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CHAPTER 7
FRESHWATER FISHES OF THE ZAMBEZI BASIN

Brian Marshall

7.1 INTRODUCTION

The Zambezi is the largest African river flowing into the Indian Ocean, draining a basin of around 1.2 to 1.5 million km^2 (estimates vary; Davies 1986). The modern river basin is the result of various geological processes that occurred during the Quaternary, which include a dramatic series of river captures, the deposition of wind-blown sands in the western part of the basin, the formation of the Rift Valley, and the rejuvenation of the erosion cycle in the eastern part. These forces have influenced its fish fauna and contributed to its present diversity (about 160 species) in the river system proper plus several hundred endemic cichlids in Lake Malawi (Bell-Cross 1972, Jackson 1986, Skelton 1994).

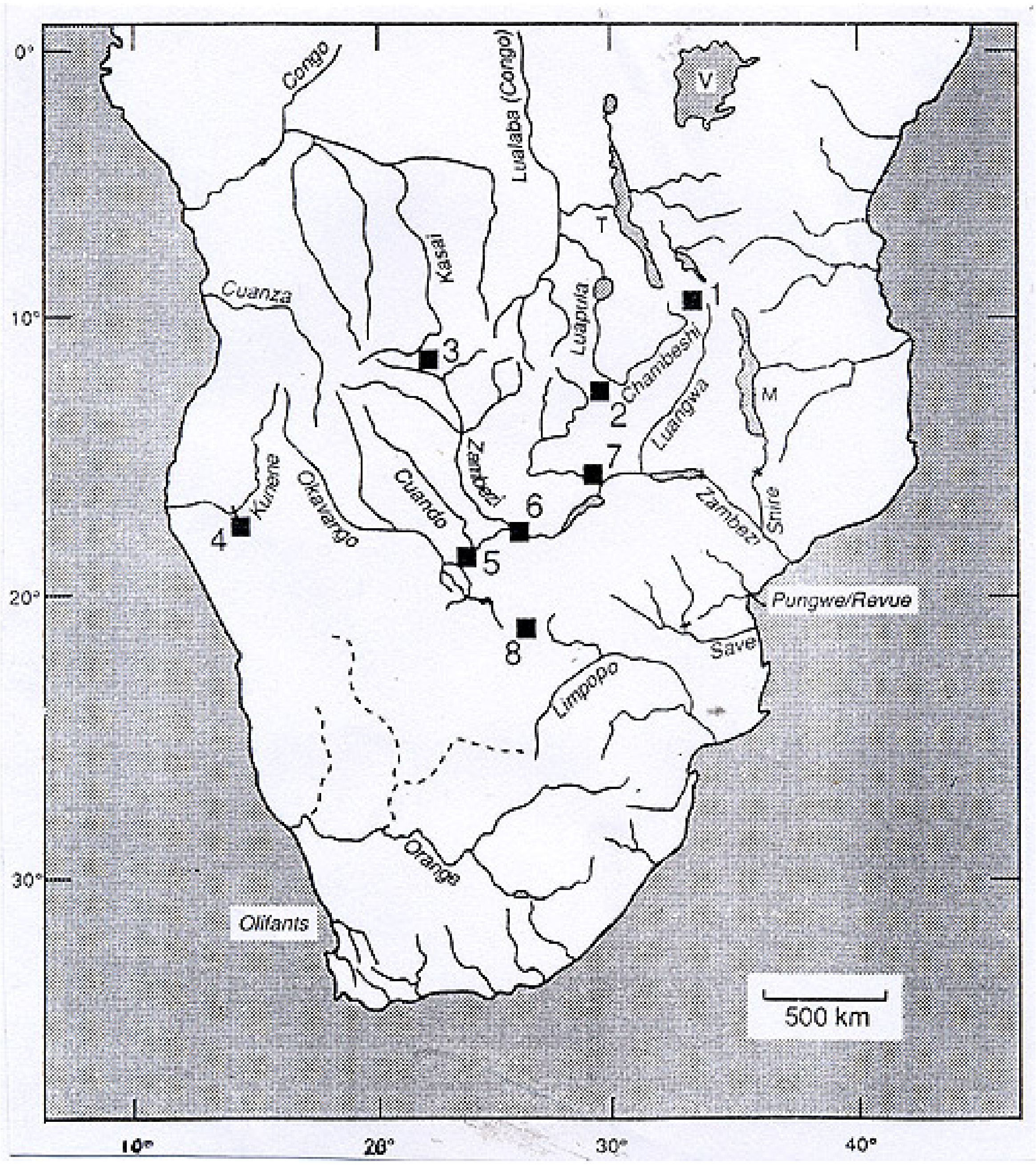
The Zambezi-Congo watershed forms a natural zoogeographical boundary that marks the northern limit of the Zambezian ichthyological province (Roberts 1975). This includes areas that were once part of the Zambezi system, such as the Cunene and Okavango basins, or the Limpopo system. Fish in the east coast rivers from the mouth of the Zambezi south to the Phongola, in northern Kwazulu-Natal, are also a part of the Zambezian system since they have been connected in various ways with the Zambezi itself. The fish populations of these rivers also include elements of the east coast fauna and they are a major component of the fauna of the Middle and Lower Zambezi as well. Some understanding of the evolution of the system and the zoogeography of the fish is essential in understanding its biodiversity and this issue is addressed in the following section.

7.2 THE ORIGIN AND ZOOGEOGRAPHY OF ZAMBEZIAN FISHES

A fundamental question in biology is why are there so many species of living things? In searching for the answer biologists need to know what determines the distribution of these species and why they occur in some areas and not others. The discipline of biogeography deals with these matters using evidence from many disciplines, including biology, geology, palaeontology and geography. This paper gives an introduction to the zoogeography of the fishes of the Zambezi Basin and it draws heavily on Skelton (1993, 1994), which should be referred to for further information.

The land surfaces of today represent the end of an immensely long period of geological activity. In the last 100 million years southern Africa has been subjected to major geological processes like the formation of the Rift Valley and associated fault systems that caused the Zambezi and Luangwa valleys. The western parts of the basin have been relatively stable over a long period of time, but the eastern parts have been subjected to considerable change, including uplifting that initiated a series of erosion cycles. In parts of Zimbabwe, for example, uplifting led to six cycles of erosion (Lister 1979) in which the eastern highlands were uplifted several times while the western Kalahari basin remained relatively static. These cycles allowed westward erosion by east coast rivers like the Limpopo and Zambezi, which captured several formerly southward-draining rivers. River capture is one of the most important geological influences on fish distribution and several major river captures in southern Africa (Figure 7.1) have influenced the distribution of fish.

Figure 7.1 The major river systems of southern Africa. The principal river captures, which are indicated by the symbol ■, are as follows: 1, the ancient link between the Upper Congo and Luangwa/pre-Lake Malawi systems, possibly via Lake Rukwa; 2, the Chambeshi-Kafue link severed by the Luapula; 3, an Upper Zambezi tributary captured by the Kasai; 4, the southward flow of the Cunene disrupted after capture by a west-flowing stream; 5, the Kwando-Okavango connection severed by tectonic movements that divert the Kwando into the Zambezi; 6, the Upper Zambezi captured by the Middle Zambezi following rejuvenation of the erosion cycle; 7, the Kafue captured by the Middle Zambezi; 8, the former link between the Upper Zambezi and Limpopo systems broken by the diversion of the former and the infilling of the Kalahari Basin. T = Lake Tanganyika, V = Lake Victoria and M = Lake Malawi.



Fish cannot move overland or live out of water for any length of time and this restricts the ways in which they can move from one river system to another. Changes in the direction of river flow, either because of earth movements or by river capture, are among the most important. Falling sea levels are also important since the courses of rivers that currently discharge separately into the sea often join at a lower sea level. For example, the Pungwe, Buzi and Zambezi rivers were probably connected when the sea level fell during the last Ice Age. The Zambezi and Pungwe are still connected by low-lying wetlands and these coastal connections must have been more extensive when the climate was wetter than it is today. Furthermore, a wetter climate may also have allowed fish to cross from one watershed to another, provided suitable marshy areas existed. Fish have been seen to move across the Congo-Zambezi watershed in this way (Bell-Cross 1965).

7.2.1 **The major fish groups**

Fish are the oldest true vertebrates and jawless fish (Agnatha) first appeared in the Silurian era (320 million years BP). They flourished for about 40 million years but most of them had disappeared by the end of the Devonian. About 60 or so species of these fish still survive today but none of them occur in Africa. The Devonian era (300 million years BP) is often called "the age of fish" since four distinct forms of jawed fish originated during this period. Only two of them have survived and flourished to the present day. The cartilaginous fish (Elasmobranchs), which include the sharks and rays, are a marine group and are found in all the oceans. A few species penetrate freshwater and one of them, the Sawfish, *Pristis microdon*, has been collected in the Lower Zambezi and the Zambezi Delta (Bell-Cross 1972). A second species, the Bull Shark, *Carcharhinus leucas*, has been taken in the Zambezi at Tete and some of its tributaries, like the Ruenya River just before the Zimbabwean border. It is said to have been taken at Chirundu (Bell-Cross & Minshull 1988), but this record is not listed in earlier books (Jubb 1960, 1967, Jackson 1961a) and it may never, in fact, have penetrated the Zambezi beyond the Cabora Bassa Gorge.

In the early Devonian, the bony fish (Osteichthyes) produced two quite distinct and possibly unrelated lineages. The first of them, the lobe-finned fish (Crossopterygii) are the ancestors of the terrestrial vertebrates. They were abundant in the Devonian but their numbers decreased after that and today they are represented only by the coelacanth and the lungfishes. The coelacanth *Coelacanthus granulatus* from the Karoo sediments of Zimbabwe, is one of the few named fossil fishes from the basin and, unusually, it was found in sediments deposited in freshwater, while all other coelacanths, including the only living species, lived in the sea (Bond 1973). The lungfish were once distributed on all continents but now have a relict distribution in Australia (1 species), South America (1 species) and Africa (4 species). One of the African species, *Protopterus annectens*, occurs in the Middle and Lower Zambezi valley while another, *P. amphibius*, is found in the floodplains of the Lower Zambezi.

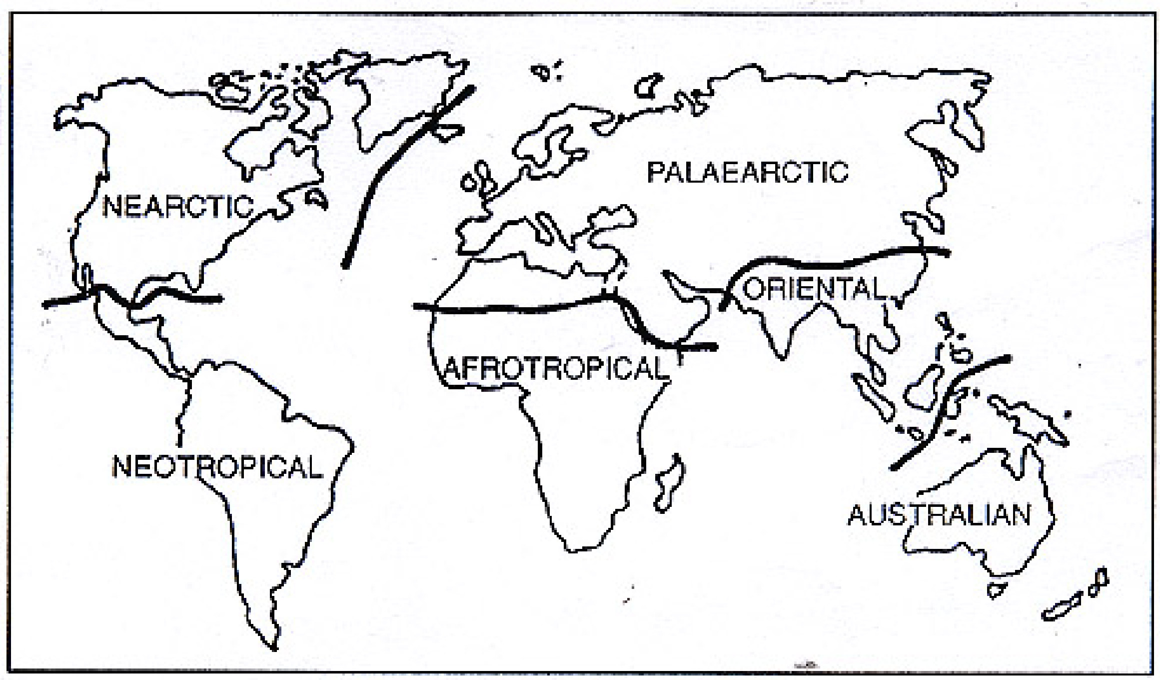
The largest and most diverse vertebrate group, with some 20,000 species, is the ray-finned fish (Actinopterygii). They come in an astonishing variety of body forms and are found in almost any water that can support fish. These range from the furthest depths of the ocean to high mountain lakes, and include inhospitable environments like hot springs and temporary pools. One of the other named fossil species found in the basin, *Namaichthys molyneuxi*, which lived in Zimbabwe about 250 million years ago (Bond 1973), is a representative of one of the most ancient bony fish groups, the Palaeoniscoidea. Primitive forms like the palaeoniscids were progressively replaced by more advanced ones during the 200 million years between the Devonian and the mid-Cretaceous. Only a few archaic bony fish have survived to the present time and none occur in the Zambezi system.

The most advanced group, the Teleostei, first appeared in the fossil record in the mid-Jurassic (130 million years BP) and by the mid-Cretaceous (90 million years BP) they had become the most abundant and successful group of bony fish. The radiation of the teleosts coincided with a period of rapid continental drift and their distribution and evolution was greatly influenced by this activity.

7.2.2 **The influence of continental drift**

In 1876 Alfred Russell Wallace divided the world into six major zoogeographical regions on the basis of their distinctive fauna that included a number of families unique to each (Figure 7.2). Although he could not have known it at the time, Wallace's regions reflect the way in which the continents moved during the last 150 million years. The linkages between the families of freshwater fishes of Africa and those in other continents clearly reflect the impact of continental drift.

Figure 7. 2 The principal zoogeographic regions of the world, after Alfred Russell Wallace. The River Nile has enabled African fish to penetrate Egypt and the Levant, and these areas could be treated as extensions of the Afrotropical.



About 150 million years ago the single supercontinent of Pangea began to break into Laurasia (North America and Eurasia) and Gondwanaland. This early split is reflected by the fact that only two Zambezian families of fish are also found in the Palaearctic and Nearctic regions (Table 7.1). One of them, the Cyprinidae, is the largest family of freshwater fish with more than 1600 species occurring throughout North America, Eurasia and Africa.

The break-up of Gondwanaland began about 70 million years ago. Australia was the first to be isolated from the rest and only one family, the Galaxiidae, occurs in both the Afrotropical and Australian regions. The sole African galaxiid species is restricted to the southern Cape and does not occur anywhere else on the continent. South America seems to have broken away next and only two families of Zambezian fish also occur in the Neotropical. The Characidae, which include well-known species like the African tigerfishes and the South American piranhas, are most diverse in the Neotropics and may have prevented the cyprinids from invading South America. The Cichlidae,

Table 7.1 The families of fish found in the Zambezi Basin and their wider distribution. N = number of species in family in the basin, FW = freshwater, M = marine.

		Afrotropical	Oriental	Neotropical	Palaearctic	Nearctic	Australian	N	Origin
Protopteridae	Lungfish	■						2	FW
Mormyridae	Snoutfish	■						9	FW
Kneriidae	Knerias	■						4	FW
Cyprinidae	Carp, barbs	■	■		■	■		46	FW
Distichodontidae	Citharinids	■						5	FW
Characidae	Characins	■		■				6	FW
Hepsteidae	African pike	■						1	FW
Claroteidae	Claroteid catfish	■						1	FW
Amphiliidae	Amphiliid catfish	■						4	FW
Schilbeidae	Butter catfish	■	■					2	FW
Clariidae	Air-breathing catfish	■	■					7	FW
Malapteruridae	Electric catfish	■						1	FW
Mochokidae	Squeakers	■						13	FW
Aplocheilidae	Killifish	■	■					4	FW
Cyprinodontidae	Topminnows	■	■		■	■		4	FW
Cichlidae	Tilapias, bream	■	■	■				31	FW
Anabantidae	Climbing perch	■	■					2	FW
Mastacembalidae	Spiny eels	■	■					3	FW
Anguillidae	Eels	■	■	■	■	■	■	4	secondary FW
Gobiidae	Gobies	■	■	■	■	■	■	2	secondary FW
Megalopidae	Tarpons	■	■	■	■	■	■	1	M
Eleotridae	Sleepers	■	■	■	■	■	■	2	M
Ambassidae	Glassies	■	■	■	■	■	■	2	M
Mugilidae	Mullets	■	■	■	■	■	■	2	M
Syngnathidae	Pipefish	■	■	■	■	■	■	2	M
Monodactylidae	Moonies	■	■	■	■	■	■	2	M
Sparidae	Sea bream	■	■	■	■	■	■	1	M
Carcharhinidae	Sharks	■	■	■	■	■	■	1	M
Pristidae	Sawfish	■	■	■	■	■	■	1	M

which include the tilapias and their allies, are most diverse in Africa and also extend into Asia with a few species in the Middle East and India.

Cichlids are one of eight families that occur in southern Asia as well as in Africa. The link between the Afrotropical and Oriental regions seems, therefore, to be rather stronger than the link between the Afrotropics and the Neotropics. Other families that occur in both regions include the air-breathing catfishes (Clariidae), many of which are similar to the well-known African catfish, *Clarias gariepinus*, the climbing perch (Anabantidae) and the spiny eels (Mastacembalidae).

Most of the evolution of African fish over the last 60 million years or so took place within the continent. Consequently, half of the fish families found in the Zambezi Basin are of African origin and are found nowhere else. Madagascar evidently broke away from Africa before this radiation took place and only three Zambezian families also occur on that island.

Finally, another eight families are of marine origin and have a global distribution in all oceans. Two goby species (Gobiidae) are found in the Zambezi and breed in fresh water. Four species of eels (Anguillidae) occur in the system but they breed at sea after spending up to 15 years in rivers and streams. The remaining six families represent estuarine species (including the shark) that occasionally penetrate fresh water and all have been collected in the lower reaches of the Zambezi.

7.2.3 **Post-Gondwana dispersion**

The freshwater fish fauna of the Zambezi Basin is made up of two major elements, the Zambezian and the East Coast. These elements evolved during the early Tertiary (about 50-60 million years BP) when the drainage patterns of southern Africa were quite different from those of the present (Figure 7.3a). The Zambezian fish fauna arose and evolved in the area of Upper Zambezi as it was then. This includes the present-day Cunene, as well as the Upper Kasai and the Chambeshi that were formerly part of the system but were later isolated through river capture. The Blotched Catfish, *Clarias stappersii*, is an example of a species whose distribution reflects its Zambezian origin (Figure 7.3b). The East Coast fauna lived in the then relatively short rivers that drained into the Indian Ocean. A few species, like the East Coast Barb, *Barbus toppini*, still retain this distribution (Figure 7.3b). Most others have been greatly modified, principally by penetrating inland along the Zambezi and Limpopo rivers.

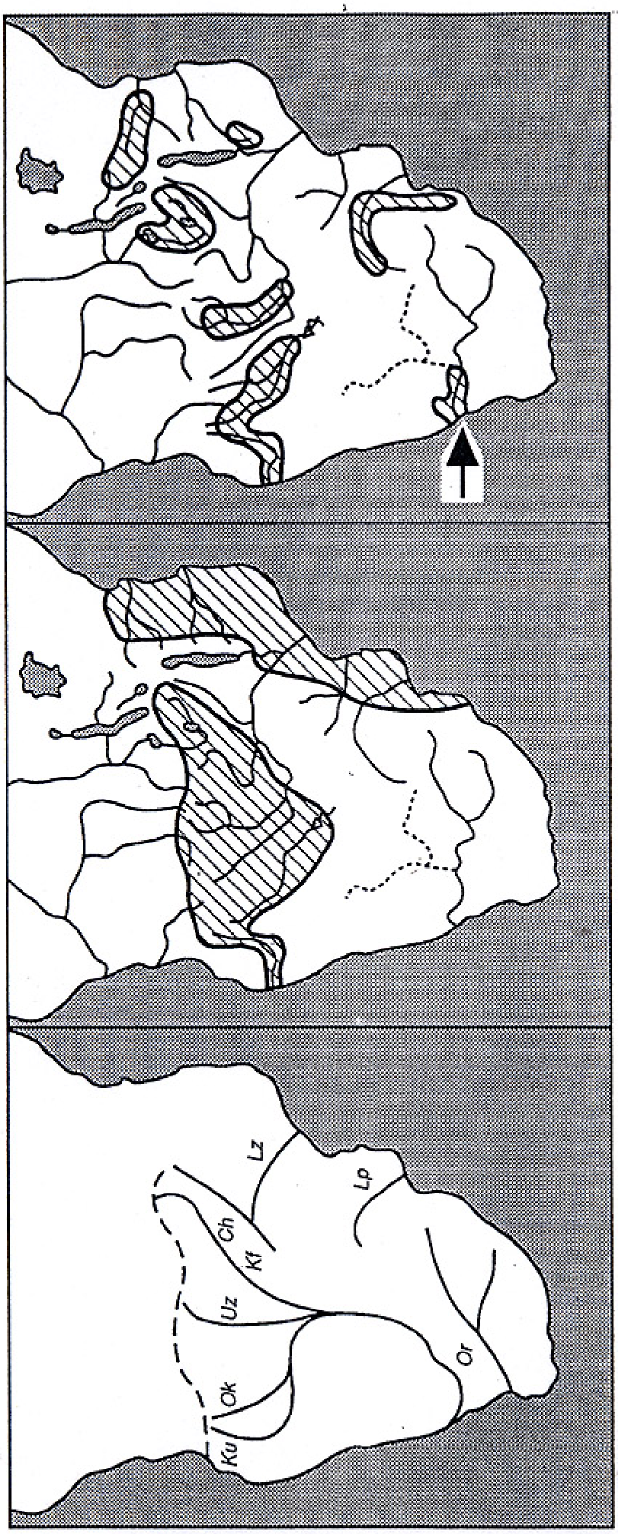
During this time, the Zambezi evidently drained into the Atlantic Ocean somewhere near the present-day mouth of the Orange River. Supporting evidence for this is provided by some species with a universal distribution in southern Africa or others like the River Sardine, *Mesobola brevianalis*, which has a fragmented but widespread distribution. It includes an isolated population in the Lower Orange (Figure 7.3c) which probably dates from the time the Zambezi discharged in this area.

Drainage patterns changed dramatically during the mid-Tertiary (about 20-30 million years BP). The course of the Upper Zambezi was diverted from the south to the southeast, i.e. from the Orange to the Limpopo. This event seems to have coincided with the infilling of the Kalahari basin (Figure 7.4a). The link between the Kafue and Chambeshi rivers was severed when the Chambeshi was captured by the Luapula to become part of the Congo drainage. The connection between the Kafue and the Upper Zambezi was severed when the former was captured by the Middle Zambezi. Evidence that the Zambezi once flowed to the Indian Ocean via the Limpopo is provided by the distribution of some Upper Zambezi fish in the Limpopo, such as the River Sardine (Figure 7.3c)

Figure 7.3 (a) Drainage patterns in southern Africa during the early Tertiary. Ku = Cunene, Ok = Okavango, Uz = Upper Zambezi, Kf = Kafue, Ch = Chambeshi, Lz = Lower Zambezi, Lp = Limpopo, Or = Orange.

(b) The typically Zambezian distribution of the Blotched Catfish, *Clarias stappersii* (left), which includes the Cunene, the upper Kasai and the Lake Bangweulu/Chambeshi system, and the typical east coast distribution of the East Coast Barb, *Barbus toppini* (right).

(c) The distribution of the River Sardine, *Mesobola brevianalis*; the isolated population in the Lower Orange (arrow) suggests an ancestral link with the Zambezi via the Kalahari.



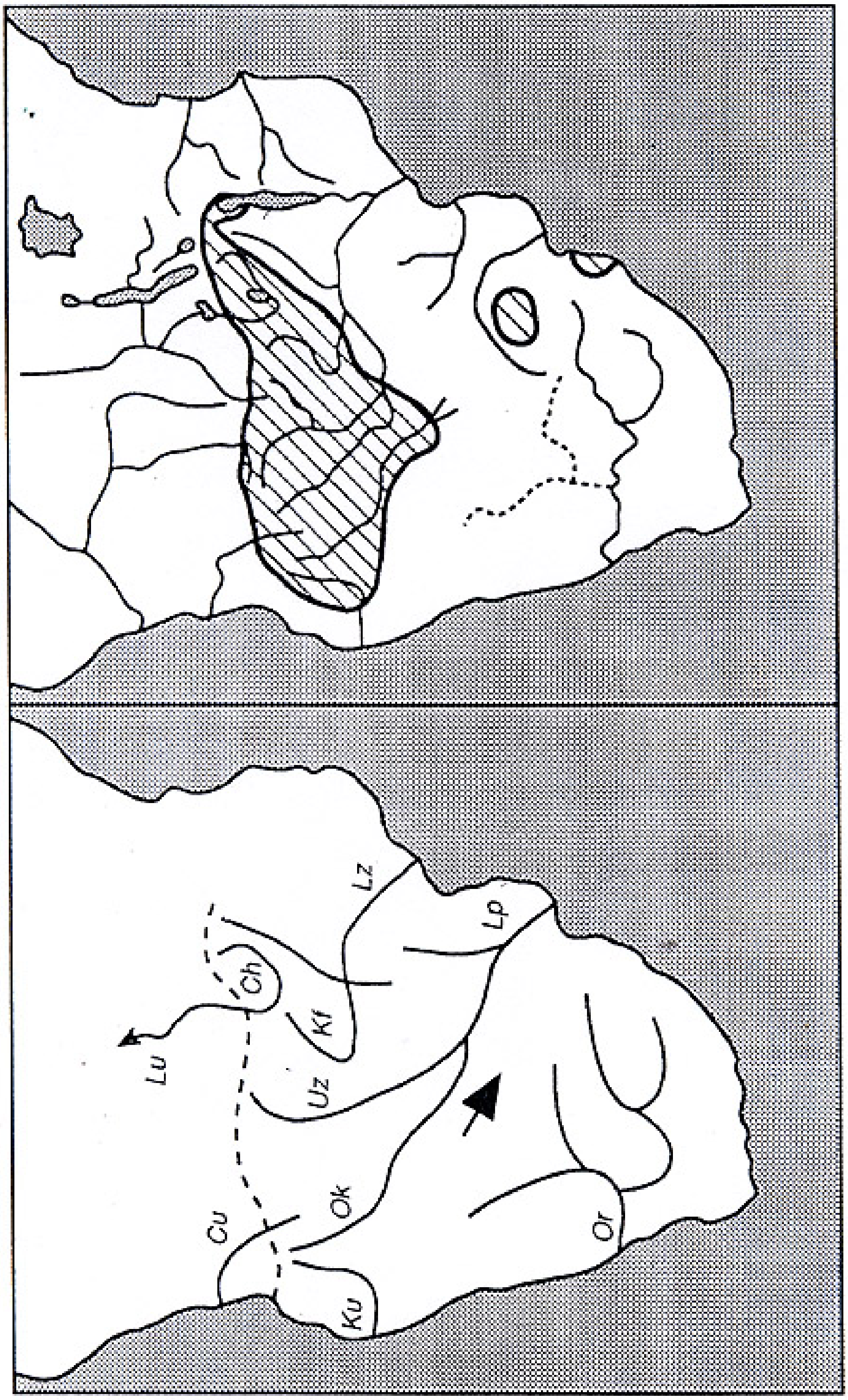
7.3(c)

7.3(b)

7.3(a)

Figure 7.4 (a) Drainage patterns in southern Africa during the mid-Tertiary. Abbreviations as in Fig. 7.3, plus Cu = Cuanza, Lu = Luapula.

(b) The distribution of the Hyphen barb, *Barbus bifrenatus*, showing its presence in rivers now isolated from the Zambezi, a relic of the former Zambezi-Limpopo connection.



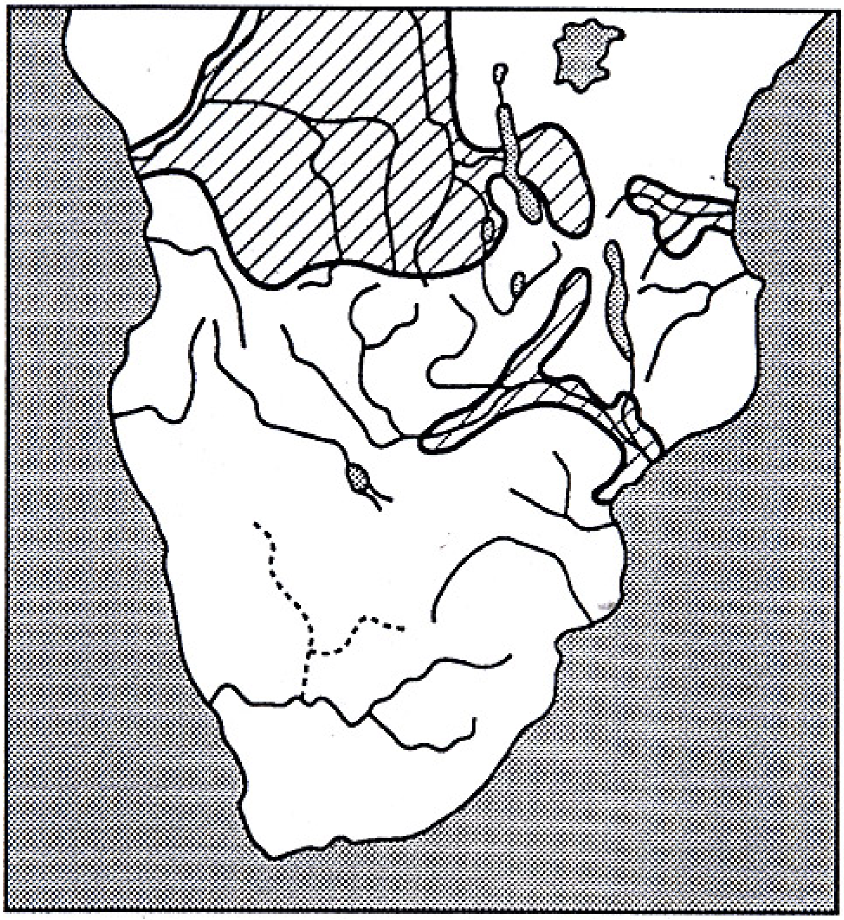
7.4(b)

7.4(a)

and the Hyphen Barb, *Barbus bifrenatus*. The latter are widespread in the Upper Zambezi and occur in the Cunene, Cuanza, Kafue and Chambeshi rivers, all streams isolated from the Zambezi by river capture. In the south an isolated population in the high-altitude tributaries of the Limpopo reflects the former connection between the two systems (Figure 7.4b).

The Hyphen Barb also occurs in the upper reaches of Lake Malawi and there was evidently a connection between the Chambeshi, the Congo and the Lower Zambezi systems in this region. The exact nature of this connection is unclear since the tectonic movements that formed the Rift Valley have obscured the evidence. Nevertheless several Upper Zambezi and Congo fish species have reached the Lake Malawi system by this route, while others have reached the Middle and Lower Zambezi, possibly via the Luangwa. They include well-known species like the Manyame labeo, *Labeo altivelis*, and the Vundu, *Heterobranchus longifilis* (Figure 7.5).

Figure 7.5 The distribution of the Vundu, *Heterobranchus longifilis*, a Congo species that was able to colonize the Middle and Lower Zambezi from the north.

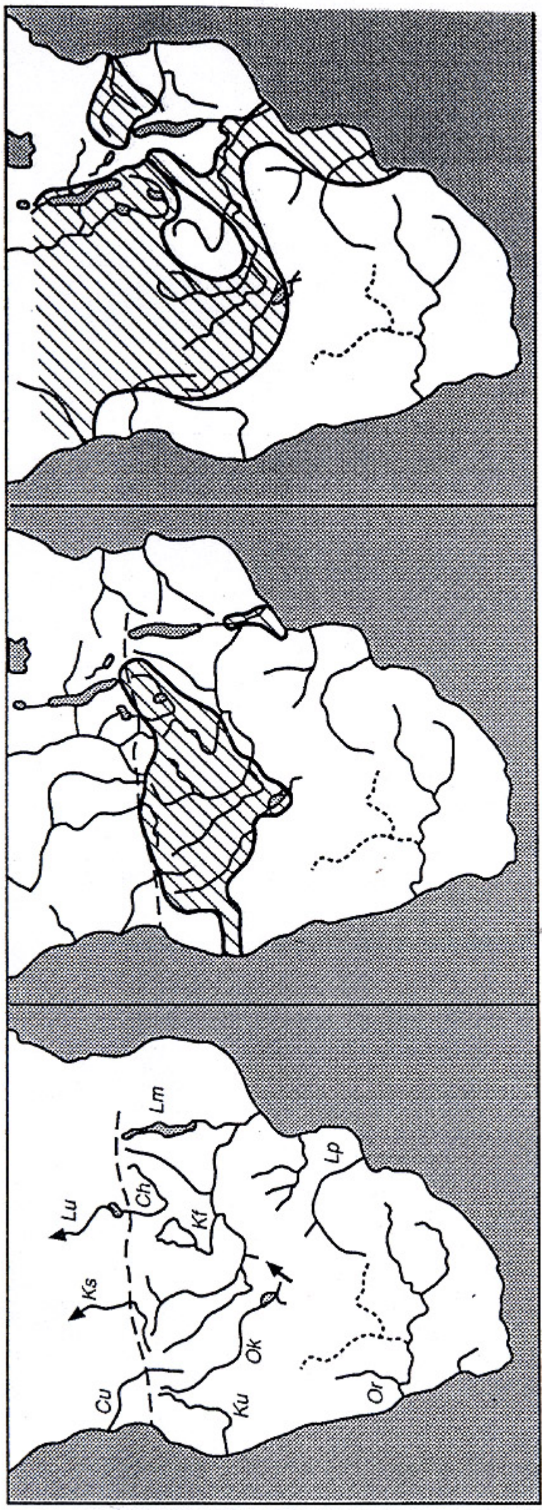


The connection between the Zambezi and the Limpopo was severed in the late Tertiary when uplift during the Pliocene (about 5 million years BP) rejuvenated the erosion cycle, enabling the Middle Zambezi to capture the Upper Zambezi, creating the Victoria Falls and the Batoka Gorge (Figure 7.6a). This enabled a number of Upper Zambezi fish to colonise the Middle and Lower sections of the river. The Sickle-fin Barb, *Barbus haasianus*, found in the Upper Zambezi and the Chambeshi as well as the Lower Zambezi, Lower Shire and Pungwe rivers, is an example (Figure 7.6b).

Figure 7.6 (a) Evolution of the modern drainage pattern in southern Africa during the late Tertiary, with the capture of the Upper Zambezi by the Middle Zambezi. Abbreviations as in Figs. 3 and 4, plus Lm = Lake Malawi. The broken line indicates the ancestral Zambezi-Congo watershed.

(b) The distribution of the Sickle-fin barb, *Barbus haasianus*, an Upper Zambezi species that was able to reach the floodplains of the Lower Zambezi.

(c) The southern distribution of the Tigerfish, *Hydrocynus vittatus*, another invader of the Middle Zambezi. It was unable to reach the Kafue or Lake Malawi because of physical barriers to its upstream movement.

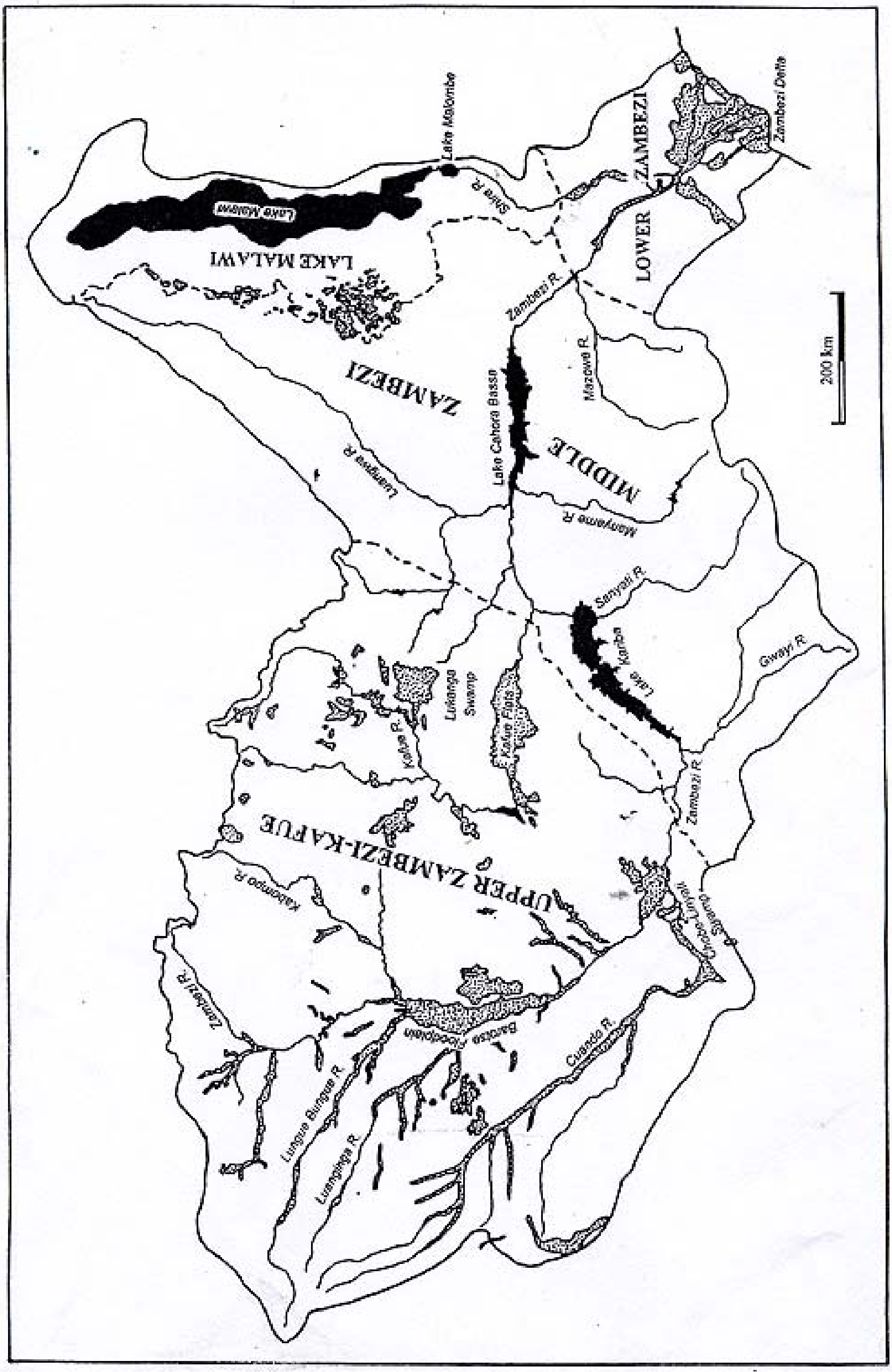


7.6(c)

7.6(b)

7.6(a)

Figure 7.7 The Zambezi Basin and its four major ichthyological divisions. The principal floodplains and wetlands are indicated by stippling, while the larger lakes and reservoirs are indicated by black shading. Based on a map drawn from data in Hughes & Hughes (1992). Note that the Okavango system is excluded, but it resembles the Upper Zambezi-Kafue by having extensive wetlands and floodplains.



The interrupted distribution of the Sickle-fin Barb came about because of its habitat preferences. It is a species that inhabits swamps and floodplains. These are widespread in the Upper Zambezi but absent in the lower river except along the coast and along the Lower Shire. Here the Sickle-fin Barb has been able to establish itself. One reason why the Middle Zambezi was so inhospitable to many Upper Zambezi species was a lack of vegetation growing in the water. This made them vulnerable to predation by the Tigerfish, *Hydrocynus vittatus*, itself an invader (Figure 7.6c). After the capture of the Upper Zambezi, it colonized the river downstream and its major tributary, the Luangwa and spread southwards into rivers of the east coast. The tigerfish could not invade the Kafue or go up the Shire into Lake Malawi because waterfalls on these rivers prevented them from moving upstream.

7.3 ICHTHYOLOGICAL REGIONS OF THE ZAMBEZI

The hydrological basin of the Zambezi can be divided into four principal ichthyological regions, each with its own distinctive fish species and families (Figure 7.7). The fish fauna in some other areas is still dominated by fish of Zambezian origin even though they are no longer linked hydrologically to the Zambezi system. The nature of these regions, and the evolution of their fish fauna, has been described in detail elsewhere (e.g. Bell-Cross 1972, Bowmaker, Jackson & Jubb 1978, Jackson 1986, Skelton 1994).

7.3.1 **The Upper Zambezi-Kafue system**

The Zambezi Basin can be divided into two distinct regions by a line extending from the Victoria Falls north-eastwards along the northern escarpment of the mid-Zambezi valley in Zambia to the northern watershed of the Luangwa. To the north and west of this line lie the drainage basins of the Upper Zambezi and Kafue rivers, the first of its four ichthyological regions. These rivers drain one of the most ancient African land surfaces that has been subjected to rather gentle pressures over millennia, leading to gradual uplift and subsidence and resulting in a landscape of "swells and depressions" and low relief (Handlos 1982). The gradients of the main rivers are gentle; the Zambezi falls by only 500 m over a distance of 1080 km from its source to the Victoria Falls (Davies 1986), while the Kafue falls by 380 m in the 1500 km between its source and the Kafue Gorge (Handlos 1982).

This topography, combined with relatively high rainfall, has produced extensive swamps and floodplains that regulate the flow of the rivers so that they seldom exhibit large variations in height. The floodplains have water on them for long periods, while the low water flows are of relatively short duration. Marginal vegetation is abundant and provides cover for small fish species, and juveniles of larger ones. These rivers have been termed "reservoir" rivers (Jackson 1986) and favour the evolution of fish species. Consequently, there are more fish species in the Upper Zambezi than in any other part of the system, except for Lake Malawi, and many of them are adapted to living in marshes.

Special features of the fish fauna include a radiation of serranochromine cichlids in the genera *Serranochromis* (6 species) and *Sargochromis* (5 species) and of mochokid catfishes in the genus *Synodontis* (7 species), while there is a larger number of small cyprinids and characids compared to the rest of the river. Other distinctive fish in this basin include the African Pike, *Hepsetus odoe*, two anabantids (*Ctenopoma multispine* and *C. intermedium*) and two mastacembelids (*Aethiomastacembelus frenatus* and *A. vanderwaali*).

In this region, the Zambezi River and its tributaries support the most species, 89 in total, of which 29.2% are cyprinids, 21.3% are cichlids and 10.1% mochokids (Table 7.2 - see end of review). The fish fauna of the Okavango is virtually the same as that of the Upper Zambezi and reflects the fact that the two systems are still intermittently connected via the Selinda spillway, which joins the Okavango and the Chobe-Linyati at periods of very high flood. Also, some of the Upper Zambezi species are only known from single specimens, e.g. *Paramormyrops jacksoni*, or a few from isolated localities, e.g. *Barbus mattozi, Schilbe yangambianus*. There are essentially no significant differences between the two systems, which is not the case as far as the Kafue system is concerned.

The Kafue was thought to have been isolated from the Upper Zambezi in the mid-Tertiary and it has fewer species than the latter (Table 7.2). It was also isolated from what is now the Zambian Congo drainage when the Chambeshi River was captured by the Luapula at about the same time. Consequently, it was not colonized by Congo species that invaded the Upper Zambezi, e.g. *Hippoptamyrus discorhynchus* and *Hydrocynus vittatus*, or the Middle Zambezi via the Chambeshi/Lake Rukwa/Luangwa River connection, e.g. *Labeo altivelis*, *Brycinus imberi* and *Heterobranchus longifilis*. The radiation of serranochromine cichlids in the Kafue is very similar to that of the Upper Zambezi, with nine species in the former compared to eleven species in the latter (*Serranochromis altus* and *S.longimanus* are absent from the Kafue). But the mochokid catfishes differ markedly, as there are only two species in the Kafue compared to eleven in the Upper Zambezi. Despite its relatively long isolation from the Zambezi, there is only one endemic species in the Kafue system, the killifish *Nothobranchius kafuensis* (although it may extend to the East Caprivi strip, in which case it loses this status).

The Cunene was isolated from the Zambezi at about the same time as the Kafue but its fish fauna is considerably different from both of those systems. Like the Kafue, it only has 66 fish species, but 9 of them (13.6%) do not occur anywhere else in the Zambezi system, and there are many more endemics. Six species, including four cichlids, are endemic to the Cunene system, namely *Kneria maydelli*, *Barbus breviceps*, *Orthochromis machadoi*, *Thoracochromis albolabrus*, *T. buysi* and *Sargochromis coulteri*. Two of the remainder have relict distributions that reflect the ancient connection between the Upper Zambezi and the Limpopo; *Labeo ruddi* occurs also in the Limpopo and Incomati systems, and there is a localised population of *Barbus argenteus* in the northern Drakensberg escarpment of South Africa. Finally, *Labeo ansorgii*, occurs in the Kwanza system in Angola as well as the Cunene.

The Chambeshi River, which once flowed into the Zambezi via the Kafue, was isolated some time in the early Tertiary when it was captured by the Luapula to become part of the Congo system. The Chambeshi and Lake Bangweulu were cut off from the Lower Luapula by the Johnston and Mumbatuta Falls and therefore have fewer species than the Lake Mweru/Luapula system (Table 7.3). Some typical Congo forms like the clupeids (sardines) failed to reach the Bangweulu system but others, like the tigerfish, *H. vittatus* and the Vundu, *H. longifilis*, did so. Nevertheless, the Chambeshi may have been a route for some of these Congo species to invade the Middle and Lower Zambezi.

7.3.2 **The Upper/Middle Zambezi boundary: waterfalls as barriers**

The transition from the Upper to the Middle Zambezi is abrupt and sharply demarcated. At the Victoria Falls the Zambezi drops by about 100 m while the Kafue falls by about 600 m in the 30 km stretch of the Kafue Gorge. Smaller tributaries of the Zambezi and the Luangwa which rise on the western plateau, such as the Kalomo, Mulungushi and Lunsemfwa, also drop steeply over the

Table 7.3 The number of species in each family in the Mweru/Luapula and Bangweulu/ Chambeshi systems of the Zambian Congo. Based on Jackson (1961a), updated as far as possible from CLOFFA (Daget *et al*. 1984, 1986, 1991). The list is probably incomplete.

	Mweru/ Luapula	Bangweulu/ Chambeshi
Protopteridae	1	
Mormyridae	15	8
Clupeidae	3	
Kneriidae	2	
Cyprinidae	25	20
Distichodontidae	2	1
Characidae	11	8
Hepsetidae	1	
Claroteidae	1	1
Amphiliidae	3	2
Schilbeidae	3	3
Clariidae	8	6
Mochokidae	8	5
Aplocheilidae	2	1
Cyprinodontidae	4	3
Cichlidae	15	10
Anabantidae	2	2
Mastacembelidae	2	1
Total number of species	103	67

escarpment. These rivers have Upper Zambezi or Kafue species in their plateau sections, but Middle Zambezi species below (Bell-Cross 1972, Balon 1974a), and the waterfalls that separate the two systems have always been regarded as major barriers.

The appearance in Lake Kariba during the late 1960s of several fish species typically found in the Upper Zambezi opened a debate on the nature of the Victoria Falls as a zoogeographical boundary. Balon (1974a, 1974b, 1978) asserted that the falls were not a major barrier to fish movements, as previous workers had thought, because fish had always been able to survive the drop over them but could not live in the harsh conditions of the river below. He postulated that the creation of Lake Kariba had changed this situation by providing a favourable habitat and, consequently, these fish were in the process of invading the system. Southern African workers challenged this view. They argued that (a) many of the alleged invaders were species that were widespread elsewhere in the Middle Zambezi, and (b) the few true Upper Zambezi invaders were more likely to have by-passed the falls through the turbines at the hydroelectric power station (Jubb 1976, Bowmaker *et al*. 1978, Marshall 1979, Kenmuir 1984). The importance of this debate, of course, lies in the general view that human activities, in the form of hydroelectric power stations, were breaking down major zoogeographical barriers in the system, which would change the species composition downstream of them.

Now, two decades later, these ideas can be examined again and there has clearly been little movement of fish across the barrier of the Victoria Falls. Twelve Upper Zambezi species have now been recorded from the Batoka Gorge below the Victoria Falls and from Lake Kariba (Table 7.4). But only two of them, the characid *Brycinus lateralis*, which may already have been in the river, and the cichlid *Serranochromis macrocephalus*, have successfully established themselves in the lake and invaded the river below the Kariba dam (Balon 1971, Marshall 1998). They almost certainly did this by passing through the hydroelectric turbines; the only other species to have done so was the introduced sardine *Limnothrissa miodon* (Junor & Begg 1971). Movement in the reverse direction, i.e. upstream, is obviously more difficult but may not be impossible since the only eel, *Anguilla bengalensis*, to have been collected from the Upper Zambezi was collected in the header dam at the Victoria Falls power station (Bell-Cross 1974).

The fact that only a few species have been able to invade the Middle Zambezi via hydroelectric turbines calls into question the importance of these structures as a means of breaking down zoogeographical barriers. Furthermore, there are no records of fish species invading the Middle Zambezi through other hydropower schemes, like that on the Kafue Gorge. Other explanations for the presence of Upper Zambezi species below the Victoria Falls should therefore be considered and the distribution of one of them, the Dash-tailed Barb, *Barbus poechii*, may provide one.

This fish is widely distributed in the Upper Zambezi and Upper Kafue drainage basins but it has also been taken from a number of places in the Zambezi system below the Victoria Falls (Figure 7.8). It occurs in the Kalomo River above the Siengwazi Falls (which has a typically Upper Zambezi fauna; Balon 1974b), in the Batoka Gorge, and again in the headwaters of the Matetsi and Deka Rivers. This distribution pattern suggests that the Batoka Gorge may be a transitional zone between the Upper and Middle Zambezi systems. It may also reflect the drainage system in the mid-Tertiary when the Zambezi flowed southwest into what is now the Kalahari Basin (another remnant of which is visible in the Ngwezi River that flows southwest to join the Zambezi west of the Victoria Falls). This drainage pattern was severed when the Middle Zambezi captured the Upper Zambezi to create the Victoria Falls, and the existing populations of *B. poechii* may therefore be relicts from this time. The same could apply to the other Upper Zambezi species and their appearance in Lake Kariba in 1968-69 may reflect the existence of some relict populations below the Batoka Gorge. Balon (1974a, 1974b, 1978) suggested that the survival of Upper Zambezi species would be assured by the new and more favourable environment of the lake, but this does not seem to have been the case. Those species collected only in the Batoka Gorge have not moved into the lake, while those collected from the lake itself seem to have disappeared or, if present, occur in very small numbers. Evidently, the lake has not offered an especially favourable environment for them and they may have failed to compete with the more numerous native species. This behaviour is more consistent with that of relict species, rather than that of strongly invasive ones.

Table 7.4 Records of Upper Zambezi fish species from the Zambezi River below Victoria Falls (Batoka Gorge) and Lake Kariba. From data in Balon (1974a, 1974b), Kenmuir (1983), Sanyanga & Feresu (1994), Anon. (1995a), Sanyanga *et al*. (1995) and Marshall (1998), as well as unpublished records from the Natural History Museum of Zimbabwe, Bulawayo (NMZB).

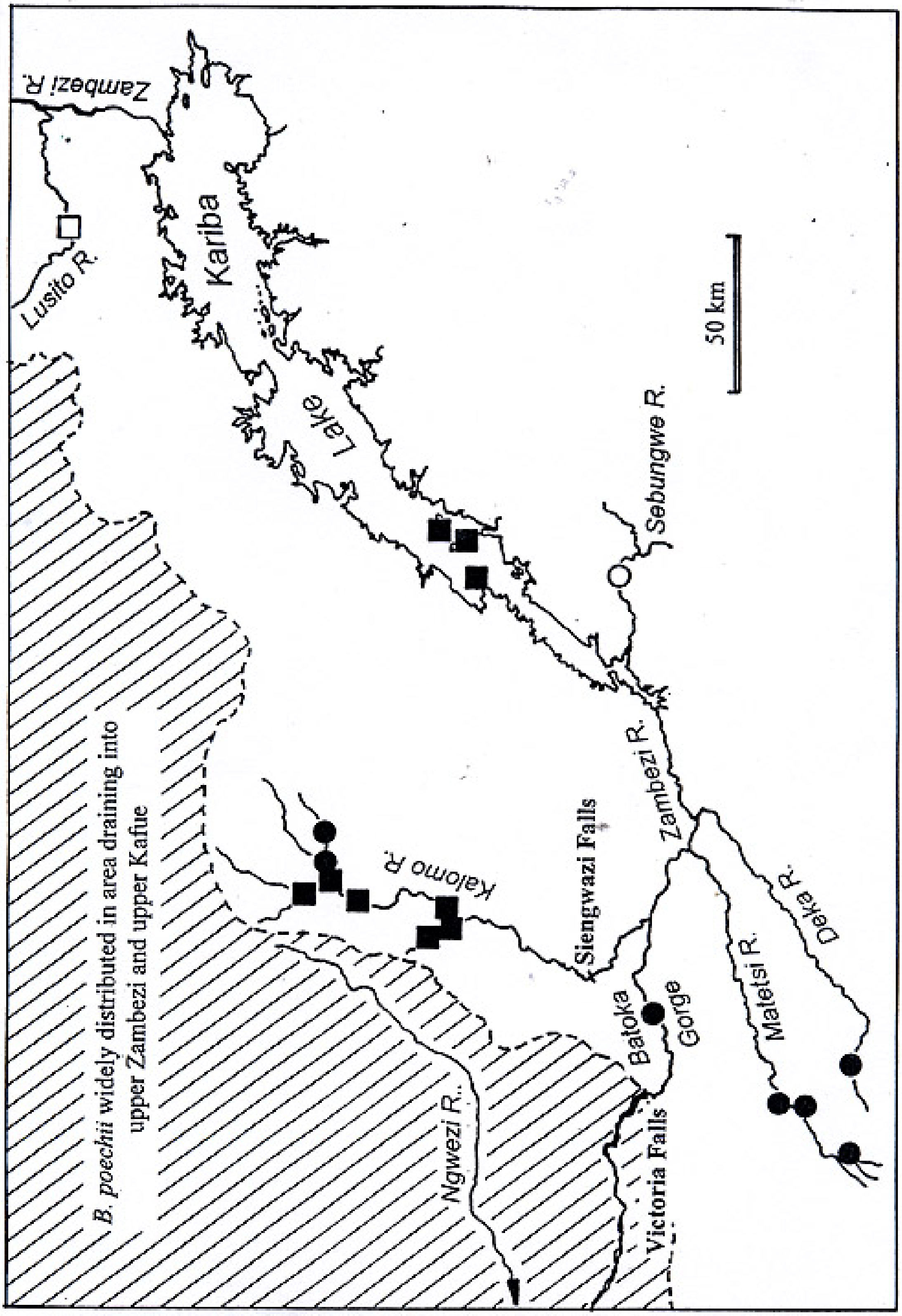
Species	Batoka Gorge	Lake Kariba	Remarks (number of specimens in brackets)
Mormyrus lacerda	●		Specimen in NMZB
Brycinus lateralis	●	●	Abundant throughout middle Zambezi
Hepsetus odoe		●	Deka R. (2) and Lake Kariba (1).
Barbus poechii	●	●	Lake Kariba, 1968-69 (9); no further records. Batoka specimen in NMZB
Barbus afrovernayi	●		Specimen in NMZB
Labeo lunatus		●	Lake Kariba, 1968-69 (1); possibly misidentified as specimen weighed only 14 g, no further records.
Hemichromis elongatus	●		Specimen in NMZB
Serranochromis robustus		●	Lake Kariba, 1968-69 (2); no further records
Serranochromis macrocephalus		●	Lake Kariba, 1966; now widespread and has reached Zambezi R. downstream
Sargochromis giardi		●	Lake Kariba, 1968-69 (127) and 1997 (1)
Sargochromis carlottae		●	Lake Kariba, 1968-69 (24); no further records
Oreochromis andersonii		●	Lake Kariba, 1968-69 (15); no further records
Aethiomastecembalus vanderwaali	●		Specimen in NMZB

The Churchill, *Petrocephalus catostoma*, is another species with a possibly relict distribution in the Middle Zambezi. It is widespread in the Upper Zambezi and is said to occur throughout the Middle Zambezi (Skelton 1993). But in Zambia it occurs only on the plateau sections of Zambezi tributaries (Jackson 1961a) and there are no records from the Zambezi itself or Lake Kariba (Jackson 1961b, Kenmuir 1983), or any of the Zimbabwean tributaries of the Zambezi (unpublished records, Natural History Museum, Bulawayo). Finally, Bell-Cross (1972) noted the presence of a catfish, which he referred to as *Clarias submarginatus*, in Lake Lusiwashi, a small waterbody on a tributary of the Luangwa. This species is not, in fact, *C. submarginatus* but probably *C. stappersii*, which occurs in the Chambeshi but not the Middle Zambezi. This probably represents a relict distribution from a time when the upper reaches of some Luangwa tributaries drained into the Chambeshi.

7.3.3 **The Middle Zambezi system**

Conditions to the east and south of the line that divides the Upper Zambezi and Kafue dividing line are very different from each other. The Middle Zambezi flows through a part of the continent that has been broken into deep troughs by the processes associated with the evolution of the African Rift Valley. The Middle Zambezi trough extends from the Victoria Falls to the Cabora Bassa Gorge, with a north-eastern extension up the Luangwa Valley. Its floor is much lower than the upper Zambezi-Kafue plateau and both rivers drop precipitously into it. The Middle Zambezi flows through several deep gorges, two of which (Kariba and Cabora Bassa) have been dammed to create huge artificial lakes.

Figure 7.8 Records of the Dash-tailed Barb, *Barbus poechii*, in the Zambezi system below the Victoria Falls. The circles denote records from the Natural History Museum, Bulawayo (NMZB) and the squares are records from Balon (1974). The open circle and square on the Sebungwe and Lusito rivers, respectively, are records for which the exact locality is not known. The shaded area is that part of the basin draining into the Upper Zambezi and Upper Kafue, where *B. poechii* is widespread.



This part of the basin is more arid than the Upper Zambezi, and its topography is more varied and geologically heterogeneous. There are few floodplains or swamps and the flow of the rivers is much more variable with short-lived floods and long periods of low flow. Their erosive power is much greater and they have little marginal vegetation, being termed "sandbank" rivers (Jackson 1986). In these rivers small fish are exposed to severe predation, because of the lack of cover (Jackson 1963), and there are fewer species than in the Upper Zambezi (a total of 56 *vs* 84). A feature of the Middle Zambezi is the lack of cichlids, with only eight species compared to 19 in the Upper Zambezi (Table 7.2). Particularly noteworthy is the absence of *Serranochromis* (although this is changing as *S. macrocephalus* is invading the system) and only one *Sargochromis* species (*S. codringtonii*). The diversity of catfish is also lower, with only two clariids (compared to six in the Upper Zambezi) and two *Synodontis* species (against seven in the upper river). Another characteristic feature is the lack of small barbs (only 17 compared to 25), that indicates the importance of predation in the sandbank rivers of the Middle Zambezi.

Families that are present in the Upper Zambezi/Kafue but absent from the Middle Zambezi, except for the transitional zone of the Batoka Gorge (Table 7.4), include the Kneriidae (possibly), Hepsetidae, Claroteidae, Aplocheilidae, Anabantidae and Mastacembelidae. Families that occur in the Middle Zambezi, but not in the Kafue or Upper Zambezi, include some of marine origin like the Anguillidae, Megalopidae and Gobiidae, and the Electric Catfish (*Malapterurus*), which is of Congo origin. This ancient connection with the Congo is reflected in the distribution of a number of Middle Zambezi species. They include the Lungfish, *Protopterus annectens*, the Cornish Jack, *Mormyrops anguilloides*, the Manyame Labeo, *Labeo altivelis*, Nkupe and Chessa (*Distichodus* spp.), which are represented in the Chambeshi by related species, the Imberi *Brycinus imberi* (Figure 7.9) and the Vundu *Heterobranchus longifilis*.

7.3.4 **The Lower Zambezi system**

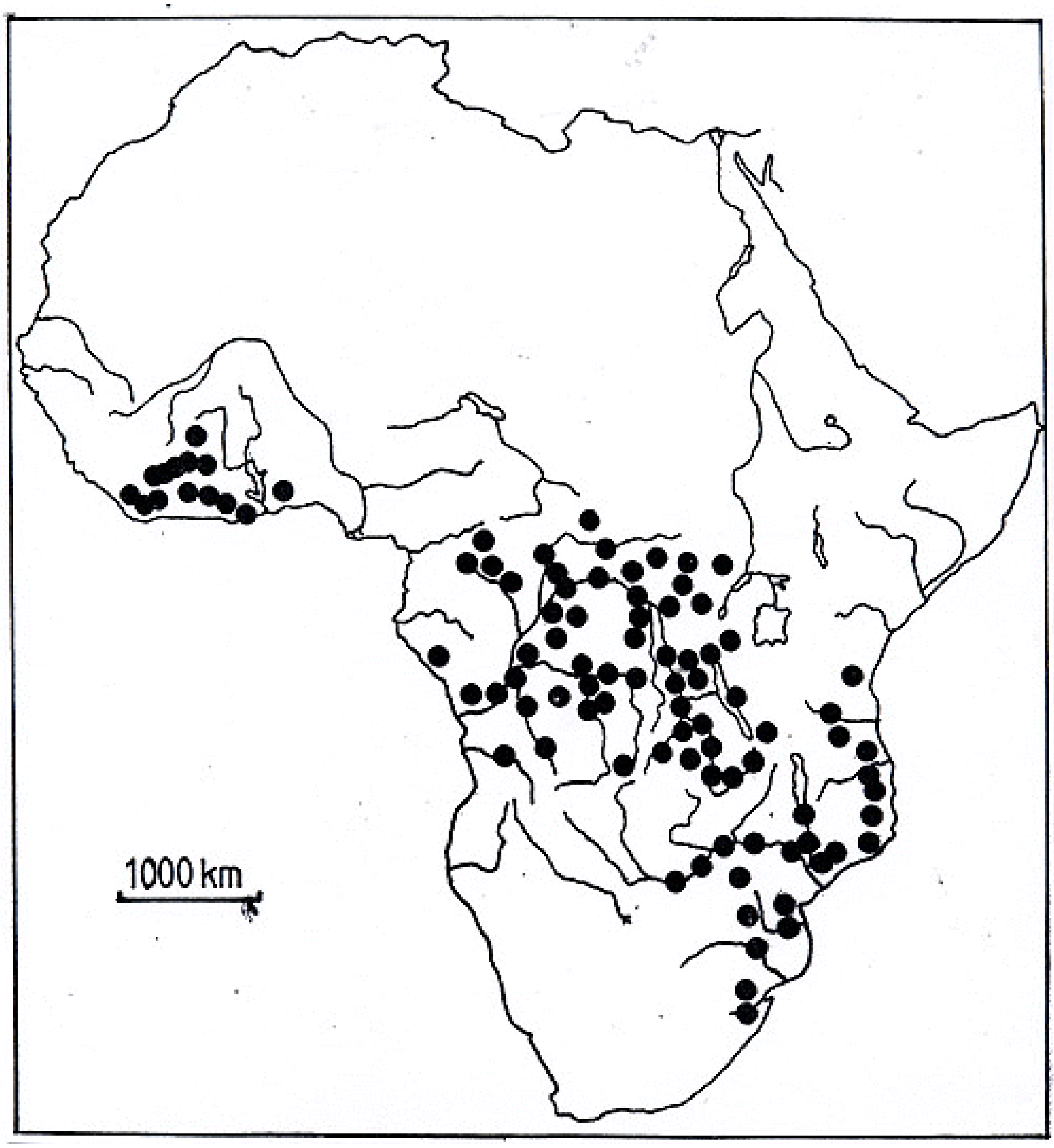
The boundary between the Middle and Lower Zambezi is poorly defined as there are no major natural barriers. The Cabora Bassa Gorge is conventionally regarded as the boundary (Bell-Cross 1972, Jackson 1986) and some marine groups, like the gobies (Gobiidae), tarpon *Megalops cyprinoides* and, occasionally, the Bull Shark *Carcharhinus leucas*, may occur inland as far as the gorge, but not beyond it. It is important to note that the Zambezi River itself, and its tributaries in particular, are still typical sandbank rivers for some distance below the gorge. The Lupata Gorge, downstream of the Zambezi-Mazowe confluence, is probably a better boundary because it marks the point where the Zambezi debouches onto the Mozambique Plain and once again becomes a floodplain system with much greater habitat diversity (Figure 7.7). These floodplains, which distinguish the Lower Zambezi, extend into the Zambezi Delta and up the Shire River almost to the Kapachira Falls.

The fish fauna contains all the elements of the Middle Zambezi, but the number of species is larger (Table 7.2), with the total rising to 83. There are several reasons for this:

(a) Some marine species enter the river from the delta (about 14 are listed in Skelton (1993) and some others have recently been collected);
(b) The occurrence of some east coast species which are typically found in the floodplains, including the East African Lungfish, *Protopterus amphibius*, the barbs *Barbus viviparus, B. toppini, B. afrohamiltoni* and *B. macrotaenia*, Barnard's Robber *Hemigrammopetersius barnardi*, the killifish *Nothobranchius orthonotus* and *N. rachovii*, the Eastern Bream *Astatotilapia calliptera* and the Black Tilapia *Oreochromis placidus*;

(c) Some species that are more typical of the Malawi region enter the Lower Zambezi in the Shire and its tributaries close to the waterfalls that separate the two systems. They include the barred minnow *Opsaridium tweddleorum*, the Silver Barb *Barbus choloensis*, the Pungwe Chiselmouth *Varicorhinus pungweensis* and the Shire Tilapia *Oreochromis shiranus*.

Figure 7. 9 The distribution of the Imberi, *Brycinus imberi*, (Paugy, 1986). Note how a species with a widespread African distribution was able to colonize the Middle and Lower Zambezi via the Chambeshi/Lake Rukwa route, but was unable to move upstream into the Upper Zambezi and Kafue because of the physical barriers on those rivers.



Some species typical of the Upper Zambezi floodplain systems reappear in the floodplains of the Lower Zambezi, having been unable to survive in the Middle Zambezi where floodplains are absent. They include the mormyrids, *Hippopotamyrus ansorgii* and *Petrocephalus catostoma*, the barbs, *Barbus haasianus* and *B. eutaenia* (Shire tributaries only), the Blunt-toothed and Snake catfishes, *Clarias ngamensis* and *C. theodorae*, the Mesh-scaled Topminnow, *Aplocheilichthys hutereaui*, and the two anabantids, *Ctenopoma multispine* and *C. intermedium*. Another family of the Upper Zambezi, the mastacembalids, is represented by *Aethiomastecembemus shiranus*, which is similar to – and possibly the same as – the Upper Zambezi species *A. frenatus* (Skelton 1993).

The fishes of the Pungwe and Buzi rivers are closely linked to those of the Lower Zambezi (Table 7.2) with a similarity index of 0.86. This reflects an ancient connection between the two rivers systems, as they were probably connected during glacial periods when the sea level was lower (Bell-Cross 1973). More recent connections may also exist via a trough of low-lying wetlands connecting the Zambezi and Pungwe as well as the coastal wetlands.

7.3.5 **The Lake Malawi system**

Lake Malawi is the southernmost lake of the African Rift Valley system and the third largest on the continent. It is estimated to be several million years old and its level is believed to have risen and fallen extensively over this period, which has contributed to the evolution of its distinctive and unique fish fauna (Owen *et al*. 1990). The lake is hydrologically a part of the Zambezi system but its fish fauna is isolated from it by the Kapachira Falls on the Shire River. Few Zambezian fish species have been able to penetrate this barrier and move into the Upper Shire or the lake itself (Tweddle, Lewis & Willoughby 1979, Tweddle & Willoughby 1979). Lake Malawi is best known for its large and diverse fauna of haplochromine cichlids, numbering perhaps 400-500 endemic species, but its non-cichlid species are equally distinct (Table 7.5).

A particular feature of the fish fauna of the Lake Malawi basin is the high degree of endemicity. The extraordinary endemicity of the cichlids – at least 99% and probably more as new species, especially from the poorly-studied Tanzanian and Mozambican shores, are described - is well known. But the same applies to the non-cichlids, where 23 of the 46 species (50%) are endemic. Many of the non-endemic species are those with a wide distribution, like the mormyrid *Mormyrops anguilloides*, the minnow *Barbus paludinosus* and the African Catfish *Clarias gariepinus*, which all occur extensively across the African continent.

7.3.6 **Similarities between components of the system**

The relationships discussed in the preceding sections can be illustrated by determining the number of species common to each sub-basin, and calculating a similarity index, as follows:

$$S = C/(N_1 + N_2 - C)$$

where S = similarity index, N_1 and N_2 = the total number of fish species in each sub-basin, and C = the number of fish species common to both.

The Lake Malawi system, because of its high endemicity, is least similar to any of the other sub-basins (Table 7.6). Similarities between the Chambeshi/Lake Bangweulu system and other parts of the basin are relatively low and rather uniform, probably because this system has fish from both the Upper and Lower Zambezi, as well as other species of Congo origin. The Chambeshi system is least similar to the Lower Zambezi because of the appearance of marine species in the latter, but rather

Table 7.5 Fishes of the Lake Malawi basin with their distributions in other systems. Based on Bell-Cross (1972) with additions from CLOFFA. The number of endemic cichlid species (281) is undoubtedly too low because many new ones have been discovered since CLOFFA 4 (Daget *et al*. 1991) was published.

Family	Species	Lower/Mid-Zambezi	Upper Zambezi	Zambian Congo	Rovuma/Rufigi rivers	Endemic
Anguillidae	*Anguilla bengalensis*	●			●	
Mormyridae	*Mormyrops anguilloides*	●		●	●	
	Petrocephalus catostoma	●	●	●	●	
	Hippopotamyrus discorhynchus	●	●	●	●	
	Marcusenius macrolepidotus	●	●	●	●	
	Marcusenius nyasensis					●
	Mormyrus longirostris	●		●	●	
Characidae	*Brycinus imberi*	●		●	●	
Cyprinidae	*Barbus arcislongae*					●
	Barbus eurystomus					●
	Barbus eutaenia	●				
	Barbus innocens			●		
	Barbus johnstonii					●
	Barbus macrotaenia	●				
	Barbus paludinosus	●	●	●	●	
	Barbus radiatus	●	●		●	
	Barbus litamba					●
	Barbus toppini	●			●	
	Barbus trimaculatus	●				
	Labeo cylindricus	●	●	●	●	
	Labeo mesops					●
	Labeo worthingtonii					●
	Opsaridium microlepis					●
	Opsaridium microcephalum					●
	Opsaridium tweddlorum	●				
	Engraulicypris sardella					●
Bagridae	*Bagrus meridionalis*					●
Amphiliidae	*Leptoglanis rotundiceps*	●	●	●	●	
	Amphilius uranoscopus	●			●	
Clariidae	*Clarias liocephalus*		●	●		
	Clarias gariepinus	●	●	●	●	

Family	Species	Lower/Mid-Zambezi	Upper Zambezi	Zambian Congo	Rovuma/Rufigi rivers	Endemic
	Clarias ngamensis	●	●	●		
	Bathyclarias (11 spp)					●
Mochokidae	*Chiloglanis neumanni*	●	●	●	●	
	Synodontis njassae					●
Cyprinodontidae	*Aplocheilichthys johnstonii*		●		●	
Aplocheilidae	*Nothobranchius orthonotus*	●				
Cichlidae	*Tilapia rendalli*	●	●	●	●	
	Tilapia sparrmanii		●	●	●	
	Astatotilapia calliptera	●				
	Pseuodocrenilabrus philander	●	●			
	Serranochromis robustus		●	●		
	Alticorpus (5 spp)					●
	Aristochromis (1 sp)					●
	Aulonacara (17 spp)					●
	Buccochromis (7 spp)					●
	Caprichromis (2 spp)					●
	Champsochromis (2 spp)					●
	Cheilochromis (1 sp)					●
	Chilotilapia (1 sp)					●
	Copadiachromis (20 spp)					●
	Corematodus (1 sp)					●
	Ctenopharynx (3 spp)					●
	Cyathochromis (1 sp)					●
	Cynotilapia (2 spp)					●
	Cyrtocara (1 sp)					●
	Dimidiochromis (4 spp)					●
	Diplotaxodon (3 sp)					●
	Docimodus (2 sp)					●
	Eclectochromis (3 spp)					●
	Exochromis (1 sp)					●
	Fossorochromis (1 sp)					●
	Genyrochromis (1 sp)					●
	Hemitaeniochromis (1 sp)					●
	Hemitilapia (1 sp)					●
	Iodotropheus (2 spp)					●

Family	Species	Lower/Mid-Zambezi	Upper Zambezi	Zambian Congo	Rovuma/Rufigi rivers	Endemic
	Labeotropheus (2 spp)					●
	Labidochromis (19 spp)					●
	Lethrinops (24 spp)					●
	Limnochromis (1 sp)					●
	Maravichromis (16 spp)					●
	Melanochromis (15 spp)					●
	Microchromis (1 sp)					●
	Naevochromis (1 sp)					●
	Nimbochromis (7 spp)					●
	Nyassachromis (6 spp)					●
	Oreochromis (5 spp)					●
	Otopharynx (12 spp)					●
	Petrotilapia (3 spp)					●
	Placidochromis (7 spp)					●
	Platygnathochromis (1 sp)					●
	Protomelas (14 spp)					●
	Pseudotropheus (31 spp)					●
	Rhamphochromis (8 spp)					●
	Sciaenochromis (3 spp)					●
	Stigmatochromis (4 spp)					●
	Taeniochromis (1 sp)					●
	Taeniolethrinops (4 spp)					●
	Tramitichromis (5 spp)					●
	Trematocranus (3 spp)					●
	Tyrannochromis (4 spp)					●
Mastacembalidae	*Aethiomastacembelus shiranus*	●				

more similar to the various basins of the Upper Zambezi, especially the Kafue, which reflects the historic connection between them.

The basins of the Upper Zambezi are all strongly similar to each other and their fish faunas are essentially the same. This applies to the Okavango but less so to the Kafue, where the similarities are lower, which is explained by the fact that it has been isolated from the Zambezi over a longer period. The Cunene is also relatively similar to the Upper Zambezi, but not to the middle and lower basins; this, too, reflects is derivation from the Upper Zambezi and lack of connection with the rest of the system.

As might be expected there are strong similarities between the basins of the Middle Zambezi. If the Upper Zambezi species that occur in the west of the Kariba area (Table 7.4) were excluded, then the similarity index between the Kariba and Cabora Bassa catchment would be considerably higher. The similarity between the two Lower Zambezi basins is also very strong, and would be higher if the marine species that occur in the Lower Zambezi were excluded. But the similarity indices between the two Middle Zambezi basins and the two Lower Zambezi ones were quite low (0.39-0.45), which reflects the presence of some Upper Zambezi and east coast species in the latter.

7.4 THREATS TO BIODIVERSITY

The continuing growth of the human population in the Zambezi Basin, and the demand for water for agriculture, industry and domestic uses, will increasingly strain water resources in some parts of the basin. These pressures will, in turn, adversely affect the biodiversity of the freshwater fishes. Stiassny (1997) has pointed out that freshwater fishes are amongst the most threatened animal groups and their biodiversity is decreasing at a faster rate than any other group. This situation will only be reversed through concerted programmes of catchment management. Setting aside protected areas is less likely to be effective for fish because rivers are linear systems whose ecology is determined by catchment processes that may have a downstream effect far distant from their origin. It is extremely difficult, therefore, to conserve particular sections of a river system unless problems elsewhere in the catchment can be controlled.

The Kruger National Park in South Africa illustrates these problems since it has a north-south orientation but its major rivers flow in an east-west direction and only a small proportion of their lengths is protected. Outside the Park, the rivers are heavily exploited for industry, mining and agriculture, and their flow ceases during the dry season (Allanson *et al*. 1990). These rivers were formerly perennial and the change has led to the extinction of six fish species (14%) out of a total of 42 in the Park (A. Deacon, pers. comm.).

7.4.1 **Climate change**

All aquatic environments depend on water and there are questions about its long-term availability, owing to climate change, throughout the basin. It is not possible to predict how global warming will influence rainfall, and therefore the water resources, of the Zambezi Basin. In Zimbabwe, the average temperature has risen by about 0.8ºC in 60 years while the average precipitation decreased by 10% in the period 1900-1994 (Unganai 1996). Records from 24 meteorological stations in Zambia, extending for periods of 30-50 years, indicate a declining trend at 24 of them, no change at six and an increasing trend at four (Anon. 1995b). The combination of reduced precipitation and increased evaporation (because of higher temperatures) has serious implications for the availability of water, and thus for fish habitats.

It is not clear if these trends are reflected in the flow of the main rivers, even though they have decreased sharply in recent years. The flow of the Zambezi at Victoria Falls, for example, seemed to increase slightly from the time records were first kept in 1907/08 until the mid-1940s (Figure 7.10). The flow then increased sharply until about 1960 and remained relatively high, but with considerable fluctuations until the end of the 1980s. Since then it has decreased rapidly and the flow in the 1990s was lower than at any time during the period of historical records. These alterations in river flow presumably reflect large-scale climatic changes but whether these represent the effect of human-induced climatic change, or some longer-term climatic cycle is still unknown.

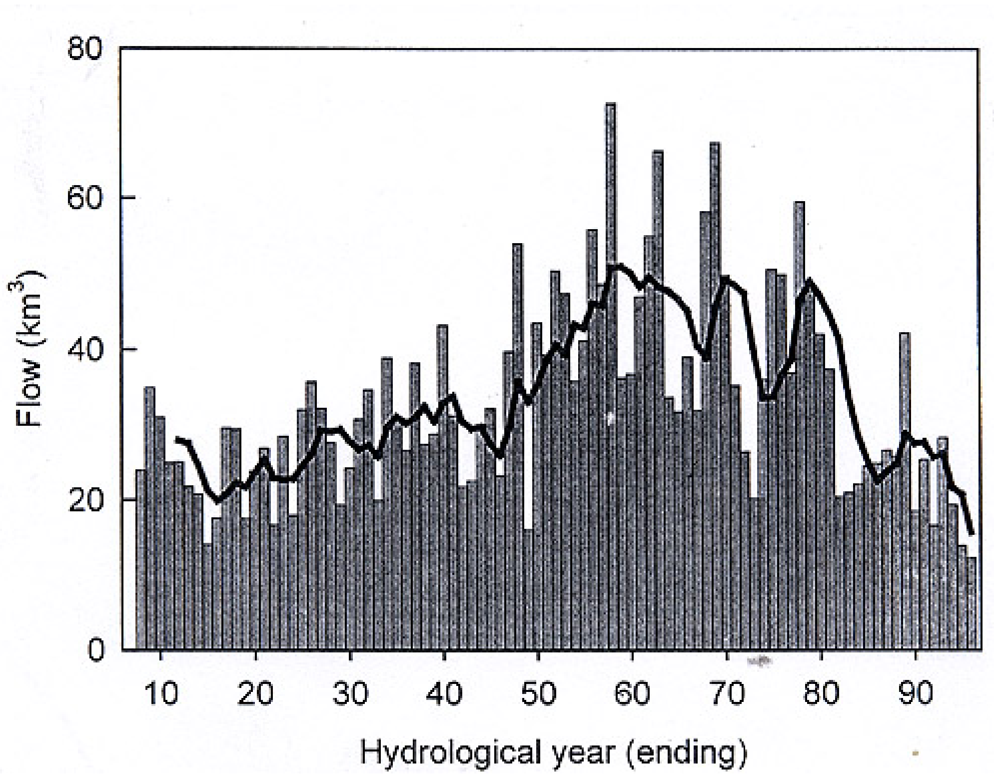
Table 7.6 The number of species in common in each of the main sections of the Zambezi Basin, including the Cunene, Chambeshi/Lake Bangweulu and Lake Malawi systems. The values in brackets are the similarity indices for each system, and the highest indices are indicated in bold type.

