THE DEVELOPMENT OF AN ECOLOGICAL MODEL TO DETERMINE FLOOD RELEASE OPTIONS FOR THE MANAGEMENT OF THE PHONGOLO FLOODPLAIN IN KWAZULU/NATAL (SOUTH AFRICA)

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ABSTRACT

The Phongolo River floodplain in KwaZulu/Natal is a river-associated wetland which was subject to regular cycles of flooding in the past. The floods were associated with seasonal summer rainfall. Through the wet and dry cycles on the floodplain there was an alternation between the aquatic and terrestrial biomes. Many of the fishes on the floodplain are dependent on this cycle for their survival.

The construction of the Pongolapoort Dam in 1969 has resulted in alterations to the timing, magnitudes and duration of the natural flooding events of the Phongolo River. This alteration has affected the fisheries. It is now necessary to simulate natural floods by artificial water releases from the dam. There are several demands on the water supply, so it has not always been possible to adhere to the natural flood regime.

This necessitated the need for an integrated management programme to ensure the sustainability of the natural resources. A practical ecological model of the fishery was developed to determine an optimum flood release scenario for the floodplain.

The relative abundances, distribution and species richness of the fishes were determined at various lakes and rivers on the floodplain. A community classification of the fishes was determined using TWINSPAN ordination. The potential yield of the fish at each site was calculated. Flood releases of varying magnitudes were simulated using Geographic Information Systems (GIS).

This information was combined in a model which can be used by resource managers to estimate the percentage species compositions of fishes at each of the lakes, and to compare the actual harvest to the potential calculated sustainable yields of fishes for various flood release regimes. Subsistence agriculture and other beneficial ecological information can be incorporated into the model to determine the effect of different flood release options for the Phongolo floodplain.

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CHAPTER 1. INTRODUCTION

Floodplain ecosystems

Wetland ecosystems are dynamic systems supporting a wide diversity of plants and animals, with a relatively high biological productivity (Bruton & Jackson 1983). Floodplains are those low-lying areas which are submerged seasonally by overspill from a river (Moses 1987), but which are otherwise dry or disconnected by levees from the river for the rest of the year, forming large open lakes (Kok 1980). In the Phongolo floodplain, a river-associated wetland (Bruton & Jackson 1983), these lakes are old river courses (ox-bow lakes) and unfilled valleys of old tributaries (Heeg & Breen 1979, 1994). Most large African floodplains follow a similar seasonal progression of events through wet and dry cycles (Gaudet 1992), and the fishes of these freshwater ecosystems are governed by associated biological rhythms (Jackson 1989). Therefore, river-floodplains are not only dynamic, but are also spatially, hydrologically and biologically complex (Power *et al* 1995).

The Phongolo floodplain ecosystem was subject to regular cycles of flooding in the past, which essentially comprised two components: the first cycle was associated with seasonal summer rainfall when spawning usually occurred, and superimposed on this was a longer term rhythm of annual rainfall variability (Jackson 1989). Within floodplain systems, there is a high variability as result of the high surface area-to-volume ratio, and continually fluctuating water levels, resulting in pronounced fluctuations of the environmental variables such as dissolved oxygen and water temperature. Through this wet and dry cycle floodplains show an alternation between aquatic and terrestrial biomes, with characteristic changes in fauna and flora (Welcomme 1973). Many of the fish populations of floodplains are therefore dependent on a natural annual cycle for their survival (Lowe-McConnell 1975, Welcomme 1979).

Natural breeding cycles

Natural breeding cycles associated with the Phongolo floodplain under a summer flood regime are as follows (Jackson 1989, Fig. 1): there is a pre-flood migration of flood-dependent fish such as *Labeo rosae* or *Hydrocynus vittatus* towards the incoming water. During the flooding period there is a large nutrient pulse when allochthonous material in the form of detritus, terrestrial plant matter and nutrients from the soil and animal faeces are incorporated into the water. During the following stage lateral migrations occur from the river into the lakes, and breeding and spawning take place in the newly available habitats. This is followed by the feeding and growth of the larvae and juveniles in refuge areas amongst the inundated vegetation. Food and refuge areas from predators are the most important ecological requirements of juvenile fish (Jackson 1962). When the flood begins to recede the flood-dependent fish move back to the river where possible and those fish tolerant of deteriorating water quality remain in the lakes (Bruton & Jackson 1983). As a result of this, the fish stocks tend to become more concentrated and many of the fish are recruited into the fishery.

Throughout the flood season, the total biomass increases and peaks at the end of the flood. It then declines through the dry season due to fishery mortality, in the form of *isiFonya* fishing, sack seining, gill netting, hook-and-line fishing, piscivorous birds (such as pelicans), and the deterioration of the lake environments due to increasing turbidity and decreasing oxygen levels (Fig. 1). The duration and timing of flooding is therefore important to the recruitment, growth and survival of fish stocks (Bruton & Jackson 1983), and periods of high water level result in a large percentage of the fish population being able to spawn successfully.

Junk *et al* (1989) proposed that the major factor controlling the biota in river-associated floodplains is the flood-pulse, when nutrients are exchanged between the river channel and floodplain lakes. The increase in and exchange of nutrients would result in an increase in biological activity. This enhanced biological activity was postulated to maintain diversity within an ecosystem (Bayley 1995). The principal agents associated with this alluvial process are the dissolved organic nutrients from the allochthonous material, including plants, detritus and sediments. These are important inputs into the nutrient pump in floodplain ecosystems (Furch *et al* 1989). Small fish play an important ecological role in converting nutrients at the base of the food chain to food for higher trophic levels, and in so doing act as a pathway for nutrients to pass from the terrestrial to the aquatic components of the ecosystem. When soils are inundated, some fish cause the nutrients in the sediments to become dispersed as a result of their nesting activities. During flooding the fishes also reverse the normal downstream flow of nutrients due to their upstream migrations (Bruton & Jackson 1983). Although flooding is important, it is essential that there is a continual water flow in the river between floods, as adequate flows are fundamental to the maintenance of essential river functioning (Osbourne *et al.* 1988).

