001$);

temperature against diaptomid I ($y = 217.1 - 8.7x$, $p > 0.001$);

and nitrate against the rotifers ($y = 1.0 + 0.05x$, $p > 0.001$).

The grouping of figured readings are such as to confirm the probability values obtained by calculation.

Quite apart from the high levels of probability found in these relationships it is unrealistic to consider any single factor being responsible for variations in plankton numbers. Nevertheless, the relationships given above can be used as indications of correlation. A more realistic analysis of the relationship between water quality and plankton density would involve the random combination of the various water characteristics in a multi-dimensional approach. It is considered, however, that this is not warranted, due to the paucity of data and the dangers inherent in applying complex analyses to field data which are subject to unknown sampling error.

5.6 The Level of Plankton Production

In order to obtain some idea regarding the level of plankton production at the Mwenda River mouth by comparison with a rich, eutrophic, water body, sampling was carried out at Lake McIlwaine in December 1970, using a comparable procedure. This lake is considered by some to be polluted, as it receives processed sewage from the city of Salisbury and is subjected to an almost constant heavy bloom of blue green algae, mainly Anacystis cyanea and Anabaena flos-aquae, so that the waters are usually an aesthetically displeasing soupy-green colour. Falconer (1971) has shown the primary production in surface waters are remarkably high, ranging between 200 mgO_2/m^3/hr in winter to 2000 mgO_2/m^3/hr in summer. The latter level is

comparable to those found by Talling (1965) in Lake George, where primary production is the highest recorded from Africa. Other chemical characteristics on the surface at the time of sampling Lake McIlwaine were: pH, 9.0; total hardness (as $CaCO_3$) 36.0 mg/l; conductivity 150 µmhos; nitrate 0.06 mg/l; ortho-phosphate 0.015 mg/l.

Zooplankton density was found, in the epilimnion of Lake McIlwaine, to range between 2160 and 4764 mg/m^3, as compared to the Mwenda densities which ranged between 0 and 979 mg/m^3 with a mean of 220 mg/m^3.

4. CONCLUSIONS

Bearing in mind the reservations imposed by the frequency of sampling which has been emphasized above, the following conclusions are reached:

1. There are quite reasonable grounds to conclude that there is an increase of plankton towards the river mouth and underneath the Salvinia mat.
2. An overall increase in plankton occurred in August 1967, following the lake's overturn the previous June (Begg, pers. comm.).
3. Apparent centres of plankton density, one under the Salvinia mat, the other away from it, were found on three of five occasions. These were not generally explicable in terms of separate populations.
4. The size composition of the zooplankton population indicated that only moderate predation pressure was being exerted by the fishes.
5. On the basis of circumstantial evidence, the most important food source was particulate organic matter, not phytoplankton, though this was a food constituent.
6. There were some indications of a rapid recovery of the plankton

population following flooding which could have been due to a recolonisation nucleus retained by the *S. lynia* mat.

7. The thermocline had no apparent effect on the vertical distribution of the plankton.

8. Plankton seemed to concentrate in areas of lowest oxygen tension. It is suggested that this is to utilize particulate organic matter, the cause of deoxygenation, where this is most abundant. Greatest concentrations of plankton were sometimes found in surprisingly low dissolved oxygen tensions.

9. Rotifer densities and nitrate concentrations showed a positive relationship ($p > 0.001$). A negative relationship was found to exist between temperature and total plankton ($p < 0.005$); diaptomid I ($p > 0.001$); and *Ceriodaphnia* ($p > 0.001$).

10. Plankton production at the Mwonda River mouth was considerably lower than subsequently found in the eutrophic Lake Mellwaine (8 to 979 mg/m^3 dry weight as opposed to 2160 to 4484 mg/m^3).

CHAPTER 7

THE BENTHOS OF LAKE WATERS

1. INTRODUCTION

For the purposes of this chapter, the term benthos refers to the animals living in or on the bottom deposits. It is considered convenient and more realistic to separate the faunal communities of the relatively ~~predominantly~~ static lake water from those of the river and its pools, hence only the bottom fauna of the lake community will be considered here, separately from the components associated with either the various aquatic macrophytes or with the drowned trees of the lake, which will be considered in the next chapter. The community of the river will be considered separately at a later date.

The original intention had been to sample the benthos over five quarterly periods from January 1967 to January 1968, at the six major stations only: on the drowned river bed, on the margins and at five and ten metres depth where sufficient depth of water allowed. This programme was carried out, but sampling of the drowned river bed was continued for eight "seasons" at an increased number of sampling points as follows: Following the first sampling period, the number of sampling points on the drowned river bed was increased to nine by the inclusion of three intermediate stations between Stations 3 and 4 (see map), for it seemed from initial results that this was the most critical stretch, being associated with the edge of the Salvinia mat. In July 1967 the number of sampling points was increased to 14 by the introduction of a single point between Stations 1 and 2, two points between 2 and 3, and a further point between 3 and 4. Some 250 m of mat had

gradually moved out of the "estuary" between January and July 1967, thus an ideal opportunity to study the effects of mat removal on the benthos occurred (particularly if this trend for clearance would persist) and was taken. This approach was enhanced by the greater uniformity of the substrate found on the drowned river bed than away from it. In order to utilise the opportunity offered by the break-up of the Salvinia mat, further samples were taken at the mat edge, and ten and 100 metres in from it. As has been shown in Chapter 4, the clearance trend did in fact persist, thus sampling of the river bed was continued at quarterly intervals until October 1968 at more or less the same number of sampling points as used in July 1967. This study may therefore be considered in two parts: the "seasonal" survey lasting five quarterly seasons and including the shoreline and intermediate depths; and the drowned river bed transect, lasting for eight quarterly seasons.

2. THE SUBSTRATES

The considerable effect that substrate can have in the distribution of benthic animals has been appreciated since before the beginning of the century (Murray and Renard, 1891) and has been recently subject to experiment, both in temperate (Cummins and Lauf, 1969) and in tropical (McLachlan, 1969; Marshall, 1971) zones. Ideally, substrate analysis should be carried out on all acceptable samples, at least in terms of carbon content, as an indication of organic matter present, and soil particle sizes. The time available for this aspect of the study only allowed for limited substrate sampling as described below.

2.1 Methods

Two methods of analysis were used. In the first, essentially rough method, the actual samples used to collect benthic organisms

were described on collection prior to washing and the volume of sand and detritus retained by 40 mesh/inch netting was ascertained. This procedure was followed for the 201 samples collected in January 1968 from all sampling points.

The second method was used on samples taken purely for this purpose at all drowned river bed transect stations in February 1969. Samples were collected by Petersen dredge, placed in large bowls and thoroughly mixed with the water taken at the same time. They were then allowed to dry out naturally and were subsampled when dry and analysed by the Department of Chemistry and Soil Science of the Rhodesian Government for particle size and carbon content. Their method of analysis for particle size was as described by Piper (1950). Carbon content was estimated using the Walkly Black (1947) method, which involved the oxidation of carbon with potassium dichromate and the measurement of carbon dioxide evolved by titration against ferrous ammonium sulphate.

2.2 Results

The results of the rough assessment method are given in Table 7.1 and the volumes of detritus found at the drowned river bed stations can be found in Fig. 7.1. Results of the carbon and particle size analysis are also given in the same figure.

The most outstanding feature observed while handling the substrate was the change which occurred in its consistency, with progression into the "estuary" and whenever samples were taken away from the drowned river bed, particularly at depths of 10 m or less. At the outermost stations of the drowned river bed samples invariably appeared as square, stratified, jelly-like cakes, with layers of smooth grey mud approximately 2 cm thick separated by 2 mm deposits

of fine vegetable debris, consisting mainly of Salvinia root hairs (Fig. 7.2). This stratification is considered to be the result of differential deposition during the rains and dry season, the thicker layer being deposited in the rains. 250 m inside Station 3 a change occurred, the samples becoming looser and with a greater proportion of vegetable matter, originating mainly from Salvinia. With progression into the estuary the samples became both looser and more sandy. Samples collected away from the drowned river bed at 15 m were similar to those from the drowned river bed. In shallower waters, however, the substrate lost its apparent uniformity. Here lacustrine deposition occurred in isolated pockets. Away from these pockets vegetable debris derived largely from the drowned trees hampered sampling considerably. Stones and grit were also common. The margins of the lake in the bay consisted of wave-washed sands within which a good deal of particulate flotsam, largely derived from Salvinia, was found.

Reference to Fig. 7.1 shows that vegetable debris retained by a 40 mesh/inch net was consistently present at low levels on the river bed from the outermost station to Parrot Bend. Thereafter a sudden increase occurred to highest levels at Jacana Bend followed by a sharp decrease to very low levels at the point of entry of the river. Results of the carbon analyses, which include all organic matter, show a consistently high level of carbon up to Jacana Bend followed by a sharp decrease with progression towards the river mouth.

Analysis of particle size show an expected gradual increase in the proportion of larger particles with progression towards the river mouth until, again, Jacana Bend was reached. Here the proportion of

TABLE 7.1 DESCRIPTION OF SUBSTRATE TYPES FOUND AT ALL STATIONS
(washed through 40/" mesh)

STATION	DEPTH m	DETRITUS ml*	SAND ml*	FIELD DESCRIPTION
	0	585	290	Sand and debris.
	4.5	38	26	Mud overlying sandy mud with a little Salvinia, leaves and twigs.
1	10	115	65	Sandy dark brown flocculent mud.
	15	130	40	Soft smooth mud with some sand and small amount of Salvinia debris.
	22	65	0	Soft smooth jelly-like mud with some fine debris. Dark grey/brown.
	0	985	480	Sand and debris.
	5	75	75	Muddy dark brown sand.
2	8.5	57	150	Dark brown sandy detritus with some mud.
	18	70	0	Soft smooth jelly-like mud with some fine debris. Grey/brown.
	0	200	255	Sand and debris.
3	4.5	650	0	Salvinia detritus overlying smooth clay-like mud.
	10	145	0	Smooth clay-like mud with some dead leaves and Salvinia.
	0	220	50	Hard reddish mud with some sand and debris.
4	6	715	0	Gritty grey/brown mud with debris.
	0	430	100	Dirty sand with Salvinia debris.
5	4	560	35	Coarse dirty sand with Salvinia debris, dead leaves and roots.
Elbow Pool		67	25	Fine sand with some red mud and detritus.
1r	20	140	0	Red/brown smooth jelly-like mud.
2a	14	125	0	Reddish-brown smooth jelly-like mud with Salvinia debris.
3a	13.5	125	0	Loose clay-like mud with traces of Salvinia debris.
3b	8	270	0	Smooth grey/brown clay-like mud with organic debris.
3c	7	660	0	Smooth brown mud with light Salvinia detritus and dead leaves.
3d	4	1057	0	Heavy Salvinia debris overlying light mud.
4a	6	800	0	Light grey/brown gritty mud with some Salvinia debris on top.
4b	6	535	0	Light grey/brown sandy mud; some Salvinia debris on top.
4c	6	565	10	Muddy grey/brown sand with Salvinia and other debris.
5	4	370	15	Coarse dirty sand with vegetable debris.
5a	5	38	10	Coarse dirty sand with vegetable debris.

* In ca 2700 ml, the van Veen dredge capacity

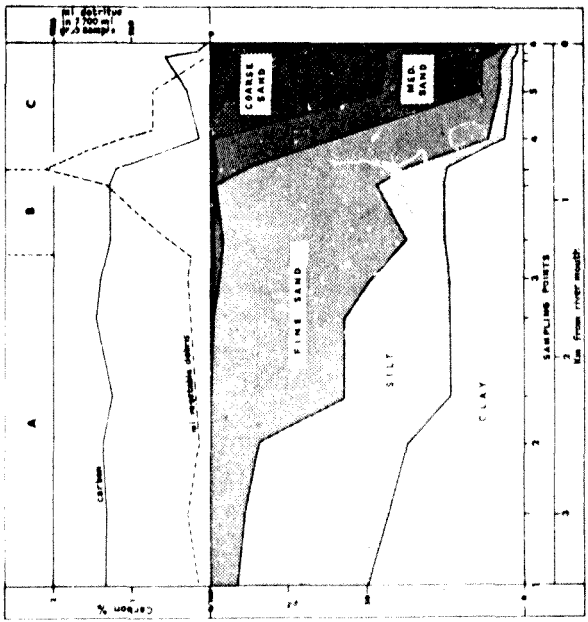


Fig. 7.1 SUBSTRATE OF THE SEVERN : RIVER BED



Fig. 7.2 A typical sample from the drowned river bed using a van Veen grab. Note the stratified layers of mud.

larger particles showed a sharp increase.

From these analyses, it would seem that the substrate of the drowned river bed outside Jacana Bend and, more particularly, Parrot Bend, was much the same. Within these points, however, a change in substrate was found which was sudden and more or less consistent.

On the basis of substrates, therefore, the drowned river bed can be broadly separated into three sections (see Fig. 7.1):

A. The bay zone. From Station 1 to approximately 250 m inside Station 3 (Parrot Bend). Characterized by a fine jelly-like mud made up of clay, silt and fine sand with a low perceptible component of vegetable debris, but a carbon content of approximately 1.4%. Within this zone particle size showed a gradual increase towards the estuary. 2.2 Km.

B. The outer estuarine transitional zone. From a point approximately 250 m inside Parrot Bend to Jacana Bend. Particles dominated by fine sand. Sharp increase in perceptible vegetable debris with inward progression. Carbon content approximately 1.4%. 0.5 Km.

C. The inner estuarine transitional zone. From Jacana Bend to the river mouth at Elbow Rapid. Sharp decrease in both vegetable debris and carbon (0.8%). Sharp increase in particle size so that substrate dominated for the most part by coarse sand. 0.8 Km.

3. THE FAUNA

3.1 Methods

Benthic samples from the shoreline were taken using a Rigosha "snapper" grab covering an area of 25 sq cm to a depth of 2.5 cm. Eight snapper grab samples constituted a single sample for analysis,

thus each sample was taken as 200 cm^2 to a depth of 2.5 cm. Five samples were taken at each station as a seasonal sample for that station, thus 1000 cm^2 constituted the seasonal collection from each marginal sampling point. A van Veen grab, sampling an area of 334 cm^2, was used for all sampling away from the margins. Although the design of the grab allows samples to be taken to a depth of 12 cm, the jelly-like consistency of the muds of the drowned river bed indicated the true depth of each sample in that substrate to be in the region of 8 to 10 cm (Fig. 7.2). Five samples taken as closely together as possible constituted the seasonal collection at sampling site, totalling a surface area of mud of 1670 sq cm. Sampling sites considered in the seasonal survey include margins and the drowned river bed at all five main stations, 5 metres at Stations 1, 2 and 5 and 10 metres at Stations 1 and 2.

Some concern has been expressed by various authors (Munro, 1965; McLachlan, 1968; Marshall, 1971) as to the efficiency of the van Veen grab in taking samples of consistent volume or area in varying substrates. Munro (1965) found in Lake McIlwaine that the number of benthic invertebrates of all types varied proportionately with the volume of the sample. McLachlan's (1968) findings from Lake Kariba suggested the opposite, namely that volume and number of animals were inversely related, in that chironomid larvae, the predominant benthos, occurred in the first 2 cm of mud, as found by Mundie (1957) in an English reservoir. Subsequently Marshall (1971) working on Lake McIlwaine, has shown that in this lake volume and the Oligochaeta are positively related whereas the Chironomidae are negatively related. The discrepancy in these findings suggest that any attempt to adjust results on the basis of the actual volume of sample taken could result

in decreasing, rather than increasing accuracy. Furthermore, a grab sample always contains a water as well as a substrate component, the volume of the latter being far more important when considering faunal density. Neither Munro (1965), McLachlan (1968) nor Marshall (1971) seem to have considered this point when relating numbers of animals to volumes of samples, which could explain the discrepancy in their findings. However sophisticated statistical cross checking may be used, faunal distribution results on the basis of grab samples are always open to error of many kinds, including amongst other factors, escape reaction by some species, "blast" effect by the pressure wave in front of the grab, differing closing patterns in different substrates by the same type of grab, differing closing patterns by different types of grab and substrate depth preferences by different species which may vary hourly. In the same way as the term "net plankton" is used to denote plankton sampled by plankton net, so also should the term "grab benthos" be used.

The rationale governing this aspect of the sampling in the present study tended towards practicality and was based firstly on the fact that quite apart from faunal distribution, any sampling method using a grab is open to error, but that for a given substrate this error should be reasonably consistent. On this basis, only "good" samples were accepted. A "good" sample was easily defined on the river bed where only uniformly sized 'cakes' (Fig. 7.2) were accepted from a grab which had closed completely without any leakage when lifted from the water. Away from the river bed the assessment of a "good" sample was more subjective, but was based on the quantity of substrate lifted which was judged after repeated sampling at a particular station to be the maximum obtainable from that substrate. Any leakage from the grab

when lifted from the water resulted in the sample being rejected. At times this was a tedious principle to maintain, particularly away from the river bed where larger sticks or gravel particles held the jaws of the grab open. On one occasion, for example, the grab had to be dropped 43 times to obtain 5 acceptable samples.

As many samples as cost/value considerations allowed were taken at each sampling point and the choice of five samples compares favourably with that of other benthic workers (Table 7.2). McLachlan (1969) using Mundie's (1957) derivation of the formula $N = \left(\frac{1.96}{Dx}\right)^2$ given in Southwood (1966) and discussed earlier with regard to the plankton, attempted to assess the accuracy of his samples on the basis of the numbers of animals collected in each. The argument against the use of this formula without transformation of data and in an essentially heterogenous habitat has been made earlier (Chapter 6). Thus the confidence limits achieved would seem questionable and the method has not been used in the present study.

TABLE 7.2

AUTHOR	SAMPLE SIZE (cm^2)	SAMPLE NUMBER	AREA SAMPLED (cm^2)
Mundie (1957)	56.5	12	55
Munro (1965)	334	6	2004
McLachlan (1969)	334	8	2672
"		4	1336
"		1	334
Marshall (1971)	100	6	600
"	334	3	1002
Downaker (-)	334	5	1670

The quarterly approach also imposes limitations on the confidence which can be placed on findings, particularly on consideration of the considerable daily variation found by Phelps et al (1969) in the Mwenda estuary subsequent to this study. These suggest, however, that conclusions based on samples taken even a week apart would be of dubious value. On this basis quarterly samples would be of equal value to fortnightly or monthly ones, for only major changes or consistent trends could be regarded as significant for either. Nevertheless, the probability of missing major changes is greater the longer the period between samples. The results presented here must therefore be viewed with some caution.

On collection, samples were immediately washed through a 40 mesh/inch netting bag and, when free of mud, stored in a 4% formaldehyde solution. In the laboratory, animals were sorted into "species" and counted. As some of the oligochaete tended to break up with this treatment, only the anterior ends of these were counted. The present state of knowledge of the species of aquatic invertebrates in Africa allows recognition to a large extent only by specialists in each group. This is particularly true in respect of larval and nymphal stages, a large proportion of which have not been described. What appeared to be different species were therefore separated following close examination and were measured and drawn with the aid of a camera lucida, before being allocated a species code. 430 different invertebrates were allocated code numbers during the course of this study, though the actual numbers of the species was subsequently found to be approximately half this number, due in part to the separate code allocation to larvae, nymphs, pupae and adults and in part to the fact that excessive care was taken to separate species to the ex-

tent that one species could be allocated several numbers. The species list is appended (App. 7.1) and grateful acknowledgement is extended to the specialists who named the various groups and who are listed in the same appendix. A reference collection of species has been kept and it is intended to produce from this a guide to the aquatic fauna of the Mwanda area of Lake Kariba separately from this study.

3.2 Results and Discussion

In this section, it is intended to consider the results of the seasonal survey and then the river bed transect, and discuss them in themselves. Comparative discussion is reserved for Section 4.

All results are presented in numbers per square metre and are appended as follows: Benthos on shoreline (App.7.2); at 5 m (App. 7.3); at 10 m (App. 7.4); and on the river bed (App. 7.5). Results from the river bed transect in 1957 and 1960 are given in Appendices 7.6 - 7.8. It was not possible to weigh faunal samples on collection as the specimens would have been required for the reference collection and sorting could only be carried out subsequent to a field trip. Biomass estimates made in Section 4.9 were therefore derived by conversion, after allocation of specimens to the reference collection.

The reference collection was kept in 70% alcohol so that hydration was necessary prior to weighing. The following procedure was followed: At least 20 specimens of each species was taken from the reference collection and placed in water for varying times, dependent on the size of species involved. Larger specimens, such as the larva of the caddis Dinarthrum spenensis, were left in water for 30 minutes while the smallest specimens (i.e. Tanytarsus larvae, Cyclo-

sathoria) were hydrated for ten minutes. Following hydration the specimens were separated and placed on filter paper to remove excess water and weighed to the nearest mg. Conversion was calculated on the basis of the number of individuals weighed. These are tabulated (Table 7.5).

Apart from considerations relating to standing crop, numerical data have been used in the analysis.

The presentation and discussion of results has been separated into two parts: the main station survey, from January 1967 to January 1968, which follows, and the drowned river bed transect, to be considered later.

3.2.1 The main station survey (February 1967 - February 1968)

3.2.1.1 Spatial differences in composition

The analysis of results as faunal composition is aimed to clarify the relative importance of the faunal groups at each sampling site, without reference to seasonal changes which have been ignored in the present context. Hence results are based on total collections from all "seasons" from each site and are tabulated by major taxa for depth in App. 7.6 and for station in App. 7.7. The total numbers of animals in each taxon collected are tabulated (Table 7.4) as are the percentages derived from these totals (Table 7.5), which are figured (Fig. 7.5).

The overall percentage composition by numbers for the entire study area indicates an overwhelming dominance (89%) by the Oligochaeta, Chaoborinae and Chironomidae (30.5%, 31.5%, 27.5% respectively) in equal proportions. The other groups found in significant numbers were the Ephemeroptera (2.0%), Trichoptera (1.9%), Ceratopogonidae (3.1%), and the Mollusca (1.0%). Interesting differences were found within the study area, however. It is most convenient in the present

TABLE 7.3 APPROXIMATE CONVERSION VALUES FROM NUMBERS TO WET WEIGHT FOR BENTHIC ORGANISMS

mg/individual	Group
0.07	Hydrachnellae, Ostracoda
0.1	Pentaneurini *mitei*, Cladotanytarsus, Tanytarsus sp. 344
0.2	Criscotopus, Ablabesmyia sp. 50
0.3	Tanytarsus *baltoatus*, T. *sarine*, Stictochironomus
0.4	Diarotanypinae
0.5	Pentaneura
0.6	Procladius, Culicoides spp. 19, 61
0.7	Cryptochironomus, Anisus
0.8	Dero, Allonais, Nais, Probezzia, Ablabesmyia, Chironomus, Polypedilum, Abiesmyia, Euthyplus, Cryptochironomus, Nilodorum, Clinon, Coenis, Chaoborus
1.0	Hemiptera
1.5	Clinotanypus, Limnochiridrilus, Auloiriblus, Aulophorus, Lumbriculidae, Glossosoleciidae, Ferrissia, Fisidia
2.5	Early instar Anisoptera
3.0	Coleoptera
4.1	Sialinus
5.1	Pyrrallidae, Hirudinea
10.0	Tipulidae, Zygoptera
13.5	Branchiura
18	Limnaea, Planorbularis, Povilla
26	Mid instar Anisoptera
50	Late instar Anisoptera, Caradina, Dissogonais, Corbicula, Hydra
320	Limnodrilus

TABLE 7.4 THE TOTAL NUMBERS/m^2 OF EACH FAUNAL TAXON COLLECTED OVER FIVE "SEASONS"

	A: BY STATIONS					B: BY DEPTH				
	1	2	3	4	5	Margins	5 m	10 m	River Bed	Total
Oligochaeta	4704	2495	147	1014	288	1472	66	12	7098	8648
Hirudinea	-	50	-	7	6	50	-	-	13	63
Odonata	12	110	50	59	-	225	-	-	6	231
Ephemeroptera	105	28	-	432	-	523	24	18	-	565
Trichoptera	106	369	60	12	6	180	148	126	99	553
Hemiptera	24	-	6	-	-	-	12	-	18	30
Coleoptera	-	-	-	100	-	100	-	-	-	100
Tipulidae	-	-	-	20	-	20	-	-	-	20
Chaoborinae	1640	3840	2928	212	420	79	1166	1710	6085	9040
Chironomidae	1915	2286	831	1165	1664	4256	1098	554	1813	7861
Ceratopogonidae	150	607	64	-	67	495	72	180	147	894
Crustacea	-	-	-	-	20	20	-	-	-	20
Mollusca	98	408	70	-	-	366	120	18	18	522
TOTAL	8700	10193	4156	3021	2477	7826	2706	2718	15297	28547
MEAN/STN (A) OR DEPTH (B)	1740	2039	1385	1510	1239	1565	90	1359	3019	

TABLE 7.5 THE PERCENTAGE COMPOSITION OF FAUNAL TAXA BY NUMBERS

	AS BY STATIONS						BY DEPTHS			OVERALL
	1	2	3	4	5	Margins	5 m	10 m	River Bed	%
Oligochaeta	54	25	4	34	12	12	2	P	45	30.3
Hirudinea	-	1	-	P	P	1	-	-	P	0.2
Odonata	P	1	1	2	-	3	-	-	P	0.8
Ephemeroptera	1	1	-	14	-	7	1	1	-	2.0
Trichoptera	1	4	1	P	P	2	5	5	P	1.9
Hemiptera	P	-	P	-	-	-	P	-	P	0.1
Coleoptera	-	-	-	3	-	1	-	-	-	0.4
Tipulidae	-	-	-	P	-	P	-	-	-	0.1
Chaoborinae	19	38	70	7	17	1	45	63	40	31.5
Chironomidae	22	22	20	39	67	58	41	24	12	27.5
Ceratopogonidae	2	6	2	-	3	7	3	7	1	3.1
Crustacea	-	-	-	-	1	P	-	-	-	0.1
Mollusca	P	4	2	-	-	5	4	1	P	1.8

P : Present

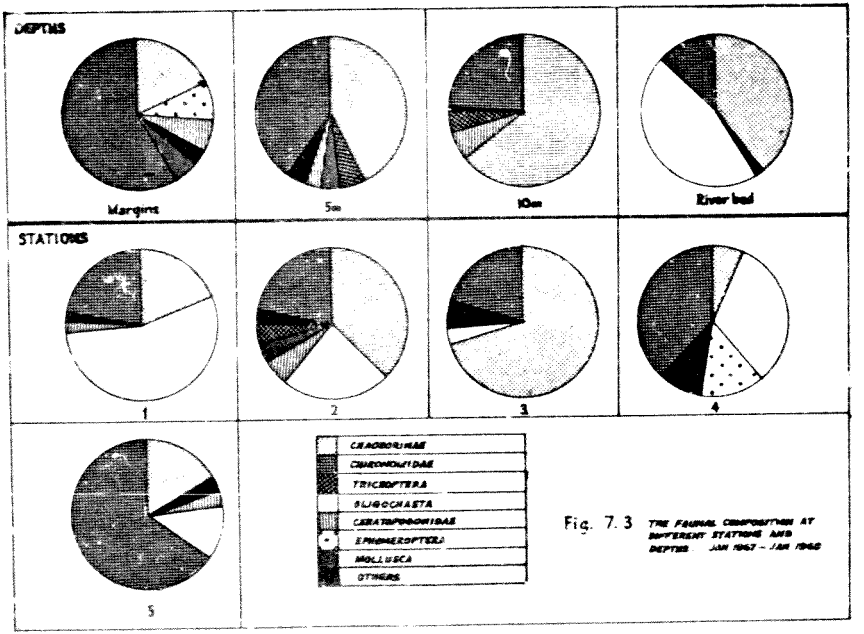


Fig. 7.3 THE FAUNAL COMPOSITION AT DIFFERENT STATIONS AND DEPTHS JAN 1967 – JAN 1968

context to consider each taxon in turn, by order of their importance as constituents.