	L. Malawi	Chambeshi	Lower Zambezi	Lower Shire	L. Cabora Bassa & catchment	L. Kariba/ Mid- Zambezi	Kafue	Chobe/Caprivi	Barotse floodplain	Okavango	Zambezi headwaters
Cunene	16 (0.04)	29 (0.28)	22 (0.17)	22 (0.19)	17 (0.17)	25 (0.24)	45 (0.53)	51 (0.52)	52 (0.54)	54 (0.55)	54 (0.54)
Zambezi headwaters	18 (0.04)	36 (0.31)	29 (0.21)	29 (0.22)	24 (0.21)	33 (0.29)	61 (**0.68**)	78 (**0.86**)	78 (**0.87**)	79 (**0.85**)	
Okavango	17 (0.04)	35 (0.30)	28 (0.21)	28 0.22)	23 (0.21)	29 (0.25)	61 (**0.69**)	80 (**0.92**)	79 (**0.91**)		
Barotse floodplain	17 (0.04)	34 (0.30)	28 (0.20)	28 (0.22)	23 (0.21)	34 (**0.31**)	59 (**0.68**)	75 (**0.85**)			
Chobe/Caprivi	17 (0.04)	34 (0.29)	30 (0.23)	30 (0.24)	25 (0.24)	35 (0.32)	59 (**0.68**)				
Kafue	16 (0.04)	32 (0.32)	24 (0.21)	24 (0.21)	19 (0.20)	27 (0.28)					
Lake Kariba/Middle Zambezi	17 (0.04)	24 (0.23)	39 (0.39)	39 (0.41)	46 (**0.72**)						
Lake Cabora Bassa & catchment	22 (0.05)	22 (0.25)	39 (0.45)	40 (0.41)							
Lower Shire	22 (0.06)	28 (0.25)	66 (**0.80**)								
Lower Zambezi	18 (0.06)	28 (0.18)									
Chambeshi	18 (0.05)										

7.4.2 **Reservoir construction**

While the construction of hydroelectric power stations has not, as yet, significantly changed the fish fauna of the Zambezi Basin the same cannot be said of another, more widespread, human activity, the construction of dams. The Middle Zambezi has been completely changed by the construction of two great reservoirs, Lakes Kariba (c. 5400 km^2 when full) and Cabora Bassa (c. 2600 km^2). The construction of dams at Mupata, Devil's and Batoka Gorges, as well as some sites below Cabora Bassa, could destroy its last remaining riverine sections. It has long been feared that this activity will affect the Lower Zambezi by reducing floods and drying out the floodplains and delta (Davies, Hall & Jackson 1975), but little is known about these issues at present. Similar fears have been expressed about the Kafue Flats, which are now regulated by the Itezhi-Tezhi Dam at their western end and the Kafue Gorge Dam at their eastern end (Handlos 1982).

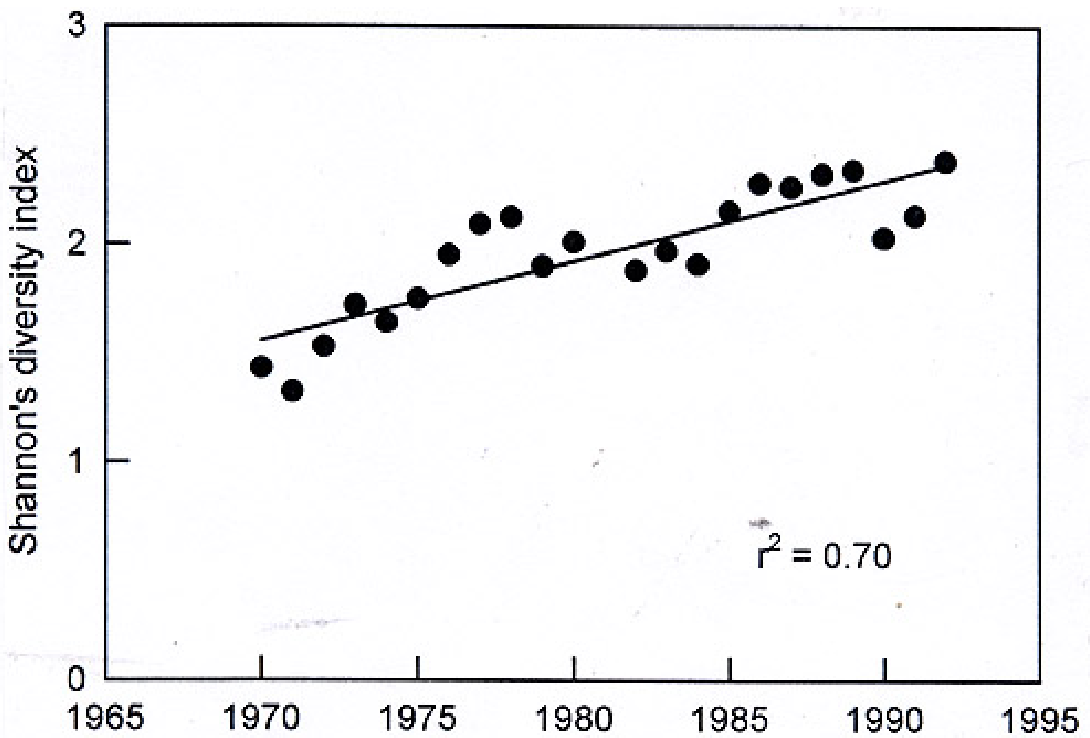
Figure 7.10 The flow of the Zambezi River (km^3) at Victoria Falls from 1907/08 to 1995/96 (columns) with a 5-year moving average (solid line) (data from Zambezi River Authority).



The most important impact of these reservoirs has been to change the composition of the fish species in the portions of the river drowned by them. Prior to the construction of Kariba, the Zambezi River was dominated by rheophilic fish species like cyprinids and distichodids (Jackson 1961b), but they declined rapidly after the dam was built. Some specialised riverine forms like the cyprinids, *Opsaridium zambezense* and *Barbus marequensis*, and the catlet *Chiloglanis neumanni*, disappeared completely from the lake. This meant that they have not been able to recolonize smaller rivers after periods of drought and the contraction in their range may have been rather greater than just the drowned section of the main river. The decline of *Labeo* and *Distichodus* was more pronounced in the larger, more lacustrine sections of the reservoir and they survive in greater numbers in the more riverine, western basins of the lake (Begg 1974).

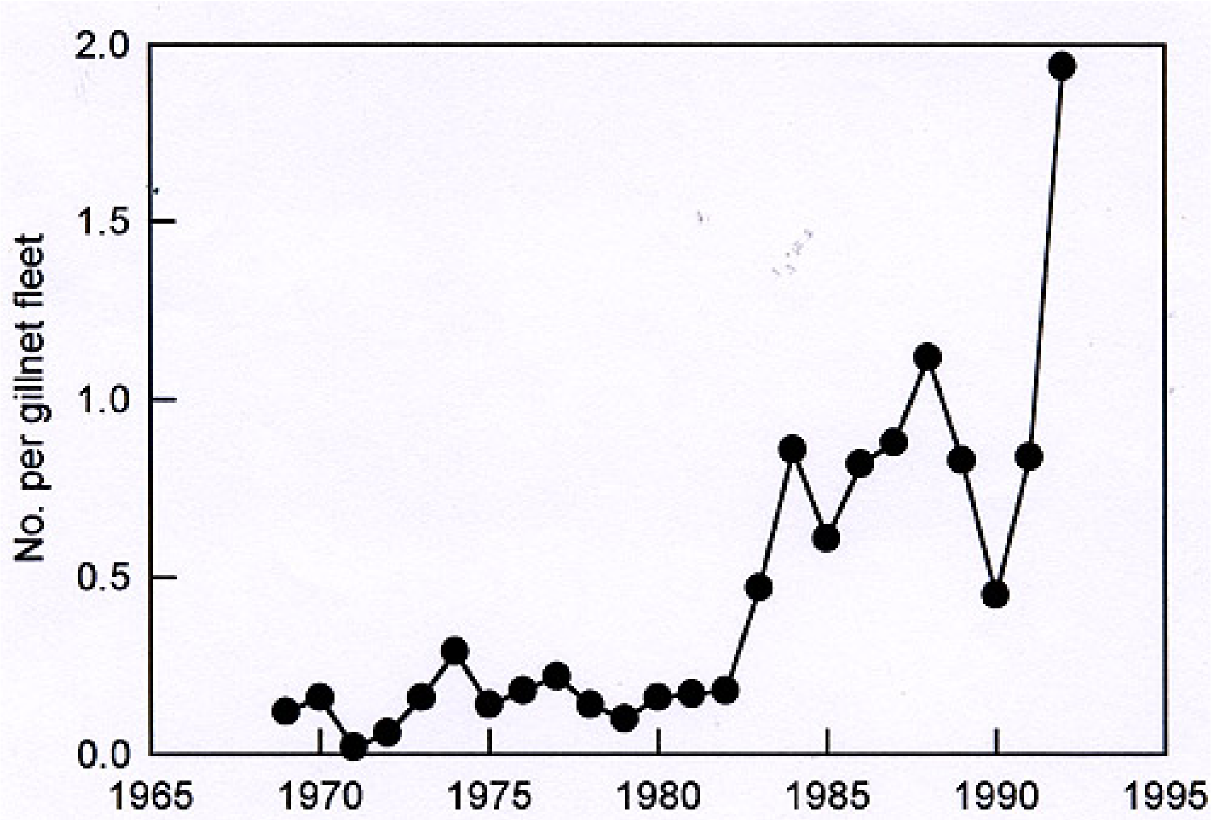
The principal beneficiaries of these reservoirs are species that can adapt to standing water. Jackson (1961b) collected very few cichlids from the river before the dam was built, and it was on the basis of these findings that the decision to stock them into the new lake was made. In reality, cichlid populations increased rapidly and they soon became the most important inshore species (Begg 1974, Kenmuir 1983, 1984). The fish fauna of Lake Kariba is still in a process of change and there seems to be a general increase in diversity (Figure 7.11). In the early years of the lake, it was dominated by only a few species of fish but others have gradually become increasingly abundant; a good example is the squeaker *Synodontis zambezensis*, which increased in abundance during the 1980s (Figure 7.12). Some of these changes may have been brought about by fishing, as suggested by Sanyanga *et al*. (1995), but perhaps more probably reflect the maturation process of the lake. These processes include the development and growth of submerged macrophytes, which have benefited some species like *Serranochromis macrocephalus* which was rare in the 1960s but is now abundant and widely distributed throughout the lake (Marshall 1998).

Figure 7. 11 Changes in the diversity of fish species in Lake Kariba, 1970-1992, indicated by Shannon's diversity index. The data are based on a weekly sampling programme using a standard fleet of gill nets ranging in size from 2" (50 mm) to 7" (175 mm) stretched mesh (redrawn from Kolding 1994).



Much of the interest in reservoirs has centred on Lake Kariba and, to a smaller extent, on Lake Cabora Bassa. Smaller reservoirs have been studied in much less detail but they may have had a significant impact on the species composition and diversity of fish. Small reservoirs are especially important in the Zimbabwean part of the Middle Zambezi, where about 7000 of them, ranging from 1 ha or less to 8000 ha in area, have been built (Figure 7.13). These reservoirs have become important features of the landscape and must have significantly changed the patterns of river flow and fish distribution. Unfortunately, little is known about these aspects and much remains to be learned about their impact.

Figure 7.12 The increase in the numbers of the squeaker *Synodontis zambezensis* in Lake Kariba, 1969-1992. Based on data from a standard fleet of gill nets ranging in size from 2" (50 mm) to 7" (175 mm) stretched mesh (redrawn from Sanyanga 1996).



The general trends among the fish fauna of small reservoirs seems to be largely similar to that in the large ones, i.e. a decline in rheophilic species like the labeos and other cyprinids, and an increase in cichlids. But they have another, and perhaps more significant, impact by providing suitable habitats for introduced species. Small reservoirs in Zimbabwe tend to have fewer species than large reservoirs but with a higher proportion of them being introduced exotics (Table 7.7). They may, indeed, be crucial to the survival of exotic species that might not be able to establish themselves in undammed rivers. If this is the case, then the construction of small reservoirs may prove to be one of the most important influences on the diversity and species composition of the Zambezi Basin.

7.4.3 **Introduced fish species**

The introduction of exotic species has the potential to change the fish fauna of the Zambezi Basin to a greater extent than almost any other human activity. The dramatic impact of the Nile perch, *Lates niloticus*, on the endemic haplochromines of Lake Victoria has heightened awareness of the potentially disastrous impact of introduced species and emphasised the need for vigilance, especially in sensitive areas like Lake Malawi (Lowe-McConnell 1993). While most of the countries in the basin have promulgated regulations to control or prohibit the importation of exotic fish species, and to monitor the movements of local fish species, they lack the capacity to enforce them and exotic fish species continue to be brought into the basin.

Figure 7.13 The distribution of reservoirs in the Zambezi Basin. Their concentration in Zimbabwe is noteworthy and greater than anywhere else in the basin (drawn from data in the FAO-ALCOM data base on inland waters).

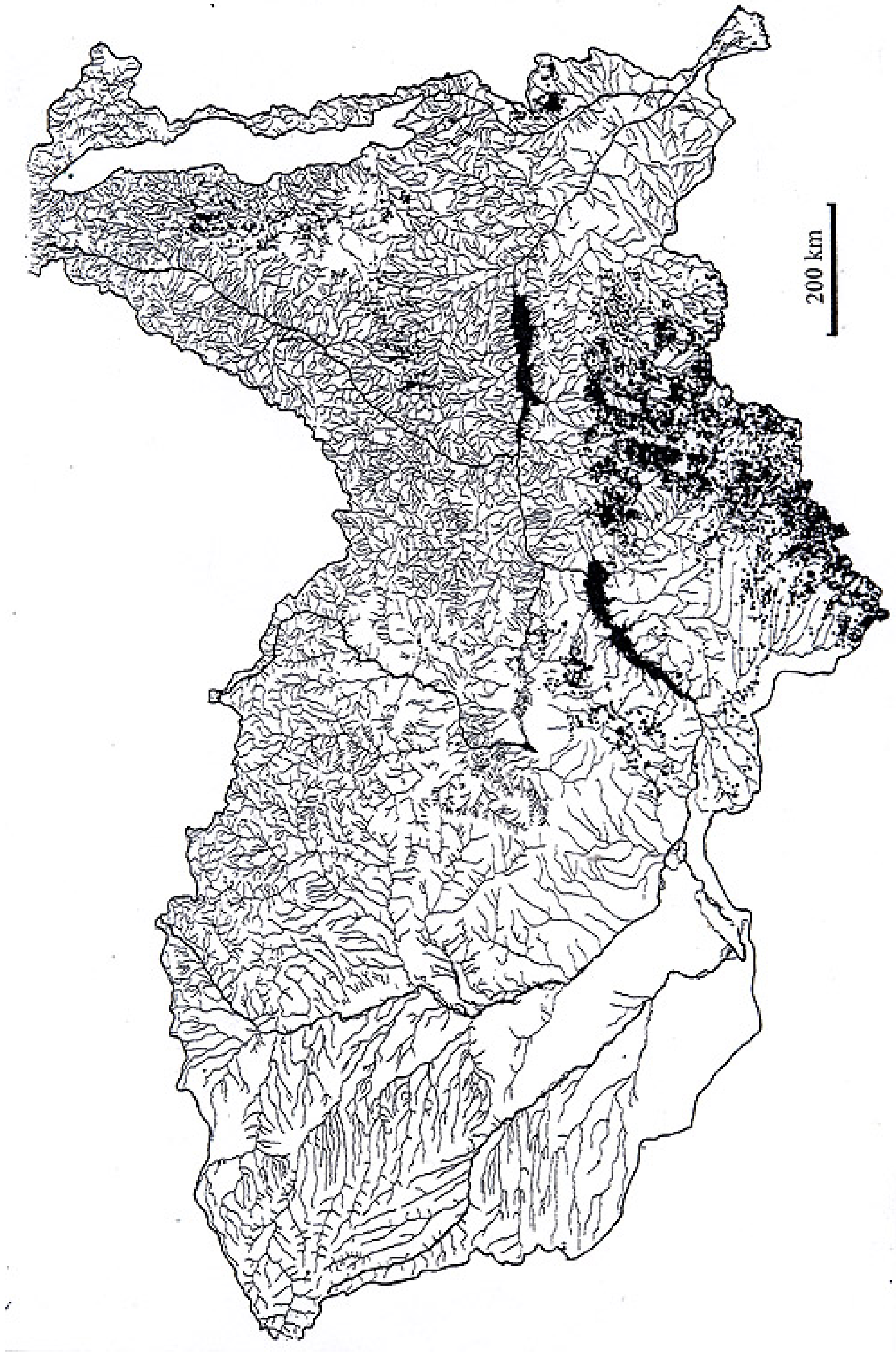


Table 7.7 The total number of fish species, and the proportion of introduced ones, in three Zimbabwean reservoirs (data from Ludbrook 1974, Marshall 1982, Marshall, Junor & Langerman 1982, Kenmuir 1983, Evans 1982, Kolding & Karenge 1985, Sanyanga & Feresu 1994 and unpublished data).

	Area (km^2)	Total no. species	No. introduced species
Lake Kariba	*c* 5400	47	4 (8.5%)
Lake Mutirikwe [1]	91.1	19	8 (42.1%)
Lake Chivero	23.6	29	8 (27.6%)
Savory dam	0.1	15	9 (60.0%)

Note: [1] Formerly known as Lake Kyle, this reservoir is not in the Zambezi Basin.

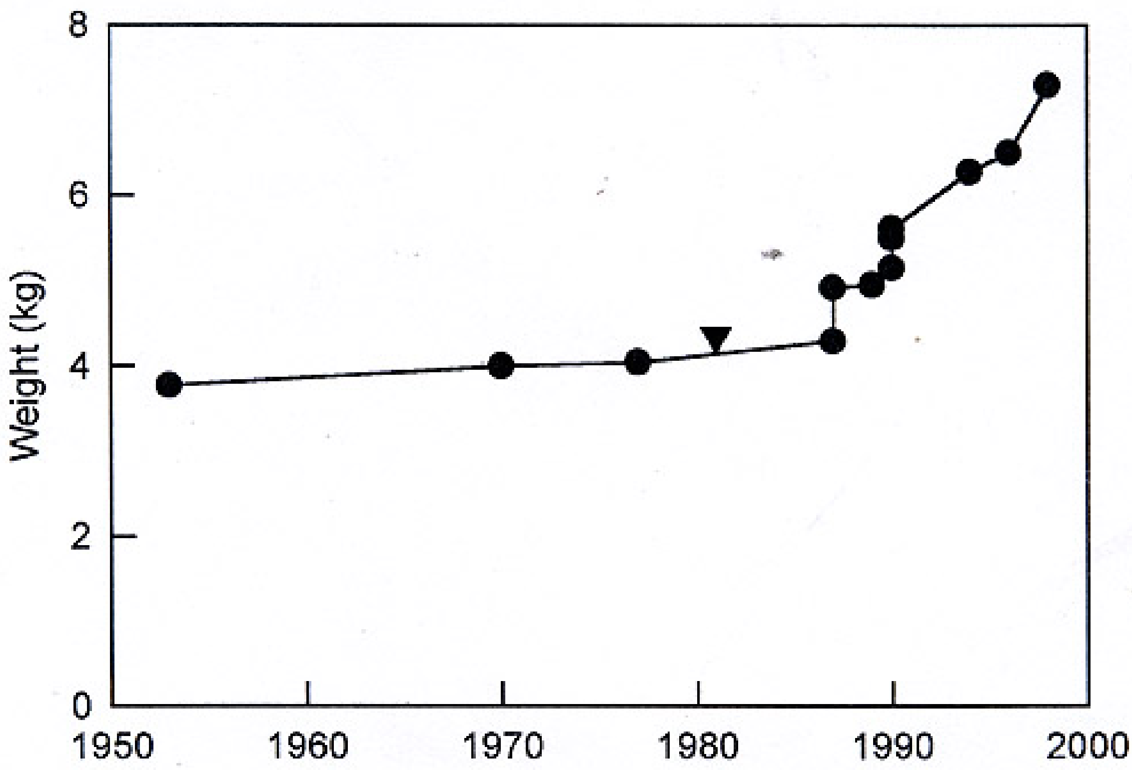
Table 7.8 Exotic fish species of non-African origin known to have been introduced into the Zambezi Basin (data from Turnbull-Kemp 1957, Toots 1970, Bell-Cross & Minshull 1988, Thys van den Audenaerde 1994 and unpublished sources).

Species	Remarks
Carassius auratus (Goldfish)	Zimbabwe; aquarium fish, occasional wild ones
Cyprinus carpio (Common Carp)	Zimbabwe *c*. 1925; widely distributed in small numbers (increasing recently in some areas) Malawi; present in Zomba area Zambia, 1946; limited distribution
Tinca tinca (Tench)	Zimbabwe *c*. 1938; extinct Zambia, 1946; failed
Catla catla (Indian Carp)	Zimbabwe *c*. 1968; failed
Ctenopharyngodon idella (Grass Carp)	Zimbabwe *c*. 1982; in fish ponds, not yet stocked Zambia, *c*. 1980s; a few in fish ponds
Salmo trutta (Brown Trout)	Zimbabwe *c*. 1907; montane waters, uncommon
Oncorhynchus mykiss (Rainbow Trout)	Zimbabwe *c*. 1910; montane waters, commonest species Malawi, 1905; montane waters. Zambia, 1942, 1947; unsuccessful
Salvilenus fontinalis (Brook Trout)	Zimbabwe, 1955; montane waters, possibly extinct
Gambusia affinis (Mosquitofish)	Zimbabwe, 1925; local populations in reservoirs around Harare Zambia, *c*. 1940s; apparently extinct
Poecilia reticulata (Guppy)	Zimbabwe; aquarium fish, now in small reservoirs around Harare Zambia; aquarium fish, apparently in streams near Kitwe
Xiphophorus helleri (Swordtail)	Zambia; aquarium fish, present in some ponds
Micropterus salmoides (Largemouth Bass)	Zimbabwe, 1932; now widespread, has reached, or been stocked into, Lake Kariba
Micropterus dolomieu (Smallmouth Bass)	Zimbabwe, 1941; probably extinct Zambia, 1947; probably extinct
Micropterus punctulatus (Spotted Bass)	Zimbabwe, 1945; probably extinct Zambia, 1945; probably extinct
Lepomis macrochirus (Bluegill Sunfish)	Zimbabwe, 1948; small, isolated populations still exist
Perca fluviatilis (Perch)	Zimbabwe, 1938; failed
Oreochromis aureus (Israeli Tilapia)	Zambia, 1983; may survive in ponds and may have escaped into the Kafue River

Until about 1950, most of the introductions were of European or North American species which were thought to be superior to the native ones, or which were valued because of their familiarity to European settlers. This attitude was encapsulated by a correspondent who wrote "to have our rivers full of trout would ... prove of the greatest benefit to our country in many ways, e.g. ... a new and very real attraction to settlers ... [allowing] the settler to indulge in the sport for which he has pined so long" (Dobell 1921). Altogether, about 17 non-African fish species are known to have introduced into the basin, principally in Zimbabwe, but also in Zambia and Malawi (Table 7.8). Fortunately, few of them have been successful.

Rainbow Trout, *Oncorhynchus mykiss*, are restricted to mountain streams in eastern Zimbabwe and in Malawi, but the other trout species have not done as well. Of the bass species, only the Largemouth Bass, *Micropterus salmoides*, has become established and is widespread in reservoirs in Zimbabwe, and has also been introduced into Lake Kariba. It is generally thought to have had little impact on the native species, but this situation may have changed following the introduction of the Florida strain in 1981. This introduction seems to have changed the character of the population, with fish growing more rapidly and to a larger size (Figure 7.14), and they appear to have become more abundant. Unpublished data from river surveys in the Harare area (Zimbabwe) indicate that bass have a severe effect on the populations of indigenous fish, especially *Barbus* species.

Figure 7. 14 Changes in the angling record for Largemouth Bass, *Micropterus salmoides*, in Zimbabwe, 1952-1998. The symbol – denotes the introduction of the Florida strain to Zimbabwe in 1981 (data from Anon. 1998).



The remaining exotics that are not extinct tend to occur in small populations with a low reproductive rate. For example, in November 1958 sixty common carp, *Cyprinus carpio*, weighing an average of 1 kg each were introduced into the Savory Dam near Harare. When the dam was drained in January 1980 there were found to be only 118 carp, only one of which weighed less than 6 kg and was estimated to be 15 years old (Evans 1982). Their failure to reproduce may have resulted from a high level of predation on their eggs and fry by the cichlids and other native species in the dam. Similarly, 1000 Bluegill sunfish, *Lepomis macrochirus*, were stocked into the dam in 1961 but only three, with an average weight of 0.8 kg, were found in 1980.

Attempts to introduce further non-African species can be expected. Aquaculturists continue to examine species like the Chinese or Indian carps, and the grass carp, *Ctenopharyngodon idella*, is currently being reared in both Zimbabwe and Zambia although it has not yet been released. Escaped aquarium fish may also be increasingly important in future and isolated populations of guppies, *Poecilia reticulata*, already occur in parts of Zambia and Zimbabwe (Thys van den Audenaerdd 1994, Gratwicke, in prep.).

Since the 1950s, the introduction of exotic species from elsewhere in Africa, including the translocation of species within the Zambezi Basin, has become much more important and is likely to have a far greater impact. So far, about 18 species are involved with nine of them being intra-basin translocations (Table 7.9). In some cases, these introductions were made for obscure or whimsical reasons; the lungfish, *Protopterus annectens*, was accidentally translocated to the Lake Malawi area, while *Tilapia zillii* were brought to Zimbabwe by President Mugabe who was persuaded – by someone in Uganda – that they would control water hyacinth (Anon. 1990). But in most cases they were done to improve fishery productivity or angling and, in contrast to the non-African species, with much more success.

The most spectacular introduction was that of the clupeid *Limnothrissa miodon* from Lake Tanganyika to Lake Kariba. Within two years of its introduction, *Limnothrissa* had colonised the entire lake and invaded the Zambezi River below the Kariba dam (Junor & Begg 1971). It later invaded Lake Cabora Bassa. The fishery on Kariba began in 1973 and now produces around 30,000 t per annum (Marshall 1995), while that on Cabora Bassa began in 1993, reached 3000 t by 1995 (FAO 1996) and may now have reached 10,000 t per annum. It may be one of the most cost-effective fishery projects ever carried out in Africa (Jackson, cited in Eccles 1985) and its ecological impacts were relatively small. It certainly had no impact on the diversity and abundance of most other fish species in the system, except for predators like *Hydrocynus vittatus* which increased in abundance (Marshall 1991). Attempts have been made to introduce *Limnothrissa* into the Itezhi-Tezhi Dam in Zambia (Mubamba 1993) but it is unclear whether they have succeeded or not.

The only other important non-cichlid introduction was that of the small sardine-like cyprinid *Mesobola brevianalis* into a small reservoir in the Eastern Highlands of Zimbabwe as a forage fish for trout. Although this species occurs in the Upper Zambezi, the stock for this introduction originally came from the Limpopo. The introduction was successful and it has since become established in the Inyangombe River (A.I. Payne & S. Temple, unpublished data) which flows into the Lower Zambezi via the Mazowe. The ecological impact of this species is unknown and it may compete with the native minnows (*Barbus* spp.), although it might have the effect of enhancing the similarities between the Upper and Lower Zambezi which already share many species.

Table 7.9 Exotic fish species of African origin known to have been introduced into the Zambezi basin. The symbol * denotes translocations within the basin (data from Toots 1970, Evans 1982, Bell-Cross & Minshull 1988, Thys van den Audenaerde 1994, Anon. 1996a and unpublished sources).

Species	Remarks
*Protopterus annectens**	Malawi; accidentally introduced to Bua River, near Nkota-Kota
Limnothrissa miodon	Lake Kariba, 1967-68; widespread and invaded Lake Cabora Bassa Zambia, 1992; Lake Itezhi-Tezhi, apparently failed
Mesobola brevianalis	Zimbabwe, *c*. 1970s; Inyangombe R., now invading Lower Zambezi
Barbus kimberleyensis	Zimbabwe, 1928; some may have briefly survived but probably extinct now
Tilapia zillii	Zimbabwe, 1990; fate unknown, possibly held in ponds
*Tilapia rendalli**	Zimbabwe, 1959; now widespread
*Serranochromis robustus**	Zimbabwe, 1965; now widespread on central plateau
*Serranochromis thumbergi**	Zimbabwe, 1 specimen, Lake Manyame (origin unknown)
*Sargochromis giardi**	Zimbabwe, 1970s; 1 specimen near Gweru (origin unknown)
*Sargochromis codringtonii**	Zimbabwe, *c*. 1978; Lake Chivero, present but rare
Astatoreochromis alluadi	Zambia, 1979; apparently unsuccessful
Boulengerochromis microlepis	Zambia, 1989; apparently unsuccessful
*Oreochromis mossambicus**	Zimbabwe, widely distributed on central plateau
Oreochromis placidus	Zimbabwe, 1955; restricted distribution in Harare area
*Oreochromis mortimeri**	Zimbabwe, widely distributed Zambia, 1950; from mid-Zambezi to Kafue system
*Oreochromis andersonii**	Zimbabwe, 1944; status uncertain, possibly abundant in some areas
*Oreochromis macrochir**	Zimbabwe, 1952; now widespread in all areas; also in lake Kariba Zambia; 1950; Congo strain into Kafue system
Oreochromis niloticus	Zimbabwe, *c*. 1982; now widespread, including Lake Kariba and Zambezi River Zambia, 1983; now established in Kafue River

The central plateau of Zimbabwe seems to have supported few cichlids prior to European settlement (Thys van den Audenaerde 1988) and extensive introductions of various species followed the construction of the reservoirs that provided suitable habitat for them. The first priority was given to enhancing tilapia stocks and *Oreochromis mossambicus, O. andersonii* and *O. macrochir* were bred in hatcheries and widely introduced into small reservoirs (Toots 1970). The latter was perhaps the most successful species and in Lake Chivero it displaced *O. mossambicus*, possibly because it was better able to deal with the increasingly eutrophic state of the lake (Marshall 1982), but it has become the dominant species in other lakes as well. Other successful species include *Tilapia rendalli* and *Serranochromis robustus*, which are now widely distributed throughout the country.

The ecological impacts of these introductions are unclear. *Tilapia rendalli* has been blamed for the destruction of vegetation and a consequent a loss of habitat for some fish and bird species (Junor 1969). In some small reservoirs on the Zimbabwean plateau, *S. robustus* replaced Largemouth Bass but became severely stunted, leading to a deterioration in their angling value (Toots & Bowmaker 1976, Evans 1982). Hybridisation of the various *Oreochromis* species is thought to have taken place, and it is generally believed that there are no longer any pure stocks left on the Zimbabwean plateau. However, the extent of hybridisation has never been fully investigated and it may have been less extensive than feared.

The translocation of these *Oreochromis* species could perhaps be justified on the grounds that they are Zambezian species that are extending their ranges with human assistance. But the same cannot be said of the most recent arrival, *Oreochromis niloticus*, which was brought to the region in the early 1980s by fish farmers in both Zambia and Zimbabwe (Thys van den Audenaerde 1994). It escaped from fish farms and is now present in the Kafue River and Lake Kariba (Thys van den Audenaerde 1994, Chifamba 1998) and in the Zambezi River below the Kariba dam. In addition, it has been enthusiastically – but illegally – translocated throughout Zimbabwe by anglers with whom it is popular because it grows larger than most of the other tilapias (Anon. 1996b). It tends to replace the other tilapias, primarily *O. mossambicus* and *O. macrochir*, and it is now the dominant species in many reservoirs. It is almost certainly in all of the major Zimbabwean tributaries of the Zambezi and can therefore be expected anywhere in the Middle or Lower Zambezi systems.

7.4.4 **Other alien species**

It is not only exotic fish that can threaten aquatic environments. Aquatic weeds like the water hyacinth (*Eichhornia crassipes*), Kariba weed (*Salvinia molesta*) and carpet weed (*Azolla filiculoides*) have caused problems throughout the basin. They can cover small water bodies and smother habitats, reducing light and oxygen and ultimately eliminating fish populations. Water hyacinth is by far the most intractable of these plants and it has become a serious problem in many parts of the Zambezi Basin. It is widespread in the Middle and Lower Zambezi, and in the Kafue system. At present, it is still largely absent from the Upper Zambezi and its tributaries and every effort should be made to prevent it from invading these areas. It is also present in the Zambezi Delta but it cannot tolerate saline water and is therefore unlikely to become a serious problem. It occurs in the Lilongwe River (Malawi), from where it could invade Lake Malawi, and the plant has indeed been found in the lake but it has not so far established itself there.

The effects of floating plants on the biota are ambiguous. They provide shelter for small fish and a habitat for invertebrates on which fish can feed but dense mats prevent photosynthesis, which makes the water below them anoxic. Recent data from the Gwebi River near Harare showed that the diversity and abundance of fish, amphibia and invertebrates was much reduced under floating mats of *Azolla filiculoides* (Gratwicke & Marshall, in prep.).

7.4.5 **Overfishing**

Overfishing is a complex term and can mean biological overfishing in which the stock is destroyed, or economic overfishing in which the catches fall to such a low level that fishing is no longer profitable. The extent of overfishing and its possible impact on biodiversity has not been well documented in the Zambezi Basin, although some information is available. Intensive fishing with small-meshed nets in shallow Lake Malombe in Malawi led to the destruction of important habitats, notably that of submerged and marginal vegetation. This contributed to the loss of the chambo (*Oreochromis* spp.) fishery and its replacement by less valuable haplochromines (Banda & Hara 1997). Another group of fish that are vulnerable to overfishing are those species that run up flooding rivers to breed, when they can be caught in large numbers, often before they have spawned. Labeos in large lakes are especially sensitive to this type of fishing and the fisheries for *Labeo victorianus* in Lake Victoria, *L. altivelis* in Lake Mweru and *L. mesops* in Lake Malawi all collapsed because of it (Jackson 1961a, Cadwalladr 1965, Msiska 1990). Overfishing may have more subtle effects, as in Lake Malawi where intensive fishing in inshore waters has reduced the number of snail-eating species, allowing snails to become more abundant and bringing schistosomiasis to areas where it did not occur previously (McKaye, Stauffer & Louda 1986). None of these fish are as yet extinct so biodiversity if measured as the presence or absence of species has not changed. Nevertheless, their abundance is much lower and the structure of the populations has changed, so they may now be much more vulnerable than before.

7.4.6 **Water abstraction and drainage of floodplains**

As the demand for water grows more will be consumed by agriculture and industry and reduce the flow in the rivers. The effects of reduced flows in southern African rivers are poorly understood although some work on these aspects is being done in South Africa (Allanson *et al.* 1990). In general, reductions in flow lead to the restriction of habitat in a stream. Adequate flows are necessary to stimulate breeding in many species of fish and it is these that are likely to decline if flows are reduced (Welcomme 1985). They will be replaced by species with a more flexible breeding pattern; in the Zambezi Basin this would entail the replacement of cyprinids by cichlids, for example.

The consumption of water and reduction of river flows will also increase fluctuations in the water levels of lakes and reservoirs, and decrease the extent of flooding on floodplains. The effects of water level fluctuations in lakes are complex and not necessarily detrimental. These fluctuations have a major impact on the mobilisation of nutrients in the littoral, which leads to an increase in invertebrate populations that are eaten by fish (McLachlan, A.J. 1970, McLachlan, S.M. 1970). On the other hand, severe fluctuations retard the development of communities of submerged vegetation, which are important substrates for invertebrates and refuges for small fish (McLachlan, A.J. 1969, Bowmaker 1973).

The impact of water level fluctuations on fish in lakes is less obvious since most of the fish species in the Zambezi system are adapted to highly changeable environments. Early workers on Lake Kariba (Jackson 1966, Harding 1966, Begg 1973) felt that large fluctuations in water level were deleterious to fishery production. These ideas were contradicted by Karenge & Kolding (1995) who found that fish catches were closely correlated with seasonal fluctuations, possibly because of their effect on nutrient inputs, but no correlation with the water levels during periods of drought.

The cycle of productivity on floodplains is, of course, determined by the hydrological cycle. The fish species are well adapted to this cycle and time their breeding to coincide with the rise and fall of the water. Fish catches on these floodplain systems are determined by the magnitude of the flood, although data from those in the Zambezi Basin are generally scarce. On the Barotse floodplain, van Gils (1988) showed that there was a positive correlation between the annual fish catch and the length of the flood season during the previous year. Thus, in 1983 and 1985, when the preceding flood season lasted only 130 days, the annual fish catch was 3500 and 4000 t respectively. In 1980 and 1981, when the flood season lasted for 210 days, the catch rose to about 6500 t. Similarly, Welcomme (1985) obtained highly significant correlations between the annual fish catches from the Kafue and Shire floodplains and the flood regime in the preceding year. However, because most of the fish caught in these fisheries were likely to be from one to two years old, he found that the best fit linear regression lines were obtained using data for both the preceding year and the year before. The equations were:

$$\text{Kafue: } C_y = 2962 + 70.54\ (0.7HI_{y-1} + 0.3HI_{y-2})$$
$$\text{Shire: } C_y = 5857 + 38.11\ (0.9HI_{y-1} + 0.3HI_{y-2})$$

where C_y = annual catch (t), HI_{y-1} = the hydrological index (a measure of flood intensity) in the preceding year while HI_{y-2} = the hydrological index two years before (Welcomme 1985).

These equations demonstrate the relationship between flooding and fisheries productivity on floodplains. In most cases, reduced flows are presently brought about by natural causes like drought, but the impact of human activities is likely to become more pronounced. Water supply to the Kafue Flats, for example, is regulated by the Itezhi-Tezhi dam upstream and by the Kafue Gorge downstream and these dams may have affected the floodplain quite considerably. Dam construction and power generation upstream might affect the floodplains of the Lower Shire, while the Zambezi Delta is affected by the Cabora Bassa dam.

The drainage and channelization of floodplains is associated with the abstraction of water, and these practices are responsible for major degradation of riverine environments and the destruction of fisheries in many parts of the world. In general, fish populations decrease in both numbers and diversity, as in the following examples (from Welcomme 1985):

(a) fish catches in the Missouri River were 2-2.5 times higher in undisturbed sections than they were in channelized ones;
(b) channelized streams in North Carolina supported a fish biomass of 55 kg/ha, compared to 175 kg/ha in unchanneled ones;
(c) the biomass of fish in the Blackwater River, Missouri, was reduced from 633 kg/ha to 147 kg/ha by channelization.

Data from African systems are generally lacking and African rivers have not so far been channelized to any significant degree. An exception is the proposal to draw water from the Okavango system (see Scudder *et al*. 1993 for details), which could have a significant impact on the biodiversity of fish. River "improvement" here is likely to cause a 60-80% decrease in fish populations (Table 7.10). A dredged section of the Boro River lacked aquatic vegetation and the associated floodplain had dried out and was severely overgrazed. The number of fish taken in December was considerably higher than the number caught in July, partly because fish are more difficult to catch in cold water and partly because only gillnets were used during the July survey.

7.4.7 **Pollution**

The continuing growth of cities in southern Africa and the commitment of its countries' governments to development means that pollution and eutrophication will become increasingly serious problems. Some pollution occurs as a result of the use of water bodies by humans as in Lesotho, for example, where dams around towns are used for washing clothes, cars and engines and for the general disposal of waste. As a result, they have become so polluted that they can support few fish other than the carp *Cyprinus carpio* (ALCOM, pers. comm.). On a larger scale, pollution from the discharge of organic matter of various kinds, acid discharges from mines and factories, and contamination by heavy metals are likely to have more serious effects on biodiversity. These problems have begun to appear in the Middle Zambezi around cities like Harare (see Moyo 1997 for examples) and in the Kafue system around the Zambian Copperbelt and Lusaka. Raw sewage discharged into the Zambezi from Livingstone (Zambia) and Victoria Falls (Zimbabwe) has contaminated the Zambezi River for a long way downstream (Feresu & van Sickle 1990). Studies to quantify the levels of heavy metal contamination have been made in Lake Kariba (Berg & Kautsky 1997) but in very few other places.

Pesticides have been widely applied throughout the region in an attempt to control tsetse fly. The aerial application of endosulphan has caused fish kills in the Okavango Delta in Botswana (Russel-Smith 1976, Fox & Matthiessen 1982), but it is not the short-term application of pesticides that poses the greatest threat to fish populations. Far more important are the long-term effects of persistent pesticides such as DDT, which is widely distributed in aquatic systems throughout the region (Greichus *et al*. 1977, 1978a, 1978b, Matthiessen 1985). Fortunately, the use of most persistent pesticides is banned in many countries and their concentrations declined after the bans were enforced (Table 7.11).

Eutrophication is likely to become a major problem and has been widely reported from parts of South Africa and Zimbabwe. The problem is mostly caused by the discharge of sewage, or sewage effluents, into the streams that flow into lakes. Eutrophication is manifested by enhanced capacity for plant growth, either in the form of rooted or floating macrophytes, or as phytoplankton which gives the water a green colouration. Primary productivity is high in eutrophic systems and in its early stages, at least, fish production is greatly increased, but if the process continues, conditions worsen and lead to a decrease in fish species diversity. In the hypertrophic Hartbeespoort Dam, for example, the fish fauna is dominated by only three species, *Oreochromis mossambicus*, *Clarias gariepinus* and *Cyprinus carpio*, and there is some evidence that their growth rates are slower than in less eutrophic systems (Cochrane 1985). Anaerobic conditions in the hypolimnion tend to become more extensive and to last longer in eutrophic systems, which increases the risk of fish kills, like the one that occurred in Lake Chivero in 1996 (Marshall 1997).

7.4.8 **Siltation**

The increasing rate of deforestation and land clearance in Africa, combined with poor agricultural practices and the unrelenting growth of the human population, is perhaps the most serious threat to small water bodies. Whitlow (1983) has shown that soil losses through erosion were over 20 times greater from cleared plots compared to protected ones at a sandveld site in Zimbabwe. There is little doubt that soil erosion is becoming an increasingly serious problem in much of southern Africa and is having a serious impact on its aquatic environments.

Large water bodies are not immune. There is evidence to show that the littoral areas of Lake Tanganyika are beginning to suffer from the blanketing effect of sediment carried into the lake (Cohen *et al*. 1993), and there are fears that something similar is happening in Lake Malawi (A.J. Ribbink, pers. comm.). This could have a serious effect on the complex community of endemic rock-dwelling cichlids ("mbuna") in the lake, all of which depend on the algal mat that grows on the rocks. In addition to blanketing the algal mats, silt reduces the food supply by preventing animals from establishing themselves on rocks, fills in refuges leading to increased juvenile mortality, and reduces light penetration which reduces available food and disrupts the breeding behaviour of cichlids. But the effect of sediments is much more detrimental in small water bodies, which, in some areas, have lost significant quantities of their storage capacities. In parts of Zimbabwe, for example, a number of small dams lost, on average, 39% of their capacity in 20 years (Magadza 1984, 1992). One dam lost 100% of its storage capacity in less than 2 years, and habitat destruction on this scale will have a severe impact on fish populations.

Table 7.10 The numbers of individual fish (N) and the number of fish species (S) caught in dredged and undredged sections of the Boro River, Okavango Delta, Botswana (data from JLB Smith Institute of Ichthyology (unpublished)). nd = no data.

	Dec1982		July1985	
	N	S	N	S
Nxaragha Lagoon (upstream)	n/d	n/d	56	15
Thamalakane River (downstream)	1126	22	53	9
Boro River (dredged)	145	18	9	5

Table 7.11 Changes in the concentration of DDT (Fg/g dry weight) in sediments and two species of fish in Lake Chivero, showing the rapid decrease in concentrations following the banning of DDT for agricultural use in 1983 (n/d = no data) (data from Greichus *et al*. 1978, Greichus 1982 and Mhlanga & Madziva 1990). The apparent increase in DDT in the sediments may reflect experimental error.

	1974	1979	1988/89
Sediments	57	n/d	76
Oreochromis macrochir >500 g	450	1270	210
Clarias gariepinus	n/d	1510	180

Table 7.12 Some indicator chemical qualities of the Middle and Lower Zambezi and major tributaries arranged in successive order from Victoria Falls to below the Shire confluence (from Bell-Cross 1974 and Davies 1986).

	Upper Zambezi (Bell-Cross)	Upper Zambezi	Kafue River	Luangwa River	Zambezi River (Tete)	Shire River	Lower Zambezi
PH		7.6	7.5	7.9	7.8	7.5	7.8
Conductivity (mS/cm)	84	75	231	147	119	315	153
Total alkalinity (mg/l $CaCO_3$)	40	33	124	57	53	110	73
Nitrate (mg/l NO_3-N)	-	0.01	-	0.15	0.16	0.18	0.13
Phosphate (mg/l PO_4-P)	3	13	-	78	121	69	78
Transparency (Secchi disc, m)	-	5.4	1.1	0.4	0.3	0.3	0.2

7.4.9 **Conclusions**

There is little doubt that conditions in the Zambezi Basin will continue to change. Human activities such as reservoir construction, the introduction of exotic species and the translocation of indigenous ones will continue. Aquatic systems will continue to be stressed even more as the human population grows and the need to balance the demand for water against the need to conserve biodiversity will become an increasing challenge for fish biologists. Added to this are the unpredictable consequences of climate change, which could lead to reduced rainfall throughout much of the basin (Unganai 1996).

Nevertheless, the magnitude of change is likely to vary in different parts of the basin. The Upper Zambezi is relatively undeveloped and its fish fauna is still intact. It generally lacks mineral resources, has limited agricultural potential and few significant dam sites, and the pace of change is likely to be relatively slow. There is a real chance, therefore, that its fish fauna can be kept in its relatively intact state, provided safeguards are instituted and maintained. The control of exotic fish species, especially *O. niloticus* should be given a high priority and fish farmers should not be allowed to use it anywhere in the basin.

The Kafue system is less secure since a large proportion of Zambia's population and most of its urban centres and industrial potential lies in its drainage basin. The Kafue Flats, a complex and important wetland (Handlos 1982), has already been affected by the construction of dams at Itezhi-Tezhi and Kafue Gorge. The influence of these dams is still unclear; they are said to have reduced the yield of fish, especially tilapias (Subramaniam 1992), but this may also be a consequence of drought and overfishing. More importantly, *O. niloticus* is now established in the Kafue (Thys van den Audenaerde 1994) and it is likely to spread throughout the Kafue Flats to the detriment of the native species, *O. andersonii* and *O. macrochir*.

The Middle Zambezi is by far the most seriously altered part of the basin and is likely to remain so since it includes its most advanced agricultural sites, and some of its largest urban areas with extensive mining and industrial areas. While the Lower Zambezi is a relatively undeveloped area, it is influenced by developments upstream, notably flow regulation and introduced species. Few of these changes can be reversed, but every effort should be made to ensure that their impact is minimised and to preserve any relatively unaltered systems that may still occur in the basin.

Finally, the Lake Malawi basin remains intact, although the species composition in the lake may be changing because of commercial fishing (Turner *et al*. 1995). The extraordinary diversity of the lake's endemic haplochromines makes it one of the world's greatest biological resources and the need to preserve it is widely recognised. The events in Lake Victoria have shown that these endemic cichlid species-flocks may be extremely vulnerable to the impact of introduced predators and it is essential that all exotic species are kept out of the lake (Lowe-McConnell 1995). So far, these efforts have been successful, but nobody should lower their guard because the pressures to spread exotic fish around are unlikely to decrease. The growing population, and increasing poverty, of Malawi may revive the suggestion that species like *Limnothrissa* should be introduced (Turner 1982) while the continuing use of *O. niloticus* in aquaculture makes it almost inevitable that it will reach Malawi.

7.5 WETLANDS OF SPECIAL INTEREST

7.5.1 **The Barotse Floodplain**

The Upper Zambezi system drains the basin from its source to the Victoria Falls. This stretch of the river is about 1440 km long, of which about 384 km flows through Angola (Bell-Cross 1974). Fishing has long been an important activity among the Lozi people of the area with a distinct social function, as well as providing a source of food (Gluckman 1941). A variety of traditional fishing gear, including gill nets made from tree bark, lift-nets, barriers, traps and baskets, are used in the fishery, but the introduction of beach seines and nylon gill nets has greatly improved productivity (Bell-Cross 1974). The Upper Zambezi is now a major source of fish in Zambia, providing about 8000 tonnes per annum or about 11.0% of the country's total supply. Most of this catch comes from the two most important wetlands in the system, (a) the Central Barotse floodplain and (b) the Southern Barotse floodplain.

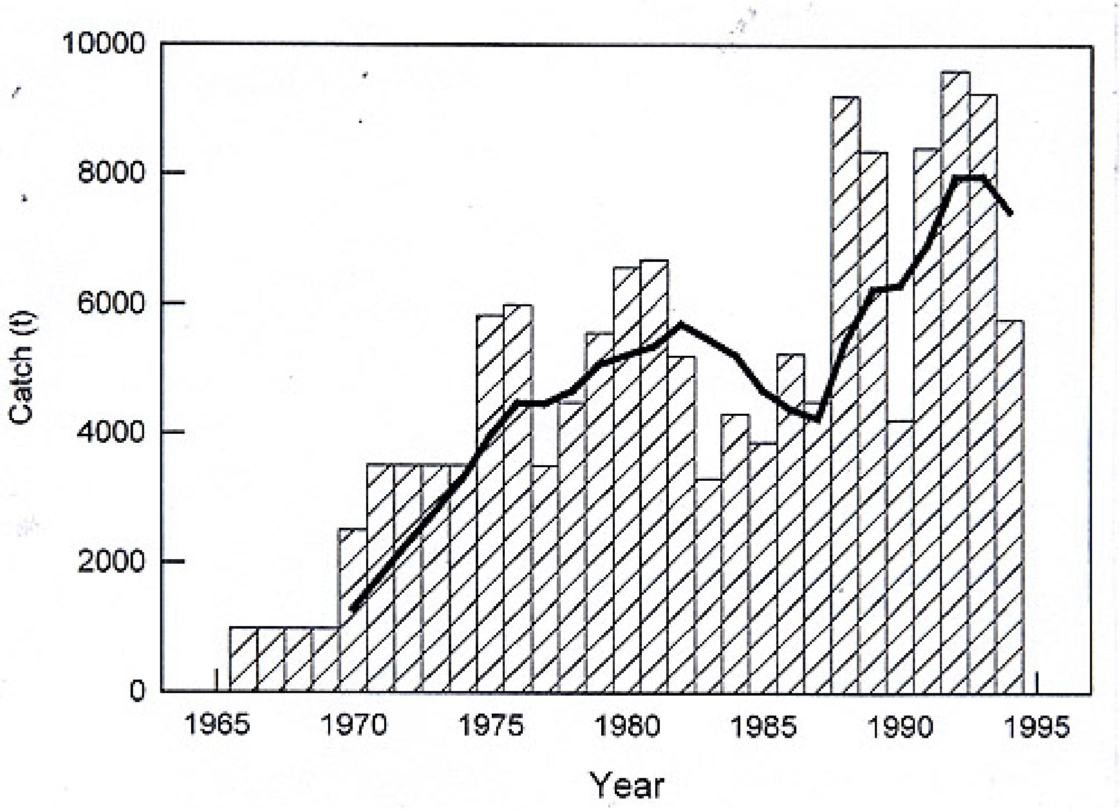
The Central Barotse Floodplain extends from Lukulu in the north to Nangweshi in the south, and is approximately 240 km long and up to 35 km wide (Bell-Cross 1974). In the flood season it covers an area of up to 7500 km^2 (Vanden Bossche & Bernacsek 1990). It is largely covered with grass but with isolated trees or clumps of trees. The dominant semi-aquatic plants along the main channel are the grass *Vossia* sp. and *Potomogeton* spp. Patches of the reed *Phragmites* occur on banks of the main channel and in the numerous lagoons and backwaters that branch off. Water lilies (*Nymphaea* spp. and *Nymphoides* sp.) are abundant in these channels and lagoons, as are dense beds of other aquatic macrophytes like *Utricularia* sp., *Najas* sp. and *Ceratophyllum* sp.

The Southern Barotse floodplain is approximately 100 km in length and is located between Sesheke and Mombova, and the main river channel marks the international boundary between Zambia and Namibia (Bell-Cross 1974). On the Zambian side the floodplain is about 8 km wide and the vegetation is similar to that of the Central Barotse floodplain, although there are more trees along the river. This floodplain is contiguous with the eastern portion of the Chobe-Linyati floodplain system.

In both floodplains, the river flows over belts of Kalahari sands and is constantly changing course owing to the erosion and redeposition of its sandy banks. These sands are very low in nutrients and the river water is therefore nutrient-poor, especially compared to the Kafue, Luangwa or Shire rivers (Table 7.12). The system is therefore unproductive and the fishery yield from the Barotse floodplain is only about half of that from the Kafue floodplain, even though they are of comparable size (Bell-Cross 1974). The catches from the Upper Zambezi vary from year to year but there is a generally increasing trend (Figure 7.15) possibly because of the growth of the human population and perhaps to an improvement in the road network which makes it easier for fishermen to market their catch. The potential yield of this system has been estimated to be around 14,000 t per annum (Vanden Bossche & Bernacsek 1990), which may be an overestimate bearing in mind the low productivity of the system..

Most of the fish species recorded from the Upper Zambezi occur on the floodplains, with the exception of a few that are restricted to its upper reaches – such as *Paramormyrops jacksoni, Barbus neefi*, *B. brevidorsalis*, *Clarias liocephalus* (Bell-Cross lists *C. submarginatus*, a synonym of *C. liocephalus*, as being widespread but this almost certainly refers to *C. stappersii*), *Hypsopanchax jubbi* and *Schilbe yangambianus*. The status of *Serranochromis coulteri* is uncertain as it appears to be limited to the headwaters of the system but it may also occur on the floodplain. The most abundant large species seem to be *Hydrocynus vittatus*, *Oreochromis macrochir*, *O. andersonii* and *Tilapia rendalli*, which together made up 56% of the catch in the gillnet fishery (Table 7.13). Gill nets are highly selective, however, and only 26 species were represented; small one like the barbs, which may be among the most numerous, are not represented in the catch because they are too small.

Figure 7.15 Fish catches from the Upper Zambezi system in Zambia. The bars indicate the catch while the continuous line is the 5-year moving average (data from Department of Fisheries, in Anon. 1995).



Little is known about the biology of the fish on the Zambezi floodplains. Bell-Cross (1974) gives some notes on the biology of each species, while Winemiller (1991) and Winemiller & Kelso-Winemiller (1994, 1996) have made more detailed biological studies of the serranochromines, the tigerfish and African pike and the squeakers. As on all floodplains, there is a distinct pattern of migration with fish moving onto the floodplain and up tributaries to breed as the water level rises and moving back to the main channel as it falls. Bell-Cross (1974) believed that an increase in river velocity was the stimulus to migration and that the depth of the water controlled fish movements. Each species had its own "depth dependency" factor, which meant that the smaller species were among the first to move onto the floodplain. Of the larger species it appeared that the cichlids were the first to migrate and the large characins among the last. He also thought that falling water levels were the stimulus for a reverse migration and he noted that small species, and the young of larger ones, tended to remain in shoals for much of the dry season. The general pattern of migration was summarised by van Gils (1988) in relation to the traditional Maalelo fishery, and the more intensive gillnet fisheries (Table 7.14).

Table 7.13 The relative abundance (% by weight) of fish species in the gillnet catch, central Barotse floodplain, 1967 survey (data from Bell-Cross 1974). Species are listed in order of abundance.

Hydrocynus vittatus	18.4
Oreochromis macrochir	17
Oreochromis andersonii	10.8
Tilapia rendalli	9.9
Hepsetus odoe	6.3
Serranochromis macrocephalus	4.9
*Serranochromis angusticeps**	4.7
Mormyrus lacerda	4.5
Clarias gariepinus	4.3
Clarias ngamensis	3.4
Serranochromis robustus	2.9
Sargochromis carlottae	2.5
Tilapia sparrmanii	1.4
Sargochromis giardi	1.6
Sargochromis codringtonii	1.6
Schilbe intermedius	0.9
Labeo lunatus	0.8
Synodontis woosnami	0.3
Synodontis nigromaculatus	0.2
Parauchenoglanis ngamensis	0.2
Marcusenius macrolepidotus	0.2

*This is presumably a mixture of Serranochromis *angusticeps* and *S. altus* since the latter had not been described at the time these data were collected.

Table 7.14 The seasonal cycle of fish abundance and fishing activity on the Barotse floodplains (from Van Gils 1988).

Jan-Apr Late rainy season	Apr-Jul Early dry season	Jul-Oct Late dry season	Oct-Dec Early rainy season
fish move up channels	fish dispersed on floodplain	fish move back to channel and lagoons	fish restricted to dry season refuges
production of young by most species	rapid fish growth	heavy losses to man and predators	reduction in fish population
almost no fishing	Maalelo fishery	intensive fishery	fishing in pools, swamps and landlocked lagoons

The Barotse floodplains seem relatively secure from a conservation point of view as the area lacks significant agricultural or mineral potential and the human population density is relatively low. There are no major dam sites that are likely to alter the flow regime and there are unlikely to be any major projects to drain or channelize the floodplains in the foreseeable future (in contrast to the Okavango, for example). At present, the fish stocks are relatively intact and there are no known alien species in the system; every effort should be made to ensure that this remains so. The main factor affecting the fish population is a continuing increase in fishing intensity, which is likely to affect the larger species first, and could change the composition of the population. Fishing could drastically reduce the numbers of some species but is unlikely to drive any to extinction.

7.5.2 **The Chobe-Linyanti system**

This floodplain system begins at the point where the Kwando River, having flowed south through Angola and the Caprivi Strip, Namibia, reaches Botswana. The Chobe flows in an ENE direction to join the Zambezi at the common borders of Botswana, Namibia, Zambia and Zimbabwe. At this point the Chobe floodplain system becomes part of the southern Barotse floodplain. The Linyanti Swamp is about 300 km^2 in extent but its size varies greatly according to the extent of the flood. Water levels in the system depend to a large extent on the height of the Zambezi floods, which causes the water to back up into it.

The only significant fishery in this system was in Lake Liambezi, located on the Chobe in Namibia and Botswana. It was located in a flat region with numerous swamps and slow-flowing rivers in a swamp system covering an area of some 300 $km^{2,}$ of which only 101 km^2 consisted of open water. The lake had an unstable recent history since it is not shown on maps published before 1950, which show only an area of reed swamp. It came into being after a drought when the local inhabitants burnt the accumulated organic matter to clear land for agricultural purposes (Seaman *et al*. 1978).

Fishing activity began in 1959 and, although there are no records from this early period, it is believed that considerable quantities of fish were captured and exported to Zambia. The fishery was investigated between May 1973 and April 1976 and some data on catches and yields are available from this period (Van der Waal 1980). The catch was made up mostly of cichlids (80.4% by weight), of which *Oreochromis andersonii* and *O. macrochir* were the most important (43% and 26%, respectively). The clariids (*Clarias gariepinus* and *C. ngamensis*) were the next most important species (12.6%) with a variety of other species making up the remainder of the catch.

Fish catches fell during this period, from 640 t in 1973-74 to 115 t in 1975-76 (Table 7.15).

Table 7.15 Fish catches and productivity of Lake Liambezi, May 1973 to April 1976 (data from van der Waal 1980).

		Yield(kg/ha)	
	Catch (t)	**Open water**	**Lake + swamp**
1973-74	636.9	63.7	21
1974-75	279.2	27.9	9
1975-76	115.3	11.5	4
Mean	343.8	34.5	11.5

According to Van der Waal (1980) this decline was not a result of excessive fishing because the number of fishermen decreased as well. Instead, he attributed it to a rise in the water level, which decreased the efficiency of the nets because (a) the nets no longer reached to the bottom of the lake, (b) the surface area of the lake doubled in size and the population density of the fish decreased, and (c) the turbidity of the water decreased, making the nets more visible and therefore less efficient. Van der Waal (1980) made various recommendations for managing this fishery, and believed that it could produce as much as 750 t/yr and thus provide a permanent living for one hundred people. Unfortunately the lake dried up during the droughts of the 1980s and no longer supports a fishery. However, recent information suggests that the lake may come into existence once again, following high flows in the Zambezi during the 1997-98 rainy season.

The species composition of the fish is similar to that of the Upper Zambezi and it is likely that the same species occur in both systems. Van der Waal (1996) collected a total of 65 species during a survey in the Caprivi area out of a total of 76 recorded from the whole Caprivi area (Van der Waal & Skelton 1984). Some idea of their relative abundance can be obtained from his data (Table 7.16) but they clearly illustrate the effect of fishing gear on estimates of relative abundance. Little work has been done on the biology of fish in the Chobe/Linyanti system. The general biology, including investigations of growth, feeding and breeding, of the larger species was investigated by Van der Waal (1980), who made some general comments on their migration, which were expanded in a later paper (Van der Waal 1998). The general pattern of migration was similar to that of the Upper Zambezi, with a total of 31 species moving between the rivers and the floodplain, compared to 12 species that remained in the river and 17 that remained on the floodplain (Table 7.17).

The conservation status of this wetland is similar to that of the Zambezi floodplains. The area has very little agricultural potential because it lies over infertile Kalahari sands, and there are no known mineral deposits of any significance. Consequently, there are unlikely to be any major drainage projects, or other developments that will significantly reduce the size of the floodplain, in the immediate future.

7.5.3 **Lower Shire**

Some small, but important, floodplains occur along the Lower Shire in Malawi. The fish species caught in these systems are typically Zambezian with *Clarias gariepinus* and *Oreochromis mossambicus* being the most important of them. The total catch ranged from 4000 to 17,000 t/yr, with a mean around 8000 t (for the period 1970-1982), which is close to the estimated potential yield (Vanden Bossche & Bernacsek 1990). The Elephant Marsh (500 km^2 flooded permanently, up to 1000 km^2 flooded during the rainy season) is the largest and most important flood plain in the system and may support as many as 4000 fishermen. These marshes are densely populated and heavily cultivated, with at least parts of them having been converted into sugar plantations. It is not known what effect this has had on fish productivity.

The fish species in the wetlands are typical of those found in the Lower Zambezi system, although most of the marine species do not penetrate upstream as far as the floodplains. The diversity and abundance of fish is related to the distance from the Shire River. The diversity of fish was greatest at a site on the river, and rheophilic species like *Hippopotamyrus discorhynchus*, *Brycinus imberi*, *Hydrocynus vittatus*, both species of *Distichodus*, *Barbus afrohamiltoni*, both species of *Labeo* and *Synodontis zambezensis* were most abundant there. By contrast, both species of *Clarias*, the cichlids *Astatotilapia calliptera*, *Oreochromis mossambicus* and *O. placidus*, and the climbing perch *Ctenopoma multispine* were more numerous away from the river on the floodplain.

Table 7.16 The relative abundance of fish species (% by numbers) in the Lake Liambezi/Linyanti swamp system, according to different methods of capture (data from Van der Waal 1985, 1998).

	Mulapo traps	Seine net (25 mm)	Seine net (50mm)	Gill nets (25-190 mm)
Petrocephalus catostoma	0.9			11.6
Pollimyrus castelnaui	1.6			
Marcusenius macrolepidotus	4.2		0.01	19.3
Mormyrus lacerda	0.03			0.02
Hydrocynus vittatus			0.02	0.02
Brycinus lateralis	0.01	7.3	0.1	2.1
Rhabdalestes maunensis	0.06			
Hepsetus odoe	0.1	1.4	3.6	2.9
Hemigrammocharax multifasciatus	0.04			
Barbus poechii	1.1	1.8	0.1	0.9
Barbus afrovernayi	4.1			
Barbus barotseensis	0.06			
Barbus bifrenatus	4.9			
Barbus multilineatus	0.07			
Barbus paludinosus	54.2			
Barbus radiatus	0.01			
Barbus thamalakanensis	0.01			
Parauchenoglanis ngamensis	0.02			
Schilbe intermedius	4.7		0.1	32.9
Clarias gariepinus	0.1	0.1	0.1	0.7
Clarias ngamensis	0.5	0.1	0.2	0.8
Clarias stappersii	0.02			
Clarias theodorae	0.4			
Synodontis leopardinus/woosnami	0.5		0.1	13.9
Synodontis macrostigma			0.04	2.6
Synodontis nigromaculatus				1.1
Aplocheilichthys johnstonii	0.2			
Aplocheilichthys katangae	0.05			
Aplocheilichthys hutereaui	0.01			
Hemichromis elongatus	0.01			
Oreochromis macrochir	0.2	16.6	60.6	1.1
Oreochromis andersonii	0.3	3.9	6.6	1.3
Tilapia sparrmanii	5.4	5.9	1.6	0.9
Tilapia rendalli	0.7	15.3	7.1	0.8
Sargochromis giardi		0.6	0.3	0.3
Sargochromis codringtonii		2.2	3.4	0.9
Sargochromis carlottae		2.4	1.1	0.1
Pharyngochromis acuticeps	0.01	35.2	4.8	2.2
Serranochromis robustus	0.06	0.1	0.2	0.02
Serranochromis macrocephalus	0.01	3.1	3.5	2.7
Serranochromis longimanus		1.5	2.9	0.6
Serranochromis angusticeps		1.3	1.8	0.9
Serranochromis thumbergi		1.1	2.2	0.3
Pseudocrenilabrus philander	13.6	0.1		
Aethiomastacembelus frenatus	0.04			
Ctenopoma intermedium	0.4			
Ctenopoma multispine	1			
Number of specimens	24,948	2,157	6,725	15,014

Table 7.17 The migration pattern of fish species in the Chobe/Linyanti and southern Zambezi floodplain system (data from Van der Waal 1998).

Group A: species that remain in the rivers	Group C: species that move between rivers and floodplains
Hippopotamyrus discorhynchus	*Marcusenius macrolepidotus*
Barbus eutaenia	*Mormyrus lacerda*
Barbus lineomaculatus	*Petrocephalus catostoma*
Labeo cylindricus	*Pollimyrus castelnaui*
Opsridium zambezense	*Barbus afrovernayi*
Hemigrammocharax multifasciatus	*Barbus barnardi*
Nannocharax macropterus	*Barbus barotseensis*
Parauchenoglanis ngamensis	*Barbus bifrenatus*
Amphilius uranoscopus	*Barbus multilineatus*
Chiloglanis neumanni	*Barbus paludinosus*
Synodontis macrostigma	*Barbus poechii*
Hemichromis elongatus	*Barbus radiatus*
	Barbus thamalakanensis
Group B: species that remain on the floodplain	*Barbus unitaeniatus*
Barbus fasciolatus	*Labeo lunatus*
Coptostomobarbus wittei	*Brycinus lateralis*
Rhabdalestes maunensis	*Hydrocynus vittatus*
Clarias stappersii	*Micralestes acutidens*
Aplocheilichthys hutereaui	*Hepsetus odoe*
Oreochromis andersonii	*Schilbe intermedius*
Oreochromis macrochir	*Clarias gariepinus*
Sargochromis carlottae	*Clarias ngamensis*
Sargochromis codringtonii	*Clarias theodorae*
Sargochromis giardi	*Synodontis leopardinus*
Serranochromis angusticeps	*Synodontis nigromaculatus*
Serranochromis macrocephalus	*Synodontis woosnami*
Serranochromis robustus	*Aplocheilichthys johnstonii*
Serranochromis thumbergi	*Pharyngochromis acuticeps*
Tilapia ruweti	*Pseudocrenilabrus philander*
Ctenopoma intermedium	*Tilapia rendalli*
Ctenopoma multispine	*Tilapia sparrmanii*

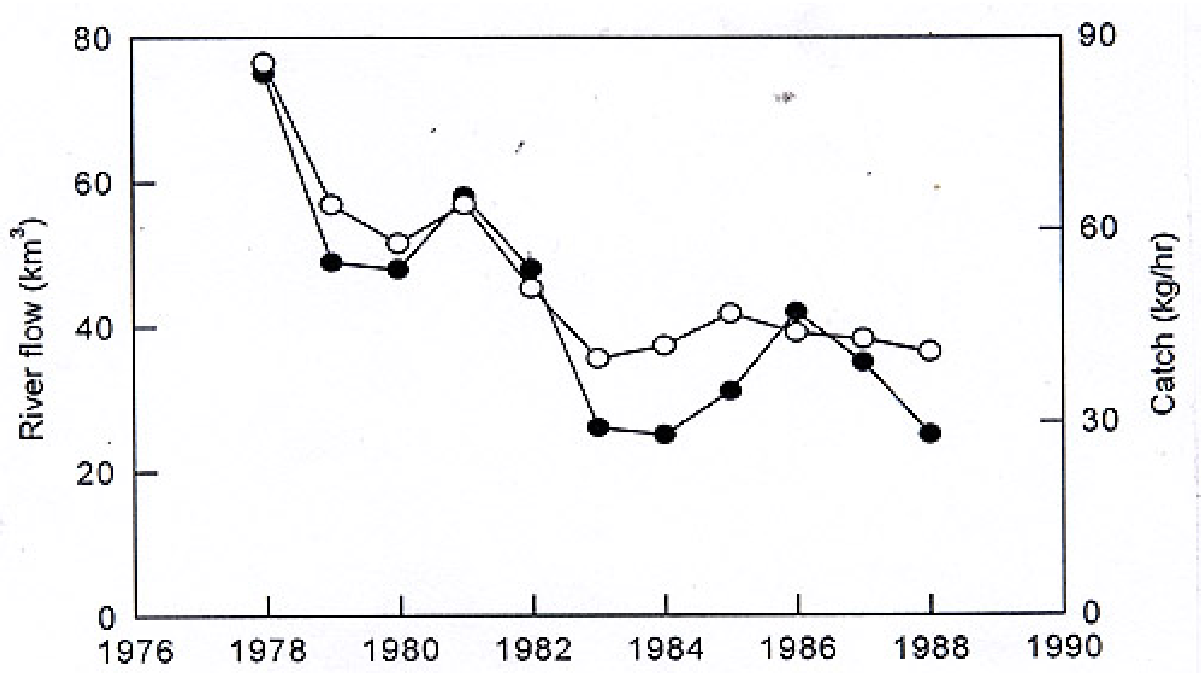
As with the Zambezi Delta, the main threats to diversity in the Lower Shire floodplains come from the possible development of large-scale irrigation farming. Crops like sugar and rice would convert more of the floodplain into agricultural land and require canalization of the river and the consumption of water. Pollution from agro-chemicals is a possibility in such a system. There is a clear need for an investigation of future proposals for development in these floodplains, an assessment of their impact, and measures to rectify some of the problems.

7.5.4 **The Zambezi Delta**

The delta of the Zambezi River is an ecologically important area where there is a transition from fresh to salt water. Its fish fauna reflects this transition by the presence of various marine species that enter freshwater (Table 7.2). The delta is an important area because of its potential for fishery production and as a nursery area for marine species, but its current fish yield is presently unknown. Unfortunately, very little is known about the ecology of the delta or the biology of its fish. There is an urgent need for investigations in view of the threats to the system.

Fears were expressed that the ecology would be severely disrupted by changes in the river flows after construction of the Cabora Bassa dam (Davies 1975, Davies *et al.* 1975). The only published data on this aspect is the evidence that the catch of prawns on the Sofala Bank, off the delta, was positively correlated with the flow of freshwater into the sea (Figure 7.16). The flow of freshwater is, of course, partly controlled by the Kariba and Cabora Bassa dams (but also by the climate). This is similar to the situation in the eastern Mediterranean where catches of fish and shrimps decreased after construction of the Aswan High Dam on the Nile (Ryder & Henderson 1975, Wadie & Abdel Razek 1985).

Figure 7.16 The relationship between the flow of the Zambezi River (●) and prawn catches (○) on the Sofala Bank, Mozambique (redrawn from data in Gammelsrod 1992).



There are few other data on the fish catches from the delta. Some information made available by IUCN indicates that the catch includes a mixture of estuarine and freshwater fish and the proportions of each will depend on the location of the fishery. Among the more important species are the mullets (*Mugil* and *Liza*) that tend to enter freshwater, and the Tarpon (*Megalops cyprinoides*) which is known to penetrate up the Zambezi as far as Tete. The distribution of fish in the delta will be determined by the salinity of the water, with marine and estuarine fish occurring in areas of high salinity, while other species will be restricted to freshwater. These distribution patterns are presently unknown.

The Zambezi Delta is, potentially, one of the most threatened of the Zambezi wetlands. Dam building is one of the threats and several dams have been proposed on the river below Cabora Bassa, e.g. Mepanda Uncua, Boroma and Lupata (Norconsult, undated). They have the potential to further alter the flow regime, already much changed by the existing dams. Another threat is the possibility of large-scale irrigation as the Zambezi Valley below Tete has areas of irrigable soil. Extensive plantations of crops such as sugar have been grown in the past in the Lower Zambezi and further development of irrigation is possible. Irrigation would further reduce the amount of freshwater flowing into the system, while large-scale agriculture brings the risk of pollution from agro-chemicals. Finally, exotic fish species could reach the delta from the Zimbabwean plateau where they are widespread. The River Sardine *Mesobola brevianalis* may have already done so, since the reports of "kapenta-like" fish in the Lower Zambezi (Williams 1998) may refer to it. The impact of exotic fish is uncertain at present, but they could have some impact on the indigenous species.

There is therefore an urgent need for a better understanding of the ecology of the Zambezi Delta. In particular, the distribution and salinity tolerance of its freshwater fishes needs to be known so that the effects of reduced fresh water inflows (and possible increases in salinity can be assessed. While the fish community consists primarily of the Lower Zambezi species listed in Table 7.2, there may be other species present, especially estuarine ones capable of living in both fresh and brackish water, and the community may be more complex than is generally realized (see Appendix 7.1).

7.6 CONSERVATION AND FUTURE DIRECTIONS

7.6.1 **Species of special conservation interest**

The conservation of fish species, like that of all other animals, requires the protection of entire ecosystems. This is a particular problem in rivers because they are linear systems and can be influenced by events in the catchment areas, often far from the area to be protected. Conservation planning therefore needs to consider if there are (a) species and (b) ecosystems of special interest that need special conservation measures. The discussion so far has clearly identified areas of interest but little has been said of species of special concern.

Species with restricted distributions and small populations are generally considered to be the most vulnerable and require special attention. Most of the fish of the Zambezi Basin, with the obvious exception of those in Lake Malawi, have relatively wide distributions and the degree of endemicity[1]

[1] It is worth defining what is meant here. An *endemic* species is one that is restricted to only one of the sub-basins listed in Table 2. Another useful term is *near-endemic*,which is a species that has a restricted distribution in (a) two sub-basins of the Zambezi system, or (b) in one sub-basin and in another river system. Some species with only a limited distribution in the Zambezi system are not considered near-endemics if they are widespread elsewhere. An example is the Yangambi Butter Catfish, *Schilbe yangambianus,* which has only been collected once in the Zambezi system but is widespread in the Congo Basin.

is generally low (Table 7.18). The greatest level of endemicity is in the Cunene system where 18% of the fish species qualify as endemics or near-endemics, which is about three times that of any other sub-basin. The reasons for this are unclear but it is probably not isolation alone, since the Cunene appears to have been cut off from the main Zambezi system for about as long as the Kafue (Skelton 1994), which has no endemics. It is possible that habitats in the Cunene are more diverse than in the Kafue, or that the river has more frequently been invaded by fish from the Congo or west coast river systems. Whatever the reasons, the Cunene is one of the most important centres of fish diversity in the southern African region and warrants further study and conservation. Unfortunately most of its length lies in Angola and little can be done at present.

The headwaters of the Okavango and Zambezi are also centres of slightly higher endemism with some species that seem to be restricted to fast-flowing streams in forested areas. The Lower Shire is the only other part of the basin with significant endemism, caused by the presence of some species typical of the Lake Malawi system entering it. An exception is *Varicorhinus pungweensis*, which also occurs in the headwaters of the Pungwe in eastern Zimbabwe. The only other endemic species in the basin are two killifish (*Nothobranchius* spp.), one endemic to each of the Kafue and East Caprivi, which are a group that typically occur in small areas. This is because of their specialized habits that enable them to live in temporary waters that are frequently isolated from other systems.

7.6.2 **Future directions**

Much of the work done on fish in the basin over the last fifty years has concentrated on fisheries. The development of fishery resources is obviously given priority because of the growth of the human population and the consequent demand for fish. Much of this work has progressed without an adequate biological base and there is a clear need for further biological investigations. This is especially important now that many fisheries have reached a level of intensity where they may be changing the composition of the fish population. The extent and impact of these changes is largely unknown. These problems have been recognised in Lake Malawi, one of the world's major centres of fish biodiversity, where a major GEF-supported project has been established. But little is being done elsewhere in the basin and this lack needs to addressed. Areas of concern include:

(a) The distribution of fish species. While this aspect is reasonably well known, there remains much to be done and areas that have been poorly investigated need further study. These include the Lower Zambezi and Delta, the Luangwa Valley and the headwaters of the Zambezi, Okavango and Cunene in Angola.
(b) Although some areas have been collected thoroughly, much of the work was done some time ago and little is known about the changes that have taken place since. It is important that some effort is made to determine the extent of change in some of these areas at least.
(c) While much of the interest centres on the larger floodplains, there are more vulnerable areas that deserve attention. They include smaller rivers and streams where changes are much more dramatic and whose fish populations may already have been irrevocably altered.

The Zambezi Basin is an area with a great diversity of fish species, and with some highly productive systems that can provide large quantities of fish for the human populations of the region. These fisheries can be sustainable with proper management, which in turn requires a proper understanding of the ecological processes that drive them. Understanding the composition of the stocks and their biological relationships is an essential first step.

Table 7.18 The number of endemic and near-endemic (see text for explanation) fish species in the major sub-basins of the Zambezi system, excluding Lake Malawi.

	Endemics	Near-endemics
Chambeshi/Lake Bangweulu	*Barbus owenae*	
	Labeo simpsoni	
	Tylochromis bangwelensis	
	Aethiomastecembelus signatus	
	N = 4 (5.9%)	
Cunene	*Kneria maydelli*	*Barbus argenteus*
	Barbus dorsolineatus	*Labeo ruddi*
	Orthochromis machadoi	*Labeo ansorgii*
	Thoracochromis albolabris	*Chetia welwitschi*
	Thoracochromis buysi	*Sargochromis gracilis*
	Sargochromis coulteri	*Schwetzochromis machadoi*
	N = 6 (9.0%)	N = 6 (9.0%)
Zambezi headwaters	*Paramormyrops jacksoni*	*Barbus breviceps*
	Barbus bellcrossi	*Hypsopanchax jubbi*
	N =2 (2.3%)	N = 2 (2.3%)
Okavango	*Parakneria fortuita*	*Barbus breviceps*
		Sargochromis gracilis
	N = 1 (1.2%)	N = 2 (2.4%)
Barotse floodplain		
Chobe/Caprivi	*Nothobranchius* sp.	
	N = 1 (1.2%)	
Kafue	*Nothobranchius kafuensis*	
	N = 1 (1.6%)	
Lake Kariba/Middle Zambezi		*Chiloglanis emarginatus*
		N = 1 (1.6%)
Lake Cabora Bassa catchment		*Barbus manicensis*
		N = 1 (2.0%)
Lower Shire		*Barbus choloensis*
		Varicorhinus pungweensis
		Opsaridium tweddlorum
		Oreochromis shiranus
		Aethiomastacembelus shiranus
		N = 5 (6.9%)
Lower Zambezi		

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Table 7.2. The fishes of the Zambezi River system (excluding Lake Malawi) together with those of the Cunene, Okavango and Pungwe-Buzi systems. Taken from Skelton (1993, 1994) with additions from other sources. The list of fish from the Chambeshi/Bangweulu is based on Jackson (1961a), updated as far as possible from CLOFFA (Daget *et al.* 1984, 1986, 1991) and is probably incomplete. ● = fish with a relatively widespread distribution, ○ = fish with a limited distribution (in some cases, known only from one specimen, numbers refer to the notes that follow at the bottom of the table.