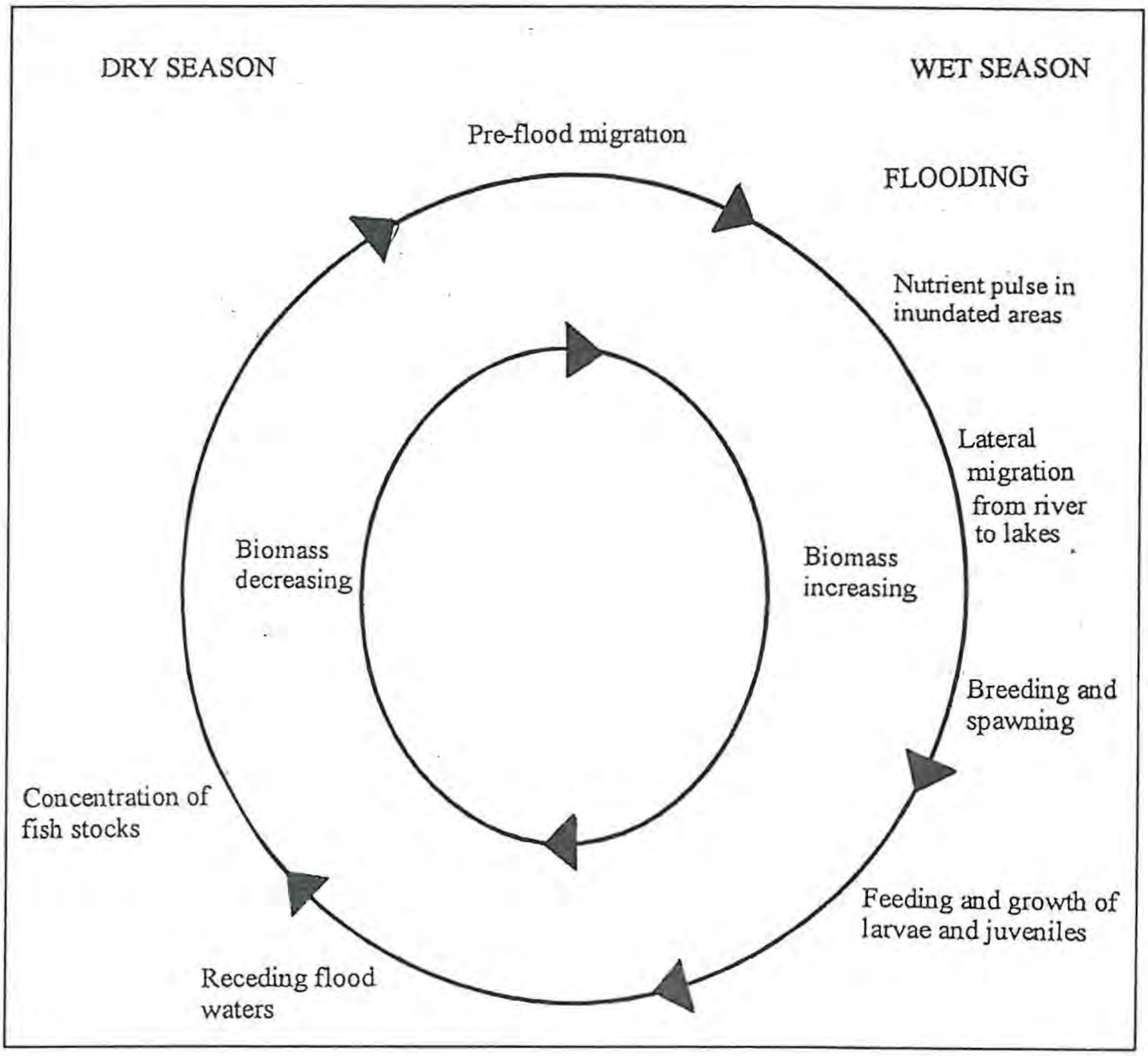

Figure 1. Natural breeding cycles of fishes associated with a summer flood regime.

The effect of environmental change on an ecosystem (such as the impoundment of a river) can only be assessed when the dynamics, including the nutrient and energy pathways, of the ecosystem are fully understood. There are two main areas of flood dependence: allochthonous energy inputs and autochthonous energy inputs. These inputs are directly effected through reduced energy input. The fishes are indirectly affected, but are also directly dependent on the floods for their breeding (Heeg & Breen 1982, 1994). Fish feed mainly in the warmer months, since they rely to an extent on the environment to regulate their metabolism (Hoar & Randall 1971). Therefore, if floods are released during the colder months, the fish would not be able to take advantage of the possible increase in food supply (brought about by the water inundation), since they are physiologically less active (Merron *et al.* 1993a). It is also true that there would be little allochthonous material available during winter to be incorporated into the water.

The amount of water released during a flood also has an effect on spawning. It is possible that if the flood levels are low some of the lakes will not be flooded. The flood-dependent fishes within these lakes will not spawn and will then resorb their gonads, resulting in limited or no recruitment into the fishery in following years. The marginal zone of the lakes on the floodplain is rich in invertebrates with a wide size range. These invertebrates provide the necessary food requirements for the juvenile fishes (Heeg & Breen 1994). If there is insufficient water, or the water level drops too rapidly after a flood release, this food source will be affected, ultimately affecting the fish stocks.

In most African floodplain systems it was found that fish production was directly proportional to the duration and extent of the flood regime (Welcomme 1979). It was also found that the flood regime in temperate floodplains affected the fisheries production (Halyk & Balon 1983). The principles governing these systems can be tested on the Phongolo floodplain.

Historical flood regime of the Phongolo River

Most of the river-floodplain ecosystems in the world have been altered by human activities (Sparks 1995), and the Phongolo floodplain is no exception. The construction of the Pongolapoort Dam upstream of the floodplain in 1969, primarily to supply water for large-scale irrigation on the Makhatini Flats (Heeg & Breen 1979), has resulted in artificial alterations to the Phongolo River and floodplain and has affected the fisheries of the floodplain (Breen & Heeg 1986). The impoundment of the water has resulted in alterations to the periodicity, magnitude and duration of the natural flooding events (Heeg & Breen 1987) and it is now necessary to simulate natural floods by artificial releases of water from the dam. The flood regime is the fundamental exogenous cue regulating the floodplain ecosystem and affects the biology of inhabiting organisms. The chemical content of the floodwaters after heavy rains affects the spawning activities of the fishes (Lake 1967). Many of the resident thirty-five species of fish occurring on the floodplain are flood-dependent spawners, spawning only during flood releases and when other environmental factors such as temperature are suitable (Coke & Pott 1969, Merron *et al.* 1985, Stallard *et al.* 1986, Merron *et al.* 1989, Merron *et al.* 1993b). The timing of floods is also important for the provision of refuge areas for juvenile fish, and for the input of energy into the water via allochthonous material. The maintenance of the Phongolo floodplain therefore relies on regular water releases from the dam that are of sufficient magnitude to flush out the system and to allow for fish migrations. The floods must also be of sufficient duration to allow for the transfer of energy-rich allochthonous organic material to aquatic components (Heeg & Breen 1982).

During the early 1970's, after the construction of the dam wall, judicious water releases from the dam closely simulated the river's natural flood patterns and had little apparent effect on the biology and ecology of selected species (Kok 1980). However, during the drought of the early 1980's no large scale water release from the dam was possible, and when water was released it was during the cooler winter months, when the fish were physiologically unable to take advantage of increased water levels and spawn (Merron *et al.* 1985). In 1984, the flood associated with Cyclone Demoina resulted in large-scale fish recruitment in all areas of the floodplain (Merron *et al.* 1985, 1993a). Since 1984 there have been only erratic water releases which have not always been synchronous with biological rhythms, and several of the flood-dependent spawners have declined in numbers (James 1992).

Heeg & Breen (1982) indicated that fish reproduction reached a peak under flow conditions resembling a natural flood regime. A reduced-aseasonal flood resulted in a decrease in allochthonous input, inhibiting the breeding of anadromous fishes. Of the fishes inhabiting the floodplain, two species have been identified as rare (*Chiloglanis swierstrai* and *Nothobranchius orthonotus*), and are listed in the Red Data Book (Skelton 1987), and 20 species are boundary species that are at the southern limit of their distribution (Skelton 1993). The need to conserve biodiversity within the system is therefore of international importance. The majority of the boundary species present in the river and floodplain lakes are important to the subsistence fishery (Kok 1980, James 1992).