Chaoborinae. The phantom midges were an extremely insignificant constituent of the marginal samples. Away from the margins, however, numbers increased and they were particularly important at 10 m and at Parrot Bend, becoming less important in deeper and shallower waters into the "estuary" and outwards towards the bay.

Oligochaeta. The Oligochaeta were a clearly dominant portion of the population of the river bed and were of some significance along the margins. Their importance as a population constituent increased with progression outwards into the bay. Coupled with their insignificance at Parrot Bend, the indications would be that they and the Phantom Midges showed a reversal of dominance.

Chironomidae. The chironomids showed increasing importance in shallowing water and were particularly important along the margins. In the same way, a marked increase in their significance as a population constituent occurs with progression towards the river mouth; from Parrot Bend towards the bay their proportion remained constant at about 20%.

Ceratopogonidae. The ceratopogonids appeared to be of greater importance towards the river mouth, until Station 5, when a slight increase in importance was found.

Trichoptera. Caddis fly larvae seemed to be of greater importance in the bay at intermediate depths than elsewhere, being more dominant where fewer oligochaeta were found.

Mollusca. The only point where the molluscs were of any significance as a population constituent was along the shoreline of the bay.

The remaining five taxa which occurred in the collections,

but which were of little overall significance, were usually associated with the shoreline. Although more or less the same number of representative taxa appeared at each station and depth, consideration of Fig. 7.3 indicates trends in the proportions of these. The analysis of overall depth composition suggests that with increased depth, or progression towards the drowned river bed, significant constituents became fewer and the important constituents more dominating. A similar type of trend is not apparent when considering the overall station composition, though the relatively large number of significant taxa at Station 2 and small number at Station 5 is of interest. These variations could be explicable on the basis that where conditions are suitable, such as the drowned river bed or Station 5, certain well adapted taxa, such as the chaoborids or oligochaets, compete with and therefore oppose colonisation by less well adapted taxa. This should also apply, however, to the shoreline where the chironomids are dominant, in that the same effect would result in their overwhelming the shoreline fauna, but this does not seem to have been the case. There is therefore some indication here that abiotic factors were primarily responsible, rather than competition.

3.2.1.2 Spatial differences in abundance

The data referred to in this section may be found in Appendices 7.7 and 7.8. Figure 7.4 illustrates the numerical abundance of taxa at each sampling site as the total collected over all "seasons". By far the most productive area sampled was the river bed away from Salvinia (Stations 4 and 5) where a considerable decrease in numbers was found. The next most numerically productive region is seen to be along the shoreline, at a considerably lower level than on the drowned river bed away from the Salvinia mat. Here, an increase was seen in

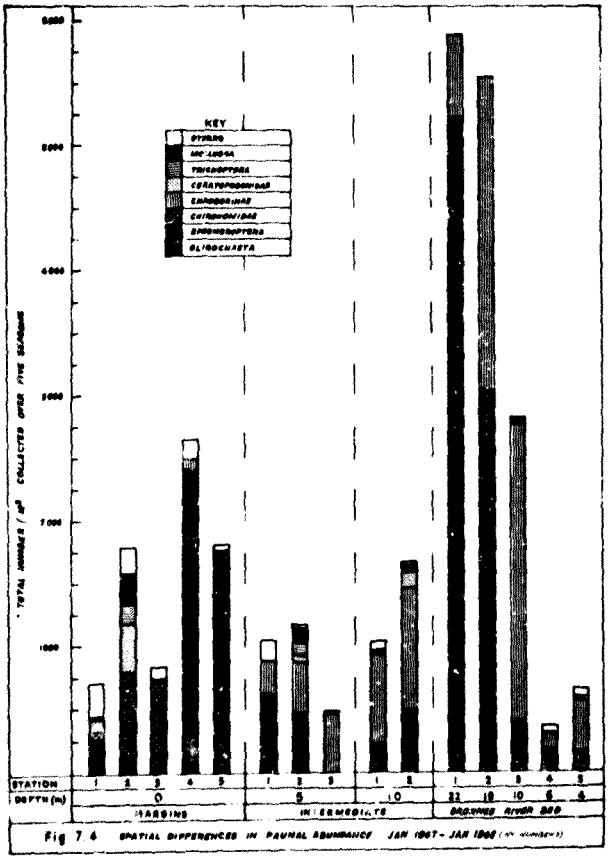


Fig 7.6 SPATIAL DIFFERENCES IN FAUNAL ABUNDANCE JAN 1967 - JAN 1968 (BY NUMBERS)

the number of animals along that part of the shoreline associated with the permanent Salvinia mat. Production at intermediate depths is lower, with lowest numerical yields, apart from the areas sampled beneath Salvinia at 5 m sites. The level of differences in mean production for all stations is given in Table 7.4.

The same table gives the mean figures for all depths sampled at each station, indicating slightly higher numerical standing crop in the bay, and particularly at Station 2, than within the "estuarine" area, where at Stations 3, 4 and 5 production is apparently more or less constant, due mainly to the relatively high production along the margins in association with Salvinia and low production away from the river bed at Station 3. When overall numbers from the areas in association with these three stations is considered, however, production at Station 3 is clearly considerably higher than at 4 and 5, due to the very limited area of the marginal habitat which causes an apparent increase at Stations 4 and 5 when mean values are considered.

The numerical distributions of the Oligochaeta, Ceratopogonidae, Mollusca and Trichoptera are similar to their importance as percentage population constituents as described in the previous section. The Chaoborinae show one major difference. Although far more important at Station 3 as a population constituent, they were in fact found in equal numbers at Station 2, but were overshadowed here by the very numerous Oligochaeta. The numbers of Chironomidae found along the margins and at intermediate depths confirm the distributional pattern indicated by the consideration of their importance as a population constituent. On the river bed, however, although increasing in importance as a population constituent towards the river mouth, the actual numbers from Station 3 inwards remain constant, at a considerably

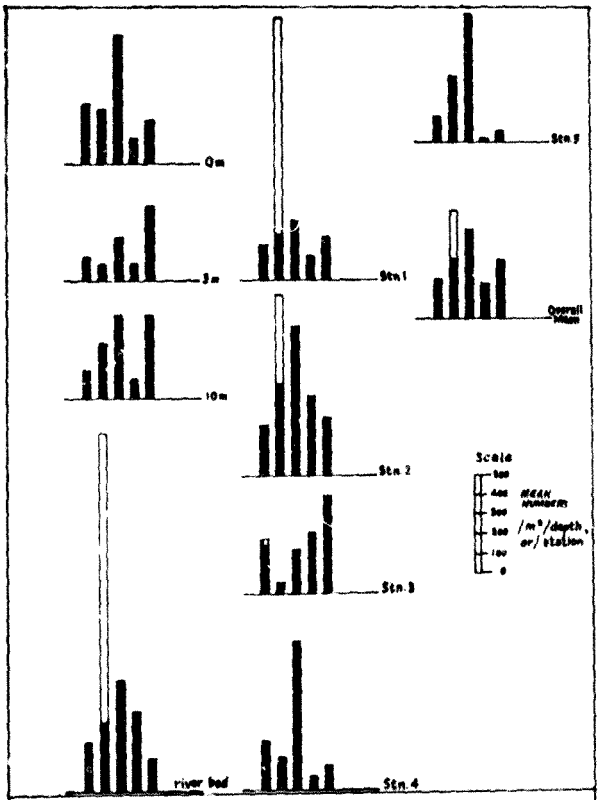


Fig. 7.5 "SEASONAL" CHANGES BY DEPTH AND BY STATION

Each histogram is in the order of Sampling Feces. Contributions by Aulodrilus in outline only

lower level than found at the bay stations. The numerically unimportant taxa may be separated into three different groups. The first includes marginal animals found throughout the study area (Odonata, Hirudinea); the second, marginal animals associated with the permanent Salvinia mat (Ephemeroptera, Tipulidae, Coleoptera, Crustacea); the third were found mainly in deeper water (Hemiptera).

3.2.1.3 "Seasonal" differences in abundance

The mean numbers/m^2 at each sampling point on the five sampling dates have been calculated and are presented as histograms (Fig. 7.5). A considerable variation between sampling dates may be seen, summarized by the overall mean "seasonal" variation. The greatest density of animals seemingly occurred in April 1967, due mainly to the very large numbers of Aulodrilus pigueti which occurred on the river bed at Stations 2 and, particularly, 1. For this reason the contribution of Aulodrilus to the mean values has been illustrated. Without Aulodrilus, it can be seen that the remaining fauna showed a trend for increase between January and July 1967, with a sharp decrease by the following October and with numbers rising again by January 1968, to higher levels than found in January 1967. A very sharp increase in the marginal fauna was found in July 1967, mainly attributable to the shoreline associated with the permanent Salvinia mat. At intermediate depths there was some indication of an overall increase during the course of the survey. "Seasonal" fluctuations of species other than Aulodrilus suggest highest numbers in July and lowest numbers in January on the drowned river bed. This pattern was followed at all the stations when the various depth zones were considered together with the marked exception of the fauna at Station 3, where the lowest density was found in April 1967.

5.2.1.4 "Seasonal" and spatial distribution of the numerically important species in each depth zone

Having presented the major spatial and seasonal changes in the benthic population, it is now necessary to consider the species involved in these changes. It has been found convenient to do this by separating the species by depth zones.

The shoreline (All stations)

Although a total of 59 species were found along the margins during the course of the survey, only eight of these constituted 70% of the shoreline population by numbers. The most important of these numerically were the Chironomus (Chironomus) sp. 47 (21%), made up of C. transvaalensis Kieffer and C. formosipennis Kieffer, which occurred in large numbers near the river mouth in July. The only other time it was found was in the same sampling point the previous January.

Stictochironomus caffrarius (sp. 8: 12%) was also of some importance but was found during the rains at the bay stations and particularly, the transitional Station 3. Clinotanypus glaridinnis (sp. 25: 7%) was very nearly always present in marginal samples, the only exception being a complete disappearance in July. It was most numerous in association with the permanent Salvinia mat at Station 4. The only remaining chironomid of importance was Criocotopus scotti (sp. 130: 4%) which occurred in some density only once during the survey, at Station 4 in July. Nemertodrilus sp. 20 (0%) and Clinotanypus glaridinnis were both uniquitous on the shoreline but showed a preference for the area close to the river mouth. Allonais sp. 127 (6%) the only other important oligochaet was found on several occasions but occurred particularly in association with chironomid Criocotopus scotti, as did the mayfly Caenis sp. 102 (8%). "Culicoides" sp. 61 (6%) was

ubiquitous, but showed a preference for the bay shoreline. It was particularly numerous at Station 2 in April. On the basis of this analysis alone no single species could be regarded as being "typical" of the margins, though the chironomids were clearly the most important constituent.

The 5 metre depth zone (Stations 1, 2 and 3 only)

A considerable decrease in numbers of species was found between the shoreline and the 5 m depth sites. 27 species were found during the course of the survey and seven of these constituted 84% of numbers collected in 5 m. Whereas only a few specimens were collected along the shoreline, the Chaoborus sp. 1 (43%), probably made up by C. edulis, C. serratoroseus and C. anomalus (Mitchell, S.M. pers. comm.) constituted nearly half of the animals collected at the 5 m sites. The larvae and pupae were ubiquitous, both in terms of "season" and station, though numbers increased towards Station 3 and comparatively few were found in October.

Tanytarsus halteatus (sp. 16: 21%) also occurred in most samples, but was markedly absent from Parrot Bend and none were found in October. Stictochironomus caffrarius (sp. 6: 11%) which was also of some importance along the shoreline, occurred mainly at Station 1 in January 1960. The remaining important chironomids Cryptochironomus sp. 7 (4%) and Procladius brevipeticulatus (sp. 15: 4%) occurred mainly in the bay in January 1960. Dipseudopsis capensis (sp. 14: 8%) was the only ubiquitous species at 5 metres and was most numerous at Station 2 in July and October. Although dead shells were frequently sampled, live Corbicula africana (sp. 32: 4%) were only found once at 5 m during the course of the survey, in October at Station 2.

The only species to be of importance both along the shoreline

and at 5 metres was therefore found to be Stictochironomus caffrarius.

The 10 metre depth zone (Stations 1 and 2)

Again, a decrease in number of species occurred between 5 and 10 metres, though this decrease could be a function of fewer sampling sites. 21 species were found and only four of these constituted 80% by numbers of animals found. The Chaoborus species alone constituted 63% of animals collected, actual numbers being more or less twice those found at 5 m. The seasonal and spatial trends at 10 m were similar to those found at 5 m. Polypedilum sp. 5 (14%) starts appearing at 10 m stations and was most numerous in April 1967 and, overall, at Station 2. "Culicoides" sp. 61 (6%) which was found to be of some importance on the margins and which occurred at 5 m sites, again became an important constituent at 10 m, predominantly at Station 2 in April. The discontinuity in depth distribution of this "species" suggests that there are more than one true species grouped in the code. Dinocloniopsis carnosis (5%) shows a similar spatial and seasonal distribution as found at 5 m.

The river bed (Stations 1 to 5, 22 m to 4 m depth)

The number of species on the river bed increased to 32 but only 3 of these constituted 80% by numbers of all animals collected. As a proportion of all the fauna collected, the numbers of Aulodrilus pigueti (sp. 3: 42%) were overwhelming. As they occurred only once in any numbers, in April at Stations 1 and 2, when very dense concentrations were sampled, the total figures reflect a greater importance than was, perhaps, actually the case. Chaoborus spp. (4%) occurred throughout the seasonal and spatial sampling, but were particularly dense in July and November at Stations 2 and 3. A seasonal difference was apparent between intermediate depths and the river bed.

In the former, densest concentrations occurred in January 1960. All did show, however, high levels of density in July and spatial concentrations at all depths showed a trend for increase towards Station 3. Polymedilium sp. 5 (6%) was found predominantly in deeper water in April and June. Greater numbers were found at Station 2, in keeping with the findings from 10 m sites.

There is some indication from the results presented above that the number of important species and depth show a negative correlation. As has been mentioned, however, this could be a function of the number of stations sampled at different depths. Conversion to number of species/station would not necessarily correct this fault, for fewer actual samples were taken, hence increasing the likelihood of missing the rarer species. This would not apply with regards the more common species, however. A marked decrease in these was apparent (Table 7.6) with increased depth, which is even more apparent if the important species from each depth zone are corrected for their contribution towards the fauna collected, by calculating the mean percentage contribution per species. A consistant trend emerges from shoreline to river bed (Table 7.8) indicating that there seemed to be an inverse relationship between depth and number of important species, which would suggest either that there was a decrease in habitat complexity from shoreline to the bed of the drowned river, or that the lacustrine niches were not fully utilised by the benthos, or a combination of both. The matter is discussed further below.

5.2.1.5 The spatial distribution of all species

The following analysis has been undertaken to ascertain habitat preference by individual species. All species were listed and marked as absent, present, abundant or occasionally abundant against the

TABLE 7.6 THE RELATIONSHIP BETWEEN THE NUMBER OF NUMERICALLY IMPORTANT SPECIES AND THE DEPTH ZONES

DEPTH (m)	STATIONS SAMPLED	NUMBER OF SPECIES	SPECIES/STATION	NO. OF IMPORTANT SPECIES AND THEIR % CONTRIBUTION TO TOTAL FAUNA	MEAN % CONTRIBUTION OF IMPORTANT SPECIES
0	5	59	12	8 : 70%	9%
5	3	27	9	7 : 64%	12%
10	2	21	10	4 : 88%	22%
River Bed	5	32	6	3 : 88%	29%

depth zones separated into bay (Stations 1 and 2), Parrot Bend (Station 3), and "Estuary" (Stations 4 and 5). The chironomid pupal "species" were disregarded as their larval linkages were imperfectly known. Spatial distributions were found to be as follows: (important species are asterisked).

1. Species found only on the shoreline:

20 species fell into this category:

(a) At the bay stations only:

Hirudinea	sp. 65, sp. 66
Ephemeroptera	Cloeon sp. 62
Odonata	sp. 57, sp. 67, sp. 160, sp. 27
	Ictinogomphus ferox
Chironomidae	Dicrotendipes fusconotatus, Nilodorum brevibucca

(b) At Parrot Bend only:

Odonata	sp. 41
Chironomidae	Cladotanytarsus pseudomanus

(c) Within the estuary only:

Ephemeroptera	Ruthrumulus sp. 55
Odonata	sp. 145
Coleoptera	Yola bakaulti, Parnaymus chalcous
Tipulidae	Limoniini (?) sp. 100
Chironomidae	Cricotopus sactii, Chironomus calligerus

(d) At bay stations and in the "estuary" only:

Oligochaeta	Allonais sp. 127*, Glossoscolecidae sp. 170,
	Nemertodrilus sp. 20*
Chironomidae	Chironomus transvaalensis*, C. formosi-
	mensis*

(e) At bay stations and Parrot Dend only:

Oligochaeta — Aulophorus furcatus

(f) At Parrot Dend and in "estuary" only:

Chironomidae — Cryptochironomus lindneri

(g) Ubiquitous along margins:

Odonata — Libellulidae sp. 167

2. Species found along the shoreline and at 5 m only:

Three species fell into this category, the mayfly Cosmis sp. 90, which was found only in the bay; the larval chironomid Stictochironomus caffrarius* which was found in the bay, but was numerous at Parrot Dend; and Pentapedilum wittei larvae which occurred in the bay and "estuary" but not at Parrot Dend.

3. Species found along the shoreline and at 10 m only:

Nil.

4. Species found along the margins and on the river bed only:

Nil.

5. Species found at 5 m stations only:

The only species in this category was the nymph of the wood boring mayfly, Povilla adusta, which would seem to have been displaced from the drowned trees (see Chapter 8).

6. Species found at 5 m and 10 m stations only:

Nil.

7. Species found at 10 m only:

Nil.

8. Species found at 10 m and in the river bed only:

Nil.

9. Species found in the river bed only:

Ten species fell into this category:

The oligochaet Dero sp. 29 and the bivalve mollusc Sphaera ferruginea were found at two points only, the former in the bay and at Parrot Bend, the latter in the bay and estuary. The other species in this category were found at single points, as follows:

(a) In the bay only:

Hemiptera	Anisops sp. 124 larvae

(b) At Parrot Bend only:

Oligochaeta	Dero dorsalis
Hemiptera	Anisops malliensis
Mollusca	Bulinus forskali

(c) In the "estuary" only:

Hirudinea	sp. 43, sp. 131
Odonata	Lestinogomphus africanus
Chironomidae	Cryptochironomus sp. 59
Ceratopogonidae	"Probezzia" sp. 72

10. Species found at all depths but the river bed:

Four species fell into this category:

The oligochaet Lemprodrilus sp. 60 and the chironomids Polypedilum deletum and Cladotanytarsus sp. 70 occurred only in the bay, whereas Ablabesmyia nilotica was ubiquitous throughout the study area away from the river bed.

11. Species found at all depths but 10 m:

Two species occurred in this category and both were ubiquitous apart from their absence from 10 m depth samples. These were the oligochaet Branchiodrilus hortensis which was most numerous on the river bed in the bay and the chironomid

Clinotanypus glaripennis" which was particularly important within the "estuary". It is very likely that the absence of these two species at 10 m sites is the result of sampling error on consideration of their otherwise widespread distribution.

12. Species found at all depths but 5 m:

Similarly, the only species falling into this category, the oligochaet Auladrilus pigueti" was widespread, though essentially of the river bed fauna in the open bay and its absence from 5 m sites is probably explicable in terms of sampling error.

13. Species found at all depths except the margins:

Four species occurred in this category:

The larvae of Cryptochironomus sp. 7 and Cryptochironomus neopilicola would appear to be truly lacustrine animals, in that they were only found in the bay away from the margins, as was the ceratopogonid "Culicoides" sp. 19. Another chironomid in this category, but showing a widespread distribution and preference for "estuarine" conditions was Clinotanypus maculatus".

14. Ubiquitous species:

The six species found in all depth zones also occurred in all parts of the study area, so that their distribution was widespread from all viewpoints. The larvae of the caddis fly Pinsendopsis capensis showed preference for areas away from the margins and was more abundant in the river bed, apparently irrespective of bay/estuarine conditions. The distribution of the Chaoborus spp. has been described in the previous section. Three larval chironomids were ubiquitous. Procladius brevipetiolatus and Tanytarsus halteatus are similar to Chaoborus in showing a preference for conditions on the drowned river bed, but within

the estuary. Polypedilum sp. 5 occurred with greater frequency in depths greater than 10 m. The remaining ubiquitous species was the ceratopogonid, "Culicoides" sp. 61, which showed preference for bay conditions.

A point of interest which emerges from the analysis is the apparent lack of species typical of the intermediate depths, which would explain the lower yields from these areas.

3.2.2 The drowned river bed transect (February 1967 to November 1968)

The collection of information for two years on the drowned river bed was undertaken in an attempt to find out firstly whether or not "seasonal" changes were repetitive and secondly, what effects the removal of the Salvinia mat had on the benthos.

3.2.2.1 The major differences in "seasonal" and spatial abundance

The numbers of animals collected in 1967 and 1968 suggests a similar level of production in these two years (Table 7.7).

The results extracted in Table 7.7 support the findings of the main station survey in that they indicate almost twice the hot season population of October and January in the cooler months of April and July. Had it not been for the isolated occurrence of large numbers of Aulodrilus pluseti in May 1967, a trend of increase from January through May to highest July levels followed by a decrease to November would have been apparent in both years, (in agreement with McLachlan's (1968) findings in the Mwenda Bay). Apart from the October 1968 findings, January and October populations were remarkably similar, as were the July populations of the two years. The decrease which appeared to occur in October 1968 is not easily explicable but cannot be taken to indicate a trend for decrease in numbers of the drowned river bed population.