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
PROTOPTERIDAE													
Protopterus annectens	Lungfish	●							●	●	●	●	●
Protopterus amphibius	East African Lungfish											●	
MORMYRIDAE													
Mormyrops anguilloides	Cornish Jack	●							●	●	●	●	●
Mormyrus lacerda	Western Bottlenose		●	●	●	●	●	●	1				
Mormyrus longirostris	Eastern Bottlenose	●							●	●	●	●	●
Mormyrus caballus		●											
Campylomormyrus tamandua		●											
Hippopotamyrus ansorgii	Slender Stone-basher		●	●	●	●	●				●	●	●
Hippopotamyrus discorhynchus	Zambezi Parrotfish	●	●	●	●	●	●		●	●	●	●	●
Marcusenius macrolepidotus	Bulldog	●	●	●	●	●	●	●	●	●	●	●	●
Petrocephalus catostoma	Churchill	●	●	●	●	●	●	●	2		●	●	●
Petrocephalus simus		●											
Pollimyrus castelnaui	Dwarf Stone-basher	●	●	●	●	●	●	●					
Paramormyrops jacksoni	Ghost Stone-basher			○									
MEGALOPIDAE													
Megalops cyprinoides	Oxeye Tarpon										●	●	●

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabóra Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
ANGUILLIDAE													
Anguilla mossambica	Long-finned Eel								•	•	•	•	•
Anguilla bicolor	Short-finned Eel										•	•	•
Anguilla marmorata	Madagascar Mottled Eel										•	•	•
Anguilla bengalensis	African Mottled Eel						3		•	•	•	•	•
KNERIIDAE													
Kneria auriculata	Southern Kneria									4			•
Kneria maydelli	Cunene Kneria		o										
Kneria polli	Northern Kneria		•	•	•	•	•	•					
Parakneria mossambica													•
Parakneria fortuita	Cubango Kneria				o								
CYPRINIDAE													
Mesobola brevianalis	River Sardine		•	•	•	•	•						
Mesobola moeruensis		•											
Opsridium zambezense	Barred Minnow			•	•	•	•		•	•	•	•	•
Opsaridium tweddlorum											•		
Barbus trachypterus		•											
Barbus breviceps	Short-headed Barb		•		•								
Barbus annectens	Broad-striped Barb								•	•	•	•	•
Barbus barotseensis	Barotse Barb	•	•	•	•	•	•	•					
Barbus bellcrossi	Gorgeous Barb			•									
Barbus lineomaculatus	Line-spotted Barb	•	•	•	•	•	•	•	•	•	•	•	•
Barbus neefi	Side-spotted Barb			•				•					

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabóra Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Barbus pseudognathodon		•											
Barbus unitaeniatus	Long-bearded Barb	•	•	•	•	•	•	•	•	•			
Barbus bifrenatus	Hyphen Barb	•	•	•	•	•	•	•					
Barbus viviparus	Bow-striped Barb										•	•	•
Barbus brevidorsalis	Dwarf Barb	•		•	•			•					
Barbos owenae		•											
Barbus thamalakanensis	Thamalakane barb			•	•	•	•						
Barbus barnardi	Black-backed Barb		•	•	•	•	•	•					
Barbus toppini	East Coast Barb										•	•	•
Barbus macrotaenia	Broad-banded Barb										•	•	
Barbus fasciolatus	Red Barb	•	•	•	•	•	•	•	•	•			
Barbus radiatus	Beira Barb	•	•	•	•	•	•	•	•	•	•	•	•
Barbus haasianus	Sickle-finned barb	•	•	•	•	•	•	•			•	•	•
Barbus trimaculatus	Three-spotted Barb	•	•						•	•	•	•	•
Barbus poechii	Dash-tailed Barb		•	•	•	•	•	•	I				
Barbus eutaenia	Orange-finned Barb	•	•	•	•	•	•	•			•	•	•
Barbus miolepis	Zigzag Barb			•	•	•	•	•					
Barbus multilineatus	Copper-striped Barb	•	•	•	•	•	•	•					
Barbus afrovernayi	Spot-tailed Barb	•	•	•	•	•	•	•	I				
Barbus argenteus	Rose-finned Barb		•										
Barbus choloensis	Silver Barb										o		
Barbus paludinosus	Straight-finned Barb	•	•	•	•	•	•	•	•	•	•	•	•
Barbus afrohamiltoni	Hamilton's Barb	•									•	•	•

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabóra Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Barbus mattozi	Papermouth		●	○		○			○				
Barbus kerstenii	Red-spotted Barb		●	●	●	●	●	●			●	●	
Barbus manicensis	Yellow Barb									○			
Barbus dorsolineatus	Cunene Barb		○										
Barbus marequensis	Large-scaled Yellowfish								●	●	●	●	●
Barbus codringtonii	Upper Zambezi Yellowfish			●	●	●	●	●					
Coptostomobarbus wittei	Upjaw Barb			●	●	●	●	●					
Varicorhinus pungweensis	Pungwe Chiselmouth										○		●
Varicorhinus nasutus	Short-snouted Chiselmouth								●	●	●	●	●
Labeo altivelis	Manyame Labeo	●							●	●	●	●	●
Labeo simpsoni		●											
Labeo ruddi	Silver Labeo		●										
Labeo congoro	Purple Labeo								●	●	●	●	●
Labeo cylindricus	Red-eyed Labeo			●	●	●	●	●	●	●	●	●	●
Labeo molybdinus	Leaden Labeo								●	●	●	●	●
Labeo lunatus	Upper Zambezi Labeo			●	●	●	●	●	I				
Labeo ansorgii	Cunene Labeo		■										
DISTICHODONTIDAE													
Distichodus mossambicus	Nkupe								●	●	●	●	●
Distichodus schenga	Chessa								●	●	●	●	●
Distichodus maculatus		●											
Hemigrammocharax machadoi	Dwarf Citharine		●	●	●	●	●						
Hemigrammocharax multifasciatus	Multi-barred Citharine		●	●	●	●	●	●					

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cuene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Nannocharax macropterus	Broad-barred Citharine			•	•	•	•	•					
CHARACIDAE													
Brycinus imberi	Imberi	•							•	•	•	•	•
Brycinus lateralis	Striped Robber		•	•	•	•	•	•	•	•	•	•	•
Alestes grandisquamis		•											
Alestes macrophthalmus		•											
Micralestes acutidens	Silver Robber		•	•	•	•	•	•	•	•	•	•	•
Micralestes humilis		•											
Bryconaethiops boulengeri		•											
Rhabdalestes maunensis	Slender Robber	•	•	•	•	•	•	•					
Hemigrammopetersius barnardi	Barnard's Robber										•	•	•
Hydrocynus goliath	Goliath Tigerfish	•											
Hydrocynus vittatus	Tigerfish	•		•	•	•	•		•	•	•	•	•
HEPSETIDAE													
Hepsetus odoe	African Pike		•	•	•	•	•	•	1				
CLAROTEIDAE													
Auchenoglanis occidentalis		•											
Chrysichthys sharpii		•											
Amarginops hildae	Hilda's Grunter												•
Parauchenoglanis ngamensis	Zambezi Grunter			•	•	•	•						
AMPHILIIDAE													
Leptoglanis rotundiceps	Spotted Sand Catlet		•	•	•	•	•	•	•	•	•	•	•
Leptoglanis cf dorae	Chobe Sand Catlet			•	•	•	•						

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobo/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Doumea alluta		•											
Amphilius natalensis	Natal Mountain Catfish									○	○		
Amphilius laticaudatus	Broadtail Mountain Catfish												•
Amphilius uranoscopus	Common Mountain Catfish	•		•	•	•	•		•	•	•	•	•
SCHILBEIDAE													
Schilbe intermedius	Silver Barbel	•	•	•	•	•	•	•	•	•	•	•	•
Schilbe bangwelensis		•											
Schilbe yangambianus	Yangambi Butterbarbel			○									
CLARIIDAE													
Clarias gariepinus	African Catfish	•	•	•	•	•	•	•	•	•	•	•	•
Clarias ngamensis	Blunt-toothed Catfish	•	•	•	•	•	•	•			•	•	
Clarias stappersii	Blotched Catfish	•	•	•	•	•	•	•	5				
Clarias liocephalus	Smooth-headed Catfish	•	•	•	•			•					
Clarias theodorae	Snake Catfish	•	•	•	•	•	•	•			•	•	
Clariallabes platyprosopus	Broad-headed Catfish			•	•	•	•						
Heterobranchus longifilis	Vundu	•							•	•	•	•	
MALAPTERURIDAE													
Malapterurus electricus	Electric Catfish								•	•	•	•	•
MOCHOKIDAE													
Chiloglanis emarginatus	Phongolo Rock Catlet								○				•
Chiloglanis fasciatus	Okavango Rock Catlet			•	•		•						
Chiloglanis neumanni	Neumann's Rock Catlet	•	•	•		•	•	•	•	•	•	•	•
Chiloglanis pretoriae	Short-spined Rock catlet								•	•			•

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Chiloglanis elizabethianus		•											
Euchilichthys guentheri		•											
Euchilichthys royauxi		•											
Synodontis zambezensis	Brown Squeaker								•	•	•	•	•
Synodontis nigromaculatus	Spotted Squeaker	•		•	•	•	•						
Synodontis nebulosus	Cloudy Squeaker								•	•	•	•	•
Synodontis woosnami	Upper Zambezi Squeaker		•	•	•	•	•						
Synodontis macrostigma	Large-spotted Squeaker		•	•	•	•	•	•					
Synodontis macrostoma	Large-mouthed Squeaker		•	•	•	•	•	•					
Synodontis leopardinus	Leopard Squeaker		•	•	•	•	•						
Synodontis thamalakanensis	Bubble-barbed Squeaker			•	•	•	•						
Synodontis vanderwaali	Fine-toothed Squeaker		•	•	•	•	•						
Synodontis ornatipinnis		•											
APLOCHEILIDAE													
Nothobranchius orthonotus	Spotted Killifish										•	•	•
Nothobranchius kuhntae	Beira Killifish												•
Nothobranchius kafuensis	Kafue Killifish							○					
Nothobranchius sp.	Caprivi Killifish						○						
Nothobranchius symoensi		•											
Nothobranchius rachovii	Rainbow Killifish										•	•	•
CYPRINODONTIDAE													
Aplocheilichthys johnstoni	Johnston's Topminnow		•	•	•	•	•	•	•	•	•	•	•
Aplocheilichthys hutereaui	Mesh-scaled Topminnow	•		•	•	•	•	•			•	•	•

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Aplocheilichthys katangae	Striped Topminnow	•	•	•	•	•	•	•	6	6	•	•	•
Aplocheilichthys moeruensis		•											
Hypsopanchax jubbi	Southern Deepbody			o									
CICHLIDAE													
Hemichromis elongatus	Banded Jewelfish			•	•	•	•		1				
Orthochromis machadoi	Cunene Dwarf Bream		•										
Pseudocrenilabrus philander	Pygmy Bream	•	•	•	•	•	•	•	•	•	•	•	
Chetia welwitschi	Angolan Bream		•										
Astatotilapia calliptera	Eastern Bream										•	•	•
Pharyngochromis acuticeps	Zambezi Dwarf Bream			•	•	•	•		•	•	?	?	
Thoracochromis albolabris	Thick-lipped Bream		•										
Thoracochromis buysi	Namib Bream		•										
Sargochromis mellandi		•											
Sargochromis carlottae	Rainbow Bream			•	•	•	•	•	1				
Sargochromis codringtonii	Green Bream			•	•	•	•	•	•	•			
Sargochromis giardi	Pink Bream		•	•	•	•	•	•	1				
Sargochromis greenwoodi	Greenwood's Bream				•	•	•	•					
Sargochromis mortimeri	Mortimer's Bream			•				•					
Sargochromis coulteri	Cunene Bream		•										
Sargochromis gracilis	Slender Bream		o		o								
Serranochromis altus	Hump-backed Largemouth				•	•	•	•					
Serranochromis angusticeps	Thin-faced Largemouth	•	•	•	•	•	•	•					
Serranochromis longimanus	Long-finned Largemouth			•	•	•	•						

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Serranochromis macrocephalus	Purple-faced Largemouth	•	•	•	•	•	•	•	•				
Serranochromis robustus	Nembwe	•		•	•	•	•	•	1				
Serranochromis thumbergi	Brown-spotted Largemouth	•	•	•	•	•	•	•					
Tylochromis bangwelensis		•											
Tilapia sparrmanii	Banded Tilapia	•	•	•	•	•	•	•	•	•			•
Tilapia rendalli	Red-breasted Tilapia	•	•	•	•	•	•	•	•	•	•	•	•
Tilapia ruweti	Okavango Tilapia			•	•	•	•						
Orthochromis machadoi			•										
Oreochromis mossambicus	Mozambique Tilapia										•	•	•
Oreochromis mortimeri	Kariba Tilapia								•	•			
Oreochromis andersonii	Three-spotted Tilapia		•	•	•	•	•	•					
Oreochromis placidus	Black Tilapia										•	•	•
Oreochromis shiranus	Shire Tilapia										•		
Oreochromis macrochir	Green-headed Tilapia	•	•	•	•	•	•	•					
ANABANTIDAE													
Ctenopoma intermedium	Black-spotted Climbing Perch	•		•	•	•	•	•			•	•	•
Ctenopoma multispine	Many-spined Climbing Perch	•		•	•	•	•	•			•	•	•
MASTACEMBELIDAE													
Aethiomastacembelus frenatus	Long-tailed Spiny Eel			•	•	•	•	•					
Aethiomastacembelus shiranus	Shire Spiny Eel										•		
Aethiomastacembelus signatus		•											
Aethiomastacembelus vanderwaali	Ocellated Spiny Eel				•	•	•		1				
AMBASSIDAE													

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabóra Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
Ambassus gymnocephalus	Bald Glassy											•	•
Ambassus productus	Long-spined Glassy											•	•
MUGILIDAE													
Mugil cephalus	Flat-headed Mullet											•	•
Liza macrolepis	Large-scaled Mullet											•	•
SYNGNATHIDAE													
Microphis fluviatilis	Freshwater Pipefish											•	•
Microphis brachyurus	Short-tailed Pipefish											•	•
SPARIDAE													
Acanthopagrus berda	Sea Bream										•	•	•
MONODACTYLIDAE													
Monodactylus argenteus	Natal Moony											•	•
Monodactylus falciformis	Cape Moony											•	•
ELEOTRIDAE													
Eleotris fusca	Dusky Sleeper											•	•
Eleotris melanosoma	Broad-headed Sleeper											•	•
GOBIIDAE													
Awaous aeneofuscus	Freshwater goby								•	•	•	•	•
Glossogobius giuris	Tank Goby								•	•	•	•	•
CARCHARHINIDAE													
Carcharhinus leucas	Bull Shark										•	•	•

				UPPER ZAMBEZI					MIDDLE ZAMBEZI		LOWER ZAMBEZI		
SPECIES	COMMON NAME	Chambeshi/ L. Bangweulu	Cunene	Zambezi headwaters	Okavango	Barotse floodplain	Chobe/Caprivi	Kafue	L.Kariba/ Mid-Zambezi	L.Cabora Bassa catchment	Lower Shire	Lower Zambezi & Delta	Pungwe & Buzi
PRISTIDAE													
Pristis microdon	Small-toothed Sawfish										•	•	•
TOTAL NO. SPECIES		67	67	87	85	81	82	64	59	48	72	77	74
TOTALS PER SECTION				95					61		83		

Notes:

1. These species have been collected in the transitional area between the Upper and Middle Zambezi, i.e. Batoka Gorge and the upper reaches of Lake Kariba. They were considered to be invaders from above the Victoria Falls, but may also be relict populations.
2. Bell-Cross (1972) and Skelton (1993) indicate that *Petrocephalus catostoma* occurs in the middle Zambezi, but there are no records of it from the main river or the Zimbabwean tributaries, but it apparently occurs in the upland sections of the Zambian tributaries (Jackson, 1961).
3. A single Mottled Eel, *Anguilla bengalensis*, has been collected from the Upper Zambezi (Bell-Cross 1975), but as it was taken in the header dam of the Victoria Falls hydroelectric power station, it was probably able to use this man-made structure to surmount the barrier of the falls.
4. Although *Kneria auriculata* is said to occur in the tributaries of the Upper Zambezi in the Eastern Highlands of Zimbabwe, there are none from these rivers in the collection of the Natural History Museum of Zimbabwe and it may be absent from them.
5. Bell-Cross (1972) reports that a specimen of *Clarias submarginatus* (which he used for *C. stappersii*, although it is now a synonym of *Clarias liocephalus*) was collected from Lake Lusiwashi, on a tributary of the Luangwa River. He suggested that this represented a connection with the Bangweulu system, but this record has been mentioned nowhere else in the literature.
6. According to Skelton (1993), *Aplocheilichthys katangae* occurs throughout the Middle Zambezi but it has never been collected in the Zimbabwean section and there are no specimens in the collection of the Natural History Museum of Zimbabwe, so its occurrence there is doubtful.

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CHAPTER 7 : APPENDIX 1
FRESHWATER FISH SURVEY OF THE LOWER ZAMBEZI RIVER, MOZAMBIQUE

Roger Bills

1. INTRODUCTION

This survey, carried out from 27 July to 14 August 1999, forms part of the Zambezi Basin Wetlands Conservation and Resource Utilisation Project. One of the aims of the project is to provide decision makers with accurate information about resources within the Zambezi Delta so that sound management policies can be implemented. The only major fish survey of the Lower Zambezi region was carried out by the German herpetologist Wilhelm Peters in 1844-45. Many of the Lower and Middle Zambezi endemics, and other more widespread Zambezian species, were discovered by Peters during this expedition. Peters published much of the descriptive work from this expedition in *Reise nach Mozambique* (1868), and most of the material was deposited in the Berlin Natural History Museum. Thus the Lower Zambezi is the type locality for large number of Zambezi fishes (Table 1). Unfortunately, Peters' notes are not sufficiently detailed to identify exact localities, with many simply being given as Tete or Quelimane.

Since Peters' expedition only a few scientists have visited the region and briefly reported on the fishes (Guy 1964, Davies 1975). Some Mozambican fisheries reports have also been published but none were of a systematic nature. This present biodiversity survey is the first systematic survey this century and is long overdue.

Two factors should be noted when considering the July 1999 collection:

1. The limits of the Lower Zambezi are rather ill-defined. Many workers have taken the upper limit to be the Cabora Bassa rapids (now the Cabora Bassa dam wall) while some consider the Shire confluence is more appropriate. Which ever is taken, during this July 1999 expedition, the upper section of the Lower Zambezi was not sampled. Only sites around Marromeu town and downstream of this point in the delta and a single site at Inhamitanga were visited. No rocky habitats were sampled and consequently several species were not collected such as *Hippopotamyrus ansorgii*, *Barbus marequensis*, *Varicorhinus* sp., *Chiloglanis* sp. and *Amphilius* spp. The absence of these rocky habitat specialists from our list must be considered simply a reflection of collecting bias.

2. Our survey was conducted in July which is the cool, low flow period. Most of the fishes are not breeding at this time and many are not very active. Probably the best time for sampling would be during the warm, wet summer, from November to January, when most fishes will be breeding. Of course accessibility during the summer would be a different problem. The rarity of some species in our samples e.g. *Protopterus* spp. and *Malapterurus electricus* was according to locals an artefact of sampling time.

Information concerning species distributions and additional biological details are largely taken from Skelton's "A Complete Guide to the Freshwater Fishes of Southern Africa" (1993a) and Smith's Sea Fishes (Smith & Heemstra 1986). Common English names follow Skelton (1993b). Photographs of habitats, fishes and fishing activities referred to in this report and available as picture files on a CD-ROM.

2. METHODS

Fish samples were collected using a variety of gill, seine and hand nets. Samples were also bought from local fishermen who were using seine and gill nets, basket traps and fish poison. Most samples were fixed in 10% formalin in the field and on returning to Grahamstown transferred to 60% propyl alcohol for long term preservation. Small specimens were placed whole into formalin while specimens larger than 20 cm were also injected with formalin. Some specimens were prepared as skeletons and some tissue samples were taken for DNA analyses. All samples were returned to the JLB Smith Institute of Ichthyology for sorting and identification. A representative collection was prepared for lodging in the Maputo Museum while the bulk of the material was held at the JLB Smith Institute of Ichthyology as a voucher collection for this study. Museum accession numbers for this collection are available on request.

All freshwater fish identifications were determined by I.R. Bills and P.H. Skelton and marine species by E.A. Anderson. The numbering of the families in the checklist follows the J.L.B. Smith Collection numbering system (Anderson, unpublished). Table 2 shows sizes, number of localities collected, habitats collected, etc.

Appendix 7.1 Table 1 Fish species whose type localities are in the Lower Zambezi region.
H = holotype, S = syntype, L = lectotype;
ZMHU (or ZMB) = Zoologisches Museum de Humbold-Universitat, Berlin,
BMNH = British Museum (Natural History), London

Species	**type locality**	**type status & no.**	**museum number**
Protopterus amphibius (Peters 1844)	Quelimane, Zambezi R.	lost	-
Anguilla mossambica Peters 1852	Lumbo, Molumbo R.	H	ZMHU 6230
Anguilla bengalensis labiata Peters 1852	Tete, Zambezi R. & Boro, Licuare R	S (4)	ZMHU 6227-8
Hippopotamyrus discorhynchus (Peters 1852)	Tete, Zambezi R.	S (4)	ZMB 3673-6
Marcusenius macrolepidotus (Peters 1852)	Tete, Zambezi R.	S (3)	ZMHU 3630, 3677, 3678
Mormyrus longirostris Peters 1852	Zambezi R.	S (2)	ZMHU 3671-2
Brycinus imberi (Peters 1852)	Zambezi R.	S (2)	ZMHU 3574
Micralestes acutidens (Peters 1852)	Zambezi R.	S (3)	ZMHU 3576
Distichodus mossambicus Peters 1852	Tete, Zambezi R.	S (2)	ZMHU 3564, 6613
Distichodus schenga Peters 1852	Tete, Zambezi R.	H	ZMHU 3565
Barbus paludinosus Peters 1852	Quelimane, Zambezi R.	S	ZMHU & BMNH 1861.3.10:6-7
Barbus radiatus Peters 1853	Tete, Revugo R.	L	ZMHU 4737
Barbus trimaculatus Peters 1852	Tete, Revugo R.	H	ZMHU 4737
Labeo altivelis Peters 1852	Mozambique	S (6)	ZMHU 3283-7
Labeo congoro Peters 1852	Tete, Zambezi R.	S (2)	ZMHU 3279
Labeo cylindricus Peters 1852	Mozambique	S (3)	ZMHU 3280-2
Opsaridium zambezense (Peters 1852)	Tete, Zambezi R.	S	BMNH1861.3.10:8-9
Synodontis nebulosus Peters 1852	Tete, Zambezi R.	H	ZMHU 3.120
Synodontis zambezensis Peters 1852	Tete, Sana & Boror, Zambezi R.	L	ZMHU 3.119
Nothobranchius orthonotus (Peters 1844)	Quelimane, Zambezi R.	S (3)	ZMHU 4754
Nothobranchius rachovii Ahl 1826	Beira, Mozambique	S (2)	ZMHU 21.389
Microphis fluviatilis (Peters 1852)	Tete, Zambezi R.	S (1?)	ZMHU 6233
Oreochromis mossambicus (Peters 1852)	Mozambique	L	ZMB 2.806-2.821
Oreochromis placidus (Trewavas 1941)	lower Buzi R., Mozambique	H	BMNH1907.7.2:19
Awaous aenofuscus (Peters 1852)	Sena, Zambezi	S (2)	ZMB 2105

3. RESULTS

3.1 Survey sites

The Zambezi River begins to split up into what is known as the delta some 20-30 kms upstream of Marromeu. The river at Marromeu and downstream to the lower delta is a large braided sand bank river. There is an extensive floodplain at Marromeu estimated at over 20 km width. The floodplain consists of river channels (which during July were not connected to the main river and so were not flowing), isolated lagoons, swamps and man-made irrigation channels. During the July 1999 expedition the floodplain channels were not flowing and the main river channel consisted of three braids at the Marromeu sugar factory.

We sampled extensively around Marromeu: the main river channel, natural backwaters and irrigation channels. We visited a site near the western edge of the of the delta for a single day and a lower section of the delta (Micelo River) for two days. We also travelled by boat from Marromeu to Malingapansi (on the Micelo River) which afforded us opportunities of collecting at various points down the main channels of the Zambezi and Micelo Rivers and interconnecting mangrove channels. Details of sample sites are given in Table 7.

3.1.2 *Habitats*

Zambezi River - main channel

At Marromeu the Zambezi River consists of two to three channels of approximately 200-300 m wide. These may be separated by islands themselves 200-300 m wide. The banks on both sides of the river were eroded sand, 6-8 m above the river level in July. The river substrate consisted of sand. River channels are more than 10 m deep in many places. In addition to the main channels there were lagoons which were clearly part of the main river at higher water levels. These had been isolated in July, sedimented partially and some were vegetated with aquatic macrophytes such at *Potamogeton pectinatus*, *Ceratophyllum* sp. and *Azolla pinnata*.

There are marginal reeds, grasses and *Polygonum*. The aquatic vegetation is sparse and dominated by floating species: *Ceratophyllum* sp., *Utricularia* sp., *Azolla pinnata*, *Ricciocarpus natans* (all native) and *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia molesta* (all exotic South American species).

Floodplain lagoons and wetlands

Large and small channels and lagoons, which during higher water levels will probably form distinct flowing channels, are present all around Marromeu. They range from large deep and extensive non-flowing river channels with large aquatic and marginal vegetation beds to very small pools with little but ephemeral invertebrate life. Certain pools are affected by rural farming and were turbid, others were fully covered with *Azolla* and some were clear.

Flooded grasslands were sampled at the northwestern edge of the Marromeu floodplain on the main road toward Inhamitanga. Water depths were shallow (<1.5 m), water was usually clear and grass cover was usually close to 100%. Few species were present in these areas possibly indicating that these areas dry out and have to be recolonised from adjacent regions.

Irrigation channels a few metres wide and up to 1 m deep were also present around Marromeu. Some of these were dry or almost so, while others appeared to remain with water for long periods as they had extensive *Azolla* cover.

Isolated pools ranging in size up to a kilometre in diameter are common on the floodplain. We visited one and it was shallow (<2 m deep), stained with humic acid, the substrate consisted of rotting plant and the lake was surrounded by a belt of 200-300 m of grassy swamp.

Appendix 7.1 Table 2 Summary details of fishes collected by the July 1999 expedition to the Zambezi Delta.

Number of sites - fish were sampled at a total of 35 sites. The number of site a species was collected at is given as a % of total sites.
% community composition - these were calculated for species from sites where the species was collected and not using the entire collection. Hopefully this will reflect more accurately abundance of species in preferred habitats. Mean, minimum and maximum % compositions are given
Estimate of abundance - R = rare, F = frequent, C = abundant. This is my opinion taken from the sample data, my knowledge of sampling techniques and fishermen's catches (not included in the data in the table).
Preferred habitats - R = main river channel, RL = lagoons associated with the main river channel, F = floodplain swamps and channels, C = creeks and small streams, V = associated with vegetation, O = open water, S = associated with the substrate.
Salinity preference - FW = freshwater (<1‰), E = estuarine (varying salinities between 1-25‰), M = marine (>25‰).

Species collected	Fish size (mm SL) (min-max)	No. of sites collected (%)	% composition		Abundance	Salinity	Preferred habitats
			mean	min-max			
Carcharinus leucas	-	-	-	-	R	FW-M	R O
Protopterus annectens brieni	197-450	6	2.4	2.4	F	FW	F V
Elops machinata	500	-	-	-	R	FW-M	R O
Megalops cyprinoides	174-322	6	1.2	0.8-1.6	F	FW-M	R O
Brachysomophis crocodilinus	630-850	3	1.9	1.9	R	M	R S
Hippopotamyrus discorhynchus	66-210	3	2.1	2.1	F	FW	R L V
Marcusenius macrolepidotus	51-258	3	22.5	22.5	C	FW	R RL F C V
Mormyrops anguilloides	218-700	6	2.6	0.8-4.3	F	FW	R RL
Mormyrus longirostris	152-240	-	-	-	F	FW	RL
Petrocephalus catostoma	41-66	3	4.2	4.2	R	FW	C V
Brycinus imberi	44-80	26	10.1	0.9-34.0	C	FW	R O
Brycinus lateralis	33-64	6	1.5	0.9-2.0	R	FW	F O
Hemigrammopetersius barnardi	29-35	6	3.2	0.5-5.8	R	FW	R O
Hydrocynus vittatus	57-380	14	2	0.9-3.3	F	FW	R O
Micralestes acutidens	13-57	23	36	6.7-89.5	C	FW	R F C O
Distichodus mossambicus	65-295	14	1.8	0.8-3.7	F	FW	R O V
Distichodus schenga	30-159	23	14.8	1.3-75	C	FW	R O
Barbus afrohamiltoni	30-87	29	11.7	0.3-73.5	F	FW	RL F C S
Barbus annectens	17-30	29	16.7	0.4-67.9	C	FW	RL F C V
Barbus haasianus	10-32	20	19.8	2.4-56.4	C	FW	RL F C V
Barbus kerstenii	24-27	3	1.4	1.4	R	FW	C V
Barbus macrotaenia	11-31	43	11.3	0.4-36.9	C	FW	RL F C V
Barbus paludinosus	10-69	49	31.8	1.6-100	C	FW	RL F C S
Barbus radiatus	20-38	9	13.2	9.5-15.4	F	FW	RL F S
Barbus trimaculatus	54-69	3	37.2	37.2	R	FW	C S
Barbus viviparus	18-34	17	17	0.4-55.6	C	FW	RL F C V
Labeo altivelis	46-195	20	12.5	0.4-33.3	C	FW	R O
Labeo congoro	89-195	17	3.5	0.8-7	F	FW	R O
Opsaridium zambezense	21-45	3	2.2	2.2	R	FW	R O
Schilbe intermedius	160-248	9	1.8	0.8-2.4	F	FW	R RL O V
Clarias gariepinus	114-490	14	5.4	0.5-19	F	FW	R RL F S

Species collected	Fish size (mm SL) (min-max)	No. of sites collected (%)	% composition		Abundance	Salinity	Preferred habitats
			mean	min-max			
Clarias ngamensis	303-307	3	1.4	1.4	R	FW	F S
Clarias theodorae	85-132	3	1.1	1.1	R	FW	C S V
Malapterurus electricus	248-318	-	-	-	R	FW	RS
Synodontis zambezensis	45-162	11	9.8	0.8-34.8	C	FW	R S
Synodontis nebulosus	-	-	-	-	R	FW	R S
Nothobranchius orthonotus	40	3	2.2	2.2	R	FW	F V
Aplocheilichthys hutereaui	36452	17	13	1.3-43.7	C	FW	RL F S V
Aplocheilichthys katangae	36492	26	11.4	0.8-63.9	C	FW	RL F S V
Microphis fluviatilis	78-177	11	6.5	2.2-26.7	F	FW-E	R S V
Microphis brachyurus	81-84	3	2.8	2.8	R	M	R S
Ambassis productus	10-96	11	22.7	0.8-40.0	C	FW-M	R O
Ambassis gymnocephalus	49	3	11.1	11.1	R	FW-M	R O
Ambassis natalensis	44-64	3	10.4	10.4	R	FW-M	R O
Leiognathus equula	20-28	3	100	100	R	E	R O
Acanthopagrus berda	16-122	6	22.4	4.7-40.0	F	E	R S O
Astatotilapia calliptera	16-58	9	1.2	0.6-2.2	R	FW	F V
Oreochromis mossambicus	9-85	46	5.5	0.8-23.4	C	FW	RL F V O
Oreochromis placidus	16-260	26	7.3	1.5-17.4	C	FW	R RL V O
Pseudocrenilabrus philander	9-71	43	12.8	1.3-59.3	C	FW	RL F C V
Tilapia rendalli	28-202	9	1.4	0.9-1.8	F	FW	RL V
Liza alata	285-330	-	-	-	F	E	R O
Valamugil seheli	23-58	6	7.4	3.8-11.1	F	E	R O
Epinephalus coiodes	-	-	-	-	F	E	R O
Terapon jarbua	31-100	9	24.5	7.3-46.2	C	E-M	R O
Sillago sihama	19-236	3	2.8	2.8	R	E-M	R S O
Glossogobius callidus	12-59	11	5.8	1.5-13.4	C	FW-E	R S O
Glossogobius giurus	235-280	3	0.8	0.8	F	FW-E	R S O
Yongeichthys nebulosus	58-72	3	3.8	3.8	R	E-M	RL S
Priolepis sp.	10-33	3	98.6	98.6	C	FW	FS
Periophthalmus argentilineatus	25-70	6	39.2	22.8-55.6	C	E-M	R S
Stenogobius kenyae	15-51	17	3.6	0.4-11.1	C	FW	R S O
Ctenopoma multispine	50-76	9	5.9	0.4-9.3	F	FW	F C V
Microctenopoma intermedium	19-33	20	2.8	0.5-10.5	F	FW	RL F C V
Solea bleekeri	12	3	0.9	0.9	R	M	R S O
Chelonodon laticeps	33-119	9	18.3	17.0-29.0	C	E-M	R O

<u>Streams draining the floodplain</u>

Two streams at the western edge of the floodplain were sampled. These were small (5 m width, <1m depth), sand substrate, vegetated streams. Their banks were forested and consequently they had considerable amounts of leaf litter. Water was brown from humic acid.

Mangrove channels

Main river and interconnecting channels in the lower delta. During July these areas were saline and tidal. Substrates were fine, soft mud. In most places vegetation was dominated by the mangrove tree *Avicenna marina*. At each of the sites we sampled there was a distinct vertical change in salinity with lower water being more saline. On exposed mud surfaces there were usually large numbers of the mudskipper *Periophthalmus argentilineatus*.

Marine lagoons near the mouth

A single site was sampled in the lagoon at the southern (marine) end of the Micelo River. Salinity was 30‰, substrates were coarse sand and water visibility was several metres. This area clearly receives little freshwater input and was dominated by marine fish species. The lagoon was estimated at 3 km wide (at its widest point) and 1 km long, its mouth (although not visited) was estimated at 500 m.

3.2 Water conductivity and salinity

Water salinity in the lower delta

Two river channels and an interconnecting backwater were sampled and tested for salinity using a salinometer. Where possible both surface and bottom samples were taken using a water bottom sampler. The two channels and backwater appear to have varying freshwater inputs indicated by both salinity and water clarity. Results are given in Table 3.

The large lagoon at the marine end of the Micelo River was dominated by salt water at the surface and on the bottom, the water clarity was high and at site ZD99/27 the substrate was coarse sand – all tending to indicate low freshwater input. This would seem to be confirmed by fishermen who informed us that the upstream connection with Zambezi main channel was either blocked or very shallow and not accessible by boat. Fishermen also informed us that at site ZD99/27 there were no crocodiles but sharks were common.

In the interconnecting mangrove channels there was salt-brackish water on the bottom but the surface water was predominantly fresh and very turbid indicating freshwater through flows even at high tide. Presumably these flows are coming from the main Zambezi channel to the north east. When the tide was out, exposed mud banks were 2-3m high and the dominant vegetation was the mangrove tree *Avicenna marina*.

The Zambezi main channel has a greater freshwater flow compared to the Micelo River, reflected in lower salinities at all levels and more turbid water in its estuary. Once we entered the Zambezi main channel at site ZD99/27 the mangroves disappeared within 2 km.

Water conductivities at freshwater sites around Marromeu and Malingapansi

Conductivity readings taken around the Marromeu area during July 1999 were high. From 14 sites around Marromeu and Malingapansi (both considered freshwater areas) we recorded a mean conductivity of 3.15 mS and a range from 1370 μS to 14.22 mS (Table 4). These data are an order of magnitude greater (i.e. more saline and conductive) than those given by Hall *et al*. (1977), who recorded water conductivity at Chinde as 140 μS.

Appendix 7.1 Table 3 Salinity of water samples in the Lower Zambezi River.

Site coordinates	Date	Site number	Time	Surface sample	Bottom sample
				parts per thousand (ppt)	
18E48'57"S 36E14'46"E	8/8/99	1	06:15	0	-
18E53'19"S 36E09'04"E	5/8/99	2	11:30	30	-
18E51'36"S 36E07'57"E	5/8/99	3	12:15	26	30
18E47'54"S 36E08'52"E	5/8/99	4	13:15	8	15
18E46'08"S 36E10'42"E	8/8/99	5	14:15	0	0
18E48'12"S 36E15'10"E	8/8/99	6	11:10	0	5
18E49'14"S 36E12'56"E	8/8/99	7	10:30	1	14
18E43'16"S 36E13'37"E	8/8/99	8	12:40	0	0
18E50'30"S 35E14'17"E	8/8/99	9	08:30	4	22

Appendix 7.1 Table 4 Conductivity and temperature of water at certain fish collection sites in the Lower Zambezi River (July 1999).

Site	Date/time	Conductivity (µS or Ms/cm)	Total dissolved solids (mg or g/l)	Temperature (ºC)
ZD99/5 river	28/7/99 09.00	2.01 mS	1.01 g/l	22.6
ZD99/6 lagoon	28/7/99 10.30	2.81 mS	1.46 g/l	24.5
ZD99/6 river	28/7/99 11.00	2.00 mS	1.00 g/l	23.0
ZD99/7 pool	28/7/99 12.00	3.29 mS	1.65 g/l	27.6
ZD99/8 backwater	30/7/99 09.00	1574 µS	788 mg/l	22.3
ZD99/10 backwater	30/7/99 12.00	1370 µS	675 mg/l	22.2
ZD99/14 stream	01/8/99 10.00	1440 µS	727 mg/l	22.3
ZD99/15 stream	01/8/99 14.45	1698 µS	861 mg/l	24.6
ZD99/22 mangrove	05/8/99 06.15	7.40 mS	3.8 g/l	23.7
ZD99/25 swamp	06/8/99 12.00	2.89 mS	1.49 g/l	22.7
ZD99/25 swamp	07/8/99 09.30	2.68 mS	1.34 g/l	20.5
ZD99/33 furrow	10/8/99 07.00	4.4 mS	2.19 g/l	18.2
ZD99/34 furrow	10/8/99 09.00	14.22 mS	7.14 g/l	20.3
ZD99/35 furrow	10/8/99 10.00	1716 µS	858 g/l	22.1
ZD99/36 swamp	10/8/99 11.00	1978 µS	992 mg/l	23.4

4. LOWER ZAMBEZI CHECKLIST

The following is a complete list of fishes recorded from the Lower Zambezi region. The families are arranged in phylogenetic order which follows the arrangement of the J.L.B. Smith Institute of Ichthyology collection (RUSI).

- * refers to numbered comments in notes below.
- # species collected during the July 1999 expedition.

Note	Scientific name	Class, Order & Family	English, Sena name
		CLASS: CHONDRICHTHYES	
		ORDER: CARCHARHINIFORMES	
		Carcharhinidae – requiem sharks	
*1#	*Carcharinus leucas* (Valenciennes 1839)		bull shark, madjibundi
		ORDER: RAJIFORMES	
		Pristidae – sawfishes	
	Pristis microdon Latham 1794		smalltooth sawfish, caixaô
		CLASS: OSTEICHTHYES	
		ORDER: LEPIDOSIRENIFORMES	
		Protopteridae – African lungfishes	
*2#	*Protopterus annectens* brieni Poll 1961		lungfish, dóe
*3	*Protopterus amphibius* (Peters 1844)		east coast lungfish, dóe
		ORDER: ELOPIFORMES	
		Elopidae – springers	
*4#	*Elops machinata* (Forsskål 1775)		springer
		Megalopidae – tarpons	
*5#	*Megalops cyprinoides* (Broussonet 1782)		oxeye tarpon, uláwa
		ORDER: ANGUILLIFORMES	
		Anguillidae – freshwater eels	kopokopo
	Anguilla bicolor bicolor McClelland 1844		shortfin eel
	Anguilla marmorata Qouy & Gaimard 1824		giant mottled eel
	Anguilla mossambica Peters 1852		longfin eel
	Anguilla bengalensis labiata Peters 1852		African mottled eel
		Ophichthidae – snake- & worm-eels	
*6#	*Brachysomophis crocodilinus* (Bennett 1833)		crocodile snake-eel
		ORDER: CLUPEIFORMES	
		Clupeidae – herrings	
*7#	*Hilsa kelee* (Cuvier 1829)		kelee shad, malola
		Engraulidae – anchovies	
*8#	*Thryssa vitrirostris* (Gilchrist & Thompson 1908)		orangemouth glassnose
		ORDER: OSTEOGLOSSIFORMES	
		Mormyridae – snoutfishes	
*9	*Hippopotamyrus ansorgii* (Boulenger 1905)		slender stonebasher
*10#	*Hippopotamyrus discorhynchus* (Peters 1852)		Zambezi parrotfish, mputa

*11# *Marcusenius macrolepidotus* (Peters 1852) bulldog, ndagumka
*12# *Mormyrops anguilloides* (Linnaeus 1758) Cornish jack, nentche
*13# *Mormyrus longirostris* Peters 1852 eastern bottlenose, nkupe
*14# *Petrocephalus catostoma* (Günther 1866) Churchill, mputa

ORDER: GONORYNCHIFORMES

Kneriidae – knerias

Kneria auriculata (Pellegrin 1905) southern kneria
Parakneria mossambica Jubb & Bell-Cross 1974 Gorongosa kneria

ORDER: CHARACIFORMES

Characidae – characins

Brycinus imberi (Peters 1852) imberi, mberi
*15# *Brycinus lateralis* (Boulenger 1900) striped robber
Hemigrammopetersius barnardi (Herre 1936) sootfin robber
Hydrocynus vittatus Castelnau 1861 tigerfish, ncheni
Micralestes acutidens (Peters 1852) silver robber

Distichodontidae – citharines

*16# *Distichodus mossambicus* Peters 1852 nkupe, xeréwa
*17# *Distichodus schenga* Peters 1852 chessa, chenga

ORDER: CYPRINIFORMES

Cyprinidae – barbs & labeos simbo

Barbus afrohamiltoni Crass 1960 plump barb
Barbus annectens Gilchrist & Thompson 1917 broadstriped barb
*18# *Barbus haasianus* David 1936 sicklefin barb
*19# *Barbus kerstenii* Peters 1868 redspot barb
*18# *Barbus macrotaenia* Worthington 1933 broadband barb
Barbus marequensis Smith 1841 largescale yellowfish
Barbus paludinosus Peters 1852 straightfin barb
Barbus radiatus Peters 1853 Beira barb
Barbus toppini Boulenger 1916 east coast barb
*20# *Barbus trimaculatus* Peters 1852 threespot barb
Barbus viviparus Weber 1897 bowstripe barb
*21# *Labeo altivelis* Peters 1852 manyame labeo
*21# *Labeo congoro* Peters 1852 purple labeo
Labeo cylindricus Peters 1852 redeye labeo
Labeo molybdinus du Plessis 1963 leaden labeo
*22# *Opsaridium zambezense* (Peters 1852) barred minnow
Opsaridium tweddlorum dwarf sanjika
Varicorhinus nasutus Gilchrist & Thompson 1911 shortsnout chiselmouth
Varicorhinus pungweensis Jubb 1959 Pungwe chiselmouth

ORDER: SILURIFORMES

Schilbeidae – butter catfishes

Schilbe intermedius Rüppell 1832 silver catfish, dambe

Amphiliidae – mountain catfishes all mpombwe?

Amphilius uranoscopus (Pfeffer 1889) stargazer mountain catfish
Amphilius natalensis Boulenger 1917 Natal mountain catfish
Leptoglanis rotundiceps (Hilgendorf 1905) spotted sand catlet

Clariidae – airbreathing catfishes

*23#	*Clarias gariepinus* (Burchell 1822)	sharptooth catfish, nsomba
*24#	*Clarias ngamensis* Castelnau 1861	blunttooth catfish, nsomba
*25#	*Clarias theodorae* Weber 1897	snake catfish, ngola
*26	*Heterobranchus longifilis* Valenciennes 1840	vundu, nhumi

Malapteruridae – electric catfishes

*27#	*Malapterurus electricus* (Gmelin 1789)	electric catfish, tinhesse (Ndau - dinda)

Mochokidae – squeakers & suckermouths

	Chiloglanis neumanni Boulenger 1911	prickleback suckermouth
*28#	*Synodontis nebulosus* Peters 1852	cloudy squeaker, nkonokono
*29#	*Synodontis zambezensis* Peters 1852	brown squeaker, nkonokono (Ndau - gorokoro)

Ariidae – sea catfishes

*30#	*Ariodes dussumieri* (Valenciennes 1840)	tropical seacatfish, bagré, mpombwe

ORDER: CYPRINIDONTIFORMES — peribanchi

Aplocheilidae – annual killifishes

*31#	*Nothobranchius orthonotus* (Peters 1844)	spotted killifish
*32#	*Nothobranchius rachovii* Ahl 1826	rainbow killifish

Cyprinidontidae – topminnows

#	*Aplocheilichthys hutereaui* (Boulenger 1913)	meshscaled topminnow
	Aplocheilichthys johnstoni (Günther 1893)	slender topminnow
#	*Aplocheilichthys katangae* (Boulenger 1912)	striped topminnow

ORDER: SYNGNATHIFORMES

Syngnathidae – pipefishes

*33#	*Microphis fluviatilis* (Peters 1852)	freshwater pipefish
#	*M. brachyurus* (Bleeker 1853)	opossum pipefish

ORDER: SYNBRANCHIFORMES

Mastacembelidae – spiny eels

	Aethiomastacembelus shiranus (Günther 1896)	Malawi spinyeel, kopokopo

ORDER: PERCIFORMES

*34 Ambassidae – glassies

#	*Ambassis productus* Guichenot 1866	longspine glassy
#	*Ambassis gymnocephalus* (Lacepéde 1801)	bald glassy
#	*Ambassis natalensis* Gilchrist & Thompson 1908	slender glassy

Leiognathidae – soapies

*35#	*Leiognathus equula* (Forsskål 1775)	slimy

Sparidae – sea breams

#	*Acanthopagrus berda* (Forsskål 1775)	riverbream, chesi

Cichlidae – cichlids

*36#	*Astatotilapia calliptera* (Günther 1893)	eastern bream, suli
*37#	*Oreochromis mossambicus* (Peters 1852)	Mozambique tilapia, nkobue
*37#	*Oreochromis placidus* (Trewavas 1941)	black tilapia, nkobue
*38#	*Pseudocrenilabrus philander* (Weber 1897)	southern mouthbrooder, suli
#	*Tilapia rendalli* (Boulenger 1896)	redbreast tilapia, ngondue

	Mugilidae – mullets	ngalazi/mangalazi
*39#	*Liza alata* (Steindachner 1892)	diamond mullet
#	*Valamugil seheli* (Forsskål 1775)	bluespot mullet
	Serranidae – rockcods & groupers	
#	*Epinephalus coiodes* (Hamilton 1822)	orangespotted rockcod, garopa
	Teraponidae – thornfishes	
#	*Terapon jarbua* Forsskål 1775	thornfish
	Sillaganidae – sillagos	
#	*Sillago sihama* (Forsskål 1775)	silver sillago
	Gobiidae – gobies	
	Awaous aeneofuscus (Peters 1852)	freshwater goby
*40#	*Glossogobius callidus* (Smith 1937)	river goby
#	*Glossogobius giurus* (Hamilton-Buchanan 1822)	tank goby
*41#	*Yongeichthys nebulosus* (Forsskål 1775)	shadow goby
*42#	*Mugilogobius mertoni (*Weber 1911*)*	
*43#	*Periophthalmus argentilineatus* Valenciennes 1837	bigfin mudhopper
*44#	*Stenogobius kenyae* Smith 1959	Africa rivergoby
	Anabantidae – labyrinth fishes	dambru
*45#	*Ctenopoma multispine* Peters 1844	manyspined climbing perch
*46#	*Microctenopoma intermedium* (Pellegrin 1920)	blackspot climbing perch
	ORDER: PLEURONECTIFORMES	
	Soleidae – soles	
*47#	*Solea bleekeri* Boulenger 1898	blackhand sole
	ORDER: TETRAODONTIFORMES	
	Tetraodontidae – pufferfishes	
#	*Chelonodon laticeps* Smith 1848	bluespotted blaasop

Notes on species

1. *Carcharinus leucas*. Several recent sightings ranging from the mouth of the Micelo River to up stream of Marromeu were reported to me during the expedition. Although not positively identified as *C. leucas* (Zambezi or bull shark) this is the most likely species to enter estuarine and riverine environments. From discussions with local fishermen it would appear to be relatively common in the lagoons and channels around the river mouth.

2. *Protopterus annectens*. Lungfish are well known by local people. We were informed that July was the wrong time to collect these and that the rainy season (late October to December) would be better. Three specimens were obtained: two from local fishermen who trapped the fish in a small backwater near Malingapansi, while a third was collected by sugar estate workers near Marromeu who dug a cocooned specimen up during ploughing operations. Local people eat this fish which was a contributing factor to why we received so few specimens.

3. *Protopterus amphibius*. Specimens collected by Peters during the 1844 expedition were identified by Trewavas (1953) as *P. amphibius*. Wier (1962) challenged the validity of Trewavas' identification while Skelton (1993b) tentatively chose to include the species in the southern African checklist. Although no specimens of this species were collected on this expedition local residents reported two types of lungfish present in the Marromeu region, both referred to as *dóe* (B. Chande, pers. comm.).

4. *Elops machinata*. A single fresh specimen, bought in Marromeu market, was apparently caught close to the town in the main channel with gill-seine nets. Skelton (1993b) removed this species from the southern African freshwater checklist. The water conductivity of the river at Marromeu around 2.0mS/cm and it was not tidal.

5. *Megalops cyprinoides*. Widespread in the main river channels up to Marromeu and in the Micelo River up to Malingapansi. Nowhere common.

6. *Brachysomophis crocodilinus*. Two specimens collected in shallow water (<20 cm) in the marine lagoon in the lower Micelo River channel. This species is characterised by oral papillae on upper and lower lips and has no caudal fin. The tail is a hardened bony tip clearly well adapted to reversing into soft sediments. Both specimens were buried in the coarse sand substrate and were presumably feeding on small fishes by ambushing them. The only two species collected with a large seine at the site were juvenile *T. jarbua* and the puffer fish *C. laticeps*.

7. *Hilsa kelee*. Caught in the lagoons and estuary of the Zambezi delta. Large fishing camps occur in the delta where this and a few other species are collected. Most fish are split or cut and sun-dried while some are smoked. They are then transported considerable distances in land. Recorded by Jackson (1975) as present in the delta but we found no indications of it moving upstream in to freshwaters. It is the most commonly seen marine-estuarine species in the Marromeu market.

8. *Thryssa vitrirostris*. No samples collected, but it was positively identified at several camps in the lower Zambezi delta. Caught by local fishermen with *H. kelee*. Not seen in Marromeu market so it appears to get sorted out of traded fish.

9. *Hippopotamyrus ansorgii*. This is species prefers rocky habitats. No habitats typical for this species were sampled and we collected no specimens. Likely to be in upper reaches of small streams in the region where suitable complex rocky habitat occurs.

10. *Hippopotamyrus discorhynchus*. A major component of the local fishery and commonly seen in the Marromeu market. Found in marginal vegetation of the main channel and lagoons along the main channel. Local fishermen were catching large numbers of this species by seine netting under grass mats. Thus it would appear to be a shoaling species.

11. *Marcusenius macrolepidotus*. Abundant in many areas, it is the most widespread mormyrid in the delta region. Habitats varied from small acidic streams draining the edges of the delta, swamps in the delta, the main channel to small pools along the Pungwe-Zambezi divide near Inhamitanga. There is a considerable amount of variation in body form within populations which we are still examining as they may represent two species. A second species, *Marcusenius livingstonii* (Boulenger 1898), occurs in parts of the Lake Malawi-Shire system (Tweddle & Willoughby 1982).

12. *Mormyrops anguilloides*. Frequently caught by local hook and line fishermen and regularly seen in the local fish market. Does not appear as common as *M. macrolepidotus*, *H. discorhynchus* or *M. longirostris,* although varying habitat requirements may account for this. It is the largest mormyrid in the Zambezi and specimens up to 75 cm seen during this trip. Good angling sites seem to be deeper "holes" in the main channel.

13. *Mormyrus longirostris*. Common in the main channel and marginal lagoons around Marromeu. A major component of the local fishery.

14. *Petrocephalus catostoma*. Only collected at one site near Camp 1 where local fisherwomen had poisoned a small stream. One of two mormyrids present there and it accounted for less than 4% of the population. The habitat was a medium sized stream, sand substrate with lots of leaf litter and marginal grasses.

15. *Brycinus lateralis*. Rare. Collected at two sites in the same backwater river channel near Marromeu. Mature adults collected together with *M. acutidens*. This species exhibits a split distribution within the Zambezi system, being abundant in the upper part of the system. The taxonomic status of the Lower Zambezi and South African stocks require examination.

16. *Distichodus mossambicus*. This and the next species are Middle and Lower Zambezi endemics described by Peters in 1852. Caught in mainstream habitats only. A component of the local fishery but not as common as the next species. On a few occasions we and fishermen caught higher numbers of *D. mossambicus,* which may indicate habitat preferences between the two *Distichodus* species. Highest numbers of both juveniles and adults of *D. mossambicus* were collected in slower flowing sections of main channels, heavily vegetated and mud substrates. Largest specimens in our samples were collected at Malingapansi in gill nets and measured 252 mm SL.

17. *Distichodus schenga*. The dominant *Distichodus* species and a major component of the local fishery. Abundant in the main river channel at Marromeu over sand substrates in fast flows. Slightly smaller than *D. mossambicus* with the typical specimens in the Marromeu market ranging from 70 to 160 mm SL.

18. *Barbus haasianus* and *B. macrotaenia*. Both species abundant around Marromeu. Found in the main river channel to seasonal swamps on the floodplain providing aquatic vegetation cover is present. Mature males of *B. haasianus* show the characteristic concave "hooked" anal fin and those in breeding condition were pink to bronze in colour. Most specimens collected were juveniles.

19. *Barbus kerstenii*. Common in drainages along the Inhamitanga-Dondo road. Habitats are well vegetated pools and streams. Two juveniles were also collected in a small stream near camp one (site ZD99/14) in vegetated habitats.

20. *Barbus trimaculatus*. Collected at a single site near Inhamitanga in pools of a perennial stream.

21. *Labeo altivelis* and *Labeo congoro*. Both species are Middle and Lower Zambezi endemics, and occur in the same habitats. *Labeo altivelis* is usually the more abundant species and forms the bulk of the artisanal fisheries catch at Marromeu. The two species can be distinguished by the shape of the dorsal fin and overall coloration. *Labeo altivelis* has a concave posterior edge to the dorsal fin, which is pointed and the body is olive with pink spots in the centres of scales. *Labeo congoro* has a rounded dorsal fin, a faint spot on the caudal peduncle and an overall dark colour to the body and fins.

22. *Opsaridium zambezense*. Collected in the Zambezi main channel at Marromeu in shallow water (<30cm) channels on one of the islands. Surprisingly only a few (5) juveniles were collected. Presumably this is a result of not collecting in the species' preferred habitats or the wrong season as they should be common in the river channel. In contrast sampling in the Buzi River on our return trip this species was one of the dominant species at most sites (also noted by Bell-Cross 1972).

23. *Clarias gariepinus*. This and the next species known locally as *nsomba* (Sena). Smaller specimens most frequently caught by us in floodplain lagoons and backwater channels. A few large adults were collected in the main channel but it does not appear to be common. Collected by local people by nets, traps, baskets, spears and hook and line. Possibly one of the few species capable of surviving under *Azolla* mats in backwaters as it is an airbreathing species.

24. *Clarias ngamensis*. Rare. Collected from several localities but always only one or two specimens. Local people do not distinguish this and the previous species.

25. *Clarias theodorae*. Collected in small streams draining the delta at camp one where it was rare. Also in small pools and streams along the Dondo-Inhamitanga road. Local fishermen clearly recognise this species as different with the name *ngola* (Sena).

26. *Heterobranchus longifilis*. Not seen during our trip although all fishermen questioned knew the fish. Clearly not very common although widespread.

27. *Malapterurus electricus*. The genus is presently being revised by Dr. Steven Norris. The species in the Middle and Lower Zambezi is likely to be renamed. Only two specimens collected, these were bought from a local fisherman who had been fishing in deep channels of the main river with a large seine net. We were told that these fish are more frequently caught during the summer.

28. *Synodontis nebulosus*. Rare. Only a few badly damaged specimens seen in fishermen's boats at the start of the trip. None were sampled by ourselves and no more were seen in the Marromeu market despite concerted searches during the last week.

29. *Synodontis zambezensis*. Only collected in the main channel and marginal lagoons. Reasonably common. Best methods were throw nets at night and gill nets.

30. *Ariodes dussumieri*. A large species attaining 50 cm. Recorded from the western Indian Ocean. A major component of the estuarine fishery. No specimens collected as only examples seen were split and dried or smoked.

31. *Nothobranchius orthonotus*. A single specimen was collected in a deep (1 m) pool at Site 13. Approximately double the size of *N. rachovii*, yellow-beige with rust red spots all over the body.

32. *Nothobranchius rachovii*. Found in a few irrigation channels and flooded grasslands around Marromeu. At these sites they were the dominant species and could be observed jumping at the surface when approached. Only adults were collected. Specimens from our collections differ slightly in colour pattern from those at the type locality, in Beira (B. Watters, pers. comm.). Male specimens from Marromeu populations tend to have spots rather than bands on the unpaired fins.

33. *Microphis fluviatilis*. Collected and described by Peters from Tete. Common in the main channel at Marromeu and Luabo. Collected over open sand substrates and in small patches of marginal grass and flotsam.

34. Ambassidae. Three species are recorded from Southern Africa. All three species are present in the Zambezi Delta. *Ambassis productus* appears to be the most widespread being present at freshwater sites at Malingapansi, mangrove channels and the Zambezi River estuary. Uncommon in the upper river sites. One of the dominant species close to the mouths together with *T. jarbua* and *C. laticeps*. The other two species were collected at single sites. Some specimens of *A. natalensis* have interrupted lateral lines which alters the keys presented in Smith's Sea Fishes and Skelton (M.E.Anderson, pers. comm.). The rostral spine and preopercular groove serration pattern enable separation of these three species.

35. *Leiognathus equula*. A few juvenile specimens collected in mangrove channels connecting the main Zambezi and the Micelo River. All specimens were collected by otter trawls with the net running at about 5-6 m deep. Salinities at these depths were 5-14‰.

36. *Astatotilapia calliptera*. Rare but widespread in backwaters, only one or two specimens caught at any site. Clearly distinguishable from *Pseudocrenilabrus philander* by the presence of several prominent bright orange egg dummies on the anal fin which were even present in non-mature specimens. In preservative these egg spots become clear and colour pattern differences are more difficult to discern. The emarginate tail is another feature helping to distinguish it from *P. philander*.

36. *Oreochromis mossambicus* and *O. placidus* are widespread in the Zambezi Delta region. Although they were found together on a few occasions they seem to exhibit habitat preferences. *Oreochromis placidus* was caught most frequently in the main channel and in lagoons associated with the main channel. We caught three

large adults at night in the fastest flowing section of main channel along the edge of a deep eroding bank. This contradicts observations by Bell-Cross (1973, 1976) that *O. placidus* prefers quiet vegetated pools.

There has been some debate about distinguishing these two species apart, particularly in juveniles (see Trewavas 1983, p. 337). We found small juveniles with three and four anal fin spines which we could also separate on colour patterns. Four anal spines were found consistently in juveniles down to 15 mm SL. This refutes the assertion by Junor (reported in Jubb & Skelton 1974) that the forth spine develops as the fishes mature.

Specimens were examined from the Moebase region of Mozambique (1997). All had three anal fin spines and exhibited typical *O. mossambicus* colour patterns. The Moebase specimens were collected from a wide variety of habitats from coastal dune lakes and swamps, large river channels to small streams. It may therefore be that the Zambezi Delta does indeed form the northern limit for *O. placidus* as suggested by Trewavas (1983).

38. *Pseudocrenilabrus philander*. Common in backwaters and marginal habitats of the main stream Zambezi. Characterised by a rounded caudal fin, the anal fin has a series of red spots.

39. *Liza alata*. Bought from local fishermen using gill-seines just above the estuary head in the main Zambezi channel. Water was less than 1‰ salinity.

40. *Glossogobius callidus* A new record for the system. It is widespread throughout rivers of the south-east coast. It has been recorded at far inland at Molopo Oog in the Upper Limpopo. Common at Marromeu and Malingapansi over sand and mud substrates of the main channel. It may be missed if large mesh nets are used or if bottom ropes of nets are not held close to the substrate on retrieval.

41. *Yongeichthys nebulosus* Collected at a single site close to the mouth of the Micelo River. Habitat was a muddy mangrove creek draining into a large lagoon (almost full sea salinity). Water was shallow (<30 cm) and clear. Appeared to be territorial as fish were seen chasing and fighting in a shallow pool. A widespread species in the Indo-Pacific region. Poisonous, with higher concentrations of the toxin tetrodotoxin in the organs.

42. *Mugilogobius mertoni* Gobies present in a side channel at Malingapansi and in shallow (10-20 cm deep) muddy pools. The pools were at the top of the tidal ebb, completely freshwater and covered with *Azolla* fern. High numbers were present; I estimate several hundred in two small pools. Identified by Helen Larson. This is a new record for the Zambezi and a northern range extension for the species. Previously known range (Smith's Sea Fishes) was southern Mozambique to Coffe Bay, South Africa.

43. *Periophthalmus argentilineatus*. We have followed Murdy (1989) as Smith's Sea Fishes is incorrect for the two southern African *Periophthalmus*. Little habitat information is available for this species in Murdy. The species was on firm mud slopes and flats where holes could be dug into the substrate. Most frequently typical mud habitats were in mangroves but at a few sites in the main Zambezi channel, where the fresh-salt boundary must have been close by, the mud was covered with an aquatic rush. Holes could be up to 3-4 m from the waters edge at high tide. Usually as holes were approached fishes left holes, skipping across the mud to the waters edge. No other species were noted as being commensal in holes.

44. *Stenogobius kenyae*. Present in main channel habitats of both the Zambezi above Marromeu and the Micelo River at Malingapansi. Not commonly caught but appears widespread. Probably our sampling method is not catching high numbers as small bottom dwellers may be passed over by seine nets being pulled too fast and slightly off the bottom.

45. *Ctenopoma multispine*. Widespread but rare. The site where greatest numbers were collected was the acidic stream near Camp 1. Preferred habitats appear to be small streams and cut off back waters where there is aquatic weed and root cover. Often caught in local fish traps.

46. *Microctenopoma intermedium*. Widespread on the floodplain and in marginal vegetation of the main channel. Appears to prefer shallow waters and extensive vegetation. Rarely caught in more than ones and twos.

47. *Solea bleekeri*. Two (11.8 mm) juveniles collected over coarse sand substrate in the estuarine lagoon of the Micelo River, salinity was 30 ‰. Previously known distribution was False Bay, South Africa to Maputo, Mozambique. This record is a considerable range extension for the species.

5. NEW RECORDS

The Zambezi checklist above is derived from Skelton (1993b), Marshall (pers. comm.) and the present survey and contains 94 species. Twenty one new records were collected during this survey and these are entirely comprised of secondary freshwater fishes such as gobies (e.g. *Glossogobius callidus*, *Stenogobius kenyae*) and estuarine and marine species (e.g. *Solea bleekeri*, *Chelonodon laticeps*) (Table 5).

Several other species were seen in fishermen's catches but not collected. These are not added to the above list as either their place of collection was not determined or they were not identified to species. Some of these species include: a juvenile kob (possibly *Johnius* sp., local name is pula), *Trichiurus* eels (possibly caught at sea, local name is *tapia*), a carangid (local name is *carapau*) and juvenile mullet (collectively called *ngalazi*).

Appendix 7.1 Table 5 New records for the Zambezi Delta collected during the July 1999 expedition.

Enter freshwater	Estuary only
Elops machinata	*Brachysomophis crocodilinus*
Ambassis productus	*Thryssa vitrirostris*
A. gymnocephalus	*Ariodes dussumieri*
A. natalensis	*Leiognathus equula*
Liza alata	*Acanthopagrus berda*
Valamugil seheli	*Epinephalus coiodes*
Glossogobius callidus	*Terapon jarbua*
Mugilogobius mertoni	*Sillago sihama*
Stenogobius kenyae	*Youngeichthys nebulosus*
	Periophthalmus argentilineatus
	Solea bleekeri
	Chelonodon laticeps

6. LOCAL FISHING METHODS

6.1 Monofilament gill nets

Monofilament gill nets are the most commonly used nets in the fishery around Marromeu. We were told that these are bought in Beira, mesh sizes ranged from 30-50 mm and the nets were very strong. We observed them being used in two distinct ways: as seine nets and as drift nets.

Seine netting. Nets were usually dragged from the canoes by hand and pulled out into deep water (<3 m) by the fishermen. They were apparently not concerned about crocodiles. The net was pulled in an arc and then the two fishermen pulled the net into the bank. Areas netted were usually shallow, slower flowing sections of the main channel. These areas are not that common and my impression was that the favoured areas were being regularly netted. These areas are also open water habitats as the fishermen are avoiding snagging the nets and because of low cover have lower numbers of fishes.

Drift netting. Nets were thrown out from a drifting canoe in the middle of the river channel. The net was usually put in at 45-90E to the flow. Once the net was fully deployed the net and boat was left to float downstream for 10-15 minutes or until the net snagged. Sometimes nets were set drifting parallel to and close to the river bank. The fishermen would thump the vegetation along the bank as they drifted downstream frightening fish into the net. Usually this operation was shorter than those in mid-channel with the net being retrieved when it reached the bottom of a vegetated section of bank.

6.2 **Fish trapping**

Traps are probably the most widespread type of fishing method in the Lower Zambezi. They are most frequently set in fences and usually where waters are receding and constrict into a channel, thus concentrating the fish. In extensive swamps which were bisected by roads, fences were set at culverts and at the head of the receding section. Fences may also be constructed in the centre of swamps with deeper holes being made by digging to attract larger fish. Here traps were baited with a variety of foods and plants.

The design of these traps is different from other regions I have visited. The traps of the area are characterised by double entrances which reduce the chance of a caught fish escaping through the mouth. This is important as traps are often left in the water for extended periods of time before being checked. With a double mouth in a trap the chances of fish escaping is reduced considerably.

6.3 **Thrust baskets**

Although not seen in operation thrust baskets are used widely in the Lower Zambezi to Buzi region. Baskets are used in groups with people walking in a line through shallow water. The basket is pushed down into the water and any fish trapped inside the basket are removed by hand. Fish are usually held on strings or bags and thrusting continues until the line reaches the bank. Thrust basket fishing is a seasonal activity. Waters are fished when they start receding and fishes are beginning to concentrate. This occurs at different times throughout the region but is usually after the summer. Thrust baskets of the area were of a different design to those seen further south in the Phongolo floodplain as they have handles built into the structure of the basket. This may be due simply to different fashions in different regions, or it could reflect differences in techniques, e.g. handles used for scooping of the basket.

6.4 **Hook and line**

Fishermen in canoes tended to use lines of several metres, large hooks and fish in deep channels and holes. Consequently, their catches usually comprised large specimens of larger species such as *Mormyrus anguilloides*, *Oreochromis* spp., *Tilapia rendalli* and, *Hydrocynus vittatus*. Women and children fishing from the banks were observed using short lines (less than two meters), small hooks and were fishing at the margins of the main channel or lagoons. Their catches were usually dominated by juveniles of *Distichodus schenga*, *Labeo* spp., *Oreochromis* spp. or adult *Brycinus imberi*. Hand made hooks were available in the Marromeu market.

6.5 **Seine netting**

None seen in operation but several large multi-filament seine nets were seen in transit and catches from these examined. Only one was observed in the Marromeu area. The catch indicated that deeper lagoons and channels of the main river had been fished as it was dominated by large specimens of mormyrids and cichlids. Seines were more common in the in the delta area and may be used more at night. A single daytime catch was almost entirely small mullet (Mugilidae spp.). Night time catches may be dominated by *Hilsa kelee*, certainly sorted catches in the process of drying are dominated by this species.

6.6 **Gill netting – multifilament nets**

Multifilament gill nets which were set in the main channel and marginal lagoons appeared to be uncommon and poorly maintained. The few nets we observed were left in the river all day and night for long periods. Nets were simply raised, checked for fish and put back in. Consequently, nets are in poor condition with many holes and probably rotting more quickly. Catches comprised large cichlids, mormyrids, labeos and *Clarias gariepinus*.

6.7 **Spearing**

We did not observe fishermen using spears but we did see one man returning from fishing. He said he had speared the *Clarias gariepinus* catfish in a shallow swamp by randomly spearing the water ahead of him as he walked through the water.

6.8 **Draining swamps**

Evidence of this activity was seen all over the region with mud walls and dried sections of swamps. We observed this activity in a swampy area close to Dondo in the Lower Pungwe system. Three women had cut off a section of swamp by the constructing a mud wall. Water was then simply poured out of the enclosure using plastic buckets and bowls. The swamp is completely drained and fish are collected by hand and held in a woven baskets. At Dondo, the most abundant large fish present was the mormyrid *Marcusenius macrolepidotus,* while the smaller fishes were a variety of *Barbus* and juvenile cichlids. We bought some of these fish and the prices was three times that in the Marromeu fish market, apparently on account of the difficulty in catching fish using this method.

6.9 **Fish poisoning**

One of the streams we visited, near camp one (ZD99/14, 01/08/99, 18E33'45"S / 35E39'46"E), had been poisoned by local women. The procedure was not observed but was described to us. Leaves and stems of the plant *Synaptolepis kirkii* were pulped and then poured into the stream as a liquid. This was apparently left for an hour or so when the women then returned to collect dead and dying fishes. The list of species found is given in Table 6.

The poison selectively killed fishes. Small fish, dominated by cyprinids, were killed first, then mormyrids (only two species present were *Marcusenius macrolepidotus* and *Petrocephalus catostoma*). Excepting the mormyrids almost no large fish were killed. Large cichlids and cyprinids were seen swimming in the area that was poisoned. The behaviour of fishes appears similar to that described for rotenone, an ichthyocide commonly used by scientists. Fishes swim in a distressed manner (on their sides and in circles) and move towards the shallows. Here they often jump out of the water onto vegetation or the bank.

At a first glance the poison had had little effect as few dead fish were visible. However, the women retrieved fishes by hauling the marginal vegetation onto the bank exposing the shallow water region and collecting fishes into small woven grass baskets. When their baskets were full fish were placed in depressions in the sand bank which were lined with leaves and then covered with damp sand.

6.10 **Catching fish by hand**

Five fishermen were observed catching fish by hand. The procedure was to drive their dugout canoe onto the edge of a vegetation mat in the main channel or in a lagoon. All the men jumped out onto the vegetation mat and walked towards the shore, splashing and thrusting their hands down into the vegetation. They have strings woven out of grass for their catches. On the two attempts we witnessed almost all members of the group caught one fish while some caught up to three. All specimens caught were large *Oreochromis* spp.

6.11 **Fish trading**

Fresh fish

Fresh fish are sold outside the Marromeu market building on grass stalls. Fish are sold unsorted and come into the market at all times of the day. The species which dominate are *Labeo altivelis*, all the mormyrids (barring *Petrocephalus catostoma*), *Hydrocyanus vittatus*, *Schilbe intermedius*, *Synodontis zambezensis*, *Clarias gariepinus* and medium sized (10-15 cm SL) cichlids of various genera, in that order of abundance. Fishermen are frequently the people doing the vending as the same people were seen on the river fishing. Sales are typically quick with the fresh catches being sold in under one hour.

Dried and smoked fish

Fish which have been split and dried and, or smoked are sold inside the Marromeu market building. Dry fish salesmen set up stalls early in the morning and remain there all day. The fish have already been sorted into sizes at least and often into species before transportation. The most common dried species is the clupeid *Hilsa kelee*. Split and smoked species commonly present are *Clarias gariepinus*, *Oreochromis* spp., *Acanthopagras berda* and small Mugilidae. The bulk of dry fish come from fishing camps in the delta and are transported up river by boat.

Appendix 7.1 Table 6. A collection of fishes from a stream near Camp 1 (Site 14, 01/08/99) poisoned by local fisherwomen.

Species	number (%)	Size (mm SL) minimum	maximum
Marcusenius macrolepidotus	81 (22.4)	50.9	172
Barbus paludinosus	66 (18.2)	25	56.1
Barbus macrotaenia	42 (11.6)	14.5	20.8
Aplocheilichthys hutereaui	33 (9.1)	11.8	20
Ctenopoma multispine	33 (9.1)	49.5	75.7
Barbus annectens	31 (8.6)	18.2	26.9
Barbus haasianus	21 (5.8)	14.6	16.5
Petrocephalus catostoma	14 (3.9)	41.2	65.6
Pseudocrenilabrus philander	11 (3.0)	18	70.8
Aplocheilichthys katangae	10 (2.8)	15.3	25.5
Barbus sp.	6 (1.7)	18.4	27.6
Microctenopoma intermedium	3 (0.8)	22.7	35.7
Oreochromis spp.	3 (0.8)	60.3	93
Clarias theodorae	3 (0.8)	85.1	132
Clarias gariepinus	2 (0.6)	129.5	142
Micralestes acutidens	2 (0.6)	32.6	35.1
Barbus afrohamiltoni	1 (0.3)	87.3	-
Total	362 (100)	-	-

7. DISCUSSION AND CONCERNS

7.1 Fishes

The size of the delta, coupled with the variety of habitats and changing seasons, make it likely that the number of recorded estuarine and marine vagrants will increase considerably with more thorough surveys. As these species form a complex and major fishery it is desirable that more thorough understanding of the fishery diversity, estuarine functioning and socio-economics of the fishery are obtained in the near future. Further surveys with these aims are recommended. If future trips are possible then a greater range of habitat types need to be surveyed, with rocky areas in upper catchments and the estuarine lower delta being the main targets. Early summer would be a better sampling period for fishes as they will be more active in warmer conditions and will be preparing to breed.

When trying to identify species of concern I am faced with several problems. The survey that has been conducted was of short duration, in the cold season, and did not survey the entire delta. The lower delta (estuary) was sampled as we travelled through it during two days, which is obviously inadequate for a proper assessment. Consequently, any comments of species presence, absence or abundance have to be viewed bearing these points in mind.

Certain tentative points can be made:

1. As there are no Lower Zambezi endemics, and habitats are widespread over a considerable area, it would appear that no species are presently threatened by extinction.

2. The riverine fauna is dominated by labeos (2), distichodids (2), characins (3) and mormyrids (4).

3. Certain species do appear to be naturally rare, e.g. *Protopterus* spp., *H. longifilis*, *Malapterurus electricus*, while others appear to have sporadic distribution patterns e.g. *Nothobranchius* spp., *Ctenopoma multispine*, *Micraoctenopoma intermedium*.

4. The fauna in the mouth area was clearly dominated during July by estuarine and marine species. It is probable that this situation will change during the summer, with increased freshwater flows pushing the estuary head closer to the mouth or even out into the sea.

7.2 **Fishing surveys**

Artisanal fishing activities in the Zambezi Delta are diverse ranging from catching fish by hand, spears, rod and line, various traditional basket traps, various seine and gill nets to poisoning. Areas fished cover most habitats from the floodplains, the main river channel to the estuary. Few areas are un-fished. Fishing pressure appeared to be high while the resource conversely appeared to be rather sparse in the main river channel during July. Catches brought into the Marromeu market were dominated by juvenile fishes ranging in size from 5-20 cm SL. Accurate assessment of the numbers of people fishing, number of boats present, the days fishing, the quantities of fish in transit through the Marromeu market and price structures could be achieved fairly easily by resident ichthyologists. This kind of simple data could provide valuable insights in to the socio-economics of the fishery and fishery dynamics throughout the seasons. Assistance with establishing such programs could be obtained from many institutions, e.g. JLB Smith Institute of Ichthyology/Department of Ichthyology, Rhodes University.

There is no regulation of the fishery, e.g. size of mesh in nets, number and size of nets, methods of setting nets. If the fishery is to remain sustainable it is likely that some sort of regulation will be necessary and that for this to be effective it must go hand-in-hand with education of local fishermen. Additional benefits to fishermen in such an education programme could be teaching of equipment maintenance, e.g. boat and net repairs. Certain activities, e.g. poisoning, although traditional are probably not sustainable with increasing populations and should be stopped. For accurate decisions in this regard assessments of the fishery must be made first.

7.3 **Concerns**

There are concerns for freshwater fishes in the Zambezi Delta and these are as follows.

1. <u>Over-exploitation of the riverine and estuarine fisheries</u>

The sugar estate at Marromeu has already attracted a considerable population within a year. With further developments the indirect effects of this needs to be considered. The use of natural resources by staff of the sugar company and the associated population, in particular fishes, mammals and trees, needs urgent attention if it is to be preserved.

In terms of fisheries, an alternative to simply increasing fishing pressure would be to establish fish farms. These could be organised in two ways:

a) as part of the sugar estates operations (large scale) and sold for commercial purposes; or

b) as rural projects (a few ponds per village) and run along subsistence lines.

In addition, areas of no development and no fishing would be desirable. These should encompass multiple habitats in the same block. Almost certainly these would require local residents' help in their maintenance. This would require an education of local residents to explain why these are necessary and what benefits local people would gain from them.

2. Effects of damming
The Zambezi is already heavily impounded and further plans to dam the river near Tete are likely to go ahead. The effects on seasonal floods and therefore on fish breeding patterns and fecundity needs to be examined. It is possible that mis-timed floods could significantly reduce fisheries catches. Projects examining fish catches over long periods of time and breeding patterns in several species, and relating this to environmental parameters, will be required to establish dam effects. These sorts of projects could be PhD programmes for young Mozambican scientists and could be supervised from numerous universities, e.g. Rhodes, Department of Ichthyology, Grahamstown.

3. Exotic plants
Effects of exotic aquatic plants such as *Salvinia* and *Azolla* can be devastating to aquatic animals: blocking out light, reducing current flows and depositing large quantities of organic material on substrates. All these cause reduced oxygenation of waters and so reduce animal productivity and alter the environment considerably. Three species of exotic aquatic plants were present in the main river channel: the water cabbage (*Pistia stratiotes*), water hyacinth (*Eichhornia crassipes*) and Kariba weed (*Salvinia molesta*).

Another plant, the aquatic fern *Azolla*, was present in large quantities in most backwaters around the Marromeu area during July 1999. Small samples were taken and these have been identified as *Azolla pinnata* a native species. It should be verified that there is no exotic *Azolla filiculoides* present in the delta.

The abundance of exotic weeds needs to be monitored seasonally and their effects studied. Control measures should be considered. *Azolla filiculoides*, for example, can be eradicated effectively using the weevil *Stenopelmus rufinasus*.

4. Eutrophication
In a summary of eutrophication in freshwater, Mason (1991) notes six effects:

- species diversity decreases;
- dominant biota change;
- plant and animal biomass increases;
- turbidity increases;
- sedimentation rates increase; and
- anoxic conditions may develop.