The fishes of the Phongolo floodplain form a crucial component of the diet of the people living on the floodplain. Approximately 98% of the people consume fish as a free source of protein (Kok 1980). The rural population living on the floodplain that relies on its natural resources is estimated to number approximately 100 000 people.

Subsistence fishery on the Phongolo floodplain

A multispecies subsistence fishery exists on the Phongolo floodplain. All species and age groups of fishes are caught using different methods. The local knowledge of fish behaviour is exploited extensively in the choice of fishing techniques. These techniques include setting *uMono* traps (funnel-shaped fish traps) in channels connecting lakes, setting gill nets in shallower water during flooding (when fish migrate to newly inundated littoral areas to feed and spawn) and *isiFonya* fishing (thrust baskets) when water levels are receding. It is difficult to collect statistics on the dispersed subsistence fishery on the Phongolo floodplain, and for this reason it is also difficult to develop a sophisticated model for its management.

Several types of subsistence fishing practices are used, but most methods are dependent on a natural cycle of flooding and drying of the lakes for their success. The traditional artisanal methods include *isiFonya* fishing, fish spears, *uMono* traps and reed seines. The introduced fishing methods include hook-and-line fishing, gill netting and sack seining (Tinley 1964). *IsiFonya* fishing, which resembles an aquatic game drive, may involve up to several hundred men and women who form a line across a lake and move forward towards the opposite end of the lake while thrusting their baskets into the water to herd and catch fish (Tinley 1964, Fig. 2). Recently, the simultaneous use of gill netting and sack-seining has been observed during *isiFonya* drives. *IsiFonya* drives are conducted throughout most of the year provided that the lakes are shallower than approximately 1.4 m as deeper water cannot be fished effectively. Approximately 180 kg of fish are harvested during an average *isiFonya* drive (Tinley 1964, James 1992); due to varying productivity between different lakes, the yields vary widely throughout the floodplain.

The use of *uMono* traps is a traditional fishing method used only by men. The traps are constructed of strong sticks and are set in channels connecting the river to the lakes or channels interconnecting lakes during flooding. *UMono* traps are often placed within a barrier of sticks set across a channel. Although traps are set for relatively short periods, they generally catch large numbers of fish (Merron *et al.* 1993a).

Gill nets are used mainly by men, although women sometimes assist by driving fish into the nets. The gill net mesh size used ranges from 75-115 mm stretch mesh, although the use of smaller mesh nets has been instituted to harvest adults of smaller, pelagic species such as the *Brycinus imberi* and *Schilbe intermedius*. Gill nets are set from boats or by wading into the water. Often fish are herded into the nets by several people. Hook-and-line fishing is usually practised by boys, although both men and women have also been observed practising this method. Sack-seining is a method of fishing practised by women and young girls. Usually two women scoop a piece of shade cloth or hessian sack into the water, while other women chase fish into the sack. They harvest primarily small species (e.g. *Barbus* spp.) and juvenile fishes (< 140 mm SL).

Figure 2. *IsiFonya* fishing on the Phongolo floodplain (drawing by Dave Voorvelt).

Management of flood releases

It is known that the alteration of flood timing, magnitude, frequency and duration disturbs the ecosystem functions (Gore & Shields 1995), including both the terrestrial (Walker & Thoms 1993) and aquatic (Toth *et al* 1993) communities. Therefore, since the construction of the Pongolapoort Dam, there has been a need for a management programme for flood releases which simulates the river's natural flow and creates floods of the correct timing and duration (Coke & Pott 1970, Heeg

& Breen 1982). The management programme should promote the fishery on a sustainable basis. In order to accomplish this an understanding of the factors promoting secondary and tertiary productivity should be obtained. To this end, much research has been performed on the floodplain and many suggestions for its management have been made: Kok (1980) suggested that water should be released from the dam during summer based on studies of the biology and ecology of several large fish species from the Phongolo floodplain. Heeg & Breen (1982, 1994) suggested that the sustainability of the floodplain resources relied on summer water releases from the Pongolapoort Dam. Merron *et al.* (1985, 1993a) after pre- and postflood surveys on the Phongolo floodplain suggested that the fisheries resource would be sustained provided a flood regime as close to natural conditions as possible was adhered to. Drewes (1988) suggested that for the most efficient functioning of the ecosystem, water should be released during the summer months. This was based on complex mathematical modelling. James (1992) suggested that water should be released during the summer season based on several years of research on the fishes of the Phongolo floodplain carried out by the Natal Provincial Administration (Nature Conservation).

Research has proved that summer water releases are the most beneficial for the fishes and the ecosystem, but there are several conflicting demands on the water supply from the Pongolapoort Dam. For a management programme to be effective on the Phongolo floodplain, it would have to take all the resource utilisers on the floodplain into account. The Department of Water Affairs and Forestry (DWA&F) prefers to release water only after the rainy season so that it can determine the period of water inundation and attenuation on the floodplain accurately. It was also proposed that a flood release programme should be formulated to take the interests of agriculture into account (Breen & Heeg 1982). This implies that no water should be released from November (when seeds are planted) to February (when they are harvested). Derman & Poultney (1985) suggested that water should be released in August and September, so that the agriculturalists can take full advantage of the rainy season. This is in conflict with the most beneficial water releases for the environment.

In developing a management strategy for the Phongolo floodplain, it must be taken into account that minimum water levels have been found to determine the habitat potentially available for fish production (Welcomme & Hagborg 1977). Welcomme (1979) found that 80 % of the variation in yield from a river-associated wetland fishery can be correlated with the flood history of the previous two years. Therefore, the lack of a flood in a given year may result in a lack of breeding in several species, which would result in a decrease in biomass and production for the next two years.

Refugia within the Phongolo floodplain

It is possible that the fishes can be exploited to local extinction during the dry-down phase as large fish kills would normally occur due to deteriorating water quality conditions. This type of fishing strategy would not affect the fishery provided that the recolonising life-history stage was protected in some refuge area (Bruton & Jackson 1983). The lakes within Ndumo Game Reserve harbour large fishes, in comparison to floodplain lakes which are harvested by people and are affected to a larger degree by artificial flood releases from the dam. The refuges in Ndumo Game Reserve are consequently essential for the management of the fishes. It is likely that only river-lake contact will provide the necessary migration route for fishes, where breeding stock can be replenished through lateral migration (Heeg & Breen 1994).

For a refuge to be viable it must retain sufficient stocks of reproductively active fishes during the dry-down which must be capable of reaching newly flooded areas, and reproduce and grow there. This implies that flood releases from the dam must be of a duration long enough to ensure that lakes near the dam are still connected to the river when the lakes in Ndumo Game Reserve and beyond are connected, to allow for the movement of fishes. If this is not possible then there should be two shorter flood releases, with an interval between them, to allow for fish movement (Merron & Weldrick 1994).

The lakes which dry out completely still continue to contribute to the ecosystem through the transference of energy to the terrestrial component through predation, decomposition and scavenging (Halyk & Balon 1983). These lakes act as refuges of energy, as much of this energy is returned to the aquatic system during subsequent flooding (Balon 1978).