TABLE 7.7 THE TOTAL NUMBERS OF ANIMALS COLLECTED "SEASONALLY" AND THE MEAN NUMBERS PER STATION

DATE	TOTAL FAUNA	NUMBER OF STATIONS	MEAN/STATION	ANNUAL MEAN
25/1-5/2/67	2712	7	387	
18-22/4/67	10324	9	1147(447*)	
17-19/7/67	9850	14	704	652
21-22/10/67	5183	14	370	(477*)
17-20/1/68	4752	14	339	
7/5/68	7932	14	566	431
24-26/7/68	8121	12	675	
29/10/68	1902	13	146	

*less *Aulodrilus pigueti*

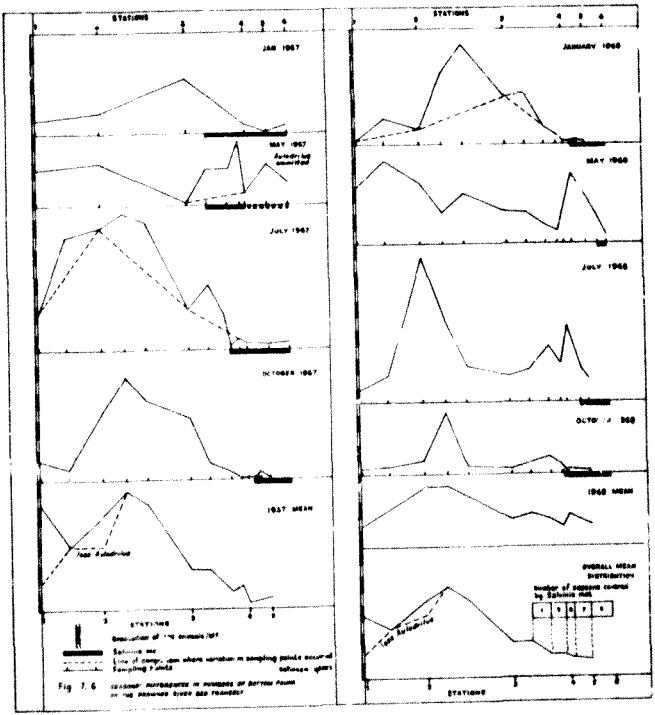

STATIONS
JAN 1967
MAY 1967
JULY 1967
OCTOBER 1967
1967 MEAN
STATIONS
JANUARY 1968
MAY 1968
JULY 1968
1968 MEAN
OVERALL MEAN
STATIONS

Fig 7.6

Figure 7.6 shows the seasonal changes in numbers of animals found at the various stations on the drowned river bed. The mean overall standing crop of animals/m^2 at each station over the two years of sampling was found to range between 219 to 1259/m^2. The results from both years indicate an increase in benthic production from the outermost bay station to 2b, a substation intermediate between Stations 2 and 3 where highest levels were found. A sharp decrease occurred to Station 3 (Parrot Bend), but the population remained more or less the same thereafter to a point approximately 150 metres outside Jacana Bend where a further decrease occurred. From this point to the river mouth, consistently low numbers of animals occurred at more or less the same level. Both the annual mean distributions do not differ very markedly from this pattern of production.

Results of the seasonal transects are not readily comparable. Characteristics consistent between the two sampling years are:

1. The outer bay stations (1 and 2) were most productive in May of both years.
2. In May of both years and in July 1968 a considerable increase in numbers of benthos occurred within the estuary.
3. From July 1967 to January 1968, and again from July to October 1968, highest yields were found between Stations 2 and 3.

The sequence replicated between the two years therefore suggest that from October to January production is low in the outer bay and within the estuary, and is highest in the intermediate zone between Stations 2 and 3. In May, highest yields occurred in the outer bay and the inner estuarine population showed an increase. By July, production at the outer stations decreased and most animals occurred in the intermediate zone between Stations 2 and 3. Only in July 1968 did

the inner estuarine population maintain the May increase, and this was probably due to the effect of removal of the Salvinia mat, discussed in Section 3.2.2.3 and 4.1. The May increases of the inner estuarine zone also cannot be attributed to normal seasonal fluctuations. In May 1957 sampling took place subsequent to unseasonal flooding of the river and supplementation of the inner estuarine population by pools benthos was very likely. In May 1960 the increase was most probably due to the Salvinia mat removal. All that may be derived from these data with any certainty is that the outer bay area showed a marked increase in production in May of each year and as a result became the most productive area, particularly as the fauna of the most consistently productive intermediate zone (Stations 2 and 3) showed a simultaneous decrease.

3.2.2.2 Faunal composition

A comparison of the percentage composition by taxa between the main station survey which included the margins and intermediate depths and the two year drowned river bed transect survey (Table 7.0), show the same taxa dominating the benthos, namely the Chaoboridae, Chironomidae and Oligochaeta. Understandably, these occurred in different proportions, the chaoborids increasing considerably in importance, from 31.5 to 45.1%, at the expense mainly of the oligochaeta (which dropped 9% to 7%) and most other groups with the exception of the chironomids, which maintained more or less the same importance as a population constituent at 29%.

Considering only the transect figures given in Table 7.0, the Oligochaeta showed a trend of decrease in importance during the survey, though there is some indication of an increase in November 1960. The most important oligochaeta were Aulodrilus pigueti, at the beginning

TABLE 7.8 'SEASONAL' CHANGES IN THE PERCENTAGE COMPOSITION OF THE FAUNA OF THE DROWNED RIVER SED

	Jan	May	July	Nov	1967	Jan	May	July	Nov	1968	Overall %
Oligochaeta	15.[illegible]	62.6	5.6	2.7	26.86	6.6	9.5	18.6	30.8	13.89	21.0
Hirudinea	-	-	0.2	-	0.07	0.[illegible]	0.1	-	-	0.05	0.1
Odonata	0.2	0.4	0.1	-	0.19	-	0.1	0.1	-	0.05	0.1
Ephemeroptera	0.4	0.2	-	-	0.10	0.1	-	0.6	-	0.23	0.2
Trichoptera	0.2	0.4	1.8	2.0	1.22	1.4	1.0	5.0	7.0	2.27	1.7
Hemiptera	1.1	0.4	0.1	0.1	0.30	-	-	-	-	-	0.2
Coleoptera	0.4	0.7	-	-	0.31	-	-	-	-	-	0.2
Culicidae	29.0	26.8	69.5	85.2	53.16	86.0	37.8	9.7	7.9	35.39	45.1
Chironomidae	51.6	8.0	19.3	6.9	16.02	5.0	50.8	63.0	44.1	45.06	29.0
Ceratopogonidae	1.8	0.5	1.6	3.2	1.50	0.6	1.1	3.9	6.0	2.40	1.9
Molluscs	-	0.3	0.[illegible]	0.3	0.33	0.3	-	1.0	4.1	0.77	0.5

of the survey, Branchiodrilus hortensis from January 1967, to May 1968, and Branchiura sowerbyi from July 1968, to the end of the survey. The Chaoborinae were at a peak over the rainy season of 1967/68 and were always an important component in 1967. A marked decrease in importance occurred from July 1968, which was contributory to the increased importance of the oligochaets from this time. The Chironomidae showed a definite increase during the course of the survey. Most important were Polypedilum sp. 5, which showed a marked seasonal increase in winter months, apart from a trend for increase during the survey; Clinotanypus nasutatus, which was always pres : and Procladius brevipeticlatus which appeared in large numbers in July 1968, and was an important component of the population in November 1968.

A trend of increase during the course of the survey was also noticeable in the Trichoptera (mainly Dibseudopsis canensis), Ceratopogonidae and Molluscs (due to the appearance of Eupera fervinea in November 1968). The Hirudinea, Odonata, Hemiptera and Coleoptera were of little importance as population constituents throughout the survey of the river bed.

The April/July increase mentioned in the previous section was due mainly, in 1967, to an increase in Aulodrilus pigueti and the Chaoborus spp. In 1968, the seasonal increase was attributable to the Chironomidae, particularly Polypedilum sp. 5.

Figure 7.7 illustrates by kite diagram the seasonal distribution and abundance of the more important species of the benthos. It was found necessary to use a variable horizontal scale as indicated, because of the wide variation in numbers between species. The figure is applicable to the rest of this section, and the following two sections, but is not used exclusively, as reference to the overall

Fig. 7.7 The seasonal distribution and abundance of the more important species of the river bed transect (1967 - 1968).

The edge of the *Salvinia* mat is denoted by the heavy stippled line.

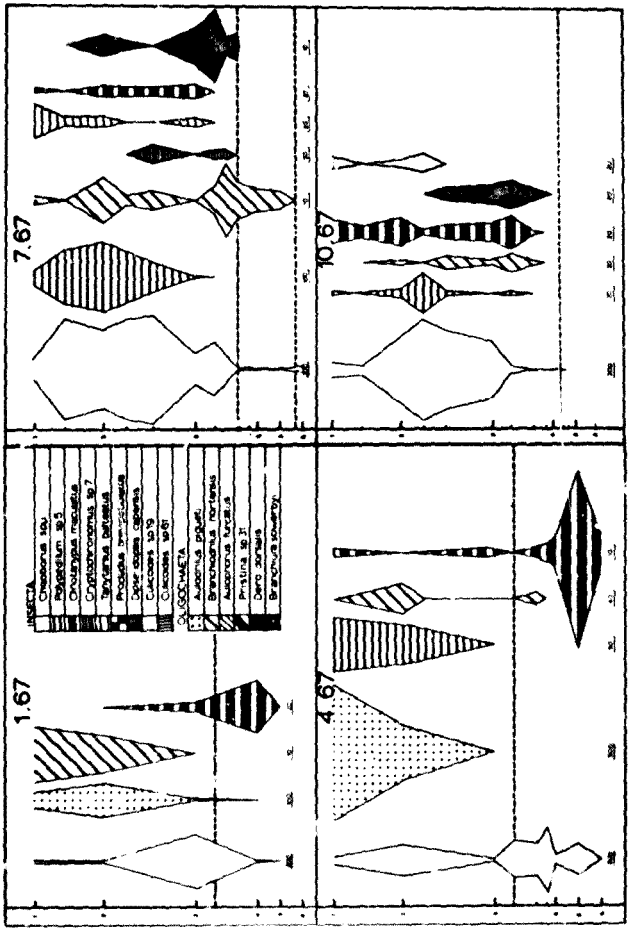


Fig. 7.7 1967

Continued overleaf

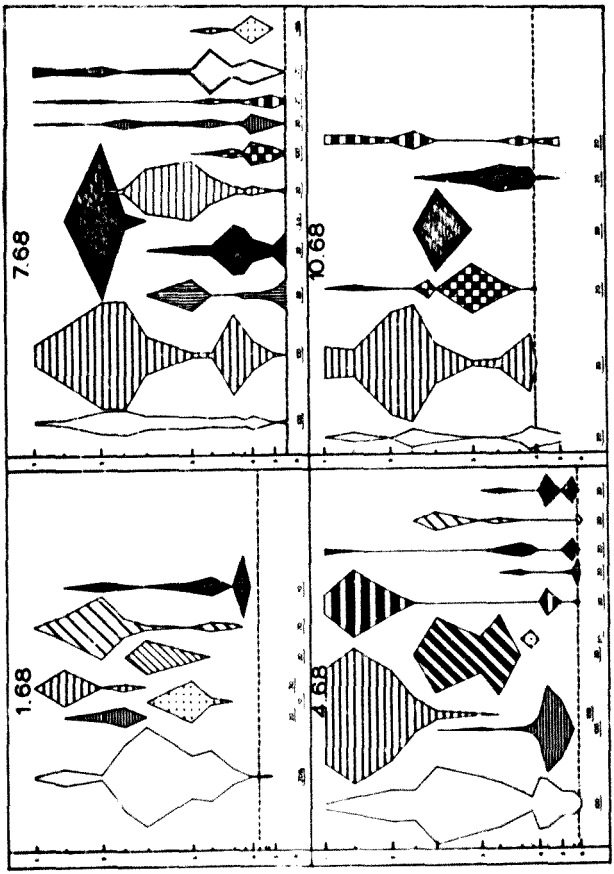


Fig. 7.7 (Continued) 1968

results (App. 7.8 - 7.16) has been made.

Consideration of the species contributory to the spatial differences in production, summarised in Fig. 7.6, is necessary. Production between Stations 1 and 2 was largely due to the presence of Aulodrilus pigueti, Branchiodrilus hortensis and, on occasion, Clinotanypus maculatus (4/68). Other species contributory towards this section of the drowned river bed, but which increased between Stations 1 and 2b and were most numerous between Stations 2 and 2b were the Chaoborus species, Polypedilum sp. 5, and Branchiura sowerbyi. The decrease in production at Station 3 was largely due to a fall off in numbers of these species. Species found predominantly between Stations 3 and 4 were Dipseudopsis capensis and, at times, Clinotanypus maculatus (1/67; 4/67). Procladius brevistriolatus, "Culicoides" sp. 19 and Dero dorsalis were largely confined to the section between Stations 3 and 5. The increase in May production in the outer bay was due largely to Aulodrilus and Polypedilum sp. 5 in 1967 and Polypedilum sp. 5 in 1968.

5.2.2.5 The effect of Salvinia on the benthos of the drowned river bed

It would appear (Figs. 7.6, 7.7) that Salvinia may be restrictive to the benthic fauna, although the trend for decrease in numbers within the estuary implies that the Salvinia is not the only factor involved, in much the same way as it was found when considering "enclosure" effects on water quality (Chapter 5). If, however, a significant increase in benthos occurs in areas freed of Salvinia, it is not unreasonable to assume that the effect of Salvinia is the most important restrictive factor. figures mentioned above show quite clearly that there is a significant increase in fauna following the depletion of Salvinia cover, which would confirm that Salvinia is restrictive

to the benthos. Not only this, but that a decrease may follow the initial increase should Salvinia recover, though on these data this could equally be the result of a seasonal effect. (October, 1968). It would appear that areas which have been covered by Salvinia and then freed of it become highly productive, at varying times after clearance (Stations 3b to 5, May and July 1968). The timing of clearance thus plays a large part in the productive sequence following clearance, highest population levels being reached between less than 8 months to between nine and twelve months after clearance, as follows:

Station 3a was cleared between May and July 1967. Standing crop [illegible] increased considerably by 17th July, when sampling was carried out, and fell away again by the following October. A trend for decrease persisted throughout the following year, a point which will be returned to below. The area between Stations 3b and 4 cleared between July and October [illegible]. A gradual increase in benthos occurred thereafter, reaching a peak in the following July, nearly a year later. The stretch between 4a and 5 cleared between January and May the following year and the population had reached a peak by May, emulating the situation at Station 3a the previous year. The implication of these results is that full utilization of the more or less virgin bottom left by the departure of Salvinia was controlled by seasonal factors. The steady fall off in numbers after the post clearance explosion of bottom fauna at 3b, the only station cleared for a sufficient period to cover the May/June period in each year, indicated that for some reason the bottom muds underneath Salvinia were capable of maintaining high populations over a single explosive period only and were thereafter unable to support further increases, even under seemingly optimal seasonal conditions.

The species involved in the colonisation of the bottom muds cleared of Salvinia did, in this case, show a sequence which could indicate early and late colonisers of virgin muds. The following species were apparently early colonisers: Cryptochironomus sp. 7, Aulodrilus pigueti, Dero dorsalis and the Chaoborus spp. Secondary colonisers included Procladius brevipeticlatus, Polypedilum sp. 5 and Dipseudopsis capensis.

4. GENERAL DISCUSSION

It has been found necessary to discuss some of the implications of the results, in themselves, in Section 3.2. The present section is basically to consider these results in relation to other findings, both within the present study and in relation to the findings of other workers.

4.1 The Effect of Salvinia on the Benthos

McLachlan (1968) found that "in the case of S. auriculata, the few samples taken (his table 27 (p 275) suggests two samples 100 metres under the mat and two samples at the mat edge at two stations) reveal a total depression of all mud fauna under a permanent mat". Bowmaker (1960, App. 1.1) in preliminary observations made in 1966 at the outset of this study, observed that the bottom mud under Salvinia "would appear to be devoid of macroscopic invertebrate life" and discussed possible reasons for this, concluding that low oxygen tensions in waters closely opposed to the mud were probably responsible. Petr (1969) found suppression of benthos under mats of Pistia in Volta lake, and also suggested low oxygen concentrations as being responsible.

The results of this study indicate that both the observations regarding Salvinia are proved to be somewhat inaccurate. A sparse

benthic population was subsequently found beneath Salvinia, on the drowned river bed, and although there may be a degree of supplementation of the benthos by animals actually living on Salvinia, which have fallen off it, and animals brought under the Salvinia by flow, certain species were found on the river bed under the mat which could not have had either source; (for example: Branchiolrilus hortensis, Procladius brevipeticulatus, and Dero dorsalis). Nevertheless there can be little doubt that Salvinia is limiting to the benthos away from the shoreline (*see* 3.2.2.3). The possible reason for this restriction should be attributable to one of the following factors:

(1) The basic trophic levels are absent due to lack of light, hence there is a shortage of food.

(2) The substrate is unsuitable, limiting colonisation.

(3) Low oxygen tensions are associated with the bottom muds, as a result of high levels of decomposing organic matter causing a microstratification of dissolved oxygen against the bottom muds and a lack of oxygen within them.

Taking the first point, many of the Chironomoni, including Polypedilum and Cryptochironomus, which are present in significant numbers in the river bed away from Salvinia, feed on detritus and the bacteria and fungi associated with it. If the lack of light and primary production were the cause of the restriction of benthos under Salvinia, these Chironomoni would almost certainly be present but they are not. The dense concentration of the apparently particulate detritus-feeding zooplankton found underneath the Salvinia (Chapter 6) indicates that lack of primary production is probably of secondary importance and that the restrictive factor/s must be related to conditions in the bottom muds.

McLachlan's (1966) experiments on substrate preferences showed that for Nilodorum brevibucca "Salvinia detritus itself does not appear to inhibit larval settlement" (p.327) and concluded that restriction by Salvinia should be attributable to some other factor. The type of substrate preferred by different species must vary, so that a general conclusion based on the behaviour of a single species is, in this context, suspect. It is possible, therefore, that the substrate underneath Salvinia could be restrictive to species other than Nilodorum.

The third possibility was that faunal restriction results from low oxygen tensions in the bottom muds beneath Salvinia. Lowest oxygen tensions within 0.5 m of the bottom underneath Salvinia occurred in January and May 1967 (Fig. 5.5) before flooding, when readings of between 2 and 10% saturation were taken. Species found at this time were Chaoborus spp., Clinotanypus nervosus and Ablabesmyia nilotica in January at Station 4, while in May fifteen different species were collected underneath the mat (App. 7.6). If the microstratification gradient is affected by oxygen tensions in the water column above the mud, as logically it should be, the above results indicate that a significant fauna was present at what may have been lowest oxygen tensions in the bottom mud. The colonisation of the mat-covered portion by Branchiodrilus hortensis during July 1967, when oxygen tensions in the water column were high and not in the two previous seasons, when tensions were at their lowest, suggest that this species' migration under the mat may have been limited by low oxygen tensions. Although, therefore, some species may not colonise the substrate under Salvinia due to a lack of oxygen (Branchiodrilus hortensis, Fig. 7.6, January, May and July 1967) others appear not to be affected to the

same degree, particularly if the reduction in number of species when higher oxygen tensions were monitored in the bottom waters is considered. Low oxygen tensions may have another effect, however. Marshall (1971) found experimentally that although Branchiura sowerbyi was capable of withstanding low oxygen tensions for a considerable period, no reproduction took place, although eggs were produced in oxygenated controls. Restriction could therefore be placed on the growth of oligochaete populations by low oxygen tensions. This restriction would not apply, however, to the insect larvae, where recruitment is dependent on the eggs produced by non-aquatic adults. Here a further limitation may be involved. The most obvious factor is the effect of the permanent Salvinia mat on the laying behaviour of the adults of benthic larvae. The assumption that an adult insect will not lay eggs on seemingly solid ground if behaviourally it requires open water for oviposition, is not considered unreasonable. This does not of course apply to the adults of the insects which live on the Salvinia mat, but those which are benthic. If this is a limiting factor on the benthic population beneath the Salvinia mat, then the most numerous species colonising this habitat must have been actively migratory. The main species, Chaoborus spp. and Glinotanypus maculatus are both extremely active in their larval stages and are both predatory and would therefore strongly suggest that the lack of oviposition above the mat-covered bottom by suitable species is an important factor in the consideration of the paucity of benthos under Salvinia.

Factors involved in the suppression of benthos underneath a permanent Salvinia mat would therefore include:

1. Substrate unsuitability.
2. Low oxygen tensions associated with decomposition in the bottom muds and unsuitable conditions for gaseous interchange at the water surface.
3. Oviposition by adults of benthic species being impaired by the false surface presented by a permanent mat, suppressing colonisation.

The consideration of supplementation of the benthic fauna on the drowned river bed beneath Salvinia by species living on Salvinia which have been dislodged can only be treated adequately when the Salvinia fauna has been considered (Chapter 8).

Supplementation by the river fauna is clearly suggested by the situation found in January 1967 (App. 7.5) in this case Stictochironomus caffrarius at Station 6, below Elbow Rapid. The same species is present near the head of the estuary in May and July 1966. The presence of Chaoborus spp. and Clinotanypus maculatus in January 1967, could also be attributable to the river. Supplementation from the river would seem to have been, on these data, insignificant. Whereas the effect of Salvinia on the drowned river bed was found to be restrictive, production seemed enhanced along the shoreline (Fig. 7.4), particularly in July 1967. The two species Chironomus transvaalensis and C. formosipennis were largely responsible for the increased numbers. A considerable number of species were involved, however, (see T.? 1.4), and apart from the Chironomus spp. mentioned above, six further species were of importance on the margins associated with Salvinia, two of which (Cassis sp. 10, Cricotopus sp.VI) were found only at stations with a permanent Salvinia mat. Although Limnodrilus sp. 20 was ubiquitous along the margins, a marked preference for shorelines

covered by Salvinia was shown. Further investigation suggested a clumped distribution in this large oligochaete, in between 2 and 20 cm depth of water. Other species found only in association with Salvinia are listed (3.2.1.3.1(c)) and include the mayfly Euthraulus sp. 53 and Chironomus calipterus. A further point worth mentioning in the present context is the importance of Stictochironomus caffrarius on the margins away from the Salvinia and its complete absence on mat-covered margins. The reverse held true for the Chironomus species. The increase in numbers of animals on margins associated with Salvinia can partly be explained by the presence of animals which live on Salvinia having been, in marginal conditions, closely associated with the marginal substrate and partly by the increased complexity of the marginal habitat caused by Salvinia.

The point has already been made that the marginal habitat covers a comparatively small area. On balance, therefore, production by benthos is restricted by Salvinia, but seemingly enhanced by the removal of Salvinia.

4.2 The Effect of Lake Level Fluctuations on the Marginal Benthos

Hynes (1961) found that with the fall in water level of a northern temperate lake, considerable mortality occurred as a result of stranding and that little change occurred in the number of marginal animals. McLachlan (1970) found similar circumstances at the Sengwa West A cleared area on Lake Kariba. A rise in water level, however, "elicited a strong response from larval communities". Chironomus transvaalensis, particularly, increased considerably. The Sengwa West cleared area is gently sloping and alluvial in nature and was a favoured grazing area for game animals. When the area was inundated by a rising water level, the shallow marginal waters were found (McLachlan, S.M. 1970) to

be rich in nutrients and poor in oxygen as a result of the inundation, initially, of dung. McLachlan (1970) suggested that the success of Chironomus transvaalensis under these conditions was the result of the species' ability to utilise the nutrient rich habitat, despite low oxygen tensions, coupled with the atypical positive phototrophic response of the larvae of this species which ensured an ability to follow the movement of marginal waters. During a further study subsequently carried out on Lake Chilwa, a tropical endorheic saline lake, McLachlan (1969) found the same increase with lake level rise, also attributable to Chironomus transvaalensis.

Reference to Fig. 5.2 (Chapter 5) shows that the only period during the survey a rise in lake level occurred was in May to June 1967, at a mean rate of 0.5 m/month. Marked increases in the mean concentration of marginal benthos occurred at the same time (Table 7.9). However, this was due to major increases at Stations 4 and 5, within the Salvinia mat, for decreases occurred at the "bay" stations. This difference would seem to indicate that "seasonal" conditions are in this case of a secondary nature and therefore cannot by themselves be used to explain the major increases which occurred within the "estuary". These are considered to be the result mainly of the rise in lake level and associated factors, for reasons which follow.