The abundance of *Azolla* in backwater channels may well be due to eutrophication and is potentially disastrous for aquatic floodplain specialists, which include many of the smaller fishes. Covering of water surfaces by *Azolla* will reduce light penetration, oxygen levels, and submerged aquatic plants. Certainly, fish biodiversity at sites where there was complete *Azolla* cover was lower than at "open" water sites in the same region of the floodplain. Whether our measurements are a reflection of sampling during different seasons, or represent real changes over the two decades, needs to be examined.

8. RECOMMENDATIONS

- Further surveys to determine biodiversity are suggested
  - in the Marromeu area during different seasons,
  - in upper regions around Caia to Tete, and
  - in the lower delta (estuary and mouth).

- A regular fisheries monitoring programme should be established (at least a 2-3 year programme).

- Fish farming enterprises to be considered to reduce pressure on fish stocks. Native tilapiine cichlids and not exotic species should be used for this.

- Local farmers should be trained in fish farming techniques.

- Monitoring of, and an eradication programme for, exotic aquatic weeds should be established.

- Regions of little or no development within the delta need to be identified for their long term protection of distinct habitat types, breeding and refuge areas for fishes.

- A programme to alleviate general habitat degradation in the delta needs to be considered in conjunction with the main industries and local people.

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Appendix 7.1 Table 7 Collection sites during the Zambezi Delta expedition (July 1999).

Site code	Date	Site description	Coordinates	Capture methods
ZD99/1	27/07/99	Zambezi R. main channel at Marromeu	18E17'23"S / 35E57'25"E	T
ZD99/2	27/07/99	Nyarugwe village near Marromeu	18E15'51"S / 35E51'40"E	T & S
ZD99/3	28/07/99	Zambezi R., main channel, upstream from Marromeu	18E15'26"S / 35E55'48"E	-
ZD99/4	29/07/99	Zambezi R., main channel, upstream from Marromeu	18E17'09"S / 35E36'53"E	S, D & fishermen
ZD99/5	29/07/99	Zambezi R., main channel, upstream from Marromeu	18E16'51"S / 35E56'38"E	S & D
ZD99/6	28/07/99	Zambezi R., main channel, upstream from Marromeu	18E16'43"S / 35E56'31"E	S, D & fishermen
ZD99/7	29/07/99	Zambezi R., main channel, upstream from Marromeu	18E16'14"S / 35E56'29"E	D net
ZD99/8	30/07/99	Floodplain channel, now chain of pools S of Marromeu	18E19'04"S / 35E54'42"E	S & D
ZD99/9	30/07/99	Irrigation channel, covered with *Azolla* fern	18E18'21"S / 35E55'09"E	S
ZD99/10	30/07/99	Same floodplain channel as ZD99/8 - further downstream	18E20'31"S / 35E54'10"E	S
ZD99/11	30/07/99	Swamp on road just N of Marromeu	18E16'11"S / 35E52'02"E	-
ZD99/12	30/07/99	Bridge on main road leaving Marromeu	18E12'39"S / 35E45'29"E	-
ZD99/13	30/07/99	Nyamisundu village - flooded grassland	18E13'42"S / 35E47'44"E	S & D
ZD99/14	36167	Stream near Camp 1	18E33'45"S / 35E39'46"E	P
ZD99/15	36167	Stream near Camp 1	18E30'00"S / 35E39' 03"E	S
ZD99/16	36167	Lake near Camp 1	18E32'50"S / 35E38'40"E	S
ZD99/17	36198	Pools along dyke near Marromeu	18E19'53"S / 35E54'54"E	-
ZD99/18	36198	Pools 20 km out from Marromeu airstrip on main road.	18E15'19"S / 35E51'19"E	S & D
ZD99/19	36226	Zambezi R., main channel, upstream from Marromeu	18E16'01"S / 35E56'19"E	S
ZD99/20	36257	Zambezi R., just downstream from Luabo	18E25'03"S / 36E06'02"E	S & T
ZD99/21	36257	Zambezi R., downstream from Luabo (mid channel)	18E34'49"S / 36E14'40"E	O
ZD99/22	36287	Mangrove fishing camp	18E48'57"S / 36E14'46"E	T, S, D & R
ZD99/23	36318	Malingapansi (Camp 2), main channel of Micelo R. (opposite bank - vegetated)	18E40'32"S / 36E06'12"E	G
ZD99/24	36318	Malingapansi (Camp 2), main channel of Micelo R. - village bank (mud)	18E40'32"S / 36E06'12"E	S & T
ZD99/25	36318	Backwater channel and muddy pools behind Malingapansi village	18E40'38"S / 36E06'07"E	S
ZD99/26	36348	Naminazi village near Malingapansi	18E39'44"S / 36E06'03"E	D & AT
ZD99/27	36379	Fishing camp on sand dune close to the mouth of the Micelo R.	18E53'36"S / 36E09'00"E	S, D & H

ZD99/28	36379	Rio Inhangurue - mangrove channel connecting Zambezi and Micelo	18E50'30"S / 36E14'17"E	T
ZD99/29	36379	Rio Inhangurue - mangrove channel connecting Zambezi and Micelo	18E49'14"S / 36E12'56"E	O
ZD99/30	36379	Zambezi main channel	18E46'20"S / 36E14'21"E	S, D & T
ZD99/31	36379	Zambezi main channel - Luabo	18E23'36"S / 36E05'26"E	T, H & LL
ZD99/32	36410	Drainage channels in sugar fields near Marromeu	18E22'56"S / 35E52'53"E	D
ZD99/33	36440	Drainage channels in sugar fields near Marromeu	18E22'54"S / 35E52'45"E	D
ZD99/34	36440	Drainage channels in sugar fields near Marromeu	18E22'39"S / 35E52'43"E	D
ZD99/35	36440	Drainage channels in sugar fields near Marromeu	18E21'35"S / 35E53'18"E	D
ZD99/36	36440	Swamp bisected by sugar plantation road	18E21'39"S / 35E53'57"E	S, D & H
ZD99/37	36471	Zambezi main channel - muddy out of current area in sugar factory harbour	18E17'09"S / 35E56'53"E	S & T
ZD99/38	36410	Sugar fields outside Marromeu (lungfish collection site)	18E19'01"S / 35E54'49"E	BD
ZD99/39	14/08/99	Tributary of the Rio Zongue near Inhamitanga (Inhamitanga-Dondo road)	18E13'33"S / 35E09'00"E	S & D
ZD99/40	14/08/99	Rio Chissadze, tributary of Rio Zongue on the Inhamitanga-Dondo road	18E16'57"S / 35E06'59"E	S & D

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CHAPTER 8
FRESHWATER MOLLUSCS
OF THE ZAMBEZI RIVER BASIN

Cornell Dudley

8.1 INTRODUCTION

The Zambezi River, its tributaries and wetlands make up one of Southern Africa's most important natural resources. Given the rapid rate of development and population growth in this region there is intensifying pressure on these resources. As a consequence, the river's wetlands and their associated biodiversity are under increasing threat. In order to more formally evaluate these resources, IUCN-ROSA, in conjunction with the Canadian International Development Agency, initiated the Zambezi Basin Wetlands Conservation and Resource Utilisation Project in 1996. This project is aimed at ensuring the wise use of the natural resources of the wetlands of the Zambezi Basin, focussing in particular on four project sites – the Barotse floodplains, the floodplains and swamps of the Chobe/Caprivi region, the wetlands of the Lower Shire Valley and the Zambezi Delta. One of the project activities is to evaluate the importance of biodiversity from a conservation perspective, both for the four wetland areas and for the wetlands of the basin as a whole. As part of this project technical reviews on the distribution, biogeography, ecology, importance, conservation interest and status of selected biological groups are required, of which this review of the basin's freshwater molluscs forms part.

The freshwater molluscs are examined from both biodiversity and biogeographical perspectives. A analysis of the fauna is presented and checklists of the basin are included. In particular, the basin's centre of biodiversity, Lake Malawi, is compared with Lake Tanganyika, and the molluscs of the river basin are discussed in relation to the other major river basins of the continent – the Congo, the Nile and the Niger. Conservation aspects are evaluated and suggestions for future investigations are presented. Also included is a discussion of the distribution and importance of the genera *Biomphalaria* and *Bulinus,* intermediate hosts of *Schistosoma* species, which are important blood flukes of man.

In most cases it is not difficult to define ecological limits for freshwater molluscs. Problems arise when coastal streams, estuaries and lagoons are considered, as a few species occupy both brackish and freshwater habitats, e.g. streams flowing into mangrove swamps, or near tidal influences. A few such species have been included in this review.

Almost all mollusc families living in freshwater are, from a geological point of view, old families, possibly dating from before the Mesozoic era. Consequently they are of world wide distribution (Danish Bilharziasis Laboratory 1998). Gastropod (snails) classification is in a continuing state of revision and it will be some time before a system comes to be generally agreed for the groups of higher rank (Brown 1994). The freshwater bivalves (mussels, clams) have been a neglected group as they are of little economic or medical importance. Their systematics are even more difficult as species show great variation in morphology with relatively few constant characters. It is easy to recognise families but generic recognition often entails anatomical examination. Without sufficient experience of the family and country of origin, defining a species is often very difficult, and occasionally impossible (Danish Bilharziasis Laboratory 1998, Mandahl-Barth 1988).

The Gastropoda, or snails, are commonly divided into two major subclasses, the Streptoneura (including the Prosobranchia) and the Euthyneura (including the Pulmonata). Prosobranchs have a comb-like gill (branchia/ctenidia) situated in the mantle cavity in front of the heart and are entirely aquatic. Attached to the foot is a horny or calcareous operculum which can be used to close the shell aperture. Sexes are separate. The group is most varied in the larger lakes and rivers of the continent and may contribute a major part of the invertebrate benthos biomass (Leveque 1972 in Brown 1994, Machena & Kautsky 1988). Species may be found to depths of 150-200 m.

Pulmonates include terrestrial as well as aquatic species and have a mantle cavity serving as a lung. No gills are present although planorbid species have a gill-like respiratory organ in the mantle cavity called the pseudobranch. An operculum is lacking. Individuals are hermaphroditic. Pulmonates are most abundant in shallower (#10 m) smaller water bodies, including seasonal rain pools.

The second class, Bivalvia (mussels and clams), has, as the name implies, a pair of hinged shells (valves) which contain a pair of gills (ctenidia) on each side of the visceral mass and a rudimentary foot, all within the mantle cavity. The larvae of the group Unionacea are parasitic on the gills of freshwater fish, while those of the group Sphaeriacea are incubated in brood chambers in the inner gills. Eventually, the young bivalves drop off and bury themselves in the mud, only their posterior end reaching up into the water. All are filter feeders.

8.2 LITERATURE REVIEW

The earliest records of freshwater molluscs in the Zambezi Basin were the result of collections made by early travellers and explorers in the middle of the 19th century. Of note were the collections of W. Peters in Mozambique and the Zambezi Valley in 1843-48 (von Martens 1859, 1879) and that of J. Kirk of the David Livingstone expedition in 1859, who collected along the Upper Shire River and, more significantly, in Lake Nyasa (Lake Malawi) (Dohrn 1865). The collections by J. Speke of the unusual thalassoid (marine-like) gastropods in Lake Tanganyika in 1858 (Woodward 1859) stimulated the first truly scientific expeditions to study freshwater organisms, including molluscs, in tropical Africa. While the focus of these expeditions was outside the Zambezi area, each of the first three (1895, 1899, 1904) visited and collected in the environs of Lake Malawi (Cunnington 1920).

The discovery that the snails *Bulinus truncatus* and *Biomphalaria alexandrina* of Egypt were the intermediate hosts of the serious human parasitic disease, bilharzia (Leiper 1915, 1918), initiated the modern phase of malacology in tropical Africa. Three important regional monographs on the non-marine molluscs followed: Mozambique (Connolly 1925, 1939), Belgian Congo (now the Democratic Republic of the Congo) (Pilsbry & Bequaert 1927) and South Africa (Connolly 1939). Although two of the three are focussed on regions outside the Zambezi Basin, all remain indispensable today as they apply to a much wider fauna and geographical area. Additionally, Haas (1936) collected widely in the basin and was one of first to add biogeographical data and considerations as regard stream basins and similar features.

In the last thirty years there has been a considerable improvement in our knowledge of freshwater mollusc biology, taxonomy and distribution within the basin. Haas (1936, 1969) and Mandahl-Barth 1988) reviewed the taxonomic disarray of the bivalves, particularly the Unionidae, consolidating the disparate fauna to a more realistic number of species. The freshwater snails of Angola were reviewed by Wright (1963), while Mandahl-Barth (1968a) published on the fauna of the upper reaches of the SE Congo Basin. In 1961, Azevedo *et al*. provided a comprehensive account of the snails and bivalves of Mozambique as did Crowley, Pain & Woodward (1964) and Mandahl-Barth (1972) for Lake Malawi. Much later, Brown *et al.* (1992) gave an account of the freshwater snails of East Caprivi and the lower Okavango River in Namibia and Botswana. Recently, in 1996, Appleton wrote an illustrated guide to all freshwater molluscs (gastropods and bivalves) of Southern Africa.

The most significant work on freshwater gastropods to date is that by Brown (1980, 1994), which reviews in great detail our knowledge on the taxonomy, biogeography, ecology, biology and medical importance of the freshwater snails of Africa. A major catalogue on the freshwater bivalves of Africa (Daget 1998) has recently been published. This text provides complete synonymies and references for every species and includes an extensive bibliography. In this review I have followed the systematics of these two works.

A large part of the work on the freshwater molluscs (particularly snails) since World War II, has been supported by the World Health Organisation and national governments in their quest to understand the complex relationships between the numerous parasites of humans and livestock (schistosomes, amphistomes and liver flukes) and their intermediate snail hosts. Substantial support remains for malacological research in the field and laboratory today and important institutional work continues to be done by the Blair Research Institute in Harare, Zimbabwe, the Biomedical Parasitology Section of the Natural History Museum in London and the Danish Bilharziasis Laboratory in Charlottenlund (Brown 1994). The latter institute has produced numerous field guides for gastropods which cover all of Africa (Danish Bilharziasis Laboratory 1977, 1982, 1987, 1989, 1993, 1998). These guides are profusely illustrated with careful line drawings and practical keys.

8.3 THE ZAMBEZI RIVER BASIN

The Zambezi River, originating on Kalene Hill in northwestern Zambia, flows nearly 2600 km before entering the Mozambique Channel. It is Africa's fourth largest river system draining approximately 1.57 million km^2 (Allanson *et al.* 1990) which includes substantial areas of Angola, Malawi, Mozambique, Zambia, and Zimbabwe, and much smaller portions of Botswana, Namibia and Tanzania. The river is often divided into three distinct biogeographic sections – the Upper, Middle and Lower Zambezi (Bell-Cross 1965b, Timberlake 1998).

The Upper Zambezi, from its source in Zambia, passes through Angola and Barotseland (Zambia) to Victoria Falls, a distance of approximately 1100 km. Also included are the Kwando River, Chobe/Caprivi and Linyanti system, the Okavango River, Okavango Swamp, Botletle River and Makadikgadi Pans system and the Kafue system. Although not always hydrologically linked, during periods of high rainfall the first two systems flow into each other and hence are unified biologically (Beadle 1981, Davies 1986, Schlettwein *et al.* 1991). The Kafue River joins the Zambezi below the Victoria Falls. The Upper Zambezi typically comprises a series of broad floodplains, such as those of Barotseland, which are separated by low sand plateaux set in a comparatively old landscape. Dense *Brachystegia* woodlands and extensive grasslands are common; swamps are scattered and generally small.

The Middle Zambezi, including its principal tributary the Luangwa, encompasses a section of similar length between Victoria Falls and the Lupata Gorge downstream from Tete. It is dominated by two large dams, Lake Kariba and Lake Cabora Bassa. Originally a 'sand bank' river (Symoens *et al.* 1981), the present character of the Middle Zambezi, since the construction of the two huge dams, is of a regulated river running through a combination of narrow gorges and broad valleys in a hot dry landscape of deciduous woodland. Floodplains are very limited. With the increased lacustrine and slow water environments in what was a fast moving river, the Upper and Middle Zambezi are becoming more ecologically homogeneous (Davies 1986, Timberlake 1998).

From the Lupata Gorge, the Lower Zambezi is broad, often comprising many anastomising channels with shifting sandbanks, until it reaches the sea at Chinde, nearly 400 km downstream (Timberlake 1998). The Shire River, which begins as an outflow from Lake Malawi and drains much of southern Malawi, passes through the Elephant and Ndindi Marshes and then joins the Zambezi River below Mutarara in Mozambique. The Zambezi Delta starts some 120 km from the coast and consists of extensive areas of grassland and wetland with few trees. Towards the coast, expansive areas of mangroves flank mud-lined tidal creeks. The coastal extent of the delta stretches 290 km from Quelimane in the north to Beira in the south (Davies 1986).

Lake Malawi lies within a narrow steep-sided rift valley biogeographically separated from the Zambezi River by a series of turbulent cataracts dropping 280 m in a distance of 80 km along the Middle Shire River.

The modern course of the Zambezi River is relatively young (1-2 million years BP) and its earlier history has been rather unstable (King 1978, Thomas & Shaw 1988). The ancient proto-Upper Zambezi, including the proto-Chambeshi, the headwaters of the Kasai, the proto-Kafue and the Kwando and Okavango rivers, drained a sizeable portion of the Central African Plateau and flowed out through eastern Botswana and northern South Africa via the Limpopo River to the sea. However, Tertiary movements altered many of the older divides between the Congo, Zambezi and Limpopo systems. The headwaters of the Upper Zambezi (proto-Chambeshi and headwaters of the Kasai, 200 km north of the present divide) were back-tilted and now flow in a reverse direction through the swamps to the Congo drainage. In the early Pliocene, violent tectonic activity caused an interruption of the flow of the proto-Kafue, Kwando and Okavango rivers causing the formation of the several palaeo-lakes in the Caprivi area. These events led to the capture of the proto-Upper Zambezi by the Middle Zambezi in the late Pleistocene. The evolution of the Middle and Lower Zambezi is less clear but there is some evidence that the river's exit at Chinde is, at least in evolutionary terms, relatively recent (Tinley 1977). Lake Malawi may have originated in the Miocene, at least its deep northern basin, but its present form is 1-2 million years old (Bowmaker *et al.* 1978, Fryer & lIes 1972).

At present, many watersheds are low between African river basins and during flood season there may be a nearly continuous sheet of water between them (Beadle 1981). For example, the Kamawafura River, a Congo tributary, and the Kanjita stream, a tributary of the Zambezi, have adequate water in channels and pools with continuous links for fish exchange. Their fish faunas indicate some exchange between the two systems via river capture and high flood levels in past pluvial periods (Beadle 1981, Bowmaker *et al.* 1978). Even the upper tributaries of the Cuanza and Cunene Rivers of Angola share watersheds with the Cubango and Kwando rivers, which drain into the Okavango Basin and Zambezi River, respectively (Beadle 1981). Such fish exchanges among river systems have considerable implications for the dispersal of some unionids which have parasitic larval stages (glochidia/lasidium) living on the gills of fish before dropping to the substrate to complete their development (Appleton 1979).

In conclusion, during the Pleistocene, extensive parts of the Central African Plateau were connected hydrologically and wetland organisms had an easy means of dispersal across them. At the same time the palaeo-wetlands fluctuated greatly in extent, primarily in response to large changes in climate.

8.4 THE MOLLUSCAN FAUNA

There are 102 freshwater and brackish water molluscs present, or very likely present, in the Zambezi Basin (including Lake Malawi). Classification of these species and sources for the records are given in Table 8.1, while Table 8.2 shows their distribution across the Zambezi Basin and their habitat.

8.4.1 **Biodiversity and distribution of groups**

Restricting the analysis to only the 90 indigenous strictly freshwater molluscs (Table 8.3), Gastropoda make up the majority of species (63 species, or 70%). This proportion is slightly smaller than that found in continental tropical Africa as a whole (76%; from Brown 1994, Daget 1998, Mandahl-Barth 1988). Gastropods are able to survive and reproduce in a wide range of freshwater environments including small temporary rain pools, floodplains, swamps, small and large rivers with diverse substrates and shallow to deep lakes. The larger bivalves tend to be restricted to the benthos (bottoms) of stable aquatic habitats like larger rivers and lakes or dams, although smaller species occur in many water bodies including small streams, pans and dams (Appleton 1996, Curtis 1991).

Endemism is high in both subclasses of gastropods, but this is due almost entirely to the contribution of Lake Malawi species (listed in Table 8.4). Out of the 23 endemics, 19 (78%) are found only in the lake. In fact, over half (52%) of all the strictly freshwater mollusc species found in the Zambezi Basin have been recorded from Lake Malawi. Endemism of bivalves is more directly associated with deep lakes and there is only one endemic *(Mutela zambesiensis)* not found in the lake.

Lake Malawi attracted the earliest collectors of molluscs in the region and by the turn of the century, 41 of the 47 species now recorded (87%) were already described. No more than a third of the Zambezi Basin species have been described this century, 15 since 1950. This is a significantly different situation to that of the terrestrial gastropods of Malawi in which approximately 50% were described in this century and nearly 12% in the last 18 years (van Bruggen 1994). Nevertheless, owing to changes in nomenclature the number of species currently accepted in the region is considerably fewer than that thought to be present early in this century. Many of the earliest species descriptions were based on superficial characters of shell size and structure with little reference to important anatomical differences (Brown 1994, Crowley *et al.* 1964, Mandahl-Barth 1988). This has been particularly true of the bivalves of the Great Lakes where in Lake Tanganyika 75 species of Unionidae were reduced to 5 species, and in Lake Malawi 15 species were reduced to 3 (Mandahl-Barth 1988). For gastropods, Crowley *et al.* (1964) cite Bourguignat as an example, listing at least 24 synonyms of *Melanoides polymorpha* that were described by him in 1889.

Among the gastropods, the Streptoneura (prosobranchs) of the basin are proprtionally under-represented when compared to the Afrotropical Region, and the Euthyneura (pulmonates) are over-represented (Table 8.3). Using the number of species by subclass and family from Brown (1994, Table 2.1), but restricting the numbers to only those families that are found in the Zambezi Basin and excluding introduced species, species of coastal brackish water and species of Palaearctic affinity, we see that the prosobranchs represent about 75% of the gastropods in the Afrotropical Region, while in the basin prosobranchs only represent 52%. However, the prosobranchs include 18 out of the 23 endemic gastropods, again 16 coming from Lake Malawi. This difference between the subclasses is more striking when we note that the Zambezi Basin contains 40% of the species of pulmonates known from the Afrotropical Region relative to the prosobranchs' 15%. The proportions of prosobranchs in Lake Malawi show only slightly more “normal” values (57% vs 43%)(see Table 8.5).

The only introduced species to the basin are four species of pulmonates – *Lymnaea columella, Helisoma duryi, Physa acuta* and *Aplexa waterloti.*

Two families, Thiaridae and Planorbidae, make up more than half (177 spp. or 60%) of the gastropod fauna of the Afrotropical Region; 50% (109 spp.) of the prosobranchs and 85% (64 spp.) of the pulmonates. These proportions vary slightly from those found for the basin as a whole – 60, 45 and 77% respectively. Between the two subfamilies of Planorbidae, the percentage of species in the Planorbinae are slightly less than expected (43% vs 54%) and the Bulininae more than expected (57% vs 46%).

For the bivalves the superfamily Unionacea (15 species) is favoured over Sphaeriacea (12 species). Nevertheless, the Sphaeriacea are proportionally better represented than Unionacea in the basin. This may be related to their broader habitat tolerance.

8.4.2 Gastropoda

Subclass Streptoneura: The prosobranchs are most varied in the larger lakes and rivers of the continent which tend to be older and more stable bodies of water. Nevertheless, species are found in all classes of freshwater habitats.

The two species of Neritidae should be present in coastal areas adjacent to the mouth of the Zambezi as Azevedo *et al.* (1961) records both species to the north and south of this part of the river. *Neritina* are found in rivers and streams just above tidal influence and hardly penetrate inland. Littorinidae, another family of brackish (and marine) habitats, may be represented, as two species of *Littoraria* are known from Mozambique (Appleton 1996).

The Viviparidae are principally species of deep lakes and rivers. With the exception of the widespread species, *Bellamya capillata* and the more restricted *B. monardi,* the remaining species are endemic to Lake Malawi. The Ampullariidae are adapted to seasonally flooded habitats as well as fast flowing streams and lake benthos. Again, it is the species found in seasonal habitats that are of wide distribution (i.e. *Lanistes ovum, Pila ovata).* The tropical African Hydrobiidae are poorly known (Brown 1994); most are associated with fast-flowing water in West Africa and the Congo Basin. The single (rare?) species from our region, *Lobogenes michaelis,* is the most widespread of this small genus as the other two species of the genus are found only in the upper reaches of the SE Congo basin.

The large family Bithyniidae is only represented by four species in our region, three so far known only as endemics with very restricted distributions (headwater streams in NE Zambia and Lake Malawi). Only *Gabbiella kisalensis* is widespread in a band across south-central Africa.

The Thiaridae, as elsewhere in Africa, are dominated by species endemic to the Great Lakes (i.e. the thalassoids of Lake Tanganyika). In our region it is the genus *Melanoides,* with nine endemic species adapted to the deep waters of Lake Malawi, that is prominent. The other melanoid, *M. tuberculata*, is successful in a wide diversity of habitats and is found in Asia and over much of tropical Africa. Two of the *Cleopatra* species seem to be restricted to the south-central band of Africa with *C. ferruginea* found throughout the eastern tropical areas of the continent.

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Table 8.1. Systematic checklist of the freshwater molluscs found in the Zambezi Basin, including Lake Malawi. Species listed in the literature as being from Zambia or Zimbabwe, or from Ethiopia to South Africa but not specifically noted as being from the Zambezi Basin (i.e. possible species), are shown by an asterisk (*). Source of data given in r. hand column.

Notes: § – species believed to have been introduced in recent historical time
B – species found in fresh to brackish waters
E – strictly endemic species

SUBCLASS STREPTONEURA (PROSOBRANCHS)

	Order Archaeogastropoda	
	Family Neritidae	
*B	*Neritina natalensis* Reeve, 1855	Brown 1994
*B	*Neritina pulligera* (Linnaeus, 1767, *Nerita*)	Brown 1994
	Order Mesogastropoda	
	Family Viviparidae	
	Bellamya capillata (Frauenfeld, 1865, *Vivipara*)	Brown *et al.* 1992
E	*Bellamya ecclesi* (Crowley & Pain, 1964, *Neothauma*)	Mandahl-Barth 1972
E	*Bellamya jeffreysi* (Frauenfeld, 1865, *Vivipara*)	Mandahl-Barth 1972
	Bellamya monardi (Haas, 1934, *Viviparus*)	Brown *et al.* 1992
E	*Bellamya robertsoni* (Frauenfeld, 1865, *Vivipara*)	Mandahl-Barth 1972
	Family Ampullariidae	
E	*Lanistes* (*Lanistes*) *nasutus* Mandahl-Barth, 1972	Mandahl-Barth 1972
	Lanistes (*Lanistes*) *neavei* Melvill & Standen, 1907	Brown 1994
E	*Lanistes* (*Lanistes*) *nyassanus* Dohrn, 1865	Mandahl-Barth 1972
E	*Lanistes* (*Lanistes*) *solidus* Smith, 1877	Mandahl-Barth 1972
	Lanistes (*Meladomus*) *ellipticus* von Martens, 1866	Azevedo *et al.* 1961
	Lanistes (*Meladomus*) *ovum* Peters, 1845	Brown *et al.* 1992
	Pila occidentalis (Mousson, 1887, *Ampullaria*)	Brown *et al.* 1992
*	*Pila ovata* (Olivier, 1804, *Ampullaria*)	Brown 1994
	Family Littorinidae	
*B	*Littoraria intermedia* (Philippi 1846, *Nerita*)	Appleton 1996
*B	*Littoraria subvittata* Reid, 1986	Appleton 1996
	Family Hydrobiidae	
	Lobogenes michaelis Pilsbry & Bequaert, 1927	Brown 1994
	Family Bithyniidae	
	humerosa group	
	Gabbiella (*Gabbiela*) *kisalensis* (Pilsbry & Bequaert, 1927, *Bulimus*)	Brown *et al.* 1992
	stanleyi group	
E	*Gabbiella* (*Gabbiella*) *balovalensis* Mandahl-Barth, 1968	Mandahl-Barth 1968b
E	*Gabbiella* (*Gabbiella*) *stanleyi* (Smith, 1877, *Bythinia*)	Mandahl-Barth 1972
E	*Gabbiella* (*Gabbiella*) *zambica* Mandahl-Barth, 1968	Mandahl-Barth 1968b
	Family Thiaridae	
	Cleopatra elata Dautzenberg & German, 1914	Brown *et al.* 1992
	Cleopatra ferruginea (I. & H.C.Lea, 1850, *Melania*)	Azevedo *et al.* 1961
	Cleopatra nsendweensis Dupuis & Putzeys, 1902	Brown *et al.* 1992
	Cleopatra smithi Ancey, 1906	Brown 1994
E	*Melanoides magnifica* (Bourguignat, 1889b, *Nyassia*)	Mandahl-Barth 1972
E	*Melanoides nodicincta* (Dohrn, 1865, *Melania*)	Mandahl-Barth 1972
E	*Melanoides nyassana* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides pergracilis* (von Martens, 1897, *Melania*)	Mandahl-Barth 1972
E	*Melanoides polymorpha* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides pupiformis* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides simonsi* (Smith, 1877, *Melania*) [1]	Brown 1994

E	*Melanoides truncatelliformis* (Bourguignat, 1889, *Nyassomelania*)	Mandahl-Barth1972
	Melanoides tuberculata (Muller, 1774, *Nerita*)	Mandahl-Barth 1972
E	*Melanoides turritispira* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
	Melanoides victoriae (Dohrn. 1865, *Melania*)	Brown *et al.* 1992
*B	*Thiara amarula* (Linnaeus, 1758, *Helix*)	Brown 1994

Family Potamididae

*B	*Cerithidea decollata* (Linnaeus, 1758, *Helix*)	Brown 1994

SUBCLASS EUTHYNEURA (PULMONATES)

Order Basommatophora

Family Ellobiidae

*B	*Melampus semiaratus* Connolly, 1912	Appleton 1996

Family Lymnaeidae

*§	*Lymnaea columella* Say, 1817	Brown 1994
	Lymnaea (*Radix*) *natalensis* Krauss, 1848	Azevedo *et al.* 1961

Family Ancylidae

*	*Burnupia caffra* (Krauss, 1848, *Ancylus*)	Brown 1994
	Ferrissia burnupi (Walker, 1912, *Ancylus*)	Gray 1980
	Ferrissia connollyi (Walker, 1912, *Ancylus*)	Gray 1980
	Ferrissia junodi Connolly, 1925	Gray 1980
E	*Ferrissia victoriensis* (Walker, 1912, *Ancylus*)	Brown 1994
E	*Ferrissia zambesiensis* (Walker, 1912, *Ancylus*)	Brown 1994

Family Planorbidae

Subfamily Planorbinae		
	Afrogyrus coretus (de Blainville, 1826, *Planorbis*)	Brown *et al.* 1992
	Biomphalaria angulosa Mandahl-Barth, 1957	Brown 1994
	Biomphalaria pfeifferi (Krauss, 1848, *Planorbis*)	Brown *et al.* 1992
	Biomphalaria rhodesiensis Mandahl-Barth, 1957	Mandahl-Barth 1957a
	Ceratophallus natalensis (Krauss, 1848, *Planorbis*)	Brown & M.-Barth 1973
	Gyraulus costulatus (Krauss, 1848, *Planorbis*)	Brown *et al.* 1992
§	*Helisoma duryi* (Wetherby, 1879, *Planorbis*)	Frandsen & Madsen 1979
*	*Lentorbis carringtoni* (Azevedo *et al.,* 1961, *Segmentorbis*)	Azevedo *et al.* 1961
	Lentorbis junodi (Connolly, 1922, 1925, *Hippeutis*)	Brown 1994
	Segmentorbis angustus (Jickeli, 1874, *Segmentina*)	Brown *et al.* 1992
	Segmentorbis kanisaensis (Preston, 1914, *Segmentina*)	Brown *et al.* 1992
Subfamily Bulininae		
africanus group		
	Bulinus africanus (Krauss, 1848, *Physopsis*)	Mandahl-Barth 1957b
	Bulinus globosus (Morelet, 1866, *Physa*)	Brown *et al.* 1992
truncatus/*tropicus* complex		
	Bulinus depressus Haas, 1936	Brown *et al.* 1992
	Bulinus natalensis (Küster, 1841, *Physa*)	Brown 1994
E	*Bulinus nyassanus* (Smith, 1877, *Physa*)	Mandahl-Barth 1972
E	*Bulinus* near *nyassanus* (Smith, 1877, *Physa*) [2]	Mandahl-Barth 1972
E	*Bulinus succinoides* (Smith, 1877, *Physa*)	Mandahl-Barth 1972
	Bulinus tropicus (Krauss, 1848, *Physa*)	Brown *et al.* 1992
	Bulinus truncatus (Audouin, 1827, *Physa*)	Brown 1994
forskalii group		
	Bulinus canescens (Morelet, 1868, *Physa*)	Mandahl-Barth 1968b
	Bulinus forskalii (Fhrenberg, 1831, *Isidora*)	Brown *et al.* 1992
	Bulinus scalaris (Dunker, 1845, 1853, *Physa*)	Brown *et al.* 1992
reticulatus group		
	Bulinus reticulatus Mandhal-Barth, 1954	Mandahl-Barth 1957b

Family Physidae	
Subfamily Physinae	
*§ *Physa acuta* Draparnaud, 1805	Brown 1994
Subfamily Aplexinae	
§ *Aplexa waterloti* (Germain, 1911, *Physa*)	Connolly 1939
CLASS BIVALVIA	
Order Filibranchia	
Family Mytilidae	
*B *Brachidontes virgiliae* (Barnard, 1964, *Musculus*)	Appleton 1996
Order Eulamellibranchiata	
SUPERFAMILY UNIONACEA	
Family Unionidae	
Cafferia caffra (Krauss, 1848, *Unio*)	Mandahl-Barth 1988
E *Coelatura hypsiprymna* (von Martens, 1897, *Unio*) [3]	Mandahl-Barth 1988
Coelatura kunenensis (Mousson, 1887, *Unio*) [3]	
Coelatura mossambicensis (von Martens, 1859, *Unio*) [3]	Mandahl-Barth 1988
E *Nyassunio nyassaensis* (Lea, 1864, *Unio*)	Mandahl-Barth 1988
Family Mutelidae	
Aspatharia pfeifferiana (Bernard, 1860, *Margaritana*)	Daget 1998
E *Aspatharia subreniformis* (Sowerby, 1867, *Anodon*)	Daget, 1998
Chambardia nyassaensis (Lea, 1864, *Spatha*)	Mandahl-Barth 1988
Chambardia petersi (von Martens, 1859, *Spatha*)	Mandahl-Barth 1988
Chambardia wahlbergi wahlbergi (Krauss, 1848, *Iridina*)	Mandahl-Barth 1988
Mutela alata (Lea, 1864, *Spatha*)	Mandahl-Barth 1988
Mutela mabilii (Rochebrune, 1886, *Mutelina*)	Appleton 1979
Mutela rostrata (Rang, 1835, *Iridina*)	Curtis 1991
E *Mutela zambesiensis* Mandahl-Barth, 1988	Mandahl-Barth 1988
Family Etheriidae	
* *Eheria elliptica* Lamarck, 1807	Mandahl-Barth 1988
SUPERFAMILY SPHAERIACEA	
Family Corbiculidae	
Corbicula astartina (von Martens, 1859, *Cyrena*)	Mandahl-Barth 1972
Corbicula fluminalis africana (Krauss, 1848, *Cyrena*)	Mandahl-Barth 1972
Family Euperidae	
Eupera ferruginea (Krauss, 1848, *Cyclas*)	Mandahl-Barth 1972
* *Eupera ovata* (Madahl-Barth, 1954, *Byssanodonta*)	Mandahl-Barth 1972
Family Sphaeriidae	
Musculium incomitatum (Kuiper, 1966, *Pisidium*)	Mandahl-Barth 1988
Pisidium kenianum Preston, 1911	Korniushin 1998
* *Pisidium ovampicum* Ancey, 1890	Mandahl-Barth 1988
Pisidium pirothi Jickeli, 1881	Mandahl-Barth 1972
Pisidium reticulatum Kuiper, 1966	Mandahl-Barth 1972
Pisidium viridarium Kuiper, 1956	Mandahl-Barth 1988
* *Sphaerium bequaerti* (Dautzenberg & German, 1914, *Eupera*)	Mandahl-Barth 1988
Sphaerium capense (Krauss, 1848, *Cyclas*)	Curtis 1991

[1] *Melanoides simonsi* may be a valid species (Brown 1994).
[2] *Bulinus* near *nyassanus* may be a new species (Mandahl-Barth 1972, Wright *et al*. 1967).
[3] Appleton (1996) and Rosenberg *et al.* (1990), citing priority, use *Coelatura* rather than *Caelatura*.

Table 8.2. Zambezi Basin mollusc checklist showing geographical distribution of species across the basin. Data derived from references listed in paper. (Bar - Barotseland, Oka - Okavango, C/C - Chobe/Caprivi, Kaf - Kafue, Ban - Bangweulu, MZV - Kariba & Mid-Zambezi Valley, CB - Cabora Bassa, LM - Lake Malawi/Upper Shire, LS - Lower Shire, Del - Zambezi Delta, IOC - Indian Ocean coast, Mw/Co - Mweru/Congo basin, rst - restricted distribution, wide - widespread distribution.)

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
GASTROPODS																		
PROSOBRANCHS																		
Neritidae																		
Neritina natalensis													?				X	rivers & streams, tidal influence. Mud in streams near mangroves
Neritina pulligera													?				X	rivers & streams, tidal influence. Mud in streams near mangroves
Viviparidae																		
Bellamya capillata		X	X	X	X	X	X		X						X		X	lakes, rivers, permanent water
Bellamya ecclesi									X							E		deeper waters on SW edge & S part of L.Malawi
Bellamya jeffreysi									X							E		live individuals found at 21m throughout L.Malawi
Bellamya monardi		X	X			X												smaller lakes, rivers; only Angola & N Namibia
Bellamya robertsoni									X							E		deep water to 86m; SE arm of lake
Ampullariidae																		
Lanistes ellipticus			?						X	X	X				X			clear streams over gravel, swamps, puddles, rivers
Lanistes nasutus									X							E		reedbeds, sand 1.5m down to 45-81m; SE arm of L.Malawi
Lanistes neavei						?									X	X		seasonal pools
Lanistes nyassanus									X	X						E		sand, reedbeds, 1.5-27m; deep, clean habitats of L.Malawi
Lanistes ovum		X	X		X	X			X	X		X			X		X	standing or slow water with muddy bottoms & vegetation, seasonal pans, lakes, rivers
Lanistes solidus									X							E		sand, weedbeds, 5-27m; commonest *Lanistes* in L. Malawi

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Ampullariidae																		
Pila occidentalis		X	X			X												from W Zambia to S Angola & N Botswana
Pila ovata							?								?		X	temporary pools, papyrus swamps, stony beaches
Littorinidae																		
Littoraria intermedia													?				X	mangrove forest, saltmarsh
Littoraria subvittata													?				X	mangrove forest, saltmarsh
Hydrobiidae																		
Lobogenes michaelis			X	X											X	X		streams over gravel, muddy pools, warm salt springs
Bithyniidae																		
Gabbiella balovalensis	X															E		stream
Gabbiella kisalensis		X	X			X				X					X		X	streams over gravel, slow waters, floodplains
Gabbiella stanleyi									X							E		littoral zone 12-95m throughout L.Malawi
Gabbiella zambica										X						E		streams?
Thiaridae																		
Cleopatra elata		X	X				X			?					X			streams, rivers & floodplains
Cleopatra ferruginea												X					X	ponds, streams, swamps, rocks in permanent rivers
Cleopatra nsendweensis		X	X	X		X						X			X		X	rivers
Cleopatra smithi						X				X					X	X		rivers, streams
Melanoides magnifica									X							E		only known from one location in L.Malawi
Melanoides nodicincta									X							E		throughout W shore of L.Malawi, depths to 27m
Melanoides nyassana									X							E		only known from SE arm of L.Malawi
Melanoides pergracilis									X							E		throughout W shore of L.Malawi down to 27m
Melanoides polymorpha									X							E		throughout L.Malawi, lakeshore down to 4.5m
Melanoides pupiformis									X							E		throughout W shore of L.Malawi down to 21m
Melanoides simonsi									X							E		lake; only known from type locality

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Melanoides truncatelliformis									X							E		lake; only known from N end of L.Malawi
Melanoides tuberculata							X	X	X			X					X	permanent waters with abundant bottom sediments; brackish waters
Melanoides turritispira									X							E		throughout lake down to 5m
Melanoides victoriae		X	X			X											X	rivers with sand or mud bottoms, floodplains
Thiara amarula													?				X	coastal freshwater above tidal influence
Potamididae																		
Cerithidea decollata													?				X	brackish water, mangrove trunks
PULMONATES																		
Ellobiidae																		
Melampus semiaratus													?				X	brackish water in mud under mangroves
Lymnaeidae																		
Lymnaea columella						X				X					?		X	Introduced; common in permanent streams, dams
Lymnaea natalensis		X	X		X	X		X	X			X	X		X		X	lakes, rivers, swamps,ditches. Pollution & desiccation-tolerant
Ancylidae																		
Burnupia caffra						?								X	?		X	V. variable sp.; stream shores & to 100m in lakes
Ferrissia burnupi									X	X							X	lakes, decaying plant stems below dam
Ferrissia connollyi										X	X						X	decaying plant stems at dam edge
Ferrissia junodi									X									decaying plant stems & submerged twigs in swamp
Ferrissia victoriensis			X			X										E		rivers attached to vegetation
Ferrissia zambesiensis						X										E		rivers
Planorbidae																		
Afrogyrus coretus		X	X			?									?		X	permanent waters with rich aquatic vegetation
Biomphalaria angulosa						X			X	X					X	X		seasonal swamps & irrigation schemes

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Biomphalaria pfeifferi		X	X	X	?	X		X	X		X		X	X	X		X	ditches, ponds, swamps, streams, irrigation channels
Biomphalaria rhodesiensis				X		X				X					X	X		lakes, hillside streams
Ceratophallus natalensis						X	X		X						X		X	marshes, slow streams, rain pools
Gyraulus costulatus		X	X			X		X				X	X		X		X	dams, lakes, aquatic vegetation, stones in slow flowing water
Helisoma duryi							X			X							X	Introduced; cooling ponds, reservoirs, pools, dams, rivers
Lentorbis carringtoni														X				aquatic vegetation in lakes, marshes, slowly flowing rivers
Lentorbis junodi						?						X	X		?		X	aquatic vegetation in marshes, slow- flowing rivers, streams, ponds
Segmentorbis angustus		X	X			X	X		X				X	X	X		X	vegetation in marshes, rocks in streams, puddles
Segmentorbis kanisaensis		X															X	permanent marshes, rain pools
Bulinus africanus				X	X	X	X	X				X	X		X		X	permanent streams, small dams
Bulinus canescens				X											X			marshes
Bulinus depressus		X	X		X	X									X		X	rivers, lakes, temporary marsh, reservoirs, dams
Bulinus forskalii				X		?	X	X	X		X	X	X		X		X	natural & artificial waters, flowing or stagnant
Bulinus globosus		X	X		X	X		X	X		X	X			X		X	streams, rivers, seasonal pools, aquatic plants in shallow water
Bulinus natalensis						X	X								X		X	small pools, slow flowing rivers, lakes
Bulinus nyassanus									X							E		coarse substrate on SW shore of L.Malawi at 1.5-15m; deep water form at 95m
Bulinus nr. nyassanus									X							E		deep water form dredged from 95m, SW shore of L.Malawi
Bulinus reticulatus				X		?	X								?		X	small briefly filled pools
Bulinus scalaris		X	X	X		X	X		X						X		X	seasonal pools lacking vegetation, floodplains
Bulinus succinoides									X							E		SW shore at 4.5m on Vallisneria aethiopica plants

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Bulinus tropicus		X	X	X		X	X			X	X				X		X	small earth dams, pools in seasonal streams
Bulinus truncatus									X						X		X	decaying vegetation in flowing to standing waters
Physidae																		
Physa acuta										X					?		X	Introduced. Stagnant & flowing water near towns
Aplexa waterloti								X									X	Introduced. Flowing & standing water modified by man
BIVALVES																		
UNIONACEA																		
Mytilidae																		
Brachidontes virgillae													?				X	brackish water, also fresh water
Unionidae																		
Cafferia caffra			X	X		X	X			X								lakes, rivers, puddles
Coelatura hypsiprymna									X							E		widespread in L.Malawi; sand, sandy mud at 3-4.5m
Coelatura kunenensis	X	X	X	X		X										X		seasonally inundated area below perennial swamps in clay bottom
Coelatura mossambicensis							X	X	X		X						X	rivers, also lake bed. Common in L. Kariba
Nyassunio nyassaensis									X							E		sand, sandy mud at 3-12m; widespread in L.Malawi
Mutelidae																		
Aspatharia pfeifferiana		X	X	X			X		X	X					X		X	lacustrine, clean sandy bottoms, high oxygen content
Aspatharia subreniformis									X							E		soft mud in shallow edges of river & lake at 4-12 m
Chambardia nyassaensis									X							X		lake, depth of 3-12m; widespread in L.Malawi & L.Tanganyika
Chambardia petersi							X	X								X		?
Chambardia w. wahlbergi		X	X	X			X		X	X							X	lacustrine, running water, ditches, small dams
Mutela alata									X							E		lakes, rivers, muddy environments

Family/species	Upper Zambezi						Middle Zambezi				Lower Zambezi				Mw/Co	rst.	wide	Habitat
	Bar	Oka	C/ C	Kaf	Ban	other	MZV	CB	LM	other	LSh	Del	IOC	other				
Mutela mabilli	X	X	X				X										X	lakes, rivers, muddy pools
Mutela rostrata		X	X				X								X		X	rivers
Mutela zambesiensis			X				X									E		?
Etheriidae																		
Etheria elliptica						X									X		X	rapids, rivers, lakes, marine?
SPHAERICEA																		
Corbiculidae																		
Corbicula astartina					X			X	X						X		X	lakes, rivers
Corbicula fluminalis africana		X	X				X	X	X						?		X	common in L. Malawi & other lakes
Euperidae																		
Eupera ferruginea		X	X			X			X			X			X		X	rivers, lakes, small dams
Eupera ovata										X							X	small lakes
Sphaeriidae																		
Musculium incomitatum			X			X	X								X			small lakes, dams
Pisidium kenianum										X					X		X	rivers
Pisidium ovampicum																	X	mountain streams
Pisidium pirothi					X	X			X						X		X	lakes, rivers, canals, depth 9-12m; most common African *Pisidium*
Pisidium reticulatum									X								X	lakes & rivers, depth 9-12m
Pisidium viridarium					X	X				X					X		X	rivers
Sphaerium bequaerti						X									X		X	rivers
Sphaerium capense		X	X			X				X					X			rivers, small lakes, dams
TOTALS 104	4	27	31	15	9	33	23	12	47	22	7	12	8	4	36	38	56	

Table 8.3. Comparison of the molluscan fauna of the Zambezi Basin with that of the continental Afrotropics (number of species). Introduced species, species with Palaearctic affinities and coastal/brackish water species are excluded. Percentages are given in brackets.

	non-endemic	endemic	totals
ZAMBEZI BASIN			
Gastropoda	40	23	**63** (70)
Prosobranchs	15	18	33 (52)
Pulmonates	25	5	30 (48)
Bivalvia	22	5	**27** (30)
Unionacea	10	5	15 (57)
Sphaeriacea	12	0	12 (43)
All Mollusca	62 (69)	28 (31)	**90** (100)
AFROTROPICAL REGION			
Gastropoda	-	-	**295** (76)[1]
Prosobranchs	-	-	220 (75)
Pulmonates	-	-	75 (25)
Bivalvia			**94** (24)[2]
Unionacea	-	-	65 (69)
Sphaeriacea	-	-	29 (31)
All Mollusca			**389** (100)

Notes: [1] N umber of species of gastropods by subclass and family derived from Brown (1994, Table 2.1), although analysis is restricted to those families found in the Zambezi Basin.
[2] Number of species for bivalves derived from Daget (1998) and Mandahl-Barth (1972, 1988).

Subclass Euthyneura: The pulmonates are most abundant in the smaller water bodies, including seasonal rain pools, and many have very extensive distributions. *Lymnaea natalensis* (Lymnaeidae), is the most widely distributed freshwater snail in Africa, though few species of *Lymnaea* occur on the continent (Brown 1994). *L. columella,* introduced to South Africa more than 50 years ago, is now found in most of the countries of Central and East Africa. *Melampus semiaratus* (Ellobiidae) is restricted to brackish habitats along the coast of East and Southern Africa and is possibly found in the Zambezi Basin.

The Ancylidae are listed as having "five plus" species in Africa by Brown (1994, Table 2.1). Within the text he lists 50 species in three genera: *Ancylus* (3 species), *Burnupia* (21 species) and *Ferrissia* (26 species). The species of *Burnupia* are considered highly uncertain with many founded on what Brown considers non-specific shell differences and most may be reduced to synonymy with *B. caffer.* Most species of *Ferrissia* are known only from the type locality and few are considered specifically distinct for similar reasons to *Burnupia.* On the other hand, the members of this genus are very small (#5 mm diam.) and are likely to be overlooked. The specific diversity of these two genera await further investigation (Brown 1994) and it is quite possible that there are no more than one or two species of *Ferrissia* in the basin. Unusually, *Ferrissia* thrive in stagnant environments (Brown 1994).

Table 8.4. Systematic checklist of the freshwater molluscs of Lake Malawi and Upper Shire. Strictly endemic species are indicated by the letter E. Source of data given in column on right.

	CLASS GASTROPODA SUBCLASS STREPTONEURA (PROSOBRANCHS)	
	Order Mesogastropoda	
	Family Viviparidae	
	Bellamya capillata (Frauenfeld, 1865, *Vivipara*)	Mandahl-Barth 1972
E	*Bellamya ecclesi* (Crowley & Pain, 1964, *Neothauma*)	Mandahl-Barth 1972
E	*Bellamya jeffreysi* (Frauenfeld, 1865, *Vivipara*)	Mandahl-Barth 1972
E	*Bellamya robertsoni* (Frauenfeld, 1865, *Vivipara*)	Mandahl-Barth 1972
	Family Ampuliarlidae	
E	*Lanistes* (*Lanistes*) *nasutus* Mandahl-Barth, 1972	Mandahl-Barth 1972
E	*Lanistes* (*Lanistes*) *nyassanus* Dohrn, 1865	Mandahl-Barth 1972
E	*Lanistes* (*Lanistes*) *solidus* Smith, 1877	Mandahl-Barth 1972
	Lanistes (*Meladomus*) *ellipticus* von Martens, 1866	Mandahl-Barth 1972
	Lanistes (*Meladomus*) *ovum* Peters, 1845	Mandahl-Barth 1972
	Family Bithyniidae	
	stanleyi group	
E	*Gabbiella* (*Gabbiella*) *stanleyi* (Smith, 1877, *Bythinia*)	Mandahl-Barth 1972
	Family Thiaridae	
E	*Melanoides magnifica* (Bourguignat, 1889, *Nyassia*)	Mandahl-Barth 1972
E	*Melanoides nodicincta* (Dohrn, 1865, *Melania*)	Mandahl-Barth 1972
E	*Melanoides nyassana* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides pergracilis* (von Martens, 1897, *Melania*)	Mandahl-Barth 1972
E	*Melanoides polymorpha* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides pupiformis* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
E	*Melanoides simonsi* (Smith, 1877, *Melania*) [1]	Brown 1994
E	*Melanoides truncatelliformis* Bourguignat, 1889	Mandahl-Barth 1972
	Melanoides tuberculata (Muller, 1774, *Nerita*)	Mandahl-Barth 1972
E	*Melanoides turritispira* (Smith, 1877, *Melania*)	Mandahl-Barth 1972
	SUBCLASS EUTHYNEURA (PULMONATES)	
	Order Basommatophora	
	Family Lymnaeidae	
	Lymnaea (*Radix*) *natalensis* Krauss, 1848	Mandahl-Barth 1972
	Family Ancylidae	
	Ferrissia burnupi (Walker, 1912, *Ancylus*)	Gray 1980
	Ferrissia junodi Connolly, 1925	Gray 1980
	Family Planorbidae	
	Subfamily Planorbinae	
	Biomphalaria angulosa Mandahl-Barth, 1957	Brown 1994
	Biomphalaria pfeifferi (Krauss, 1848. *Planorbis*)	Mandahl-Barth 1972
	Ceratophallus natalensis (Krauss, 1848, *Planorbis*)	Mandahl-Barth 1972
	Gyraulus costulatus (Krauss, 1848, *Planorbis*)	Mandahl-Barth 1972
	Segmentorbis angustus (Jickeli, 1874, *Segmentina*)	Brown 1994

Subfamily Bulininae
africanus group

	Bulinus globosus (Morelet, 1866, *Physa*)	Mandahl-Barth 1972
truncatus/*tropicus* complex		
E	*Bulinus nyassanus* (Smith, 1877, *Physa*)	Mandahl-Barth 1972
E	*Bulinus* near *nyassanus* (Smith, 1877, *Physa*)[2]	Mandahl-Barth 1972
E	*Bulinus succinoides* (Smith, 1877, *Physa*)	Mandahl-Barth 1972
	Bulinus truncatus (Audouin, 1827, *Physa*)	Gray 1984
forskalii group		
	Bulinus forskalii (Ehrenberg, 1831, *Isidora*)	Mandahl-Barth 1972
	Bulinus scalaris (Dunker, 1845, *Physa*)	Gray 1981a

CLASS BIVALVIA

Order Eulamellibranchiata

SUPERFAMILY UNIONACEA

Family Unionidae

E	*Coelatura hypsiprymna* (von Martens, 1897, *Unio*)[3]	Mandahl-Barth 1988
	Coelatura mossambicensis (von Martens, 1859, *Unio*)[3]	Mandahl-Barth 1988
E	*Nyassunio nyassaensis* (Lea, 1864, *Unio*)	Mandahl-Barth 1988

Family Mutelidae

E	*Aspatharia subreniformis* (Sowerby, 1867, *Anodon*)	Daget, 1998
	Chambardia nyassaensis (Lea, 1864, *Spatha*)	Mandahl-Barth 1988
	Chambardia wahlbergi wahlbergi (Krauss, 1848, *Iridina*)	Mandahl-Barth 1988
E	*Mutela alata* (Lea, 1864, *Spatha*)	Mandahl-Barth 1988

SUPERFAMILY SPHAERIACEA

Family Corbiculidae

Corbicula astartina (von Martens, 1859, *Cyrena*)	Mandahl-Barth 1972
Corbicula fluminalis africana (Krauss, 1848, *Cyrena*)	Mandahl-Barth 1972

Family Euperidae

Eupera ferruginea (Krauss, 1848, *Cyclas*)	Mandahl-Barth 1972

Family Sphaeriidae

Pisidium pirothi Jickeli, 1881	Mandahl-Barth 1972
Pisidium reticulatum Kuiper, 1966	Mandahl-Barth 1972

Notes:[1] *Melanoides simonsi* may be a valid species (Brown 1994).
[2] *Bulinus* near *nyassanus* may be a new species (Mandahl-Barth 1972, Wright *et al*. 1967).
[3] Appleton (1996) and Rosenberg *et al.* (1990), citing precedence, use *Coelatura* rather than *Caelatura*.

Table 8.5. Comparison of the molluscan fauna of Lake Malawi (including Upper Shire River) with Lake Tanganyika (number of species). Percentages are given in brackets.

	non-endemic	endemic	total
LAKE MALAWI			
Gastropoda	16	19	**35** (74)
Prosobranchs	4	16	20 (57)
Pulmonates	12	3	15 (43)
Bivalvia	8	4	**12** (26)[1]
Unionacea	3	4	7 (58)
Sphaeriacea	5	0	5 (42)
All Mollusca	24 (51)	23 (49)	**47** (100)
LAKE TANGANYIKA			
Gastropoda	21	38	**59** (82)[2]
Prosobranchs	8	37	45 (76)
Pulmonates	13	1	14 (24)
Bivalvia	4	9	**13** (18)[1]
Unionacea	2	8	10 (82)
Sphaeriacea	2	1	3 (18)
All Mollusca	25 (35)	47 (65)	**72** (100)

Notes: [1] Number of species for bivalves derived from Daget (1998) and Mandahl-Barth (1972, 1988).
[2] Number of gastropod species derived from Brown (1994, Table 12.10).

The Planorbidae are by far the largest family of pulmonates in the basin. Inhabitants of temporary water sites, the family is dominated by the genera *Bulinus* (13 species) and *Biomphalaria* (3 species), both in numbers of species and in distribution. The success of *Bulinus* may be attributed to its ability to aestivate for many months in dry mud. *Biomphalaria* has less ability in this regard and is perhaps less successful in the drier parts of Africa (Brown 1994). Of particular significance for both *Biomphalaria* and *Bulinus* is that they are the intermediate host of many species of *Schistosoma.* Of greatest concern by far are the species *S. mansoni* and *S. haematobium,* the causes of bilharzia throughout Africa. *Biomphalaria* is the most important vector of *S. mansoni* as all species have at least one compatible strain of the parasite (Brown 1994). *S. haematobium* is transmitted entirely by *Bulinus* spp., of which *B. africanus, B. globosus* and *B. truncatus* are particularly important.

The only planorbid species with a restricted range are the endemics of Lake Malawi (*Bulinus nyassanus, B.* nr. *nyassanus* and *B. succioides*) and *Biomphalaria angulosa, B. rhodesiensis* and *Lentorbis carringtoni.* The two *Biomphalaria* are found in southern Tanzania, southeast Congo, northeastern and central Zambia and Lake Malawi. *L. carringtoni* ranges through the coastal areas from Mozambique to Natal. The introduced species *Helisoma duryi* can now be found throughout Africa. Two species of Physidae were also probably introduced, but as the taxonomy of this family is unstable it is unclear how many species are present (Brown 1994).

Biomphalaria pfeifferi occurs in a great variety of habitats, including man-made ones such as irrigation channels, and the species is found from Arabia through tropical Africa. Its success seems to be limited along the east coast by high temperatures, and by low temperatures in the African "temperate" highlands (Brown 1994). It is the most important vector of *S. mansoni.*

The taxonomy of *Bulinus* is highly complex and species are not yet defined satisfactorily (Brown 1994, Brown & Rollinson 1996). The genus is normally divided into four groups based on shell characteristics, anatomy, chromosome number and molecular properties. These groups are *africanus*, the *truncatus/tropicus* complex, *forskalii* and *reticulatus.* All are represented in the basin. The genus is highly successful in small seasonal water bodies, though the Lake Malawi endemics are deep water species.

The *africanus* group includes *B. africanus* and *B. globosus,* the group with the greatest range of the genus in Africa. Both species are common in various natural and artificial situations, including lake margins, permanent swamps and irrigation systems, small water bodies that may be flowing or stagnant, perennial or temporary, and are sometimes polluted (Brown 1994).

The *truncatus/tropicus* complex is represented by seven species in the Basin, including the three endemics of Lake Malawi. Species are found in similar habitats to the *africanus* group. The *natalensis/tropicus* group is distributed along the east coastal third of Africa from Ethiopia to South Africa. However, there is some separation, possibly by temperature, between *B. natalensis* and *B. tropicus,* the latter associated with cooler and higher altitude environments than the former (Brown 1994). The distribution of *B. tropicus* is more equatorial, being found from East Africa through the Congo to most of tropical West Africa. An unusual feature of *B. truncatus* is its tetraploid chromosome composition. It is an extremely variable species and many named species have been synonymized with *B. truncatus.* Brown (1994) lists six of the most widely used names. Only *B. truncatus* of this complex is a natural vector of *S. haematobium.*

The *forskalii* group contains *B. canescens, B. forskalii* and *B. scalaris,* no species of which is a natural carrier of *S. haematobium* flukes. *B. forskalii* has an Afrotropical distribution, while *B. scalaris* is more limited to eastern, southern and south-central Africa. *B. canescens* is only found in central Angola, SE Congo and possibly central Zambia. Again, habitats are similar to other species of the genus.

The only representative of the *reticulatus* group is *B. reticulatus,* an inconspicuous species widely scattered in eastern and southern Africa. It is found in small rain pools and is not a natural host of *S. haematobium* (Brown 1994).

8.4.3 **Bivalvia**

Order Filibranchia: Only one Filibranchia is listed as a possible species for the Zambezi Basin. Appleton (1996) records *Brachidontes virgiliae* in the fresh to brackish waters on the coast of Mozambique to the Western Cape, but it has not been recorded from the basin.

Order Eulamellibranchiata: The remaining 27 bivalve species belong to the Eulamellibranchiata (mussels, clams and pill clams) and are true freshwater species. The systematics of this order is not satisfactory, although it was much improved by Mandahl-Barth's 1988 monographic treatment (see also Danish Bilharziasis Laboratory 1998). His reasons for the historical proliferation of described "species" and taxonomic chaos is as follows. Many inland waters are very isolated leading to genetic isolation of their bivalve fauna. There is a wide variety of biotopes which leads to new forms, i.e.

individuals adapt or perish. Yet such aquatic habitats are by nature unstable and of short duration, preventing the evolution of full new species. Consequently, the fauna has many forms at subspecific or variety level. Contributing to this often superficial variation in the Unionidae is their fertilisation and dispersal characteristics. There is no copulation, and fertilisation is external and accidental to some degree ensuring much crossbreeding. Dispersal of the parasitic larval stage is passive meaning that immature individuals, transported far from their place of origin, must adapt or perish. Much of this considerable adaptability is expressed in shell shape.

Superfamily Unionacea: This superfamily is represented in the basin by the families Unionidae, Mutellidae and possibly Etheriidae. The Unionidae (Í 15% of the Afrotropical fauna) includes the widespread genera *Coelatura* (=*Caelatura,* Daget 1998, Rosenberg *et al.* 1990) and *Cafferia.* A third genus, *Nyassunio,* (considered by Mandahl-Barth (1972, 1988) as *Caelatura*) is found only in Lakes Malawi and Tanganyika. *Coelatura* is well known for its extreme plasticity of shell form which has led to approximately 200 supposed species or subspecies having been described in the past. Mandahl-Barth's (1988) analysis reduced these to no more than 24 species, two of them endemic to Lake Malawi and the Upper Shire River. More recently, Daget (1998) listed 28 valid species but under four genera, *Coelatura, Mweruella, Nitia* and *Nyassunio*. '*Coelatura*' (i.e. not in the strict sense of Daget) are principally species of large lakes and dams and perennial rivers. The remaining species, *Cafferia caffra,* is found throughout the southern part of the continent in smaller bodies of water. As with *Coelatura,* it is extremely variable in form.

The biggest bivalves, the Mutelidae, are better represented in the Zambezi region (around 23% of the Afrotropical fauna), including three endemics – *Mutela alata, M. zambesiensis* and *Aspatharia subreniformis.* However, as Mandahl-Barth (1988) points out, this family is rather confusing as it lacks useful taxonomic characters. Numerous species in the past have been based on the size, shape and thickness of the shell which he feels are of little specific value. He concludes by saying that it is impossible to decide how many species there are in Africa. *Aspatharia,* formerly a large genus of 34 species, has been reduced to 15, of which only two occur in our region (Daget 1998). *Chambardia* includes three of the seven species currently recognised out of the more than 50 described forms (Daget 1998). The genus is primarily an inhabitant of large lakes or dams. The taxonomy of the *Mutela* is difficult. Mandahl-Barth's (1988) attempt at unravelling the confusing taxonomic history of the genus is itself convoluted and confusing to a non-specialist. His admittedly unsatisfactory classification has reduced the plethora of named species (around 75) to a manageable 13. *Mutela* are large (Í 100 mm) bivalves of both lakes and perennial rivers, and four species are found in the Zambezi Basin.

The last unionid family, the Etheriidae, is now considered to be represented in Africa by only one species, *Etheria elliptica.* It has not been specifically cited for our region, but as it is common and its distribution is noted to cover tropical Africa (Mandahl-Barth 1988), it is included in the checklist. Its preferred habitats are exposed rocky shores of great lakes and fast running rivers, rapids, cataracts and waterfalls, all of which are common in the basin.

Superfamily Sphaeriacea: This superfamily includes Corbiculidae, Euperidae (Korniushin 1998 *in lit.)* and Sphaeridae. All have representatives in the Zambezi Basin. Corbiculidae, the largest of the Sphaeriacea (generally #30 mm), contains only two species, *Corbicula astartina* and *C. fluminalis.* The latter originally was thought to represent at least 42 species (Mandahl-Barth 1988). Both occur over much of the continent in lakes and dams and the larger rivers. In our region, *C. fluminalis* is represented by the subspecies (or form) *africana.*

The two genera of Sphaeridae, *Sphaerium* (=?*Musculium,* Korniushin 1998 *in lit.)* and *Pisidium,* are tiny clams (#l2 mm and #5 mm respectively). They are found in all types of water bodies, often in very large numbers, and most species have very extensive distributions in Africa.

The last family, Euperidae, is often included in Sphaeridae and contains one small genus *Eupera*. Two species, *E. ferruginea* and *E. ovata*, occur over large portions of Africa. Azevedo *et al.* (1961) recorded *E.* (as *Byssanodonta*) *crassa* from central and coastal Mozambique. However, Daget (1998) considered this a mis-identification of *E. ferruginea*.

8.5 BIOGEOGRAPHY

8.5.1 Lake Malawi

Lake Malawi is of special significance within the Zambezi Basin. Its fauna (Table 8.4) is so distinct that biologically it has only a slight relationship to the rest of the basin. Non-endemics, with the exception of *Lanistes ellipticus* and *Biomphalaria angolensis*, are extremely widespread on the continent (i.e. *Bellamya capillata, Melanoides tuberculata, Lymnaea natalensis, Biomphalaria pfeifferi, Ceratophallus natalensis, Bulinus* spp., *Coelatura caffra, Chambardia wahlbergi, Corbicula fluminalis,* etc.).

The molluscs of Lake Malawi are often compared to those of the other Great Lake, Lake Tanganyika (Beadle 1981; Brown 1978, 1994). Table 8.5 summarises the fauna of the two lakes. While proportions of endemic gastropods are similar, Lake Tanganyika has a more diverse prosobranch assemblage, centred mainly around the unusual thalassoid group which includes a rich fauna of rocky shores. Like Lake Malawi, the species of pulmonates are similar in number (14-15) and most are of extremely widespread distribution.

A comparison of the bivalve richness is perhaps not valuable as the number of species indicated for Lake Tanganyika does not appear to be representative, particularly for the Sphaeriacea. What is significant is the proportion of endemics, which is considerably greater than that of Lake Malawi and again indicates the great age and stability of this deep lake. Lake Tanganyika also has two monotypic genera.

Since Lake Malawi is a deep, relatively stable environment of considerable age, why has there not been a speciation of the prosobranchs as found in Lake Tanganyika? Three reasons have been proposed. Firstly, Lake Malawi is somewhat younger and shallower than Lake Tanganyika and has been subject to more significant changes in water depth and, possibly, salinity (Lake Malawi, 1-2 million years BP, Fryer & Iles 1972; Lake Tanganyika, up to 6 million years BP, Brown 1994). Secondly, Lake Malawi has a very diverse snail-eating fish fauna that inhabits the rocky shoreline. Thirdly, the initial stock of Lake Malawi gastropods had different genetic characteristics (founder effect).

Owen *et al.* (1990) show that no more than 25,000 years ago, Lake Malawi was 250-300 m shallower than it is at present, and only 200 years ago the lake was 120 m lower than current levels. They claim that a large proportion of the *mbuna* rock-dwelling cichlid fish species would have had to evolve in this short period. Such fluctuations in water levels would certainly prove stressful on both fish and snail populations. However, such drastic changes would not take place 'overnight'. Both fish and snails should have been able to move vertically with the changing water levels as in many places the shores of the lake are steep-sided with rocky habitats extending to considerable depths (Beadle 1981). Bowmaker *et al.* (1978) feel that large variations in lake level would have had little impact on cichlid biology but may have been of considerable importance for speciation. Brown (1994) notes that the two main isolating mechanisms proposed for Lake Tanganyika and other African Rift Valley lakes are (a) habitat fragmentation (e.g. the division of a rocky shoreline by the soft substrata of a river delta or sandy beaches), and (b) changes in lake level where populations evolve independently in separate small lakes while water level in the main basin is low. Both would have promoted speciation.

Fryer (1959) noted that Lake Malawi had a more diverse snail-eating fish fauna than Lake Tanganyika, while McKaye, Stauffer & Louda (1986) recorded more than a dozen molluscivorus fish species at Cape Maclear. Fryer proposed that it is these rock inhabiting fish that prevent snails from invading the rocky shoreline, but Beadle (1981) doubts this explanation. Yet in recent years the transmission of *Schistosoma haematobium* in tourist areas such as Cape Maclear has increased (Cetron *et al*. 1993) and it has been suggested that over-fishing of the snail-eating fishes may be the reason for the multiplication of the bilharzia snail vector *Bulinus globosus* (Cetron *et al.* 1996, Stauffer *et al.* 1997, but see Msukwa & Ribbink 1997).

Beadle (1981) makes a third and perhaps more significant point. Evolution works with the material available. The present prosobranch endemic array in Lake Malawi is clearly different from that found in Lake Tanganyika. Malawi's endemics occur in the genera *Bellamya, Gabbiella, Lanistes, Melanoides* and *Bulinus.* With the exception of one *Melanoides* species, the endemics of Tanganyika are derived from the thalassoid stock. Beadle suggests that of most importance was the peculiar genetic characteristics of the ancestral stock. Perhaps in Lake Malawi this stock could not evolve to forms adaptable to the rigorous conditions on wave-swept rocks.

8.5.2 **Zambezi Basin**

Pilsbry and Bequaert noted early in this century (1927) that the outstanding features of the freshwater molluscan fauna of the Afrotropical Region were its taxonomic poverty and uniformity over immense areas (Í 500 species, Brown 1994, Daget 1998, Mandahl-Barth 1988). While this is true for the pulmonates, and to some degree the bivalves (Appleton 1979, 1996), the prosobranchs show much more diversity with 'centres of endemism' in the Congo Basin, Lake Tanganyika, Lake Victoria and Lake Malawi. Nevertheless, species richness remains low relative to other invertebrate groups in Africa such as terrestrial snails (Í 5500 species, van Bruggen 1995) and insects (>1000 species of Odonata; >550 species of aquatic insects for Malawi alone, Dudley 1998). Although Pilsbry and Bequaert's point is certainly true, intriguing questions regarding speciation and biogeography remain (Brown 1994).

The Zambezi Basin mollusc fauna is clearly Afrotropical. Numerous species (i.e. *Melanoides tuberculata, Lymnaea natalensis, Gyraulus costulatus, Biomphalaria pfeifferi, Bulinus forskalii, Cafferia caffra, Pisidium pirothi* and *Chambardia wahlbergi*) extend far southwards well into Natal in South Africa through the 'tropical corridor' (Poynton 1964) along the eastern coastal areas of the continent. Many species reach their southern limits in the Pongola River region north of Natal, a major 'subtraction' zone (Brown 1994). Their southern geographical ranges show various degrees of restriction and they do not occur, or are sparsely represented, in the highlands of more equatorial latitudes, as seen in the genera *Biomphalaria* and *Bulinus.*

The southern limits of the fauna in the western and central parts of Africa lie at far lower latitudes, many species scarcely penetrating south of the Cunene and Okavango river systems and the Caprivi

Strip wetlands. For most species, aridity and, perhaps to a lesser degree, temperature may be the limiting factors (Brown 1994, Brown *et al.* 1992, Curtis 1991). Certainly the more narrowly tropical species of west and central tropical Africa (i.e. species of *Bellamya*, *Lanistes, Gabbiella, Cleopatra, Melanoides, Segmentorbis, Mutela* and *Sphaerium)* have the Zambezi River and the highlands of Zimbabwe as their southern limit. The Limpopo River valley has not provided western faunal elements access to Mozambique and the coastal corridor in recent geological time (Brown 1978).

The tropical molluscs categorised by Brown (1978) as broadly tropical include Zambezi Basin species such as *Melanoides tuberculata, M. victoriae, Lymnaea natalensis, Gyraulus costulatus, Ceratophallus natalensis, Biomphalaria pfeifferi, Bulinus africanus, B. forskalii, B. natalensis/tropicus, Physa acuta* and *Corbicula fluminalis africana.* These species have wider temperature tolerances and are able to live in both high cool and low warm tropical climatic conditions.

The gastropod faunas of Angola, Mozambique, Natal and East Africa are summarised in Table 8.6 and compared with that of the Zambezi Basin as a whole. It is clear that there are a small number of ubiquitous species (3 prosobranchs, 9 pulmonates) that occur over enormous geographical areas. Removing these species from the analysis gives a different picture. For the prosobranchs there is little significant overlap except for the Zambezi Basin with Mozambique and Angola. In fact, 12 of the 15 species of these two countries are found in the basin. The situation with the pulmonates is somewhat different. Shared species, notably over the 'base-line' number of nine, occur over a broad band of Africa from Angola to Mozambique as well as north to East Africa and south to Natal. A recent examination of the molluscs (gastropods and bivalves) of eastern Transvaal's Kruger National Park substantiates this similarity with 19 of its 21 indigenous species being found in the basin (De Kock & Wolmarans 1998).

It is perhaps more relevant to compare the freshwater mollusc species of the Zambezi Basin with those of the other three largest river basins in Africa – the Congo (Zaire), the Nile and the Niger.

8.5.3 **The Congo Basin**

The Congo River system has survived in its present state without great change at least through the Pleistocene. Much of the main river in the middle section of this basin was really almost lacustrine in character, similar to the great lake that occupied the basin during the Pliocene (Bailey 1986). The Luvua River tributary drains a huge area, much of this (the Luapula-Bangweulu-Chambeshi system or Zambia-Zaire (Congo) system of Bowmaker *et al.*1978) probably captured from the Zambezi River. This system may have been the corridor by which Zambezi fish penetrated the Congo Basin as 18 species are shared solely by the two systems. However, Bell-Cross (1965a) found 16 species of fish in pools on the Muhinga watershed plain between the Zambezi and Congo systems (extreme NW Zambia) and points out that higher rainfall would have enabled these fish (and molluscs?) to move from one system to another. The present Congo is the seventh longest river in the world (4370 km) and has the second largest basin (4 million km^2). Rainfall in the central basin occurs virtually throughout the year. Because the Congo straddles the equator and drains floodwaters alternately from north and south of the equator as the wet seasons change, fluctuations in water level are minimised ('reservoir' rivers) (Symoens *et al.* 1981).

8.5.4 **The Nile Basin**

The Sahara has long been the major hindrance to the movement of Afrotropical snails northward as well as Palaearctic species southward, and the connection of freshwater snail faunas of North Africa (Egypt) and tropical Africa is now restricted to the slender 6695 km thread of the Nile River.

Although certainly old in geological terms, the Nile has waxed and waned so frequently that, whenever time allowed an endemic fauna to evolve, a later recession largely destroyed it. Indeed the equatorial part of the Nile did not reach the Mediterranean until the mid-Pleistocene and may have ceased flowing on several occasions (Dumont 1986). The most recent 'last pluvial' occurred about 12,500 years BP (Beadle 1981) and it is during these periods of high water levels that faunal exchanges between central Africa, the Mediterranean and Asia must have occurred. The present basin (3 million km^2) is a fairly homogeneous ecosystem except for the East African Great Lakes, and the fauna is overwhelmingly African (Dumont 1986).

Table 8.6. Comparison of the freshwater gastropods of the Zambezi Basin with those of Mozambique, Natal, Angola and East Africa (Tanzania, Uganda and Kenya). Introduced species, coastal/brackish water species and species endemic to Great Rift Valley lakes (i.e. Lake Malawi, Lake Tanganyika, Lake Victoria) are not included. *Burnupia* and *Ferrissia* are treated in the aggregate as genera. Figures are approximate and are derived from Brown (1978, 1994).

	Total Species (no.)		
Geographical area	Prosobranchs	Pulmonates	Total
Zambezi Basin (ZB)	17	23	40
Mozambique	9	13	22
Natal	5	18	23
Angola	11	16	27
East Africa	27	29	56
	Species in Common (no./total no.)		
Mozambique/Natal	4/10	13/18	17/28
Mozambique/Angola	5/15	9/20	14/35
Natal/Angola	3/12	10/24	13/36
ZB/Mozambique	9/17	13/23	22/40
ZB/Natal	4/18	16/25	20/43
ZB/Angola	8/20	11/28	19/48
ZB/East Africa	5/39	20/32	25/71
Z/M/N/A/EA	3/43 (7%)[1]	9/39 (23%)[2]	12/82 (14%)

Notes: [1] *Bellamya capillata*, *Lanistses ovum* and *Melanoides tuberculata*.
[2] *Lymnaea natalensis*, *Burnupia* sp, *Ferrissia* sp, *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Segmentorbis kanisaensis*, *Bulinus africanus*, *B. globosus* and *B. forskalii.*

8.5.5 The Niger Basin

The "Nilotic" river basins of northern and western Africa, particularly the Nile and the Niger, have had geologically recent and substantial inter-connections (Beadle 1981). More humid conditions at the beginning of the Quaternary forced the proto-Upper Niger (then part of the Senegal River system) north to form an endorheic lake. Eventually this river was forced northeastwards where it broke through to join the Lower Niger. During this period there was an intermittent connection with Lake Chad, a connection which periodically still exists. Lake Chad was connected to the Nile through Bahr el Ghazal in recent prehistoric times (Beadle 1981, Welcomme 1986). The present Niger River is the third longest in Africa, yet it is poorly endowed with permanent tributaries as much of the river passes through very arid terrain (#400 mm rainfall/year). Rainfall is seasonal over most of the 1.12

million km^2 basin and the resultant strong flood regime imposes an annual cycle of flood and drawdown that produces a constant but repetitive habitat instability ('pulse stable'). Water levels rise and fall sharply so that spates are of short duration and may occur a number of times a year. Such rivers are called 'sand bank' rivers (Symoens *et al.* 1981).

8.5.6 **Comparison Between Basins**

Table 8.7 provides a comparison of the freshwater snails of the Zambezi Basin with those of the Congo, Nile and Niger. Species from associated large lakes, coastal (brackish water) species, Palaearctic species and introduced species are not included.

The Congo system is the outstanding system for species richness (96 species) and endemics (60 species), particularly among the prosobranchs (74 and 57 species respectively). The Nile and Zambezi systems are a poor second and third in species richness and, like the Niger, very poor in endemics. Another notable feature is the high proportion of pulmonates in all three systems when compared to the Congo River. Only the Niger has fewer pulmonate species (14) than the Congo (22). The pulmonates of the Nile show the greatest richness (29 species) and endemism (6 species).

Table 8.7 also provides a comparison of the species found in common in the four river systems. The Congo system, being the geographically closest has the greatest species overlap with the Zambezi (29 species). A reasonable agreement is also seen between the Nile and the Zambezi (21 species). However, similarities with the Niger are probably near the minimal number found for any comparison between regions (12 species). For example, see the Natal, Mozambique, Angola and East African comparisons in Table 8.6. In fact, this value is identical to that of the four systems as a whole. Most of the species common between systems belong to the pulmonates, reaching 65% similarity for the Zambezi/Congo comparison.