Floodplain fishery yields

The standing stocks and yields of fishes may be relatively low in small floodplain ecosystems due to the presence of many small and juvenile fishes (Bruton & Jackson 1983), compared to the yields from larger river floodplains (Welcomme 1979). Within the Phongolo floodplain it is possible that the yields from the harvested lakes would be significantly lower than from those within Ndumo Game Reserve, which are not fished (Weldrick & Merron 1994). Based primarily on gill net catches, Lagler *et al.* (1971) have estimated that the standing stock of fishes on the Kafue floodplain in Zambia may be 350 - 500 kg.ha^{-1}. Standing stocks in different parts of the Okavango Delta are estimated to be between 10 and 700 kg.ha^{-1} (Fox, 1976), with the higher figure applying to nutrient-enriched lagoons. Yields are calculated as one-third of the standing stock (Lagler *et al.* 1971), based on the actual yield and biomass on the Kafue floodplain. Welcomme (1979) plotted catch (kg) against flooded area (ha) for various river floodplains and was able to deduce that normally exploited floodplains should produce 40 - 60 kg.ha^{-1}.y^{-1} on a sustained basis.

On the Phongolo floodplain, in addition to being affected by water releases from the dam, the fishes are heavily utilised by people. However, the floodplain lakes are potentially highly productive since they have abundant macrophytes and plankton, are relatively shallow and warm and have a regular nutrient input (James 1992). Coke & Pott (1970) estimated that the annual potential yield from the floodplain lakes in their natural state was 112 kg.ha^{-1}. This was based on the productivity of the Phongolo floodplain compared to that of Lake Kariba (Harding 1964, Kemp *et al* 1967) which was estimated at 45 kg.ha^{-1} in the shallow areas (Hickling 1961). A potential yield of approximately 500 tonnes per annum was calculated by Kok (1980) based on the total flooded area of the floodplain at 10 350 ha calculated by Breen *et al* (1978). The area at mean retention level (MRL) of 2 700 ha is considered a more accurate estimation for the potential area for the fishery (Heeg & Breen 1982). The average potential yield estimated by Heeg & Breen (1982) was between 500 and 750 tonnes per annum, while James (1992) estimated a yield of 385 tonnes per annum, based on an average standing stock of 37 kg.ha^{-1} estimated by Welcomme (1979). James (1992) states that a more realistic yield would be between 150 and 250 tonnes per annum. This is equivalent to between 55 and 93 kg. ha^{-1}. y^{-1}. The apparent decrease in yield can be attributed to several factors: irregular water releases often asynchronous with biological rhythms of fish; overfishing primarily as a result of an increase in human population residing immediately around the floodplain, from 40 000 (Heeg & Breen 1979,1994) to 100 000 (Poultney *pers comm* 1995); and reduced productivity of lakes due to an increase in pollution from human effluent (raw sewage, washing, etc.), agricultural runoff and poor agricultural practises.

Heeg & Breen (1979) estimated a yield of 400 tonnes per annum (1978) for the subsistence fishery as based on a population of 40 000 people, which was 100 tonnes below the estimated potential yield. It would appear that with the increase in human population, the subsistence fishery is at or near its carrying capacity. With the rapid human population growth in Maputaland it is likely to outstrip the yield of the fishery to a greater extent in the future. It is therefore necessary to consider introducing a total allowable catch for the floodplain, admittedly a difficult task for a dispersed, subsistence fishery. Suggestions on other ways of accommodating any increase in yield by rural people include the use of small mesh gill nets, fish farming, prohibiting gill netting in inlet channels during flood releases and summer flood releases (Merron & Weldrick 1994).

The calculation of the potential yield has been purely theoretical, based on values calculated by Welcomme (1979) for tropical African floodplains, which have then been compared to the values for the Phongolo floodplain. The calculations have not taken the actual fishing pressure or natural mortality into account, and have been based on the total flooded area, and not the area at MRL. More accurate calculations would be based on the fishery area at MRL, and would be compared to the actual harvest, taking fishing pressure and natural mortality into consideration.

Integrated management

The sustainable utilisation and conservation of the fishes of the Phongolo floodplain cannot be carried out in isolation from other environmental threats which affect the floodplain ecosystem. Fishes can be adversely affected by a number of other environmental problems such as deforestation, unplanned agricultural development, loss of riparian vegetation and encroachment of cattle (all potentially resulting in soil erosion and increased sediment loads in lakes and rivers). The destruction of riparian vegetation decreases the allochthonous energy inputs into the ecosystem which can impact negatively on fishes. The change in land use patterns over the last decade brought about by increased human population is straining an already heavily utilised resource base, such as the encroachment of people onto sensitive ecological areas, and cutting and burning riverine vegetation for agricultural purposes. Increased slash/burn shifting agriculture leads to a decreased flood attenuation regime on the floodplain and increased water velocity down the floodplain during flood releases. Levees may be altered, necessitating more frequent and deeper openings of the channels into the lakes. Modifications to levees may also result in a shorter period of river-lake connections which would affect migrations of fishes into and out of lakes. Altering flood attenuation patterns also has implications for predicting the degree of inundation of floodplains and potential fish productivity. Lowering levees to ensure the flooding of lakes at a lower magnitude flood release could result in a faster rate of drainage within lakes (Merron & Weldrick 1994). This would affect the marginal areas of the lakes necessary for providing food and refuge for juvenile fish.

It is clear, therefore, that an integrated management programme is required in an attempt to promote the sustainable utilisation of all the natural resources on the Phongolo floodplain. One of the main components of the holistic approach would be to re-establish a natural flood regime programme. If resource models are to be of any value in ecosystem management, they must take as many interactions as possible into account. The interactions include physical, biological and cultural interactions, which ultimately determine the productivity of the fishery (Welcomme & Hagborg 1977) and the ecosystem.

The aim and design of the study

The principal aim of the study was to develop a practical ecological model for the management of the Phongolo floodplain for various flood release options.

In order to achieve this aim the study was designed in the following sequential manner:

1. The relative abundance, distribution and species richness of the smaller fish (> 140 mm SL) were determined. The demography of the smaller fishes of the Phongolo floodplain has not previously been quantified, but they are as important to the subsistence fishery as the larger fish species.
2. The relative abundance, distribution and species richness of the larger fish (< 140 mm SL) were determined.

The relative abundance, distribution and species richness of the fishes would be necessary in the model for resource managers to determine likely species compositions at each of the lakes. This information would be incorporated into tables where the percentage contribution of the fishes to biomass and abundance could be determined.

3. The biomass of the smaller fishes were determined at each particular site and throughout the floodplain based on the above abundance results. The biomass estimates were determined to estimate the potential yield of the small fish species which could be taken from the fishery.
4. The catch-per-unit effort of the larger gill netted species was determined to calculate the potential

yield.

The biomass and potential yield estimates of the fishes are necessary in the ecological model because they would enable resource managers to predict the potential yield at each of the lakes. These values are necessary to compare to the actual harvest from the floodplain to manage the fishery sustainably.

5. A community classification was carried out for the small and large fish species with the use of TWINSPAN ordination.

A community classification is necessary in the model so that lakes and habitat types with similar environmental variables and habitat types could be grouped together. This would allow for efficient management. Each group could be managed according to certain criteria, instead of each individual lake. This classification would be ecologically important as it allows an understanding of the groups of lakes in an attempt to simplify a complex ecosystem for management purposes.