Apart from their distances from the river mouth and mat edge, the major differences affecting the marginal fauna at Stations 4 and 5 are the degree of slope and associated factors. Station 4 is very steep and Station 5 gently sloping where marshland, similar to the bay stations 1, 2 and 3. At Station 4, the July increase was due to thirteen different species, notably Allonais sp. 12, Dero sp. 102 and Criocotopus scotti. At 5, however, only three species were

TABLE 7.9 SEASONAL [illegible]ATION IN MARGINAL POPUL[illegible]TIONS (numbers/m^2)

STATIONS	1	2	3	4	5	MEAN
January 1967	360	400	20	420	280	298
April 1967	201	720	128	167	125	268
July 1967	6	216	90	1666	1266	649
October 1967	75	375	66	155	25	119
January 1968	2	84	540	250	119	213

collected, Chironomus transvaalensis and C. formisimilis constituting 80% by numbers of a considerable population. As Brundin (1957) has pointed out, the Orthocladiinae (which include Cricotopus) do not have an effective erythrocruorin system and are unable to withstand low dissolved oxygen tensions. On the other hand the large Chironomus larvae are both physiologically and, possibly, morphologically adapted to withstand low oxygen tensions, having erythrocruorin and elongated abdominal gills. Conditions at Stations 4 and 5 on the basis of the above, would therefore seem to have been markedly different. The cause of these differences would appear to be the result of the shoreline slope. Mitchell (1970) reports on a phenomenon frequently noted against the shoreline of a Salvinia mat following a rise in water level, namely that a gap is formed between the mat and shoreline which is later colonised by a rapid growth of Salvinia. At Station 4, however, due to (1) the steepness of the shoreline and the volume of water in contact with a sparse deposition of Salvinia debris; (2) high oxygen tensions resulting from effective surface interchange, and (3) a short clearance to the margin resulting from the steepness of the shoreline, colonisation by many species was allowed which either required readily available oxygen (Cricotopus, Caenis sp.), were negatively phototropic or were weak migrators. The flat shore at Station 5 was observed prior to May 1967, to have a deep compact cover (ca 20 - 30 cm) of stranded Salvinia left by the high 1966 water level which had appreciably decomposed in its deeper layers prior to the May/July inundation. With flooding, therefore, the margin of the water moved comparatively rapidly and although subject to effective surface interchange of gases, the oxygen tensions following organic decomposition were probably extremely low. As they were, in fact, at Sengwa

(McLachlan, S.M. 1970) under conditions allowing free surface interchange. Both population increases would seem, therefore, to have resulted from a rise in water level. On the one hand, however, the short migratory distance and seeming availability of oxygen allowed colonisation by many species and on the other the comparatively long migratory distance, high nutrient level and low oxygen concentration provided an apparently ideal habitat for Chironomus. Why then, the decrease in fauna at the stations in the bay, where the slope is similar to that at Station 5? The only conclusion that can be drawn a this difference, is that the nutrient level at these stations was considerably lower and that Chironomus requires, particularly, a high nutrient level, as was supplied in this case by the stranded Salvinia. On this premise the limitation imposed by a rapidly extending margin not experienced at Station 4 was the [illegible] use of the low marginal population [illegible] the bay.

It would therefore seem that the implication of McLachlan's work, that a rise in water level [illegible] an increase in marginal fauna in widely separated lake types due to colonisation by Chironomus transvaalensis, cannot be applied generally. On the basis of these results the rise in water level should be accompanied by both a rapid movement of the margin and a high nutrient level to allow successful colonisation by this species. The implications of the absence of this species at Station 4 are either that the nutrient level was not sufficiently high, or that C. transvaalensis and C. formosipennis are particularly susceptible to competition.

Other factors could obviously be involved in these interesting faunal differences so that further work on the effects of a rising lake level on different substrates and slopes and at different nutrient

levels are clearly necessary and are likely to yield valuable information.

4.3 The Effect of Substrate on the Benthic Standing Crop of the Drowned River Bed

On the basis of substrate analysis, the drowned river bed has been zoned into three areas: Area A (the bay zone), from Station 1 to 250 m inside Station 3 (3a); Area B (the outer transitional zone), to Jacana Bend (3c); Area C (the inner transitional zone), to the river mouth (Fig. 7.1). Zonation on the basis of standing crop (Fig. 7.6) places the outer, productive, zone from Station 1 to a point somewhere between 2b and 3; the outer transitional zone from this point to between 3a and 3b; the inner transitional zone from here to the river mouth. Factors other than substrate, analysed in the way they have been here, would therefore appear to be of greater importance to the standing crop.

4.4 The Effect of Depth and Associated Factors on the Benthos.

Consideration of the spatial differences in composition of the benthos (3.2.1.1) led to the tentative conclusion that with increased depth or progression towards the drowned river bed, constituents of the benthos of proportional significance became fewer and more dominating. The reason suggested for this was that under suitable conditions certain well-adapted taxa competitively excluded less well-adapted taxa. Against this suggestion, however, was the fact that along the shoreline where the chironomids were clearly in overall dominance, the greatest diversity of species was found. This seemed to have ruled competitive exclusion out and suggested rather that abiotic factors were primarily responsible. Subsequently it has been shown that one of the reasons for the overall dominance of chironomid larvae along the shoreline

were the very dense concentrations of Chironomus associated with a rise in water level. This suggests that competitive exclusion may still have been a significant factor in the decrease of faunal variety with depth.

Consideration of the spatial differences of the numerically important species (3.2.1.4) also indicated a negative correlation between numbers of species and increasing depth. The tentative conclusion drawn from these data was that there was either a decrease in habitat complexity from the shoreline to the drowned river bed or that lacustrine niches had not yet been filled at the time of sampling.

There would seem to be little doubt, therefore, that the variety of animals decreased with depth and that numbers increased; (see 3.2.1.2/4) a situation analagous to marine fishes in the Tropics (= shoreline) and Temperate (= river bed) regions. However, any attempt to explain this phenomenon without further study is open to criticism. Nevertheless, factors which must have a considerable bearing include nutrient levels, light, substrate and a degree of competition from established deep water species. The suggestion that all deep water niches had not yet been filled, which stems from the comparative youth of Lake Kariba, is more questionable, bearing in mind, particularly, the comparative simplicity of the drowned river bed as a habitat; the similarity of the fauna to profundal benthos of long-established lakes, described by Odum (1969) as having little variety; and the relatively high production of the deeper waters.

4.5 Distribution of the Benthos in Relation to Water Quality

Underflow resulting from flooding of the river did not at any time coincide with sampling of the benthos of the drowned river bed (Table 7.10). The scouring and displacement effect of these, which

are likely to have been both selective and considerable, are therefore unknown.

TABLE 7.10 BENTHIC SAMPLING PERIODS IN RELATION TO FLOW (m^3/s)

SAMPLING DATE	FLOODING DATE	VOLUME OF FLOOD	COMMENT
	10.12.66	20	45-50 days prior to sampling
25.1 - 5.2.67	8.1.67	25	17-25 days prior to sampling
10.4 - 22.4.67	2.5.67	61	Sampling before flood
7.1 - 20.1.68	25.1.68	15	Sampling before flood
	8.2.68	6	Sampling before flood

The distribution of the benthos cannot be related to water quality by itself unless radical changes in water quality can be associated with major changes in either the quantity or quality of the fauna. Water quality has been seen (Chapter 5, 2.0.5) to have shown a gradual trend of change from the edge of the Salvinia mat to the open bay stations and little seasonal change apart from flooding periods and increased phosphates and pH fluctuations during November 1967. These differences could be associated with the faunal differences but are insufficient in themselves to have been of overriding importance. The effects of enclosure and the Salvinia mat on water quality have also been discussed (Chapter 5, 2.0.6/7) and there can be little doubt that these two factors could have of their effect on the benthos in this indirect manner. Nevertheless, it is not possible to draw even vague conclusions regarding the effect of water chemistry on the benthos, apart from those considered above, relating to Salvinia and lake

level fluctuations.

4.6 The Categorisation of the Benthos

Consideration of the spatial distribution of all species of benthos (3.2.1.5) suggests that certain species may be regarded as typical of certain habitats. On these data marginal species would include libellulid sp. 167, Nilodorum brevibucca, Allonais sp. 127, Nemertodrilus sp. 29, Aulophorus furcatus, Chironomus transvaalensis and C. formosipennis. Shallow water species of coarser sediments include Stictochironomus caffrarius, Pentapedilum wittei and Caenis sp. 90. Deep water species of finer, more uniform sediments include Dero sp. 29, Eumera ferruginea, Aulodrilus nigueti, Chaoborus spp., Polypedilum sp. 5, Cryptochironomus sp. 7, Cryptochironomus neonilicola and Branchiodrilus hortensis. Although any study of the lake as a whole would be inclined to categorise all species found in this study to be of the area associated with river mouths, species closely associated, or "estuarine" species for the purposes of this study, include Cryptochironomus lindneri, Lestinogomphus africanus, Clinotanypus claripennis, C. maculatus and "Probezzia" sp. 72. Ubiquitous species include Pseudocleon gaerensis, Procladius brevistriolatus, Tanytarsus balteatus and "Culicoides" sp. 61.

4.7 Faunal Stability

Any study of a developing ecosystem such as Lake Kariba must of necessity consider indicators of change in a dynamically unstable situation. A study monitoring these changes should ideally be carried out over a longer period than it was possible to use here. Nevertheless, major faunal developments of species occurring in large numbers during the two year transect could be indicative of development. Whether there were true long term changes or not will only be seen

clearly with further studies. Temporal frequency data of some species are figured (Fig. 7.8). With the above reservation, Branchiodrilus hortensis and Chaoborus spp. show a decrease during the course of the survey which could indicate a "phasing out" of these species. Aulodrilus pigueti could also be included, but this is most unlikely in the light of the violence of population change which occurred over a short period. Dipseudopsis capensis, Polypedilum sp. 5, Cryptochironomus sp. 7, Procladius brevipeticlatus and Branchiura sowerbyi would seem to show a "phasing in". Clinotanypus nemulatus, which is not figured, showed an essentially stable population during the course of the survey, as did the narrow-headed "Culicoides" sp. 61. The broad-headed Culicoides sp. 19, on the other hand, became more numerous towards the latter part of the survey.

It is necessary to seek confirmation of these impressions by comparison with McLachlan's (1969) findings from 1963 to 1966. All the above species were found by McLachlan associated with bottom muds. Aulodrilus pigueti, Branchiodrilus hortensis and Chaoborus were marked as being present (as opposed to abundant) during McLachlan's work, so that there is some indication of an increase of these species until 1969. Dipseudopsis capensis, Cryptochironomus sp. 7 (= McLachlan sp. 15) and Branchiura sowerbyi are also marked as being only present, so that the probability of their "phasing in" is greater. McLachlan found Procladius in some density in the estuarine mud, however, so that although there is a possibility of this species having increased, this is uncertain. Polypedilum sp. 5, which in these data is shown as "phasing in", has been an important component of the fauna of deep water bottom muds for some time, so much so, that McLachlan (1969) following Brundin (1958) has classified Kariba as being a "Polypedilum

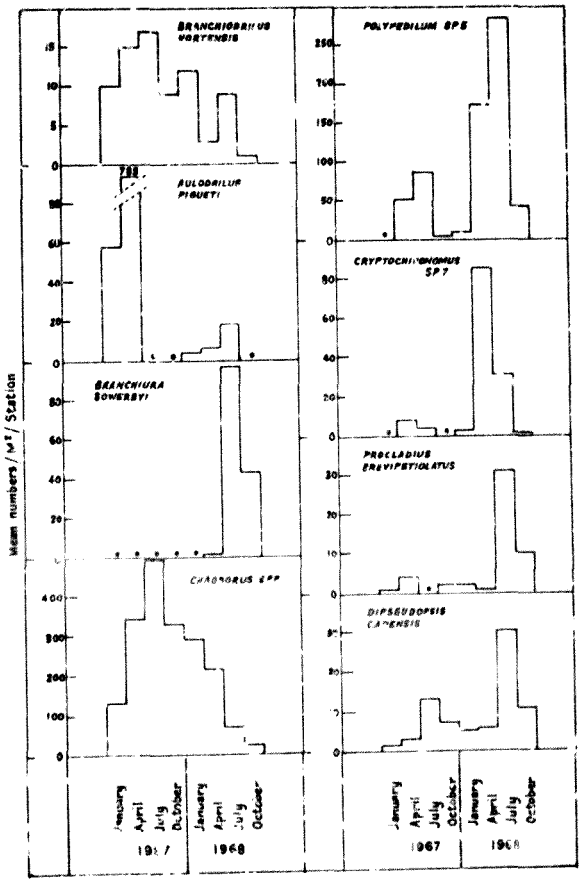


Fig. 7.8 TEMPORAL CHANGES IN ABUNDANCE OF SOME IMPORTANT FAUNAS OF THE BROXNED RIVER BED

* NO ANIMALS FOUND

lake" on the basis of the frequency of occurrence of his Polypedilum sp. 10(1) which is the same species as is being considered here (sp. 5). It is therefore unlikely to be "phasing in", although on these data, colonisation of the "estuarine" habitat took place in 1966. Clinotanypus maculatus held much the same position in 1967 and 1968 as previously, as did the ceratopogonid "Culicoides" sp. 61. Taxonomic difficulties mitigate against earlier comparisons of "Culicoides" sp. 19. These data are presented for comparison by subsequent workers, for confirmation of trends is necessary from later sampling.

The increasing numbers of Branchiura sowerbyi and, possibly, Procladius brevistylatus suggest an enrichment of the bottom muds in the drowned river bed, as these two species are typical of the eutrophic Lake McIlwaine (Marshall, 1971). This enrichment could be either a function of detritic accumulation in the "estuary" with time, or the result of the break-up of the permanent Salvinia mat.

4.8 Chaoborus in Relation to Zooplankton Density

TABLE 7.11 A COMPARISON OF THE DENSITY OF CHAOBORUS IN THE BENTHOS AND PLANKTON CONCENTRATIONS

PERIOD	CHAOBORUS CONCENTRATION	PLANKTON CONCENTRATION
January 1967	Station 3	Very low, highest in vicinity of Station 3
July 1967	Stations 1a to 2b	Density centre at Stations 2 and 4
October 1967	Stations 2a to 3	Density centre at Station 4, bottom, reasonable concentration at 2 and 3
January 1968	Stations 2a to 2b	Station 2 to 3, Station 5

The May findings have been omitted as benthic sampling took place before flooding; planktonic, after.

Chaoborus is widely known to be planktonic by night and benthic by day (Otum, 1960). As both planktonic and benthic sampling was carried out by day it follows that Chaoborus spp. were collected mainly in the benthic samples. Consideration of coincidental samples, from January 1967 to January 1968, (Fig. 7.0, 6.2) shows a similarity in seasonal fluctuation of plankton and Chaoborus. There is also some spatial correlation between density of Chaoborus on the transect and plankton density centres, particularly in July 1967 and January 1968 (Table 7.11). High numbers of Chaoborus were never found, however, in association with plankton density centres underneath the Salvinia mat. Being dark, it would be expected that Chaoborus would have remained planktonic underneath the Salvinia mat which could explain their paucity in benthic samples, but they were not collected with plankton here, and must, therefore, have been in low numbers underneath the Salvinia mat.

4.9 Standing Crop

The conversion values given in Table 7.3 have been used to assess the mean standing crop of the study area, using the numerical data from the seasonal survey. These are given in Table 7.12.

TABLE 7.12 THE MEAN STANDING CROP IN MG WET WT/M^2 OF THE SEASONAL SURVEY 1967/68

SITE	BIOMASS
Shoreline (0 metres)	4225
5 metres	1005
10 metres	909
Drowned river bed (3 - 22 metres)	1065
Overall	1304

Clearly the most productive zone, as biomass, is the shoreline, though this is mainly due to the very large Nemertodrilus sp. 28 which was commonly found in association with Salvinia at Stations 4 and 5. Without this species, the mean biomass of the margins was found to be 1143 mg/m^3, which is similar to the findings on the river bed and at 5 and 10 metre depth stations.

Unfortunately McLachlan's (1969) values are expressed as cuticle-free dry weight and are not comparable with these estimations. Petr's (1969) estimates of bottom fauna standing crop of Volta Lake in water shallower than 10 m are similar to the 1504 mg/m^2 estimated from the results of this work. At Kete Krachi, annual estimates of approximately 1700 to 3000 mg/m^2 were found, at Yeji 2090 to 2570, at Kpandu 770 to 1700 and at Dodi, near the dam wall, 650 to 710 mg/m^2. Petr (1969) found, however, that the bottom fauna was largely confined to waters shallower than 10 m, and between the year 1966 and 1968, a marked decrease in standing crop occurred as the lake matured.

By comparison the standing crop estimates made at the eutrophic Lake McIlwaine in 1968 are considerably higher. Marshall (1971) estimated the following standing crop for the different depth zones:

0 – 5 m	:	6.011 g/m^2
5 – 10 m	:	15.212 g/m^2
10 – 20 m	:	2.607 g/m^2

4.10 The Bottom Fauna Food Web

Literature on the feeding habits of the larvae of, particularly, African aquatic insects is sparse. In order to attempt clarification of the feeding habits of the important constituents of the bottom fauna so that a significant food web could be constructed, the mouth-parts of those genera upon which direct feeding observations have not

been made have been studied.

It is known that the larval Chironomini are feeders of particulate organic matter (Wirth and Stone, 1956), in some cases collected by the use of salivary webs spun across the mouth of the larval tube, irrigated by a current set up through the tube by the body movements of these animals and periodically eaten. Larval Tanytarsini are also known to use salivary webs to catch food particles; in some species, webs are spun on special extensions of the larval tube. This has been found both in America and Africa (Wirth and Stone, 1956; Scott, 1967). On the other hand the Tanypodinae are known generally to be predatory (Wirth and Stone, 1956; Pennak, 1953). The "herbivorous", species (here usage implies animals eating both living and dead particulate organic matter) are essentially sedentary; the predatory species, errant.

In the larval chironomids of the Mweola River mouth, a clear gradation in the following characteristics of the mouth parts may be seen (Fig. 7.9):

1. A simplification of the grinding molar type mandibles of the "herbivores" with several teeth, to the simple, lengthened spear-like mandible of the predators.
2. An increased curvature of the predatory mandible culminating in the acutely hooked mandible of Clinotanypus. These two series are considered the most important indicators of the type of feeding.
3. The separation of the labial plate by a non-toothed central lobe and reduction in tooth complexity.
4. The absence of presence of the lingua, found only in the Tanypodinae.

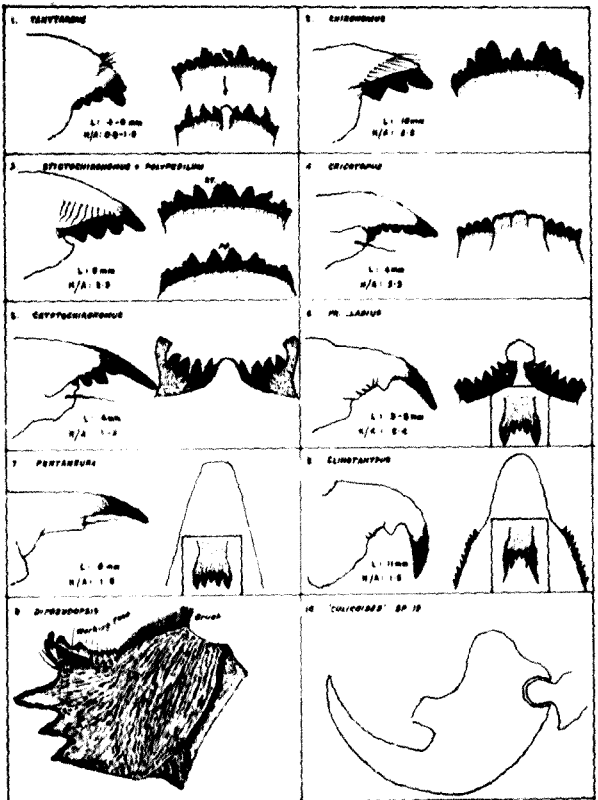


Fig. 7.9 THE GRADATION OF MANDIBLE, LABIAL PLATE AND LIMBUS IN THE LARVAE OF THE MAIN CHIRONOMID GENERA OF THE NIGERIAN RIVER MOUTH (1-8)
MANDIBLE OF THE LARVAE OF DIPLOCLADIUS CAPENSIS AND 'CULICOIDES' SP.19 (9 AND 10)
L: APPROXIMATE LENGTH OF FULLY MOULTED LARVA. H/A: RATIO OF HEAD/ANTENNAL LENGTH

An attempt has been made to correlate both size and antennal length (as head/antennal length ratio) with the above characteristics, but a clear gradation was not found. Apart from Chironomus, the "herbivorous" end of the series are smaller. H/A ratios were confused by the gradation of characteristics within the Tanytarsinii (Fig. 7.9.1) where both short and extremely long antennae were found, the former being indicative of a sedentary, herbivorous, role; the latter of an errant, predatory one. It is of interest to note that although mandibles retain "herbivorous" characteristics throughout the Tanytarsinii series, the labial plate shows a tendency towards predatory characteristics, in that some species show a separation of the labial teeth by the non-toothed central lobe. Thus on balance the Tanytarsinii are considered herbivores, but there is some likelihood that some of them may be predatory. The herbivorous Chironomini all have short antennae and a clear gradation can be seen in the Tanypodinae where both antennae and head capsules lengthen in close correlation with the predatory characteristics of the mandible and labial plate (Fig. 7.9, 6 - 9).

On the basis of the mouthparts, some of which are figured (Fig. 7.9), the series, starting with the most herbivorous and ending with the most predatory, is as follows: Chironomus, Tanytarsus, Polypedilum, Stictochironomus, Cricotopus, Cryptochironomus, Procladius, Ablabesmyia and Clinotanypus. As far as Stictochironomus, in the series, mouthparts are clearly of a "herbivorous" nature. It is probable also, judging by some of the dense associations of Cricotopus ($330/m^2$) which were found which are uncharacteristic of predatory animals, that Cricotopus is also herbivorous. Cryptochironomus is more difficult to classify on the basis of mouthparts, but as these were found in

even denser associations than Criocorus (502/m^2) it is probable that these are also herbivores. Procladius is far more likely to be predatory on the basis of its mandibles and Ablabesmyia and Clinotanypus are almost certainly predatory. It cannot be concluded, however, that these last three genera are entirely predatory. There are some indications that Procladius could be an omnivore (quite dense concentrations (156/m^2), short antennae, herbivorous-like labial plate, small size) and the likelihood of imbibition by Ablabesmyia and Clinotanypus of particulate organic matter cannot be ruled out. Their errant nature (observed in aquaria), the clearly developed mouthparts, comparatively sparse concentration and long antennae suggest that these two are, however, essentially predatory. In the analysis of the food web the latter three genera have been considered to be predators.

The Oligochaeta and Mollusca are all considered "herbivorous", and the mouthparts of the trichopteran Dipseudopsis (Fig. 7.9.9) with the mandibular brush and setae, coupled with their tube dwelling habit, suggest strongly that they are also herbivorous. This has been confirmed as far as practically possible by the examination of gut contents. Chaoborus is an observed predator, particularly of zooplankters (Chapter 6), and has itself been observed to be predated upon by the ceratopogonid "Culicoides", (Fig. 7.9.10) which seems to have paralysing salivary properties (Mitchell, S., pers. comm.).

Two further species must be considered, although they were of little importance in benthic samples. These are the large anisopteran nymphs of Macromia which are errant, and the cryptic Ictinogomphus nymphs, both of which occurred with such frequency in the gut contents of fishes, the mormyrids in particular, that they must have played a significant role in the feeding web of the bottom fauna. Both are predatory

and previous experience has shown that the only way to capture the nymphs of these species in any numbers is by employing a fast-moving dredge, a method not used in this survey of the bottom fauna.

On the basis of the above categorisation of the feeding habits of the bottom fauna, the food webs of the seasonal survey and the river bed transect series have been illustrated (Figs. 7.10, 7.11) showing the relative proportions by numbers of the components. Two points become clear on consideration of the food webs. The first is the considerable contribution made by zooplankton, particularly to the benthic secondary consumers through Chaoborus and to the bottom fauna numbers as a whole. The second is the seeming lack of utilisation of a considerable proportion of the primary consumers in higher trophic levels. This point will be reconsidered when the feeding of fishes is dealt with in a later chapter. The relative proportions of the constituents have already been considered (Sections 3.2.2.1, 3.2.2.2).

5. CONCLUSIONS

The conclusions which may be derived from these data, bearing in mind the reservations imposed by the frequency of sampling, are summarised below.

1. Oligochaeta, Chaoborinae and Chironomidae dominated the fauna of the bottom muds in varying proportions according to depth and substrate, constituting 89% by numbers of animals collected in the seasonal survey and 95% of the river bed population.
2. The most productive area, numerically, was the river bed away from the Salvinia mat. Considerable decrease in bottom fauna occurred under the Salvinia mat, where the drowned river bed was least productive. Margins, when considered numerically, were next most productive, particularly in association with the Salvinia mat.