The prosobranchs of the Zambezi River have no affinity with those of the Nile or the Niger River. Except for the extremely widespread *Pila ovata, P. wernei, Lanistes ovum* and *Melanoides tuberculata,* most prosobranchs are limited to a single river basin. The Congo River, which is believed to have captured some of the headwaters of the Upper Zambezi River, shows no more than a weak affinity, with 12 species in common. Three species, *Lanistes neavei, Lobogenes michaelis* and *Cleopatra smithi,* are only found in the Upper Zambezi and in the SE headwaters of the Congo. Two other species, *Lanistes ellipticus* and *Gabbiella kisalensis*, are found in the same two areas but have wider distributions, including the Middle Zambezi as well as southern Angola and the Caprivi/Okavango wetlands. The remaining seven species. *Bellamya capillata, Lanistes ovum*, *Pila ovata, Cleopatra elata, C. ferruginea, C. nsendweensis* and *Melanoides tuberculata*, have much more extensive distributions.

The pulmonates show a much greater overlap between the river systems and geographical regions. This is undoubtedly related to their preference for shallow ephemeral bodies of water, their ability to aestivate and their high reproductive and dispersal powers. These are all characteristics which would favour pulmonate colonisation of the 'sandbank' rivers. Among the three basins, pulmonate richness and endemism seem, in part, to be related to basin size. Characteristic of the pulmonates' successful invasion of broad geographical areas is that no less than ten species of the total possible (32) are found in all four river systems (*Lymnaea natalensis, Burnupia* sp., *Ferrissia* sp., *Afrogyrus coretus, Gyraulus costulatus, Segmentorbis kanisaensis, Biomphalaria pfeifferi, Bulinus globosus, B. forskalii* and *B. truncatus*).

Table 8.7. Comparison of the freshwater molluscs of the Zambezi Basin with those of the Congo, Nile and Niger basins. Strictly endemic species from the Great Rift Valley lakes (i.e. Lake Malawi, Lake Tanganyika, Lake Victoria) and introduced species are not included. *Burnupia* and *Ferrissia* are treated in the aggregate as genera. Species endemic to the various basins are shown in brackets (E). All figures approximate and derived from Brown (1994), Daget (1998), Mandahl-Barth (1972, 1988).

	Total Species (no.)					
Gastropoda	Prosobranchs		Pulmonates		Totals	
	no.	end.	no.	end.	no.	end.
Congo (C)	74	57 (77)	22	3 (14)	96	60 (63)
Zambezi (Z)	17	2 (12)	23	0 (0)	40	2 (5)
Nile(N)	16	4 (29)	29	6 (21)	45	10 (22)[1]
Niger (Ni)	7	0 (0)	14	0 (0)	21	0 (0)
Bivalvia [2]	Unionacea		Sphaeriacea		Totals	
	no.	end.	no.	end.	no.	end.
Congo (C)	22	13 (59)	12	1 (8)	34	14 (41)
Zambezi (Z)	13	1 (8)	12	0 (0)	25	1 (4)
Nile (N)	10	0 (0)	8	1 (13)	18	1 (6)
Niger (Ni)	11	1 (9)	4	0 (0)	15	1 (7)
	Species in Common (no.)					
Gastropoda	Prosobranchs		Pulmonates		Totals	
	no.	%Pro	no.	%Pul	no.	%
Z/C		12	15	17	65	2928
Z/N		3	10	18	51	2132
Z/Ni	2	9	10	38	12	25
Z/C/N/Ni	2	2	10	26	12	9
Bivalvia	Unionacea		Sphaeriacea		Totals	
	no.	%Uni	no.	%Sph	no.	%
Z/C		4	13	9	60	1328
Z/N		3	15	5	33	823
Z/Ni	3	14	3	23	6	18
Z/C/N/Ni	2	5	3	17	5	8

Notes: [1] The 8 Palaearctic species indicated by Brown (1994, Table 12.16) are not included.
[2] Bivalve species with Palaearctic affinities, coastal/brackish water species and the endemic species of Madagascar and associated islands are excluded.

Prosobranchs of African freshwater systems, like those of other continents, are more varied than the pulmonates (Brown 1994). Prosobranchs are more adapted to the relatively stable aquatic environments of deep lakes and large equatorial rivers (i.e. Lake Malawi, Congo River). Pulmonates, on the other hand, have difficulty invading deep water as most species need to regularly fill their lung with air. They also do not do well in turbulent rivers. Yet, being self-fertilising hermaphrodites, they have great reproductive powers and, consequently, are well adapted for dispersal to and colonisation of smaller, seasonal and, therefore, less stable water bodies. Such environments would not favour the evolution of new species. Any population developing specialised genotypic characteristics would not survive in the long run unless fortunate enough to be passively dispersed to a new favourable habitat. Under such conditions, more generalised characteristics with greater dispersal powers would be favoured.

A similar comparison of the bivalves (Table 8.7) supports this analysis. The Congo system remains the richest, although showing less dominance with a total of 34 species (14 endemic). The Zambezi system (25 species), the Nile (18 species) and the Niger (15 species) follow. What is remarkable is the almost complete lack of endemics in these three river basins. Another feature noted is the much higher proportion of the larger Unionacea relative to the smaller Sphaeriacea in the Congo and Niger systems (>60%) when compared to the other two basins (56 and 52%). The Unionacea make up 69% of the bivalves of the continent as a whole (Table 8.3). Again the Zambezi shares more species with the Congo (13) than with the Nile (8) or the Niger (6), and it is the Sphaeriacea which form the majority of them.

Thirty of the 41 species of the Unionacea mentioned here are confined to a single river system (although they may be present elsewhere), the exceptions being *Aspatharia pfeifferiana, Chambardia wahlbergi, Mutela mobilli, M. rostrata* and *Etheria elliptica*, the last two species occurring in all river basins. Like the pulmonates, the Sphaeriacea show the most overlap between geographical areas. Only seven species (41%) are limited to a single basin (again, they may occur elsewhere), while six species (*Corbicula fluminalis, Eupera ferruginea, Pisidium kenianum, P. pirothi, P. viridarium* and *Sphaerium hartmanni*) are found in three or more basins. Perhaps it is the superfamily's ecological versatility that provides the answer. However, it must be remembered that species delineation in bivalves is on the whole weaker than that of the gastropods, as is our knowledge of bivalve distributions. Therefore, the more conservative systematic treatment of Mandahl-Barth's (1988) has been used in the above analysis rather than that of Daget's (1998). Consequently, the results shown in Table 8.7 are very tentative.

The wide diversity of the Congo Basin mollusc fauna, particularly the prosobranchs, may be attributed to the great variety of habitats, the huge size of the system and its probable permanence and isolation through the Quaternary, first as a great lake and then as a river system. The Congo has been sufficiently isolated for a long enough time to evolve more endemic species than any other African water system. Of all the great basins it has been the least affected by earth movements or great climatic changes during the Pleistocene (Beadle 1981). In contrast, the other basins were being drastically altered by violent disruptive earth movements and fluctuations in climate (rainfall, surface water and temperature) (Welcomme 1986, Dumont 1986, Davies 1986, King 1978, Bowmaker *et al.* 1978), and this instability of 'sandbank' rivers continues today. Both the Nile and the Niger now flow through extremely arid regions. The area of the Middle and Lower Zambezi (before the large dams were built) was reduced to a fast flowing stream between rocks and sandbanks in the dry season. In flood, it overflowed and inundated large expanses of surrounding land. With respect to freshwater molluscs, environmental instability is a common feature of these three river systems, both over an evolutionary time scale and an annual time scale.

In conclusion, the Zambezi River system has a species richness considerably superior to the nearly equivalent sized Niger system. It is also slightly richer than the Nile with respect to Prosobranchs and Unionacea species numbers. Nevertheless, it is extremely poor in endemics and clearly Lake Malawi is the biodiversity heart of the basin. The high proportion of pulmonate (and Sphaeriacea?) species is to be expected as the stability and aquatic resources needed for prosobranch diversity are not available in the Zambezi system. Also expected, because of the pulmonates' preference for shallow unstable water bodies and their great ability to disperse and colonise such water bodies, is the uniformity of the species complexes over the four systems.

8.6 *BIOMPHALARIA, BULINUS* AND SCHISTOSOMIASIS

The driving force of modern malacology has been the importance of species of *Bulinus* and *Biomphalaria* as intermediate hosts of the serious human parasitic diseases – urinary (*Schistosoma haematobium*) and intestinal bilharzia (*S. mansoni*). After World War II, the World Health Organisation (WHO) and various national health authorities began to give serious consideration to the possible control of this blood fluke. This financial support and vigorous investigative effort has advanced knowledge for many species besides those of medical and veterinary importance.

Georg Mandahl-Barth, founder and first director of the Danish Bilharziasis Laboratory, has contributed many papers on mollusc biology, ecology and systematics including important regional faunas (Mandahl-Barth 1968a on SE Congo; 1972 on Malawi) and a comprehensive publication on the little-studied freshwater bivalves of Africa (Mandahl-Barth 1988). Others, such as C.A. Wright (1963, Angola, snails) and D. Brown *et al.* (1992, Namibia, snails; 1994, Africa, snails) of the Medical Research Council and the Biomedical Parasitology Section of the Natural History Museum in London, Azevedo *et al.* (1961, Mozambique, molluscs) of the Institute of Tropical Medicine in Lisbon, and C. Appleton (1979, south-central Africa, bivalves; 1996, southern Africa, molluscs) of the Department of Zoology and Entomology, University of Natal in South Africa, have provided comprehensive accounts of the molluscs of the Zambezi Basin as a direct outcome of their investigations of snails of medical importance. The most current information regarding the distribution of schistosomiasis (and consequently the snails *Biomphalaria pfeifferi* and *Bulinus africanus* and *B. globosus*) is the *Atlas of the Global Distribution of Schistosomiasis* (Doumenge *et al.* 1987), where each country is documented by text and maps.

Biomphalaria pfeifferi and *B. angulosus* are host to *S. mansoni,* although the latter species only occurs within the Zambezi Basin in Lake Malawi. However, the prevalence of *S. mansoni* is much less than that of *S. haematobium* in almost all areas. In Mozambique the highest rates occur near Tete (25%) with lower rates at Chinde (<1%), where population densities are too low to maintain significant infection foci points. Nearly 30% of all districts examined were without infection. In the past, prevalence rates were <10% in Malawi, even in the Southern Region. At present, rates vary between 20-30% with foci in the highlands overlooking the Shire Valley. The area of infection is increasing but rates remain about one third that of *S. haematobium.* Overall, more than half of the 524 bodies of water surveyed in the 1950s harboured *B. pfeifferi* in Mozambique and Malawi. The main endemic areas in Zimbabwe are in the northeast of the country with two-thirds of the population infected near the border with Zambia. The disease was seldom recorded in the drier northern Matabeleland. *B. pfeifferi* is ubiquitous in Zambia but the prevalence of intestinal bilharzia is very low (0-10%), being about one-fourth that of the urinary disease. Sturrock (1978, in Doumenge *et al.* 1987) points out two factors that seem to have a major influence on the distribution of the snail intermediate host in certain parts of the central plateau (1000-1300 m) with a continental climate. Low nocturnal temperatures limit the growth and life span of the snails and the water bodies, located on granite-based soils, have a low calcium and carbonate content which is unfavourable to the survival of *B. pfeifferi* and *Bulinus* spp. The most suitable areas are the flat valley bottoms with impeded drainage. Intestinal bilharzia and *B. pfeifferi* are found throughout the far upper reaches of the Kwando, Lungue Bongo and Luena Rivers in Angola and the Okavango and Chobe rivers in Namibia.

Bulinus africanus and *B. globosus* are the only known natural hosts of *Schistosoma haematobium* in the Zambezi Basin. According to Brown (1994), the most important and widespread of these is *B. globosus* as *B. africanus* inhabits the cooler climatic areas of southern Africa. Nevertheless, both species are recorded as being hosts in areas of all countries that lie within the basin except Malawi (Brown 1994, Table 5.2) and Namibia (Brown *et al*. 1992), where *B. globosus* is the only species (but see Brown & Rollinson 1996).

Urinary bilharzia is endemic throughout the Zambezi Basin with prevalence rates reflecting human population densities and favourable snail habitats and transmission conditions. In Mozambique, *B. globosus* was ubiquitous and found in one third of all suitable sites examined; *B. africanus* being found in only 6%. Prevalence rates were high (80%) in the lower reaches of the Zambezi River as far as Chinde, but upstream at Tete rates decline (Í 40-50%). Infection rates along the shores of Lake Malawi ranged from 30-50% with prevalence increasing southward reflecting increasing human densities. In the Lower Shire River Valley rates were extremely high at 90-95%. In Zimbabwe, prevalence rates tend to be higher in the wetter and cooler sites of the tributary headwaters of streams feeding the Zambezi River from the northern highlands. To the east in northern Matebeleland, infection rates are closer to 20% reflecting the drier conditions and sparse population. Infection rates appear to be lower in the sparsely populated districts of Zambia, being 5-10% in the Luangwa Valley and the Kafue River area, but reaching nearly 40% in the Zambezi headwaters in Northwest Province, the Gwembe Valley near Kariba and the Zambezi River. Significant infection rates persist into the upper reaches of the Zambezi in Angola and within the more southern Chobe/Caprivi wetlands of Namibia.

Notable *Bulinus* species absent from Brown's (1994) list of hosts of *S. haematobium* are *B. forskalii* and *B. tropicus,* both widely distributed species in Africa and in the Zambezi region. He points out that if the parasite were to evolve compatibility with these two common snails the prevalence of urinary schistosomiasis would be greatly increased.

8.7 CONSERVATION

The centre of molluscan endemism is Lake Malawi and, as such, it should be the focus of conservation concern. At present, the 1996 IUCN Red List of Threatened Animals lists eight species of gastropods from Lake Malawi as Vulnerable (*Bulinus nyassanus*) or Endangered (*Bellamya ecclesi, B. jeffreysi, B. robertsoni, Lanistes nasutus, L. nyassanus, L. solidus* and *Bulinus succinoides*, Baillie & Goombridge 1987). The criteria used were primarily based on the presence of small isolated fragmented populations and upon an assumed decline of various population parameters. All lake endemics are documented from small collections from only a few isolated lakeside localities; their actual distributions in the lake are unknown. These populations need further collection and analysis to establish their conservation status. Additionally, the doubtful specific status of *M. simonsi* and *B.* nr. *nyassanus* might be clarified through new collections. At present, the lakeshore and Upper Shire River environments have not been greatly affected by development and, without clear evidence to the contrary, these endemic populations would seem secure. Similar points could be made regarding the endemic bivalves *Coelatura hypsiprymna, Nyassunio nyassaensis, Chambardia nyassaensis* and *Mutela alata*.

Outside the Lake Malawi area, endemics include *Gabbiella stanleyi, G. zambica* and *Mutela zambesiensis,* the first two only known from their type localities (Chitipa, E Zambia and Mankoyo, NW Zambia respectively) and have not been collected since. Whether these three species are as strictly endemic as records indicate can only be determined by further investigations. If truly of such limited distribution, their survival would not be assured.

The only other species endemic to the basin, and of equally restricted distribution, are *Ferrissia victoriensis* and *F. zambesiensis.* However, endemism and rarity are unlikely. The genus is widespread in tropical Africa, but their shells are so small (2-6 mm dia) that these species are often overlooked (Brown 1994). The number of species is also uncertain as many were founded on shell differences, and few are likely to be distinct. Further study of *Ferrissia* (and *Burnupia*) is required to firmly establish the distinctness of the Ancylidae species (Brown 1994).

8.8 FURTHER INVESTIGATIONS

Of the four principal wetlands of the Zambezi Basin, the Chobe/Caprivi area has been the most thoroughly studied (Brown *et al*. 1992, Curtis 1991, Curtis & Appleton 1987). Currently 20 species of gastropods have been identified from this wetland (Tables 8.2 and 8.8). With the exception of *Bellamya monardi,* which is restricted to the Cunene and Okavango river systems, all are widely distributed species of east, central and southern Africa. Brown *et al.* (1992) were disappointed to find no unique species in the Caprivi and they explained this finding in terms of hydrology and ecology. The Chobe/Caprivi watershed is poorly defined to the north east, allowing faunal exchange with a vast area of Central Africa. Also, without extensive stony rapids in the lower Okavango there is no 'high energy' niche which seems to have driven prosobranch speciation in West Africa. As noted earlier in this review, they found a considerable overlap (26%, 9 species) with the fauna of the Sudd region of the Nile (Brown *et al.* 1984), more than 3000 km to the north. Both lists were made up of snails that thrive in water bodies that are temporary to a greater or lesser degree and occupy seasonal water scattered over large areas of Africa. Curtis (1991) lists 11 species of bivalves from the Chobe/Caprivi wetlands, including only four Sphaeriacea. As with the gastropods, all except *Mutela zambesiensis,* which is endemic to the Central Zambezi, are found over considerable areas of east, central and southern Africa.

Table 8.8. Comparison of the published records of the molluscan fauna of four major wetland areas in the Zambezi Basin (number of species).

	Barotse floodplains	Chobe/ Caprivi	Lower Shire Valley	Zambezi Delta
Gastropoda				
Prosobranchs	n/a	9	n/a	7
Pulmonates	1	11	2	11
Subtotal	1	20	n/a	18
Bivalvia				
Unionacea	2	7	n/a	1
Sphaeriacea	n/a	4	n/a	2
Subtotal	2	11	n/a	3
Total	**3**	**31**	**2**	**21**

Note: Comparative data is scanty and should be treated with caution. There are no records available for some areas, particularly the Lower Shire.

The upper reaches of the Zambezi which extend into the south eastern areas of Angola were investigated by Wright many years ago (Wright 1963), and it would appear that there is much to learn about the molluscs of that vast country. The relatively ancient headwaters of the Zambezi to the north, associated with the Lungwebungo, Zambezi, Kabompo and Kafue Rivers, appear to have affinities with the moister Congo Basin, and may contribute new species. As Timberlake (1998) notes, it is here that both flora and fauna include genera and species more typical of the Congo Basin and species diversity for many groups is higher than elsewhere in the Zambezi Basin owing, in part, to it being a mixture of species from two regions.

The Barotse floodplains, the Busango and Lukango swamps and the Kafue floodplains are, except for isolated records, unknown as far as freshwater molluscs are concerned. However, because of the unstable hydrology characteristic of these regions, most species likely to be found would be widespread species similar to those found in the Chobe/Caprivi system.

The Lower Shire Valley wetlands have also not been studied systematically with regard to molluscs. As these marshes have a history of extreme instability and have been greatly modified by human activity, they are unlikely to include species of narrow distribution. Productive areas of investigation might be the rocky gorge environments of the Middle Zambezi and the Middle Shire, though again their relatively unstable aquatic environments would work against any unique forms.

Azevedo *et al.*'s (1961) survey of Mozambique, though now rather dated, forms the basis of what we know about the Zambezi Delta wetlands. For similar reasons to those proposed above, future studies of this region are unlikely to uncover new species, but will probably provide new records of freshwater/tidal interface species which are known to occur north or south of the delta (Neritidae, Assimineidae, Elloblidae and Mytilidae). The bivalves are essentially unknown, though again there should be no surprises within the strictly freshwater families.

An area of potential interest, but not strictly part of the present Zambezi River system, is the Chambeshi River/Bangweulu Lake/Luapula River system (The Zambia/Zaire [Congo] System of Bowmaker *et al.* 1978). The Luapula River, after passing over the Johnston and Mumbatuta Falls, enters Lake Mweru which ultimately drains into the Luvua River, a major tributary of the Lualaba and Congo Rivers. In 1948 Schwetz and Dartevelle published the first comprehensive analysis of the freshwater molluscs of this area, recording 33 species of which ten were considered endemic. The vast collections of L. Stapper, made just prior to the First World War, formed the basis of this study. Twenty years later Mandahl-Barth (1968a) reviewed the molluscs of this region and his results, based on a slightly larger geographical area (including the smaller bodies of water just to the east, which he called High Katanga, and west of the Luapula River), and a more current taxonomy, listed 72 species, 22 being endemic or near endemic. The current list of recognised species (Table 8.9), based on the recent works of Brown (1994) and Daget (1998), includes 71 species. Nineteen of these are endemic if the Upper Lufira River of Mandahl-Barth's High Katanga is included.

Perhaps 1 million years BP, the Luapula River, above the Johnston and Mumbatuta Falls, is thought to have captured the Chambeshi River in the vicinity of the Bangweulu Swamps (Thomas & Shaw 1988). The molluscan fauna provides some negative support for this idea. Except for two endemics of Lake Mweru, *Cleopatra smithi* and *C. johnstoni,* which also occur in the Luapula River just above Johnston Falls, and *Ferrissia zambiensis* which is doubtfully endemic (see Brown 1994), the Chambeshi River/Bangweulu Lake region does not contain any unique snail species or snail species with Congo affinities. Of the 24 species known from this system, 21 are widespread and found in the Zambezi Basin. However, one endemic bivalve, *Coelatura choziensis,* is present in Lake Bangweulu as is a derived form (*schomburgki*) of *Mutela h. hargeri,* an endemic of Lake Mweru. A second endemic, *Coelatura luapulaensis,* is found in the middle Luapula River below the lake but above the falls. Ten of the remaining 14 bivalves are also found in the Zambezi Basin. Lake Bangweulu and associated swamps are considered unproductive and with limited habitat diversity by Bowmaker *et al.* (1978) and may not be very old.

Table 8.9. Systematic checklist of the freshwater molluscs found in the Lake Mweru/Luapula River/Lake Bangweulu/Chambeshi River system (Zambian/Congo System) and "High Katanga", based on Brown (1994) and Mandahl-Barth (1968a, 1988).

Notes: E - species endemic to this greater region
§ - species believed to have been introduced in recent historical time

Columns: B - Chambeshi River/Lake Bangweulu, Upper Luapula region (above Johnston Falls)
M - Lower Luapula River/Lake Mweru region
K - "High Katanga" (middle and upper Lufira River and area near Lubumbashi)
? - Presence questioned by Mandahl-Barth (1968a)

CLASS GASTROPODA
SUBCLASS STREPTONEURA (PROSOBRANCHS)

Order Mesogastropoda

		B	M	K
	Family Viviparidae			
	Bellamya capillata (Frauenfeld, 1865, *Vivipara*)	●	●	
E	*Bellamya contracta* (Haas, 1934, *Vivipara*)			●
E	*Bellamya crawshayi* (Smith, 1893, *Viviparus*)		●	
E	*Bellamya mweruensis* (Smith, 1893, *Viviparus*)		●	
E	*Bellamya pagodiformis* (Smith, 1893, *Viviparus*)		●	
	Family Ampullariidae			
	Lanistes (*Lanistes*) *neavei* Melvill & Standen, 1907			●
	Lanistes (*Meladomus*) *ellipticus* von Martens, 1866			●
	Lanistes (*Meladomus*) *ovum* Peters, 1845	●	●	●
	Pila ovata (Olivier, 1804, *Ampullaria*)			?
	Hydrobiidae			
	Lobogenes michaelis Pilsbry & Bequaert, 1927			●
	Lobogenes spiralis Pilsbry & Bequaert, 1927			●
	Bithyniidae			
	humerosa group			
	Gabbiella kisalensis (Pilsbry & Bequaert, 1927, *Bulimus*)	●		●
	Thiaridae			
E	*Cleopatra johnstoni* Smith, 1893	●	●	
E	*Cleopatra mweruensis* Smith, 1893		●	
	Cleopatra nsendweensis Dupuis & Putzeys, 1902		●	●
E	*Cleopatra obscura* Mandahl-Barth, 1968			●
E	*Cleopatra smithi* Ancey, 1906	●	●	
	Melanoides anomala (Dautzenberg & Germain, 1914, *Melania*)			●
E	*Melanoides crawshayi* (Smith, 1893, *Melania*)		●	
E	*Melanoides imitatrix* (Smith, 1893, *Melania*)		●	
E	*Melanoides mweruensis* (Smith, 1893, *Melania*)		●	

SUBCLASS EUTHYNEURA (PULMONATES)

Order Basommatophora

		B	M	K
	Family Lymnaeida			
	Lymnaea (*Radix*) *natalensis* Krauss, 1848	●	●	●
§	*Lymnaea* (*Radix*) *columella* Krauss, 1848			?
	Family Ancylidae			
	Burnupia caffra (Krauss, 1848, *Ancylus*)	?	?	●
E	*Burnupia kimiloloensis* Pilsbry & Bequaert, 1927			●
	Burnupia mooiensis (Walker, 1912, *Ancylus*)			●
	Ferrissia fontinalis Mandhal-Barth, 1968			●
E	*Ferrissia zambiensis* Mandhal-Barth, 1968	●		
	Family Planorbidae			
	Subfamily Planorbinae			
	Afrogyrus coretus (de Blainville, 1826, *Planorbis*)	?		●
	Biomphalaria angulosa Mandahl-Barth, 1957	●		
	Biomphalaria pfeifferi (Krauss, 1848, *Planorbis*)	●	●	●
	Biomphalaria rhodesiensis Mandahl-Barth, 1957	●		
	Biomphalaria sudanica (von Martens, 1870, *Planorbis*)	●		
	Ceratophallus natalensis (Krauss, 1848, *Planorbis*)	●		
	Gyraulus costulatus (Krauss, 1848, *Planorbis*)	●		●
	Lentorbis junodi (Connolly, 1912, *Hippeutis*)	?		
	Segmentorbis angustus (Jickeli, 1874, *Segmentina*)	●		●
	Segmentorbis excavatus Mandahl-Barth, 1968			●
	Subfamily Bullininae			
	africanus group			
	Bulinus africanus (Krauss, 1848, *Physopsis*)	●		
	Bulinus globosus (Morelet, 1866, *Physa*)	●	●	●
	truncatus / *tropicus* complex			
	Bulinus natalensis (Kuster, 1841, Physa)	●		●
	Bulinus tropicus (Krauss, 1848, *Physa*)	●	●	●
	Bulinus truncatus (Audouin, 1827, *Physa*)			●
	forskalii group			
	Bulinus canescens (Morelet, 1868, *Physa*)			●
	Bulinus forskalii (Ehrenberg, 1831, *Isidora*)	?	?	●
	Bulinus scalaris (Dunker, 1845, 1853, *Physa*)	●		●
	reticulatus group			
	Bulinus reticulatus Mandhal-Barth, 1954	?		
	Family Physidae			
	Subfamily Physinae			
§	*Physa acuta* Draparnaud, 1805			?

CLASS BIVALVIA

Order Eulamellibranchiata

		B	M	K
	SUPERFAMILY UNIONACEA			
	Family Unionidae			
E	*Coelatura choziensis* (Preston, 1910, *Unio*) [1]	●		
E	*Coelatura gabonensis* (Küster, 1862, *Unio*) [1]		●	
E	*Coelatura kipopoensis* Mandahl-Barth 1968 [1]			●
E	*Coelatura luapulaensis* (Preston, 1913, *Unio*) [1]	●		●
E	*Mweuruella mweruensis* (Smith, 1908, *Unio*)		●	
E	*Prisodontopsis aviculaeformis* Woodward, 1991		●	
	Family Mutelidae			
	Aspatharia pfeifferiana (Bernardi, 1860, *Margaritana*)	●	●	●

		B	M	K
	Chambardia dautzenbergi (Haas, 1936, *Aspatharia*)	●		●
	Chambardia rubens rubens (Cailliaud, 1823, *Anodonta*)	●	●	●
E	*Mutela hargeri hargeri* Smith, 1908		●	
E	*Mutela hargeri schomburgki* Haas, 1936	●		
	Mutela rostrata (Rang, 1835, *Iridina*)		●	
	Etheriidae			
	Etheria elliptica Lamarck, 1807	●	●	●
	Euperidae			
	Eupera ferruginea (Krauss, 1848, *Cyclas*)	●	●	●
	SUPERFAMILY SPHAERIACEA			
	Family Corbiculidae			
	Corbicula africana (Krauss, 1846, *Cyrena*)	?	●	?
	Corbicula astartina (von Martens, 1859, *Cyrena*)	●		
	Family Sphaeriidae			
	Musculium hartmanni bangweolicum Haas, 1936	●		●
	Musculium incomitatum (Kuiper, 1966, *Pisidium*)	●		●
	Pisidium kenianum Preston, 1911			●
	Pisidium langlelyanum Melvill & Ponsonby, 1891	●		
	Pisidium priothi Jickeli, 1881	●		
	Pisidium viridarium Kuiper, 1956	●		
	Sphaerium bequaerti (Dautzenberg & Germain, 1914, *Eupera*)	●	●	
	Sphaerium (or *Musculium*?) *capense* (Krauss, 1848, *Cyclas*)	●		●

[1] Appleton (1996) and Rosenberg *et al*. (1990), citing precedence, use *Coelatura* rather than *Caelatura.*

On the other hand, Lake Mweru and the lower Luapula, separated from the Chambeshi River/Lake Bangweulu region by the two waterfalls and never thought to have been part of the Zambezi River system, have a relatively large number of endemic snails (10 species, prosobranchs: *Bellamya* (3), *Cleopatra* (4), *Melanoides* (3)) and bivalves (3 species, Unionacea: *Mweruella* (1), *Prisodontopsis* (1), *Mutela* (1)) more characteristic of the Congo system. Still, 16 of the 29 species known from this region are found in the Zambezi Basin. Schwetz and Dartevelle (1948) describe the present physiographic and bathymetric characteristics of Lake Mweru and the Lower Luapula River in some detail. However, as Brown (1994) points out, Lake Mweru must have been much deeper to have existed long enough to develop such a distinct assemblage, and both the lake and its molluscs now seem to be near the end of their life.

8.9 CONCLUSIONS

Freshwater molluscs do not really seem very useful in understanding changes in biodiversity across the Zambezi Basin. There are few, if any, endemics in this large area except for the isolated, ancient and stable habitat of Lake Malawi. However, among basins such knowledge may provide a measure of the stableness of the aquatic regime over geological time. Most of the major river basins of the continent have similar evolutionary histories in this regard and consequently very similar faunas. The exception is the Congo. What can be said is that the biodiversity of these aquatic organisms, whether unique or not, reflects the quality of the wetland ecosystem. In other words, a "full" mollusc faunal complement at one site, even if nearly the same as at other sites, would suggest an aquatic ecosystem in reasonable shape and supportive of a full community of other aquatic invertebrates.

As Brown (1994) pointed out at the close of his introduction to his book, *Freshwater Snails of Africa and their Medical Importance,* a rich mollusc fauna is usually a sign of a healthy and sustainable aquatic ecosystem and it is the uncontaminated water from such systems on which the well-being of rural African communities depend.

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CHAPTER 9
REVIEW OF ODONATA ASSOCIATED WITH THE WETLANDS OF THE ZAMBEZI BASIN

Moira FitzPatrick

9.1 INTRODUCTION

With the increase in demand for arable land, the wetlands of the Zambezi Basin are under threat. In order to preserve these ecosystems an understanding of the biodiversity is important. Odonata are reliable indicators of the condition of aquatic and terrestrial ecosystems and are also ecologically important as they are major predators in these systems. Odonata are also relatively easily caught and are therefore ideal for monitoring changing conditions in the Zambezi wetlands. Although the Odonata, a primitive and ancient group of insects, are better documented than most invertebrate groups, it is unfortunate that data from the Zambezi Basin are scattered throughout many publications and hence this report is a consolidation of previous work in the basin, with particular reference to the Barotse floodplains, the Okavango Delta, the Lower Shire wetlands and the Zambezi Delta, highlighting shortcomings of the available data. Potential threats and conservation of Odonata populations are highlighted.

The Odonata are familiar insects in aquatic environments as they depend on water for most of their life cycle. In southern and central Africa the order Odonata consists of two suborders – the Anisoptera, or dragonflies, and the Zygoptera, or damselflies (Figure 9.1). The Anisoptera are stronger fliers and more robust than the more delicate Zygoptera. The more powerful fliers are capable of long sustained flight and thus adults are liable to spread further afield. This is evident in the Zambezi basin where 92 of the species collected are widespread throughout the Afrotropical region (Africa south of the Sahara) compared to 43 which have localised (limited) distributions (see Table 9.1). Some of the Anisoptera even extend their range to other continents such as *Pantala flavescens* to Europe, Asia, Australia and America and *Paragomphus genei* to Europe. In general, the Zygoptera, with their weak flying ability, tend to be more localised, e.g. *Lestes amicus* and *Pseudagrion assegaii*; of the 75 species found in the Zambezi Basin 31 are localized. *Agriocnemis exilis*, although the smallest and most delicate species, has a wide distribution throughout Africa as the adults are wafted from place to place by air currents.

The distribution of the Odonata is largely governed by the physical and vegetational conditions of the water and the nature of the substrate (Pinhey 1978). The structure of the vegetation, more than its composition, is significant to these predatory insects, providing perches for adults and, in certain genera, providing sites for egg laying and nurseries. More importantly, the vegetation provides shade and thus has an effect on the water temperature and microclimate, which together with salinity and strength of currents, control diversity of Odonata. Many species favour open stagnant pools, pans or swamps. Others prefer flowing streams, some hover over waterfalls, while there are those which are only found in the diffuse light of pools or slow moving streams which are well shaded with trees. Many species, however, are more tolerant of a wider range of conditions (eurytopic) and they are more widely distributed throughout southern and central Africa.

Figures 9.1; 9.2 and 9.3

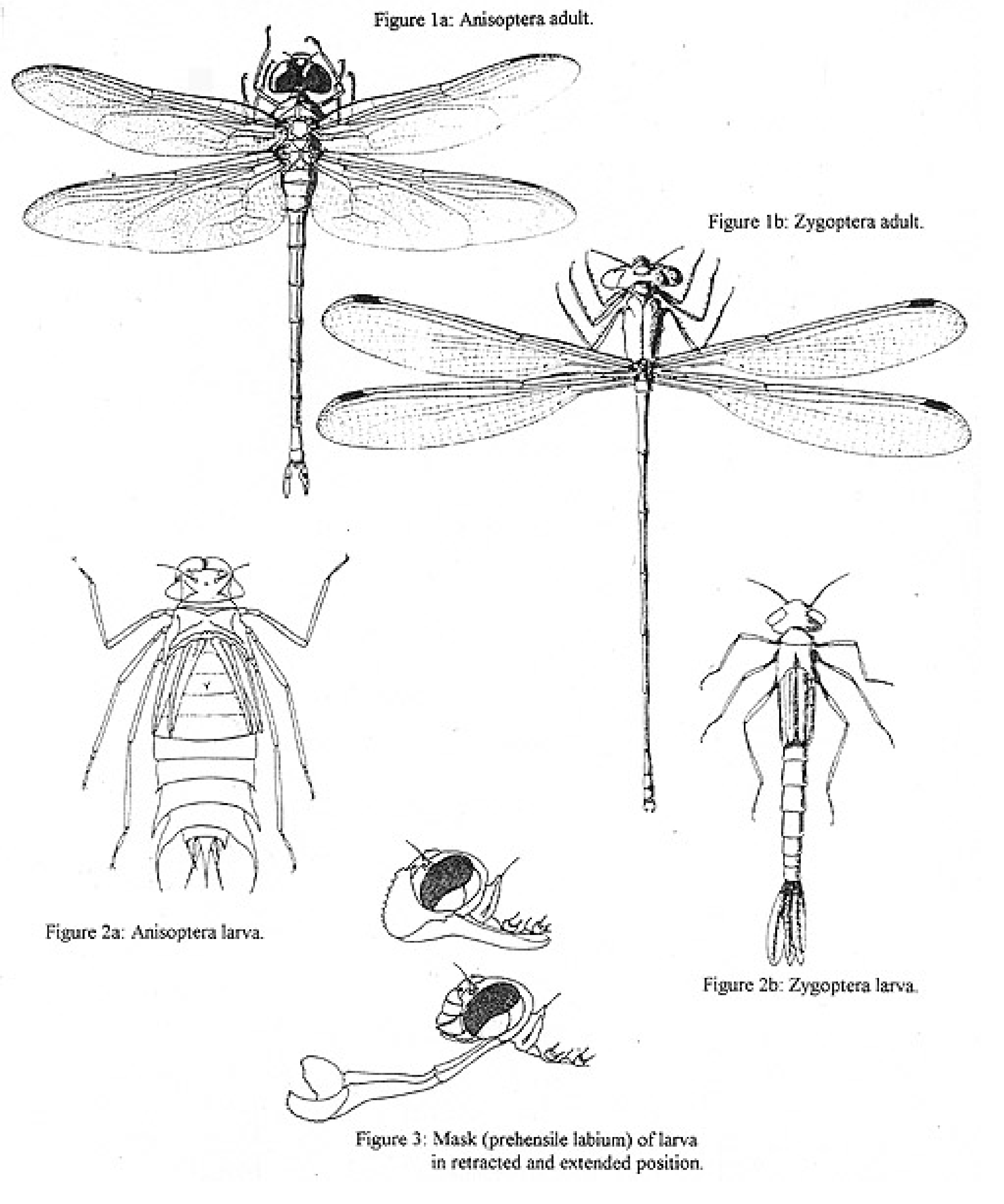

Figure 1a: Anisoptera adult.

Figure 1b: Zygoptera adult.

Figure 2a: Anisoptera larva.

Figure 2b: Zygoptera larva.

Figure 3: Mask (prehensile labium) of larva in retracted and extended position.

9.2 PREVIOUS WORK

Although the Odonata are abundant throughout the Zambezi Basin, especially in the wetlands, there has been little work done on the group. Sporadic collecting in the basin was done by Elliot Pinhey and this work resulted in taxonomic revisions and checklists published between 1950 and 1982, but little collecting has been done since then. Pinhey's collecting trips included the Mwinilunga district, Zambia in 1963, 1965 and 1972 (148 species recorded); a number of collecting expeditions to the Okavango and Chobe swamps during the years 1967-1976 (84 species recorded); various trips to Victoria Falls and Katombora between 1953 and 1963; trips to northern Malawi via Mpatamanga gorge along the lower Shire River (30 species recorded) in 1966 and 1970. He also collected in Mozambique between 1947 and 1973, but there are very few records (18 species) from the Zambezi Delta area. However, a recent collecting trip carried out under the Wetlands Biodiversity Assessment project increased the number of species to 31. Recent collecting also carried out under this project in March/April 1999 increased the number of species known from there from 5 to 33 (26 Anisoptera and 7 Zygoptera). Many of the earlier specimens are housed in the Natural History Museum, Bulawayo and form the basis of the attached checklist. All the specimens collected up to 1980 were identified by Pinhey, and are included in his publications. The only ecological work undertaken on the basin was carried out along Lake Kariba by Balinsky (1967) and is discussed below.

9.3 LIFE CYCLE

The adults of both suborders are insect predators which catch prey on the wing. Their legs are well developed, and situated in a forward position for catching and holding prey, and also for perching. Adults are diurnal and prefer warm areas, and males may display territorial behaviour. After mating, female Anisoptera generally lay their eggs directly into the water, tapping its surface with their abdomens to help withdraw the protruding eggs from their genital pores after which the eggs sink slowly to the bottom. Female Aeshnidae (Anisoptera) and Zygoptera have a spiny, sheathed ovipositor with which they make a number of slits in plant stems, either above or below the surface of the water, where they lay their eggs. The larvae, or nymphs, (Figure 9.2) are predators, feeding on invertebrates and small fish which they seize by shooting out the long prehensile labium (Figure 9.3). Some larvae live in mud, debris or among stones, while others are active scramblers amongst aquatic plants. Mature larvae climb up grass or reed stems, tree trucks, branches or rocks, until they are at or above the surface of the water, where they shed their last skin to become soft, teneral adults (newly emerged adults without full colouration and hardening of the cuticle). As soon as they are capable of flight they seek shelter and rest until their wings and body have hardened.

9.4 CONSERVATION AND POTENTIAL THREATS

Balinsky's (1967) work is the only ecological study of Odonata in the Zambezi Basin, but some work has been done around Pietermaritzburg and Kruger National Park, South Africa. The results of these studies are similar to those done elsewhere and are used as a basis for this discussion.

Savanna rivers, including the Zambezi, have variable water flows due to seasonal rainfall and drought, and any slight fluctuation in flow rates causes changes in the biotope (Stewart & Samways 1998). This causes a high turnover of Odonata species resulting in a dynamic species composition through migration of species to and from the changing sites. Odonata are most abundant from November to January, at the start of and early in the wet season, but their numbers decrease later in the season after the rivers begin to flood since few species can survive in fast flowing water. Their numbers decline again in the cool dry season from July to August (Pinhey 1951). This pattern differs in eurytopic and widespread species, which generally occur throughout the year.

9.4.1 **Importance of aquatic and riparian vegetation**

The cover provided by exposed aquatic macrophytes is the most important environmental factor for most Odonata as it provides nurseries for nymphs and perches for the adults, as well as shade and protection from predators like birds and larger Anisoptera (Samways & Steytler 1996, Stewart & Samways 1998). Consequently, the species diversity is greater at sites with diverse aquatic macrophytes, in contrast to sites without vegetation where the diversity is low, dominated by a few species that favour such conditions. Any change in the aquatic vegetation results in a change in the structure of the Odonata population. The introduction of an exotic weed, *Salvinia molesta*, to Lake Kariba, and *Pistia stratiotes* and *Eichhornia crassipes* to the Sabie, Crocodile and Letaba rivers in South Africa, have led to an increase in the species diversity (Balinsky 1967, Stewart & Samways 1998), but it would be unwise to allow these invasive and detrimental weeds to flourish merely to increase Odonata diversity. In any case the species favouring these weeds were neither rare, localised endemics nor threatened species.

Water temperature is also an important environmental factor as, among other things, it affects egg development (Samways & Steytler 1996). Water temperature and sunlight-versus-shade are interrelated, as a river with a deep riparian strip that shades the water surface will be cooler. The adults prefer specific sunlight-versus-shade regimes. The physiognomy of the vegetation and not its species composition determines the presence or absence of dragonfly species). Only highly eurytopic zygopterans are found in areas without shade along the banks and with very few aquatic macrophytes. It has therefore been suggested that there should be at least a 20 m strip of riparian vegetation between the edge of the water and the edge of any cultivation to maximise Odonata diversity (Samways & Steytler 1996).

9.4.2 **Effects of dam construction**

Construction of dams will change currents, vegetation and water temperature, which in turn will affect the dragonfly population. The diversity of Odonata in natural habitats is far richer and less uniform than that of artificial bodies of water where it is poorer and more restricted (Balinsky 1967). The species composition also changes with the rarer, localised species being replaced by common, widespread species. The management of impoundments should aim to create and maintain a large variety of biotopes, with a suitable range of plant architectures and occasional small areas of bare ground if the Odonata diversity is to be maintained. Dams and reservoirs with aquatic macrophytes can be important refugia for species not occurring locally, thus providing an important recolonisation source, particularly after disasters such as heavy flooding or periodic high silt load (Stewart & Samways 1998).

9.4.3 **Other effects on Odonata populations**

Droughts, as well as disturbances such as water extraction and the removal of riverine and wetland vegetation are the main causes of species loss (Stewart & Samways 1998). Fluctuations in flow rate and high silt loads cause the destruction of river bank vegetation leaving exposed dry sandbanks reducing species diversity. The growth of exotic trees on the banks can also shade out natural bushes and reeds which are the preferred ovipositing sites of many species. Natural disturbances such as animals trampling and grazing the vegetation and churning the water tend to cause a temporary local reduction in the species diversity (Stewart & Samways 1998), but the continuous presence of cattle could pose a more serious threat. Pollutants such as sewage effluent and fertilizer runoff will make aquatic environments unsuitable for many Odonata species.

There is strong evidence that differences in Odonata assemblages along rivers indicate particular types of human disturbance (Samways & Steytler 1996, Stewart & Samways 1998) and may be useful indicators for river management. Environmental conditions are generally characterized by the proportion of eurytopic species (wide biotope tolerance) to stenotopic species (narrow biotope tolerance), by the number of Anisoptera to Zygoptera species, and also simply in terms of which species are present or not. A highly disturbed river has fewer stenotopic to eurytopic species and proportionally more Anisoptera species, as well as a low species richness (Stewart & Samways 1998). A reference for water management could be obtained by making further collections in the Zambezi Basin, which could then be used to assess changing environmental conditions in future.

9.5 AREAS OF HIGH SPECIES RICHNESS

The deserts and arid parts of central Africa are obviously unfavourable for Odonata. Only those species capable of widespread dispersal because of their ability to fly strongly (like many anisopterans) can populate the waters in such areas. Endemic species are absent (Brinck 1955). On the other hand, in areas of higher rainfall and permanent water there is a richer fauna containing many endemics. The Zambezi River is one of the few rivers of the region that does not dry up or split into muddy pools during years of extreme drought and will therefore always have Odonata along its banks.

The areas that are richest in number of species and genera, but not necessarily in numbers of individuals, are swampy areas along forested tropical streams, which also have a number of endemics. The total number of species from these areas in Africa exceeds 250 (Pinhey 1978) and the upper Zambezi in the Mwinilunga District is one such area with twelve endemics being recorded (*Crocothemis brevistigma, Prodasineura flavifacies, Aciagrion nodosum, Ischnuragrion nodosum, Diastatomma selysi, Onychogomphus kitchingmani, O. quirkii, Anax mouri, Allorhizucha longistipes, Nesciothemis fitzgeraldi, Trithemis bifida, T. anomala*). Another area rich in Odonata is the Okavango Delta with seven endemics (*Agriocnemis ruberrina, Enallagma angolicum, Pseudagrion deningi, Anax bangweuluensis, Trithemis aequais, Macromia paludosa, Phyllogomphus brunneus*). There are similarities between the populations in the Zambian/Angolan streams and swamps, and the swamps of the Okavango Delta although individual populations are variable, being most dense in quiet pools well stocked with standing and floating vegetation. The reason for the marked similarity between palustrines of Zambia and those of the Okavango Delta is not clearly understood (Pinhey 1978). In the later Tertiary period there is believed to have been a large western drainage basin, and it is also believed that the Upper Zambezi was not connected to its middle and lower reaches but followed a fault line across the Caprivi at or near the Kwando River, which flowed southwards to join the Limpopo.

Species associated with the east coastal lowland forests and bush between Natal and East Africa are also found in the main river valleys, especially along the middle and lower Zambezi River, and in the lowland forests of Malawi (Pinhey 1978). There are eight endemics found in these areas.

Most of the collecting along the Zambezi wetlands has been in the Mwinilunga District in northwestern Zambia and along the Okavango. The large number of species and endemics (see Table 9.1) found in these wetlands in comparison to other areas is more likely to reflect the collecting effort rather than an absence of Odonata. As no collecting has been done in recent years it is not possible to state if any of the species listed below are still present in the area. It is assumed that the collecting that has taken place was done with a sweep net and no quantitative data are available. The larval biotopes are also not known and it is not possible to determine which species, if any, are threatened and should be awarded special conservation status. The species that have been collected from the Middle Zambezi, Lower Shire (Mpatamanga Gorge) and the Zambezi Delta are all widespread ones.

9.6 GAPS IN KNOWLEDGE AND FUTURE RESEARCH

Very little is known about the ecology and habitats of the Odonata of the Zambezi Basin. No collecting has taken place for over 20 years except for two recent trips to Barotseland and the Zambezi Delta, which collected mainly widespread and common species from pools and marshes. No sampling to determine population status has been done, so the present status of all species is not known. Mwinilunga (148 species) and the Okavango (84 species) are the best collected areas. The Odonata of the Barotse floodplain (33 species), Lower Shire (Mpatamanga Gorge) (32 species) and the Zambezi Delta (31 species) are very poorly known, and species collected so far from these areas have all been widespread ones (Table 9.1). As the Zygoptera are more localised and are more affected by environmental conditions than the Anisoptera, any future collecting and monitoring work should concentrate on them. For monitoring purposes there is also a need to standardize collecting techniques such as the catch-per-unit-effort method (Clark & Samways 1996).

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Table 9.1 Distribution of Odonata in the Zambezi Basin with particular emphasis on the wetlands. Data are collated from the checklist below and additional collections

(Mwi=Mwinilunga, Bar=Barotse floodplain, Okav=Okavango & Chobe swamps, Kat-VF=Katombora to Victoria Falls. L.Shire = Lower Shire, Mpatamanga Gorge). Localised refers to limited distribution as used by Pinhey.

Family/Species	**Upper Zambezi**				**M.Zam.**	**Lower Zambezi**		**Local dist.**	**Wide. dist.**
	Mwin	**Bar**	**Okav**	**Kat.-VF**		**L.Shire**	**Delta**		
ZYGOPTERA									
Lestidae									
Lestes amicus	X			X				X	
Lestes dissimulans			X	X					X
Lestes ochraceus	X				X				X
Lestes pallidus			X	X					X
Lestes pinheyi	X		X	X					X
Lestes tridens	X							X	
Lestes uncifer	X			X			X		X
Lestes virgatus	X				X				X
Protoneuridae									
Chlorocnemis marshalli		X							X
Chlorocnemis wittei	X							X	
Elattoneura glauca	X		X		X	X			X
Elattoneura tropicalis	X			X					X
Mesocnemis singularis				X		X			X
Prodasineura flavifacies	X							X	
Coenagrionidae									
Aciagrion africanum	X								X
Aciagrion gracile	X				X		X		X
Aciagrion congoense							X	X	
Aciagrion heterosticta				X				X	
Aciagrion macrootithenae	X							X	
Aciagrion nodosum	X							X	
Aciagrion steeleae	X		X					X	
Aciagrion zambiense	X							X	
Agriocnemis angolensis	X			X				X	
Agriocnemis exilis	X	X	X	X		X	X		X
Agriocnemis forcipata	X								X
Agriocnemis gratiosa			X	X					X
Agriocnemis pinheyi	X						X		X
Agriocnemis ruberrina			X					X	
Agriocnemis victoria	X	X	X						X

Family/Species	**Upper Zambezi**				**M.Zam.**	**Lower Zambezi**		**Local dist.**	**Wide. dist.**
	Mwin	**Bar**	**Okav**	**Kat.-VF**		**L.Shire**	**Delta**		
Ceriagrion bakeri	X							X	
Ceriagrion bidentatum	X		X					X	
Ceriagrion glabrum	X	X	X	X	X		X		X
Ceriagrion katamborae			X	X				X	
Ceriagrion kordofanicum	X						X		X
Ceriagrion platystigma	X								X
Ceriagrion sakeji	X		X					X	
Ceriagrion sanguinostigma	X							X	
Ceriagrion suave	X		X	X	X				X
Ceriagrion whellani	X	X							X
Enallagma angolicum			X					X	
Enallagma glaucum		X							X
Enallagma sinuatum	X								X
Enallagma subtile				X	X				X
Ischnura senegalensis			X	X	X		X		X
Ischnuragrion nodosum	X							X	
Pseudagrion acaciae			X	X	X	X	X		X
Pseudagrion assegaii			X	X				X	
Pseudagrion chongwe	X							X	
Pseudagrion coelestis		X	X	X			X		X
Pseudagrion commoniae			X	X	X		X		X
Pseudagrion deningi			X					X	
Pseudagrion fisheri	X		X					X	
Pseudagrion gamblesi	X								X
Pseudagrion glaucescens	X		X	X					X
Pseudagrion greeni	X							X	
Pseudagrion hageni	X								X
Pseudagrion hamoni	X		X	X	X	X	X		X
Pseudagrion helenae			X			X	X	X	
Pseudagrion kersteni	X				X	X			X
Pseudagrion kibalense	X							X	
Pseudagrion makabusiensis	X							X	
Pseudagrion massaicum			X		X	X			X
Pseudagrion melanicterum	X								X
Pseudagrion nubicum				X	X				X
Pseudagrion rufostigma	X		X	X				X	
Pseudagrion salisburyense	X			X					X
Pseudagrion sjöstedti	X		X	X					X
Pseudagrion spernatum	X			X					X

Family/Species	**Upper Zambezi**				**M.Zam.**	**Lower Zambezi**		**Local dist.**	**Wide. dist.**
	Mwin	**Bar**	**Okav**	**Kat.-VF**		**L.Shire**	**Delta**		
Pseudagrion sublacteum	X		X	X	X	X			X
Pseudagrion sudanicum			X	X	X				X
Pseudagrion williamsi	X							X	
Chlorocyphidae									
Chlorocypha frigida	X							X	
Chlorocypha luminosa	X								X
Chlorocypha wittei	X							X	
Platycypha caligata	X			X	X				X
Calopterygidae									
Phaon iridipennis	X		X	X	X	X			X
Umma distincta	X							X	
Total Zygopotera (77)	**55**	**7**	**31**	**31**	**18**	**10**	**13**	**31**	**45**
ANISOPTERA									
Gomphidae									
Cinitogompus dundoensis			X					X	
Crenigomphus cornutus	X			X				X	
Crenigomphus hartmanni	X			X		X			X
Diastatomma selysi	X							X	
Gomphidia quarrei			X	X					X
Ictinogomphus ferox		X	X	X					X
Lestinogomphus angustus			X	X					X
Neurogomphus uelensis							X		
Neurogomphus wittei				X				X	
Notogomphus praetorius	X								X
Onychogomphus kitchingmani	X							X	
Onychogomphus quirkii	X							X	
Paragomphus cataractae				X				X	
Paragomphus cognatus	X								X
Paragomphus elpidius			X	X	X				X
Paragomphus genei			X	X	X		X		X
Paragomphus nyassicus				X				X	
Paragomphus sabicus				X	X				X
Paragomphus zambeziensis				X	X			X	
Phyllogomphus brunneus			X	X				X	
Aeshnidae									
Acanthagyma sextans	X								X
Aeshna wittei	X							X	
Anax bangweuluensis			X					X	

Family/Species	**Upper Zambezi**				**M.Zam.**	**Lower Zambezi**		**Local dist.**	**Wide. dist.**
	Mwin	**Bar**	**Okav**	**Kat.-VF**		**L.Shire**	**Delta**		
Anax congoliath	X							X	
Anax imperator	X		X	X	X		X		X
Anax mouri	X							X	
Anax speratus	X			X		X			X
Anax tristis	X		X	X					X
Gynacantha sevastopuloi	X							X	
Gynacantha vesiculata	X								X
Gynacantha villosa	X			X					X
Heliaeschna cynthiae	X							X	
Heliaeschna triervulata	X							X	
Hemianax ephippiger			X	X	X				X
Corduliidae									
Macromia bifasciata		X	X	X	X				X
Macromia bispina	X							X	
Macromia congolica				X				X	
Macromia kimminsi	X		X						X
Macromia overlaeti				X				X	
Macromia paludosa			X	X				X	
Macromia picta		X	X	X	X	X			X
Macromia unifasciata	X							X	
Libellulidae									
Acisoma panorpoides		X	X	X	X		X		X
Acisoma trifidum	X								X
Aethiothemis bequaerti	X							X	
Aethiothemis diamangae	X							X	
Aethiothemis discrepans	X		X			X			X
Aethiothemis mediofasciata	X							X	
Aethriamanta rezia	X	X	X	X					X
Allorrhizucha klingi	X								X
Allorrhizucha longistipes	X							X	
Allorrhizucha preussi	X							X	
Archaephlebia victoriae				X				X	
Atoconeura biordinata	X								X
Brachythemis lacustris	X		X	X	X	X	X		X
Brachythemis leucosticta		X	X	X	X	X	X		X
Brachythemis wilsoni			X						X
Bradinopyga cornuta	X					X			X
Chalcostephia flavifrons	X		X	X			X		X
Crocothemis brevistigma	X							X	

Family/Species	**Upper Zambezi**				**M.Zam.**	**Lower Zambezi**		**Local dist.**	**Wide. dist.**
	Mwin	**Bar**	**Okav**	**Kat.-VF**		**L.Shire**	**Delta**		
Crocothemis divisa	X								X
Crocothemis erythraea		X					X		X
Crocothemis sanguinolenta	X		X	X	X	X			X
Crocothemis saxicolor	X				X			X	
Diplacodes deminuta		X						X	
Diplacodes lefebvrei	X	X	X	X	X		X		X
Diplacodes okavangoensis	X	X	X					X	
Eleuthemis buettikoferi	X			X					X
Hadrothemis camerensis	X								X
Hadrothemis defecta	X								X
Hadrothemis scabrifrons	X						X		X
Hadrothemis versuta	X								X
Hemistigma albipuncta	X	X	X	X	X		X		X
Monardithemis flava	X							X	
Nesciothemis farinosum			X		X				X
Nesciothemis fitzgeraldi	X							X	
Notiothemis robertsi	X								X
Olpogastra fuelleborni				X	X	X			X
Olpogastra lugubris		X	X	X		X			X
Orthetrum abbotti	X			X	X				X
Orthetrum angustiventre	X								X
Orthetrum austeni	X								X
Orthetrum brachiale	X	X	X	X		X	X		X
Orthetrum chrysostigma		X	X	X	X	X	X		X
Orthetrum guineese	X								X
Orthetrum hintzi	X								X
Orthetrum icteromelas	X	X	X	X					X
Orthetrum julia	X						X		X
Orthetrum machadoi	X		X						X
Orthetrum macrostigma	X							X	
Orthetrum microstigma	X								X
Orthetrum monardi	X								X
Orthetrum robustum	X		X					X	
Orthetrum saegeri	X							X	
Orthetrum stemmale							X		
Orthetrum trinacrium	X	X	X		X		X		X
Palpopleura jucunda	X				X				X
Palpopleura lucia	X	X		X			X		X
Pantala flavescens			X	X	X	X			X

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
Parazyxomma flavicans			X	X					X
Philonomon luminans	X		X	X					X
Porpacithemis dubia	X							X	
Porpax asperipes	X								X
Porpax risi	X								X
Rhyothemis fenestrina			X	X					X
Rhyothemis mariposa	X							X	
Rhyothemis notata	X	X	X	X					X
Rhyothemis semihyalina		X	X	X	X				X
Sympetrum fonscolombei			X						X
Sympetrum navasi		X	X						X
Tetrathemis polleni						X	X		X
Thermochoria equivocata	X								X
Tholymis tillarga	X	X	X	X	X	X	X		X
Tramea basilaris			X	X	X				X
Tramea burmeisteri		X							X
Trithemis aconita	X			X					X
Trithemis aequalis			X					X	
Trithemis annulata	X	X	X	X	X	X	X		X
Trithemis anomala	X							X	
Trithemis arteriosa	X		X	X	X	X	X		X
Trithemis bifida	X							X	
Trithemis dichroa	X								X
Trithemis donaldsoni					X	X			X
Trithemis dorsalis	X								X
Trithemis furva	X								X
Trithemis hecate		X	X						X
Trithemis kirbyi		X	X	X	X	X			X
Trithemis monardi	X		X	X					X
Trithemis nuptialis	X								X
Trithemis pluvialis	X								X
Trithemis pruinata	X								X
Trithemis stictica	X		X	X	X				X
Trithemis werneri					X	X			X
Urothemis assignata				X	X		X		X
Urothemis edwardsi		X	X	X	X		X		X
Zygonyx atritibium	X							X	
Zygonyx eusebius	X							X	
Zygonyx flavicostus	X								X

Family/Species	Upper Zambezi				M.Zam.	Lower Zambezi		Local dist.	Wide. dist.
	Mwin	Bar	Okav	Kat.-VF		L.Shire	Delta		
Zygonyx natalensis	X			X		X			X
Zygonyx torridus	X		X		X	X			X
Total Anisoptera (140)	**93**	**26**	**53**	**57**	**34**	**22**	**23**	**44**	**94**
TOTAL SPECIES (217)	**148**	**33**	**84**	**88**	**52**	**32**	**36**	**75**	**139**

9.8 CHECKLIST AND ECOLOGICAL NOTES

The following checklist has been compiled from:

a) specimens in the Natural History Museum, Bulawayo.
b) Pinhey, E. (1962). A descriptive catalogue of the Odonata of the African Continent (up to December 1959) Part 1-2. *Publicaçoes Culturais da Companhia de Diamantes de Angola* **59**: 1-322.
c) Additional references listed below.

ZYGOPTERA

LESTIDAE (21)

Lestes amicus *Martin, 1910*
Very local and gregarious, preferring wet patches in forest or swamp-forest.
Distribution: Zimbabwe, Mozambique, Angola, S Tanzania.

Lestes dissimulans *Fraser, 1955*
Found in swamps and grassy pools, quiet streams, sometimes temporary rain pools
Distribution: Widespread; S Mozambique, Transvaal, Zimbabwe, Botswana, Zaire, Angola, Tanzania, Kenya, Uganda, DRC, Gabon, Chad, Nigeria, Senegal.

Lestes ochraceus *Selys, 1862*
Usually found at stagnant reedy or grassy pools or quiet streams.
Distribution: Zimbabwe, Malawi, Zambia, DRC, Tanzania, Kenya, Uganda, S Sudan, Cameroon, Nigeria, Burkino Faso.

Lestes pallidus *Rambur, 1842*
Common and widespread species found in open country, favouring grassy or reedy pools and streams, or at times the bush, grass or low vegetation at some distance from water. Also occurs at grass-fringed pools in arid sandy waste lands.
Distribution: Throughout Afrotropics, except in forests.

Lestes pinheyi *Fraser, 1955*
Found at reedy or grassy pools; most commonly in palustrine swampy conditions.
Distribution: Zimbabwe, Zambia, E Angola, DRC, Nigeria.

Lestes tridens *McLachlan, 1895*
Very local in open reed beds or at reedy, grassy margins of small or large pools, even lakes.
Distribution: Natal, Transvaal, Mozambique, Zimbabwe, Zambia, E Angola, Zaire, Tanzania, Kenya, Uganda, Somalia, Nigeria.

Lestes uncifer *Karsch,1899*
A rather uncommon species, found near reedy pools or streams but generally amongst bush or clumps of tress nearby.
Distribution: Natal, Mozambique, Zimbabwe, Zambia, DRC, Tanzania, Uganda, Somalia, Nigeria.

Lestes virgatus *(Burmeister, 1839)*
Locally common and widespread species found in woodland or forest, sometimes in thick bush. Favours small pools, or sluggish forest streams.
Distribution: E Cape northwards, inland & coastal to Ethiopia, equatorial, C & W Africa.

PROTONEURIDAE
Chlorocnemis marshalli *Ris, 1921* (10)
Found in heavy forest, sometimes montane forest, but quite often in thick patches of bush.
Distribution: Zimbabwe, Zambia, Malawi, Mozambique.
Chlorocnemis wittei *Fraser, 1955* (10)
Distribution: Zambia, DRC.

Elattoneura glauca *(Selys, 1860)* (8,18)
Locally common and gregarious on banks of streams, particularly in shade of trees
Distribution: Widespread throughout the Afrotropics.

Elattoneura tropicalis *Pinhey, 1974* (5,15,18)
On banks of well shaded streams and rivers.
Distribution: Zambia, Malawi, DRC, Uganda.

Mesocnemis singularis *(Karsch, 1891)* (8,18,22)
Frequents fast waters of rivers and streams; appears to be gregarious.
Distribution: Widely distributed in Afrotropics.

Prodasineura flavifacies *Pinhey, 1981* (24)
Only known from Ikelenge (Mwinilunga).

COENAGRIONIDAE
Aciagrion africanum *Martin, 1908*
Prefers swamps or swampy verges of streams.
Distribution: Zimbabwe northwards to DRC.

Aciagron congoense *(Sjöstedt, 1917)*
Slow streams or reedy and grassy pools.
Distribution: Malawi, Tanzania, Uganda, Mozambique, Zambia

Aciagrion gracile *(Sjöstedt, 1909)*
Found at quite reedy or grassy pools, streams and swamps.
Distribution: Malawi, Tanzania, Uganda, Mozambique, Zambia, Zimbabwe.

Aciagrion heterosticta *Fraser, 1955*
Found in swamps or swampy pools verging on slow streams.
Distribution: Uganda, DRC, Zambia.

Aciagrion macrootithenae *Pinhey, 1972*
Found in swamps and eggs possibly laid through mud or through submerged plants into mud.
Distribution: Angola, DRC, Upper Zambezi.

Aciagrion nodosum *(Pinhey, 1964)*
Found in swampy gallery forest streams.
Distribution: Only in Mwinilunga area.

Aciagrion steeleae *Kimmins, 1955* (18)
Found in swamps or the swampy margins of streams, pools and lakes.
Distribution: Zambia, Angola, Botswana.

Aciagrion zambiense *Pinhey, 1972*
Found in swamps near or in gallery forest.
Distribution: Zambia, E Angola.

Agriocnemis angolensis *Longfield, 1945* (18)
Distribution: Angola, Namibia.

Agriocnemis angolensis spatulae *Pinhey, 1974* (8,18)
Only known from Ikelenge Swamp, Mwinilunga.

Agriocnemis exilis *Selys, 1869*
Distribution: Nigeria, Uganda, Tanzania, Malawi, Zambia, Mozambique, Zimbabwe, Botswana, DRC, Angola.

Agriocnemis forcipata *Le Roi, 1915*
Distribution: Sudan, Cameroon; Central African Republic, Uganda, DRC, Zambia.

Agriocnemis gratiosa *Gerstaecker, 1891* (18)
Distribution: Sudan, Tanzania, Uganda, Malawi, Zambia, Mozambique, Botswana, Natal.

Agriocnemis pinheyi *Balinsky, 1951*
Distribution: Zambia, Zimbabwe, Mozambique, Natal.

Agriocnemis ruberrina *Balinsky, 1961* (18)
Only known from Natal and Okavango Swamps.

Agriocnemis victoria *Fraser, 1928* (18)
Distribution: Sierra Leone, Nigeria, Cameroon, Central African Republic, Uganda, DRC, Angola, Zambia, Botswana.

Ceriagrion bakeri *Fraser, 1951* (3)
Distribution: Uganda, Nigeria, Upper Zambezi.

Ceriagrion bidentatum *Fraser 1941* (3, 18)
Local in forests of Central and tropical Africa.
Distribution: Uganda, Angola, Zambia, DRC, Nigeria, Zambezi Basin.

Ceriagrion glabrum *(Burmeister, 1839)* (18)
A common species in streams and pools well supplied with reeds.
Distribution: Widely distributed over the Afrotropics and parts of Arabia.

Ceriagrion katamborae *Pinhey, 1961* (2,9,18)
Found in swampy streams.
Distribution: Upper Zambezi.

Ceriagrion kordofanicum *Ris, 1924*
Distribution: Sudan, Kenya, Uganda, Upper Zambezi.

Ceriagrion platystigma *Fraser, 1941* (3)
Distribution: Uganda, Cameroon, DRC, Zambia, S Nigeria, Upper Zambezi.

Ceriagrion sakeji *Pinhey, 1963*
Found in swampy streams.
Distribution: Upper Zambezi.

Ceriagrion sanguinostigma *Fraser, 1955*
Distribution: DRC, Upper Zambezi.

Ceriagrion suave *Ris, 1921* (3,18)
Distribution: Fairly widespread; almost abundant in some localities. Zimbabwe, DRC, Angola, Kenya, Nigeria, Botswana, Zambia.

Ceriagrion whellani *Longfield, 1952* (3)
Fairly localised species.
Distribution: Zimbabwe, Zambia, DRC, Lake Victoria, Sierra Leone.

Enallagma angolicum *Pinhey, 1966* (18)
Distribution: Zambia, Botswana, Angola.

Enallagma sinuatum *Ris, 1921*
Apparently rather scarce.
Distribution: DRC, Natal, Zimbabwe, Zambia, S Tanzania.

Enallagma subtile *Ris, 1921* (18)
Occurs on rivers and streams.
Distribution: South Africa, DRC, Tanzania, Kenya, Zimbabwe, N Nigeria.

Ischnuragrion nodosum *Pinhey, 1964* (5)
Known only from the Ikelenge area, Mwinilunga.

Ischnura senegalensis *(Rambur, 1842)* (9 18)
Widespread in most freshwater habitats and has a very high tolerance of ecological conditions.
Distribution: Throughout the African continent and Asia.

Pseudagrion acaciae *Förster, 1906* (8,18)
Distribution: Widespread in Africa.

Pseudagrion assegaii *Pinhey, 1950* (18)
Very local species.
Distribution: Transvaal, Botswana, Zimbabwe, Zambia, S DRC.

Pseudagrion chongwe *Pinhey, 1961*
Distribution: Angola, N Zambia.

Pseudagrion coelestis *Longfield, 1945* (18)
Fairly localised species.
Distribution: Angola, Botswana, Zimbabwe, Zambia.

Pseudagrion commoniae *Förster, 1902* (18)
Distribution: Zimbabwe, N Botswana, Mozambique northwards to Kenya.

Pseudagrion deningi *Pinhey, 1961* (18)
Distribution: Bangweulu & Okavango Swamps.

Pseudagrion fisheri *Pinhey, 1961* (18)
Distribution: Angola, Zambia.

Pseudagrion gamblesi *Pinhey, 1978* (19)
Large species found at fast flowing waters, often near cascades or rapids where the streams or rivers are open, with grasses and sedges on the banks.
Distribution: Natal, Transvaal, Zimbabwe, Mozambique, Zambia, Kenya.

Pseudagrion glaucescens *Selys, 1876* (18)
Favours streams and rivers rather than pools.
Distribution: Mozambique, Zambia, Botswana, Zimbabwe, Kenya.

Pseudagrion greeni *Pinhey, 1961*
Distribution: Zambia.

Pseudagrion hageni *Karsch, 1893* (18)
Distribution: Nearly all tropical and subtropical Africa.

Pseudagrion hamoni *Fraser, 1955* (8)
Prefers rivers or streams with adequate fringe vegetation and shade.
Distribution: Zimbabwe, Mozambique northwards to Kenya, DRC, Uganda, Nigeria, S Sudan.

Pseudagrion helenae *Balinsky, 1964* (1,18)
Distribution: Zambia, Botswana, Malawi.

Pseudagrion kersteni *(Gerstaecker, 1869)* (8)
One of the commonest Zygoptera. Frequents streams or pools but not swamps.
Distribution: Most of Afrotropics.

Pseudagrion kibalense *Longfield, 1959*
Distribution: Localised species; Uganda, DRC, Zambia.

Pseudagrion makabusiensis *Pinhey, 1950*
Found very locally on rushes or grasses in very sluggish parts of streams.
Distribution: Zambia, Zimbabwe.

Pseudagrion massaicum *Sjöstedt, 1909* (8,18)
Locally common over streams, pools or even broad rivers, flying strongly and low over the water; settling on leaves of water lily etc. Rather swift for a Coenagriid.
Distribution: Cape northwards to Kenya, Uganda, DRC, Angola.

Pseudagrion melanicterum *Selys, 1876*
Distribution: Zambia, DRC, Uganda, Cameroon, Nigeria, W Africa.

Pseudagrion nubicum *Selys, 1876* (18)
Locally common and gregarious in summer over stagnant pools.
Distribution: Zimbabwe to Sudan and W Africa.

Pseudagrion rufostigma *Longfield, 1945* (18)
Favours swamps rather than streams or rivers.
Distribution: Angola, Zambia, Botswana, Zimbabwe.

Pseudagrion salisburyense *Ris, 1921* (18)
Common and gregarious along grassy banks of streams and pools throughout the year.
Distribution: southern & eastern Africa.

Pseudagrion sjöstedti *Förster, 1906* (18)
Found along rivers and streams, sometimes over pools and swamps.
Distribution: subtropical & tropical Africa.

Pseudagrion spernatum *Selys, 1881*
Distribution: South Africa, Mozambique, Zimbabwe, Zambia.

Pseudagrion sublacteum *(Karsch, 1893)* (8,18)
Somewhat local species found flying over rather fast-flowing rivers or broad streams, not over still pools, and sometimes at edges of rapids. Has rather a strong flight for a Coenagriid.
Distribution: South Africa, Botswana, Zimbabwe, Mozambique, Kenya, Uganda, Nigeria.

Pseudagrion sudanicum *Le Roy, 1915* (18)
Distribution: Zimbabwe, Uganda, Botswana.

Pseudagrion williamsi *Pinhey, 1964* (7)
Distribution: Angola, N Zambia.

CHLOROCYPHIDAE

Chlorocypha frigida *Pinhey, 1961* (2)
A shy dragonfly, appearing in sunlit spots at forested streams and waterfalls.
Distribution: Upper Zambezi.

Chlorocypha luminosa *(Karsch, 1893)* (3)
Distribution: Widespread & common; Tanzania, Malawi, Zimbabwe, Mozambique, Zambia, Ghana, Nigeria.

Chlorocypha wittei *(Fraser, 1955)* (18)
Distribution: DRC, Angola, Zambia.

Platycypha caligata *(Selys, 1853)* (18)
Common on streams or rivers; not a swamp species.
Distribution: Tanzania, Somalia, DRC, Mozambique, Zambia, Zimbabwe, Namibia, Angola.

CALOPTERYGIDAE
Phaon iridipennis *(Burmeister, 1839)* (18)
Locally common on shaded streams and pools in forest or even clumps of bush.
Distribution: All tropical and subtropical Africa.

Umma distincta *Longfield, 1933* (11)
Distribution: DRC, Zambia, Angola.

ANISOPTERA

GOMPHIDAE
Cinitogomphus dundoensis *(Pinhey, 1961)* (18,9)
Found in swampy areas.
Distribution: Angola, Zambia, Botswana.

Crenigomphus cornutus *Pinhey 1956* (18)
Favours long grass near the margins of fast flowing rivers and streams.
Distribution: Upper Zambezi.

Crenigomphus hartmanni *(Förster, 1898)* (8)
Found over pools and streams, settling on low vegetation.
Distribution: From South Africa to Tanzania, DRC, Angola.

Diastatomma selysi *Schouteden, 1934*
Distribution: Upper Zambezi.

Gomphidia quarrei *(Schouteden, 1934)* (18)
Locally common near wooded fringe of rivers.
Distribution: DRC, Uganda, Angola, Botswana, Zimbabwe.

Ictinogomphus ferox *(Rambur, 1842)* (18)
Common, found on reedy pools or rivers.
Distribution: Natal to East, Central and tropical W Africa.

Lestinogomphus angustus *Martin, 1912* (18)
Favours the wooded fringes or fast flowing rivers.
Distribution: Kenya, Uganda, DRC, Zambia, Botswana, Zimbabwe.

Neurogomphus uelensis *(Schouteden, 1934)*

Neurogomphus wittei *Schouteden, 1934* (5)
Only found in grasslands at Katombora Rapids.

Notogomphus praetorius *(Selys, 1878)*
Found on banks of reedy streams, rivers and pools.
Distribution: South Africa, Zimbabwe, Zambia, Angola, DRC.

Onychogomphus kitchingmani *Pinhey, 1960*
Only known from Mwinilunga area.

Onychogomphus quirkii *Pinhey, 1964* (5)
Only known from Mwinilunga area.

Paragomphus cataractae *Pinhey, 1963*
Only known from Katombora.

Paragomphus cognatus *(Rambur, 1842)*
Common species in open, rocky streams.
Distribution: From Cape Province to Ethiopia, and from Kenya westwards to Nigeria.

Paragomphus elpidius *(Ris, 1921)* (18)
Found near river margins, sparingly in swamps.
Distribution: Natal, along Zambezi River, Malawi, DRC, Kenya, Uganda.

Paragomphus genei *(Selys, 1841)* (18)
Found near rivers, streams and pools. Commonest and most widespread of the African Gomphidae.
Distribution: From South Africa to S Europe.

Paragomphus nyassicus *Kimmins, 1955*
Distribution: Malawi, Zimbabwe.

Paragomphus sabicus *Pinhey, 1950* (18)
Found on well flowing rivers and streams.
Distribution: Sabi Valley to Zambia, Mozambique.

Paragomphus zambeziensis *Pinhey, 1960*
Only known from Upper and Middle Zambezi.

Phyllogomphus brunneus *Pinhey, 1976* (18)
Only known from Upper Zambezi.

AESHNIDAE

Acanthagyma sextans *(McLachlan, 1895)* (3)
Distribution: West Africa, Angola, Zambia.

Aeshna wittei *Fraser, 1955* (23)
Distribution: DRC, Zambia.

Anax bangweuluensis *Kimmins, 1955* (18)
Distribution: Zambia, Botswana.

Anax congoliath *Fraser, 1953* (3)
Distribution: DRC, Zambia.

Anax imperator *Leach, 1815* (18)
Distribution: recorded from nearly all of the Afrotropical Region, except at higher altitudes.

Anax mouri *Pinhey, 1981* (23)
Only known from Mwinilunga area.

Anax speratus *Hagen, 1867* (8,18)
Tends to favour rivers or streams more than pools.
Distribution: Most of continental Afrotropics.

Anax tristis *Hagen, 1867* (18)
Widespread and powerful flier, often seen over pools rather than rivers and streams.
Distribution: Zimbabwe to Kenya, Uganda, Namibia, Central & W Africa and neighbouring islands.

Gynacantha sevastopuloi *(Pinhey, 1961)* (2)
Distribution: Uganda, Malawi, Zambia.

Gynacantha vesiculata *Karsch, 1891*
Distribution: Afrotropics.

Gynacantha villosa *Gruenberg, 1902* (18)
Distribution: Mozambique, Malawi, Zambia, Botswana, Tanzania, Uganda, DRC, Nigeria.

Heliaeschna cynthiae *Fraser, 1939* (3)
Distribution: Angola, NW Zambia.

Heliaeschna trinervulata *Fraser, 1955*
Distribution: Angola, DRC, Upper Zambezi.

Hemianax ephippiger *(Burmeister, 1839)* (18)
Distribution: Common migrant found over nearly all of Africa and neighbouring islands.

CORDULIIDAE

Macromia bifasciata *(Martin, 1912)* (18)
Harks up and down in forest or thick bush, near streams or over rivers and lakes.
Distribution: W Africa, DRC, Zambia, Botswana, .Zimbabwe.

Macromia bispina *Fraser, 1954*
Distribution: Uganda, Upper Zambezi.

Macromia congolica *Fraser, 1955*
Distribution: DRC, Zimbabwe.

Macromia kimminsi *Fraser, 1954* (18)
Distribution: Kenya, Uganda, Botswana, Zambia.

Macromia overlaeti *Schouteden, 1934*
Distribution: DRC, Zambia.

Macromia paludosa *Pinhey, 1976* (18)
Only known from S Zambia and N Botswana.

Macromia picta *Selys, 1871* (8,18)
Common in bush country harking up and down, occasionally gregarious.
Distribution: South Africa, Zimbabwe, Malawi, Botswana, Zambia, Tanzania, Kenya, Uganda, DRC, Angola, Nigeria.

Macromia unifasciata *Fraser, 1954*
Distribution: DRC, Zambia.

LIBELLULIDAE
Acisoma panorpoides *Rambur, 1842* (18,25)
Found on quiet rivers or streams, pools or swamps.
Distribution: Africa and Oriental Regions.

Acisoma trifidum *Kirby, 1889*
Distribution: Kenya, Uganda, DRC, Zambia, Angola, Cameroon, W Africa.

Aethiothemis bequaerti *Ris, 1919*
Distribution: DRC, Zambia.

Aethiothemis diamangae *Longfield, 1959* (3)
Distribution: Angola, Zambia.

Aethiothemis discrepans *Lieftinck, 1969* (18)
Found in reedy or grassy pools.
Distribution: DRC, Zambia, Botswana, Malawi, Central Africa to Nigeria.

Aethiothemis mediofasciata *Ris, 1931*
Distribution: Angola, Zambia.

Aethriamanta rezia *Kirby, 1889* (18)
Settles on reeds or twigs over or near water. Not a common species.
Distribution: Mozambique, Botswana, Zambia, DRC, Tanzania, Kenya, Uganda, W Africa.

Allorhizucha klingi *Karsch, 1890*
Found in dense forest.
Distribution: DRC, Angola, Zambia, Cameroon, W Africa.

Allorhizucha longistipes *Pinhey, 1964* (5)
Only known from Mwinilunga area.

Allorhizucha preussi *Karsch, 1891*
Distribution: Uganda, DRC, Zambia, Cameroon.

Archaeophlebia victoriae *Pinhey, 1963*
Only known from Victoria Falls.

Atoconeura biordinata *Karsch, 1899*
Found in thick bush or forest fringing streams and rivers.
Distribution: Afrotropical region.