6. Flood releases of varying magnitudes were simulated using Geographical Information Systems (GIS). This enabled various flood release scenarios to be graphically represented, thus illustrating the effect of various floods on the floodplain rivers and lakes. The simulated flood releases are necessary to predict the potential available area for the fishery at various flood releases. The available area will affect the habitat types, fish communities and potential yields from the fishery. From the GIS, the potential affect on subsistence agriculture could be determined for various flood release options.

CHAPTER 2. THE STUDY AREA

The Phongolo River originates on the Drakensberg escarpment in northern Natal/Swaziland, 550 km from the sea. It flows eastwards for 310 km where it passes between the Lebombo and Ubombo mountain ranges through the Pongolapoort Gorge where it was impounded in March 1970 by an 89.3 m high dam wall. From the gorge, the river continues to flow eastwards for 6 km, where it turns north to flow at a shallow gradient of 1:3 000 for the next 240 km. It is here that the floodplain exists, where the water spills the banks of the Phongolo River during the rainy season into lower lying areas adjacent to the river. On the floodplain there are approximately 90 lakes (65 named and 25 unnamed) which are depressions of various sizes and depths. The Phongolo River is joined by the Ngovuma River and the Sutu River, which drain from the Transvaal and Swaziland respectively, and then crosses the Mozambique border to become the Rio Maputo which enters the sea near Delagoa Bay (Fig. 3, Appendix 1). On either side of the floodplain there is an area of fertile soil which is referred to as the Makhatini Flats in Maputaland (Hensley 1969), and this is where most of the commercial agriculture in the area is carried out. The floodplain varies in width between 0.8 and 4.8 km from the Pongolapoort Dam to the Sutu River confluence, and has a maximum inundation area of approximately 10 265 ha during peak floods (Coke 1976). The mean retention level of the lakes and river was estimated at 2 700 ha, including the lakes on the Sutu floodplain, as the latter are influenced by the Phongolo floodplain system (Heeg & Breen 1994).

Geology and Geomorphology

The geology and geomorphology of the Phongolo floodplain was described by several workers, but have been summarised by Kok (1980, Fig. 4): Acid volcanic tuffs and breccia, rhyolite and dacite of the Stormberg Series constitute the Lebombo mountains, which are tilted at a 15-20^0 declination eastwards as a result of continental drift (Kok 1980). During the following Cretaceous period, the sea reached as far inland as the Lebombo mountains, and off-shore sediments accumulated on the floodplain. Within these flat sediments two distinct layers are discernible. During the Miocene period a thin layer of conglomerates and sandy limestone was deposited. The deep red sands along the north-western banks of the floodplain from the Mlambongwenya River to Ndumo Game Reserve are a result of weathering of exposed portions of this layer (Kok 1980). The Port Durnford beds were formed during the Pleistocene when sandy materials were deposited on the Miocene formation.

The coastline advanced eastwards as the sea level gradually decreased. At each of the positions where the coastline was located during the lowerings, a long-shore dune system was developed. Sands of Recent age were formed during the weathering of these systems. This long-shore dune formation resulted in the deflection of the Phongolo River northwards on the Maputaland plain. The Phongolo River deeply incised its course into the relatively soft Cretaceous sediments at sea levels up to 100 m below present level, and as the sea level rose, alluvial silts and gravels were deposited by the river filling in the incised valley to form the present terraces and floodplain. Some of the lakes are a result of the incompletely filled portions of the former incised valley, and others are a result of the river meandering across the low gradient, forming true ox-bow lakes (Kok 1980).

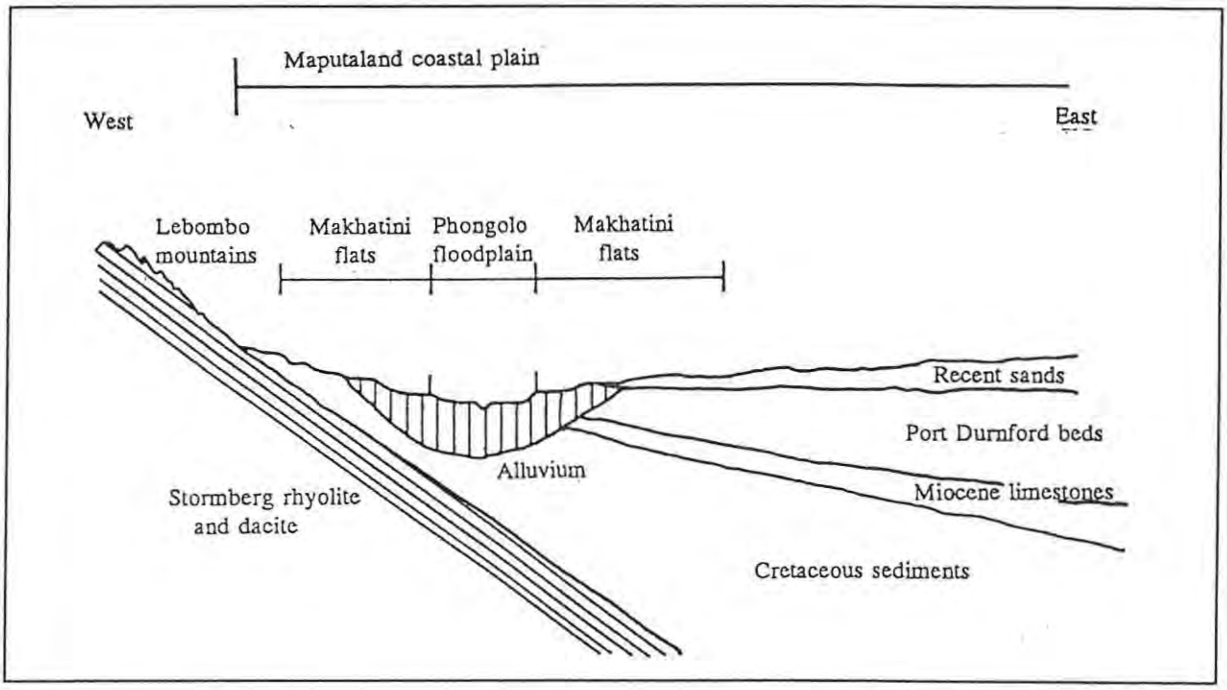

Figure 4. Diagrammatic representation of a geological section of the Phongolo floodplain and Makhatini flats (after Kok 1980, Heeg & Breen 1994).

Soils

The soils of the Phongolo floodplain are divided into two major groups (Hensley 1969): The first soil group is the sandy soils lying east of the floodplain and on the western bank north of the Mlambongwenya River. Randomly located below these soils is a slowly permeable cemented layer which affects their drainage. Where this layer occurs near the surface, ephemeral lakes are formed during the wet season in localised depressions of the flats (Kok 1980). The second soil group is the terrace soils extending throughout the floodplain and westwards off the plain and south of the Mlambongwenya River. In the well drained areas, permeable oxisol soils, including leached, red, apedal, sandy clay loams and clays, are found. As the drainage deteriorates, the soils become darker with finer particles resulting in decreased permeability. The vertisols, including saline, calcareous black clays, appear as black impermeable saline soils. Vertisols are usually associated with cyclical wet and dry environments.