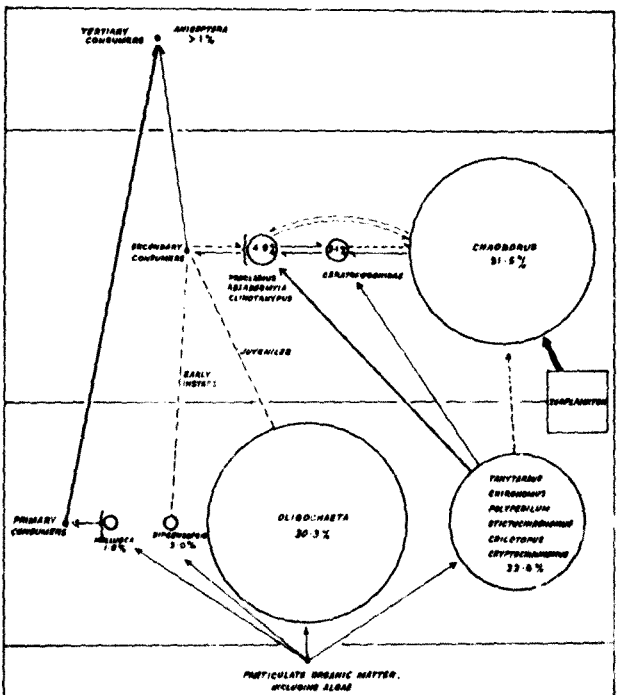


Fig. 7.10 FOOD WEB OF THE BOTTOM FAUNA FROM ALL DEPTHS SHOWING RELATIVE ABUNDANCE BY NUMBERS OF CONSTITUENTS, FISH EXCLUDED JAN 1967 - JAN 1968

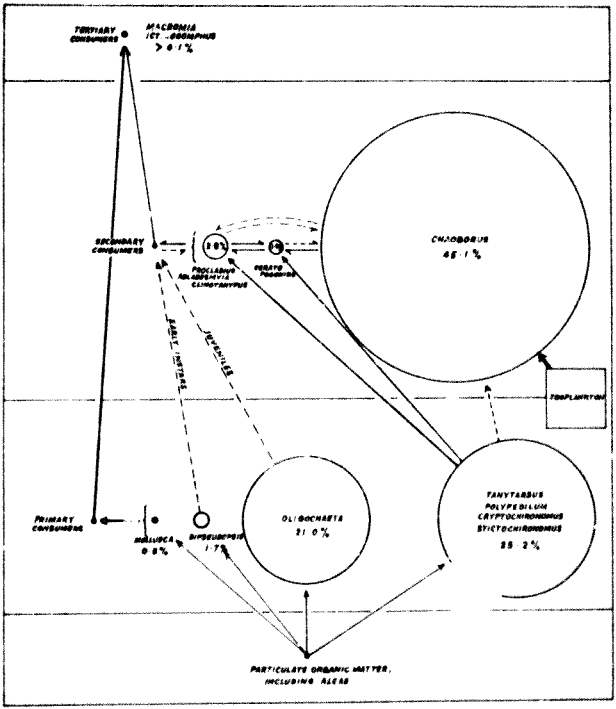


Fig 7.11 FOOD WEB OF THE BOTTOM FAUNA OF THE RIVER OED SHOWING THE RELATIVE ABUNDANCE BY NUMBERS OF CONSTITUENTS, FISH EXCLUDED. JAN 1967 - NOVEMBER 1968

10 metre depths were next most productive numerically and 5 m depths were least productive. Considered as biomass, the margins were clearly the most productive, particularly when associated with Salvinia, mostly as a result of the presence of the large oligochaete Lamprodrilus. There was little difference in mean standing crop at 5 metres, 10 metres and the drowned river bed.

3. The bottom fauna was most numerous during winter months.

4. The area consistently most productive on the drowned river bed occurred between Stations 2 and 3, some 2 Km. from the point of entry of the river.

5. The only clear-cut replicable seasonal change which occurred on the drowned river bed was the increase in numbers of bottom fauna at the outermost stations in May of each year, due to the presence of Aulodrilus pigueti and Polycelilum sp. 5 in 1967 and to Polypedilum sp. 5 in 1968.

6. The restrictive effect Salvinia was found to have on bottom fauna possibly results from a combination of the following factors:

   a. Substrate unsuitability

   b. Low oxygen tensions

   c. Oviposition by adult insects being impaired by the false surface of the mat.

7. The larvae of Chironomus are known to actively colonise lake margins in association with a rise in water level. The implication of the occurrence and absence of Chironomus larvae under these conditions in this study, indicate that for successful colonisation a rapid marginal movement (hence gently sloping shoreline) coupled with high nutrient levels are necessary.

8. Different substrates, as analysed in this study, showed no cor-

relation with benthic productica. It is considered that substrates require more careful analysis than those traditionally used, for requirements of benthic animals are probably far more subtle than these methods show.

9. Variety of animals and depth were negatively correlated. For several reasons it is considered that this was not primarily due to a lack of suitable species resulting from the comparative youth of Lake Kariba.

10. No correlation could be made between water quality and benthic productivity.

11. Some benthic animals have been tentatively categorised into marginal species, shallow water/coarse sediment species, deep water/fine sediment species and "estuarine" species.

12. An attempt has been made, by analysis for trends of increase, stability or decrease of the more numerous species of the river bed over the two-year sampling period, to ascertain whether any species could be either colonising, stable or decolonising. Comparison with McLachlan's (1969) findings suggests that some species fall into these categories, but confirmation is necessary from later sampling.

13. An apparent increase which occurred in the populations of Branchiura sowerbyi and Procladius brevipeticlatus which are tropical eutrophic indicators, suggests an increasing detritic accumulation in the vicinity of the river mouth, due either to increasing maturation or to the disintegration of the permanent Salvinia mat.

14. The pattern of Chaoborus density in the bottom muds both seasonally and spatially (away from Salvinia) suggests the possibility of some correlation with plankton density centres.

15. The mean standing crop estimate of 1804 mg/m^2 is similar to Petr's (1969) estimates from Lake Volta, and considerably lower than those of Marshall (1971) from the eutrophic Lake Mollwaine which ranged from 2.6 to 15.2 g/m^2.

16. The relative composition of the components of the within-benthos food web indicates the importance of Chaoborus to productivity of the benthos in that its main source of food is zooplankton. A considerable proportion of the primary consumers are not readily available to higher trophic levels within the benthos. The question will be reconsidered when feeding relationships of fish are dealt with.

CHAPTER 8

THE FAUNA OF SUBSTRATES OTHER THAN BOTTOM MUDS

1. INTRODUCTION

In order to fulfil one of the main aims of the study it was necessary to subjectively determine what appeared to constitute major habitats and to sample these as adequately as cost considerations allowed; determining whenever possible seasonal variations of fauna, but, more importantly, the species composition of various habitats in terms of presence, importance and feeding relationships. The principle underlying this approach basically involved the question of availability to and utilization of the faunal components, at species level, by fish.

The major benthic habitats (substrates) chosen at the outset of the study were the bottom muds, the drowned trees and the Salvinia mat. During the course of the field work an invasion by rooted aquatic macrophytes occurred which has been described (Chapter 4) and the importance of which has been emphasised previously (Bowmaker, 1968, 1970; Donnelly, 1969). As these plants invaded the study area sampling was initiated on them. They included Potamogeton pusillus, Ceratophyllum demersum and Lagarosiphon ilicifolius.

This chapter will consider the results of sampling of all these substrates, apart from the bottom muds.

2. THE FAUNA OF THE DROWNED TREES

It was considered unlikely, prior to inundation, that the trees of Lake Kariba would readily disintegrate, due to the very hard woods of the vegetation to be flooded and the seasoning effect of submersion.

Whereas this would have seemed to have held true for totally submerged trees, exposed trees, particularly at their extremities, were observed to be in the process of disintegrating during the course of this study. Terminal material was rapidly stripped off the trees following inundation and some suggested biological effects of this have been published (Bowmaker, 1968, 1970).

2.1 Methods

Due to the difficulty of obtaining a uniform substrate to sample, the methods used were qualitative, though an effort was made to collect approximately the same quantity for each sample. Samples were collected over three seasons, during April, August and November 1967. At Stations 3 and 4 samples were taken from dead trees standing both in and clear of the Salvinia mat. Samples were collected from bark and twigs within 1 m of the water surface, except on one occasion when a branch was collected accidentally from the bottom at 10 m depth by grab in April. The twigs and bark were broken off and placed in a 40 mesh/inch bag under the water, which, when full, was washed into a container in the boat. The fauna was sorted from the collected material by eye. Animals utilising cracks or borings emerged as the material dried out. Sorting was continued until no further movement could be found in dry material. Washing in a formaldehyde irritant bath seldom elicited further emergence of animals. An attempt was made to obtain more quantitative results by the use of standard wooden blocks. Sets of five were suspended on buoyed chains at five metre depth intervals at all stations. The blocks were constructed of two 1 cm thick meranti planks, 15 cm x 10 cm, screwed together and drilled with three 5 mm holes at their interphase, so that on being unscrewed fauna utilizing the holes could be collected. The use of styrofoam buoys was

ruled out in the Mwanda area due to their rapid destruction by crocodiles. Cost considerations dictated the use of metal cans. These buoys were unsuitable (some had been used as targets, others disintegrated) and all the wooden blocks and chains were eventually lost. This part of the project was abandoned and the results obtained too scattered and discontinuous to be of value. No attempt was made to relate numbers of animals to the species of dead tree sampled, due to recognition problems, though both the species of tree and state of disintegration could have a considerable effect on results. Sampling carried out in December 1972, strongly indicated on subjective assessment a major increase in the tree fauna; the surface material of the trees was found to be honeycombed with Povilla borings, offering a greatly improved substrate for these animals particularly. Over 700 specimens were collected from the drowned trees.

2.2 Results

Full results are appended (App. 8.1). Thirty-five species were collected from the drowned trees and six of these constituted 85% of the total number collected, the wood-boring nymph of the mayfly Povilla adusta contributing 63% by itself. Other important species were the larvae of the caddis Economus thomasoti (7.3% of total animals collected), nymphs of the mayfly Euthraulus sp. 53 (6.9%), the ceratopogonid pupa sp. 356 (3.5%), the larvae of Chironomus (Niloiorum) sp. 358 (2.9%), and Dicrotendipes fusconotatus (2.5%). Oligochaeta, Crustacea, Odonata and Mollusca were infrequently found and only in small numbers. No single station appeared to be more productive than any other, on the basis of the rough method used.

Of the important species, Povilla and Niloiorum occurred in all "seasons" sampled, whereas Euthraulus was not collected in April,

though it occurred in large numbers in August and with less frequency in November. *Dicrotendipes* larvae were not collected in August.

TABLE 8.1 A COMPARISON OF THE FAUNA OF CLOSELY ASSOCIATED DROWNED TREES WITHIN AND AWAY FROM THE SALVINIA MAT

	APRIL		AUGUST		NOVEMBER		TOTAL	
SPECIES	IN	AWAY	IN	AWAY	IN	AWAY	IN	AWAY
Pyrilla adusta	58	0	69	5	107	11	234	16
Economus thomasetti	6	0	3	0	5	0	14	0
Euthraulus sp. 55	1	0	1	6	0	0	2	6
Nilodorum sp. 358	5	0	0	0	5	0	10	0
Dicrotendipes fuscomotatus	0	6	0	0	2	2	2	8

Table 8.1 indicates that *Salvinia* probably exerts a considerable effect on the fauna of the drowned trees, particularly in the case of *Pyrilla adusta*, where very large numbers were found on the trees in association with *Salvinia* as opposed to the relatively sparse population on trees, never more than 10 m distance away, which were clear of the mat. Although the method used was only roughly quantitative, the considerable and consistent difference was probably significant. There was also a possibility that numbers of *Nilodorum* sp. 358 and *Economus thomasetti* also showed an increase in association with the mat.

2.8 *Discussion*

The drowned trees appear to be extremely important to secondary productivity in Lake Kariba. Although no adequate sampling of periphytic development on the drowned trees was undertaken, this was observed to be considerable, particularly in close association with the surface and seemingly more abundant in areas closer to the river mouth. Not only did the drowned trees provide a relatively stable substrate suitable for periphytic development in the photic zone, but increased the area

for this development very considerably. In terms of overall productivity this increase in periphytic development would have to be balanced against a decrease in phytoplanktonic production. Nevertheless, the considerable differences in the specific makeup of the fauna typical of drowned trees from other habitats, particularly in the instance of Povilla adusta, which if this habitat had not been available would have been sparse if at all present, suggests that by increasing habitat and therefore species diversity in the lake, the drowned tree substrate can only increase overall productivity. This would be particularly applicable to fisheries productivity if the fish species present were predominantly insectivorous rather than planktivores. Being of lotic origin the majority of the fishes would logically be of the former rather than the latter category. Under the circumstances present in the study area at the time of this study therefore, it is considered that the drowned trees, as a substrate for periphytic development and by increasing habitat and therefore species diversity, increased secondary production. On consideration of the enormous substrate area involved, the role of the drowned trees in the whole lake must have been considerable. The subject will be reconsidered after presentation of fish feeding data (Chapter 11).

The increase in numbers of Povilla in association with Salvinia would seem to have been related to development of early instars. In trees associated with Salvinia, nymphs were generally smaller than found in trees away from the mat. The implication of these findings was that Salvinia formed a suitable substrate for the development of early instars, hence increasing the population on trees associated with Salvinia.

Petr (1971) considers that the present fisheries productivity of the Volta Lake is largely dependent upon the explosion of the Povilla

adults population associated with the drowned trees. This situation has not been reported on Lake Kariba, which could be related to differences in the type of woodland inundated. The softer forest woods of the Lake Volta area provide a more suitable substrate for the wood-boring nymphs than the hard, predominantly Colophospermum woodlands inundated by Lake Kariba. Indeed, McLachlan (1968) reports that a significant increase in the Povilla population of Lake Kariba only took place after drawdown and attack on the dead trees below high water level by terrestrial beetles.

The importance of inundated trees in terms of resource management will be considered in a later chapter.

3. THE FAUNA OF THE SALVINIA MAT

One of the main aims of this study was to ascertain the effects of Salvinia on both biotic and abiotic components of the "estuarine" area. It has been shown that a quite considerable negative effect is exerted on the fauna of the bottom muds by the mat. It followed that an assessment of the fauna actually living within the mat was necessary. This investigation did not, however, consider the essentially terrestrial fauna living above the water surface, even though, potentially, this component could have interacted with the aquatic fauna and had considerable effect on it. Obvious terrestrial components included large numbers of spiders and the Jacana (Actophilornis africanus) the latter frequently having been observed to turn over Salvinia leaves and take off aquatic animals from the undersurface.

3.1 Methods

Initial sampling was entirely qualitative and has been reported on (Bowmaker, 1968). Quantitative sampling was initiated in April,

1967. At this time it was hoped that the fauna of the Salvinia mat would be investigated separately in depth and concurrently by another worker who started his investigation at this time, so that emphasis was placed on other aspects of this study. Unfortunately the separate study of Salvinia fauna was discontinued, but has been reported (Alp, 1968).

Initially, quantitative sampling was undertaken using a .125 m^3 open-ended box, designed for the purpose and made from aluminium, taking a sample 0.25 m^2 in area. The box was plunged into the Salvinia to a depth of 0.5 m and a 20 mesh/inch framed gauze bottom slid into place on slots. The whole box was then lifted from the water and the entrapped vegetation washed to remove the fauna which was then sorted from the debris, while alive, against a white background. The Salvinia was then thoroughly squeezed by hand to remove excess moisture and weighed. The samples were found to be so considerable that time mitigated against replication. This method was used again in July 1967, but thereafter, when it was clear that the separate Salvinia study was not to continue, a different method allowing replication (usually 3 - see Table 8.2) was started. This method involved scooping a sample of Salvinia out of the water using a dish of 80 cm diameter and 20 cm deep. The dish was pushed sideways under the mat and brought to the surface in as abrupt a movement as possible. After the vegetation sample had been washed to remove the fauna (see below), the hand-squeezed Salvinia was weighed. At the time of taking samples, the Salvinia box was used to take three samples of weed which were similarly treated, to remove excess moisture, and weighed, giving an estimate of Salvinia density at the sampling site. Thus the faunal density could be related either to surface area of mat or to live weight of weed less excess water, allow-

TABLE 6.2 THE SIZE, DISTRIBUTION AND FREQUENCY OF SAMPLING OF THE *SALVINIA* MAT

	BAY				INTERMEDIATE						PERMANENT MAT						
STATION	1		2		3		3/4	4		4a	+10m	+50m	5		6		SAMPLE AREA (m^2)
DATE	EM	S	EM	S	EM	S	C	EM	S	EM	C	C	EM	C	C		
April 1967	-	-	-	-	-	2	2	-	1	-	-	-	-	2	-		0.25
July 1967	-	-	-	-	1	2	-	-	3	-	-	-	-	3	-		0.25
November 1967	-	-	2	3	2	3	-	3	3	3	3	3	3	3	3		0.125
Jan/Feb 1968	3	3	3	-	3	3	-	3	3	3	3	3	-	3	-		0.125

EM: Open water edge of *Salvinia*
S: Shoreline edge of *Salvinia*
C: Centre of *Salvinia* mat
EM: Edge of permanent mat
6: Above Kihov Rapid when backflooded

ing the opportunity for comparison with either bottom muds or productivity (in terms of fauna/unit live plant weight) of other aquatic macrophytes.

Prior to squeezing the Salvinia for weighing, individual plants were agitated vigorously in three separate water baths before being passed through graded meshes of 20, 40 and 60 meshes/inch; thereafter being sorted separately, alive against a white background. The method was tested by washing five times, the last time in a 1% formaldehyde solution, and found to extract 89% of the fauna by numbers, error resulting from retention mainly of Ceratopogonidae and Hirudinea (Fig. 8.1). Samples usually produced approximately 150 individuals, the more abundant species occurring in markedly similar numbers in replicates, whereas rarer species showed little consistency between replicates. Sample size and extraction technique was considered satisfactory in terms of the requirements of the study. The sorting of animals was greatly facilitated by their movement and the use of a flat triangular net designed for the purpose and used when hand sorting became difficult. This sorting net, used in all vegetation samples, had a 10 cm base and 12 cm height, the apex being attached to a handle, across which was stretched 60/mesh/inch netting. By scooping through a sample, agile animals and debris could be extracted and removed. After careful scrutiny for movement of faunal components the debris was discarded. Thus a sample was satisfactorily cleaned of all debris and animals.

The use of the Salvinia bar to ascertain weed density and the hand squeezing method gave results of surprising consistency for any given part of the weed mat. Standard errors for three replicates ranged between 0.4 and 14.6% (Table 8.3) but were frequently found to be within 10% fiducial limits, suggesting a reasonably good method for the

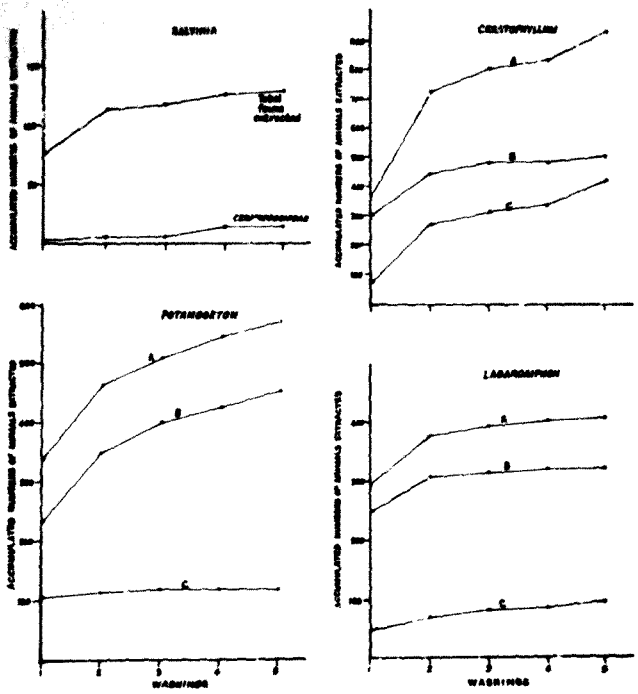


Fig. 8.1 Test washings for faunal extraction from different vegetation substrates

A: Total numbers of animals extracted
B: Numbers extracted less Chironomidae
C: Chironomidae extracted

TABLE 8.5 THE COMPACTION OF SALVINIA AT SAMPLING SITES AS G LIVE WEIGHT/M^2 (excess water removed by hand squeezing)

STATION	NOVEMBER 1967		FEBRUARY 1968	
	$\bar{x}$(g/m^2)	$\frac{s}{\bar{x}}$%	$\bar{x}$(g/m^2)	$\frac{s}{\bar{x}}$%
1 S	5452	4.79	10,880	4.24
1 EW	5432	-	2,888	7.90
2 S	-	-	-	-
2 EW	-	-	2,702	5.75
3 S	3500	0.99	8,068	0.41
3 EW	0700	-	3,368	4.91
4 S	2480	-	7,928	5.89
4 EW	8440	-	4,932	14.64
4m EW	4040	12.00	3,988	4.86
4m + 10 m	14,452	5.38	15,300	7.01
4m + 30 m	12,188	5.50	15,300	9.55
5	18,700	1.19	13,408	6.97

estimate of Salvinia compaction.

Sampling points varied during the course of the study, but until it was known that the separate study of the Salvinia fauna was no longer to be carried out, coverage was minimal. Thereafter, however, replicated sampling was undertaken at a greatly increased number of stations. Sampling was usually undertaken at at least one of the bay stations (1 or 2), being taken from the margin of the mat and against the shoreline; at Stations 3 and 4, also at the margin and shoreline; at the edge of the permanent mat (4m), 10 m and 50 m inside the mat edge; at Station 5 at the margin and shoreline and, when backflooding permitted, above the Elbow. Details of sampling sites, sample size and replication are tabulated in Table 8.2.

After separation of animals from the vegetation, samples were preserved in 4% formalin and sorted to code species level in Salisbury. After this second sorting and drawing by camera lucida, animals were allocated code numbers and added to the reference collection.

Data collected in April and July 1967, are therefore limited and suspect; in November 1967 and January 1968, coverage and replication was such as to give reasonably reliable information.

8.2 Results

Full results of faunal analysis are appended (App. 8.2 - 8.5) and, in keeping with other chapters, data have been extracted and tabled where relevant within the text.

8.2.1 Salvinia Compaction

Results of the estimation of Salvinia compaction are given in Table 8.3. During November 1967, the Salvinia at Station 1 was evenly compacted from shoreline to weed edge. At Stations 3 and 4, however, compaction was far greater against the weed

margin than the shoreline, the former being mature or even senescent blocks of weed, the latter, younger and therefore less compacted, having probably developed along the shoreline following the rise in water level earlier in the year. By February, the situation at Stations 1 to 4 had reversed with greater compaction along the shoreline. This is more difficult to explain, but could have been due to the disappearance of senescent marginals and the maturation of shoreline plants, coupled with the rapid outward expansion, and therefore lower compaction, of marginal plants following the availability of nutrient associated with river flooding.

Estimates of compaction in the permanent estuarine mat on the transect 4a to 5 were more consistent. Whereas densities ranged between 2 and 11 kg/m^2 along the marginal bands of Salvinia, the mat edge was found on both occasions to be close to 4 kg/m^2. Ten metres into the mat this rose abruptly to 15 kg/m^2 and remained at approximately this figure to Station 5, varying little between November and February.