Brachythemis lacustris *(Kirby, 1889)* (8)
Locally gregarious in swampy conditions.
Distribution: In suitable swampy areas throughout tropical and subtropical Africa.

Brachythemis leucosticta *(Burmeister, 1839)* (18,8)
Found over cleared banks of any pool or even near a temporary puddle.
Distribution: Throughout most of the African Continent, S Europe and W Asia.

Brachythemis wilsoni *Pinhey, 1952* (18)
Distribution: Sudan, Nigeria, Uganda, Botswana.

Bradinopyga cornuta *Ris, 1911* (18,8)
Favours rocks near faster running streams or rivers.
Distribution: South Africa, Mozambique, Malawi, Zimbabwe, Tanzania, Kenya, Zambia.

Chalcostephia flavifrons *Kirby, 1889* (18)
Prefers reedy or grassy pools and swamps to rivers and streams.
Distribution: Most of Afrotropical region.

Crocothemis brevistigma *Pinhey, 1961* (2,3)
Only known from the Mwinilunga area.

Crocothemis divisa *Baumann, 1898*
Found over streams in forest or bush, with rocks on which to settle.
Distribution: Zimbabwe, Malawi, Zambia, Tanzania, Kenya, Uganda, DRC, Sudan, Cameroon, W. Africa.

Crocothemis erythraea *(Brullé, 1832)*
Very common throughout southern Africa.

Crocothemis sanguinolenta *(Burmeister, 1839)* (18,8)
Locally found on rocks in open country on rivers, streams, pools and swamps.
Distribution: Throughout continental Afrotropical region.

Crocothemis saxicolor *Ris, 1919* (2,3,8)
Local over or near rocky streams or pools.
Distribution: Zimbabwe, Zambia, Malawi.

Diplacodes deminuta *Lieftinck, 1969*
Localised species of shallow marshes.

Diplacodes lefebvrei *(Rambur, 1842)* (18,8)
Abundant at quieter waterways, pools, swamps, or margins of rivers.
Distribution: Over all continental Africa.

Diplacodes okavangoensis *Pinhey, 1976* (18)
Swamp species found from the Okavango Delta to W Zambia.

Eleuthemis buettikoferi *Ris, 1910*
Distribution: Zambia, Tanzania, Uganda, W Africa.

Enallagma glaucum *(Burmeister, 1839)*
Very common species at ponds throughout southern Africa.

Hadrothemis camerensis *(Kirby, 1889)*
Distribution: DRC, Uganda, Cameroon, W Africa, Angola, Zambia.

Hadrothemis defecta *(Karsch, 1891)*
Distribution: DRC, Cameroon, Angola, W Africa, Mozambique, Zambia, Zimbabwe.

Hadrothemis scabrifrons *Ris, 1909*
Distribution: Tanzania, Kenya, DRC, Cameroon, Zambia.

Hadrothemis versuta *(Karsch, 1891)*
Distribution: W Africa, DRC, Zambia.

Hemistigma albipuncta *(Rambur, 1842)* (18)
Common and widespread in open swamp, reedy pools in bush, woodland or forest.
Distribution: Over most of continental Afrotropics.

Monardithemis flava *Longfield, 1945*
Distribution: Angola, Zambia.

Nesciothemis farinosum *(Förster, 1898)* (18)
Common species favouring open country, grassland or swamps, in bush or woodland.
Distribution: Over all continental Afrotropics.

Nesciothemis fitzgeraldi *Longfield, 1955*
Distribution: Zambia.

Notiothemis robertsi *Fraser, 1944*
Distribution: Uganda, Nigeria, Cameroon, DRC, Zimbabwe, Zambia.

Olpogastra fuelleborni *Gruenberg, 1902* (18)
Species settles on bushes overhanging the river.
Distribution: South Africa, Zimbabwe, Malawi, Tanzania, Kenya, Sudan, DRC, Angola, Nigeria.

Olpogastra lugubris *Karsch, 1895* (18,8)
Found at reed fringed rivers, streams or large reedy pools.
Distribution: Namibia, Zimbabwe, Botswana, Zambia, Malawi, Tanzania, DRC, Mozambique, Kenya, Uganda, Sudan, W Africa.

Orthetrum abbotti *Calvert, 1892*
Distribution: Most of the Afrotropical region.

Orthetrum angustiventre *(Rambur, 1842)* (3)
Distribution: Angola, W Zambia, N Uganda, S Sudan, N Nigeria, W Africa.

Orthetrum austeni *(Kirby, 1900)*
Distribution: Zambia, DRC, Cameroon, W Africa.

Orthetrum brachiale *(Beauvios, 1805)* (18,8)
Common in bush country, sometimes in forest.
Distribution: Throughout continental Africa.

Orthetrum chrysostigma *(Burmeister, 1839)* (18)
Found in streams, rivers, pools in open country. Highly tolerant of temperature gradients and possibly also pH values.
Distribution: Throughout most of continental Africa; also neighbouring Asia and Europe.

Orthetrum guineese *Ris, 1909*
Found over streams in bush or forest.
Distribution: Natal to Tanzania and Somalia, Angola, Zambia, Nigeria, W Africa.

Orthetrum hintzi *Schmidt, 1951*
Found over streams and pools in bush or forest.
Distribution: Natal to Kenya, Angola, Zambia northwards to Nigeria and W Africa.

Orthetrum icteromelas *Ris, 1909* (18)
Found over warmer streams and pools in bush country.
Distribution: Natal, Mozambique, Tanzania, Angola, Botswana, Zambia, Cameroon, Sudan.

Orthetrum julia *Kirby, 1900*
Distribution: South Africa to Ethiopia, Angola, Zambia, Mozambique, DRC, Nigeria, W Africa.

Orthetrum machadoi *Longfield, 1945* (18)
Common in swamps.
Distribution: Most parts of the Afrotropics.

Orthetrum macrostigma *Longfield, 1945*
Distribution: Angola, Zambia, Tanzania, DRC.

Orthetrum microstigma *Ris, 1911*
Distribution: Angola, Zambia, Cameroon, Uganda, Kenya, W Africa.

Orthetrum monardi *Schmidt, 1951*
Distribution: Zambia, DRC, Kenya, Nigeria, Cameroon.

Orthetrum robustum *Balinsky, 1965* (18)
Favours woodland.
Distribution: Botswana, Zambia.

Orthetrum saegeri *Pinhey, 1966*
Distribution: DRC, Uganda, Cameroon, Zambia.

Orthetrum stemmale stemmale *(Burmeister, 1839)*
Thick bush or forest in warmer areas.
Distribution: Mozambique and Transvaal to equatorial E and W Africa, also Madagascar and Mauritius.

Orthetrum trinacrium *(Selys, 1841)* (18)
Prefers rivers, streams and pools in rather open country.
Distribution: Natal to North Africa, mainly in the E half.

Palpopleura jucunda *Rambur, 1842* (18)
Locally common at grassy pools and swamps.
Distribution: Most of continental Afrotropics.

Palpopleura lucia *(Drury, 1773)* (18,8)
Inhabits pools, swamps and the calmer stretches of streams and rivers.
Distribution: Locally abundant over most of continental Afrotropics.

Pantala flavescens *(Fabricius, 1798)* (18)
Distribution: Throughout Africa and neighbouring islands, Europe, Asia, Australia, Americas.

Parazyxomma flavicans *(Martin, 1908)* (18)
A shy species, only found in the shade of trees.
Distribution: Zimbabwe, Botswana, Malawi, DRC, Uganda.

Philonomon luminans *(Karsch, 1893)*
Prefers reedy pools in warm open country, not common in the central swamps.
Distribution: Natal northwards to Somalia, central and W Africa.

Porpacithemis dubia *Fraser, 1954*
Distribution: DRC, Zambia.

Porpax asperipes *Karsch, 1896*
Distribution: DRC, Angola, Zambia, Cameroon, W Africa.

Porpax risi *Pinhey, 1958* (7)
Very local species found in swamps.
Distribution: Zimbabwe, Mozambique, Zambia, Angola.

Rhyothemis fenstrina *(Rambur, 1842)* (18)
Occurs in great numbers, fluttering on the verge of forests, thick bush or woodland, near swamps.
Distribution: Botswana, northwards to Uganda and west equatorial Africa.

Rhyothemis mariposa *Ris, 1913* (18)
Distribution: Namibia, Zambia, Angola, DRC.

Rhyothemis notata *(Fabricius, 1781)*
Distribution: Botswana, Zambia, DRC, W Africa.

Rhyothemis semihyalina *(Désjardins, 1832)* (18)
Found at reed fringed rivers and streams, grassy or reedy pools and swamps.
Distribution: Continental Africa.

Sympetrum fonscolombei *(Selys, 1837)* (18)
Found in many of the more open, often arid regions.
Distribution: Scattered localities throughout continental Africa.

Sympetrum navasi *Lacroix, 1921* (18)
Common on swampy verges.
Distribution: Uganda, Zambia, Botswana, W Africa.

Tetrathemis polleni *(Selys, 1869)* (8)
Local species on quiet well shaded pools or sluggish streams under shade, at low elevations.
Distribution: Natal to Kenya, DRC, Uganda, Nigeria.

Thermochoria equivocata *Kirby, 1889*
Distribution: Uganda, Zambia, DRC, Cameroon, W Africa.

Tholymis tillarga *(Fabricius, 1798)* (18)
Distribution: Throughout Afrotropics; Asia and Australia.

Tramea basilaris *(Beauvois, 1817)* (= *Trapezostigma basiliare*) (18)
Found flying swiftly over small or large bodies of water in open country or forest clearings.
Distribution: Most of Afrotropics and Asia.

Tramea burmeisteri *Kirby, 1889* (= *Trapezostigma burmeisteri*)
Very common, widespread species.

Trithemis aconita *Lieftinck, 1969* (18)
Found in thick bush fringing rivers and streams.
Distribution: Natal to Kenya coast, Zambezi valley to Mwinilunga, Malawi, DRC, W Africa.

Trithemis aequalis *Lieftinck, 1969* (18)
Settles on reeds or sedges in streams or on low vegetation away from the banks.
Distribution: Zambia, Okavango.

Trithemis annulata *(Beauvois, 1805)* (18,8)
Found on or near rivers, streams and pools; settling frequently on reeds, grasses or rocks.
Distribution: Widely distributed in Africa and Asia.

Trithemis arteriosa *(Burmeister, 1839)* (18,8)
Found over or near most freshwater sources, whether stagnant or fast flowing, throughout the year. Not a swamp species, being found only on the fringes.
Distribution: Widely distributed; the most abundant anisopteran in Africa.

Trithemis anomala *Pinhey, 1956*
Found in open swamps, reedy pools.
Distribution: Only known from NW Zambia.

Trithemis bifida *Pinhey, 1970*
Found in thick gallery forest.
Distribution: Mwinilunga area, Zambia.

Trithemis dichroa *Karsch, 1893*
Small species found in forest or thick bush, quite streams and pools.
Distribution: W Africa, Cameroon, Uganda, DRC, Zambia.

Trithemis donaldsoni *(Calvert, 1899)*
Local, not usually abundant. Generally in bush country, on rivers and streams; sometimes in rather arid places.
Distribution: Natal, Zimbabwe, Malawi, Mozambique northwards to Kenya, Somalia, Ethiopia, DRC, Uganda, Nigeria.

Trithemis dorsalis *(Rambur, 1842)*
On streams and pools in open country.
Distribution: South Africa, Mozambique, Kenya, Zimbabwe, Angola, Zambia, DRC.

Trithemis furva *Karsch, 1899*
On streams, rivers or reed-fringed pools, in the open or even in forest. Often very abundant.
Distribution: Probably throughout continental Africa.

Trithemis hecate *Ris, 1912* (18)
This species prefers reedy pools and swamps or quietly flowing streams. Settles on reeds, sedges and grasses growing in the water.
Distribution: South Africa, Botswana, Zimbabwe, Mozambique, Zambia, Tanzania, DRC, Uganda, Cameroon, Chad, Mali.

Trithemis kirbyi *Selys, 1881* (18,8)
Usually settles on rocks or stones in the bed of fast or slow flowing stream and rivers in open country.
Distribution: South Africa, Namibia, Botswana northwards to equatorial Africa, Sudan, Ethiopia, India, Pakistan.

Trithemis monardi *Ris, 1919* (18)
Found on reedy pools or swamps, or sluggish reed fringed rivers.
Distribution: Angola, Zambia, Malawi, Mozambique, Zimbabwe, Botswana, Namibia.

Trithemis nuptialis *Karsch, 1894*
Normally a species of heavy forests, breeding in slow forest streams.
Distribution: Zambia, Angola, DRC, Uganda, W Africa.

Trithemis pluvialis *Förster, 1906*
Locally common species which settles on vegetation near or over running or slow-flowing streams.
Distribution: South Africa to Angola, DRC, E Africa.

Trithemis pruinata *Karsch, 1898*
Very local species which tends to fly in thick bush or forest near small streams.
Distribution: Central and Equatorial West Africa.

Trithemis stictica *Burmeister, 1839* (18)
Locally common in swamps, pools or streams in bush or open country or open forest areas.
Distribution: South Africa, Botswana northwards to Ethiopia and W Africa.

Trithemis werneri *Ris, 1912* (8)
Inhabits river valleys or low-lying plains. Generally settles on bare twigs of low bushes or other low plants near the river up to about 200 m from the river.
Distribution: Eastern half of Africa from Limpopo to Zambezi valley to S Malawi, rivers in lowlands of Kenya and Uganda.

Urothemis assignata *(Selys, 1872)* (18)
Common at reedy pools or streams.
Distribution: Natal, Mozambique, Zimbabwe, Zambia, Malawi north to Ethiopia.

Urothemis edwardsi *(Selys, 1849)* (18)
Prefers rivers or broad stream to pools.
Distribution: Natal, Mozambique, Zimbabwe, Botswana, Zambia northwards to Sudan.

Zygonyx atritibiae *Pinhey, 1964* (5)
Distribution: Zambia, DRC, Angola.

Zygonyx eusebia *(Ris, 1912)* (5)
One of the largest libellulids in the world.
Distribution: DRC, Angola, Zambia.

Zygonyx flavicosta *(Sjöstedt, 1899)* (5)
Distribution: DRC, Uganda, Angola, Zambia, W Africa.

Zygonyx natalensis *(Martin, 1900)* (18,5)
Usually very common at waterfalls and rapids.
Distribution: South Africa, Zimbabwe, Mozambique, Angola, DRC, Tanzania, Kenya, Uganda, W Africa.

Zygonyx torridus *(Kirby, 1889)* (18)
Distribution: Over most of continental Africa.

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CHAPTER 9 : APPENDIX 1
LIST OF ODONATA COLLECTED FROM BAROTSELAND

Odonata specimens were collected from the Barotseland area by Rafael Chiwanda and Philip Mhlanga from 20 March to 4 April 1999. Localities collected were:

Ndau School transect:	15°25'41"S / 22°57'49"E
Ndau School area:	15°25'S / 22°58'E
Sefula:	15°23'11"S / 23°10'07"E
Mongu:	15°17'46"S / 23°08'36"E
Kalabo:	14°58'10"S / 22°38'27"E
Kalabo, 5 km west:	14°54'58"S / 22°34'02"E

List of Species Collected (nomenclature follows Pinhey).

ZYGOPTERA
Coenagrionidae
Agriocnemis exilis
Agriocnemis sp.nr. exilis
Agriocnemis sp.nr. falcifera
Agriocnemis victoria
Ceriagrion cf. glabrum
Ceriagrion whellani
Enallagma glaucum
Pseudagrion coelestis
Pseudagrion cf. coelestis (female)
Pseudagrion sp. (female)

ANISOPTERA
Gomphidae
Crenigomphus sp.
Ictinogomphus ferox

Cordullidae
Macromia bifasciata
Macromia picta
Macromia sp. (female)

Libellulidae
Acisoma panorpoides
Acisoma sp.
Aethriamanta rezia
Brachythemis leucostricta
Crocothemis erythraea
Crocothemis sp.?
Diplacodes deminuta
Diplacodes lefebvrii
Hemistigma albipuncta
Olpogastra lububris
Orthetrum brachiale
Orthetrum cf. brachiale
Orthetrum chrysostigma
Orthetrum icteromelas cinctifrons
Orthetrum trinacrium
Palpopleura lucia
Rhyothemis semihyalina
Tholymis tillarga
Tramea burmeisteri
Trithemis annulata
Trithemis hecate
Trithemis kirbyi
Trithemis sp.
Urothemis edwardsi

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CHAPTER 9 : APPENDIX 2
ODONATA SURVEY OF THE ZAMBEZI DELTA

Richard Kinvig

1. INTRODUCTION

The single most important cause of insect extinctions is the destruction of natural biotopes (Pyle *et al.* 1981). Wetlands world-wide are under the continuous threat of human disturbance. These disturbances include increased expansion of human populations, an increase in agriculture and the dumping of waste into waterways. In the past only a small amount of research has been done on the habitat preferences of African Odonata, yet it is known that several are under threat due to wetland disruption (Samways 1992).

Odonata, both adults and larvae, are valuable indicators of water quality and landscape disturbance (Watson *et al*. 1982, Castella 1987). They are good indicators due to their total reliance on water for their lifecycle and if the water quality is poor then the species will not proliferate. The water need not necessarily be polluted, but may have to higher silt load and therefore exclude the Odonata larvae. They are also an important and widespread component of freshwater ecosystems, being top predators (Corbet 1962). Many male Odonata are closely associated with particular biotopes (Steytler & Samways 1994). This may lead to exclusions, and therefore a range of biotopes are needed to suit the individual males and this is provided by large tracts of wetland.

Elliot Pinhey and some technicians from Bulawayo did the only work that has been carried out in this area in the early 1960s. Most of the expeditions into Mozambique were in the south, mainly to Maputo (Pinhey 1981). It was therefore important for us to get a collection of species for the area and then compare these to the previous collections done by Pinhey from 1947 to 1971 in the same area.

The study undertaken was to get information on the status and species list of the Marromeu complex, a wetland complex in the lower Zambezi Delta. The chosen sites are described with a brief history and description, for each of the species collected, and their distributions across Africa will be documented as well as their status.

2. SAMPLING SITES

The Odonata were collected using a sweep net and walking through the vegetation. The sampling was not done along transects. All species were captured in a random sampling of the sites.

2.1 Site A: Safrique 7/8 June 1999. 18^{0}26'52" S / 35^{0}53'46" E

Sampling took place in semi-cultivated lands, a short walk from the village of Safrique. The principle subsistence crop was rice and dominated the cultivated lands. The land was dry for the area and therefore the plants were small and shrivelled. In addition, but to a lesser extent was sorghum. In the grasslands adjoining the cultivated fields, the vegetation was made up mainly of *Vigna* spp., banana plants and Ilala palms (*Hyphaene coriacea*). The Ilala palms and the banana plants provided areas for the Odonata to shelter in. Where the *Pennisetum polystachion* grew to about 1.8 m high it provided shelter and retained moisture. The grass and Banana plants provided shelter for the predominantly more fragile species like *Ceriagrion glabrum* and other Zygoptera.

The larger Anisoptera could be found hawking over the open grass, examples of these being *Anax imperator* and *Crocothemis erythraea*. This area was sampled on two consecutive days and would fall into the class of "dry wet grasslands". The soil was a dry black loam that was very difficult to penetrate when so dry. Dry man- made channels traversed the cultivated lands.

2.2 Site B: Vila Nova 9/10 June 1999. 18^{0}23'42" S / 35^{0}54'27" E

Vila Nova is a small settlement 10 km from the town of Marromeu. It was sampled on two consecutive days. The area was wet with a small hand-dug canal approximately 3 m wide. On the one side of this canal was a settlement containing about 10 houses with the people dwelling in these houses, growing subsistence crops.

The crops comprised of rice, sugarcane, bananas, pineapples, coconuts and a very small amount of maize. In the Marromeu complex, crops and dwellings bound all water bodies. This therefore does not provide a true reflection of natural habitat for the Odonata, but they seemed to thrive in these environments. There was a small proportion of natural vegetation comprising *Pennisetum polystachion* and tall papyrus. It was difficult to sample "dry wet grassland", but in the end this area was deemed suitable. The main Odonata seen were *Orthetrum trinacria*, *Crocothemis erythraea* and *Trithemis arteriosa*. Again, *Ceriagrion glabrum* was prevalent for the damselflies. The species *Agriocnemis* sp. nr. *pinheyi* was found at this site for the first time. It was found around a well-sheltered clump of sugarcane.

2.3 **Site C: River bank along the Zambezi** 3 km range from Marromeu factory to Chinde
11 June 1999

The vegetation was typical of the habitat: *Eichhornia* spp., *Salvinia* spp. and *Ipomea* spp. Away from the waters edge at the high water mark there were stands of moribund grass. In and around the areas of human habitation and cultivation there were many species of weed including *Tagetes minuta*, *Senecio* spp., *Ageratum houstonianum* and *Bidens pilosa.* The sampling on this day was done from a canoe. It was done between 9:00 and 13:30. The areas sampled were specifically near the riverbanks, as no species seemed to be found over open water except for *Pseudagrion acaciae*. This is not very usual for species of damselflies as they are usually confined to areas that are well vegetated, and where the water is not flowing very strongly. *Trithemis annulata* was found integrating with *Crocothemis erythraea* and the two species of *Orthetrum* (*chrysostigma* and *trinacria*). This species of *Trithemis* seemed to be quite aggressive towards all other species of dragonfly. *Brachythemis leucosticta* was found in large numbers in and around a mud flat where they spent their time proportionately between hawking and sunning themselves. The *Pseudagrion spp.*, *Ceriagrion spp.* and the single *Enallagma spp.* were found predominantly over the *Salvinia spp.* in the areas of backwater.

2.4 **Site D: River bank, 4 and 6 km south of Marromeu** 18^{0}18'18" S / 35^{0}59'58" E
12 June 1999. 18^{0}19'51" S / 36^{0}01'25" E

In both the 4 and 6 km sites there was no human habitation with the habitat being natural with open sand spits and areas covered with tall reeds and grass. In these two sites, the most commonly seen dragonfly was *Crocothemis erythraea* that could be seen hawking close to the vegetated areas of the spits. The dragonflies found were all fairly common to this type of habitat, except for one species that was recorded only once and was captured hawking over the grass on the island (*Neurogomphus uelensis*). No *Pseudagrion acaciae* were found and this may therefore infer that this species of damselfly has a relationship with *Salvinia spp*. as it was only near to it and on the adjacent open water.

2.5 **Site E: Bambani Area** 13 June 1999. 18^{0}18'09" S / 35^{0}53'21" E

This site can be described as "dry wet grassland". Small channels traversed the short grass, which made up this site. There were no species of special interest to be found here and the species that we did find could be called common to all areas studied.

2.6 **Site F: Palm grove, north of Marromeu** 14 June 1999. 18^{0}13'05" S / 35^{0}46'21" E

The palm-grove that we went to was completely disturbed by humans. Many of the palms had been cut done for use as canoes. The ground below the palms had been cleared, sorghum, and sugarcane planted in the place of the natural vegetation. There was also human habitation of the area and all the problems that go along with people, for example paths, large areas cleared around the houses and livestock. It was interesting to note, however, that the smallest damselfly in Africa (*Agriocnemis exilis*) could be found in the moribund areas of the sorghum and the sugarcane. The behaviour of the *Anax imperator* was as in Site A where it was hawking along the man-made paths.

2.7 **Site G - Palm savanna, south of Marromeu** 15/16 June 1999. 18^{0}28'08" S / 35^{0}53'43" E

Site Gilboa was situated 4 km south of Safrique and was sampled on two consecutive days as it was easily accessible and was the least disturbed site. Both coconut and ilala palms were in abundance and the grass growth was moribund. There were no channels or man-made canals and hence the site was very dry. This could explain the lack of Odonata as only one individual was found in the entire sampling period. The entire sampling period was six hours. This was broken into three and a half hours on the first day and two and a half on the second day.

3. SPECIES AND THEIR STATUS

The species found in the Marromeu area and their distribution across sampling sites are shown in Appendix 9.2 Table. 1. Each species is described below.

Agriocnemis exilis – Found throughout Mozambique. They are gregarious at reedy pools, swamps, sluggish streams. They make very brief flights and are fairly inconspicuous. Distribution: South to equatorial Africa, Madagascar, Mauritius and Réunion.

Agriocnemis sp. nr. *pinheyi* – This species has never been described before and therefore distribution and status are unknown.

Ceriagrion glabrum – This species has been found extensively throughout Mozambique and the rest of the Afrotropical region of Africa. Its status is common and was collected by Pinhey 50 km west of Marromeu.

Ceriagrion kordofanicum – The only records of this species previously recorded in Mozambique were by Moura, who found them at Vila Fontes in 1947. They were not previously seen in the Marromeu area. This species will only be found at low altitudes and on streams that have surface vegetation. They are found in Malawi, Kenya, Uganda and Sudan.

Enallagma spp. – The individual found was a female and further identification is impossible.

Ischnura senegalensis – The most common and abundant zygopteran. This species will be found all over continental Africa the islands and Asia. It will not be found in densely vegetated areas and is highly tolerant of saline waters. The absence of this otherwise common species, in the Marromeu complex is interesting since it is usually habitat non-specific. This lack of huge numbers could be due to seasonality. It must however be remembered that this is only an inferred reason and I have no proof.

Pseudagrion acaciae – This species is found on open water rivers with fast flowing currents and is seldom seen on small streams. It is found from Natal to Kenya, Zaire and Angola. It was recorded in Dondo and Chimoio by Pinhey in 1947. From the information available to me it does not look like it was recorded previously at Marromeu.

Pseudagrion coelestis – This species has only been found in Angola and Zimbabwe. There is no record of it having been recorded in the whole of Mozambique. There is also no description of its habitat, but when found it was close to the backwaters of the Zambezi that had surface vegetation. There is no record of its status, and it was uncommon in the study area.

Pseudagrion hamoni – Found in Mozambique, but not in the area that was studied by me. It prefers shady areas with lots of surface vegetation. In Mozambique, it has been found at Cabora Bassa dam. It is found from Zimbabwe to Kenya, Sudan and equatorial West Africa.

Pseudagrion helenae – This species has only been found in Northern Rhodesia (Bechuanaland). It was found under the same conditions as the above species. There is no mention of its status, but was uncommon in the study area.

Acisoma panorpoides – This is a common dragonfly that has been found all over Afrotropical Africa as well as Madagascar. It prefers quiet streams and stagnant pools with a surface vegetation of the type *Nymphaea*.

Anax imperator – This is a migratory species of dragonfly that is found throughout Africa, Europe and western Asia. It has a typical large dragonfly behaviour of hawking up and down slow moving rivers and open tracts of land.

Appendix 9.2, Table 1 Odonata species found in the Marromeu area, June 1999.

Family/Species	Site						
	A	B	C	D	E	F	G
ZYGOPTERA							
Coenagrionidae							
Ceriagrion glabrum (Burmeister, 1839)	X	X	X	X	X		
Ceriagrion kordofanicum (Ris, 1924)			X				
Pseudagrion acaciae (Förster, 1906)			X				
Pseudagrion coelestis (Longfield, 1947)			X				
Pseudagrion hamoni (Fraser, 1955)			X				
Pseudagrion helenae (Balinsky, 1964)			X				
Ischnura senegalensis (Rambur, 1842)			X	X			
Enallagma sp. (female)			X				
Agriocnemis exilis (Sélys, 1872)						X	
Agriocnemis sp. nr. pinheyi		X	X				
ANISOPTERA							
Gomphidae							
Neurogomphus uelensis (Schouteden, 1934)				X			
Aeshnidae							
Anax imperator (Leach, 1815)	X					X	
Libellulidae							
Orthetrum chrysostigma (Burmeister, 1839)			X		X		
Orthetrum trinacria (Sélys, 1841)		X	X				
Palpopleura lucia (Drury, 1773)	X	X			X		
Hemistigma albipuncta (Rambur, 1842)	X				X		
Acisoma panorpoides (Rambur, 1842)		X		X	X		
Diplacodes lefebvrii (Rambur, 1842)	X	X	X				
Crocothemis erythraea (Brullé, 1832)	X	X	X	X	X		
Brachythemis lacustris (Kirby, 1889)				X			
Brachythemis leucosticta (Burmeister, 1839)			X				
Trithemis annulata (Beauvois, 1807)			X				
Trithemis arteriosa (Burmeister, 1839)		X					
Urothemis assignata (Sélys, 1872)			X				
Urothemis edwardsii (Sélys, 1849)		X	X				X

Brachythemis lacustris – This species is gregarious at pools and rain puddles. Sometimes several individuals of the same sex are noted to sit on the same perch. This was noted when in the study area. They prefer open bush country from Mozambique to Ethiopia and West tropical Africa.

Brachythemis leucosticta – Recorded throughout Mozambique and Zimbabwe. It is scarcely disturbed by human intruders and this was noticed as sometimes one would stand on them while they were resting. They are found in most parts of Africa, southern Europe, Madagascar and western Asia.

Crocothemis erythraea – Very common dragonfly found in open country near streams, rivers and open expanses of water. It is found throughout Mozambique and Africa as well as Asia and Europe. It did not display any unusual behaviour or habitat preferences while observed.

Diplacodes lefebvrii – This species is common on pools or quiet margins of rivers, hence the reduction in numbers on the Zambezi itself, in open grasslands, in sparse or thick bush and even thin broad-leafed woodland. Nearly all of Africa and neighbouring islands as well as southern Europe and western Asia.

Hemistigma albipuncta – This is an abundant dragonfly. It often aggregates around open swamp, reedy or stagnant pools and is even common in forest. It may be dominant in the forests of Mozambique. It is found in most parts of Afrotropical Africa at lower elevations, except in Cape Province.

Neurogomphus uelensis – This species was first recorded in the Belgian Congo. This is all the information that can be found on it. I would therefore infer that it is a new species to Mozambique. It was found hawking over short grass near the Zambezi River.

Orthetrum chrysostigma – Found throughout central and northern Mozambique. It prefers open areas and does not venture into forest. It is highly tolerant of temperature gradients and pH gradients. It occurs in most parts of Africa and has a separate subspecies in Sierra Leone.

Orthetrum trinacria – Found to frequent still waters and mud pools. Found throughout Africa from Natal to Palaearctic North Africa. This individual species tends to fly low and for longer periods than other members of the genus. This behaviour was not noticed.

Palpopleura lucia – Found extensively in Mozambique. There are two forms and they may be found together, this not being the case in our study site. They prefer areas of swamp, reeds, grasses and twigs as these are used as perches. They are found in open country or bush and not forest. Where these individuals were caught supports this description, as does the resting on reeds, twigs and grasses. Found extensively throughout Africa.

Trithemis annulata – Found throughout Mozambique. As with the above species they were recorded by Pinhey at Marromeu. They are common in open bush, semi-arid zones, on rivers, streams, pools and swamps. All the areas mentioned by Pinhey were supported by my findings. They can be found throughout Africa, southern Europe and western Asia.

Trithemis arteriosa – This species is common to the majority of water bodies in Africa. It can usually be found all year round. They are highly tolerant of pH and temperature gradients. Most parts of Africa and western Asia.

Urothemis assignata – This species was last recorded by Pinhey at Marromeu in 1967, and has been recorded throughout Mozambique. It has a preference for reedy pools, lakes and sometimes swamps. It will always settle on the same perch even if chased away and this behaviour was noted. It sometimes hovers, but flies low. Natal to Ethiopia and equatorial Africa; also Madagascar.

Urothemis edwardsii – This is very similar to the above species but prefers more open expanses of water. Settles on high perches and is not readily driven away. Found 50 km west of Marromeu by Pinhey. Ranges from Natal to the Sudan, Angola and equatorial Africa and also Algeria.

4. DISCUSSION

There are only seven matching species in the review checklist and the1999 survey. This may be ascribed to the fact that the checklist is from past records and was probably formulated from previous work done by Pinhey and the technicians from Bulawayo as well as Moura and the Ferreiras.

The more fragile species found in the 1999 study may be remnants from the summer and hence their low numbers and poor appearance (in terms of wing wear). The more fragile species include certain of the *Pseudagrion* and the *Agriocnemis* genus as well as the *Enallagma* genus. The one female *Enallagma* collected may be a remnant female which survived from the summer. The environment and the climate of this area do not vary much and can be described as semi-tropical. This allows for a higher survival rate of individuals throughout the year.

It must be said that the Odonata in general seem to have adapted well to changes brought about by man. In certain cases these anthropogenic influences may have helped the Odonata to increase their range as more micro-habitats have been created as a result. For example, the development of canals may provide corridors for the Odonata adults and larvae to move along as they are filled by natural streams and rivers. Both robust and fragile species co-exist and the numbers of certain species are extremely high. I would also postulate that at any time in the year there would be large numbers of Odonata, this being related to climate suitability and food availability.

In conclusion, the Odonata assemblage appears to be well represented and thriving, judging by the diversity of Odonata collected.

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CHAPTER 10
REVIEW OF WETLAND LEPIDOPTERA OF THE ZAMBEZI BASIN

Alan Gardiner

10.1 INTRODUCTION

The Lepidoptera is one of the largest insect orders with more than 150,000 species worldwide, of which more than 12,000 are thought to exist in Africa. The bright and attractive wings make them a familiar group to the general public. Adult Lepidoptera are readily distinguished from other insects by the presence of scales, often brightly coloured, on the wings, head and body. In all Lepidoptera, apart from a few of the more specialized families, there is a spur-like structure (an epiphysis) on the fore tibia, a structure that does not occur in other insects. Together with the way in which the mouthparts are modified to form a coiled, sucking tube (proboscis), this is characteristic of the group (Henning 1985).

The attractiveness of butterflies and larger moths has given them considerable appeal amongst amateurs. Because of collecting and research by these amateurs and a few professional entomologists, butterflies are now perhaps the best known invertebrate group in terms of both taxonomy and distribution. This, in addition to other biological traits, makes them an important group for biodiversity studies. These traits are:

(a) the group is sensitive to changes in the environment,
(b) large numbers may be present, so that time spent in the field quickly yields a substantial data set,
(c) families that are relatively easy to identify can be selected, and for some regions detailed taxonomic information is available,
(d) they can be collected in a quantitative manner.

There are many Lepidoptera of economic and social importance. They have an obvious agricultural importance, both as pests and pollinators, but some species are also valued as food. For example, the larva of a Saturnid moth, the mopane worm (*Imbrasia belina*), is collected and dried for human consumption and is a common part of the human diet from the northern half of South Africa through to central Zambia. Another emperor moth larva eaten throughout the Zambezi basin is *Cirina forda*. Around Victoria Falls, the branches of one of its larval food plants, *Burkea africana*, are broken in order to collect the caterpillars. The importance of lepidopteran larvae as food has often been written about, for example Chavanduka (1975) illustrated the importance of insects as a source of protein, Defoliart (1995) reviewed "edible insects as mini-livestock", and Roberts (1998) states "There is little doubt that the emperor moth *Gonimbrasia* [*Imbrasia*] *belina* is one of the major economically important insects in Southern Africa". In some parts of its range the cost of this insect per kilogram is more than the price of dried meat.

This chapter firstly reviews existing information on the Zambezi Basin (Section 10.3), covering the major works on Lepidoptera and collections from the area. Taxonomy and taxonomic works are not covered. In the next section (10.4), the Zambezi River itself is divided into six faunal sections. Species recorded from each section and any noticeable and obvious features of the fauna are given.

Thirdly, in Section 10.5, the wetland species occurring along the Zambezi are discussed. For each species, information on its diagnosis, habitat, habits, conservation status and distribution is given. Finally, in Section 10.6 the faunal regions are discussed from a biogeographical viewpoint.

10.2 HIGHER CLASSIFICATION

Butterflies were regarded as a suborder of the Lepidoptera – the Rhopalocera or 'club-horned' – to distinguish them from the suborder Heterocera, or 'varied-horned', moths. Today, the differences between butterflies and moths are considered so slight that this division is no longer justified (Skaife 1979). Most butterflies are brightly coloured, the tips of their antennae are swollen and they fly by day. The caterpillars are seldom hairy, although some are armed with spines. Also, with the exception of some of the more primitive species, the pupae are not enclosed in cocoons. A more fundamental difference between butterflies and moths is that the wings on each side of a butterfly are not linked together by a jugum or a frenulum – except, again, in a few of the most primitive species found in Australia. Instead, at the front of the hindwing there is a rounded lobe, known as the humeral lobe, which presses against the underside of the forewing when the insect is in flight.

Butterflies form two superfamilies – the Hesperioidea, comprising one African family (the Hesperiidae), and the Papilionoidea with five families (the Nymphalidae, Pieridae, Lycaenidae, Riodinidae and Papilionidae). The Hesperioidea differs from the Papilionoidea in having the antennae set widely apart at the base, and the peripheral veins of both wings are not stalked.

10.3 EXISTING INFORMATION

This review principally focuses on butterflies as meaningful conclusions can be drawn from this group. Emperor moths are also mentioned, but unfortunately only general distributions of this group are available as it has not been collected to the same extent. Although Pinhey (1962) has described the hawk moths of central and southern Africa, and d'Abrera (1986) has published *Sphingidae Mundi*, the taxonomy and distribution records for the group are still poor. Important emperor moth records are mentioned in the appropriate section.

Most of the data in this review has been collected by amateur butterfly collectors. Some of this information is available as checklists, but more detailed information is housed in private collections. There are several large private collections. Those relevant to the Zambezi Basin are: (a) Steve Collin's collection, now known as ABRI (African Butterfly Research Institute) in Nairobi, Kenya. This also contains Alan Heath's Zambian collection and collections from Zambia and Malawi by Ivan Bampton, Colin Congdon and Ray Murphy; (b) C.B. Cottrell's collection housed in Harare, and (c) the Gardiner collection, housed in Bulawayo. Some smaller collections are those of the late Rob Pare housed in Bindura, and Ian Mullin's collection housed in Harare. The Natural History Museum of Zimbabwe in Bulawayo also has a fine collection of specimens from south central Africa, to which many collectors have contributed. Of particular note are the collections of E.C.G. Pinhey. The collections of Rob Pare and half of the Gardiner collection have been put onto an electronic database.

There are noticeable gaps in collecting along certain parts of the Zambezi, in particular from where the Zambezi leaves NW Zambia and enters Angola downstream to Katima Mulilo. A small amount of collecting has taken place at Zambezi and Lukulu, but these collections are in the UK and not available for study. There has also been little collecting from Luangwa through to the Zambezi Delta.

Carcasson's (1995) *African Butterflies* provides the most recent information on the taxonomy of African butterflies, and nomenclature used in this review follows this. Apart from d'Abrera (1980, 1997), *Butterflies of the Afrotropical Region,* there are no references that cover the butterflies of the Zambezi Basin. Field guides such as Migdoll (1988) and Williams (1969) cover only a limited number of species. Evans (1937) provided a catalogue of the African Hesperiidae housed in the British Museum, while Henning (1989) published a comprehensive book on the Charaxinae butterflies of Africa. Another significant work is that by Ackery and Vane-Wright (1984) on milkweed butterflies of the world which provides useful taxonomic and ecological information on the African species. The fauna of various parts of the basin is covered by a number of books and publications, of which the most important are given below. Checklists for Zambian butterflies are given by Neave (1910), Dening (1979) and Heath (1982), while Pinhey and Loe (1977) provide a small guide to some of the species. Heath is about to publish a checklist of Zambian butterflies using the collections of Denning (early 1950s), Cottrell (late 1950s), Pinhey (1970s), Heath (late 1970s), Gardiner and Blease (1980s), Terblanche (1990s), and Bampton and Congdon (late 1990s). The most useful information on the butterflies of Zimbabwe and Mozambique is given in Pennington (1978, 1994), *Butterflies of Southern Africa*. This text includes a few keys and relies on its colour plates for species identification; it also includes country-based distributions. The first volume, on the Hesperiidae, Papilionidae and Pieridae, of a series of five on butterflies of southern Africa has recently been published (Henning *et al*. 1997), but this excludes those species that are not found in South Africa. Other texts that provide information on species found in Zimbabwe include Cooper (1973), Murray (1935), Pinhey (1949a, 1949b, 1965) and van Son (1949, 1955, 1963, 1979). Torben Larsen (in prep.) compiled a checklist to the butterflies of Botswana, and it is from this that most of the Chobe records given here are taken. In addition to many other localities, Torben's checklist contains most of the information collected by Pinhey (1968, 1971, 1972, 1974). In the 1960s and 1970s Pinhey carried out a significant amount of collecting in the Victoria Falls area, the results of which are presented in Pinhey (1975). The most significant published information available for the butterflies of Malawi, which also covers the Zambezi to a limited extent, is that by Gifford (1965). This provides a keyed checklist to the Malawi butterflies and colour plates.

10.4 ZAMBEZI FAUNAL REGIONS

The Zambezi Basin covers a vast geographical area, and it is not possible, with the present resources, to cover the entire basin. In this preliminary study, the Zambezi River is looked at from its origin in northwestern Zambia through to the delta on the Mozambique coast. An attempt has been made to divide the river into six faunal sections. The dividing line between sections is not clear-cut, although the separation is logical and based on habitat differences – a combination of geographical and floristic factors.

The fauna described for each section, apart from the first, are those species recorded from the vegetation in or alongside the Zambezi. If only wetland species were being considered, little difference would be found between the different sections of the Zambezi, with the possible exception of the first. The main factors separating butterfly faunas along the Zambezi are probably climatic conditions and the type of woodland, and not the presence of wetlands.

For the first section, the tributaries near the source of the Zambezi and their associated dambos have been included. Lepidoptera from other tributaries of the Zambezi have not been included, except for the Chobe and part of the Lower Shire. More detailed work on the Lepidoptera of the Zambezi Basin as a whole is being carried out by WWF in Harare. For each faunal region, important or noticeable species and features of the fauna are noted, along with species of conservation concern. A list of all species recorded from the Zambezi River area is given in Table 10.1 (at the end of this review).

10.4.1 **Section 1: Northwestern Zambia and the neighbouring part of Angola**

The northern border of Zambia is influenced by two river systems, that of the Congo and that of the Zambezi. The northern Zambian border is in fact a watershed which separates the waters of the Congo from those of the Zambezi. All the rivers and streams immediately to the north of the border fall within the catchment of the Lualaba River, which eventually becomes the Congo. Evergreen riverine forest stretching back to the great central rainforest of Africa extends close to Zambia's northern border, and the longest tributary of the Lualaba reaches right to the border of northwest Mwinilunga, a very short distance from the source of the Zambezi. Hence there is a strong influence from the central forest block, and many of these species occur in this region of Zambia, for example species from the genera *Charaxes* and *Euphaedra*.

The Zambezi has its source in Mwinilunga at an altitude of approximately 1370 m altitude. This first part of the Zambezi, around Kalene Hill, has an unusually rich fauna with many species also occurring on eastern tributaries of the Zambezi headwaters. Many expeditions resulting in good collections have been made to this area (e.g. Denning, early 1950s; Cottrell, late 1950s; Pinhey, 1970s; Heath, late 1970s; Gardiner and Blease, 1980s; Terblanche, 1990s).

The rainforest biome contrasts strongly with the surrounding deciduous or semi-deciduous forests that cover much of Zambia. In general, the influence of the main Congo rainforest zone extends across the north of the country in the form of strips or patches of riverine, evergreen, moist forest, including swamp forest. The richness of the fauna of the area surrounding the source of the Zambezi is principally due to the forest along its margins.

These forests influence the butterfly fauna in two ways. They provide specialized microclimates, and they provide a different range of host plants. Thus species which require the deep shade of the forest floor are common in the forests near Kalene Hill. Plant families common there, such as Lauraceae, are hosts for species such as *Papilio hesperus*. Riverine evergreen habitats also exist to a limited extent in other parts of the country, and here butterfly species occur which prefer evergreen hostplants not normally found in savanna habitats.

In many of the northern riverine habitats, the occurrence of rainforest fauna is patchy, with each patch differing in its species composition. For example, along a small, shady stream, one may see the White Banded Swallowtail (*Papilio echerioides homeyeri)*, the small Riodinin *(Abisara rogersi*) and possibly Euthaline forest floor species (e.g. *Aterica galene* and *Catuna crithea pallidior*). In contrast, in another patch the unusual lycaenids *Dapidodigma demeter nuptus* and *Argyrocheila inundifera* may be found.

Wet, thickly forested areas at the sources of streams may contain unusual species. The source of the Zambezi, some miles north of the Mwinilunga–Ikelenge road, is home to deep shade species of the forest floor such as *Bicyclus sebetus, B. trilophus* and *B. sophrosyne overlaeti*. The Zambezi source has also provided a record of the rare and beautiful *Charaxes acuminatus cottrelli*. Not far away, near the Ken Suckling Mission on the Luakela River, Blease found the only known Zambian colony of the African Leaf Butterfly, *Kamilla ansorgei,* in April 1988. Similar habitats occur in the northern Luapula Province, for instance along the Kalungwishi River and in Northern Province. Here, *B. sebetus* also occurs, together with unusual *Charaxes* such as *C. lucretius schofieldi* and *C. eudoxus zambiae*.

Of all these habitats, the most notable is the Isombo and Mudileji cluster of streams to the west of Kalene Hill which flow into the Zambezi inside Angola. These forests are not connected to the Congo rainforest to the north, and appear to represent a relict fauna from past pluvial periods. First noted in 1954, these relatively small evergreen areas had been undisturbed throughout the colonial period due to their proximity to the Angolan border; by mutual agreement people could pass through them but not settle within them. They survived intact until the 1970s, but their status today is not clear owing to a large influx of refugees from Angola. It has been reported that the Isombo forest has been cut down to make way for cassava fields and fish ponds. Thus, an appreciable number of species listed in Table 10.1 may no longer occur within Zambia. However, if there are other relict patches in the same neighbourhood, these species may still survive.

A common swallowtail butterfly in these forests is the green *Papilio phorcas congoanus*, otherwise recorded only from Mufulira and the Kalungwishi. It reoccurs as a different subspecies *P. p. nyikanus*, far to the east in the Afromontane forests on the Nyika Plateau. The subspecific differences suggest an absence of widespread interconnected gene flow since before the last northern glaciation and its contemporary arid period in Central Africa (possibly 22,000 BP). Other notable Swallowtails are the large *Papilio hesperus* and *Graphium ridleyanus*, a remarkable reddish *Acraea* mimic.

Among the Pieridae, the unusual delicate, translucent-winged *Pseudopontia paradoxa* is so distinctive it has been placed in its own monotypic subfamily. This species was bred for the first time by Heath (1977), who observed specimens laying on the plant *Rhopalopilia marquesii* growing along the Jimbe River. There are two subspecies – *P. paradoxa paradoxa* occurs in forests from Sierra Leone through to the northern Democratic Republic of Congo (DRC), and *P. paradoxa australis* occurs in central and southern DRC, Angola and northwestern Zambia. It is suggested *Pseudopontia paradoxa australis* is placed on IUCN's list of Vulnerable species because of its close relationship with riverine vegetation and unique taxonomic status. Another two wet forest pierids are *Leptosia hybrida vansomereni* and *L. nupta*.

Large acraeine species found in the forest are *Acraea epaea*, *A. macarista* and *A. umbra macaroides*, while common danaines are *Amauris niavius* and *A. tartarea.* The satyrines *Gnophodes betsimena parmeno,* and the previously mentioned *Bicyclus* species, as well as *B. mesogena, B. mandanes* and *B. dubia*, occur in deep shade.

The family Nymphalidae are represented by *Lachnoptera anticlea*, *Kamilla cymodoce,* several forest *Neptis* species (e.g. *N. nemetes, N. nicoteles*) and the common *Pseudoneptis bugandensis ianthe*. The splendid scarlet male of *Cymothoe sangaris luluana* may be seen after the rains sunning itself on leaves near the Isombo River, and in the deep shade one may see *C. herminia katshokwe*. The splendour of these are matched by large *Pseudacraea*, such as *P. kuenowi, P. boisduvali, P. lucretia protracta* and the smaller green spotted *P. semire*. Three dark purple-blue forest floor species of *Euriphene* (*E. pallidior, E. incerta theodota* and *E. saphirina trioculata*) may sometimes be found in large numbers flying alongside *Catuna crithea pallidior* and *Aterica galene.* Even more spectacular in the understorey are the large purple, yellowish, orange and reddish *Euphaedra* such as *E. overlaeti, E. herberti katanga, E. katangensis, E. cooksoni,* and *E. crawshayi*. The Isombo area has eight *Euphaedra* species. These fly from ground level to shoulder height, while the four *Bebearia* species, particularly the large and striking *B. plistonax*, tend to skim the ground.

Notable lycaenids fluttering in the shade are the white *Oboronia guessfeldti* and the delicate hairstreak *Oxylides faunus*. The very large hesperiid *Gamia shelleyi* may be seen flying along the streams. In July, well into the dry season (and normally only found in Cameroon and the DRC), the rare *Artitropa cama* appears.

There are also many spectacular rainforest species of the genus *Charaxes* belonging to the *Tiridates* group, notably *C. numenes aequatorialis, C. tiridates tiridatinus, C. imperialis lisomboensis, C. ameliae amelina* and *C. pythodoris*. Rainforest *Charaxes* of other groups include *C.eudoxus* (which occurs in Zambia as three subspecies), *C. lucretius* (two subspecies), *C. anticlea proadusta, C. hildebranti katangensis*, and the black *C. etheocles carpenteri* and *C. cedreatis*. While virtually all of these species are found in the strips of evergreen forest at Kalene Hill, many also occur in other forest patches across northern Zambia.

In this northern region of Zambia there are species, such as *Acraea mirifica* and *Zeretis fontainei*, restricted to marshy areas. A number of other acraeines, although not found exclusively in marshy places, prefer them. Two species quite tightly linked to marshes are *Acraea rahira*, which feeds on Polygonaceae, as well as on *Erigeron* (Asteraceae), and *A. ventura* which utilises *Cassia* plants. Less closely linked to marshes are *A. acerata* and *A. periphanes*, both of which utilize a range of herbaceous and shrubby host plants. Other nymphalids that are mainly seen in marshy places are *Junonia ceryne, Neptis jordani* and the False Fritillary, *Pseudargynnis hegemone*.

A number of emperor moths can be found in northwestern Zambia. One species only recorded from this region is Kuhne's Lunar Moth, *Argema kuhnei.* The genus *Argema* is the well-known group of Moon or Lunar Moths; these moths produce a silky cocoon. They are yellow or green in colour with very long hindwing tails; *Argema kuhnei* has a chrome-yellow ground colour with some greenish yellow basal tints. It is also likely to occur in the Shaba Province of the DRC, although it has not yet been recorded there.

From northwest Zambia the Zambezi flows southwest into Angola and has no direct connection with the Lualaba catchment. No collections from this part of Angola have been noted and we have no idea of the ecological state of the riverine forests. Having passed in a wide arc through Angola, the Zambezi re-emerges to form the Barotse Plain.

10.4.2 **Section 2: Barotse Floodplain**

Apart from collections made by C.B. Cottrell and a small recent collection by the BFA, very little collecting has taken place in this area. At Mongu, Cottrell recorded a rare and interesting species, *Erikssonia acraeina* (for notes on its ecology see Henning 1984). This species is on the IUCN list of Vulnerable species and only a few scattered populations have been found in central and southern Africa. Although not a swamp species, being found on the higher ground at Mongu, it would be of interest to know if it still occurs in this area. Its food plant is *Gnidia kraussiana*.

Most of the species recorded from this section are either wetland species (such as *Neptis jordani*, *Leptotes pulcher* and *Acraea acerata*) or common migrants (for example, *Belenois aurota*). *Mylothris rubricosta*, unlike many of this mistletoe-feeding genus, uses herbaceous Polygonaceae as their food plants. It is a true marsh species.

One group of emperor moths found in this section of the Zambezi are those belonging to the genus *Bunaeopsis*. These are normally brightly coloured moths with yellow and red background colours and black stripes. They have well developed eyespots on both the fore and hindwings. The larvae are usually adorned with short thick spines and feed mostly on sedges and grasses.

10.4.3 Section 3: Senanga to Victoria Falls, including the Chobe/Linyanti swamps

After leaving the Barotse floodplain towards Victoria Falls, the Zambezi passes through dry forests on Kalahari sands. Some information is available for species collected just above Victoria Falls at Kazungula by Pinhey in the 1960s and 1970s, and there is reliable information available for the Chobe system (Larsen, in prep.). Amongst the few species of interest in this area, the most important are the true marsh species, *Mylothris rubricosta* and *Leptotes pulcher*, dealt with later. Most species from this section have wide distributions, but a few, such as *Acraea atergatis* and *A. atolmis*, are linked to the Kalahari sand system. These two acraeas are particularly common in the Livingstone-Victoria Falls area, through the northwestern part of Zimbabwe and west through Botswana to Ovamboland in Namibia.

Because of the microclimate produced by the Victoria Falls, some interesting taxa occur in the "rainforest". The rainforest fauna is noticeably different to that of the surrounding area. Of particular note is the unusual *Acraea anemosa* form *albiradiata*, which has only been taken in this forest and at Katima Mulilo in Namibia. Nothing is known about the population at Katima Mulilo, but at Victoria Falls the population is Conservation Dependent (cd). This taxon with its limited distribution (only two small populations being known), should be given special conservation status. Other species found at Victoria Falls are listed by Pinhey (1975).

Within the forest there are some large and attractive butterflies. The genus *Papilio* is represented by *Papilio nireus lyaeus*, with its black background and blue or green bands, the common and widespread *P. demodocus*, which is mainly black and yellow in colour, and *P. constantinus*, a black and yellow species similar to *P. demodocus* but with tails. In and outside the forest one will also come across *Graphium leonidas*, *G. antheus* and *G. porthaon*, the latter two have very long and attractive swordtails on their hindwings. This is one place where *Graphium porthaon* can be found in large numbers; its food plant, *Friesodielsia obovata*, is common in the surrounding Kalahari sands. The other noticeable large species is the white *Nephronia thalassina*. The male flies quite rapidly and is a delicate pale blue in colour, while the female is a slower flier and is either off-white in colour or, in form *sinalata*, has an attractive yellow hindwing. This seems to be the commoner form at Victoria Falls. The Clouded Mother-of-Pearl, *Salamis anacardii nebulosa,* is a large attractive Nymphalid that can be found inspecting the understorey bushes.

Recently, Henning and Henning (1994) described *Charaxes zambeziensis* from the Victoria Falls. However, it is likely that this species is not valid as the male is probably *Charaxes vansoni* while the female is probably *C. fulgarata*, the female of which has many attractive forms. Some have blue hindwings with blue and black forewings, while others have blue hindwings with blue, white and black forewings, while yet others have a whitish blue hindwing with light blue and black forewings. The food plant of *C. fulgarata* is the tree *Amblygonocarpus andogensis* which is common in the vicinity of the Falls. There is a fine specimen of this tree outside the Victoria Falls railway station, at times females can be seen ovipositing on it.

The genus *Acraea* is also common in the rainforest and surrounding bush. In fact, four species were described from specimens caught near the Falls – *A. atergatis*, *A. atolmis*, *A.axina* and *A. aglaonice* were all described by Westwood in 1881. Of these, *A. atolmis* is particularly noticeable during the dry season as the male is bright scarlet in colour.

An interesting record from the Palm Grove area of Victoria Falls is an attractive little lycaenid *Spindasis brunnea*. Two specimens were taken in 1938 by R.W. Barney and are the only records for southern Africa. As there are records in the British Museum of *S. brunnea* from Ndola, also caught by R.W. Barney but in 1941, it is possible that the 1938 specimens were labelled Victoria Falls by mistake.

Ypthimomorpha itonia, the Swamp Ringlet, is common in the surrounding swampy areas. Another small ringlet, *Ypthima cataractae*, was described from the Victoria Falls by van Son in 1955. It has, however, been synonymised with *Y. granulosa* (Kielland, 1982) which is found in grassy and swampy areas from East Africa through to Zimbabwe. The other wetland species that have been recorded from the Falls are *Acraea acerata*, *Catacroptera cloanthe*, *Mylothris rubricosta* and *Eicochrysops hippocrates*. Other wetland species that should occur there are *Acraea rahira*, *Neptis jordani*, *Leptosia alcesta*, *Cacyreus lingeus*, *Cupidopsis cissus*, *Leptotes pulchra* and *Parnara monasi*.

10.4.4 **Section 4: Victoria Falls to Tete**

The butterfly fauna from the gorges below Victoria Falls through to Tete is typical of more hot, arid areas. This section could be divided into two subsections – the area above Kariba dam wall and the part below. Below Kariba dam, the Zambezi is joined by the Kafue River at an altitude of around 500 m, and then by the Luangwa River at Luangwa at around 370 m. A list of butterflies collected from Cabora Bassa by M.C. & G.V. Ferreira is given in Pinhey (1976).

The presence of Pieridae, or Whites, is a noticeable feature of this section of the Zambezi Valley and it is common to see massive migrations of this group. The species normally involved are *Catopsilia florella* and *Belenois aurota*. With these one may find other species such as *Graphium porthaon* and *Phalanta phalantha*. The migrations normally happen during the early months of summer, and the butterflies fly from north-west to south-east.

Another White that catches the eye is *Nephronia argia*, with its peculiar underside markings. The hindwing underside is a deep yellow in colour, while the forewing underside is white with the basal half a red-orange colour. It is a rapid flier and only when perched can the underside colouration be seen; in flight the white uppersurface shows. *Eronia leda* is also common; the male is bright yellow in colour with a orange tip, while in the wet season the female is almost completely yellow (in the dry season it also has a orange tip).

The genus *Colotis* is well represented in this section, with its variously tipped forewings. Examples are *C. vesta*, *C. celimene amina* (male with its crimson streaked wingtips), *C. ione* (male with purple wingtips), *C. danae annae* (male with its scarlet apical patches), *C. antevippe gavisa* (male with its reddish-orange apices), *C. eris* (male with golden apical spots), and *C. euippe mediata, C. pallene* and *C. evagore antigone* (the smaller yellow or orange-tipped *Colotis).* Most of these species are fairly widespread. A particularly widespread species is the small *C. amata*, which is also found in hot, dry places in south Asia. Similarly, the Zebra White (*Pinacopteryx eriphia*) is found almost everywhere in drier localities. The small white *Nepheronia bucqueti* occurs in open places, while the large satyrine *Melanitis leda* can be found commonly in the shady ravines or thickets.

Between Chirundu and Kanyemba, Hancock (in the 1980s) and Gardiner (in the 1990s) have recorded the rare *Dixeia leucophanes* in thickets, a species restricted to this region, low-lying areas in Mozambique and parts of the Sabi Valley in Zimbabwe. It is a medium-sized white butterfly and a rapid flier. Many Whites fly together with *D. leucophanes*, including its close ally *D. doxo*.

In the Mana Pools area in thick riverine bush, especially along the small rivers that enter the Zambezi, some beautiful *Charaxes* can be found. The most spectacular of these is *Charaxes cithaeron joanae*. The male has bright iridescent blue spotting on the forewing upperside, while the hindwing upperside has a large pale blue discal patch. The female has a wide and solid white discal band on the forewing, and the hindwing has a large blue-white discal patch. Another common *Charaxes* is *C. ethalion binghami*, one of the Black Charaxes.

The only wetland butterfly species to have been recorded from this section are *Catacroptera cloanthe*, *Leptosia alcesta* and *Leptotes pulcher*. It is likely there will be fewer wetland species here compared to other sections, but others that should be found are *Ypthimomorpha itonia*, *Acraea rahira*, *Cacyreus lingeus*, *Eicochrysops hippocrates* and *Parnara monasi*.

A rare emperor moth, the Frog Foot *Antistathmoptera daltonae*, has been collected from Chirundu. It is a large orange-brown species with very long tails which are even longer than those of the Moon Moth. Of the two subspecies, the typical *A. d. daltonae* is from the Usumburu mountains in north east Tanzania, while the Chirundu subspecies, *A. d. rectangulata*, has also been recorded from low altitude forest in Mozambique and Malawi.

10.4.5 **Section 5: Tete to Mopeia**

Below Tete and closer to the Zambezi Delta, the Shire River enters the Zambezi. Although little collecting has taken place in the Lower Shire marshes, the following marsh species have been recorded: *Neptis jordani*, *Catacroptera cloanthe*, *Junonia ceryne*, *Leptosia alcesta*, *Cacyreus lingeus* and *Parnara monasi*. Some information on this area can be found in Gifford (1965). In highland areas further up the Shire and its tributaries, such as Cholo and Zomba, there are many endemic and interesting species. For instance, on Cholo Mt. *Eretis herewoodi* is only found in marshy glades near forest.

10.4.6 **Section 6: Zambezi Delta**

There appears to have been no collecting in this area except for a recent trip carried out by this project. As the field trip was done late in the season and a poor species list was obtained it is difficult to draw any conclusions. Most species collected were eclectic which may indicate: (a) the area is much disturbed and modified by human activity, (b) due to the time of year only common and obvious species were present, and/or (c) only the conspicuous species were caught. If the low species count is due to human impacts there may be concern for the environmental health of the area. Of the species recorded from the area, a few, such as *Euphaedra neophron*, confirm the link the area has with the eastern forests and woodlands. Four wetland species were collected: *Eicochrysops hippocrates*, *Ypthimomorpha itonia*, *Neptis jordani* and *Parnara monasi*. At least an additional six species should be found: *Leptosia alcesta*, *Leptotes pulcher*, *Cacyreus lingeus*, *Cupidopsis cissus*, *Acraea rahira* and *Catacroptera cloanthe*.

10.5 WETLAND SPECIES

Species listed as wetland species are those that have a close relationship with wetlands. Most are dependant on swamp plants such as *Polygonum* as larval food, and therefore only occur within or very close to swamps (for example, *Mylothris rubricosta*). Some wetland species, such as *Catacroptera cloanthe*, may be found in other moist habitats. The habitat and habits of each species give an indication of how tightly bound the species is to the swamp or wetland habitat. A list of butterflies considered to be wetland species is given in Table 10.2.

Over the rest of Africa there are only about 15 additional wetland, swamp or marsh associated species – *Mashuna mashuna* occurs in high level dambos on the Zimbabwe highveld; *M. upemba* occurs in dambos in the Shaba Province of the DRC, SW Tanzania and Angola; *Acraea bettiana* occurs in swamps above 2100 m in western Uganda, Rwanda, Burundi and eastern DRC; *A. rangatana* occurs in swamps above 2100 m in Kenya, Rwanda to Uganda and eastern DRC; *A. odzalae* is found in the DRC; *A. hecqui* in south Kivu, DRC; *A. pierrei* in north Kivu, DRC; *A. guichardi* in western Ethiopia; *A. necoda* in the Ethiopia highlands; *Metisella meninx* in wet meadows in South Africa; and *M. midas* in high level dambos in eastern Africa. The following species of *Pseudonympha* are restricted to marshy ground in high mountainous regions – *P. varii* and *P. swanepoeli* in South Africa and *P. cyclops* and *P. arnoldi* in eastern Zimbabwe.

The health of a wetland can be indicated by the presence or absence of certain species, particularly if one takes into account the abundance of the component species. A sudden decrease in numbers of a species, if change due to climatic conditions can be ruled out, can be a warning that there has been a marked change in the environment. Other groups such as dragonflies and mayflies, however, may be better indicators of water quality.

10.5.1 Species Descriptions

1. ***Leptosia alcesta inalcesta*** Bernardi, 1959 — African Wood White

Diagnosis: This flimsy white butterfly is easily identified in our region by its black tip and black postdiscal spot.
Habitat & habits: It has a distinctive slow bouncing flight. Found in many different shady habitats from forests to riverine thickets in low hot valleys, it is seldom or never found far from water. Its favoured habitat is along rivers. Though on the wing throughout the year, it is generally more plentiful in late summer and autumn.
Conservation status: Although its numbers may be influenced by human impact, it is unlikely to be under any threat.
Distribution: The species has a wide distribution occurring from the Natal coast, through Zimbabwe and Zambia to East Africa. A different subspecies is found in West Africa. It may be found along the whole length of the Zambezi.
Food plants: *Capparis brassii*, *C. fasicularis* (Pennington 1994), *C. tomentosa* and *Maerua juncea* (Henning *et al*. 1997).

2. ***Mylothris rubricosta rubricosta*** (Mabille), 1890 — Swamp or Papyrus Dotted Border

Diagnosis: This and the next species are readily recognized by their white colour and the costa on their under and upperside being bordered by a distinctive orange streak (hence the specific name *rubricosta*). In the past *M. rubricosta* was considered to be a subspecies of *M. bernice*, but in *M. rubricosta* the marginal forewing spots are not produced along the veins, while in *M. bernice* the marginal spots along the costa project inwardly along the veins.

Habitat & habits: The larval food plant (*Polygonum*) is intermixed with papyrus, so the butterfly often lives completely away from dry ground. The flowers of *Polygonum* are a favourite nectar source for the species. Records are from August to April. The flight is light and floating with an occasional fluttering movement; it always flies low down and often amongst the reeds. Seldom seen more than a few metres away from its swamp habitat.
Conservation status: Low Risk, least concern.
Distribution: There are two subspecies, one in eastern and southern Africa from Ethiopia through to Zambia, Angola, northern Botswana, northwestern Zimbabwe and Malawi, and a second subspecies in the east of the DRC. Within the Zambezi Basin, this species is widespread (although localised) along the Zambezi above the Victoria Falls and along the Kafue, while in Malawi it will probably be found in the Lower Shire. In Botswana it is only known to occur in the panhandle of the Okavango and in the northwestern part of the delta, but is also likely to occur in the Kasane area since there are records from the Kazungula Rapids just inside Zimbabwe.
Food plants: *Polygonum* spp. (Polygonaceae), and on *Polygonum barbatum* in East Africa.

Table 10.2. Wetland Lepidoptera species from the Zambezi Basin.

Family Pieridae	Acraeinae
Pierinae	11. *Acraea rahira rahira*
1. *Leptosia alcesta inalcesta*	12. *A.ventura ventura*
2. *Mylothris rubricosta*	13. *Acraea mirifica*
3. *Mylothris bernice*	14. *Acraea acerata*
	15. *Acraea periphanes*
Family Lycaenidae	
Polyommatinae	Nymphalinae
4. *Eicochrysops hippocrates*	16. *Catacroptera cloanthe*
5. *Leptotes pulcher*	17. *Junonia ceryne ceryne*
6. *Cacyreus lingeus*	
7. *Cupidopsis cissus*	Limenitinae
	18. *Neptis jordani*
Theclinae	19. *Pseudargynnis hegemone*
8. *Zeretis fontainei*	
9. *Zeretis sorhagenii*	**Family Hesperidae**
	Hesperinae
Family Nymphalidae	20. *Parnara monasi*
Satyrinae	21. *Borbo micans*
10. *Ypthimomorpha itonia*	

3. ***Mylothris bernice overlaeti*** Berger, 1981 (no common name)
Diagnosis: See preceding species for identification.
Habitat & habits: Also an inhabitant of swampy areas.
Conservation status: Vulnerable.
Distribution: There are five subspecies of this butterfly. The nominate subspecies is from Gabon and Cameroon, while the other four occur in the DRC; one of them (*M. bernice berenicides*) also occurs

in Rwanda, Burundi and Uganda. Although it has only been recorded from Ndola in our region, there is the possibility that it may be found in the upper reaches of the Zambezi.
Food plants: *Polygonum* spp.

4. ***Eicochrysops hippocrates*** Fabricius, 1793 White Tipped Blue
Diagnosis: The sooty ground colour and the prominent white tips of the forewings make the male a distinctive little butterfly. The female is very different, looking like a small *Euchrysops*, but the chalky underside with fine black markings is different from that genus and similar to that of the male.
Habitat & habits: Because of its host plants, which are almost wholly aquatic, this species is restricted to habitats with permanent water (swamps and river banks). It is a spring and summer butterfly. Males are perching species, usually sitting with the wings two-thirds open on the host plant, and they are extremely aggressive for their size. The flight is also rather rapid for such a delicate species. Both sexes visit flowers. Its illustrated life history is shown in Clark & Dickson (1971).
Conservation status: Not under any threat, but may be of use as an indicator of the health of the aquatic system.
Distribution: The species is found throughout most of Africa and Madagascar. Although widespread, this species tends to be localized within the Zambezi Basin, it is found from the origin of the Zambezi through to Victoria Falls. There are few records from Botswana, but it is not infrequent along the Chobe River from Serondella to Kazungula, though rarely in any numbers. It has not been seen in the hot and dry parts of the Zambezi below Victoria Falls to Chirundu.
Food plants: Larvae have been recorded on *Polygonum* and *Rumex* (Polygonaceae).

5. ***Leptotes pulcher*** (Murray), 1874 Beautiful Zebra Blue
Diagnosis: The upperside ground colour of the male of this small butterfly is a light and vivid violet; the female is also a lighter colour than the other *Leptotes*. The underside has more striking whitish marginal and submarginal markings than other members of the genus.
Habitat & habits: Almost exclusively tied to marshy habitats.
Conservation status: Although rare this species is not under any threat.
Distribution: There are records from most of Africa, though the species appears to be absent from many areas - widespread, local, but quite rare. Found intermittently at various localities along the entire length of the Zambezi, even in the hot parts such as Mlibizi and Deka. In Botswana it is chiefly found in the Okavango and Chobe river systems. Larsen (in prep.) states "where the Chobe river runs over stony ground between Kasane and Kazungula the species may be quite common, but it is usually not numerous". A spring and summer insect.
Food plants: Has been recorded on *Sesbania sesban* (Fabaceae: Papilionoideae).

6. ***Cacyreus lingeus*** (Stoll), 1782 Bush Bronze
Diagnosis: The upperside of this small butterfly is dark blue in the male and a lighter blue with white and brown in the female. The underside is a mosaic of white and brown.
Habitat & habits: Favourite habitat is the banks of streams through woodland. It has a weak fluttering flight and is often found settled on vegetation next to the river.
Conservation status: Not under any threat.
Distribution: Found throughout sub-Saharan Africa. Although its favourite habitat is along rivers in woodlands of various types, it is also found on the margins of forests. Within the Zambezi Basin it can be found in many places along the Zambezi and Chobe rivers where these pass through woodland.

Food plants: *Plectranthus*, *Salvia*, *Calamintha*, *Lavandula*, *Mentha* and *Hemizygia flabellifolia* (Lamiaceae).

7. ***Cupidopsis cissus*** (Godart), 1824 Common Meadow Blue

Diagnosis: A largish lycaenid, both sexes have rounded wings without tails. Male light blue, forewing with a narrow dark margin and apical area, hindwing anal angle with a red and black submarginal spot. The female is similar to the male but the blue areas are reduced and have several red and black hindwing submarginal spots. Underside is light grey with submarginal red markings and dark postdiscal spots.

Habitat & habits: Found in wet grasslands, grassy meadows and dambos; less often in woodlands. It is normally seen fluttering around flowers in the grass, although at times it flies quite rapidly just above them.

Conservation status: Not under any threat, but may be of use as an indicator of the health of grassland systems.

Distribution: Found throughout Africa and the Madagascar. There are indications that the West African, the South and East African and Madagascan populations may be subspecifically distinct. Along the length of the Zambezi this species is found in grasslands, but is probably rare in the middle sections.

Food plants: *Eriosema* sp., *Vigna* sp. Feeds on flowers and by burrowing into developing seeds; visited by ants.

8. ***Zeretis fontainei*** Stempffer, 1956 Fontain's Gem

9. ***Zeretis sorhagenii*** (Dewitz), 1879 Scarce Gem

Diagnosis: These two species are very distinctive, the underside being orange and black with numerous metallic silver-blue spots and the upperside is black-brown with orange spots. In *Z. sorghagenii* these orange spots are along the margin, while in *Z. fontainei* they are dispersed over the uppersurface.

Habitat & habits: Although these two species are not true swamp species, they are dambo-associated, very localized and rare. Within the region they have only been found in Mwinilunga District (the record of *Z. sorhagenii* from Kazungula by R.H.R. Stevenson in 1933 remains a mystery as it has not been seen there since). *Z. sorghagenii* was found in a small wet dambo a few hundred metres from the Zambezi River on Hillwood Farm. Similarly, *Z. fontainei* was found on a large wet dambo about 40 km SE of Mwinilunga. Both species fly little and remain in small colonies, often sitting on the ground or low vegetation.

Conservation status: Vulnerable.

Distribution: *Zeritis fontainei* has only been recorded from the DRC and NW Zambia. *Zeritis sorhagenii* also has a restricted distribution, having been found in Angola, southern DRC and in one locality in Mwinilunga District.

10. ***Ypthimomorpha itonia*** Hewitson, 1865 Swamp or Lesser Ringlet

Diagnosis: Apart from the eye-spots this species is uniformly brown above. There are usually 6 or 7 ocelli on the hindwing underside arranged in a straight line, some or all of which are also present on the upperside. These ocelli make it distinguishable from all its close relatives in the genus *Ypthima*, which have only 1 or 2 ocelli. Ocelli are sometimes reduced to tiny points during the dry season. The underside of the hindwings is crossed by two more or less distinct, straight brown discal bands, and the forewing eye-spot is usually oval in shape.

Habitat & habits: A smallish butterfly normally associated with moist environments such as swamps, marshes, bogs and permanent river margins. As long as the habitat is moist it matters little

whether the surroundings are arid, rainforest or semi-montane habitats. The flight is weak with a slight bobbing movement as it makes its way through the grass and swamp vegetation – a similar flight pattern to species of the genus *Ypthima*.
Conservation status: Not under any threat, and may be of use as an indicator of the health of the aquatic system.
Distribution: Found over most of Africa in savanna habitats, usually on somewhat swampy ground, but it does not go further south than N Botswana, Victoria Falls and E Zimbabwe. This species is likely to be found along the whole length of the Zambezi. In Botswana records are from Kazungula to Kasane, on the floodplain inside the main Chobe Forest, and in the northern Okavango.

11. ***Acraea (Actinote) rahira rahira*** Boisduval, 1833 Marsh Acraea
Diagnosis: The species can be recognized simply by the characteristic radial streaks at the margin of all four wings; the hindwing underside has no marginal lunules. The ground colour is lighter than that of the upperside, but the black discal spots are usually interconnected by orange streaks; there are also orange marginal streaks.
Habitat & habits: The habitat is always a marshy place (including the edges of dams) or floodplain. It may sometimes be extremely numerous. Flight is low down and very weak, not wandering very far from its food plant. The species is greatly attracted to the flowers of *Polygonum*, on which it often perches. The lifecycle is illustrated in van Son (1963).
Conservation status: Not under any threat, and may be of use as an indicator of the health of the aquatic system.
Distribution: Restricted to marshy habitats in southern, eastern and central Africa (N Botswana, Zimbabwe and Namibia to Kenya and Uganda). There are three subspecies, one in S Tanzania, one in W Kenya and Uganda, and the nominate one covering the rest of its distribution. It occurs along most of the Zambezi wherever its larval food plant occurs, and in the swampy parts of the Chobe/Linyanti system.
Food plants: *Persicaria attenuata* (formerly *Polygonum pulchrum*) and *Conyza canadensis* (=*Erigeron canadense*).

12. ***Acraea ventura ventura*** Hewitson, 1877 Banded Orange Acraea
Diagnosis: A small to medium orange species, with black borders on both fore and hindwings enclosing orange spots along the margins. The black submarginal bar is always fully formed from the costa to outer margin isolating the orange apical area on the forewing. The hindwing underside has orange submarginal and discal markings. The female is similar but with a large dark apical area enclosing a whitish band.
Habitat & habits: Most often found in marshy grassland, and wide ranging. It has having a slow floating flight except when disturbed, when it flies with a rapid and slightly zig-zag movement.
Conservation status: Not under any threat.
Distribution: The nominate subspecies is widespread in the northern part of Zambia, Shaba Province of DRC through to Malawi and S Tanzania. *A. v. ochrascens* occurs in Kivu Province of the DRC, Rwanda, Burundi, NW Tanzania, Uganda and W Kenya, although some authors regard it as form *ochrascens*. It is found in the first section of the Zambezi, and although not recorded from the Lower Shire marshes it may occur here as it has been recorded from swamps near Mt Mulanje.
Food plants: Possibly *Senna* species.

13. ***Acraea mirifica*** Lathy, 1906 Dark Marsh Acraea
Diagnosis: The male of this species is unmistakable with the upperside being dark brown to black with a broad yellowish-white subapical band. The hindwing has a few yellow submarginal spots,

while the underside is cream with black spots arranged in the normal acraea pattern. The female is unlike the male and is mid-brown with a dark border to both wings and an apical patch on the forewing.
Habitat & habits: Found in marshy vegetation adjoining streams. The males do not venture away from their marshy habitat and sit on grass stems awaiting the approach of females.
Conservation status: Vulnerable.
Distribution: Northern part of Zambia, Bihe District of Angola, and the Shaba and Lualaba districts of the DRC. This rare, localized species is found in marshy areas next to streams in upper parts of the Zambezi. There is a colony in a small marsh along the Sakeji River on Hillwood Farm, the first tributary of the Zambezi.

14. ***Acraea acerata*** Hewitson, 1874 The Falls Acraea
Diagnosis: The upperside of this small butterfly is yellow-orange with broad black margins. There is a black submarginal bar from the costa to the outer margin isolating the yellow-orange apical area on the forewing. The yellow on the forewing does not intrude into the cell. The hindwing has one or two spots in the discal area near the costa.
Habitat & habits: Normally found near water. It is a weak flier and tends to prefer vegetated areas near marshes.
Conservation status: Not under any threat.
Distribution: Found sporadically over most of the Afrotropical Region north of the Zambezi and Cunene. Although the species is usually found near water, in certain areas it has moved into cultivated patches near rivers or in very wet areas, where it can be a pest on sweet potatoes. Occurs in Barotseland through to Victoria Falls and along the Chobe River at Shakawe and Kasane. It probably also occurs along the Lower Shire and has also been recorded from Blantyre and Mulanje.
Food plants: *Solanum*, *Ipomoea*, *Lepistemon*, *Merremia*, *Vernonia*, *Passiflora* and *Zea* (van Someren & Rogers 1926).

15. ***Acraea periphanes*** Oberthur, 1893 (no common name)
Diagnosis: A medium sized polymorphic species. The ground colour is light orange-brown, both wings have numerous spots, forewing with or without black apical patch, and veins darkened towards the apex margins. The female is similar but usually duller brown, sometimes greyish-brown with a light area at the distal half of the forewing.
Habitat & habits: Found in marshy grassland. It is a fairly strong flier.
Conservation status: ?Vulnerable.
Distribution: Within its habitat it is found in Angola, N Zambia, N Malawi, S and W Tanzania and the DRC (Haut-Lomani, Lualaba and Haut-Shaba provinces). In the Zambezi Basin it is restricted to the northern part of Zambia and the adjoining area of Angola.

16. ***Catacroptera cloanthe*** (Stoll), 1781 Pirate
Although this is a widespread and common species, it is included here as it is often found along stream banks and in marshy areas.
Diagnosis: The specires is orange-brown with dark brown spots and bars on the forewing and a submarginal row of blue centred eyespots on the hindwing. Unusual features of this butterfly are the tufts of cilia at the ends of the veins at the margins of both wings, and the hairy body and wing underside. The sexes are similar.
Habitat & habits: Although preferring marshy areas and stream banks, it can be found in most grassy landscapes. Specimens are usually encountered singly and are wary, normally gliding away quickly when approached. Description of the early stages is given in van Son (1979).

<u>Conservation status</u>: Not under any threat.
<u>Distribution</u>: Found throughout sub-Saharan Africa, with subspecies *C. cloanthe ligata* from Senegal to Cameroon and the nominate subspecies through the rest of Africa. Found along the whole length of the Zambezi.
<u>Food plants</u>: *Justicia protracta*, *Ruellia cordata* and *Asclepias* spp.