Climate

The climate is typically warm to hot and humid, subtropical (Schulze 1965), with two distinct seasons (Kok 1980). Summer extends from November to March, and has a mean monthly temperature of 24°C, with the mean maximum above 30 °C and a monthly precipitation rate of 50 to 100+ mm. During summer there are high evaporation rates due to the high temperatures and high wind speeds. The prevailing winds in summer are north-easterly. These north-easterly winds are occasionally interrupted by shorter periods of south-easterly winds which are accompanied by thunderstorms and unstable weather conditions. Winter extends from April to September with mean monthly temperatures slightly cooler (17 to 22 °C). During winter there is no frost at night, and there is a low mean monthly precipitation of 10 to 15 mm.

Vegetation

The vegetation of the floodplain can be divided into marginal and aquatic components (Musil *et al.* 1973, Fig. 5). The marginal floral communities are divided into 6 components along a habitat preference moisture gradient from 1 (moist) to 6 (dry) (Table 1):

Table 1. Marginal floral communities of the Phongolo floodplain (after Kok 1980).

	Dominant community	Type	Habitat description
1	*Phragmites australis*	Reed	Relatively flat swampy areas, poor drainage
2	*Phragmites mauritianus*	Reed	River levees, feeder channels and lake margins, fluctuating water level
3	*Cyperus fastigiatus* *Echinocloa pyramidalis*	Sedges	Marshy areas
4	*Cynodon dactylon*	Grass	Mud flats surrounding some lakes, heavily grazed on by cattle in dry season
5	*Ficus sycomorus*	Tree	Short stretches on some lake margins and river levees
6	*Acacia xanthophloea*	Tree	Transition between aquatic and terrestrial environments

The aquatic floral components are divided into four categories, from the marginal areas of the lakes, to the littoral areas to the open water areas (Table 2).

Table 2. Aquatic floral communities of the Phongolo floodplain (after Kok 1980).

	Dominant community	Type	Habitat description
1	*Cyperus fastigiatus* *Echinocloa pyramidalis*	Sedges	Wet marginal areas of lakes
2	*Ludwigia stolonifera* *Nymphaea lotus* *Nymphaea caerula*	Rooted marginal aquatic macrophytes, floating leaves	Shallow littoral areas of lakes
3	*Pistia stratioles* *Trapa natans* *Azolla pinnata*	Floating aquatic macrophytes	Slightly deeper littoral zones
4	*Ceratophyllum demersum* *Lagrosyphon* sp. *Najas pectinata* *Najas marina* *Potamogeton crispus*	Submerged aquatic macrophytes	Relatively low turbidity

These latter submerged macrophytes are the most important primary producers, although all of the macrophytes comprising the floodplain vegetation are important in the efficient functioning of the ecosystem. Many of the macrophytes can be classified according to environmental gradients such as water depth and pH (Musil *et al.* 1973). This is important since many fish communities are also associated with particular vegetation types. Therefore, if these habitats are likely to change, then so too are the particular fish communities in the area.

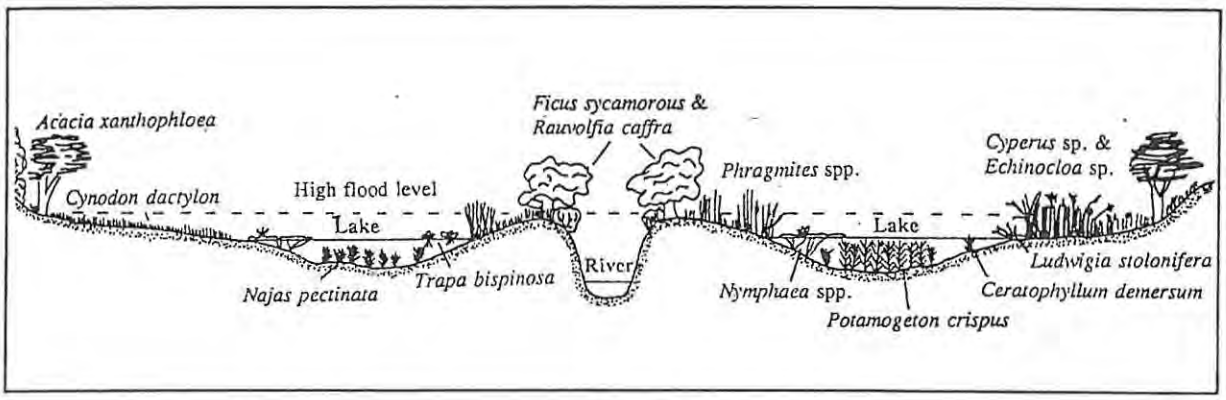

Figure 5. Vegetation types on the Phongolo floodplain (after Kok 1980).

The dam, floodplain rivers and lakes

There are approximately 90 lakes on the floodplain. Seventeen of these lakes have been selected as representative of each particular habitat type occuring on the floodplain. The selected lakes are the most important lakes in the subsistence fishery as they are the larger more perennial water bodies, as opposed to the other lakes which are less permanent. The lakes fall into four main hydrological categories as described by James (1992): those with their own catchments, and not usually filled by the Phongolo River (such as Lake Mayazela); those susceptible to flooding by the Sutu River (such as Lake Banzi); those with separate inflow and outflow points that are flushed out by floods (such as Lake Sokhunti); and those with only one inflow and outflow which are not flushed out (such as Lake Mhlolo). Apart from these hydrological categories, the lakes have been characterised by other environmental variables (Table 3).

The Pongolapoort Dam is one of the largest dams in South Africa. It has a very high turbidity during the summer rainy season due to runoff from agricultural lands in the Transvaal. As a result of this, the water released into the Phongolo River from the dam has a high sediment load. In the Phongolo River below the dam wall there are some areas where the river becomes shallow, with rocky areas forming rapids. The rapids are suitable habitats for rheophilic fish species, such as *Chiloglanis swierstrai* and *Labeo cylindricus*. At the New Bridge over the river, artificial rapids have been created.

Table 3. Characteristics of the representative lakes and rivers on the floodplain. The explanations for the abbreviations of the sites can be found on Fig. 3, Appendix 1.

Site	Area (ha)	Temperature (°C)	Substrate Type	General characteristics
Pho		15 - 27	Rocky - sandy	Turbid with peripheral aquatic vegetation, some rapid areas
Sti		15 - 22	Rocky	Deep, fast-flowing, turbid, little aquatic vegetation
May	25.8	20 - 31	Muddy	Own catchment, shallow, turbid, little aquatic vegetation
Nhl	37.9	20 - 28	Muddy	Own catchment, relatively deep, little aquatic vegetation
Mkh		22 - 30	Muddy - sandy	Shallow swampy pools with own catchment, very eutrophic, densely vegetated
Mzi	74.2	23 - 30	Sandy	Shallow, turbid, little aquatic vegetation
Mla		19 - 27	Sandy	Shallow, clear, little aquatic vegetation
Ntu	23.5	20 - 27	Muddy	Shallow, clear, dense aquatic vegetation
Nsi		20 - 28	Sandy - muddy	Shallow, clear, abundant aquatic vegetation
Mth		20 - 28	Sandy - muddy	Shallow, clear, abundant aquatic vegetation
Tet	115.9	24 - 30	Sandy - muddy	Shallow, clear, abundant aquatic vegetation
Kha	74	23 - 30	Sandy - muddy	Shallow, turbid, dense aquatic vegetation
Men	32.2	21 - 29	Sandy - muddy	High conductivity, clear, abundant aquatic vegetation
Sha	49.2	20 - 28	Sandy - muddy	Shallow, clear, abundant aquatic vegetation
Sok	101	20 - 27	Sandy	Deep, clear, little aquatic vegetation
Mhl	56	21 - 29	Muddy	High conductivity, clear, abundant aquatic vegetation
Bum	58.4	21 - 28	Muddy	Relatively deep, turbid, some aquatic vegetation
Ngo	22.1	22 - 30	Muddy	Shallow, very turbid, little aquatic vegetation
Nam	63.4	22 - 30	Muddy - sandy	Shallow, turbid, eutrophic, little aquatic vegetation
Nya	183.4	20 - 27	Muddy - sandy	Relatively deep, turbid, high conductivity, little aquatic vegetation
Ban		20 - 28	Muddy	Relatively deep, turbid, abundant aquatic vegetation
Sut		16 - 27	Sandy	Turbid, fast-flowing annual river