3.2.2 Faunal composition

Although a relatively wide range of approximately 98 species were found in association with the Salvinia mat, the fauna was dominated by the Ephemeroptera, Odonata, and to a lesser extent, the Chironomidae (Table 8.4) totalling 66% by numbers of the fauna sampled. McLachlan's (1969) earlier sampling in the same area produced similar results (Table 8.4). Species typical of Salvinia were not numerous however. The mayflies, for example, were represented by only one species, Ruthrrulus sp. 55, in any great numbers; similarly the Chironomidae were largely represented by the larvae of Clinotanypus alarcininia and Ablabesmyia sp. 80. In contrast, a wide range of

TABLE 8.4 MEAN SEASONAL DIFFERENCES (in numbers/m^2) OF MAJOR TAXA COLLECTED FROM SALVINIA THROUGHOUT THE STUDY AREA

TAXON	APRIL		JULY		NOVEMBER		FEBRUARY		TOTAL	%	McLACHLAN (1969) % by Nos.	NUMBERS OF SPECIES
	Nos/m^2	%	Nos/m^2	%	Nos/m^2	%	Nos/m^2	%				
Oligochaeta	-	-	31	4.1	44	3.7	39	3.3	114	3.45	12	4
Hirudinea	4	1.3	1	-	-	-	4	0.3	9	0.18	1	3
Crustacea	14	8.8	15	1.7	61	5.1	100	8.5	198	6.42	-	9
Hydrachnellae	1	0.2	-	-	134	11.2	8	0.7	143	5.56	-	4
Ephemeroptera	48	17.8	268	35.9	429	35.9	206	17.7	951	27.55	15	6
Odonata	82	30.0	255	38.6	241	20.2	327	28.2	905	25.18	37	11
Hemiptera	6	2.1	1	0.1	1	0.1	1	-	9	0.17	-	3
Trichoptera	-	-	-	-	P	-	P	-	P	0.02	-	2
Coleoptera	14	5.0	3	0.4	4	0.4	4	0.3	25	0.52	-	19
Culicidae	43	15.7	23	3.1	83	6.9	98	8.4	247	7.58	-	2
Chironomidae	20	7.4	96	12.8	104	8.7	232	19.7	452	13.65	31	14
Ceratopogonidae	6	2.1	36	2.2	70	5.9	87	7.4	199	6.12	4	7
Other Diptera	1	0.2	-	-	1	0.1	7	0.6	9	0.29	-	5
Gasteropods	26	9.6	8	1.1	22	1.8	57	4.9	113	3.33	-	6
Fish	-	-	-	-	P	-	P	-	-	-	-	
Eggs and Larvae	-	-	-	-	P	-	-	-	-	-	-	3
TOTAL:	275		735		1194		1170		3374			98

*Percentages calculated from total numbers collected in each season.

odonate nymphs seemed to utilise the Salvinia substrate and many different species were observed ovipositing, on the plants, in any open water which occurred between plants or against the mat margin, including Trithemis, Urothemis, Pseudagrion, Ceriagrion and Ictinogomphus ferox. Nevertheless, the Odonata utilising the Salvinia mat were again strongly dominated by the libellulids, probably of one or two species (see Section 8). These points need consideration in greater detail.

Species typical of the Salvinia substrate, in that they were more numerous here than elsewhere, were not necessarily a dominant proportion of the Salvinia fauna and Table 8.5 has been compiled to illustrate this point, by extraction of species using two criteria. The first of these depended on the numerical importance of individual species; the second, on the proportion each species constituted as a representative of its taxonomic group, covered by the general phrase "major taxon".

The Oligochaeta were overwhelmingly represented by a species of Allonais (sp. 127). The large Nemertodrilus sp. 20 and Branchiura sowerbyi were collected on the shoreline only and probably arose from the bottom muds.

A large proportion of the Crustacea collected were ostracods, particularly species 212 (Stenocypris sp ?) and 277. Cyclocypretta hislopi was the single most important crustacean and the larger freshwater shrimp Caridina nilotica was frequently collected.

Of the Hydrachnellae, Rhinophormurus sp. 277 occurred infrequently in very large numbers, constituting 06% of all mites collected.

Although six species of mayfly nymphs were collected, the

TABLE 8.5 THE IMPORTANT CONSTITUENTS OF THE *SALVINIA* FAUNA

MAJOR TAXA	SPECIES	CODE	% OF MAJOR TAXON	% OF TOTAL	
OLIGOCHAETA	*Allonais* sp.	127	97.0	3.4	***
CRUSTACEA	*Caridina nilotica*	172	7.6	0.5	
	Cylaestheria hislopi	209	27.4	1.8	*
	Stenocypris (?) sp.	212	18.6	1.2	
	Ostracoda sp.	277	25.9	1.7	*
HYDRACHNELLAE	*Rhinophoracarus* sp.	178	86.4	4.8	***
EPHEMEROPTERA	*Baetiumulus* sp.	55	89.6	24.7	***
ODONATA	*Trithemis annulata*(?) Early instar	253	12.0	3.1	**
	Libellulidae	261	65.5	16.4	
	Urthetrum sp.(?)	262	7.9	2.1	
	Early instar Coenagriidae	251	9.3	2.3	
COLEOPTERA	*Hydrovatus* spp.	245	25.5	0.1	*
	Hydrocanthus spp.	276	24.2	0.1	*
CHIRONOMIDAE	*Clinotanypus clarripinis*	25	54.2	7.4	**
	Pentaneura (*Ablabesmyia*) sp.	50	30.0	4.1	***
CULICIDAE	*Aëdeomyia africana*	135	94.2	7.2	***
CERATOPOGONIDAE	Short head "*Probezzia*"	72	57.5	3.5	**
GASTEROPODA	*Aplexus corutus*	256	66.5	2.3	***

: Species successfully utilizing the *Salvinia* substrate but found elsewhere.

* : Species more successfully utilizing the *Salvinia* substrate but found elsewhere.

** : Species most successful on *Salvinia* but which utilize other substrates with reasonable success.

*** : Species which probably find *Salvinia* an essential substrate to maintain high numbers.

Ephemeroptera were overwhelmingly represented by Euthraulus sp. 55 (90%). This species was ubiquitous on the Salvinia and constituted the single most important numerical component of the fauna (25%).

Libellulid dragonfly nymphs were also very numerous in the Salvinia mat (particularly in early instars) far more so than coenagriid zygopterans. It is probable that there has been some confusion regarding the separation of species due to the difficulties associated with the recognition of early and late instars of the same species. The comparatively large number of eleven species which have been tabled could in fact be fewer than this. The Odonata will be considered in more detail in a later section of this chapter (see Section 8).

The Coleoptera showed the greatest species diversity in the Salvinia mat, 19 species being collected. They were, however, numerically unimportant, constituting only 0.52% of the total collected, suggesting a random utilisation of an essentially unsuitable substrate.

Two predatory tanypod chironomids, Clinotanypus alarvipinis and Ablabesmyia sp. 50 together constituted 84% of chironomids sampled, although 14 species occurred. Similarly culicids were dominated by a single species, Aëdeomyia africana (94%) and the ceratopogonids by sp. 72 (57%). Each constituted respectively 7% and 3.8% of the total faunal sample.

The gasteropod molluscs showed a similar phenomenon with Anisus coretus dominating (68%) the six species collected and itself constituting 2.6% of total faunal samples.

Summarising these findings, it is clear that the Salvinia mat constitutes a rather specialised habitat, with usually only a single

species from each major taxon utilising it efficiently. The [illegible] of important components, at species level, of the Salvinia mat is therefore a relatively short one and, in order of numerical importance, is as follows:

Bathyaulus sp. 53

Libellulidae

Clinotanypus glarricinis

Adiocnyia africana

Rhinocnoracarus sp. 170

Ablabesmyia sp. 50

Probezzia sp. 72

Allonais sp. 127

Anisus cornutus

Apart from an unknown number of libellulid anisopterans, eight species only were therefore of numerical importance in the Salvinia mat. The Crustacea were atypical in having more species with similar numerical proportions.

5.2.3 Variations in faunal density

Total faunal counts are tabulated as numbers/m^2 and/kg (Table 6.6) and figured by "seasons" and major taxa in Figures 6.2 to 6.4 as numbers per square metre of Salvinia. For reasons given when discussing methods, little reliable information regarding seasonal change may be derived from the results. The relatively low population figures for April and July could easily be sampling artefacts. Spatial distribution of faunal constituents are more reliable and variation in this respect occurred as follows:

Oligochaeta

Oligochaetes were not found in April 1967, but in July occurred

TABLE 8.6 TOTAL NUMBERS OF ANIMALS SAMPLED IN RELATION TO AREA AND LIVE WEIGHT OF SALVINIA

	1		2		3		3/4		4		4a	+10	+50		5	6		
	S	E	S	E	S	E	E	S	C	E	E	C	C	S	C	C	$\bar{x}$	s
No/m^2																		
APRIL	n	n	n	n	257	n	627	n	168	n	n	n	n	n	36	n		
JULY	n	n	n	n	1414	n	n	n	345	n	n	n	n	n	541		1024	693
NOVEMBER	n	n	475	736	416	1005	n	920	2694	557	1626	2023	718	1886	1305			
FEBRUARY	359	1263	2630	1001	n	678	n	1509	n	1317	1032	1903	570	n	721	n		
No/Kg live weight																		
JULY	n	n	n	n	148	n	n	n	24	n	n	n	n	n	n	n		
NOVEMBER	n	n	95	136	119	104	n	109	n	321	157	112	133	40	100	227	145	113
FEBRUARY	33	38	326	496	n	126	n	190	n	267	260	105	76	n	54	n		

S : Shoreline E : Edge of weed C : Central sample n : no sample s : standard deviation from mean

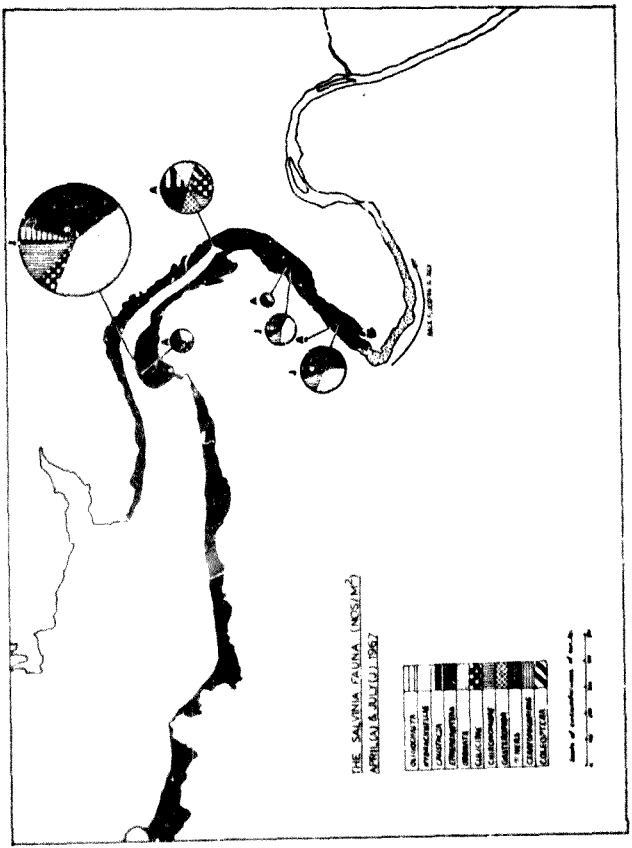


Fig. 8.2

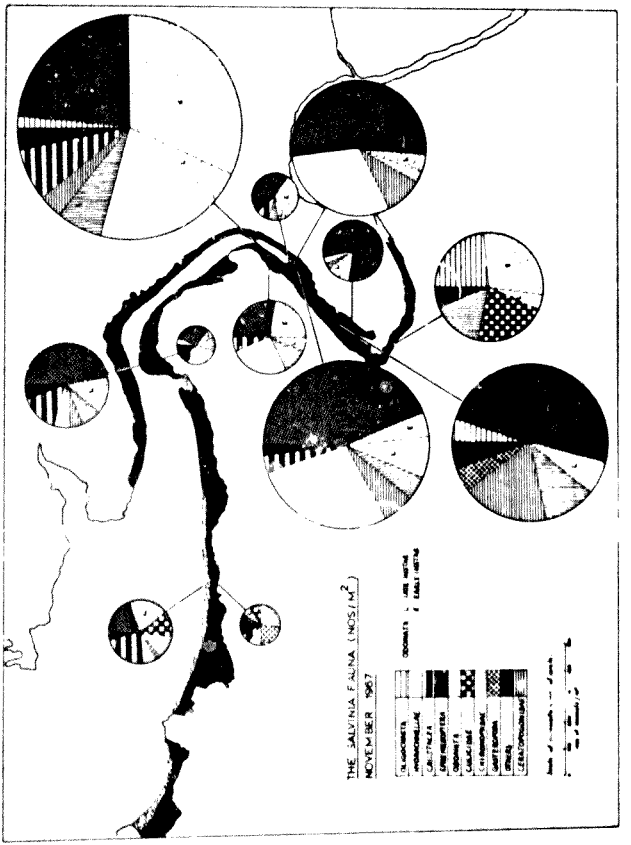


Fig. 8.3

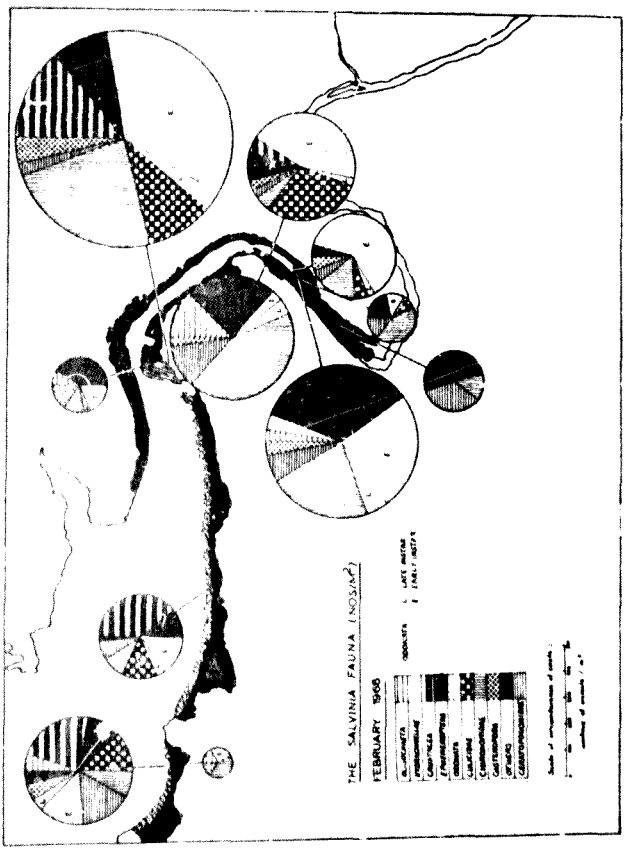

THE SALVINIA FAUNA (NOSAM)
FEBRUARY 1966
OLIGOCHETA
CRUSTACEA
COLEOPTERA
CHIRONOMIDAE
OTHERS

Fig. 8.4

at Station 3 at the weed edge and within the weed mat at Station 4 in small numbers. In November small numbers were again found on the weed edge, but this time of permanent mat, and within the mat at Station 5. A much larger number, composed entirely of a new species of Allonais, occurred in the mat covering the back-flooded river, not previously sampled. In February 1968, oligochaetes were collected widely, Allonais sp. (127) being dominant and occurring in largest numbers against the shoreline at Station 4. Taken as a whole therefore, the oligochaeta showed no clearly discernable distributional trend by the method and frequency of sampling used.

Hydrachnellae

No mites were collected in April and July 1967, but were probably present, being lost through the mesh of the "Salvinia box". In November 1967, they were collected in large numbers, particularly just within the mat edge. This distributional pattern was mainly due to the large number of Rhinophormarus sp. 178 which occurred. Arrenurus sp. 238 was found to occur in the Salvinia against the shoreline at Station 4 only, where large numbers were found. In February 1968, the numbers decreased considerably, but the pattern of distribution was repeated in that largest numbers occurred in the permanent mat within 50 m of the mat edge, but away from it. An apparent pattern of preference of areas associated with the mat edge, but away from it, may be deduced from these results.

Crustacea

Apart from what seemed an atypical distribution of small numbers of crustaceans in July 1967 (Station 5), the preferred habitat of Crustacea utilising the Salvinia substrate clearly appeared to be

either loose weed or against the edge of the Salvinia.

Ephemeroptera

Although mayfly nymphs occurred in association with Salvinia at most sampling points, a clear preference for the permanent Salvinia mat is indicated by the results. This observation holds true for Euthraulus sp. 55 only, however, for the baetid nymphs 62 and 98 occurred in larger numbers at Stations 1 to 5, showing a reversal of dominance, Cosmis sp. 98 being more numerous at Station 5.

Odonata

Odonata nymphs were consistently present at all sampling stations. Variation occurred in proportions of numbers of late and early instars, however. Late instars were usually found at the bay stations and deep within the permanent mat. Early instars showed a clear increase in association with the mat edge or loosely compressed Salvinia, suggesting that oviposition occurred in open water patches and dispersion resulted in the wider distribution of late instars.

Culicidae

Mosquito larvae and pupae were consistently associated with open water at the edge of the Salvinia mat, being most numerous in February 1968, when they were widespread, in this habitat, throughout the study area. An inconsistent dense population was sampled in the Salvinia covering the back-flooded river in November 1967, which in the light of other distributional results could be related to the relatively recent invasion of this area by Salvinia.

Chironomidae

Chironomid larvae, which were overwhelmingly represented by the Tanypodinae, were first found in appreciable numbers in July 1967, when no discernable distributional pattern was apparent. In November

the distribution of tanypod larvae was inconsistent in that largest numbers were found at both the bay stations and within the permanent mat; a circumstance not explicable in terms of specific constituents. Larvae of Orthocladiinae were most commonly found in association with the weed edge and the few Chironomini which were found occurred up the river in association with invasive Salvinia. In February, orthoclads and Chironomini were too infrequent for any distributional comment. The tanypods, which were present in far larger numbers than found previously, showed a more marked preference for compacted mat along the shoreline and within 50 metres of the edge of the permanent mat.

Gasteropods

Gasteropod molluscs seemed to occur in greatest concentrations in association with the edge of the permanent mat in April and were not found in July 1967. In November, two foci of concentration were found, on the shoreline at Station 2 and the other deep within the permanent mat at Station 5. In February 1968, the distributional variability was sustained by the presence of gasteropods at most stations except within the permanent mat, largest concentrations being found at Stations 1 and 3 associated with both the edge of the weed and the shoreline. The variability of seasonal results suggests that gasteropod populations were clumped during 1967, and showed an overall increase in February 1968.

Ceratopogonidae

Ceratopogonid larvae were not found prior to November 1967, when large numbers occurred at most sampling points, decreasing somewhat by the following February. Larvae were widely distributed, showing little preference for any particular habitat on the basis of the analysis considered here.

The spatial distribution of taxa in relation to depth of occurrence within the Salvinia mat are summarised in Table 8.7. The fauna inhabiting Salvinia may be categorised in three main groups on the basis of these data.

1. Widespread fauna. This category includes the Oligochaeta, late instar Odonata, Gasteropoda and Ceratopogonidae.
2. "Edge fauna". Included here are the Crustacea, Cloeon, sp. 82, early instar Odonata, Culicidae and orthoclad chironomids.
3. "Within fauna". This category includes those animals best adapted to both withstand and utilise the most stringent conditions imposed by compacted Salvinia. Included are the Hydrachnellae, heptagenid mayflies and tanypod chironomids.

It could be expected that the components of the "edge fauna" would show a decrease with progression towards the river mouth as the effects of the Salvinia mat became more marked, whereas the "within" faunal components would increase for the same reason. Consideration of the components of these categories show that variations occurred as follows: The Crustacea and bactids of the edge fauna did show a trend for decrease with progression into the "estuary". On the other hand, the Odonata were generally more numerous at intermediate stations and the culicids and ostracods remained more or less constant. A similar variability was found in the distribution of the "within" fauna. The heptagenid mayflies showed a definite increase into the estuary, whereas the mites and tanypod chironomids showed an increase from the bay to the intermediate zone, a decrease towards the permanent mat and an abrupt increase within the mat. Hence no general correlative trend was found in this respect.

The results of faunal distribution over the entire study area

TABLE 8.7 THE RELATIVE IMPORTANCE OF MAJOR TAXA IN RELATION TO SITUATION IN THE STUDY AREA AND OCCURRENCE AT THE EDGE OF OR WITHIN THE SALVINIA MAT

	EDGE OF SALVINIA			WITHIN SALVINIA		
	*BAY	INTERMEDIATE	*PERMANENT MAT	*BAY	*INTERMEDIATE	*PERMANENT MAT
Oligochaeta		X	X	X	XX	X
Hydrachnellae	X	X		X	XX	XXX
Crustacea	XXX	XXX	X	X	X	X
Heptageniidae	XX	XX	X	X	X	X
Baetidae	XX	XX			XX	
Early instar Odonata	XX	XXX	XXX	X	X	X
Late instar Odonata	XX	XX	X	X	XX	XX
Culicidae	XX	XX	XX			
Tanypodinae	X	X	X	XX	XXX	XXX
Orthocladiinae	X	X	X			
Gastropoda	X	X	X	X	X	X
Ceratopogonidae	X	X	X	X	X	X

*Bay : Stations 1 and 2 Intermediate : Station 3 Permanent mat : Stations 4 and 5

give some indication of habitat preferences of the Salvinia fauna. Consideration of distribution within the permanent Salvinia mat only, without the added complication of shoreline effects, should aid in clarifying habitat preferences shown by the species concerned, if compared with their overall distribution. Data pertaining to distribution of species important within the permanent mat have therefore been extracted (Table 8.8) to allow comparison.

In November 1967, distribution of the oligochaete Allonais sp. 12" suggests that the preferred habitat of this animal was deep within the mat at this time. By February 1968, this trend was reversed however, so that the indefinite conclusion drawn from the overall distribution pattern persists. Nevertheless, the species is an important constituent of the Salvinia fauna and only occurs in small numbers on the drowned trees, Ceratophyllum and Lagarosiphon, so that although no consistent distributional pattern emerges from these results, it is clear that without the presence of Salvinia, Allonais would have been scarce if not entirely absent from the study area.

The heptagenid ephemeropteran Euthraulus sp. 53 shows obvious preference for the permanent mat away from open water in November 1967, when it was found in large numbers. Although present throughout the mat in the following February, however, an overwhelming preference for the station 10 m away from the mat edge was indicated by distribution. The distribution of this species within the mat therefore tends to confirm the conclusions drawn earlier, that the large numbers of Euthraulus sp. 53 found would have probably been absent from the study area had it not been for the presence of the Salvinia substrate.

Consideration of the early (sp. 261) and late instar libellulids

TABLE 8.8 RESULTS (as numbers/m^2) OF THE IMPORTANT CONSTITUENTS OF THE PERMANENT MAT TRANSECT, NOVEMBER 1967 and FEBRUARY 1968

SPECIES	CODE	NOVEMBER 1967				FEBRUARY 1968			
		4m	+10m	+50m	5	4m	+10m	+50m	5
Allomais sp.	127	26	0	11	82	2	39	20	11
Baetralus sp.	53	184	852	889	940	55	618	120	322
Libellulidae late instar	262	9	24	68	68	8	49	10	28
Libellulidae early instar	261	194	0	88	0	642	474	55	0
Clinotanypus nervosus	25	17	24	55	124	38	222	90	28
Ablabesmyia sp.	50	0	24	33	82	86	112	105	56
Probezzia sp.	72	5	150	114	316	6	68	55	220
Probezzia sp.	210	0	0	11	27	6	39	40	6
Rhin.chorocerus sp.	178	0	504	547	0	0	58	0	0
Ablabesmyia africana	135	5	0	0	0	53	-	30	11
Aquasa convexa	256	0	0	0	82	29	68	25	0
*TOTAL FAUNA		550	1626	2023	1886	1024	1853	570	721

*Includes species other than those listed.

(sp. 262) confirms the distribution derived from overall findings, early instars being associated with the permanent mat edge and late instars distributed more or less evenly to deep within the permanent mat.

The tanypod chironomids Clinotanypus glarrinipis and Ablabesmyia sp. 50 both showed an increase into the permanent mat in November 1967, and greatest concentrations within 50 m of the mat edge the following February, with a marked decrease deep within the mat. The November distribution confirms the suitability of compressed mat to these species, and the February distribution which is common to several different species is discussed below.

Procladius sp. 72 is consistent in showing an increase into the mat both in November and February, strongly suggesting "salviniaphyllie" tendencies in the species. This was not apparent on consideration of broader distribution as a result of a screening effect by the distribution of other ceratopogonid larvae. Procladius sp. 210 shows a similar distribution in November, but this is changed in February to the same distribution as found in the Tanypodinae (see below).

The mite Rhinophorocarus sp. 178 is clearly associated with the Salvinia some distance from the mat edge, but conditions deep within the mat become limiting at some distance between 50 and 250 m from the edge. On the basis of overall distribution, this limitation on distribution would not be expected, as largest numbers of these mites were associated with the permanent mat.

The culicid Aëdeomyia africana is clearly associated with the mat edge although some were found 50 m in from the edge, where contact with the water surface for respiratory purposes must have been difficult, bearing in mind compaction of the mat. Occurrence of this species deep within the mat in February 1968, is considered below.

The gasteropod mollusc Anisus gyrotus also shows a variation in distribution, occurring deep within the mat in November 1967, where it was absent the following February, although significant concentrations occurred near the mat edge.

5.2.4 Flow effect

Most of the species considered above (including: Allonais sp. 127, perhaps Rithrmulus sp. 53, the tanypod chironomids, Probosmia sp. 210 and Anisus gyrotus) showed a peculiar variation between November 1967, where they were present in largest numbers deep within the mat, and February 1968, when the concentration occurred between 10 and 50 metres from the mat edge. This variation has tended to obscure the object of this analysis; the confirmation or not of the suitability of Salvinia as a substrate for various species. In itself however, this seasonal change is of interest for it suggests displacement of the fauna. Three alternatives resulting in displacement were possible. The first is that conditions deep within the Salvinia mat were optimal to certain species. When the river flows conditions are changed to such a degree that migration away from the river mouth occurs to that part of the mat where conditions are most optimal and most like the situation deep within the mat in the dry season. The second alternative is that flow displaced the fauna downstream, towards the mat edge, in February 1968. The unsuitability of edge conditions led, however, to an active dispersion back into the mat which at the time of sampling had progressed to at least 50 m in from the mat edge. The third alternative was that the main flooding effect was confined to Station 5, affecting the fauna here only.