17. ***Junonia ceryne ceryne*** (De Boisduval), 1847 Marsh Commodore
<u>Diagnosis</u>: One of the smaller *Junonia*. Ground colour is brown with a broad pale red-brown median band across both wings which is paler proximally. The dry season form *tukuoa* has more angular wings and the forewing is more falcate. Sexes are similar.
<u>Habitat & habits</u>: Locally common in marshes along streams and rivers. It flies slowly, but can put on considerable speed when disturbed, frequently settling on low vegetation or the ground with their wings open. The life history is given by van Son (1979).
<u>Conservation status</u>: Not under any threat.
<u>Distribution</u>: The nominate subspecies occurs from the Transkei up the Indian Ocean coast to Kenya, from Zimbabwe to Angola and across the DRC to Uganda, Kenya and Ethiopia. The second subspecies, *J. c. ceruana*, occurs in Cameroon, Nigeria and Guinea. Found in the upper Zambezi, the Lower Shire marshes and the delta.
<u>Food plants</u>: *Pycnostachys reticulata*, *Plectranthus* sp., *Scabiosa* sp., *Coleus* sp. and *Plastostema* sp.

18. ***Neptis jordani*** Neave, 1910 Jordan's Sailer
<u>Diagnosis</u>: All *Neptis* have a characteristic black and white appearance. This small, distinctive species has its forewing submarginal lines in areas 3, 4 and 6 clearly interrupted by dark veins and the white band narrows towards the costa, giving the outer edge a kink. The sexes are similar.
<u>Habitat & habits</u>: The species shows a preference for riverine and grassy marshes. Its flight is low and comparatively slow, and it frequently settles on low-growing vegetation close to the edge of the water.
<u>Conservation status</u>: Not under any threat.
<u>Distribution</u>: Found from N Botswana to Zambia, DRC, Rwanda, Burundi, Tanzania, Malawi, Mozambique and E Zimbabwe. Recorded from the upper reaches of the Zambezi and along the Chobe River. It is probably absent from the Middle Zambezi but reoccurs in the Lower Shire and Zambezi Delta.

19. ***Pseudargynnis hegemone*** (Godart), 1819 False Fritillary
<u>Diagnosis</u>: A medium sized butterfly, orange with numerous black spots. Similar to *Phalantha phalanta*, but it can be distinguished by the more rounded wings and different arrangement of spots. Sexes are similar. Seasonally variable, the wet season form differs from the dry season form *nyassae* in the heavier black spotting.
<u>Habitat & habits</u>: The species is not so tied to marshy areas as others listed here, and is found in both marshes and open glades on forest edges. It flies with a gliding motion just above the vegetation, settling often with its wings open.
<u>Conservation status</u>: Not under any threat.
<u>Distribution</u>: Found in marshy areas from Cameroon to Angola and eastwards to Zambia, Malawi, W Tanzania, W Kenya and S Sudan. Found in the Zambezi headwaters and, although not recorded from the Lower Shire, it may occur here as there are records from Cholo and Mt Mulanje. A single 1934 record from Lomagundi in Zimbabwe has never been substantiated and is probably erroneous.

20. ***Parnara monasi*** (Trimen), 1889 Water Watchman

Diagnosis: This little butterfly looks much like a *Borbo* but the antennae are noticeably shorter. There is a single spot in the forewing cell, while the hindwing has a row of regularly placed white spots on both the upper and the under surfaces. The spots on the hindwing underside are often framed with dark scales. The male differs from most *Borbo* in lacking the spot in space 1b, but it is present in the female.

Habitat & habits: As the common name implies, this species is associated with water, flying in grass along rivers and lakes and occasionally on the edge of bush. Illustrated life history is given in Pennington (1978).

Conservation status: Not under any threat.

Distribution: Found over most of Africa, but is not particularly common. It seems to be missing from large areas which seem superficially suitable. Although widespread, it is not common along the Zambezi and has only been recorded from Mongu, the Shire lowlands and the Zambezi Delta. In Botswana it is essentially linked to the Okavango and Chobe river systems.

Food plants: *Saccharum* and various riverine grasses.

21. ***Borbo micans*** (Holland), 1896 Marsh Swift

Diagnosis: The upperside of the male has a distinctive orange-brown colouring with ochrous spots. The underside is similar but slightly lighter in colour. The female is similar in colour but is quite distinctly spotted (large hyaline spots on forewing with a non-hyaline discal spot near the inner margin).

Habitat & habits: An inhabitant of marshes, swamps and marshy areas along rivers. In these habitats it flies low and relatively slowly over the grass, often settling on conspicuous blades. The males establish relatively small territories (5-10 m^2) where they perch on blades of grass from which they dart out and chase off intruders. The females seem to fly at random in the swampy area, presumably searching for suitable food plants.

Conservation status: Not under any threat.

Distribution: Found throughout sub-Saharan Africa (in South Africa only one specimen has been taken near Kosi Bay). So far it has been recorded only from the upper section of the Zambezi and the Chobe/Linyanti system. It is likely to occur from the source through to Barotseland, and may even occur around Kazungula. It should then reoccur somewhere near Nhamilabue and go through to the Zambezi Delta.

Food plants: Possibly swamp grasses (Poaceae).

10.6 DISCUSSION

10.6.1 Butterfly faunas

The area around the source of the Zambezi and the surrounding river systems is rich in butterfly and emperor moth species (Table 10.3). Approximately half of Zambia's total butterfly species can be found in this area. Of the 21 wetland species listed, 18 are found in Mwinilunga District, and probably also the remaining three. The first section of the Zambezi contains species which are distributed from south central Angola through the Shaba Province of the DRC and over much of Zambia, excluding the drier parts of the Zambezi Valley. This faunal assemblage is known as Zambesian following Carcasson (1964). Typical or characteristic species include *Graphium taboranus*, *Belenois rubrosignata*, *Bicyclus cottrelli*, *B. cooksoni*, *Neocoenyra cooksoni*, *Physcaeneura pione*, *Charaxes bohemani*, *C. guderiana*, *C. penricei*, *C. fulgurata*, *Euriphene iris*, *Pseudacraea poggei*, *Neptis jordani*, *Junonia touhilimasa*, *J. artaxia*, *J. actia*, *Acraea guillemei*, *A. asema*, *A. omrora*, *A. mansya*, *A. periphanes*, *A. chaeribula*, *A. mirifica*, *Liptena homeyeri*, *L.*

eukrines, *Deloneura subfusca*, *Deudorix kafuensis*, *Iolaus australis*, *Iolaus violacea*, *Lepidochrysops pampolis*, *Euchrysops katangae*, *Sarangesa astrigera*, *S. pandaensis*, *Abantis zambesiaca*, *Metisella kambove*, *M. angolana*, *Teniorhinus harona*, *Meza larea*, *Fresna nyassae* and *Brusa saxicola*. Many of these species are absent from the other sections of the Zambezi (Table 10.1).

Although there is little material from Barotseland, the small amount of collecting that has taken place suggests this section has affinities with both the Zambesian and Kalahari faunas, but possibly more with the former. Species linking it with this zone are *Sallya benguelae*, *Charaxes guderiana* and *Neptis jordani*, while *Acraea atolmis* and *A. atergatis* link it with the Kalahari zone. Most of the species so far collected are eclectic (widespread) species, suggesting incomplete collecting. In addition to the five true wetland and swamp species listed, a further eight should be present (*Leptosia alcesta, Acraea rahira, Junonia ceryne, Ypthimomorpha itonia, Cacyreus lingeus, Cupidopsis cissus, Eicochrysops hippocrates* and *Parnara monasi*). It is estimated that the number of species would increase at least four-fold if further collecting in swamps and woodlands was carried out.

The next section, from Senanga to Victoria Falls, include species more typical of the Kalahari system, but still contains elements from the Zambesian region such as *Neptis jordani* and *Charaxes fulgurata*. Similarly the Chobe/Linyanti system, although having strong affinities with the Kalahari, also has affinities with the Zambesian region. An indication of this is the presence of species such as *Charaxes bohemani*, *C. guderiana* and *Neptis jordani*. Species characteristic of the Kalahari region are *Charaxes phaeus, C. zoolina, Graphium porthaon, Colotis agoye, C. amatus calais, C. celimene amina, C. danae annae, C. evenina evenina, C. ione, C. pallene, Aloeides damarensis, A. molomo, Anthene amarah, Azanus jesous, A. moriqua, Crudaria leroma, Epamera mimosae rhodosense, Iolaus bowkeri tearei, Lepidochrysops plebeia, Spindasis phanes, Zintha hintza hintza, Gegenes pumilio, Sarangesa seineri* and *Spialia delagoae*. Of the 20 wetland species listed in the review, nine have been recorded from the Chobe/Linyanti area, and it is likely that a few additional wetland species such as *Catacroptera cloanthe* will also be found.

The fourth section of the Zambezi is more typical of the drier Kalahari zone, which includes parts of Matabeleland, the former northern Transvaal, the northeastern Cape, Botswana, the western half of Namibia and southern Angola. In addition to the species mentioned above, other species characteristic of this zone that occur in this section are *Charaxes vansoni, Colotis vesta mutans, Dixeia doxo parva, Nepheronia buquetii buquetii, Lepidochrysops glauca* and *Bicyclus ena.* The genus *Colotis* is well represented in this section with 13 species having been recorded, followed by Section 3 with 11 species. The high number of *Colotis* species in this section is an indication of its adaptation to hotter and drier conditions. The more eastern part of this section is wetter, as shown by species such as *Charaxes cithaeron joanae*, *Euphaedra neophron neophron* and *Euriphene iris*.

On entering the Lower Shire a few of the more wet-adapted species, such as *Charaxes pollux geminus*, *Euphaedra neophron neophron* and *Neptis jordani*, are seen. This region, apart from having swamp-adapted species, shows affinities with the Kalahari and Zambesian zones. Although only six wetland species have been recorded, it is likely that a further eight will be found (*Mylothris rubricosta, Acraea rahira, A. acerata, Ypthimomorpha itonia, Cupidopsis cissus, Eicochrysops hippocrates, Leptotes pulcher* and *Borbo micans*).

Due to the paucity of records from the area below the Shire, little can be said about Section 6. It is likely that the portion from the Shire to the Zambezi Delta will contain species characteristic of the lowland eastern woodland and forests such as *Appias lasti, Euxanthe wakefieldi, Charaxes violetta,* *C. lasti, Euryphura achlys, Neptis goochi, Hypolimnas deceptor, Acraea rabbaiae, A. satis, Pentila tropicalis, Argiolaus lalos, Axiocerces punicea, Anthene lasti* and *Gorgyra subflavida*. In the area around the delta, coastal species such as *Colotis eunoma*, which appears to be restricted to littoral sand dunes, may be found, along with many of the common dry-adapted species.

Table 10.3 Number of butterfly and emperor moth species (not including subspecies) for the six faunal sections of the Zambezi River, including those possibly in Section 5.

Family/subfamily	Section of Zambezi						
	1	**2**	**3**	**4**	**5**	**6**	**Total**
Nymphalidae							
Acraeinae	42	6	14	12	3	3	54
Charaxinae	32	3	13	15	7	0	41
Argynninae	3	1	1	1	2	0	3
Danainae	6	1	1	1	2	2	7
Libytheinae	0	0	0	1	1	0	1
Limenitinae	62	7	10	9	8	0	66
Nymphalinae	26	8	12	14	15	13	26
Satyrinae	33	4	10	11	11	3	41
Riodinidae	1	0	0	0	0	0	1
Papilionidae	16	4	10	5	7	3	19
Pieridae	35	13	25	31	26	6	47
Lycaenidae	103	7	53	33	30	9	155
Hesperiidae							
Coeliadinae	3	0	2	1	1	0	3
Hesperiinae	80	3	16	11	8	4	87
Pyrginae	25	1	14	9	4	1	37
Total butterflies	**467**	**58**	**181**	**154**	**125**	**44**	**588**
Saturnidae (emperor moths)	57	36	38	45	42	3	63

Along the length of the Zambezi there are also many butterfly species that are particularly adaptable (eclectic species). These are able to establish themselves in a great variety of habitats throughout Africa. Most are species of open formations and occur almost everywhere except on the higher mountains and under extreme desert conditions. Their presence within forests is usually due to their ability to colonize such man-made habitats as road edges, footpaths, clearings, plantations and gardens. These adaptable species include *Papilio demodocus, Belenois gidica, B. creona, B. aurota,* *Mylothris agathina, Catopsilia florella, Eurema hecabe, E. brigitta, E. desjardinsii, Danaus chrysippus, Hamanumida daedalus, Neptis saclava, Byblia anvatara, Byblia ilithyia, Eurytela dryope, Hypolimnas misippus, Junonia oenone, J. hierta, J orithya, Cynthia cardui, Acraea encedon, A. eponina, Deudorix antalus, Anthene definita, Lampides boeticus, Zizula hylax, Zizeeria knysna, Coeliades forestan, Tagiades flesus* and *Peliopidas mathias*.

The Zambezi passes through four broad faunal regions – the Zambesian, Kalahari, Eastern Woodland and Coastal – and is therefore rich in butterfly diversity. This diversity is particularly noticeable when one considers the higher taxonomic categories. For example, certain genera found on the western side of the rift, such as *Liptena*, *Epitola*, *Oxylides* and *Telipna*, are not present or scarce in the east. Genera with their centres of origin in East or Southern Africa, such as the lycaenid genera *Capys* and *Cnodontes*, are either absent or rare in the western forests. The Zambezi Basin, has genera from both the western and eastern regions with 146 genera having been recorded from along the river itself.

The Zambezi Valley may also act as a barrier to butterfly movement. Some species found just north of the valley are not present in the south, for instance *Belenois crawshayi*. Many of these species are associated with miombo woodland and are probably unable to move across the hot, low-lying Zambezi Valley.

10.6.2 **Conservation**

The major concern for conservation is the small riverine forests to the west of Kalene Hill in the extreme northwest of Zambia. These forests provide the habitat and food plants for many of the unusual species recorded from this area, it is important to have an on-the-ground assessment so that the present state of the forest patches is truly known. Once an area of rainforest has been laid bare, its immense ecological complexity is unlikely to regenerate within historical time.

Most wetland butterfly species are closely linked to wetlands and would not be able to survive without them, with the possible exception of *Cacyreus lingeus, Leptosia alcesta, Cupidopsis cissus, Ypthimomorpha itonia* and *Catacroptera cloanthe* which can survive in drier habitats. Wetland species of particular interest are *Acraea periphanes, A. mirifica, Mylothris rubricosta, Zeretis fontainei* and *Z. sorhagenii*. The others are widely distributed in Africa and are not under any threat on a continental basis. All five species of interest have been recorded from the first section of the Zambezi; the only one recorded from other sections (2 and 3) is *M. rubricosta* which has a wider distribution than the others but is rather localized. Of these five species, *Zeritis fontainei* and *Acraea mirifica* have the most restricted total distributions, and the Zambezi Basin holds an important proportion of the global population. These two species are the most threatened, either due to habitat destruction or drying-out of their habitats.

10.7 CONCLUSIONS

The Mwinilunga area of the Zambezi is the most important area within the basin for butterfly diversity. This applies to both wetland and riparian species. In addition, two wetland species considered to be under global threat occur in this section. The Zambezi from Victoria Falls through to Tete has a distinctive fauna consisting of the more dry-adapted species, but none are under threat.

It is clear, from the paucity of records, that further research is required in the Barotseland area and in the Zambezi Delta. Although only 58 species are listed here for Barotseland, the presence of

Erikssonia acraeina suggests other species of interest may be present and many more could be added to this list. Further research in the Barotseland area is required to confirm and assess the affinities and importance of this section compared to the others. The present information suggests it forms a strong link between the wet Zambesian zone and the drier Kalahari zone, with a possible predominance of the Zambesian elements. With further collecting it is likely that this section would rank as the second most diverse part of the Zambezi.

It is probable that the low number of species from the Lower Shire is due to inadequate sampling, but the number of species is still expected to be lower than for Barotseland. It appears to form a link between the drier Kalahari, wetter Zambesian and eastern forest or woodland zones. Unfortunately, conclusions cannot be drawn for the Zambezi Delta. It should contain many elements from the East African woodlands and costal zones, and some of the rare coastal species are expected to occur.

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Table 10.1 List of species and subspecies from various butterfly families or subfamilies recorded from various parts of the Zambezi. (These do not equate to the faunal sections described earlier.)

●	species found in swamp or wetland habitats
Mwi	Mwinilunga area of northwestern Zambia (including the Mudwiji plains and Ikelenge District)
Bar	Barotse floodplains
C/C	Chobe/E.Caprivi/Linyanti swamps
VF	Victoria Falls
UZ	all other Upper Zambezi localities
V-K	Mid Zambezi from below Victoria Falls to Kariba dam wall
K-T	Mid Zambezi from below Kariba dam wall to Tete
LSh	Lower Shire Valley
P	species not recorded but likely to be found in Lower Shire Valley
LZ	other localities in the Lower Zambezi

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
NYMPHALIDAE										
Acraeinae										
Acraea (Acraea) acara acara *Hewitson, 1865*								X		
Acraea (Acraea) acrita *Hewitson, 1865*		X		X	X	X				
Acraea (Acraea) aganice nicega *(Suffert), 1904*		X								
Acraea (Acraea) aglaonice *Westwood, 1881*				X	X		X			
Acraea (Acraea) anemosa *Hewitson, 1856*		X		X	X	X			P	
Acraea (Acraea) asema *Hewitson, 1877*								X	P	
Acraea (Acraea) atergatis *Westwood, 1881*		X	X	X	X					
Acraea (Acraea) atolmis *Westwood, 1881*		X	X	X	X	X				
Acraea (Acraea) axina *Westwood, 1881*					X					
Acraea (Acraea) buettneri *Rogenhofer, 1889*		X								
Acraea (Acraea) caldarena *Hewitson, 1877*			X	X	X	X		X		
Acraea (Acraea) cepheus cepheus *(Linnaeus), 1758*		X								
Acraea (Acraea) chaeribula *Oberthur, 1893*		X								
Acraea (Acraea) diogenes *Suffert, 1904*		X								
Acraea (Acraea) eltringhamiana *Le Doux, 1932*		X								
Acraea (Acraea) epaea epaea *(Cramer), 1779*		X								
Acraea (Acraea) guillemei *Oberthur, 1893*		X								
Acraea (Acraea) leucographa *Ribbe, 1889*		X								
Acraea (Acraea) lygus *Druce, 1875*				X	X	X				
Acraea (Acraea) macarista macarista *(Sharpe), 1906*		X								
Acraea (Acraea) mansya *Eltringham, 1911*		X								
Acraea (Acraea) natalica *Boisduval, 1847*		X	X	X	X	X	X	X		X
Acraea (Acraea) neobule neobule *Doubleday, 1847*		X		X		X	X			
Acraea (Acraea) omrora umbraetae *Pierre, 1988*		X								
Acraea (Acraea) oncaea *Hopffer, 1855*								X		
Acraea (Acraea) periphanes *Oberthur,1893*	●	X								
Acraea (Acraea) poggei poggei *Dewitz, 1879*		X								
Acraea (Acraea) stenobea *Wallengren, 1860*										
Acraea (Acraea) umbra macarioides *(Aurivillius)*		X								
Acraea (Acraea) zetes acara *Hewitson, 1865*							X			
Acraea (Acraea) zetes zetes *(Linnaeus), 1758*		X								
Acraea (Actinote) acerata *Hewitson, 1874*	●		X	X	X	X				
Acraea (Actinote) alciope *(Hewitson), 1852*		X								

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
Acraea (Actinote) alicia alicia *(Sharpe), 1890*		X								
Acraea (Actinote) cabira *(Hopffer), 1855*								X		
Acraea (Actinote) encedana *(Pierre), 1976*		X								
Acraea (Actinote) encedon encedon *(Linnaeus), 1758*		X	X	X	X	X			P	X
Acraea (Actinote) eponina *(Cramer), 1780*		X		X	X	X	X			X
Acraea (Actinote) esebria esebria *Hewitson, 1861*		X								
Acraea (Actinote) induna induna *(Trimen), 1895*		X								
Acraea (Actinote) jodutta jodutt *(Fabricius), 1793*		X								
Acraea (Actinote) johnstoni praelongata *(Hancock & Heath), 1988*		X								
Acraea (Actinote) mirifica *(Lathy), 1906*	●	X								
Acraea (Actinote) ntebiae dewitzi *(Carcasson), 1981*		X								
Acraea (Actinote) obeira burni *(Butler), 1896*							X	X		
Acraea (Actinote) oreas angolanus *Lathy, 1906*		X								
Acraea (Actinote) peneleos pelasgius *Grose-Smith, 1900*		X								
Acraea (Actinote) perenna perenna *(Doubleday), 1847*		X								
Acraea (Actinote) pharsalus pharsaloides *(Holland), 1892*		X								
Acraea (Actinote) rahira rahira *Boisduval, 1833*	●	X		X		X				
Acraea (Actinote) servona servona *Godart, 1819*		X								
Acraea (Actinote) sotikensis *Sharpe, 1892*		X								
Acraea (Actinote) speciosa speciosa *(Wichgraf), 1909*		X								
Acraea (Actinote) ventura ventura *(Hewitson), 1877*	●	X								
Pardopsis punctatissima *(Boisduval), 1833*							X	X		
Charaxinae										
Charaxes achaemenes achaemenes *Felder & Felder, 1867*		X	X	X	X	X		X	X	
Charaxes acuminatus cottrelli *van Someren, 1963*		X								
Charaxes ameliae amelina *Joicey & Talbot, 1925*		X								
Charaxes anticlea adusta *Rothschild, 1900*		X								
Charaxes anticlea proadusta *van Someren 1971*		X								
Charaxes bohemani *Felder & Felder, 1859*		X		X	X			X		
Charaxes brutus angustus *Rothschild, 1900*		X								
Charaxes brutus natalensis *Staudinger, 1885*				X	X			X	X	
Charaxes candiope candiope *(Godart), 1824*				X		X		X		
Charaxes castor castor *(Cramer), 1775*		X								
Charaxes cedreatis *Hewitson, 1874*		X								
Charaxes cithaeron joanae *van Someren, 1964*								X		
Charaxes dilutus dilutus ? *Rothschild, 1898*		X								
Charaxes diversiforma *van Someren & Jackson, 1957*		X								
Charaxes drucaenus proximans *Joicey & Talbot, 1922*		X							P	
Charaxes ethalion binghami *Henning, 1982*								X		
Charaxes ethalion ethalion *(Boisduval), 1847*					X					
Charaxes etheocles carpenteri *van Someren & Jackson, 1957*		X								
Charaxes eudoxus mechowi *Rothschild, 1900*		X								
Charaxes eupale veneris *White & Grant, 1989*		X								
Charaxes fulgurata *Aurivillius, 1898*		X			X					
Charaxes fulvescens monitor *Rothschild, 1900*		X								
Charaxes guderiana guderiana *(Dewitz), 1879*		X	X	X	X	X	X	X		
Charaxes hildebrandti katangensis *Talbot, 1928*		X								

Species **Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Charaxes howarthi *Minig, 1976*	X								
Charaxes imperialis lisomboensis *van Someren, 1975*	X								
Charaxes jahlusa argynnides *Westwood, 1864*							X		
Charaxes jahlusa rex *Henning, 1978*							X		
Charaxes jasius saturnus *Butler, 1865*	X		X	X	X	X	X	X	X
Charaxes like catachrous *van Someren & Jackson, 1952*	X								
Charaxes lucretius intermedius *van Someren, 1971*	X								
Charaxes lucretius schofieldi *Plantrou, 1989*	X								
Charaxes manica *Trimen, 1894*							X		
Charaxes nichetes pantherinus *Rousseau-Decelle, 1934*	X								
Charaxes numenes aequatorialis *van Someren, 1972*	X								
Charaxes penricei penricei *Rothschild, 1900*	X			X					
Charaxes phaeus *Hewitson, 1877*			X		X		X		
Charaxes pollux geminus *Rothschild, 1900*								X	X
Charaxes pollux pollux *(Cramer), 1775*	X								
Charaxes protoclea azota *(Hewitson), 1877*	X								
Charaxes protoclea catenaria *Rousseau-Decelle, 1934*	X								
Charaxes pythodoris pythodoris *Hewitson, 1873*	X								
Charaxes vansoni *van Someren, 1975*					X				
Charaxes varanes vologeses *(Mabille), 1876*	X	X	X	X	X	X	X	X	X
Charaxes variata *van Someren, 1969*	X								
Charaxes zoolina zoolina *(Westwood), 1850*			X	X	X		X	P	
Euxanthe crossleyi crossleyi *(Ward), 1871*	X								
Euxanthe wakefieldi *(Ward), 1873*							X		
Argynninae									
Lachnoptera anticlia *(Hubner), 1819*	X								
Phalanta eurytis eurytis *(Doubleday), 1847*	X							P	
Phalanta phalantha aethiopica *(Rothschild & Jordan), 1903*	X	X	X	X	X	X	X	X	X
Danainae									
Amauris (Amaura) damocles hyalites *Butler,1874*	X								
Amauris (Amaura) dannfelti restricta *Talbot, 1940*	X								
Amauris (Amauris) niavius niavius *(Linnaeus), 1758*	X								
Amauris (Amauris) ochlea ochlea *(Boisduval), 1847*								P	X
Amauris (Amauris) tartarea tartarea *Mabille, 1876*	X								
Danaus (Anosia) chrysippus aegyptius *(Schreber), 1759*	X	X	X	X	X	X	X	X	X
Tirumala petiverana *(Doubleday), 1847*	X								
Libytheinae									
Libythea labdaca laius *Trimen, 1879*							X	P	
Limenitinae									
Aterica galene galene *(Brown), 1776*	X								X
Bebearia aurora theia *Hecq, 1989*	X								
Bebearia orientis orientis *(Karsch), 1895*							X		X
Bebearia plistonax *(Hewitson), 1874*	X								
Bebearia schoutedeni *(Overlaet), 1954*	X								
Bebearia senegalensis katera *(van Someren), 1939*	X								
Byblia anvatara acheloia *(Wallengren), 1857*	X		X	X		X	X	X	X
Byblia ilithyia *(Drury), 1773*		X	X	X					

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
Catuna crithea pallidior *Rothschild, 1918*		X								
Crenidomimas concordia *(Hopffer), 1855*		X								
Cymothoe caenis *(Drury), 1773*		X								
Cymothoe herminia katshokwe *Overlaet, 1940*		X								
Cymothoe sangaris luluana *Overlaet, 1945*		X								
Euphaedra cooksoni *Druce, 1905*		X								
Euphaedra harpalyce serena *Talbot, 1928*		X								
Euphaedra herberti katanga *Hecq, 1980*		X								
Euphaedra neophron neophron *(Hopffer), 1855*								X	X	X
Euphaedra overlaeti *Hulstaert, 1926*		X								
Euphaedra ruspina *(Hewitson), 1865*		X								
Euphaedra simplex *Hecq, 1978*		X								
Euphaedra zaddachi crawshayi *Butler, 1895*		X								
Euptera elabontas *(Hewitson), 1871*		X								
Euptera freyja *Hancock, 1984*		X								
Euptera hirundo lufirensis *Joicey & Talbot, 1921*		X								
Euptera pluto primitiva *Hancock, 1984*		X								
Euriphene (Euriphene) incerta theodota *(Hulstaert), 1924*		X								
Euriphene (Euriphene) iris *(Aurivillius), 1903*		X						X		
Euriphene (Euriphene) saphirina trioculata *(Talbot), 1927*		X								
Euriphene (Euriphene) tadema nigropunctata *(Aurivillius) 1901*		X								
Euriphene (Euryphura) chalcis *(Felder & Felder), 1860*		X								
Eurytela dryope angulata *Aurivillius, 1898*		X	X	X				X	X	X
Eurytela hiarbas lita *Rothschild & Jordan, 1903*									X	X
Hamanumida daedalus *(Fabricius), 1775*		X	X	X	X	X	X	X	X	X
Neptidopsis ophione nucleata *Grunberg, 1911*		X								
Neptis alta *Overlaet, 1955*		X		X	X			X		
Neptis conspicua *Neave, 1904*		X								
Neptis gratiosa *Overlaet, 1955*		X								
Neptis jordani *Neave, 1910*	●	X	X	X		X			X	X
Neptis kiriakoffi *Overlaet, 1955*		X								
Neptis laeta *Overlaet, 1955*		X	X	X						X
Neptis melicerta *(Drury), 1773*		X								
Neptis nementes nementes *Hewitson, 1868*		X								
Neptis nicoteles *Hewitson, 1874*		X								
Neptis nysiades *Hewitson, 1868*		X								
Neptis saclava marpessa *Hopffer, 1855*		X	X	X	X	X	X	X	X	X
Neptis serena serena *Overlaet, 1955*		X		X	X	X				
Neptis trigonophora melicertula *Strand, 1912*		X								
Pseudacraea boisduvalii boisduvalii *(Doubleday), 1845*		X								
Pseudacraea dolomena dolomena *(Hewitson), 1865*		X								
Pseudacraea eurytus eurytus *(Linnaeus), 1758*		X								
Pseudacraea kuenowii kuenowii *Dewitz, 1879*		X								
Pseudacraea lucretia expansa *(Butler), 1878*		X		X		X		X	X	X
Pseudacraea poggei *(Dewitz), 1879*		X								
Pseudacraea semire *(Cramer), 1779*		X								
Pseudargynnis hegemone *(Godart), 1819*	●	X								

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
Pseudathyma callina *(Grose-Smith), 1898*		X								
Pseudoneptis bugandensis ianthe *Hemming, 1964*		X								
Sallya amulia intermedia *(Carcasson), 1961*		X								
Sallya benguelae *(Chapman), 1872*		X	X							
Sallya boisduvali boisduvali *(Wallengren), 1857*		X								
Sallya consors *(Rothschild & Jordan), 1903*		X								
Sallya garega *(Karsch), 1892*		X								
Sallya moranti dubiosa *(Strand), 1911*		X								
Sallya pechueli rhodesiana *(Rothschild), 1918*		X								
Sallya sp. near amulia *(Cramer), 1777*		X								
Sallya trimeni trimeni *(Aurivillius), 1898*		X								
Nymphalinae										
Catacroptera cloanthe cloanthe *(Stoll), 1781*	●	X	X		X	X	X	X	X	
Cynthia cardui *(Linnaeus), 1758*		X	X	X	X	X	X	X	X	X
Hypolimnas anthedon anthedon *Doubleday, 1845*		X					X	X	X	X
Hypolimnas misippus *(Linnaeus), 1764*		X	X	X	X	X	X	X	X	X
Junonia actia *(Distant), 1880*		X						X		
Junonia antilope *(Feisthamel), 1850*		X	X	X	X	X	X	X	X	X
Junonia archesia archesia *(Cramer), 1779*		X			X				X	X
Junonia artaxia *Hewitson, 1864*		X			X		X	X	X	X
Junonia ceryne ceryne *(Boisduval), 1847*	●	X	X						X	X
Junonia cuama *Hewitson, 1864*		X							X	X
Junonia hierta cebrene *Trimen, 1870*		X	X	X	X	X	X	X	X	X
Junonia natalica natalica *(Felder & Felder), 1860*		X	X	X	X	X	X	X	X	X
Junonia octavia sesamus *(Trimen), 1883*		X	X	X	X	X	X	X	X	X
Junonia oenone oenone *(Linnaeus) 1758*		X	X	X	X	X	X	X	X	X
Junonia orithya madagascariensis *Guenee, 1865*		X	X	X	X	X	X	X	X	X
Junonia pelarga *(Fabricius), 1775*		X								
Junonia rauana osborni *(Holland), 1920*		X								
Junonia sinuata sinuata *(Plotz), 1880*		X								
Junonia sophia infracta *Butler, 1888*		X								
Junonia terea elgiva *Hewitson, 1864*		X								
Junonia touhilimasa *Vuillot, 1892*		X						X		
Junonia tugela pyriformis *Butler, 1896*		X								
Kamilla cymodoce *(Cramer), 1777*		X								
Salamis anacardii nebulosa *Trimen, 1881*		X			X	X		X		
Salamis parhassus *(Drury), 1782*		X							X	X
Vanessula milca latifasciata *Joicey & Talbot, 1928*		X								
Satyrinae										
Bicyclus angulosa selousi *(Trimen), 1895*		X					X		X	X
Bicyclus anynana anynana *(Butler), 1879*				X	X		X	X	X	
Bicyclus anynana centralis *Condamin, 1968*		X								
Bicyclus cooksoni *(Druce), 1905*		X								
Bicyclus cottrelli *(van Son), 1952*		X	X			X	X	X		
Bicyclus dubia *(Aurivillius), 1893*		X								
Bicyclus ena *(Hewitson), 1877*					X		X	X		
Bicyclus mandanes *Hewitson, 1873*		X								

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Bicyclus mesogena mesogena *(Karsch), 1894*		X								
Bicyclus moyses *Condamin & Fox, 1964*		X								
Bicyclus safitza safitza *(Westwood), 1850*		X							X	X
Bicyclus sandace *(Hewitson), 1877*		X								
Bicyclus sebetus *(Hewitson), 1877*		X								
Bicyclus sophrosyne overlaeti *Condamin, 1965*		X								
Bicyclus suffusa suffusa *(Riley), 1921*		X								
Bicyclus trilophus trilophus *(Rebel), 1914*		X								
Bicyclus vansoni *Condamin, 1965*		X								
Bicyclus vulgaris *(Butler), 1869*		X								
Coenyropsis bera *(Hewitson), 1877*		X					X		X	X
Gnophodes betsimena parmeno *Doubleday, 1849*		X								
Henotesia centralis *Aurivillius, 1903*		X								
Henotesia perspicua *(Trimen), 1873*									X	X
Henotesia phaea katangensis *Overlaet, 1955*		X								
Henotesia simonsii *(Butler), 1877*				X	X	X	X		X	X
Henotesia teratia *(Karsch), 1894*		X								
Melanitis leda helena *(Westwood), 1851*		X	X	X	X	X	X	X	X	X
Melanitis libya *Distant, 1882*		X						X		
Neocoenyra cooksoni *Druce, 1907*		X								
Physcaeneura pione *Godman, 1880*		X						X	X	X
Ypthima antennata antennata *van Son, 1955*					X		X		X	X
Ypthima asterope asterope *(Klug), 1832*						X			X	X
Ypthima condamini condamini *Kielland, 1982*									X	X
Ypthima congoana *Overlaet, 1955*		X								
Ypthima diplommata *Overlaet, 1954*		X	X							
Ypthima granulosa *Butler, 1883*				X	X	X				
Ypthima impura paupera *Ungemach, 1932*		X	X							
Ypthima praestans *Overlaet, 1954*		X			X					
Ypthima pulchra *Overlaet, 1954*		X								
Ypthima pupillaris pupillaris *Butler, 1888*		X								
Ypthima recta *Overlaet, 1955*		X								
Ypthima rhodesiana *Carcasson, 1961*							X	X		
Ypthimomorpha itonia *(Hewitson), 1865*	●	X		X	X	X				X
RIODINIDAE										
Abisara rogersi dollmani *Riley, 1932*		X								
PAPILIONIDAE										
Graphium adamastor *(Boisduval), 1836*		X								
Graphium almansor almansor *(Honrath), 1884*		X								
Graphium angolanus angolanus *(Goeze), 1779*		X	X	X	X	X			X	X
Graphium antheus *(Cramer), 1779*		X	X	X	X	X	X	X	X	X
Graphium leonidas leonidas *(Fabricius), 1793*		X	X	X	X	X	X	X	X	X
Graphium poggianus poggianus *(Honrath), 1884*		X								
Graphium policenes policenes *(Cramer), 1775*		X								
Graphium porthaon porthaon *(Hewitson), 1865*				X	X	X		X	P	

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Graphium ridleyanus *(White), 1843*		X								
Graphium schaffgotschi *(Niepelt), 1927*		X	X							
Graphium taboranus *(Oberthur), 1886*		X								
Papilio constantinus constantinus *Ward, 1871*					X	X			P	
Papilio dardanus cenea *Stoll, 1790*										X
Papilio dardanus dardanus *Brown, 1776*		X								
Papilio demodocus demodocus *Esper, 1798*				X		X	X	X	X	X
Papilio echerioides homeyeri *Plotz, 1880*		X								
Papilio hesperus hesperus *Westwood, 1843*		X								
Papilio mackinnoni theodori *Riley, 1921*		X								
Papilio nireus lyaeus *Doubleday, 1845*		X		X	X		X	X	X	X
Papilio nireus nireus *Linnaeus, 1758*		X								
Papilio phorcas congoanus *Rothschild, 1896*		X								
PIERIDAE										
Appias epaphia contracta *(Butler), 1888*								X	X	X
Appias sabina sabina *(Felder & Felder), 1865*		X								
Belenois aurota aurota *(Fabricius), 1793*		X	X	X	X	X	X	X		
Belenois calypso welwitschii *Rogenhofer, 1890*		X								
Belenois crawshayi *Butler, 1894*		X								
Belenois creona severina *(Stoll), 1781*		X	X	X	X	X	X	X	X	X
Belenois gidica abyssinica *Lucas, 1852*		X	X	X	X	X	X	X	X	
Belenois rubrosignata rubrosignata *(Weymer), 1901*		X								
Belenois thysa thysa *(Hopffer), 1855*		X								
Belenois zochalia agrippinides *(Holland), 1896*									X	
Catopsilia florella *(Fabricius), 1775*		X	X	X	X	X	X	X	X	X
Colias electo hecate *Strecker, 1900*		X								
Colias electo pseudohecate *Berger 1940*									X	X
Colotis agoye agoye *(Wallengren), 1857*				X		X				
Colotis amatus calais *(Cramer), 1775*				X		X		X		
Colotis antevippe gavisa *(Wallengren), 1857*		X	X	X	X	X	X	X	X	X
Colotis auxo *(Lucas), 1852*								X		
Colotis celimene amina *(Hewitson), 1866*		X		X			X	X		
Colotis celimene celimene *(Lucas), 1852*									X	
Colotis danae annae *(Wallengren), 1857*				X			X	X	X	
Colotis eris eris *(Klug), 1829*		X	X	X	X	X	X	X	X	X
Colotis euippe mediata *Talbot, 1939*		X	X	X	X	X	X	X		
Colotis euippe omphale *(Godart), 1819*				X	X	X	X	X	X	X
Colotis evagore antigone *(Boisduval), 1836*		X	X	X	X	X	X	X	X	X
Colotis evenina casta *(Gerstaeker), 1871*		X						X	P	
Colotis evenina evenina *(Wallengren), 1857*				X						
Colotis ione *(Godart), 1819*				X				X	P	
Colotis pallene *(Hopffer), 1855*				X				X		
Colotis regina *(Trimen), 1863*		X					X			
Colotis subfasciatus ducissa *(Dognin), 1891*		X							P	
Colotis vesta mutans *(Butler), 1877*							X	X		
Colotis vesta rhodesinus *(Butler), 1894*		X								

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Dixeia doxo parva *Talbot, 1943*							X	X	X	
Dixeia leucophanes *Vari, 1976*								X		
Dixeia pigea *(Boisduval), 1836*		X			X					
Eronia leda *(Boisduval), 1847*		X			X		X	X	X	
Eurema brigitta brigitta *(Stoll), 1780*		X	X	X	X	X	X	X	P	X
Eurema desjardinsii marshalli *Butler, 1898*		X	X	X	X	X	X	X	X	X
Eurema hapale *(Mabille), 1882*		X	X						X	X
Eurema hecabe solifera *(Butler), 1875*		X	?	X	X	X	X	X	X	X
Eurema senegalensis *(Boisduval), 1836*		X								
Leptosia alcesta inalcesta *Bernardi, 1959*	●	X						X	X	X
Mylothris agathina agathina *(Cramer), 1779*		X	X	X	X	X	X	X	X	X
Mylothris alcuana shaba *Berger, 1981*		X								
Mylothris bernice *Berger 1981*	●	?X								
Mylothris rubricosta rubricosta *(Mabille), 1890*	●	X	X	X	X					
Mylothris rueppellii haemus *(Trimen), 1879*								X		
Mylothris rueppellii rhodesiana *Riley, 1921*		X							X	X
Nepheronia argia argolisia *(Stoneham), 1957*		X								
Nepheronia argia mhondana *(Suffert), 1904*					X		X	X	P	
Nepheronia buquetii buquetii *(Boisduval), 1836*								X		
Nepheronia thalassina sinalata *(Suffert), 1904*		X			X		X	X	X	X
Pinacopteryx eriphia eriphia *(Godart), 1819*		X		X	X		X	X		
Pseudopontia paradoxa australis *Dixey, 1923*		X								
LYCAENIDAE										
Actizera lucida *(Trimen), 1883*		X							X	X
Alaena amazoula nyasana *Hawker-Smith, 1933*								X		
Alaena interposita hauttecoeuri *Oberthur, 1888*		X								
Alaena lamborni *Gifford, 1965*									X	
Alaena nyassa nyassa *Hewitson, 1877*									X	
Aloeides damarensis damarensis *(Trimen), 1891*				X						
Aloeides molomo krooni *Tite & Dickson, 1973*				X						
Aloeides molomo mumbuensis *Riley, 1921*					X					
Anthene amarah amarah *(Guerin-Meneville), 1849*				X	X	X		X		
Anthene contrastata mashuna *(Stevenson), 1937*				X		X	X			
Anthene crawshayi crawshayi *(Butler), 1899*		X								
Anthene definita definita *(Butler), 1899*		X							X	X
Anthene hobleyi *(Neave), 1904*		X								
Anthene kersteni *(Gerstaecker), 1871*		X							X	
Anthene lemnos lemnos *(Hewitson), 1878*		X								
Anthene ligures *(Hewitson), 1874*		X								
Anthene liodes *(Hewitson), 1874*								X	X	
Anthene lunulata *(Trimen) 1894*		X		X		X			X	
Anthene nigropunctata *(Bethune-Baker), 1910*		X								
Anthene princeps princeps *(Butler), 1876*				X			X			
Anthene rubricinctus anadema *(Druce), 1905*		X								
Anthene sp.		X								
Anthene sp.nr. wilsoni *Talbot, 1935*		X								

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Aphnaeus erikssoni *Trimen, 1891*		X								
Argyrosheila inundifera *Hawker-Smith, 1933*		X								
Aslauga marshalli ? *Butler, 1899*		X								
Aslauga purpurascens *Holland, 1890*		X								
Aslauga vininga *(Hewitson), 1875*		X								
Axiocerses amanga *(Westwood), 1881*				X		X		X	X	X
Axiocerses bambana *Grose-Smith, 1900*									X	X
Axiocerses tjoane *(Wallengren), 1857*				X	X	X		X		
Axiocerses tjoane rubescens *Henning & Henning, 1996*		X								
Azanus isis *(Drury), 1773*		X								
Azanus jesous jesous *(Guerin-Meneville), 1849*				X		X				
Azanus mirza *(Plotz), 1880*		X								
Azanus moriqua *(Wallengren), 1857*				X		X				
Azanus natalensis *(Trimen), 1887*							X			X
Azanus ubaldus *(Stoll), 1782*						X				
Baliochila hildegarda *(Kirby), 1887*		X								
Cacyreus lingeus *(Stoll), 1782*	●	X							X	X
Cacyreus marshalli *Butler, 1898*				X						
Cacyreus virilis *Aurivillius, 1924*				X					P	
Citrinophila terias *Joicey & Talbot, 1921*		X								
Cnodontes pallida *(Trimen), 1898*								X		
Cnodontes vansomereni *Stempffer & Bennett, 1953*								X		
Crudaria leroma *(Wallengren), 1857*				X	X	X				
Cupidesthes arescopa orientalis *(Stempffer), 1962*		X								
Cupidopsis cissus *(Godart), 1824*	●	X		X						
Cupidopsis jobates jobates *(Hopffer), 1855*				X		X				
Deloneura subfusca *Hawker-Smith, 1933*		X								
Deudorix (Actis) mimeta mimeta *(Karsch), 1895*		X								
Deudorix (Hypokopelates) kafuensis *Neave, 1910*		X								
Deudorix (Pilodeudorix) caerulea *Druce, 1890*							X			
Deudorix (Pilodeudorix) zeloides *(Butler), 1901*		X								
Deudorix (Virachola) antalus *(Hopffer), 1855*			X	X		X	X	X	X	X
Deudorix (Virachola) dinochares *Grose-Smith, 1887*				X	X		X	X		
Deudorix (Virachola) diocles *Hewitson, 1869*							X		X	
Deudorix (Virachola) jacksoni *Talbot, 1935*		X								
Deudorix (Virachola) lorisona coffea *Jackson, 1966*					X					
Eicochrysops hippocrates *(Fabricius), 1793*	●	X	X	X	X	X				X
Eicochrysops messapus mahallakoaena *(Wallengren), 1857*		X		X		X				
Eicochrysops pinheyi *Heath, 1985*		X								
Epitola carcina *Hewitson, 1873*		X								
Epitola sp.		X								
Epitola katerae *Jackson, 1962*		X								
Epitola mpangensis *Jackson, 1962*		X								
Epitola subgriseata ? *Jackson, 1964*		X								
Epitola viridana viridana *Joicey & Talbot, 1921*		X								
Eresina toroensis *Joicey & Talbot, 1921*		X								
Erikssonia acraeina *Trimen, 1891*			X							

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Euchrysops barkeri *(Trimen), 1893*										X
Euchrysops katangae *Bethune-Baker, 1923*		X								
Euchrysops malathana *(Boisduval), 1833*		X		X	X	X		X	X	X
Euchrysops osiris osiris *(Hopffer), 1855*		X		X	X	X		X		X
Euchrysops severini *Hulstaert, 1924*		X								
Euchrysops subpallida *Bethune-Baker, 1923*		X								
Freyeria trochylus *(Freyer), 1843*		X	X	X		X	X	X	X	X
Hemiolaus caeculus caeculus *Hopffer, 1855*				X	X	X	X	X	X	
Hemiolaus caeculus vividus *(Pinhey), 1962*		X								
Hewitsonia kirbyi kirbyi *Dewitz, 1879*		X								
Hypolycaena buxtoni buxtoni *Hewitson, 1874*		X							X	
Hypolycaena liara *Druce, 1890*		X								
Hypolycaena phillipus phillipus *(Fabricius), 1793*		X	X	X	X	X	X		X	
Iolaus (Aphniolaus) pallene *(Wallengren), 1857*					X				P	
Iolaus (Argiolaus) aequatorialis *(Stempffer & Bennett), 1958*		X								
Iolaus (Argiolaus) cottrelli *(Stempffer & Bennett), 1958*		X								
Iolaus (Argiolaus) silarus *Druce, 1885*		X		X		X	X	X		
Iolaus (Epamera) australis *Stevenson, 1937*		X								
Iolaus (Epamera) bakeri *(Riley), 1928*		X								
Iolaus (Epamera) mimosae rhodosense *(Stempffer & Bennett), 1959*				X	X					
Iolaus (Epamera) nasisii *(Riley), 1928*						X				
Iolaus (Epamera) sidus *Trimen, 1864*								X		
Iolaus (Epamera) violacea *(Riley), 1928*		X								
Iolaus (Iolaphilus) trimeni *Wallengren, 1875*		X		X	X					
Iolaus (Stugeta) bowkeri nyasana *(Talbot), 1935*									X	
Iolaus (Stugeta) bowkeri tearei *(Dickson), 1980*				X	X	X		X		
Lachnocnema bibulus *(Fabricius), 1793*									P	X
Lachnocnema durbani *Trimen, 1887*									P	X
Lampides boeticus *(Linnaeus), 1767*			X	X		X		X	X	
Lepidochrysops chloauges *(Bethune-Baker), 1923*				X	X					
Lepidochrysops cinerea cinerea *(Bethune-Baker), 1923*		X								
Lepidochrysops glauca *(Trimen), 1887*					X		X	X	P	
Lepidochrysops pampolis *(Druce), 1905*		X								
Lepidochrysops patricia? *(Trimen), 1887*					X	X				
Lepidochrysops plebeia plebeia *(Butler), 1898*				X						
Lepidochrysops pterou ssp. *(Bethune-Baker), 1923*		X								
Lepidochrysops sp. A		X								
Leptomyrina (Letomyrina) hirundo *(Wallengren), 1857*										X
Leptotes babaulti *(Stempffer), 1935*		X						X		
Leptotes brevidentatus *(Tite), 1958*								X		
Leptotes jeanneli *(Stempffer), 1935*		X								
Leptotes pirithous pirithous *(Linnaeus), 1767*		X		X	X	X		X	X	X
Leptotes pulchra *(Murray), 1874*	●	X	X	X				X		
Liptena eukrines *Druce, 1905*		X								
Liptena fulvicans *Hawker-Smith, 1933*		X								
Liptena homeyeri homeyeri *Dewitz, 1884*		X								
Liptena lualaba *Berger, 1981*		X								

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Liptena praestans congoensis *Schultze, 1923*		X								
Liptena xanthostola xantha *(Grose-Smith), 1901*		X								
Mimacraea marshalli marshalli *Trimen, 1898*		X								
Mimacraea skoptoles *Druce, 1907*		X								
Myrina silenus silenus *(Fabricius), 1775*		X								
Neurellipes gemmifera *(Neave), 1910*		X								
Oboronia guessfeldti *(Dewitz), 1879*		X								
Ornipholidotos overlaeti *Stempffer, 1947*		X								
Ornipholidotos peucetia peucetia *(Hewitson), 1866*		X								
Oxylides faunus albata *(Aurivillius), 1895*		X								
Pentila inconspicua? *Druce, 1910*		X								
Pentila pauli elisabetha *Hulstaert, 1924*		X								
Pentila pauli nyassana *Aurivillius, 1898*									X	X
Pentila pauli obsoleta *Hawker-Smith, 1933*					X					
Pentila tropicalis tropicalis *(Boisduval), 1847*					X					
Pentila umangiana meridionalis *Berger, 1981*		X								
Phlyaria heritsia virgo *(Butler), 1896*		X								
Pseudonacaduba aethiops *(Mabille), 1877*		X								
Pseudonacaduba sichela sichela *(Wallengren), 1857*		X							P	
Spalgis lemolea *Druce, 1890*					X					
Spindasis brunnea *Jackson, 1966*					X					
Spindasis ella *(Hewitson), 1865*				X		X	X	X		
Spindasis homeyeri *(Dewitz), 1887*		X								
Spindasis modestus heathi *D'Abrera, 1980*		X								
Spindasis mozambica *(Bertolini), 1850*		X								
Spindasis natalensis *(Westwood), 1851*				X	X	X			P	
Spindasis phanes *(Trimen), 1873*				X	X			X		
Tarucus sybaris sybaris *(Hopffer), 1855*				X		X				
Telipna ruspinoides katangae *Stempffer, 1961*		X								
Teratoneura isabellae congoensis *Stempffer, 1954*		X								
Thermoniphas distincta *(Talbot), 1935*		X								
Thermoniphas fontainei *Stempffer, 1956*		X								
Thermoniphas micyclus colorata *(Ungemach), 1932*		X			X					
Triclema nigeriae *(Aurivillius), 1905*		X								
Tuxentius calice calice *(Hopffer), 1855*		X		X				X		
Tuxentius melaena melaena *(Trimen), 1887*		X		X					P	
Uranothauma antinorii felthami *(Stevenson), 1934*		X								
Uranothauma falkensteini *(Dewitz), 1879*		X								
Uranothauma poggei *(Dewitz), 1879*		X								
Zeritis fontainei *Stempffer, 1956*	●	X								
Zeritis sorhagenii *(Dewitz), 1879*	●	X								
Zintha hintza hintza *(Trimen), 1864*				X	X	X				
Zizeeria knysna *(Trimen), 1862*				X		X		X		X
Zizula hylax *(Fabricius), 1775*				X	X	X		X	X	X

Species	Section	Mwi	Bar	C/C	VF	UZ	V-K	K-T	LSh	LZ
HESPERIIDAE										
Coeliadinae										
Coeliades forestan forestan *(Stoll), 1782*		X		X	X	X	X	X	X	X
Coeliades libeon *(Druce), 1875*		X				X				
Coeliades pisistratus *(Fabricius), 1793*		X								
Hesperiinae										
Acada biseriata *(Mabille), 1893*		X		X			X			
Acleros mackenii *(Trimen), 1868*		X							P	
Acleros ploetzi *Mabille, 1890*		X								
Andronymus caesar philander *(Hopffer), 1855*		X						X		
Andronymus fenestrella *Bethune-Baker, 1908*		X								
Andronymus marcus *Usher, 1980*		X								
Andronymus neander neander *(Plotz), 1884*		X						X		
Ankola fan *(Holland), 1894*		X								
Artitropa cama *Evans, 1937*		X								
Astictopterus abjecta *(Snellen), 1872*		X								
Astictopterus punctulata *(Butler), 1895*		X								
Borbo borbonica borbonica *(Boisduval), 1833*		X		X	X	X			X	X
Borbo detecta *(Trimen), 1893*		X								
Borbo fallax *(Gaede), 1916*		X		X		X				X
Borbo fanta fanta *(Evans), 1937*							X			
Borbo fatuellus fatuellus *(Hopffer), 1855*		X		X	X		X	X	X	X
Borbo gemella *(Mabille), 1884*				X	X	X	X			
Borbo holtzi *(Plotz), 1883*		X								
Borbo micans *(Holland), 1896*	●	X		X						
Borbo perobscura *(Druce), 1912*		X								
Borbo sirena *(Evans), 1937*		X								
Brusa allardi *Berger, 1967*		X								
Brusa saxicola *(Neave),1910*		X								
Caenides dacela *(Hewitson), 1876*		X								
Caenides halma *(Evans), 1937*		X								
Caenides leonora *dux (Evans), 1937*		X								
Ceratrichia flava semlikensis *Joicey & Talbot, 1921*		X								
Ceratrichia semilutea *Mabille, 1891*		X								
Fresna cojo *(Karsch), 1893*		X								
Fresna nyassae *(Hewitson), 1878*		X								
Gamia shelleyi *(Sharpe), 1890*		X								
Gegenes hottentota *(Latreille), 1824*		X		X	X	X				
Gegenes niso brevicornis *(Plotz), 1884*		X	X	X	X	X				
Gegenes pumilio *(Hoffmansegg), 1804*				X		X	X			
Gorgyra aretina *(Hewitson), 1878*		X								
Gorgyra diva *Evans, 1937*		X								
Gorgyra johnstoni *(Butler), 1894*		X								
Gorgyra moquerysii *Holland, 1896*		X								
Hypoleucis ophiusa ophir *Evans, 1937*		X								
Kedestes brunneostriga *(Plotz), 1884*		X								

Species	**Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Kedestes callicles *(Hewitson), 1868*					X	X	X			
Kedestes heathi *Hancock & Gardiner, 1982*		X								
Kedestes michaeli *Gardiner & Hancock, 1982*		X								
Kedestes mohozutza *(Wallengren), 1857*		X								
Kedestes nerva paola *(Plotz), 1884*		X								
Kedestes pinheyi *Hancock & Gardiner, 1982*		X								
Kedestes protensa *Butler, 1901*		X								
Kedestes straeleni *Evans, 1956*		X								
Lepella lepeletier *(Latreille), 1824*		X								
Metisella angolana *(Karsch), 1896*		X								
Metisella formosus linda *Evans, 1937*		X								
Metisella kambove *(Neave), 1910*		X								
Metisella midas midas *(Butler), 1894*		X							P	
Metisella willemi *(Wallengren), 1857*		X								
Meza larea *(Neave), 1910*		X								
Monza punctata punctata *(Aurivillius), 1910*		X								
Paracleros biguttulus *(Mabille), 1890*		X								
Pardaleodes incerta *(Snellen), 1872*		X								
Parnara monasi *(Trimen), 1889*	●			X					X	X
Paronymus nevea *(Druce), 1910*		X								
Parosmodes morantii morantii *(Trimen), 1873*		X				X	X	X		
Pelopidas mathias *(Fabricius), 1789*		X	X	X	X	X	X		X	X
Pelopidas thrax inconspicua *(Bertolini), 1850*		X		X					P	X
Platylesches affinissima *Strand, 1921*		X								
Platylesches batangae *(Holland), 1894*		X								
Platylesches chamaeleon *(Mabille), 1891*		X								
Platylesches galesa *(Hewitson), 1877*		X								
Platylesches lamba *Neave, 1910*		X								
Platylesches moritili *(Wallengren), 1857*		X							P	
Platylesches picanini *(Holland), 1894*		X								
Platylesches robustus robustus *Neave, 1910*		X								
Platylesches shona *Evans, 1937*			X							
Platylesches tina *Evans, 1937*		X								
Prosopalpus debilis *(Plotz), 1879*		X								
Prosopalpus styla *Evans, 1937*		X								
Pteroteinon caenira *(Hewitson), 1867*		X								
Pteroteinon ceucaenira *(Druce), 1910*		X								
Semalea arela *(Mabille), 1891*		X								
Semalea proxima *(Plotz), 1886*		X								
Semalea pulvina *(Plotz), 1879*		X								
Teniorhinus harona *(Westwood), 1881*		X		X	X		X			
Teniorhinus ignita *(Mabille), 1877*		X								
Tsitana wallacei *(Neave), 1910*		X								
Xanthodisca vibius *(Hewitson), 1878*		X								
Zenonia zeno *(Trimen), 1864*		X								
Zophopetes cerymica *(Hewitson), 1867*		X								

Species **Section**	**Mwi**	**Bar**	**C/C**	**VF**	**UZ**	**V-K**	**K-T**	**LSh**	**LZ**
Zophopetes dysmephila *(Trimen), 1868*			X						
Pyrginae									
Abantis bamptoni *Collins & Larsen, 1994*	X								
Abantis contigua *Evans, 1937*	X								
Abantis paradisea *(Butler), 1870*			X					P	
Abantis venosa, *Trimen, 1889*	X					X	X		
Abantis vidua *Weymer, 1901*	X								
Abantis zambesiaca *(Westwood), 1874*	X							X	X
Calleagris hollandi *(Butler), 1897*	X								
Calleagris jamesoni jamesoni *(Sharpe), 1890*	X		X						
Calleagris lacteus *(Mabille), 1877*	X								
Caprona pillaana *Wallengren, 1857*			X		X				
Celaenorrhinus bettoni *Butler, 1902*	X								
Celaenorrhinus galenus *(Fabricius), 1793*	X								
Eagris decastigma *Mabille, 1891*	X								
Eagris lucetia *(Hewitson), 1875*	X								
Eretis melania *Mabille, 1891*	X								
Gomalia elma elma *(Trimen), 1862*			X		X		X		
Katreus hollandi *(Druce), 1909*	X								
Katreus holocausta *(Mabille), 1891*	X								
Leucochitonea levubu *Wallengren, 1857*				X	X		X		
Netrobalane canopus *(Trimen), 1864*	X								
Sarangesa astrigera	X								
Sarangesa brigida brigida *(Plotz), 1879*	X								
Sarangesa laelius *(Mabille), 1877*	X								
Sarangesa lucidella lucidella *(Mabille), 1891*			X	X		X			
Sarangesa maculata *(Mabille), 1891*	X								
Sarangesa motozi *(Wallengren), 1857*				X					
Sarangesa pandaensis deningi *Evans, 1956*	X								
Sarangesa phidyle *(Walker), 1870*			X	X		X	X		
Sarangesa seineri seineri *Strand, 1909*			X	X	X	X			
Spialia colotes transvaaliae *(Trimen), 1889*							X		
Spialia delagoae *(Trimen), 1898*			X						
Spialia diomus ferax *(Wallengren), 1863*			X						
Spialia dromus *(Plotz), 1884*	X							X	
Spialia mafa mafa *(Trimen), 1870*			X	X	X				
Spialia secessus *(Trimen), 1891*	X								
Spialia spio *(Linnaeus), 1764*	X		X		X		X		X
Tagiades flesus *(Fabricius), 1781*	X	X	X	X	X	X	X	X	X
Totals: 612 taxa	**472**	**60**	**144**	**119**	**111**	**89**	**131**	**126**	**96**

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CHAPTER 10 : APPENDIX 1
LIST OF LEPIDOPTERA COLLECTED FROM BAROTSELAND

Lepidoptera specimens were collected from the Barotseland area by Rafael Chiwanda and Philip Mhlanga from 20 March to 4 April 1999. Localities collected were:

Ndau School transect: 15°25'41"S / 22°57'49"E
Ndau School area: 15°25'S / 22°58'E
Sefula: 15°23'11"S / 23°10'07"E
Mongu: 15°17'46"S / 23°08'36"E
Kalabo: 14°58'10"S / 22°38'27"E
Kalabo, 5 km west: 14°54'58"S / 22°34'02"E

List of Species Collected (nomenclature follows Pennington 1994, second edition).

BUTTERFLIES
Family Nyphalidae
Sub-tribe Melantini
Melantis leda helena
Ypthima impura?

Tribe Acraeni
Acraea acerata
Acraea atergatis
Acraea atolmis
Acraea caldarena
Acraea encedon encedon
Acraea natalica

Tribe Charaxinae
Bybilia ilithya
Charaxes achamenes achamenes
Eurytela dryope angulata
Hamanumida daedalus
Neptis jordani
Neptis laeta
Precis antelope
Precis ceryne
Precis octavia sesamus
Precis oenone oenone

Family Lycaenidae
Tribe Hypolycaenini
Deudorix antalus
Eicochrysops trochilus
Freyeria trochylus
Hypolycaena phillipus
Lampides boeticus
Leptotes pulcher

Family Pieridae
Eurema brigitta brigitta
Eurema hapale
Mylothris agathina
Mylothris rubricosta rubricosta

Family Hesperidae
Gegenes niso niso
Pelopidas mathias
Platylesches shona

MOTHS
Macroglossium trochilus
Othreis materna

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CHAPTER 10 - APPENDIX 2
LEPIDOPTERA SPECIES COLLECTED FROM THE ZAMBEZI DELTA

Nicola Feltham

1. INTRODUCTION

As is the case with most wetlands world-wide, the biodiversity of the Zambezi Basin is under threat from increasing human population growth and associated impacts. Little is known about the biodiversity of this area, therefore it is important to document the species present in the basin so that, as human impact increases, changes in faunal population numbers and species occurrence may be monitored.

Butterflies have long been recognized as indicators of environmental health (Feltwell 1986, Kremen & Razafimahatratra 1990, New 1997). Ecological indicators, as defined by Noss (1990), are "species that signal effects of perturbations on a number of other species with similar habitat requirements". Although there are many other insect groups that may serve as ecological indicators (Brown 1991), a wide range of butterfly families are particularly good candidates for both practical and biological reasons – they are often involved in highly specific plant-herbivore and plant-pollinator interactions (Ehrlich & Raven 1964, Pullin 1995), and there is good taxonomic knowledge of butterflies and they are easy to identify in the field (Pollard & Yates 1993). The widespread butterfly population and species losses reported by many researchers (e.g. Pyle *et al.* 1981, New 1997), frequently as a consequence of habitat fragmentation, often reflect the decline of a number of other taxa with similar habitat requirements.

This study details butterfly species diversity in one of the four IUCN Zambezi Basin Wetlands Biodiversity Project areas, namely the wetlands of the lower Zambezi Delta in what is called the Marromeu Complex. The sites chosen are described, the butterfly species at each site catalogued and a brief description of the known distribution and environmental requirements of each butterfly species is given. Cognisance of the status of butterflies as environmental indicators is taken and brief conclusions about the condition of environmental health made on the basis of the findings.

2. SAMPLING SITES

2.1 Site A: Safrique — $18^0$26'52" S / $35^0$53'46" E

Sampling took place in semi cultivated lands, a short walking distance from the village outskirts. Rice was the principal crop, but owing to the dry soil conditions, plants were very stunted. Sorghum was also growing in the fields. *Vigna* spp. were abundant in the grassland and banana plants and Ilala palms (*Hyphaene coriacea)* in the area provided sheltered habitats for insect species. Along the edges of the cultivated fields, *Typha* sp. grew very tall and formed a moist environment at ground level. The area falls into the "dry wet grasslands" of the Marromeu complex as small water channels cross the area, although not filled with any water at the time. The soil was dry, black loam. This area was sampled on two consecutive days.

The most common butterflies in the area were *Danaus chrysippus, Hyalites eponina, Papilio demodocus demodocus* and *Eurema brigitta brigitta*, all highly eurotopic species. *Bicyclus safitza* and *Ypthimiomorpha itonia* were only found in association with *Typha* sp.

2.2 Site B: Vila Nova — $18^0$23'42" S / $35^0$54'27" E

This site, 10 km south of Marromeu town, was sampled on two consecutive days; traps were set with banana bait. The area was very swampy; a tributary bisected the area and tall papyrus and *Typha* grew at the water's edge. A small settlement was situated on one bank of the tributary and associated rice paddies had been planted very close to the water in one area of the site. Coconut, *Phoenix* palms and bananas grew on one bank. Very little habitat in the immediate vicinity of permanent bodies of water throughout the Marromeu complex remain completely uncultivated. As a result, it was logistically very difficult to locate sampling areas described as "swampy wet grasslands" that were completely free of human interference. *Neptis laeta* was particularly common here as was *Amauris ochlea.* The traps failed to catch anything except four *Bicyclus safitza safitza* individuals. *Bebearia orientis orientis* was found in association with its larval host, *Phoenix reclinata* (wild date palm), and also flying around banana trees.

2.3 **Site C: River bank along the Zambezi** 3 km range from Marromeu factory

Much of the day was spent observing insects from a canoe over an area which extended up and down from the factory in Marromeu. Very few butterflies were seen over the water or at the water's edge (from 9.00 to 11.00 only three butterfly individuals were observed, these being the common African Monarch and *H. eponina*). *Papilio demodocus demodocus* and *P. dardanus cenea* individuals were common around a small village on the river bank south of Marromeu. *Eurytela dryope* was seen flying around its larval host, *Ricinus communis* (the castor oil plant). The vegetation was typical of this environment: *Salvinia* sp., *Eichornia* sp., *Ipomea* sp. (?) and other water weeds predominated at the water's edge. Farther from the water, grass grew in rank stands. Where there was human habitation, common weeds such as *Bidens pilosa*, *Ageratum houstonianum, Tagetes minuta* and *Senecio* sp. grew in abundance around the houses and in the areas cultivated with vegetables, sugarcane and *Ricinus communis*.

2.4 **Site D: River bank, 4 and 6 km south of Marromeu** $18^0$18'18" S / $35^0$59'58" E

$18^0$19'51" S / $36^0$01'25" E

As over the area covered at Site C, very few butterflies were seen in the vicinity of the river, except around human habitation where crops had been planted and plant weeds flourished. *Danaus chrysippus aegyptius* and *Hyalites eponina* were the only species seen with any regularity.

2.5 **Site E: Bambani Area** $18^0$18'09" S / $35^0$53'21" E

Like Site A, this area can be described as "dry wet grassland". Short grassland and small water channels made up this area, again depleted in butterfly fauna. Although nearby areas had been cultivated, the site itself was not. Relatively high abundance of blues and skippers is perhaps a reflection of the cropped vegetation and the presence of larval food plants, *Indigofera sp* (Clover Blue), *Oxalis corniculata* (Sooty Blue) and water-side grasses (the skippers).

2.6 **Site F: Palm grove, north of Marromeu** $18^0$13'05" S / $35^0$46'21" E

Undisturbed palm savanna, free of human habitation was a particularly difficult habitat to find in the Marromeu complex. Site F can perhaps be described as a palm grove since the ground beneath the coconut and Ilala palms was heavily cultivated with sugar-cane and sorghum. Around the houses, weed plants (in particular *Ageratum houstonianum*) grew in abundance. Traps set here with banana bait and left overnight revealed no new species.

2.7 **Site G - Palm savanna, south of Marromeu** $18^0$28'08" S / $35^0$53'43" E

This site is situated 3-4 km south of Safrique and was sampled over two consecutive days since it was relatively accessible, given the logistical problems of reaching palm savanna that was not inhabited. Both coconut and Ilala palms were abundant in the area; grass growth was dense. No water bodies were present and consequently the site was very dry. Sampling in this area was very poor with an average of three species being observed every hour; these butterflies being the eurytopic species present at each of the other sites. Traps yielded a *Melantis leda helena* and a *Papilio demodocus demodocus*. Significantly, it was observed that while walking through the homesteads to reach this area, far more butterflies were observed than when at the site. The pansies and other *M. leda helena* were caught around houses, vegetable gardens and other planted crops. *Asystacia gangetica* grew prolifically in vicinity of houses.

3. DISTRIBUTION AND ENVIRONMENTAL REQUIREMENTS

The various species found are described below. Table 1 shows the distribution between sites.

Appendix 10.2 Table 1 Butterfly species collected in the Marromeu area in June 1999 (* not common; ** common; *** very common).

Scientific name	Common name	Site							
		A	B	Ci	Cii	D	E	F	G
NYMPHALIDAE									
Danainae									
Danaus (A.) chrysippus aegyptius	African Monarch	***	**			**	**		***
Amauris (A.) ochlea ochlea	Novice Friar	***	***					***	**
Satyrinae									
Bicyclus safitza safitza	Common Bush Brown	**	***		***			**	
Ypthimomorpha itonia	Marsh Ringlet	**	**						**
Melantis leda helena	Common Evening Brown								*
Acraeinae									
Hyalites (H.) eponina	Dancing Acraea	***	***	***	***	**	***		
Hyalites encedon encedon	Common Mimic Acraea	*	**	*					
Acraea (Stephenia) natalica natalica	Natal Acraea		*						
Nymphalinae									
Bebearia orientis orientis	Eastern Palm Forester		**						
Euphaedra neophron neophron	Gold-banded Forester				**				
Hamanumida daedalus (sighted)	Guinea-fowl				**				
Aterica galene theophane	Forest-glade Nymph				*				
Neptis jordani	Jordan's Sailor						**		
Neptis laeta	Common Sailor		***					**	
Byblia anvatara acheloia	Common Joker							*	
Eurytela dryope angulata	Golden Piper			*				*	
Hypolimnas misippus	Common Diadem			*					
Precis (Junonia) oenone oenone	Blue Pansy			*					
Precis (J.) natalica natalica	Brown Pansy								*
Precis (J.) orithya madagascariensis	Eyed Pansy	*						**	*
Vanessa (Cynthia) cardui	Painted Lady		*					*	
LYCAENIDAE									
Miletinae									
Lachnocnema bibulus	Common Woolly Legs							**	
Lachnocnema durbani	D'Urban's Woolly Legs	*							
Polyommatinae									
Leptotes pirithous / brevidentatus	Common Blue	*							
Azanus natalensis	Natal Spotted Blue					*			

Scientific name	Common name	Site							
		A	B	Ci	Cii	D	E	F	G
Euchrysops sp.									*
Euchrysops malathana	Common Smoky Blue			*	*				
Euchrysops osiris	Osiris Smoky Blue	**							
Euchrysops barkeri	Barker's Smoky Blue	*							
Eicochrysops hippocrates	White-tipped Blue			*					
Zizeeria knysna	Sooty Blue						**		
Zizina antanossa (?)	Clover Blue	*					**		**
Freyia trochylus	Grass Jewel Blue		*						
PIERIDAE									
Pierinae									
Catopsilia florella	African Migrant	*							
Eurema (M.) brigitta brigitta	Broad-bordered Grass Yellow	***	***		***	**		***	***
Belenois creona severina	African Common White							**	
Mylothris agathina	Common Dotted Border	***		**				***	***
Leptosia alcesta inalcesta	African Wood White							*	
Appias epaphia contracta	Diverse White	**	**						
PAPIOLIONIDAE									
Papiolioninae									
Papilio demodocus demodocus	Citrus Swallowtail	***							***
Papilio dardanus cenea	Mocker Swallowtail			**					
Papilio nireus (sighted)	Green-banded Swallowtail								
HESPERIIDAE									
Pyrginae									
Spialia spio (?)	Mountain Sandman		*						
Hesperiinae									
Borbo fallax (?)	False Swift						*		
Borbo fatuellus fatuellus	Long-horned Swift		*						
Pelopidas thrax inconspicua	White Banded Swift		*						
Parnara monasi (?)	Water Watchman						*		

Danaus (A.) chrysippus aegyptius African Monarch
A very common butterfly that occurs all through the Afrotropical region and beyond. The species flies throughout the year at almost all altitudes and in most habitats. Larval host: members of Asclepiadaceae family.

Amauris (A.) ochlea ochlea Novice Friar
A widespread species in the eastern portion of Africa, particularly in coastal forests of KwaZulu-Natal and Mozambique. Although widespread, this species is not as common as others in the genus and in some years emerges in very small numbers. It is generally more common during the summer months so it is perhaps

surprising that the butterfly was so abundant during the sampling period (winter) around Marromeu. Larval host: members of Asclepiadaceae family.

Bicyclus safitza safitza Common Bush Brown
This species is very common throughout the Afrotropical region, particularly in rainforests. Individuals were caught in traps set with banana bait at Site B, Vila Nova. Larval host: grasses, in particular *Ehrharta erecta*.

Ypthimomorpha itonia Marsh Ringlet
This butterfly is found along the eastern border of Zimbabwe and in Mozambique, usually in marshy places. Larval host: not confirmed, but possibly waterside grasses.

Melantis leda helena Common Evening Brown
The species has an extensive range over the Afrotropical, Palaearctic and Indo-Australian regions. This particular subspecies occurs in a wide diversity of habitats; its range extends from wooded areas in Mozambique to coastal bush in the Transkei to the bushveld of northern South Africa, Zimbabwe, Botswana and N Namibia. This subspecies flies year-round, but is more plentiful during winter. Larval host: bristle grasses, kikuyu grass, sugar cane, *Cynodon* spp.

Hyalites (H.) eponina, Dancing Acraea
This species is described in Pennington's Butterflies (Pringle *et al.* 1994) as being extremely common, widespread throughout the Afrotropical region and ubiquitous along the eastern wide of southern Africa. Indeed, this was the most abundant butterfly on the wing in the Marromeu complex during the study period. Larval host: *Hermannia* and *Triumfetta* spp.

Hyalites encedon encedon Common Mimic Acraea
This butterfly is found throughout most of the eastern parts of southern Africa at all times of the year and is particularly common along the coastal areas of Natal and Mozambique. Larval host: *Commelina* spp.

Acraea (Stephenia) natalica natalica Natal Acraea
This is another very common species that is found along the eastern side of southern Africa, most often in wooded terrain. Larval host: members of Passifloraceae family.

Bebearia orientis orientis Eastern Palm Forester
This subspecies is widespread in Mozambique and has also been recorded along the eastern Zimbabwe border. Individuals were observed in the Marromeu complex in association with palm trees, the larval host-plant and caught in traps set at Site F. Larval host: *Phoenix reclinata* (wild date palm).

Euphaedra neophron neophron Gold-banded Forester
This species is widespread in Mozambique and also occurs along the eastern border of Zimbabwe. Although Pare has described the food plant as occurring abundantly along the middle part of the Zambezi River and its tributaries (Pringle *et al.* 1994), this species was not found along the Zambezi in the Marromeu complex, but only in the forests away from the water's edge. Larval host: members of the Sapindaceae family

Hamanumida daedalus Guinea-fowl
This butterfly is very common in Zimbabwe and Mozambique and also occurs in the Natal Midlands, Swaziland, northern parts of South Africa, N Namibia and Botswana. It flies throughout the year. Larval host: members of the Combretaceae family.

Aterica galene theophane Forest-glade Nymph
This species is widespread in Mozambique, common in the Dondo and Savane forests (Pringle *et al.* 1994) and also occurs along parts of the E Zimbabwe border. Larval host: members of the Combretaceae family.

Neptis jordani Jordan's Sailor
Specimens of this species have been recorded before from Dondo, Buzi River and Moribane forest in Mozambique and at specific spots in Zimbabwe. Larval host: not confirmed.

Neptis laeta Common Sailor
This is the most widespread and common southern African *Neptis.* It was particularly common at Site B. Larval host: various plants, including *Dalbergia, Brachystegia boehmii, Albizia adianthifolia* and *Acalypha* spp.

Byblia anvatara acheloia Common Joker
This butterfly is common across the eastern coast of southern Africa to Zimbabwe and N Namibia. Although usually observed throughout the year, few individuals of this species were observed. Larval host: members of Euphorbiaceae family.

Eurytela dryope angulata Golden Piper
This species is not nearly as common as *E. hiarbas*. It is to be found along the KwaZulu Natal coast, northern parts of South Africa, throughout Zimbabwe and Mozambique. Larval host: *Ricinus communis* (castor oil plant).

Hypolimnas misippus Common Diadem
An interesting mimic of other species, this butterfly is widespread throughout the Afrotropical region. Larval host: *Ageratum houstonianum* (floss flower), *Asystasia gangetica*.

Precis (Junonia) oenone oenone Blue Pansy
Another widespread species, this butterfly is common in most of southern Africa and flies throughout the year. Larval host: members of Acanthaceae family including *Asystasia gangetica*.

Precis (J.) natalica natalica Brown Pansy
This species occurs widely over Zimbabwe and Mozambique and is commonly seen in Natal throughout the year. Larval host: members of Acanthaceae family including *Asystasia gangetica*.

Precis (J.) orithya madagascariensis Eyed Pansy
Although these butterflies are generally not as common as others in the genus, individuals of this species were seen more regularly around Marromeu than *P. oenone* and *P. natalica*. Larval host: members of Acanthaceae family and *Plectranthus* spp.

Vanessa (Cynthia) cardui Painted Lady
This highly ubiquitous species is known throughout the world. Larval host: numerous plants, many of which are regarded as weeds (e.g. thistles).

Lachnocnema bibulus Common Woolly Legs
Found in woody and open savanna habitats throughout the eastern portions of the subcontinent, this species is regarded as being locally common and on the wing all year-round. Larval host: Psyllids (Homoptera).

Lachnocnema durbani D'Urban's Woolly Legs
Similar distribution and status to common woolly leg butterfly. Larval host: Coccids and membracids (Homoptera).

Leptotes pirithous / brevidentatus Common Blue/Short-toothed Blue
Species of this genus are difficult to distinguish from one another. *L. pirithous* is common almost everywhere in southern Africa and its distribution extends into Europe and even Asia. *L. brevidentatus* is similarly well distributed and coexists with L. *pirithous* down the east side of South Africa. This species does not appear

to have been previously collected from Mozambique. Larval host: *Plumbago auriculata* and various members of Fabaceae family.

Azanus natalensis Natal Spotted Blue
Although this species is commonly found in thornveld in KwaZulu-Natal, the northern regions of South Africa and the eastern parts of Zimbabwe, it appears that it has not been collected before in Mozambique (it is likely though that the specimen is an alternative species of *Azanus*). Larval host: *Acacia* spp.

Euchrysops sp.
*S*pecies remains unidentified and therefore its distribution is unknown.

Euchrysops malathana Common Smoky Blue
This inconspicuous blue butterfly is described in Pringle *et al*. 1994 as abundant in many parts of southern Africa, but Mozambique is not included in its distribution. Larval host: various *Vigna* spp. (Fabaceae family).

Euchrysops osiris Osiris Smoky Blue
*T*his species is seldom seen in large numbers and is more commonly found in Zimbabwe than Mozambique. Larval host: various *Vigna* spp. (Fabaceae family).

Euchrysops barkeri Barker's Smokey Blue
Although common in localised parts of South Africa, this species is rare in the northern parts of South Africa and has only been collected in Zimbabwe and Mozambique on a limited number of occasions. Larval host: various *Vigna spp*. (Fabaceae family).

Eicochrysops hippocrates White-tipped Blue
*T*his species is abundant in localized spots across a wide area of southern Africa. Larval host: *Polygonum sp, Rumex sp.*

Zizeeria knysn Sooty Blue
Described as the most common of all small blues from southern Africa. Larval host: *Oxalis corniculata*, *Euphorbia* sp. and a variety of other plants.

Zizina antanossa (?) Clover Blue
In comparison to *Z. knysa*, this species is rare, has a more restricted distribution and has not been described from Mozambique. Larval host: *Indigofera* spp*., Desmodium incanum*.

Freyia trochylus Grass Jewel Blue
*A*lthough widespread in distribution, this inconspicuous species is not found often. Larval host: *Indigofera cryptantha, Heliotropium* sp.