The water temperature range throughout the floodplain is between 15°C and 31°C. It seldom drops below 15°C, as the floodplain is situated in a sub-tropical climatic zone. pH values have not been included in Table 3, as they are highly variable within and between lakes, as a result of fluctuating water temperatures and different soil types on the east and west side of the Phongolo River. The lakes range from deep, sandy and clear with little aquatic vegetation to lakes which are relatively shallow, muddy, turbid, with extensive aquatic vegetation.

CHAPTER 3. SAMPLING SITES, METHODS AND GENERAL TECHNIQUES

Sampling occurred from December 1993 to April 1995. Sampling was carried out on bimonthly field excursions (duration of approximately two weeks each), over eight months, except during flood release periods (August 1994 and February 1995) when pre- and postflood surveys were also carried out.

Sampling sites

The following sites were chosen as representative of most of the fish habitats occurring on the Phongolo floodplain (Fig. 3, Appendix 1): Phongolo River below the dam wall, Phongolo River at Mabunga, Phongolo River at the New Bridge, Phongolo River at Makhani Drift, Mayazela, Nhlanjana, Mkhonjeni, Mzinyeni, Mlambongwenya River, Ntunte, Nsimbi, Mthikeni, Tete, Khangazini, Mengu, Shalala, Sokhunti, Mhlolo, Bumbe, Ngodo, Namanini, Mandlankunzi, Nyamithi, Banzi, Isolated rainpool within Ndumo Game Reserve (Emathimini Enkulu) and the Sutu River at Fontana. At each of these sites fish were caught using at least one of the following methods.

Methods

The methods of fish capture in the rivers and lakes included gill netting, seine netting, rotenone and electrofishing. These methods are described below, and the type of method used at each site is indicated in Table 4.

Gill netting

Multifilament gill nets of stretch mesh sizes 35 mm, 40 mm, 45 mm, 60 mm, 75 mm, 85 mm, 90 mm, 100 mm, 110 mm and 120 mm were used. Four fleets were used and these were standardised for each survey and each lake. The gill nets were set overnight at all the sites with the exception of Ndumo Game Reserve, where biological conditions (hippopotami and crocodiles) made this impractical. In Ndumo Game Reserve the nets were set during the day when they could be monitored regularly. The catches from the game reserve cannot theoretically be directly compared with the catches from the rest of the floodplain as they were set during different periods of day and for different times. Nocturnal fish movement may differ somewhat from diurnal movement. But, for the purposes of the ecological model it has been assumed that these catches can be directly compared to each other. The gill nets were used to compare the species compositions within each of the lakes, and to estimate the potential yields, although there were no replications of the gill nets within each lake for particular survey. Replication was not practical due to time constraints. It has been assumed that there was no fish migration in the lakes where the gill nets were set, and that the catch was directly related to abundance. Gill netting captures only those fish in the particular area of the lake that they were set in at that time, it does not take fish movement into account. It is also more selective towards pelagic than bethic species. Despite this, it is likely that for fishery purposes that the data would still give accurate results, as gill nets are one of the major types of gear used on the floodplain, so the same species would be selected for by local fishermen as the management suggestions have been based on. The time of day which the gill nets were set is also limiting, as those set in the day would not take the nocturnal species into account, and vice versa. There is also a degree of escapement from gill nets which is difficult to quantify.

Seine netting

Seine nets were extensively used at the sampling sites. A 25 m x 1 m (0.5 cm mesh size) seine net, a 2 m x 1 m (0.5 cm mesh size) minnow seine net and a 1 m x 1 m (0.5 cm mesh size) minnow seine net were used. The large seine net was pulled by at least two people along the periphery of the sampling sites, except in Ndumo Game Reserve where it was pulled along the periphery of the lakes with the aid of a power boat. It was pulled out in a perpendicular direction initially for approximately 10 m and then pulled parallel to the shore in a half circle covering an area of approximately 100 m^2 in 1 m deep water. The minnow seines were drawn through the water by two people in a direction perpendicular to the shore and then raised. The limitations with seine netting is that seine nets are pulled manually or by power boat, and so many of the fish are scared away. It was found to be effective provided that the area of the seine was not disturbed. There was also some escapement, with some of the larger fish jumping over the net. The seine netting was limited to a distance of approximately 10 m offshore and / or by water depth.

Rotenone

Rotenone is an ichthyocide of powdered derris root derivative of 6.8% active ingredient. This ichthyocide is miscible with water after pretreatment with 50% iso-propanol. Concentrations of rotenone at approximately 10 ppm were effective after 10 to 30 minutes depending on water temperatures. Rotenone sampling was the most effective sampling technique and was used in areas where gill nets or seine nets could not be used, such as heavily vegetated areas in lakes or very dry lakes to obtain estimates of fish biomass. The areas where rotenone was applied were noted and were blocked off by the enclosure of nets where possible. The site was worked for 2 to 4 hours by which time the majority of fishes had been collected. The site was revisited over a period of 48 hours when possible to collect any remaining fish that were not immediately affected by the rotenone.

Rotenone is the most effective method for determining the total species composition and abundance of a given area (Pardue & Huish 1981). In order to estimate the fish biomass accurately, a large area must be rotenoned. This is due to the concentration of fish in small areas and isolated pools (Lowe-McConnell 1975, Welcomme 1979), resulting in an overestimate of the total fish biomass available on the floodplain. (The fish biomass calculated can be correlated to the percentage inundation for different water releases). But, it was not practical to use rotenone on large areas as it would have been time-consuming, labour intensive to capture the dead fish, and expensive. The larger areas were generally utilised by people for domestic purposes, making the application of rotenone difficult without disturbance to the people.

Electrofishing

The electrofisher was used in the periphery of most lakes and in the shallow areas in the Phongolo and Sutu Rivers. It was most efficient in the Phongolo River in the fast-flowing rapid areas. Due to the low conductivity of the water in most of the lakes, this technique was not very effective. The fish were only mildly affected and were able to recover fast enough to swim away before being caught.

In addition to the above sampling methods, fish caught by local people using traditional fishing methods were analysed when possible. This method gave an estimation of the total number, species composition and size composition of fishes caught over a particular sampling period and the effort of a particular fishing method. More extensive surveys would be required to determine the actual harvest from the subsistence fishery.

Table 4. Methods of fish capture at each site.