A flood of approximately 15 m^3/s occurred shortly prior to sampling on 25th January 1968 (sampling taking place between 29th January

and 2nd February), the plunge point being at Station 5, deep within the mat. This strongly suggests that physical displacement was an important factor in the distribution of the mat fauna, and is supported by the apparent lack of effect on Probezzia sp. 72, previously found to be particularly tenacious animals, (see test washing, Fig. 8.1) at Station 5. Yet the evidence suggests (Chapter 6) that zooplankton may be retained by the mat to a degree that recolonisation of waters beneath Salvinia occurs a short period after flooding. As these animals are less well adapted to anchor themselves in the wood mat than the fauna found in it and as these are displaced it would seem fallacious to argue that zooplankton is retained by Salvinia. It would therefore seem unlikely that zooplankton is retained by Salvinia, where active flow is experienced in the Salvinia roots, namely above the plunge point. Retention, if it occurs, would therefore seem to take place downstream of the plunge point, of both zooplankton and the Salvinia fauna, apart from Probezzia sp. 72 and, to a lesser extent, Euthyraulus sp. 55.

When holding faunal samples with Salvinia in aquaria, it was noticed that all faunal components (apart from molluscs and oligochaets) dislodged from the plants swam actively upwards with great persistence until reaching the plant substrate once more. Under minor flooding conditions the effect of this behaviour would be to displace the mat fauna downstream, forming concentrations below the plunge point. Major floods would, however, be extremely destructive to the mat fauna.

The available evidence suggests therefore that flooding is the major factor affecting faunal distribution during the rainy season, and that although distribution is essentially passive, there must also

be a degree of active movement to explain the distribution away from the mat edge, and concentrations of fauna 10 m within the mat. It is probable therefore that the first two alternatives given above also have some bearing on faunal distribution during the rains.

8.2.5 The effect of compaction on faunal density

Consideration of the wide variation in results related to density/m^2 (Figs. 8.2 - 8.4) in relation to a seeming consistency of results related to density/kg (Fig. 8.5), suggests that faunal density is directly related to compaction, or the amount of substrate available. The conclusion which could understandably be drawn from these figures proves erroneous however, for the standard deviation of results, per m^2, in relation to the mean is proportionately less than for results per Kg (see Table 8.6).

8.2.6 Biomass

The biomass was estimated by conversion from mean numbers of each species in the same way as for the animals of the bottom muds, and contributions by the various components are given in Table 8.9. Biomass results are presented in mg/m^2, and by conversion using the overall mean compression value of the Salvinia, in mg wet weight of species/Kg live weight of Salvinia. For comparative purposes, it is considered more realistic to consider only the Salvinia roots as a substrate for aquatic animals, so that the proportion contributed by the roots to total plant weight of a wide range of growth forms of Salvinia was ascertained (roots/total plant weight: 0.480; $\bar{x}$: 0.0142; 3%) and values/Kg plant converted to value/Kg root. The mean total values were estimated to be approximately 4.2 g wet weight/m^2 Salvinia, 0.5 g wet weight/Kg live weight of Salvinia and 1 g wet weight/Kg live weight of Salvinia "root".

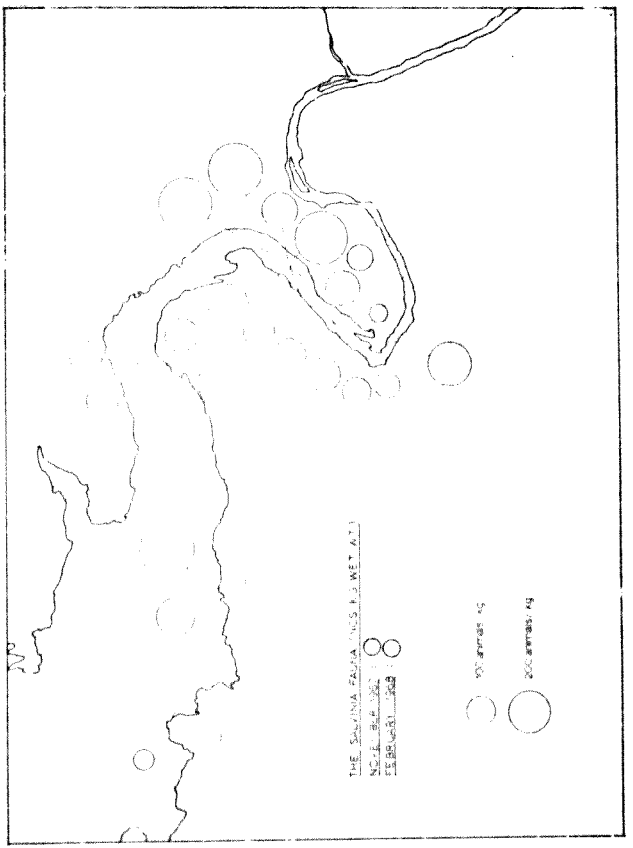

THE SOUTHERN RHODESIA WET AREA
NOVEMBER 1961
FEBRUARY 1962
100 grammes =5
200 grammes =5

Fig. 8.5

TABLE 3.8 MEAN STANDING CROP OF THE SALVINIA FAUNA (mg wet weight of animal/kg live weight of Salvinia)

	mg/m²	mg/Kg	mg/Kg root only
Hirudinea	3.5	0.4	0.8
Oligochaeta	157.7	16.3	34.0
Caridina	250.0	29.8	61.7
Cyclocypteris	14.7	1.7	3.5
Ostracoda	1.8	0.2	0.4
Orthocladiinae	0.8	0.2	0.4
Euthaxulus	201.0	23.8	49.6
Baetidae	44.6	5.3	11.0
Pyrilla	25.6	3.0	6.2
Zygoptera	241.0	28.5	59.4
Early instar Anisoptera	417.8	49.4	102.9
Mid instar Anisoptera	767.0	90.7	188.9
Late instar Anisoptera	1610.0	190.5	396.8
Hemiptera	1.7	0.2	0.4
Trichoptera	0.2	P	P
Coleoptera	15.6	1.9	4.0
Culicidae	61.7	7.3	15.2
Hydrachnellae	3.9	0.5	1.0
Chironominae (Larvae)	0.4	0.1	0.2
Tanypodinae (Larvae)	131.4	15.6	32.5
Chironomidae (Pupae)	2.1	0.5	0.8
Ceratopogonidae	43.5	5.2	10.8
Other Diptera	30.0	3.5	7.3
Bicmonalaria	128.5	15.2	31.7
Bulinus	4.9	0.6	1.2
Lymnaea	39.8	4.7	9.8
Anisus	16.2	1.9	4.0
Ferrissia	0.2	P	P
*TOTAL:	4196.9	496.5	1034.2

*Derived from species table

As a substrate, therefore, Salvinia compared favourably with the bottom muds, even where these were most productive.

The only value comparable with results obtained by McLachlan (1969) is that of 4.2 g wet weight/m^2. He estimated 754 mg dry weight/m^2, and using his own conversion values from dry to wet weight, this approximates to 5.7 g wet weight/m^2, a figure of remarkable similarity considering both the variation in methods of estimation and the more limited sampling carried out by McLachlan.

Consideration of the components as biomass changes the importance of various groups (Table 6.10); in particular the Odonata show overwhelming dominance as biomass, to the cost of the mites, mayflies, mosquitoes and chironomids in particular. The molluscs are not emphasised when considered as biomass in this instance, as the species involved (Anisus) is a small one.

TABLE 6.10 FAUNAL COMPONENTS OF SALVINIA IN TERMS OF PERCENTAGE NUMBER AND PERCENTAGE WEIGHT

	% NUMBERS	% WEIGHT
Oligochaeta	3.5	3.3
Hirudinea	0.2	0.1
Crustacea	6.4	6.3
Hydrachnellae	5.6	0.1
Ephemeroptera	27.6	6.5
Odonata	25.2	72.5
Hemiptera	0.2	0.1
Trichoptera	0.1	0.1
Coleoptera	0.5	0.4
Culicidae	7.6	1.5
Chironomidae	13.7	3.5
Ceratopogonidae	6.1	1.0
Other Diptera	0.3	0.7
Gasteropoda	3.3	4.5

4. THE FAUNA OF VASCULAR HYDROPHYTES

4.1 Introduction

The importance of the role played by vascular hydrophytes has been mentioned previously (Chapter 4); as food directly to grasing invertebrates and fish, as a substrate for periphytic development and benthic animals, and, perhaps most importantly in Lake Kariba, where a major factor governing the fish population is the intense predation pressure exerted by Hydrocynus, as protective cover for juvenile fishes. McLachlan found, in fact, that benthic productivity alone increased in the region of 500% in association with floating macrophytes. Welch (1952) states that *generally speaking* "the greater the development of larger aquatic vegetation, the greater the biological productivity of a body of water". On the other hand, in certain circumstances competition by macrophytes may decrease phytoplankton productivity, as is the case in free-floating macrophytes such as Salvinia, for both are utilizing the same source of nutrient in the water. But, as Kofoid (in Welch, 1952) has pointed out, phytoplankton production may actually be enhanced by the rooted macrophytes; by the eventual release of nutrient derived from bottom deposits where normally it would not be available to phytoplankton, a circumstance considered to contribute considerably to the high productivity of the tropical endorheic Lake Chilwa, Malawi (Howard Williams, pers. comm.).

4.2 Methods

A convenient quantitative assessment of the total fauna of littoral macrophytes is a problem which has still to be overcome satisfactorily. Although many attempts have been made (for example, see Welch, 1952; Macan 1965) to solve this problem by the use of

volumetric grab devices, cages left in situ, sweeping through a set distance with a standard-sized scraper net, each method is subject to inconsistent error and is essentially unsuitable, although several samplers, including those devised by Gerkin, Macan, Gillespie and Brown, and Cocklands' modification of Macan's sampler, have been recommended (Edmonson and Winberg, 1971). Faunal density can be related to dry and wet weight of substrate, quadrat area and actual area of substrate. It would seem obvious that the latter method is the most realistic. A method for the assessment of plant surface area has been devised by Harrod and Hall (1962) which is relatively simple once a particular plant has been calibrated. Surface area in itself does not, however, take into account the type of microhabitat offered by the plant. The area of a broad flat leaf of the Stellis type, for example, bears little relationship to the same area of a plant with small densely tufted leaves such as Ceratophyllum. In the same way the former offers far less substrate area for any given volume of water. The difficulties involved in sampling of macrophytic faunas is so problematic that many workers have tended to ignore this important habitat. Others have ignored non-emergent fauna and used the more convenient method of emergence traps, a technique reviewed by Mundie (1971). Another method, which allows emergent insects to be related to wet weight of substrate is considered later in this chapter.

The method used in this study relates faunal density to wet weight of substrate as follows:

A basin 80 cm in diameter and 20 cm deep was slipped gently sideways into the weed bed. It was then tilted to the horizontal and moved slowly sideways until the vegetation swayed into it. The weed stems were then clamped to the edge of the basin where they came into con-

tact with it by hand and the whole gently raised above the water surface into the boat. In the process the stems broke off, usually where they were clamped against the edge of the dish. Typical samples of Potamogeton and Ceratophyllum may be seen in Figure 8.6. Washing procedure to remove fauna was the same as for Salvinia. When washing was completed the plants were placed in a 60 mesh plankton net and either allowed to drip dry or were spun by hand to remove excess water and then weighed. Extraction curves for the three plant species sampled are given in Fig. 8.1. The extraction method was most effective on Lagarosiphon (c. 5% lost) and less effective on Potamogeton (c. 9% lost) and Ceratophyllum (c. 12% lost). In all cases the great majority of the more tenacious animals were chironomid larvae. The washing water containing the faunal sample was split through 20, 40 and 60 mesh/inch sieves and sorted alive.

Sampling of the Potamogeton and Ceratophyllum was initiated in April 1967, and continued quarterly until February and May 1968, respectively. Sampling of Lagarosiphon was initiated when this plant first appeared in July 1967, and continued to February 1968. Quarterly sampling was undertaken wherever dense beds of plants were found within the study area. Three replicates were taken at each chosen site. Like the fauna of Salvinia, a numerical similarity of the more numerous species on all the substrates was found between replicates.

In all cases the stands of plants were dense, giving the impression at the water surface of occupying approximately 50% of the available space. The substrate offered by each varied considerably, however. Lagarosiphon, for example, has long stems (up to 3 m) approximately 2 mm thick from which arise, at intervals of about 3 mm, whorls of tough, brittle leaves about 10 mm long which arise alternately and

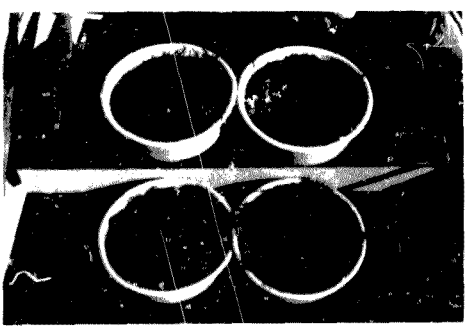


Fig. 8.6 Typical samples of *Paratendipes albimanus* (bottom) and *Potamothrix moldaviensis* (top) for faunal extraction.

recurve downwards and towards the stem. The whole forms a narrow spiral of protective interconnected cages under the recurved leaves. Ceratophyllum is also thin-stemmed and has well defined nodes and internodes, the latter about 2 cm long. About 12 leaves of more or less the same length as the internode, arise from each node. The leaves are more or less circular in section, thinning distally and bifurcating twice. Each whorl is closely opposed to the stem at its base and angles away from the stem distally, the whole plant giving the impression of a series of brushes. The great majority of the fauna is found within these "brushes" which appear to be a highly effective substrate. Potamogeton is more delicate than the plants already mentioned. 1 mm wide and 8 cm long delicate flat leaves arise about 1 cm apart along a 1 mm thick stem. The density of the plant is related more to an increased number of stems than the morphology of the leaves and a very different microhabitat would seem to be offered.

4.3 Results

Full seasonal result are appended (App. 8.6 to 8.8). The frequency of sampling used does not allow an analysis of spatial differences in the estuary between stands of the same species and the quantitative parameter chosen, that of numbers/Kg wet weight of substrate, mitigates against accurate quantitative comparison between substrates in absolute terms, due to their widely varying habit. Analysis of seasonal changes of fauna is also suspect, perhaps less so than the above, so that these results are presented (Table 8.11). The true value of sampling the macrophytes lies in the comparison of their faunal composition.

TABLE 6.11 THE MEAN FAUNAL COLLECTIONS (in numbers/kg wet weight substrate) OF THE AQUATIC MACROPHYTES BY "SEASONS"

	1967			1968			
	April	July	Nov.	Feb.	May	Total	Mean
Potamogeton	258	487	545	1451	709	3260	652
Ceratophyllum	1642	3439	1256	1648	405	8390	1678
Lagarosiphon	-	1649	1649	923	1551	5772	1442

4.3.1 Faunal density and "seasonal" change

The table (6.11) gives results of mean faunal numbers/kg wet weight of substrate for each sampling period. The mean densities of animals on each kg of substrate suggests, with reservation, that Lagarosiphon and Ceratophyllum may be classed separately, as substrates, from Potamogeton and would seem to be equally more effective than Potamogeton per unit plant weight. This observation is supported by the morphological differences between the three substrates, for Ceratophyllum and Lagarosiphon obviously offer a greater surface area per unit weight than Potamogeton.

Little can be said about the "seasonal" changes in the fauna of Potamogeton, for the two May samples vary considerably. Perhaps the increase in February 1968, was sufficiently large to warrant the observation that an increase occurred during the rains. Again, the April and May results over the two years differ so widely for the fauna of Ceratophyllum that little can be said, unless the decrease between July 1967, and May 1968, is sufficiently consistent a trend to warrant comment. The faunal density on Lagarosiphon, in contrast, was seemingly consistent during the sampling period.

4.3.2 Faunal composition

Although quite wide variation between the percentage frequency of major taxa in each of the rooted macrophytes occurred, the order of importance remained the same (Table 8.12). On all substrates, the most important animals numerically were the chironomid larvae ($\bar{x}$: 52%) followed by molluscs (27%), crustaceans (11%), dragonflies (6%), and then mayflies (3%). The same table shows the faunal variations which occurred in each substrate. More or less the same number of species was found on each substrate: at least 30 species occurred on Ceratophyllum, 36 on Lagarosiphon and 34 on Potamogeton. Consideration of the more important species found on the rooted macrophytes (Table 8.13) suggests that these may be categorized, on the basis of apparent substrate preferences, as follows: (most important species on each substrate are asterisked).

TABLE 8.12 THE PERCENTAGE BASED ON NUMBERS OF FAUNAL COMPOSITION OF ROOTED MACROPHYTES BY MAJOR TAXA

	CERATOPHYLLUM	POTAMOGETON	LAGAROSIPHON	$\bar{x}$
Oligochaeta	0.4		0.7	0.4
Hirudinea		P*		P
Crustacea	12.4	5.5	14.2	10.7
Hydrachnellae		0.3	0.1	0.1
Ephemeroptera	2.0	1.7	5.5	3.1
Odonata	7.1	4.1	6.2	5.8
Trichoptera	P	1.1	0.7	0.6
Lepidoptera	0.9	0.3	0.2	0.4
Hemiptera	P		P	P
Chironomidae	45.9	70.1	37.9	51.6
Ceratopogonidae	0.1	0.3	0.3	0.1
Culicidae	P		0.2	0.1
Mollusca	30.7	15.0	34.0	26.8

*P: present

TABLE 8.15 THE PERCENTAGE COMPOSITION (BASED ON NUMBERS) OF IMPORTANT SPECIES ON ROOTED AQUATIC MACROPHYTES

SPECIES	CODE	CERATOPHYLLUM	POTAMOGETON	LAGAROSIPHON
OLIGOCHAETA				
Branchiodrilus hortensis	8	0.1	-	-
Dero sp.	29	-	-	-
Limnais sp.	127	0.3	-	P
CRUSTACEA				
Caridina nilotica	172	0.1	4.9	-
Cyclocypris hislopi	209	11.8	0.3	15.2
EPHEMEROPTERA				
Euthraulus sp.	53	-	-	0.1
Cloeon sp.	82	1.6	1.2	3.4
Povilla adusta	133	0.2	0.2	2.1
TRICHOPTERA				
Ecnomus thomasetti	91	0.3	0.2	0.3
COENATA				
Zygoptera	-	6.6	3.4	0.5
Anisoptera	-	0.4	0.8	0.3
LEPIDOPTERA				
Pyralidae	-	0.9	0.3	0.2
CHIRONOMIDAE				
Pentaneurini vitiosi	55	5.7	27.6	0.4
Ablabesmyia nilotica	66	3.6	0.9	3.6
Cladotanytarsus pseudomancus	70	0.5	12.7	4.8
Cricotopus scutti	139	5.6	6.2	9.2
Tanytarsini fuscocinctus	140	16.8	-	5.6
Tanytarsus sp.	[illegible]	3.9	-	-
CERATOPOGONIDAE				
Narrow head "Culicoides"	61	-	0.1	-
Medium head "Probezzia"	210	-	0.2	-
Long head "Probezzia"	334	0.1	-	0.3
MOLLUSCA				
Biomphalaria pfeifferi	12	7.5	1.2	4.4
Bulinus (Physastra) sp.	30	26.0	13.7	25.6
Lymnaea natalensis	65	0.1	0.4	0.3
Aplexa marmorata	256	1.4	-	-
Ferrissia sp.	308	P	0.5	3.9

1. SUBSTRATE SPECIFIC

(a) Lazarosiphon: Dero sp. 29, Ferrissia cawstoni, Euthraulus sp. 55 (?), and Povilla adusta (?)

(b) Ceratophyllum: Tanytarsus sp. 344, Anisus coretus and Pyralidae (?)

(c) Potamogeton: Ceratopogonidae spp. 61 and 210

2. "TYPE" SUBSTRATE SPECIFIC

(a) Brush type (Lazarosiphon and Ceratophyllum): Allonais sp. 127, Cyclaestheria hislopi,* Dicrotendipes fusconotatus,* "Probezzia" sp. 334, Physopsis sp. 30* and Zygoptera.

(b) Potamogeton type: Caridina nilotica,* Pentanodilum wittei,* Ablabesmyia nilotica, Cladotanytarsus pseudomancus,* Lymnaea natalensis and Anisoptera (?)

3. NON-SUBSTRATE SPECIFIC

Cloeon sp. 13, Bellamya thomasseti, Gricotopus sp. 1 and Biomphalaria pfeifferi.

A considerable proportion of animals using the plants as substrates therefore showed an apparent choice between brushy type plants, irrespective of species, as opposed to the Potamogeton type. This conclusion is considered not to be attributable to sampling error for two reasons. Firstly, the percentage composition of many species were markedly similar on the brush type substrate and dissimilar on Potamogeton too frequently to be entirely attributable to sampling artefact (Table 8.13, Cyclaestheria, Zygoptera, Anisoptera, Pentanodilum, Ablabesmyia, Bulinus and Lymnaea). The second reason was the frequent occurrence of representatives to each substrate type from the same major taxa which seemed specific to that substrate type. For example,

Caridina occurred mainly on Potamogeton, whereas Cyclocaetheris was present mainly on the other two substrates; Pentaneidilum occurred mainly on Potamogeton and Dicrotendipes on the "brush" substrates. The same interchange can be seen between Bulinus and Lymnaea, and within the Ceratopogonidae and Odonata. In each case there is a strong suggestion of different species occupying similar niches and the implication is that the categories are valid, for similar niches occupied by different species imply different habitats.

The further conclusion which may be drawn from these results is that Ceratophyllum and Lagarosiphon seem to offer a separate habitat from Potamogeton, particularly with regard to the "type substrate specific" animals, which constitute the major part of the populations on the "brush" type plants (c. 55% by numbers, 70% by weight).

Biomass estimations of the aquatic macrophytes, which have been calculated from the individual species level, are most conveniently considered in relation to each other and Salvinia, in the section below.

5. THE VARIETY AND ABUNDANCE OF ANIMALS ON THE DIFFERENT SUBSTRATES

Biomass has been estimated from mean numbers of individual species as for other benthos and obviously changes the emphasis of numerical importance from smaller to larger species (Tables 8.14 and 8.15).

The fauna found on Ceratophyllum was dominated by molluscs (Table 8.14) which contribute 78% of the biomass of the population, and to a lesser extent by the Odonata. Although the chironomid larvae did not form a significant part of the biomass of this substrate, the large numbers of these which occurred emphasized their significance as a population constituent.

TABLE 8.14 THE BIOMASS OF FAUNAL COMPONENTS OF THE AQUATIC MACROPHYTES (OVERALL MEAN RESULTS IN MG/KG WET WEIGHT OF SUBSTRATE)

	CERATOPHYLLUM	LAGAROSIPHON	POTAMOGETON	SALVINIA*
Hirudinea	-	-	P	0.8
Oligochaeta	6.4	6.4	-	34.0
Crustacea	148.6	134.6	1601.8	65.6
Hydrachnellae	-	P	P	1.0
Ephemeroptera	133.2	718.2	58.6	66.8
Trichoptera	4.8	7.2	4.0	P
Odonata	1063.0	792.0	300.1	748.0
Hemiptera	P	-	-	0.4
Coleoptera	-	-	-	4.0
Pyralidae	66.3	15.3	10.2	-
Culicidae	P	P	-	15.2
Chironomidae	364.7	247.3	169.6	34.2
Ceratopogonidae	0.8	3.2	2.2	10.8
Other Diptera	-	-	-	1.3
Molluscs	2618.3	2375.8	564.2	46.7
TOTAL:	4406.1	4302.0	2711.2	1034.8

*Weight of submerged part of plant only - Not collected P : Present

TABLE 8.15 THE PERCENTAGE COMPOSITION BY BIOMASS OF THE FAUNA OF VARIOUS SUBSTRATES

	CERATOPHYLLUM	LAGAROSIPHON	POTAMOGETON	SALVINIA	DEAD TREES
Hirudinea	-	-	-	0.1	0.4
Oligochaeta	0.2	0.2	-	3.3	1.1
Crustacea	3.4	3.2	59.1	6.3	-
Hydrachnellae	-	-	-	0.1	-
Ephemeroptera	3.0	16.7	2.2	6.5	97.6
Trichoptera	0.1	0.2	0.2	-	0.4
Odonata	24.1	18.5	11.1	72.3	0.1
Hemiptera	-	-	-	-	-
Coleoptera	-	-	-	0.4	0.1
Pyralidae	1.4	0.4	0.4	-	-
Culicidae	-	-	-	1.5	-
Chironomidae	8.3	5.8	6.3	3.3	0.7
Ceratopogonidae	-	0.1	0.1	1.0	0.3
Other Diptera	-	-	-	0.7	0.2
Mollusca	59.4	55.2	20.8	4.5	0.2

The fauna of Lagarosiphon closely followed that of Ceratophyllum, except for more frequent occurrence of ephemeropteran nymphs. On Potamogeton, however, there was a marked difference. The molluscs were far less dominant (21%) as biomass and the population was largely composed of crustaceans (59%), with Odonata (11%) and chironomids (6%) also important constituents.