Catopsilia florella African Migrant
This species flies almost year-round and is often very abundant during seasonal migrations. It inhabits the whole of southern Africa. Larval host: various species of *Cassia* (Fabaceae).

Eurema (M.) brigitta brigitta Broad-bordered Grass Yellow
This species is far more common than others in its the genus and indeed more common than most of the Pierids. Larval host: *Hypericum aethiopicum, Cassia mimosoides*.

Belenois creona severina African Common White
*A*nother very common butterfly, this species also is often seen in large scale migrations. Larval host: *Boscia* spp*., Capparis* spp*., Maerua angolensis*.

Mylothris agathina Common Dotted Border
The distribution of this common species has, in recent years been shown to be increasing as the species adapts to additional food plants. Larval host: *Tapinathus rubromarginatus, Erianthemum dregei, Tieghemia quinquenervia, Ximenia caffra, Osyris lanceolata, Colpoon compressum.*

Leptosia alcesta inalcesta African Wood White
*T*his species is common from the KwaZulu-Natal coast through Swaziland, the northern parts of South Africa, Mozambique and into Zimbabwe. Larval host: *Capparis* spp.

Appias epaphia contracta Diverse White
*T*his species is widespread throughout Africa. Larval host: *Boscia* spp, *Capparis* spp*., Maerua angolensis*.

Papilio demodocus demodocus Citrus Swallowtail
"Abundant everywhere and throughout the year in subtropical Africa is no exaggeration for this ubiquitous butterfly" (Pringle *et al.* 1994). Larval host: a wide variety of tree species including *Clausena anisata, Calodendrum capense, Vepris* spp. and citrus trees.

Papilio dardanus cenea form *cenea* Mocker Swallowtail
This is the most common form of this subspecies of butterfly and is widely distributed over the eastern parts of southern Africa. Larval host: a variety of tree species including *Clausena anisata, Xymalos monospora, Vepris* spp. and citrus trees.

Papilio nireus lyaeus Green-banded Swallowtail
This subspecies is widespread in KwaZulu-Natal, Swaziland, the northern regions of South Africa and Mozambique. Larval host: a wide variety of tree species including *Clausena anisata, Calodendrum capense, Vepris* spp. and citrus trees.

Spialia spio (?) Mountain Sandman
This is a very common skipper that inhabits most of southern Africa. Larval host: *Hermannia* spp., *Hibiscus* spp., *Triumfetta* spp.

Borbo fallax (?) False Swift
A commonly occurring skipper that is distributed over the eastern parts of southern Africa in particular. Larval host: *Ehrharta* sp.

Borbo fatuellus fatuellus Long-horned Swift
Another commonly occurring skipper especially in coastal bush. Larval host: *Ehrharta erecta* and *Setaria megaphylla*.

Pelopidas thrax inconspicua White Banded Swift
This species is widespread over the whole of Africa and known to occur very commonly along the Zambezi River. Larval host: *Imperata cylindrica* and *Ehrharta erecta.*

Parnara monasi (?) Water Watchman
This species has occasionally been recorded as far as Beira; it's distribution appears to be scattered across southern Africa. In suitable localities this species can be common in winter. Larval host: waterside grass.

4. DISCUSSION

To a certain extent, fluctuations in butterfly assemblage structure may be attributed to taxonomic variations and the associated seasonal, ecological and biological differences (New 1997). Indeed, weather and large-scale climatic patterns have long been recognized as major factors in population dynamics of small ectothermic animals (Andrewartha & Birch 1954). Butterflies, being heliotherms, are generally associated with fine, sunny weather (Shapiro 1975, Pollard 1988, Pollard & Yates 1993). too, gives good evidence for a causal relationship between butterfly abundance and weather.

It is unfortunate that the heavy rains that were experienced in Mozambique over late summer/early winter delayed our trip for over a month. It is almost certain that a greater number of butterfly species would have been recorded had sampling taken place earlier in the year when temperatures were warmer and winter not so far progressed. The species list for the Marromeu complex can not therefore be regarded as comprehensive as sampling needs to be carried out throughout the year to allow for seasonal fluctuations in species availability.

Season, weather and vegetation have been shown to be highly correlated (Warren 1985). It could therefore be argued that insect populations and their respective food supplies are responding to the same environmental variables and there is no real causal basis to the relationship between the two. Sparks and Parish (1995) and Feber *et al.* (1996) suggest this is unlikely and indeed, butterfly distribution did appear to be related to vegetation in the Marromeu complex (discussed below). However, changes in season remain paramount in determining butterfly presence in this and other areas (New 1997).

Butterfly utilization of plants, at least for nectar, appeared to be opportunistic. The plants with the most nectar-laden flowers tended to be exotic weeds and as a result more butterflies feed on them. Exotic plant presence indicated butterfly presence. The butterfly assemblage in the Marromeu complex seemed to be largely composed of highly vagile, migrant species whose distributions as generalists are influenced by abundant nectar sources. Jackson (1987) has noted preference for exotic nectar sources particularly by migratory species which may reasonably be expected to be more adaptable to a variety of food sources. These resources were located around human settlements; as is often the case, exotic weeds flourished in these areas of disturbance. This association with exotic weeds could however be a function of season (few indigenous plants flowering during winter) which reinforces the importance of sampling throughout the year. Low levels of species richness can also be attributed to the predominance of a limited number of crops, namely sugarcane and sorghum. Uncommon species and those with localized distributions were found by Jackson (1987) to prefer indigenous nectar plants. The distribution of more sedentary species (such as the Blues and Skippers) of the Marromeu complex appeared to be determined more by larval host plants presence.

Butterfly abundance and species diversity was also a consequence of microhabitat heterogeneity. Sparsely-vegetated patches of earth in warm, sunny and sheltered conditions have been described as being the most suitable for butterflies (for Nymphalids in particular; Vickery 1998). Such conditions prevailed in the villages where earth had been cleared around the houses and the natural vegetation thinned or removed for garden replacement.

To conclude, many of the butterfly species found in the Marromeu complex utilize exotic plant species which are pioneers of bare ground and areas of disturbance. These weeds flower prolifically and attract nectar-feeding insects, especially eurytopic butterflies. Owen (1971) reports that a remarkable proportion of common African butterflies now utilize agricultural weeds that have been introduced with crops as larval food-plants and these species have consequently expanded their range and increased their numbers. This suggests that an area such as the Marromeu complex where the natural vegetation has been disturbed to such a great extent, an assemblage of fewer, yet abundant, butterfly species is to be found. If butterflies are to be regarded as indicators of environmental health, there is concern for overall plant and animal species biodiversity in this part of the Zambezi Basin.

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CHAPTER 11
REVIEW OF AQUATIC INVERTEBRATES OF THE ZAMBEZI BASIN

Brian Marshall

11.1 INTRODUCTION

The invertebrates are an enormously diverse group of animals, falling into about 35 phyla (Barnes 1986) depending on the system of classification adopted. Some workers include the animal-like protists (Protozoa); others divide the Arthropoda into several different phyla, while the invertebrate chordates are also frequently included amongst them. Some of these phyla are very large; for example there are about 50,000 described molluscs and at least 750,000 arthropods. The greatest diversity of invertebrates occurs in the oceans and on land where the arthropods are the dominant forms. But they are also abundant in freshwater, where about 13 phyla are represented (Edmondson 1959, Durand & Lévêque 1980, 1981). Current thinking is that there may be 36-45 protozoan phyla (Corliss 1984, Margulis 1990) and 32-38 phyla of metazoan (animals) phyla (Minelli 1993) making a total of 68-83 phyla. Total number described varies, but Hammond's review (1992) seems to be well respected. Mollusca is considered to have over 100,000 species (Brusca & Brusca 1990), while the Insecta is estimated to have more than 950,000 species presently described (Hammond 1992). Large as these numbers are, they represent only the tip of the iceberg of invertebrate biodiversity, which is expected to be 10-30 million species (Hammond 1992).

Despite being far more diverse and abundant than vertebrates in aquatic systems, the ecology of invertebrates has generally been neglected in the Zambezi Basin. The reasons are obvious; the vertebrates are mostly relatively large and conspicuous (in the case of birds or mammals) or of importance as food or for recreation (especially fish). Furthermore, the vertebrates are much easier to identify and there is a wide range of guidebooks available to the layman. By contrast, invertebrates are much more difficult to identify and specialist knowledge is usually required. Invertebrate groups that have been studied in detail include the vectors of human or animal diseases like some gastropod molluscs or mosquitoes. Even in these species, though, investigations tend to be orientated to control measures and the prevention of disease transmission rather than towards biology or ecology.

This review must necessarily be an inadequate one. The literature on invertebrates is very extensive and sometimes rather specialised, and no one person can be familiar with all of it. In preparing this review, I have concentrated on invertebrates in ecosystems and on papers that describe the diversity and composition of invertebrate communities. Adequate coverage of the taxonomic literature would be impossible to achieve, and I have not attempted it.

One of the major difficulties in dealing with aquatic invertebrates in tropical Africa is the lack of adequate guidebooks. Fortunately, many groups are cosmopolitan and general books published elsewhere can be used to identify them at least to the level of family and, in some cases, to genus. One of the most useful books for African workers is the two-volume *Flore et Faune Aquatiques de l'Afrique Sahelo-Soudanienne* (Durand & Lévêque 1980, 1981). Its major drawback is that animals are identified only to family and generic level. Unfortunately, it is not readily available in anglophone Africa, including most of the Zambezi Basin, where in any case many would be deterred by the fact that it is written in French. Keys for the identification of southern African forms are currently being prepared in South Africa and these should help to fill the need for English-language identification guides.

Another major difficulty is that many taxa are in need of revision. This becomes particularly important if an attempt to compare faunas in different systems is to be made. Workers in the field who lack taxonomic expertise often use names that have been used by someone else without any check on their accuracy. An example of this problem is the cyclopoid *Mesocyclops leuckarti*, which is referred to by this name in much of the literature from the Zambezi Basin. But a recent revision of the genus (Van der Velde 1984) showed that *M. leuckarti* does not occur in Africa. So which species is being referred to? No one knows, because reference collections are rarely made.

The most useful source book to the literature on African freshwater invertebrates is the bibliography produced by Davies, Davies, Frazer & Chutter (1982). This work has been used extensively in preparing this review and readers should refer to it for further references. Unfortunately, it carries references only to 1980 and there has been no subsequent revision.

Most invertebrate phyla include parasitic forms as well as free-living ones and in some cases (e.g. Platyhelminthes) the former are more important than the latter. Many human parasites that have an aquatic phase, or are transmitted by aquatic organisms, are responsible for diseases like bilharzia, malaria, river blindness, and so on. This review makes no attempt to deal with parasitic forms or the diseases that they might be responsible for, being restricted to free-living species only in order to keep it to a manageable size.

It would be highly desirable if checklists of the aquatic invertebrates of the Zambezi Basin could be produced. In practical terms this is very difficult because most groups have not been thoroughly collected, indeed the gaps in our knowledge of these animals are very striking. Furthermore, the taxonomic literature that would be needed for such an exercise is very scattered and much of it is in museum journals with a very limited distribution. Few libraries in the countries of the Zambezi Basin have the resources to obtain these papers. One of the major problems for workers in the basin is that most of the specimens are available in museums in Europe or North America and difficult to access and therefore effectively lost to local workers. However, good collections of certain groups are found in various institutions in South Africa.

11.2 INVERTEBRATE GROUPS

KINGDOM PROTISTA

The protists are single-celled organisms but with a complex structure, now generally grouped together as a separate kingdom but formerly treated as unicellular plants or animals. Although not generally regarded as invertebrates, they can be very important ecologically in pelagic ecosystems (Dumont 1986, Hecky & Kling 1981). The animal-like protists (protozoa) are heterotrophic, and free-living or parasitic. Free-living forms all live in an aqueous medium, which may include the interstitial water in the soil as well as water in ponds or lakes. The principal forms of free-living animal-like protists in freshwater include:

Phylum Rhizopoda: The rhizopods, also known as the Sarcodina, include the naked amoebas (e.g. *Chaos*) and testaceous forms, i.e. enclosed in a shell of some kind (e.g. *Difflugia*, *Chlamydophrys*). The systematics of the group was said to be chaotic (Dragesco 1980) and is probably still in need of revision. Most of these amoebae are soil animals and there seems to have been little published in Africa on forms living in a more typical aquatic environment. The bibliographies in Dragesco (1980) and Davies *et al*. (1982) suggest that most of the literature dears with free-living forms in the soil or with parasitic ones, and there seem to be few papers on truly aquatic forms. The paper by Green (1963) that discusses rhizopods in the Sokoto River in West Africa may contain some information relevant to the Zambezi system.

Phylum Actinopoda: This phylum includes the heliozoans (mostly freshwater) and radiolarians (mostly marine), both amoeboid animals frequently enclosed in a spherical silicaceous skeleton. Their fine needle-like pseudopods (known as axopods) are greatly extended and radiate from the centre of the body. They may be floating as part of the zooplankton, or benthic, in which case they may be sessile, stalked forms. They are extremely delicate organisms and little is known about them, especially in Africa. Apart from some comments in Dragesco (1980) there seems to be nothing available about this group on the continent.

Phylum Ciliophora: The ciliates are a large, diverse and complex group with a great variety of sub-cellular microstructures. There are thought to be about 1000 species living in freshwater (Dragesco 1980) and they occur in almost any kind of aquatic habitat being free-living, sessile or parasitic. As with the other protozoan groups, there are few data on African ciliates and none on those of the Zambezi system. The papers by Dragesco (1966, 1970, 1972a, 1972b, 1973) may be of value.

KINGDOM ANIMALIA

Phylum Porifera: The sponges are an important group of animals in marine systems, but a few species occur widely in freshwater. In West Africa, there are thought to be about 11 species in 7 genera and two families (Boury-Esnault 1980) and the number in the Zambezi Basin is possibly similar. This group has not been studied in detail and the African literature is sparse. Papers that might have data of value to anyone working in the basin include some on sponges in the Bangweulu-Mweru system (Brien 1967, 1969, 1970a, 1970b), Lake Tanganyika (Brien 1974) and South Africa (Burton 1958). Papers from the Zambezi Basin itself include the description of a new genus and species from Lake Malawi (Brien 1972, 1973), raising the possibility that there may be a degree of endemism among the sponges of this lake. Penny (1986) notes that there are about 13 species in the Zambezi River, particularly near Victoria Falls. Other reports on sponges come from Lake Kariba (Begg & Junor 1971a, 1971b), the Mwenje dam, Zimbabwe (De Drago 1976) and Namibia. Two unidentified species have been recorded from the Kwando and Chobe rivers, and another from the Kavango River (Curtis 1991).

Phylum Cnidaria: The members of this phylum (also known as the Coelenterata) are almost exclusively marine, being represented in freshwater only by the hydras and some medusae. The hydras live in small streams and pools and are little known; virtually nothing has been published about the African forms, apart from some taxonomic descriptions from Kenya (Cox & Young 1973), the Congo (Semal-van Gansen 1953) and South Africa (Omer-Cooper 1964). It is possible that the species described in these papers might occur in the Zambezi Basin, but more work remains to be done.

Much more has been done on the medusae, of which there is only one African genus, *Limnocnida*, with only two species, *L. tanganicae* and *L. indica* (Goy 1980). The former is the only one reported from the Zambezi Basin (Jordaan 1935, Pitman 1965, Begg & Junor 1971b, Oldewage & Shafir 1991, Curtis 1991). Mills (1973), who reported on a population explosion in the Mwenda estuary, Lake Kariba, is the only author to have presented any quantitative data on this species. Edney (1939) published a brief account of the behaviour of *Limnocnida* and its responses to external stimuli.

Phylum Platyhelminthes: This phylum is best known for its parasitic forms, which include the flukes (Monogenea and Trematoda) and the tapeworms (Cestoda). Many of these parasites are transmitted by aquatic vectors and are responsible for a number of diseases in animals and humans. A considerable effort has been made to control bilharzia and liver flukes, among others, and there is a considerable literature on these parasitic flukes (see Chapter 8). There is one free-living platyhelminth class, the Turbellaria, which are abundant animals in suitable habitat, but they are inconspicuous and little is known about the African species (Gourbault 1980). Curtis (1991) reported that an unidentified species had been collected from rainwater pools in the eastern Caprivi, but there seem to be no other reports about turbellarians in the Zambezi Basin. Some papers that might be useful include Ball (1974), de Beauchamp (1951), Kawakatsu (1972), Marcus (1955, 1970), Young (1976) and Young & Young (1974). Weir (1969) described the fauna of some temporary pools in the Hwange National Park, Zimbabwe, from which he recorded two turbellarians, *Castrada* sp. and *Phaenocerca foliacea*, each of which occurred in five out of 12 pools.

Phylum Nemertea: Freshwater nemerteans are widely distributed but inconspicuous animals that live upon the vegetation in rivers, streams and lakes, or amongst detritus on the bottom. They are thought to be related to the flatworms (Turbellaria) and there is only a single freshwater genus, *Prostoma*. Some work has been done on nemerteans in Kenya (Gibson & Young 1974, Young & Gibson 1975), but there are no reports from anywhere else in Africa.

Phylum Gastrotricha: A small phylum of about 460 species, including both marine and freshwater forms. They are said to be common animals in ponds, streams and lakes and most are benthic (Brunson 1959). There are no data from Africa.

Phylum Nemata (Nematoda): The nematodes (roundworms) are amongst the most widely distributed and abundant of all animals. Free-living nematodes occur in almost any habitat and there are many parasitic forms that attack almost every kind of plant and animal. Aquatic vectors transmit many of the parasitic forms that cause diseases in humans and animals. The most important of these is river blindness (onchocerciasis), which is widespread in west and central Africa, and much of the literature on freshwater nematodes in Africa stems from efforts to control this disease.

There is some literature on parasitic nematodes in freshwater fish (Khalil 1971, Khalil & Polling 1997). The references Andrassy (1984) and Jairajpuri & Ahmad (1992) should also be mentioned.

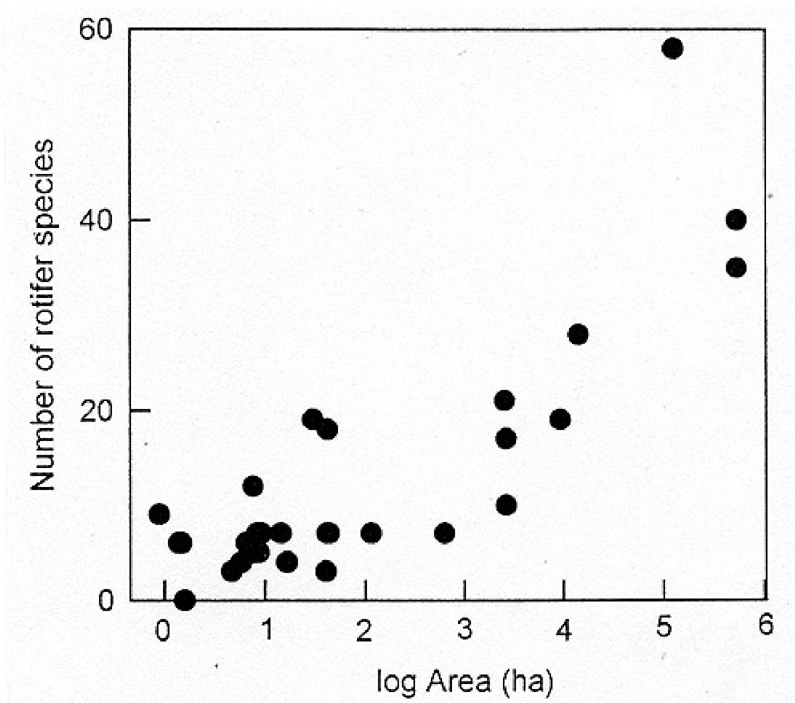
Despite the fact that they are abundant and widespread, very little is known about free-living aquatic nematodes in Africa, possibly because they are very difficult to identify. The literature is very sparse and nothing that could be related to the Zambezi Basin was found, apart from a paper by Coomans, Rashid & Heyns (1995) that presumably refers to free-living nematodes in the Okavango Delta, Botswana. In a comment that could apply to whole basin, Curtis (1991) noted that little was known about free-living nematodes in Namibian waters and that there might be a number of endemic species in the country. Some works that might contain relevant data include Andrássy (1970), Heyns (1976) and Meyl (1957).

Phylum Rotifera: The rotifers (also known as Rotatoria), or wheel-animalcules, are microscopic animals, usually about 100-600 µm in size, occasionally reaching 1 mm (Pourriot 1980). The vast majority live in freshwater where they may be sessile or free-living, and only a few species are marine or parasitic. They are important constituents of the zooplankton in lakes. In the Zambezi Basin they have mostly been investigated as components of the plankton. With the exception of

Green & Carey (1965), who examined samples from the Kafue River, all of the work on rotifers comes from lakes and reservoirs, especially Lake Kariba. A list of rotifers in Lake Liambezi is given in Seaman *et al.* (1978), who also briefly describe their vertical migration over a 24-hour period. Dudley (pers. comm.) notes that there are 12 species known from Malawi, although the majority of these are in Lake Chilwa, just outside the basin.

Some of the earliest records of rotifers from Lake Kariba appear in Thomasson (1965), while Bowmaker (1973) gives some quantitative data on rotifers in the zooplankton. These data are of particular interest since they pre-date the introduction of kapenta, *Limnothrissa miodon*, into the lake. At that time rotifers were relatively insignificant in the plankton, making up 3% by weight. This situation changed after the sardines eliminated the larger crustacean zooplankton and rotifers now make up over 80% of the zooplankton (Marshall 1991, 1997). Andersson & Stenson (1989) briefly noted the possible impact of predation on the morphology of *Brachionus calcarus* in the lake. Other studies were concerned with their distribution in the lake (Magadza 1980; Green 1985) and the seasonal cycle of *Keratella cochlearis* in relation to thermal stratification (Begg 1974), or their diurnal movements in relation to predation by kapenta (Begg 1976). Finally, some data on rotifers is available from a series of small impoundments near Marondera and in the Nyanga District, Zimbabwe (Green 1990) and from Lake Chivero (formerly Lake McIlwaine) and Cleveland dam, both near Harare (Elenbaas & Grundel 1994). It is possible to prepare lists of rotifers from these papers (Table 11.1) but few clear patterns are evident, apart from the much greater number in Lake Kariba. This is to be expected since there seems to be an association between the size of a water body and the number of rotifer species (Figure 11.1). The most widespread species found in all of these waters, was *K. cochlearis*, which made up 74-94% of the rotifers in Lake Kariba and 20-84% of those in the other reservoirs. This species has been discussed in relation to its entire African distribution (Green 1987) and some data from Zimbabwe are included in that paper.

Figure 11.1 The number of rotifer species in various lakes and reservoirs in relation to their surface area. Data from various sources in Green (1990) and Elenbaas & Grundel (1994).



Phylum Annelida: The annelids (segmented worms) are most abundant in the oceans but two groups, the Oligochaeta and the Hirudinea, are predominantly freshwater forms. There are five families of aquatic oligochaetes and they are important members of the benthos in rivers and lakes (Brinkhurst 1966, Brinkhurst & Jamieson 1973, Lauzanne 1980). Despite being abundant animals, they have not been investigated in much detail anywhere in the Zambezi Basin, apart from some work done in Lake Chivero in Zimbabwe. Martin & Giani (1995) described a new species from Lake Malawi. Other references for the region are Beddard (1908) and Martin & Giani (1995).

Lake Chivero is highly eutrophic and the bottom sediments are rich in organic matter, conditions that favour oligochaetes, which are able to tolerate the anoxic conditions that occur at the mud-water interface. The principal species in the lake were *Branchiura sowerbyi* and *Limnodrilus hoffmeisteri* with occasional specimens of *Dero digitata* (Brinkhurst 1970). They preferred to live in sediments with organic detritus and were abundant at depths ranging from 2-20 m. They were able to invade the deeper sediments in winter when the lake was isothermal and were therefore the most abundant benthic species in this zone (Marshall 1972, 1973, 1978, 1982). About thirty years later the benthos of the lake was re-investigated and oligochaetes were still abundant, although *Branchiura sowerbyi* seemed to be absent, probably reflecting the increasing severity of pollution in the lake (Marshall 1995).

The only other data on oligochaetes in the Zambezi Basin come from lakes Kariba and Liambezi. Bowmaker (1973) found that there was a greater diversity in Lake Kariba than in Lake Chivero, with *Aulodrilus pigueti*, *Branchiodrilus hortensis*, *Branchiura sowerbyi* and *Dero dorsalis* being present. They made up about 20-30% by weight of the benthos and were presumably eaten by fish, although there was no evidence of them in any stomach contents. The lack of resistant species like *Limnodrilus hoffmeisteri*, which is capable of surviving in extremely polluted situations, reflects the unpolluted state of Lake Kariba. *Ilyodrilus* and *Limnodrilus* were present at most stations in Lake Liambezi, sometimes in quite large numbers (>1000 per m^2). This was particularly the case in areas where the bottom was strewn with hippopotamus dung (Seaman *et al*. 1978), again reflecting the ability of oligochaetes to live in areas with high organic matter and low oxygen.

Another important group of aquatic annelids are the Hirudinea (leeches) which are widespread and sometimes abundant animals. They seem to have been almost completely overlooked in the basin, except perhaps for some data from Namibia where two families and 15 species are known. *Placobdelloides jaegerskioldi* and *Asiaticobdella fenestrata* were found only in the eastern Caprivi (Oosthuizen & Curtis 1990, Curtis 1991) but might be expected elsewhere in the Okavango or Upper Zambezi systems. Publications that may have some useful data include Sawyer (1986), Sciachitano (1959, 1962, 1963) and Soós (1970).

Phylum Ectoprocta: The moss animals are generally placed in the phylum Bryozoa but it is often suggested that the phylum should be spilt into the Endoprocta (entirely marine) and Ectoprocta (entirely freshwater). They are inconspicuous, sessile branched animals that superficially resemble algae or moss (Wiebach 1980). They are largely overlooked and may be more common than generally supposed. Very little is known about these animals in the Zambezi Basin, apart from some records for Namibia where five species in two families have been recorded. The three species of *Plumatella* (*P. emarginata, P. punctata* and *P.repens*) are cosmopolitan, while *Lophopodella capensis* and *L. thomasi* occur elsewhere in southern Africa (Curtis 1991).

Table 11.1. The genera of rotifers from some water bodies (mostly dams) in the Zambezi Basin. The numbers indicate the numbers of species of each genus in each water body. Data from Green (1985, 1990), Seaman *et al*. (1978) and Elenbaas & Grundel (1994).

	Lake Kariba	Lake Liambezi	Mutoko (Sweet Valley)	Mtemwa	Lake Chivero	Edinburgh	Joberini	Gwaai	Cleveland	Nyambuya	Udu	Rhodes	Moodie	Claremont	Purdon	Gulliver	Mare	Troutbeck	Large Connemara	Small Connemara
Altitude (m)	485	929	1260	1340	1350	1350	1410	1420	1560	1600	1676	1707	1768	1813	1920	1951	1951	2134	2255	2270
Aneuraeopsis	2	1			1	1		1											1	1
Ascomorpha	1										1	1	1		1			1		
Asplanchna	1	1		1	1	1			1	1							1			
Brachionus	4	4	2		3	2			5											
Cephalodella																	1	1		
Colurella																				1
Conochilus	1		1	1			1			1		1	1						1	1
Epiphanes		1			1															
Euchlanis	1				1				1											
Filinia	3	1			1				2											
Gastropus									1											
Hexarthra	1	1			1		1		1					1						
Keratella	2	2	1	1	2	1	2	1	3		1	1	1	1	1	1	1	1	1	2
Lecane	6	1			1				1						2			1		3
Lepadella					1										1					1
Mytilina		1							1											
Polyarthra	1			1	1	1	1		1	1	1		1	1		1	1			
Pompholyx												1								1
Synchaeta	1		1	1		1		1			1	1	1	1		1				
Tetramastix		1																		
Trichocerca	5	1	1	2	3	2		3	2	1	3	1	2	3	2	2	1			1
Trichotria	1																			
Totals	30	15	6	7	17	9	5	6	19	4	7	6	7	7	7	5	5	4	3	11

Phylum Mollusca: The molluscs are an important group of freshwater invertebrates and the gastropods have been studied in some detail because of their importance as vectors of parasites that cause human and animal diseases. They have been reviewed separately (Chapter 8).

Phylum Tardigrada: The systematic position of the tardigrades (water bears) is unclear, some authors treat them as allies of the annelids, others the arthropods, but they are probably best retained as a separate phylum (Barnes 1986). They are minute animals usually about 0.3-0.5 mm long, although some reach 1.2 mm. They mostly inhabit the water film surrounding the leaves of mosses and lichens but some are freshwater species, living in bottom detritus or on algae and aquatic mosses. Because of their small size, they are rarely encountered and nothing is known about them in the Zambezi Basin. One of the few papers on African tardigrads is Iharos (1969) but the review by Ramazzotti (1972) may mention African species.

Phylum Arthropoda: The arthropods are an enormous assemblage of animals with at least 750,000 described species, three times the number of all other animals combined (Barnes 1986). The adaptive diversity of the arthropods has enabled them to live in almost all habitats and they are the most successful of the invaders of the terrestrial environment. Nevertheless, they have also been very successful in aquatic environments and are diverse and numerous animals in all freshwater systems.

<u>Subphylum Chelicerata</u>: The chelicerates are primarily terrestrial being represented by well-known forms like the spiders, the scorpions and their allies, and the ticks and mites. Some mites have become aquatic and they can be quite abundant at times. In spite of this, little is known about them in Africa and no data are available from the Zambezi Basin. A useful paper is that of Jansen van Rensburg (1976) which gives a key to the families of water mites in the Afrotropical region. Other papers that describe water mites from central and South Africa and should be of some value to workers in the Zambezi Basin include Bader (1968), Dippenaar-Schoeman & Jocqué (1997), Viets (1959, 1968, 1971, 1980), Viets & Böttger (1974a, 1974b) as well a general review of African water-mites (Viets 1953).

Many spiders are associated with water, but there are no truly aquatic species in Africa (Lawrence 1970). None are able to swim but they can dive below the surface for short periods or run rapidly on the surface. The best-known semi-aquatic spiders are the fish-eaters, *Thalassius* spp., which are large animals able to catch small fish and tadpoles. There are several species in this genus and they are widely distributed but little known.

<u>Subphylum Crustacea</u>: The crustaceans are the only arthropod subphylum that is primarily aquatic. The majority of its 42,000+ species is marine but there are numerous freshwater forms. Functionally, but not taxonomically, the subphylum can be split into three groups: the fairy shrimps and their allies that live in seasonal pools, the microcrustacea, and the relatively large decapods. The are also a number of parasitic species, especially among the Copepoda, which infest fish and crabs, but these have not been taken into account here. A general introduction to the African crustaceans can be found in Rey & Saint-Jean (1980), Dussart (1980, 1989), Kiss (1980) and Monod (1980). Dussart (1989) gives a more detailed list of the calanoid copepods. The known crustacean fauna of Malawi is about 130 species, including Decapoda (C. Dudley, pers. comm.).

(a) *Crustacea of seasonal pools*
The crustacea that live in seasonal pools are primarily the classes Branchiopoda (order Anostraca) (fairy shrimps) and Ostracoda (seed shrimps). They are mostly ephemeral and survive periods of

drought by the production of resistant eggs. Consequently, they tend to be most numerous in arid or semi-arid areas. Of the countries in the Zambezi Basin, Namibia seems to have the greatest diversity with some 35 ostracod species, of which 18 may be endemic (Curtis 1991). At least five of them are confined to very arid regions of Namibia and Botswana while only ten are widespread in Africa.

Little is known about these animals elsewhere in the basin. General reviews of these groups include Kiss (1980) and Rey & Saint-Jean (1980), while other works include the description of a new species from Zimbabwe (Hartland-Rowe 1969) and a detailed review of the family Streptocephalidae in Africa (Hamer, Brendonck, Coomans & Appleton 1994a, 1994b). These papers suggest that about eight species of *Streptocephalus* may occur in the basin: *S. caffer* (Zimbabwe), *S. macrourus* (Botswana, Namibia), *S. indistinctus* (Zimbabwe, Namibia), *S. ovamboensis* (Namibia), *S. trifidus* (Zimbabwe), *S. vitreus* (Zimbabwe) and *S. cladophorus* (Namibia). Another species, *S. wirminghausi* has also been collected from pans in the middle Zambezi valley in Zimbabwe (Hamer 1994). Other genera commonly found in seasonal pools, including *Branchipodopsis* and *Triops* have also been reviewed recently (Truxal 1990, Hamer & Appleton 1996, Hamer & Rayner 1995). The authors point out that very little collecting has been done outside South Africa and Namibia, and there may be other species elsewhere in the basin.

Weir (1969) recorded *S. vitreus* and *Caenastheriella australis* in pools in the Hwange National Park, Zimbabwe, where they occurred in six of the 12 pools that were sampled. There seems to be no other data on these species from the Zambezi Basin.

(b) *Microcrustacea*

The microcrustacea are principally found amongst the classes Copepoda (principally the orders Calanoida and Cyclopoida), Branchipoda (suborder Cladocera) and Ostracoda. Rey & Saint-Jean (1980) give a general introduction to the African cladocerans, while Dussart (1980) and Kiss (1980) do the same for the copepods and ostracods, respectively. More specialised papers include Rayner (1992, 1994) and Martens (1984, 1990).

They are generally sparse in running waters, although some records are available from the Zambezi and Kafue rivers (Jackson 1961, Hall, Davies & Valente 1976, Green & Carey 1965). Similar species occurred at all sites, with *Diaphanosoma excisum*, *Daphnia* spp. and *Bosmina longirostris* being the most common cladocerans, and *Tropodiaptomus* and *Mesocyclops* sp. the commonest copepods. Non-planktonic species included *Alona* sp. and *Chydorus* sp.

Most of the work on these microcrustaceans has been carried out in lakes and reservoirs. The zooplankton of Lake Kariba has been studied in considerable detail (see review by Marshall 1997) because of its importance as a food resource for the sardine *Limnothrissa miodon*, which now accounts for about 60-70% of the lake's fish production. Some data from the period before *Limnothrissa* were introduced are available in Bowmaker (1973) against which the changes brought about by the sardine can be assessed. These changes are typical of those that follow the introduction of planktivorous predators anywhere in the world and involve the elimination of larger species like daphniids and larger copepods until only small ones like *Bosmina* and rotifers are left (Table 11.2). The suggestion that these changes reflect a "stressed" ecosystem (the implied stress is high levels of DDT in the water) made by Berg (1995) can therefore be discounted.

Table 11.2. Changes in the relative abundance (%) of zooplankton in Lake Kariba, following the introduction of *Limnothrissa miodon* in 1967-68. Data from Marshall (1991).

	1967-68	1970	1972	1975-76
Diaptomids	14.3	0.2	0	+
Cyclopoids	4.7	12.5	10.1	13.8
Nauplius larvae	11.1	16.4	17.1	3.1
Bosmina	7.4	15.9	17.1	10.5
Ceriodaphnia	69.3	14.3	0	0.3
Diaphanosoma	2.2	0.2	0	+
Daphniids	0.9	0.2	0	0
Rotifers	+	40.3	55.7	72.3

+ = change, but unmeasured.

As in other lakes, the zooplankton make diurnal migrations up and down the water column and the sardines follow them closely (Begg 1976), which emphasises their importance as a food resource. Indeed, the condition and abundance of the kapenta closely follows the abundance of plankton (Cochrane 1984, Marshall 1988). From this efforts to determine the factors that influence the distribution and abundance of zooplankton were made, revealing the importance of the rivers and the nutrients they bring in to the lake (Magadza 1980, Marshall 1997, Masundire 1994). Other factors of importance were predation by the sardines (Masundire 1989a, 1991, 1992) and water transparency (Masundire 1989b).

The presence of kapenta in Lake Cabora Bassa has also focussed interest in its zooplankton. Its species composition is similar to that of Lake Kariba, with the larger species having been eliminated in open water and the small *Bosmina longirostris* being the dominant species (Gliwicz 1984, Mandima 1997). The impacts of predation were well illustrated by Gliwicz (1986a) who described a distinct lunar cycle amongst the zooplankton, which depended on the fact that the water of Lake Cabora Bassa is very turbid. At full moon, when light penetration was greatest, the kapenta were able to see the larger zooplankton and they were eliminated. As the moon waned, light penetration decreased and larger forms like *Diaphanosoma* at first, followed by *Daphnia*, began to appear. As the moon waxed this sequence was reversed. The crustacean zooplankton were also important in Lake Cabora Bassa because they filtered out clay particles and so influenced water transparency (Gliwicz 1986b).

Relatively little work has been done on the zooplankton of Lake Malawi, in spite of its large size. Jackson *et al.* (1963) gave a brief and mostly qualitative synopsis of the zooplankton community, and this was followed by Fryer (1957a, 1957b, 1957c). More information became available after the FAO fishery expansion project, which provided data on seasonal variation in abundance and vertical migration of the most abundant species (Degnbol & Mapila 1982). Twombly (1983) also investigated seasonal variation. Lake Malawi supports a number of pelagic fish species and the zooplankton is an important component of their diet (van Lissa 1982, Thompson & Irvine 1997). Most of the inshore fish species in the lake also utilise zooplankton at some stage of their lives, usually as juveniles (McKaye, Makwinja, Menyani & Mhone 1985).

A major advance in knowledge of the zooplankton of Lake Malawi was brought about by the ODA/SADC study of its pelagic resources. In this study the biomass, production, spatial distribution and seasonal variation of the microcrustacea throughout the lake was investigated (Irvine 1995a, Irvine & Waya 1995). A comprehensive study of feeding in pelagic fish species demonstrated the importance of the zooplankton to fishery productivity (Allison, Thompson, Ngatunga & Bulirani 1995). Because of the success of *Limnothrissa* in lakes Kariba and Cabora Bassa it was suggested that this fish might be introduced into Lake Malawi, which would have altered the composition of its zooplankton (Turner 1982). This suggestion was severely criticised on the grounds that the impacts of a zooplanktivorous fish would cascade unpredictably throughout the fish community of the lake bringing about irreversible and possibly adverse changes (Eccles 1985, McKaye *et al*. 1985). Finally, the biology of the most important species, the copepod *Thermodiaptomus cunningtoni*, was studied in detail by Irvine, Waya & Hart 1995).

Elsewhere in the Zambezi Basin, zooplankton has been investigated in Lake Liambezi (Seaman *et al*. 1978), and in Lake Chivero and Cleveland Dam near Harare. The latter studies dramatically illustrate the effects of eutrophication, since the zooplankton density in eutrophic Lake Chivero was generally about three times more abundant than it was in the oligotrophic Cleveland Dam (Elenbaas & Grundel 1994). Magadza (1994) used zooplankton to assess the state of pollution in Lake Chivero. Zooplankton associations in a number of small reservoirs near Marondera and Nyanga, Zimbabwe, provide a comprehensive list of species from those area, while other data are available from three reservoirs elsewhere in Zimbabwe (Magadza 1977). Magadza (1981) also published a checklist of the free-living entomostraca (Copepoda and Cladocera) of Zambia. A discussion of the altitudinal distribution of crustacean zooplankton in Africa (Green 1995) includes data from his earlier work.

It is possible to prepare checklists of microcrustacea for some places in the Zambezi Basin (Table 11.3). In most cases, the number of species ranges from 10 to 19 and the presence of only 11 species in Lake Malawi is probably an artifact since it refers only to planktonic forms. The large number of species in the Kafue and Bangweulu systems comes about because of the inclusion of many non-planktonic forms, primarily in the family Chydoridae. This reflects the swampy nature of both these systems that allows these species to survive without being eliminated by fish.

(c) *Macrocrustacea: the Decapods*

The Decapoda, which include the crabs, crayfish and shrimps, are primarily marine but they do include a number of freshwater species. The identification of freshwater crabs is particularly difficult (Monod 1980) but there appears to be only one true freshwater genus, *Potamonautes*, in the Zambezi Basin. This is the common river crab and it is not clear how many species are present, although Curtis (1991) suggest that three species occur in Namibia. Little is known about their ecology, apart from an estimation of their abundance (Turnbull-Kemp 1960) and their importance as food for otters, trout and eels (Butler & Du Toit 1994, Butler & Marshall 1996) in streams in the Eastern Highlands of Zimbabwe. Records of crabs from the Zambezi Basin are given in Cumberlidge (1997).

The shrimp *Caradina nilotica* is widely distributed in Africa and occurs throughout the Zambezi Basin, but little is known about it. Some general observations on their presence in Lake Kariba were made by Begg & Junor (1971b). The pelagic shrimp *Limnocaradina tanganicae* was said to have been introduced into Lake Kariba from Lake Tanganyika (Bell-Cross & Bell-Cross 1971) but its fate is unknown. Some exotic species, including the Louisiana Red Crawfish *Procambarus clarkii* (Zambia) and the giant Malaysian prawn *Macrobrachium rosenbergii* (Malawi and Zimbabwe) have been brought to the basin for aquaculture purposes (Mikkola 1996). *Macrobrachium* are known to have escaped from a fish farm at Kariba and they have been caught at various places in the lake but they are unlikely to become established, as their larvae need to grow in saline water. *Procambarus* can breed in freshwater and has become a problem in Lake Naivasha, Kenya, by destroying beds of submerged macrophytes that were important breeding areas for fish and reducing the numbers of leeches, clams and other invertebrates (Harper, Mavuti & Muchiri 1994). So far, there is no evidence that alien decapods have escaped into any natural systems in the basin, but the situation needs to be monitored closely.

Table 11.3. The microcrustacea of some waters in the Zambezi Basin. Data from Twombly (1983), Irvine (1995a), Green (1985, 1990), Elenbaas & Grundel (1994), Seaman *et al*. (1978), Magadza (1981) and Curtis (1991).

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
Calanoida: Diaptomidae										
Tropodiaptomus cunningtoni	●									
Tropodiaptomus hutchinsoni		●						●		
Tropodiaptomus kraepelini	●	●						●		
Tropodiaptomus longispinis									●	
Tropodiaptomus simplex									●	
Tropodiaptomus worthingtoni			●	●	●	●				
Tropodiaptomus sp.nov.										●
Thermodiaptomus congruens							●			●
Thermodiaptomus mixtus			●	●	●					
Thermodiaptomus syngenes		●						●		
Lovenula falcifera										●
Cyclopoida: Cyclopidae										
Afrocyclops gibsoni					●					
Cryptocyclops inopinatus										●
Cryptocyclops linjanticus								●	●	
Tropocyclops confinis								●		
Tropocyclops prasinus								●	●	
Tropocyclops tenellus					●			●	●	
Mesocyclops aequatorialis	●									
Mesocyclops dussarti			●							
Mesocyclops ogunnus		●			●			●	●	
Mesocyclops sp.						●				
Thermocyclops decipiens				●	●					
Thermocyclops hyalinus		●						●	●	
Thermocyclops macracanthus					●	●				
Thermocyclops neglectus	●	●						●	●	

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
Thermocyclops oblongatus			●			●				
Thermocyclops retroversus					●					
Thermocyclops tenuis								●		
Thermocyclops sp.						●	●			●
Macrocyclops albidus	●	●						●	●	
Microcyclops bicolor								●	●	
Microcyclops varicans		●		●					●	
Microcyclops rubelloides									●	
Eucyclops dubius	●									
Eucyclops euacanthus								●		
Eucyclops serrulatus								●	●	
Eucyclops stuhlmani								●	●	
Paracyclops fimbriatus									●	
Cladocera: Sididae										
Pseudosida szalayi									●	
Diaphanosoma excisum	●	●	●	●	●	●	●	●	●	●
Diaphanosoma sarsi									●	
Cladocera: Daphniidae										
Daphnia laevis		●	●	●	●	●				
Daphnia longispina		●						●		
Daphnia lumholtzi	●	●	●							
Daphnia pulex			●	●	●	●		●		
Daphnia rosea						●				
Daphnia sp.					●	●				
Ceriodaphnia dubia		●	●	●				●		
Ceriodaphnia quadrangula					●	●				
Ceriodaphnia reticulata							●			●
Ceriodaphnia sp.	●									
Simocephalus serrulatus						●			●	
Simocephalus vetulus					●				●	
Scapholeberis kingi									●	
Moina dubia							●	●	●	
Moina micrura	●	●		●						●
Moinadaphnia macleayi								●		
Bosminidae										
Bosmina longirostris	●	●	●	●	●	●	●	●	●	
Bosminopsis deitersi		●						●		

Group / species	Lake Malawi	Lake Kariba	Lake Chivero	Cleveland Dam	Marondera	Nyanga	Lake Liambezi	Zambia (Kafue system)	Lake Bangweulu	Namibia (East Caprivi & Kavango R.
Macrothricidae										
Ilyocryptus spinifer								●	●	
Ilyocryptus sp.										
Macrothrix triserialis									●	
Macrothrix sp.				●			●			●
Chydoridae										
Chydorus barroisi									●	
Chydorus eurynotus									●	
Chydorus globosus									●	
Chydorus hybridus									●	
Chydorus pubescens									●	
Chydorus sphaericus									●	
Chydorus sp.			●	●		●	●			
Acroperus harpae									●	
Alona affinis								●		
Alona guttata								●	●	
Alona karua									●	
Alona rectangula								●	●	
Alona sp.							●			●
Alonella excisa									●	
Oxyurella singalensis									●	
Camptocercus rectirostris									●	
Euryalona occidentalis								●	●	
Graptoleberis testudinaria								●	●	
Leydigia acanthrocercoides									●	
Pleuroxus chappuisi								●	●	
Pleuroxus denticulatus								●	●	
Pleuroxus sp.							●			●
Kurzia latissima								●		
Kurzia longirostris									●	
Totals	11	16	11	12	15	14	10	33	44	11

Giant shrimps (*Macrobrachium* spp.) occur in the estuarine and lower reaches of rivers draining into the Indian Ocean and will occur in the Zambezi Delta as well as up the lower reaches of the Zambezi River itself. Monod (1980) gives a guide to the West African species but nothing about the East African ones could be located.

Subphylum Insecta

The insects are the largest and most diverse group of animals and their primary radiation has taken place in the terrestrial environment. Many insect orders have aquatic forms, almost all of which occur exclusively in inland waters. Most aquatic insects, with the exception of the Coleoptera (beetles) and Hemiptera (bugs), live in the water during their larval or nymphal stages and in the terrestrial environment as adults. In some cases the adult phase of the life cycle can be very short, lasting only a few hours or a few days, as in the Ephemeroptera and some dipteran groups like the chironomids. Because of their ability to fly adult insects have considerable powers of dispersion and most species would be expected to have a wide distribution. But too little is known about the distribution of aquatic insects in Africa to make any conclusions about their distribution and degree of endemism. Their ability to fly also allows insects to recolonize water bodies after drought and they are among the earliest invertebrates to appear in streams after the rains (Harrison 1966).

Most taxonomic studies deal with adult forms because larval ones frequently lack distinctive morphological characteristics. Many ecological papers therefore list insects to generic level only, while some of the methods for assessing water quality by means of biotic indices require identification to family only. Useful references at this level include Volume 2 of the *Flore et Faune Aquatiques de l'Afrique Sahelo-Soudanienne* (Durand & Lévêque 1981) and the SASS handbook (Thirion, Mocke & Woest 1995). A more detailed general work is Scholz & Holm (1985) which deals with all the orders of insects in southern Africa.

For accurate identifications it is necessary to refer to the primary taxonomic literature, which is often scattered and difficult to find. Some taxonomic papers, which contain data of interest to anyone working in the Zambezi Basin, are included in the discussion of each order, but the list is incomplete and can only be a general guide.

Order Collembola

The springtails are abundant in the terrestrial environment but still have to live in humid situations. Some are amphibious but only a few species live in water. Forge (1981a) gives a general outline of the group but nothing is known about aquatic collembola in the Zambezi Basin, although Magadza (1968) studied shoreline terrestrial collembola under *Salvinia* mats around Lake Kariba.

Order Plecoptera

Stoneflies are relatively uncommon, occurring mostly in small streams, and they have been neglected in the Zambezi Basin where most work has been carried out on lakes or reservoirs. Dejoux (1981) gives a general guide to African forms, while Hynes (1952a, 1952b) described the neoperlids of the Afrotropical region. Zwick (1976) is a general catalogue of Plecoptera that includes African species. No work from anywhere in the basin could be located.

Order Ephemeroptera

The mayflies are a very important group especially in running waters, but they have received little attention in the Zambezi Basin. General works on African mayflies include Demoulin (1970, 1981) and Peters & Edmunds (1964). The list of Ephemeroptera in the Natural History Museum of Zimbabwe includes species from many parts of the basin and is a useful introduction to this group (Gillies 1974). They, too, have been neglected in the basin because they are most abundant in small flowing streams and relatively rare in the standing waters that have been investigated most intensively. One exception is the widespread African mayfly *Povilla adusta*, which is one of the few to occur in standing waters. It has been recorded in Lake Kariba where it is an important food item for some fish species (Bowmaker 1973, Joubert 1975, Mitchell 1976a). It has been studied extensively elsewhere in Africa (Hartland-Rowe 1953, 1955, 1957, 1958). In Lake Kariba *P. adusta* was able to colonise the drowned trees, where it made up from 77 to 93% of the insect biomass (McLachlan 1970b, Boon 1984).

Order Odonata
The dragonflies and damselflies are well-known aquatic species because the adults are relatively large, brightly-coloured, and conspicuous diurnal forms. Their taxonomy is relatively well known and, thanks to the work of Eliot Pinhey, it is possible to make lists for various parts of the Zambezi Basin. This work has been reviewed separately (see Chapter 9).

Order Orthoptera
The grasshoppers and locusts are almost exclusively terrestrial and it is not clear if any aquatic species occur in Africa. The group Tetrigidae will take to water and swim below the surface to escape their enemies. The South American species *Paulinia acuminata* is of some interest because it was brought to the region as a biological control agent to control the aquatic weed *Salvinia molesta*. It is a small, flightless, polymorphic species (Meyer 1979) that lives on and underneath *Salvinia* plants, swimming well under water when necessary. It now occurs in the Chobe-Linyanti system, and in Lakes Kariba and Cabora Bassa. Its efficacy as a biological control agent is debatable; Mitchell & Rose (1979) suggested that it did control the weed on Lake Kariba but Chisholm (1979) and Marshall & Junor (1981) were more sceptical.

Order Hemiptera
The waterbugs are widespread and abundant in most aquatic habitats, especially small streams and pools, including seasonal ones. They include well-known forms like the pond-skaters (Gerridae), backswimmers (Notonectidae), water scorpions (Ranatridae), Belastomatidae and Coixidae. There is a large literature on the group, but little from the Zambezi Basin. Worldwide reviews of some important groups include the work of Hungerford (1933), Hungerford & Matsuda (1960) and Andersen (1995) while general works on African hemipterans include de Sallier Dupin (1976) and Dethier (1981). Drake (1963) described some new species from central Africa (which may include parts of the Zambezi Basin) while Hutchinson (1933) considered their zoogeography in Africa. The only known ecological study from anywhere in the basin dealt with species found in temporary pools in the Hwange National Park (Weir, 1966).

Order Neuroptera
The lacewings and their allies are typically terrestrial with only a few aquatic species. The papers by Elouard (1981) and Tjeder (1957) may be useful to workers in the Zambezi Basin, while Smithers (1957) described two species from Zimbabwe.

Order Trichoptera
Caddisflies are amongst the most important members of stream communities and are well known in South Africa, primarily through the work of K.M.F. Scott. She produced an extensive bibliography on African trichopterans (Scott & Scott 1969) and a general overview of the group in southern Africa (Scott 1986). A general account of the group is given in Marlier (1981) while the papers by Scott (1970, 1976) are of interest to workers in the basin. One of the few investigations from anywhere in the Zambezi Basin is that of Boon (1986) who described net spinning in *Amphipsyche senegalensis* in Lake Kariba. This species normally inhabits running water but it is likely that water movements around the trees enabled it to survive in the lake.

Order Coleoptera

The beetles are the largest order of animals and are an extraordinarily diverse, but predominantly terrestrial group. As might be expected, there are a number of aquatic families that are most commonly found in streams, ponds and seasonal waters, rarely in large lakes or rivers. They are unusual amongst aquatic insects in that both larval and adult forms are aquatic, although the adults can survive out of water and fly readily. The most important families are the Dytiscidae (giant water beetles) and the Gyrinidae (whirligig beetles) and these have been investigated in most detail. Forge (1981b) gives a useful general introduction to African water beetles, while Brinck (1955a, 1955b, 1955c) dealt with African gyrinids, and with the gyrinids of Malawi and Mozambique (Brinck 1960a, 1960b) which are relevant to the Zambezi Basin.

The Dytiscidae of southern Africa were dealt with by Omer-Cooper who published a series of ten papers on dytiscids from Malawi and Zimbabwe (eight of them summarised in Omer-Cooper 1965a, the others in Omer-Cooper 1965b, 1967). According to this work, there were some 27 dytiscid genera in the basin with about 142 species. However, there are 150 species of Dystiscidae in Malawi alone according to Dudley (pers. comm.). The most diverse genera were *Hydrovatus* (19 species), *Cybister* (19 species) and *Laccophilus* (18 species). These estimates are probably incorrect now because further dytiscid collections have been made. They include some from South Africa and Zimbabwe (Bertrand & Legros 1967) and Namibia (Hebauer 1995). Bistrom (1996) reviewed the dytiscid genus *Hydrovatus* as well as naming a new species and giving distributional records of others in Namibia (Bistrom 1995). The dytiscids of parts of the Zambezi Basin, at least, seem therefore to be relatively well known.

Few of the smaller beetle families have been reviewed on a regional or continental scale, with the exception of a review of the Dryopidae of the Afrotropical region (Bertrand 1967). Finally, an important series of papers deals with the larval stages of the aquatic beetles of the Afrotropical region (Bertrand 1961, 1962, 1963, 1964, 1965, 1966, 1969a, 1969b). These would be of considerable value to anyone working on benthic fauna in small pools where beetles are likely to be abundant.

Of some interest are the weevils (family Curculionidae) that have been introduced into various countries in the basin to control alien aquatic weeds. They are not themselves aquatic since their larvae live in the plants and not in the water, but they are of importance in ecological terms through their possible impact on the floating weeds. One of the earliest to be imported from South America was *Cyrtobagous singularis* to control *Salvinia molesta* (May & Sands 1986, Sands & Kassulke 1986). This species is well established in the Caprivi Strip (Kwando and Chobe systems) (Schlettwein 1985) and northern Botswana (Proctor 1984). *Neohydronomus affinis* has been used to control water lettuce, *Pistia stratiotes,* in Zimbabwe and Botswana (Chikwenhere & Forno 1991, Chikwenhere 1994a). Other South American weevils, *Neochetina bruchei* and *N. eichhorniae*, have been used to control water hyacinth, *Eichhornia crassipes*, with considerable success in some areas like Lake Chivero (Chikwenhere 1994b). The insect has been introduced onto Lake Kariba to control the outbreak of water hyacinth there and it is likely to spread to Lake Cabora Bassa and other parts of the Zambezi.

Order Diptera

Many dipteran families have aquatic larval stages, among them the Culicidae (mosquitoes), Simuliidae (blackflies) and Ceratopogonidae (biting midges) that are vectors of human and animal diseases. Other aquatic dipterans include the Tabanidae (horseflies), Chironomidae (non-biting midges) and Chaoboridae (ghost midges), which are all of considerable ecological importance. In all aquatic dipteran families, only the larvae and pupae live in water; the adults emerge to a terrestrial existence. General comments on the biogeography of Diptera in southern Africa are given in Bowden (1978), while Elouard (1982) gives a general introduction to the order and some of its less important families. An important source, which gives keys to families, subfamilies and genera of all dipteran families, is Crosskey (1980) and it has been used to estimate the number of species in the principal families of aquatic diptera (Table 11.4). The estimates are almost certainly too low because little collecting has been done in many areas and the distribution of most species is still poorly known. It is likely that many new species have been described since this catalogue was published in 1980. Malawi has approximately 62 species of mosquitoes, 23 species of blackflies, 116 species of horseflies and 31 species of non-biting midges (C. Dudley, pers. comm.).

The craneflies (Tipulidae) are the largest family in the Diptera but they have generally been little studied. Their biology is poorly known, especially in Africa and there seems to have been little work done in the Zambezi Basin (which may explain why there are so few species that have been recorded from it; Table 11.4). The only relevant paper seems to be that of Alexander (1963).

The psychodids are a small family with only about 100 Afrotropical species (Table 11.4), although this number is likely to increase with further collecting. The larvae live in a variety of aquatic habitats, including foul ones like the biological filters of sewage works. They can become very abundant in these situations and play an important part in breaking down the organic matter in sewage. Nothing seems to be known about their ecology anywhere in Africa.

Table 11.4. The approximate number of aquatic Diptera in the Afrotropical region, and in the Zambezi Basin. Estimated from data in Crosskey (1980). Zambezi Basin records are based on species recorded from Angola, Malawi, Mozambique, Zambia and Zimbabwe.

	Afrotropical Region		Zambezi Basin	
	Genera	Species	Genera	Species
Tipulidae	55	1321	33	97
Psychodidae*	20	100	8	12
Culicidae	13	605	9	137
Simuliidae	3	165	3	31
Chaoboridae	2	11	1	5
Chironomidae	97	372	57	123
Ceratopogonidae	35	625	21	75
Tabanidae	30	722	21	268
Total	255	3921	153	748

* excludes the subfamily Phlebotominae, the larvae of which are not aquatic.

Mosquitoes (Culicidae) are particularly important in Africa because they are vectors of malaria. Major efforts to control the disease have been made for almost a century and there is now a huge literature on the physiology and behaviour of adult mosquitoes, as well as on disease transmission and control efforts. Much less is known about their biology and ecology during their larval and pupal phases in the aquatic medium. Hopkins (1952) and Rickenbach (1981) give a general introduction to African mosquitoes, while Khamala (1968) illustrates East African species. Jupp (1996) published a similar volume for southern Africa and it should be valuable for anyone working in the Zambezi Basin. The Anophelinae were reviewed by Gillies & de Meillon (1969) and the zoogeography of *Aedes* is discussed by Reinert (1970). An extensive checklist, with distribution maps, of Zimbabwean mosquitoes was published by Reid & Woods (1957), but this is probably out of date now if only because of the discovery that some species are actually species complexes.

These species complexes involve several morphologically identical species that can only be separated by cytological or biochemical means. The best known is the *Anopheles gambiae* complex, which has been studied in detail because one of the four species that make up the complex is a vector of malaria (Green 1970, 1972, Mahon, Green & Hunt 1976). Attempts to find methods to separate the species by morphological techniques have not been particularly successful (Zahar, Hills & Davidson 1970). The extent to which species complexes occur among species that do not transmit malaria is unknown, although there is evidence that they exist among *Aedes aegyptii*, the vector of yellow fever (Paterson, Green & Mahon 1976).

Second in importance to mosquitoes in Africa is the family Simuliidae (blackflies). In west and central Africa they are important vectors of onchcerciasis (river blindness), while in South Africa they are important pests of livestock, having become abundant after river flow patterns changed through regulation. Neither of these problems is particularly serious in the Zambezi Basin where much less attention has been paid to simuliids, in contrast to those in other parts of the continent. Important general guides to the African Simuliidae include Freeman & de Meillon (1953), Crosskey (1962, 1969) and Phillipon (1981). Palmer (1991) produced a regional checklist for southern Africa.

Other biting flies also have aquatic larval forms. The ceratopogonids are small biting midges, of which the best known is the genus *Culicoides* that, apart from their nuisance value, transmit various human and animal diseases. A general guide to African ceratopogonids is provided by Cornet (1981) while more detailed information is available in a series of 12 papers by de Meillon & Wirth (the most recent is de Meillon & Wirth (1991) and contains bibliographic information on the others). Very little is known of their larval biology and ecology, i.e. during their aquatic stage, in the basin. Braverman (1978) described some of the characteristics of their breeding sites around Harare, Zimbabwe, as well as some aspects of their biology and abundance (Braverman 1977, Braverman & Phelps 1981).

Another large and important group of biting flies with aquatic larvae is the Tabanidae (horseflies), which are significant mostly because of their nuisance value to domestic animals, although they do transmit some diseases. General guides to the tabanids of Africa are available in Oldroyd (1952, 1954, 1957) and Taufflieb (1981), while Travassos Santos Dias (1988) listed species from southern Africa. Goodier (1967) published a list of 88 species of Zimbabwean horseflies, although not all of them may have occurred in the Zambezi Basin, while Clarke (1968) and Phelps & Vale (1975) investigated their seasonal occurrence in Zambia and Zimbabwe, respectively.

An important family of non-biting midges is the Chaoboridae, whose larvae are important components of both the benthos (early instars) and zooplankton (late instars) (Mitchell 1976b). It is a relatively small family with perhaps only four species occurring in the Zambezi Basin; *Chaoborus edulis* (the most widespread and the only one apparently in Lake Malawi), *C. anomalus, C. ceratopogones* and *C. pallidipes* (Mitchell 1975, 1988, Irvine 1995b). Chaoborids are especially important in Lake Malawi, where dense swarms of adult lakeflies rising in a narrow column from the lake's surface are a visually striking feature. The FAO fishery expansion project concluded that

Chaoborus (the larvae are predaceous) competed for plankton resources with pelagic fish, which accounted for the low pelagic productivity of the lake (Turner 1982). It is likely that the quantity of zooplankton eaten by *Chaoborus* was overestimated and Irvine (1995b, 1997) estimated that it consumed 10-20% of the crustacean zooplankton production. The impact of this is probably reduced by the fact that *Chaoborus* is itself an important resource for many fish species living in the lake (Allison *et al*. 1995, Thompson & Irvine 1997).

Chaoborus was abundant in Lake Kariba during its early years when it was the major open-water predator on zooplankton (Bowmaker 1973, Mitchell 1975, 1988). This situation changed after the kapenta *Limnothrissa miodon* was introduced in 1967-68, which quickly reduced the population of *Chaoborus* in the lake (Marshall 1991). It is certainly absent from the zooplankton in open water but may still occur in protected shallow water areas, as other larger planktonic species do (Green 1985). Otherwise *Chaoborus* can only be expected to occur in the lake if it is carried there as part of the invertebrate drift in the inflowing rivers (Mills 1976). The same situation occurs in Lake Cabora Bassa where *Chaoborus* is rarely recorded (Gliwicz 1984). Elsewhere in the Zambezi Basin, chaoborids have been reported from a number of localities around Harare and in the Zambezi valley (Mitchell 1988).

The largest family of non-biting midges is the Chironomidae and they are widespread in all water bodies. Dejoux (1981) gives a good general guide to the family, while the main taxonomic study of African chironomids is Freeman (1955, 1956, 1957, 1958), although Cranston & Edward (1998) review the African genus *Afrochlus* and discuss the phylogeny of the subfamily Podonomonae. A review of the genus *Dicrotendipes*, which is widespread in Africa and known from both lakes Kariba and Chivero, is given in Efler (1988). Descriptions of larvae and pupae from Lake Kariba (McLachlan 1969a) and Malawi (McLachlan 1971) are of interest as they are among the few papers on the juvenile stages of these insects in Africa. He also provides a cautionary note on the use of prolegs, anal papillae and 'gills' in larval taxonomy, since these structures vary in relation to the conductivity of the water (McLachlan 1976). Despite the extensive work that has been done on African chironomids, new forms continue to be discovered, e.g. the records of *Doithrix* and *Georthoclades*, the first from the Afrotropical region, which came from the Zambezi Basin (Seuther & Andersen 1996).

Some chironomids are able to live in the small ephemeral rock pools that commonly occur in many parts of the basin, and fill up after rainfall (McLachlan 1981, 1983, 1988, McLachlan & Cantrell 1980). One of them, *Polypedilum vanderplanki*, is a cryptobiotic species and can survive the dry season as a larva through an extraordinary ability to survive for many years in an almost completely desiccated state (cryptobiotic). Although these rock pools may only last for a few days they amount to permanent habitats for this species. The other rock pool species, *Chironomus imicola*, is unable to survive like this and must seek new pools as an adult. In contrast to *P. vanderplanki* it has a very short life cycle, averaging 12.2 days from egg to adult.

Much of the interest in chironomids stems from their importance as benthic animals, where they have an important function in cycling detritus and as food for fish. Species in the subfamily Chironominae are also able to survive in polluted situations where oxygen is deficient because the blood of the larvae has an oxygen-transporting substance, which gives them a bright red colour (hence the name “blood worms”). Most of the work on chironomids in the Zambezi comes from Lake Kariba, as part of McLachlan’s (1974) investigation into the evolution of lake ecosystems. He was particularly interested in the effects of water level fluctuations (McLachlan 1970a) and the impact of aquatic macrophytes (McLachlan 1969b) on chironomid communities. Chironomids were also fairly numerous (about 11% of the biomass) on the drowned trees in the early years after the lake was created (McLachlan 1970b), but they had decreased in importance (to only 0.001% of the biomass) by the 1980s (Boon 1984). The relationship between chironomids and sediments was investigated in the field (McLachlan & McLachlan 1971) and in the laboratory (McLachlan 1969c).

Chironomids were also investigated in Lake Chivero in an attempt to determine the effect of eutrophication (Marshall 1978, 1982). Their abundance here was strongly seasonal and related to fluctuations in water level; as at Kariba the chironomids increased in numbers as the lake level rose and nutrients were released from the exposed shore. But in Lake Chivero, chironomid larvae were restricted to the first few metres, with the deeper sediments being dominated by oligochaetes. There was little change in their abundance over thirty years (Marshall 1995) despite the increasing severity of pollution in the lake. Few other data are available on benthos from anywhere in the basin, apart from some brief comments in Seaman *et al*. (1978) who noted that chironomids were among the dominant benthic species in Lake Liambezi.

Finally, benthic insects, especially chironomids, have been investigated because of their importance as fish food. Work on fish feeding has been centred on Lake Kariba where Mitchell (1976a) and Joubert (1976) both recorded a wide range of insects in the diet of most fish species. Even the almost exclusively piscivorous tigerfish, *Hydrocynus vittatus*, fed on invertebrates during its juvenile stages (Kenmuir 1975). Similarly, in Lake Chivero Munro (1967) and Marshall & van der Heiden (1977) found that almost all fish species fed on benthic insects and other invertebrates. This emphasises their importance in aquatic systems.

11.3 CONSERVATION

11.3.1 **Conservation of invertebrates**

Little importance has been attached to the conservation of invertebrates in Africa and it is probably true to say that most people on the continent are quite indifferent to the idea. Indeed, most would probably prefer to eliminate them, supporting campaigns against snails, mosquitoes or blackflies without any regard for the consequences to other species. This is a shortsighted attitude, of course, since invertebrates are vital for the functioning of ecosystems, processing organic matter and nutrients, as food for other animals, and as biological control agents for a variety of pest species. This view is reflected in the relative paucity of papers dealing with the conservation of aquatic invertebrates. Of the Zambezi Basin countries, only Namibia has made any attempt to draw up a checklist of species and articulate a conservation policy (Curtis *et al*. 1998).

Aquatic systems throughout the basin are subject to various human activities that affect their biota in one way or another. Of particular concern is the use of pesticides to control mosquitoes (vectors of malaria), tsetse flies (nagana) or snails (bilharzia) because of their impact on non-target species. Very little is known about the impact of these operations on aquatic invertebrates apart from an evaluation of the effect of a molluscicide on stream fauna (Harrison & Mason 1967) and some work on the impact of endosulfan, used to control tsetse, in the Okavango Delta (Russel-Smith 1976, Russel-Smith & Ruckert 1981).

Other activities that have an impact on aquatic systems include agriculture and land clearance, pollution and siltation, but very little is known about their effect on aquatic invertebrates. Organic pollution in streams around Harare, as elsewhere in the world, caused a loss of insect species with only chironomids being able to survive in the most affected areas (Marshall 1972). Even amongst the chironomids, only *Chironomus* is able to resist severe pollution, while other genera, like *Procladius, Tanypus, Pentaneura, Dicrotendipes* and *Nilodorum*, were dominant in less severely affected areas.

Little attention has been paid to the introduction of alien invertebrate species, apart from some brought in as biological control agents and others for aquaculture purposes. Many insect species have remarkable powers of dispersal because of their powers of flight and the ability to use the winds to carry them long distances. The increase in air travel has assisted many species, especially mosquitoes, to spread, which explains how species like *Aedes aegyptii* and *Culex pipiens* reached southern Africa (de Moor 1992). Both are potential disease vectors and their appearance is a cause for concern.

At present, temporary waters are the most vulnerable ecosystems in the region. The invertebrate species that live in them are well adapted to arid conditions and can survive drought but, because many of them are relatively large, they cannot survive fish predation. The introduction of fish into these pools, which often follows when they become permanent after water is pumped into them, can have a serious impact on the invertebrate fauna. Such a situation occurred in the Hwange National Park where some seasonal pools became permanent when water was pumped into them to supply game animals during the dry season. The pools were stocked with Catfish, *Clarias gariepinus* and the diversity of insects (mostly Hemiptera) and other invertebrates was greatly reduced (Weir 1972). In this case, the consequences were perhaps not serious since none of the species were endemic and there are numerous other seasonal pans in the park which cannot support fish. But some seasonal pools support endemic crustacean species and these populations are at risk if fish are introduced into these pools. An example of this danger is illustrated by the possible extermination of hitherto undescribed and endemic crustacea in Rhino Ridge Pool in South Africa that followed the introduction of fish into it (Martens & de Moor 1995). Ironically, this occurred in a nature reserve where managers were attempting to improve a bird observatory.

11.3.2 **The present state of knowledge**

The destruction of the crustaceans in the Rhino Ridge Pool came about through ignorance. It was done by conservationists for the best of motives – to improve and develop a bird observatory and educational facility – but without any realisation that unique species may have existed. This reflects the need for a greater understanding of aquatic invertebrates and their importance. This understanding will not be achieved without investment in basic taxonomy and ecological studies. At present, most invertebrate taxonomists are based in Europe and North America, with very few in South Africa, and few African countries have the resources to employ taxonomists, give them the special training they need and maintain the museum collections that have to be built up. Unfortunately donor funding for biodiversity is increasingly linked to human social interests and the culture of utilizing resources (Attwell & Cotterill, in press); funding for naming and counting species is increasingly difficult to obtain.

One exception to this is the increasing use of aquatic invertebrates to monitor water quality and programmes to accomplish this are well developed in some countries, like Australia (Chapman 1995) and South Africa (Chutter 1998). Little has been done in the Zambezi Basin, apart from some work in streams around Harare (Gratwicke, in press), but it is hoped that more will follow. Projects like this should stimulate an interest in invertebrates and bring their importance in aquatic systems to a wider range of people.

11.4 CONCLUSIONS AND RECOMMENDATIONS

The knowledge of aquatic invertebrates is generally rather sparse in most parts of the Zambezi basin. It is difficult for field workers to do much on them since they can usually only be identified by people with specialist knowledge and access to appropriate microscopes. The scattered nature of the literature and the lack of good field guides is another impediment to understanding. Also, while funding may become available for fisheries investigations, which have an obvious economic justification, it is rare for projects in invertebrate biology to be funded adequately (an obvious exception is those species of medical or veterinary importance). These comments apply to the basin as a whole, but there are some areas where more detailed information on some invertebrate groups is available.

11.4.1 Summary of knowledge by area

A preliminary assessment of the state of knowledge of aquatic invertebrates from the various sections of the Zambezi Basin is given in Table 11.5, and briefly outlined below.

Upper Zambezi

As in most of the basin, invertebrates have been studied only in localized areas. The most important of these is the Kavango and Chobe systems in Namibia, from which collections have been made. While attempts have been made to list all the aquatic macro-invertebrates known from Namibia, relatively little is known of their biology.

Middle Zambezi

Data are available from some parts of the Middle Zambezi system. Lakes Kariba and Chivero have been studied in some detail, with data available for the benthos (notably molluscs, Chironomidae (Diptera) and oligochaetes), and the planktonic microcrustacea and rotifers. The planktonic crustacea of Lake Cabora Bassa have also been investigated in some detail but nothing else is known about the invertebrates of this lake. Smaller reservoirs have been investigated to a lesser extent but the detailed checklists of rotifers from Zimbabwe are a noteworthy contribution. River systems have been largely neglected, apart from a few studies in stream ecology in Zimbabwe and some data from the Kafue River, collected a long time ago.

Lower Zambezi

Almost nothing has been published on invertebrates of the Lower Zambezi, which remains a priority area for further investigations.

Lake Malawi

The aquatic invertebrate fauna of Malawi seems to be quite well known and lists of species have apparently been prepared, although they are not readily available (C. Dudley, pers. comm.). The lake itself is of special importance since it has a number of endemic species amongst the molluscs and the crustacea (and probably other groups, too).

11.4.2 Use of aquatic invertebrates for monitoring

Knowledge of aquatic invertebrates is likely to become increasingly necessary in future for anyone involved in managing water quality. It is well known that communities of aquatic invertebrates respond to changes in the physical and chemical environment in which they live. In many parts of the world attempts have been made to use this fact to detect water pollution and to manage water quality. A simple method of determining the state of the aquatic invertebrate community, and use

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Table 11.5. State of knowledge about the major invertebrate groups in the Zambezi Basin (1 = none/virtually none; 2 = very poor to poor; 3 = moderate to good).

	Upper Zambezi			Middle Zambezi			Lower Zambezi			Lake Malawi		
Group	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology	Taxonomy	Distribution	Ecology
Protozoa [1]	1	1	1	1	1	1	1	1	1	1	1	1
Porifera [2]	2	1	1	2	1	1	1	1	1	2	1	1
Cnidaria [3]	2	1	2	2	1	2	2	1	2	2	2	2
Turbellaria	1	1	1	1	1	1	1	1	1	1	1	1
Rotifera [4]	2	3	1	3	3	2	2	1	1	1	2	1
Nematodes	1	1	1	1	1	1	1	1	1	1	1	1
Oligochaetes [5]	2	3	1	2	2	3	1	1	1	2	2	1
Crustacea [6]	3	3	1	3	3	3	1	1	1	3	3	3
Chelicerata	1	1	1	1	1	1	1	1	1	1	1	1
Insecta [7]												
a) Ephemeroptera [8]	2	1	1	2	1	1	1	1	1	2	1	1
b) Odonata [9]	3	3	1	3	3	1	3	2	1	3	2	1
c) Coleoptera [10]	2	2	1	2	2	1	2	1	1	2	2	1
d) Diptera [11]	2	2	1	3	3	2	1	1	1	2	3	1
Mollusca	3	3	1	3	3	2	3	2	1	3	3	1

Notes:

1. Ciliates are important pelagic species in Lakes Tanganyika and Kivu, but not apparently in Lake Malawi or anywhere else in the Zambezi Basin. This seems to be linked to the impact of planktivorous clupeids; in Lake Kivu the ciliates only appeared after the larger zooplankton were eliminated by *Limnothrissa*.
2. Records of sponges are available from the Okavango and Chobe systems in Namibia (UZ), Lake Kariba and Mwenje Dam (MZ), and from Lake Malawi from which several species have been described. Nothing is known of their ecology.
3. The taxonomy of cnidarians is well known as far as medusae are concerned since there is only one species (sometimes thought to be two), but less in known about polyps. The only ecological study of jellyfish comes from Lake Kariba.
4. The rotifers are especially well-known in the Middle Zambezi, thanks to the work of Green in Africa in general, and Lake Kariba and other reservoirs in particular. Very little is known about their ecology.
5. The oligochaetes have been studied intensively in Lake Chivero (MZ), from which some ecological data are available. Other collections have been made in the Okavango system (UZ), Lake Kariba (MZ) and Lake Malawi.
6. The planktonic crustacea are generally well known in all systems except perhaps the Lower Zambezi. Their ecology has been studied in considerable detail in Lakes Kariba and Cabora Bassa (MZ) and Lake Malawi. Less detailed studies are available from a number of reservoirs in Zimbabwe (MZ) and Lake Liambezi (UZ).
7. The smaller insect orders have not been studied intensively in the basin, where most work has concentrated on the larger orders like the Diptera.
8. The taxonomy of southern African Ephemeroptera is quite well known, thanks to the work of K.M.F. Scott, but their ecology has not been studied in much detail anywhere in the basin.
9. The Odonata are well known from a taxonomic point of view – perhaps more so than any other insect order – through the work of Elliot Pinhey. The same cannot be said about their ecology, which has been little studied anywhere in the basin.
10. Some coleopteran groups, like the family Dytiscidae, are quite well known but their ecology is poorly understood.
11. Dipteran groups that are of medical or veterinary importance are well known, as are some others like the Chironomidae, which have been studied extensively in Lake Kariba.
12. Of all the invertebrate groups, the molluscs are best known taxonomically because there are relatively few species (compared to the insects) and their medical importance requires accurate identification. Their ecology has been studied in most detail in Lake Kariba and parts of Zambia and Zimbabwe (MZ), partly in relation to bilharzia control. Lake Malawi has a large mollusc fauna, with a number of endemic species, which has not been thoroughly studied.

it as an index of water quality, has been developed in South Africa. It has been termed SASS (South African Scoring System).

The system involves collecting a sample of invertebrates from a stream or river using a standardised net and following defined methods (Chutter 1998). The invertebrates collected are tipped into a tray and the types recorded. It is generally only necessary to record each type to family level, which is usually possible with standard guides. Each family is given a number from 1 to 15, which reflects its sensitivity to changes in water quality; the most tolerant families are ranked 1 and the least tolerant 15. The SASS score is the sum of the numbers against each recorded taxon, the ASPT or average score per taxon is the SASS score divided by the number of taxa. Unaltered water will have high SASS or ASPT scores while very low scores will be recorded in severely polluted systems.

This system has been very successful in South Africa in assessing water quality over extensive catchment areas (Chutter 1998) and has been successfully adapted for use in Zimbabwe (Gratwicke, in press). The SASS method is presently most suited to riffles in streams and small rivers, but it can probably be adapted for use in larger rivers and floodplain systems. Its advantage is its simplicity; the only equipment needed is a hand net and some basins, buckets, and so on, and most invertebrates can easily be identified to family level. Furthermore, the invertebrate community is continuously exposed to pollutants and therefore responds to sporadic discharges that are not easily detected by chemical analysis.

Biomonitoring of this kind could allow a network of pollution monitoring stations to be established throughout the Zambezi basin, with a rather higher density in areas where pollution problems are known to exist. The costs of running such a programme are generally within the means of most government departments within the region although donor funding might be needed to train personnel, provide some equipment, and so on.

11.4.3 **Recommendations**

Conservation agencies should make more effort to recognize the importance of invertebrates. They are by far the most numerous animals in aquatic systems, and also the least known. They represent the largest gap in our understanding of biodiversity, and this alone warrants more study. Most of them have no obvious economic or social value so this means that a fundamental change in the approach taken by most agencies, who will have to recognize that the study of biodiversity is intrinsically important.

Some of the steps that might be taken include:

(a) Scientists and specialists could be asked to summarize all the available data on particular invertebrate groups. This would have to involve a review of the primary taxonomic literature, an evaluation of all specimens available in museums throughout the world, and an opportunity to locate the grey literature available in countries of the region. This would obviously be a costly business and could not be done without a significant commitment of funds over a long period.

(b) At the same time museum resources in the basin need to be strengthened. This would have to include funds for the appointment and training of new curators, as well as operating funds so that they can establish and expand collections, and to publish their work. It has to be accepted that invertebrate identification requires trained specialists who require lifelong practice before becoming fully conversant with their special groups. This requires long-term financing.

(c) Some short-term projects that would stimulate interest in invertebrates could also be established. One example might be to establish a basinwide programme to assess water quality using the SASS system, with appropriate modifications. Such a programme would obviously need a co-ordinator, but local people could be trained to sample in their own areas and the requirements for equipment are relatively small.

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