The fauna of Salvinia was clearly dominated by the biomass of Odonata (72%) and carried a relatively minor molluscan component. Ephemeroptera and Crustacea were both significant as weight constituents of the fauna (c. 6%), whereas chironomid larvae were even less important than on the rooted macrophytes (3%). It is noteworthy that four extra taxa found on Salvinia, with biomass contributions greater than 0.1%, did not occur on other macrophytes, or only occurred at less than 0.05% biomass.

The fauna of the drowned trees was atypical in being completely dominated by ephemeropteran nymphs (97%) when considered as biomass, although a quite wide variety of animals were found on this substrate.

It is clear that the fauna of substrates considered above, even at family or order level, are distinct as a group from the fauna of the bottom muds when faunal constituents are considered. In the same way, a further distinct faunal category was found in the riverine pools. It had been intended to include an analysis of this community in the present study but time considerations mitigate against this. Preliminary analysis has shown however, a clear dominance of Hemiptera and Coleoptera in the pools and although there is a degree of similarity between the faunas found in bottom deposits of both pools and lake, the marked species diversity of the pools, coupled with this abundance of Hemiptera and Coleoptera, suggests a further habitat within the study

area. This is understandable when considering the relative ages of the two habitats.

At this stage in the discussion, therefore, the drowned trees and aquatic macrophytes (typified by a dominance of Gasteropoda, Odonata and Ephemeroptera) may be clearly separated from the bottom muds (typified by the Oligochaeta, Chironomidae and Chaoborinae) and the riverine pools (typified by the Hemiptera and Coleoptera).

Consideration of the faunal components at species level should clarify the similarity, or not, of the substrates other than the bottom muds of the lake and the riverine pools. This is most conveniently accomplished by dealing with each major taxon to assess specific faunal differences.

HIRUDINEA — The leeches showed a clear preference for Salvinia as a substrate and were infrequent elsewhere.

OLIGOCHAETA — Only one species (Allonais sp. 127) occurred with any frequency on the macrophytes, having been absent from Potamogeton only, and also having shown a clear preference for Salvinia.

HYDRACHNELLAE — The new species of Rhinophorangris (sp. 178) was clearly the most numerous mite, but occurred only in association with Salvinia. Other mites occurred, but in small numbers only.

EPHEMEROPTERA — Baetid nymphs were found on all substrates, but occurred in the greatest concentrations on Lagarosiphon. Euthraulus sp. 55 showed a clear preference for Salvinia, although it was also of some importance on the drowned trees and occurred on Lagarosiphon. As a

numerical component of Salvinia, this species was found to be an important constituent. The large nymphs of Povilla adusta provided a most significant role in the standing crop of the study area. It formed 97% of the biomass on the drowned trees, was also an important component of the Lagarosiphon fauna (17%) and was found on all substrates. The role played by this species elsewhere has already been discussed (Chapter C.2.3).

TRICHOPTERA — The larvae of Ecnomus thomasetti, though never of any importance, occurred on all substrates, though infrequently found on Salvinia.

ODONATA — An interesting apparent interaction between anisopterans and zygopterans occurred between substrates. Whereas the Anisoptera were a clearly dominant component of the Salvinia fauna (72% biomass) where liballulid nymphs were abundant and formed 92% of the odonate biomass, the Zygoptera formed 95% and 90% of the odonate biomass on Ceratophyllum and Lagarosiphon respectively. Potamogeton appeared to be intermediary between these two extremes, the Zygoptera only constituting 64% of biomass of the Odonata. Although of obvious importance on the living macrophytes, dragonfly nymphs occurred infrequently on the drowned trees, only early instar nymphs being found. Further consideration is given to the Odonata in a later section of this chapter (D.3).

HEMIPTERA

Hemipterans were most infrequent on the macrophytes and seemed always to be of neustic origin. Gerrid eggs were found on Ceratophyllum, however, so that the emergent tips of vegetation could play an important role in the life cycle of neustic hemipterans.

COLEOPTERA

Surprisingly few beetles were collected from the aquatic macrophytes; their contribution to faunal biomass was therefore insignificant. No beetles were found on the rooted macrophytes and only a few on Salvinia. Samples from drowned trees produced two species of larvae, one a dytiscid, the other the hydrophyllid Berosus, apart from an adult hydrophyllid.

LEPIDOPTERA

The larvae and pupae of pyralid moths were common on the rooted macrophytes, on which the larvae fed, and were absent from Salvinia and the drowned trees. They were invariably found on the terminal tufts closely associated with the water surface, and seemed to show a preference for Ceratophyllum.

CULICIDAE

Aëdes vig. africanus was the only mosquito which occurred with any frequency in association with the substrates being considered, and showed a clear preference for Salvinia, where it constituted an important component of the population. No mosquito larvae were collected in association with either Potamogeton or the drowned trees.

CHIRONOMIDAE

It is perhaps more realistic to consider aspects of chironomid density numerically. The rooted macrophytes clearly carried much higher numbers of chironomid larvae than Salvinia. As a numerical faunal component of Potamogeton (70%) the chironomids were of greater importance than on either Ceratophyllum (48%) or Lagarosiphon (54%), but a larger biomass was found, per unit substrate, on Ceratophyllum (365 mg/kg) and Lagarosiphon (247 mg/kg) than Potamogeton (170 mg/kg), while Salvinia could again clearly be separated from the rooted macrophytes, carrying only 33 mg/kg.

TABLE 8.16 THE PROPORTIONS OF CHIRONOMIDAE COLLECTED ON DIFFERENT SUBSTRATES (% as a constituent)

	CER.	LAG.	POT.	SAL.	TRE.
% Chironominae	64	41	33	0.8	83
% Orthocladiinae	10	23	10	1.2	0
% Tanypodinae	26	36	57	90.2	9
% Pupae	40	54	52	2	15

It is of interest to note, firstly, the broad components of the chironomid populations found on the various substrates and, secondly, the proportion of pupae collected. These percentages are tabulated above (Table 8.16), the substrates being denoted by their first letters. There would appear to have been an inverse relationship in terms of the proportions of the chironomid fauna between the Chironominae and Tanypodinae;

the former dominating the tree population and decreasing thereafter, in the sequence Ceratophyllum, Lagarosiphon, Potamogeton and Salvinia, where it formed an insignificant constituent. On the other hand, the Tanypodinae showed an exactly opposite sequence of importance. The Orthocladinae seemed independent of this relationship, having been more consistently present throughout the substrates, apart from Salvinia, and were invariably represented by Cricotopus sectii, though various other species occurred. On the trees, the Chironominae were largely represented by Dicrotendipes fusconotatus and Nilodorum sp. 350. D. fusconotatus was also an important constituent of the Ceratophyllum population and occurred on Lagarosiphon. On Potamogeton, Pentapedilum wittei was the main representative and this species also occurred on Ceratophyllum and Lagarosiphon. Cladotanytarsus pseudogranosus was also a significant component of Potamogeton and occurred on all other substrates apart from the trees. Of the Tanypodinae, Ablabesmyia sp. 50 was clearly the most important and was peculiar to Salvinia. Ablabesmyia nilotica was found on all substrates, but was most important on Potamogeton. The only other tanypod of any significance was Clinotanypus glarripinis which was most commonly found on Salvinia, occurring on the dead trees

and Ceratophyllum, but not elsewhere.

Consideration of the pupal constituents of chironomid populations (Table 8.16) indicates a clear differentiation between the rooted macrophytes, where more or less half the population consisted of pupae, and the dead trees and Salvinia, the pupal constitution of each to the chironomid biomass amounting to 2% and 13% respectively. Clearly, Salvinia was an unsuitable substrate for the pupae of the overwhelmingly tanypod population component.

CERATOPOGONIDAE

The ceratopogonid species 72 (short head "Probezzia") was found to be an important constituent of the Salvinia fauna and occurred quite frequently on the trees but not elsewhere. Species 210 (medium head "Probezzia") was also significant in the Salvinia population and occurred on Potamogeton but not on the trees or other rooted macrophytes, where, in the latter instance, another species peculiar to those alone occurred (species 334, long head "Probezzia"). Generally speaking, apart from within Salvinia "roots", the ceratopogonids were not significant population constituents.

MOLLUSCA

The molluscs were found to be extremely important population constituents of the rooted macrophytes, particularly on Lagarosiphon and Ceratophyllum. Here the main representatives were Biomphalaria pfeifferi and B. Physopsis sp. 30, the latter having

been found on all substrates and the former on all substrates except the trees, though it is almost certainly present here. Lymnaea natalensis was also present on all substrates, but never in large numbers. Anisus sorotus was confined to Ceratophyllum and particularly, Salvinia, where it occurred in large numbers. The only other gasteropod found on these substrates was Ferrissia cowstoni which occurred on Salvinia, Potamogeton and Lagarosiphon, and seemed to show a preference for the latter.

The above considerations are summarised in Table 8.17, which attempts to indicate the importance of different species by combination of two viewpoints; the relative abundance of individual species and their importance as components of a substrate population, i.e. a species abundant on a given substrate but relatively unimportant as a population constituent on this substrate rates equally with a species which is more abundant on another substrate, but is an important constituent of the given substrate population. The table is, therefore, somewhat subjective, but is based on two objective observations.

In the consideration of abundance and distribution of the animals on the various substrates, there are eight clear cases where distributional patterns separate Salvinia from the other substrates. This would seem to indicate that Salvinia could be regarded as a separate habitat. In three cases, distributions are confined to trees suggesting that these too, could be regarded as separate. In a further four cases distributions are common to both trees and Salvinia but not the other substrates. There are, therefore, a total of seven instances

TABLE 8.17 THE DISTRIBUTION AND IMPORTANCE OF THE DOMINANT SPECIES ON THE DIFFERENT SUBSTRATES

SPECIES	CODE	DEAD TREES	SALVINIA	CERATOPHYLL.	LAGAROSIPHON	FILAMENTOUS
OLIGOCHAETA						
Dero sp.	29	X			X	
Allonais sp. nov.	127	X	XXX	X	X	
CRUSTACEA						
Caridina nilotica	172	X	X	X		X
Cralaeotheria hislopi	209	X	XX	XX	XX	X
HYDRACHNELLAE						
Rhinochoncarus sp.	178		XXX			
EPHEMEROPTERA						
Euthraulus sp.	53	XX	XXX		X	
Cloeon sp.	58	X	X	X	XX	X
Povilla adusta	143	XXX	X	X	XX	X
TRICHOPTERA						
Cheumatopsyche thomasetti	91	XX	X	X	X	X
ODONATA						
Coenagriidae	-	X	X	XXX	XXX	XX
Libellulidae	-	X	XXX	X	X	XX
LEPIDOPTERA						
Pyralididae	-			XX	X	X
CHIRONOMIDAE						
Clinotanypus clarrisimis	25	X	XX	X		
Pentaneurini	35			X		XXX
Pentaneura (Ablabesmyia) sp.	50		XXX			
Ablabesmyia nilotica	68	X	X	X	X	XX
Cladotanytarsus pseudomancus	78		X	X	X	XX
Cricotopus scotti	139	X	X	X	XX	X
Dicrotendipes fuscocostatus	148	XX		XXX	X	
Chironomus (Kiefferiella) sp.	358	XX				
CULICIDAE						
Aldesmyia africana	155		XXX	X		
CERATOPOGONIDAE						
Short head "Probezzia"	72	XX	XXX			
Medium head "Probezzia"	210		XX			X
Long head "Probezzia"	354			X	X	
MOLLUSCA						
Biomphalaria pfeifferi	12		X	XXX	XXX	XX
Bulinus depressus	30	X	X	XXX	XXX	XX
Lymnaea natalensis	65		X	X	X	XX
Aplexa soratus	286		XXX	XX		
Ferrissia caxaiani	306		X		XX	X

KEY: X - Present in substrate
XX - Either numerous on substrate or more commonly found on substrate
XXX - Either abundant on substrate or most commonly found on substrate i.e., species typical of substrate

where distributions suggest the drowned trees as a separate habitat, of which four show an association with Salvinia. As there is a reasonable case to support the separation of Salvinia (8 clear-cut instances of animals peculiar to Salvinia only) as a habitat, the four instances where distribution is common to both substrates tend to support the separation of the drowned trees as a habitat also. The tentative conclusion would therefore be, on the basis of species distribution, to further subdivide the plant substrates into Salvinia and drowned tree habitats. At this stage in the discussion therefore, benthic habitats in the study area may be separated in the following way:

A. Pools

B. Bottom muds

C. Vascular plants

(1) Drowned trees

(2) Salvinia

(3) Rooted hydrophytes

The separation of the rooted hydrophytes is less distinct in these considerations, though there is some evidence to support the separation of Potamogeton from Lagarosiphon and Ceratophyllum (which have many common distributional patterns) which was discussed earlier on consideration of numerical abundance similarities (3.4.2).

The dangers of quantitative comparison of the different substrates has been previously emphasised. Comparison is considered permissible, however, if it is clearly understood that all the comparison implies is that plant A, as a substrate, carries a larger/smaller mean biomass per unit ight of plant A than plant B carries per unit weight of plant B. For the sake of convenience this will be termed "carrying

capacity". The varying carrying capacities of the plant substrates have been estimated as:

Ceratophyllum	: 4.4 g wet wt/kg live weight of plant
Lagarosiphon	: 4.3 g wet wt/kg live weight of plant
Potamogeton	: 2.7 g wet wt/kg live weight of plant
Salvinia	: 1.0 g wet wt/kg live weight of "root"

These figures indicate quite strongly that the tentative separation, based on species distribution, of Ceratophyllum and Lagarosiphon/Pot.. ton/Salvinia is valid. The results suggest therefore, that habit.. category C(2), the rooted hydrophytes, may be further separated into (a) Brush type and (b) Potamogeton.

McLachlan's (1969) results differ greatly from those given above both in order of carrying capacity and of values. He found that "the floating mats (Salvinia and Ludwigia) supported nearly seven times more than submerged vegetation (Potamogeton and Ceratophyllum)". He gives his results as dry wt/100 g dry wt of substrate, so that direct comparison of values can only be vague estimates and are not considered to be of value. However, in this study the carrying capacity of the rooted (submerged hydrophytes) was 2.7 to 4.4 times better than for Salvinia, a difference not easily attributable to sampling error. It can only be assumed that during early invasive stages, as seemed to be the case during McLachlan's sampling, plant substrates had not had a chance to develop their full carrying capacity; a premise which receives some support from the emergence of Odonata from aquaria (0.0).

The proportions of Mollusca in the biomass seemed closely related to the total carrying capacity of each substrate. The molluscan component from each substrate has been subtracted, therefore, with

the following results:

Ceratophyllum	1700	mg wet/kg wet.
Lagarosiphon	1926	
Potamogeton	2147	
Salvinia	909	

Thus the major difference in carrying capacity between the "brush" substrates and Potamogeton was attributable to the presence of a larger proportion of molluscs in the former. Without the molluscs the carrying capacity of rooted macrophytes was very similar, about twice that of Salvinia. Clearly, Salvinia had a lower carrying capacity and if considered in terms of environmental area, considerably lower, as a result of limitation on depth and therefore volume of water column colonisable.

96 species were found on Salvinia, yet the rooted macrophytes and drowned trees yielded a relatively consistent and much lower number, between 34 and 38. It is difficult to find an explanation for this phenomenon unless it could have been attributable to "edge effect" as a result the wide variety of contact with different habitats experienced by Salvinia, such as margins, the river, trees, etc. Certainly, certain species seemed peculiar to Salvinia alone and the implication is that this plant, in itself and quite apart from edge effect, offers both a series of specialised habitats and a general substrate utilisable by many species.

It is not possible to compare the standing crop of rooted macrophytes directly with that of the bottom muds. They do, however, carry roughly 4 times the biomass found in Salvinia, weight for weight of substrate, and Salvinia, area for area, carries again about 3 times the biomass of the bottom muds. Very roughly therefore, the rooted

hydrophytes would carry 16 times the biomass of the bottom muds, even if the "performance" column (sensu McLachlan, 1969) was limited to the depth of Salvinia, at extremis about 0.5 m. As the performance column of rooted hydrophytes can extend to about 7 m this would emphasise the increased productivity considerably. These figures are essentially rough even if the distillation of considerable sampling, but the point that is made is that there was a very considerable increase in standing crop of benthos following the establishment of rooted aquatic macrophytes.

6. TROPHIC REPRESENTATION

The crops of a representative selection of Zygoptera were removed and permanently mounted in Swann's modification of Berlese's medium. The clearing action of this mountant allowed the inspection of crop contents. The experience gained from the careful separation of benthos for coding allowed relatively easy recognition of most animals from their parts. Chironomid head capsules are clearly revealed by the technique described and as they are persistent, give an indication of zygopteran food preferences. The results achieved from the crop contents of 102 zygopteran nymphs collected from the rooted macrophytes, as percentage occurrence, were as follows:

	%	
CHIRONOMINAE		27%
Dicrotendipes	55.5	
Psectrocladius	4.5	
Cladotanytarsus	5.0	
Unrecognisable	45.1	
ORTHOCLADINAE		6%
Cricotopus	5.8	
TANYPODINAE		7%
Ablabesmyia	6.3	

The main reason, apart from the persistence of head capsules, allowing the recognition of contents was that the prey were injested whole, with very little damage. Similarly, on two occasions Ablabesmyia were found injesting Dicrotendipes. These also were injested whole, on both occasions head first, whereas the Zygoptera injested chironomid larvae from both anterior and posterior ends. Usually one or two larvae were present in the gut, but up to four recognizable head capsules occurred at one time. In contrast, the Anisoptera appeared to masticate food before injection and on the few occasions that contents were recognizable, these were of animals larger than the chironomid larvae, such as Povilla. Theoretically, therefore, the Zygoptera could only injest prey of the chironomid shape whereas the Anisoptera could utilise larger animals. This was tested in aquaria and it was found that the theory seemed to hold true for Zygoptera, whereas Anisoptera injest (and masticate) both larger prey and smaller prey of the chironomid type. The observations on Ablabesmyia suggest that these also may only injest smaller cylindrical or soft animals and that the size of prey intake is limited by the size of the buccal orifice of the head capsule. Thus the limitation of chironomid larvae, as prey to Ablabesmyia would be head capsule size, which would have to be smaller than the buccal orifice of the predator. The limitation of prey size and shape for Zygoptera could explain their paucity on Salvinia, as suitable prey is particularly sparse.

In determining the proportional trophic representation by biomass, components were separated into the following groups:

Secondary predators - Zygoptera, later instar Anisoptera nymphs.

Primary predators - Early instar Anisoptera, Tanypodinae larvae, Ceratopogonidae.

Utilisable herbivores - Chironominae and Orthocladinae larvae, Ephemeroptera nymphs, Cyclaestheria, Ostracoda, Culicidae, Oligochaeta.

Non-utilizable herbivores - Gasteropoda, Pyralidae, Caridina.

The reason behind the separation of the herbivores is derived from the fact that a large proportion are either not utilised or utilised only in a limited way. The gasteropods, for example, cannot be ingested by either the primary or secondary predators listed, due to the presence of the shell. Similarly, Caridina is too large and swift to form a significant part of prey and the habit of the pyralid moth larvae of utilizing only terminal material associated with the water surface would tend to rule out their significant usage as prey.

The proportions of total biomass each of these groups constituted on the different macrophytes is listed below (Table 9.10). Ceratophyllum and Lagarosiphon are combined as one substrate (the "Brush type") for reasons given earlier.

TABLE 9.10 PROPORTIONS OF POPULATION BIOMASS OF THE DIFFERENT SUBSTRATES SEPARATED AS TROPHIC LEVELS

	BRUSH TYPE		POTAMOGETON		SALVINIA	
	Biomass	%	Biomass	%	Biomass	%
Secondary predators	915	21	500	11	740	67
Primary predators	50	1	55	2	135	12
Utilisable "herbivores"	702	16	103	7	121	11
Non-utilisable "herbivores"	2665	61	2171	00	100	10

There is, on the basis of these data, a marked imbalance between utilisable herbivores, which should theoretically be of greater biomass, and predators. Predatory biomass in each case is greater than prey biomass, particularly in Salvinia. Another interesting point is the definite decrease in the non-utilisable component of the Salvinia fauna.

The imbalance of the trophic biomass pyramid suggests an inversion situation, known to be typical of standing crop of planktonic (Harvey, 1950, and Riley, 1956, in Odum, 1959) but atypical of benthic communities. Three explanations for the situation are available:

1. The rate of energy turnover of the primary consumers, particularly of the chironomids, crustaceans and ephemeropterans, is considerably higher than for the Odonata.
2. The Odonata utilize their own earlier instars. This has been observed amongst Anisoptera in aquaria.
3. A major source of energy for the predators is derived directly from zooplankton. Zooplankton densities in association with the Salvinia mat, for example, were such as to make this supposition reasonable.

It is probable that all three of these alternatives contribute to the stability of the apparent inverted biomass pyramid of the fauna of rooted hydrophytes.

Aquarium evidence has shown that Anisoptera are eager to predate on Paralia. The probable explanation for the overwhelming dominance of these animals on the drowned trees lies in their wood-boring habit which makes them difficult to prey on. The lack of cover for Anisoptera on the drowned trees also make this an unsuitable substrate for them, for they are particularly vulnerable here to predation by fishes.

7. OBSERVATIONS ON FISH ASSOCIATED WITH THE HYDROPHYTES

Fish were taken during collection of macrophyte samples. In Potamogeton the species collected were Tilapia mortimeri juveniles and adult Barbus fasciolatus and Hemihaplochromis philander. Tilapia mortimeri juveniles were also collected from Ceratophyllum, but the most frequent species collected were Alestes lateralis. A. lateralis larvae and fish eggs, presumably of this species, were commonly found in this substrate throughout the year. Larvae and eggs of a different species (see Chapter 10) were found in shoreline Salvinia. Tilapia mortimeri were also collected in Salvinia samples as was the minnow Nannaethiops brevianalis.

Large numbers of small fishes were usually seen in association with the Salvinia mat. These were recognizable as being, mainly, shoals of juvenile Tilapia mortimeri and individuals and shoals of the two minnows Aplocheilichthys sp. and Nannaethiops. Tilapia juveniles were frequently seen in association with individual wind-blown Salvinia plants in open water.

During the course of the study, particularly during 1968, a very dense population of Alestes lateralis was observed to occur in the Lagarosiphon and Ceratophyllum beds. Some idea of the density of this species can be gained from the fact that, using a mealie-meal porridge baited concertina net with a 0.5 m diameter opening, up to 200 individuals could easily be caught within a few minutes. It is of interest to note that currently (1972) the same results are obtainable in Lagarosiphon beds, but the species now involved are Alestes imberi, A. lateralis, and Micralestes acutidens. These observations will be referred to again in a later chapter.

The aquatic macrophytes would seem, therefore, to be an important

habitat for juvenile and small fishes.

8. OBSERVATIONS ON THE ODONATA

8.1 The Emergence of Odonata from "Breeding" Aquaria

The knowledge of nymphal and larval forms of African aquatic insects is as yet largely in its infancy, and imposes irritating restrictions on accuracy in hydrobiological studies. In an attempt to overcome, at least partly, this imposition, breeding aquaria were used to correlate early stages of development with imagines, most of which can now be accurately named. Initial trials of breeding individual specimens at the Research Station indicated the unsuitability of this method, for on many occasions by the end of a field period, few emergences had taken place and non-emergents had to be discarded. The method which was eventually evolved which is described below, although having the drawback of occasional mass emergences resulting in difficulties in relating pupal/nymphal casts to imagines, was found to be more suitable.

The technique used involved the collection of samples of the various hydrophytic substrates of more or less constant size shortly before the end of a field trip. These samples were placed in large heavy gauge polythene bags, with a liberal amount of both water and air, and crated for transmission to Salisbury. On arrival, always within 40 hours of collection, samples were placed into large glass aquaria (120 x 50 x 45 cm) containing approximately 270 litres of matured tap water overlying a layer of clean sand. These aquaria were aerated and covered with a dome of mosquito gauze. Emergent adults were collected daily using a suction device, killed with chloroform and transferred to vials of 70% alcohol. Exuviae were collected on the water surface or from dowels placed vertically in the tanks to facilitate emergence and were

Author Bowmaker Alan Philip Macgowan
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