Site	Methods
Phongolo River	Gill nets, seine nets, rotenone, electrofisher
Mayazela	Seine nets, rotenone
Nhlanjana	Gill nets, seine nets, rotenone
Mkhonjeni	Seine nets
Mzinyeni	Gill nets, seine nets, rotenone
Mlambongwenya River	Seine nets, rotenone
Ntunte	Seine nets, rotenone
Nsimbi	Seine nets, rotenone
Mthikeni	Seine nets, rotenone
Tete	Gill nets, seine nets, rotenone
Khangazini	Gill nets, seine nets, rotenone
Mengu	Seine nets, rotenone
Shalala	Seine nets, rotenone
Sokhunti	Gill nets, seine nets, rotenone
Mhlolo	Gill nets, seine nets, rotenone
Bumbe	Seine nets, rotenone
Ngodo	Seine nets, rotenone
Namanini	Seine nets, rotenone
Mandlankunzi	Gill nets, seine nets, rotenone
Nyamithi	Gill nets, seine nets
Banzi	Gill nets, seine nets
Sutu River	Seine nets, rotenone

These sampling methods were used in combination due to particular constraints and limitations of each individual method. Each type of gear is selective, and so a combination of gear types allowed for the most comprehensive survey.

General techniques

Measurement

All fishes caught in gill nets were measured to the nearest millimetre, from the tip of the snout to the point of flexure of the caudal fin (standard length, SL), and weighed in the field to the nearest gram on a 3.0 kg digital balance. Where gonad and stomach samples were required for laboratory analysis, the abdominal cavity was cut open and the entire viscera were removed, labelled and preserved in 10% buffered formalin.

Preservation and curation

All fishes caught in seine nets or with rotenone were fixed in 10% formalin solution and dispatched to the JLB Smith Institute of Ichthyology, in Grahamstown. These fishes were identified, sorted and weighed immediately and were then preserved in 50% iso-propanol. All specimens were housed in the JLB Smith Institute of Ichthyology.

Reproductive seasonality

The reproductive seasonality was determined for gill netted species by macroscopic examination of the gonads and assigning a gonad maturation index (GMI) of between 1 and 6 (after Nikolsky 1963). Specimens showing little or no gonad development (stages 1 & 2) were considered undeveloped, whilst those with developed gonads (stages 3, 4, 5 and 6) were considered mature. The spawning of species was further substantiated by the presence or absence of juvenile fishes caught in seine nets and minnow seines.

Biomass estimates

The biomass estimates for the small fishes were determined using seine net catches in a measured area of water. The biomass values were determined in $kg.ha^{-1}$ and were then converted to potential yields at one third of the biomass estimates (Lagler *et al* 1971) per annum. The potential yield was calculated at one third of the biomass for the Kafue floodplain by using the following equation:

$$Y_N = B_N \,.\, Y_X / B_X$$

where B_N is the biomass, Y_N is the potential yield, B_X is a known biomass for a particular year, and Y_X is a known harvest for the same year. These calculations were substantiated by Welcomme (1979) for several other African floodplain fisheries. The constraints of accepting potential yield as one third of the biomass are that during low water levels, the potential yield will be overestimated, and at high water levels the potential yield will be underestimated.

Catch-per-unit effort calculations

For the gill net data the catch-per-unit effort (CPUE) was determined using to the following formula:

$$\text{CPUE} = \frac{\text{kg of fish}}{\text{m}^2 \text{ of gill net x hours set}}$$

It can be assumed that catch is related to abundance (Cushing 1968), and since the catch was not predetermined, but rather a chance outcome from applying a predetermined effort, the catch should be proportional to effort and abundance (Robson & Regier 1971). The calculated CPUE was then converted to biomass in kg.ha^{-1} (according to Robson & Regier (1971)), which was then converted into potential yields per annum.

Community classification

A community classification of the smaller fish species was determined using TWINSPAN (two-way indicator species analysis) ordination, and the environmental variables of sites were classified using a cluster analysis stored on the Rhodes University's mainframe computer.

TWINSPAN was used to classify and ordinate fish communities within the sites based on species composition according to number or mass. Ordinations based on a group of differential species that tended to occur together was formed using TWINSPAN, and a division based on these species was made. The ordination was then divided into communities. The communities were identified according to indicator species. The catch effort was standardised to draw comparisons between sites over the different sampling periods. A cluster analysis was used to group the sites based on environmental variables (Merron & Weldrick 1994).

TWINSPAN is a polythetic divisive technique (Hill 1979, Gauch & Whittaker 1981) where the data is initially ordinated by reciprocal averaging, then those species characterising the reciprocal averaging axis extremes are emphasised to polarise the samples. The samples are then divided into two clusters by breaking the ordination axis near its middle (Hill 1992). The sample division is refined by a reclassification using species with maximum values for indicating the poles of the ordination axis. The division process is then repeated on the two samples to give four groups, etc., until each group has no more than a chosen minimum number of members, or else the number of divisions (levels) is stipulated (Gauch 1982). The results may be displayed as a dendrogram showing resultant sample hierarchy, using the sequences of divisions as integral levels or computing the levels as the average distances between samples in ordination space (Gauch & Whittaker 1981). Basically, TWINSPAN operates by ordering the data sets and classifying samples using dichotomies, in order to identify the most important features of the data set (Merron 1991).

Gauch (1982) recommends TWINSPAN for hierarchical classification because of its robustness and effectiveness as a consequence of being polythetic and divisive. Other advantages of TWINSPAN are the use of the original data set, integrated classifications of both samples and species, the production of an arranged data matrix, ordering of samples sequentially to place the most similar samples together, making dendrograms clearer, and minimal computer requirements (Hill 1992).

TWINSPAN classification divides complete data sets into distinct groups on the basis of differences between the various samples or groups of samples. This grouping allows the homogeneity of the samples to be observed (Hill 1992). The division process was terminated at the fifth group level as additional variance, explained by subsequent divisions, was low and caused the division of particular communities into meaningless groups.

Geographical Information System (GIS)

The Phongolo floodplain is not a static ecosystem and the availability of the water resource and fish stocks can change annually. GIS was used to simulate flood releases of varying magnitudes on the Phongolo floodplain. It can be used for fisheries resource and habitat management (Giles & Nielson 1992), but this requires continual expert updating of the database. The data sets for the flood manipulation included slope and hydrological features.

The GIS package used was pc ARC INFO for digitising, editing and annotation, and ARCVIEW (ver. 2) for manipulation and display.

Different levels of floodplain inundation were simulated and the advantages and disadvantages to the species composition and relative abundance of fish from flood releases at different seasons of the year and of various magnitudes and durations from the dam were determined.

The levels of floodplain inundation on GIS were determined using contour levels drawn from 1 : 50 000 maps of the Phongolo floodplain. The contour levels are not 100 % accurate, but can be correlated to various historical magnitudes of actual flood releases. For the purpose of the ecological model it has been assumed that each of the contour levels correlates to a particular flood level.

CHAPTER 4. THE FISH FAUNA

The fish fauna of the Phongolo River and floodplain consists mainly of tropical taxa as the floodplain is climatically an extension of a tropical to sub-tropical zone (Bruton & Kok 1980). To date 40 species belonging to 11 families have been collected from the floodplain, which include marine migrants. The dominant characteristics of the fish species (after Skelton 1993) are shown in Table 5, and some of the fishes important in the subsistence fishery are illustrated in Figure 6. Of all the species recorded on the floodplain, 20 are boundary species, occurring no further south than the Phongolo system.

The optimum spawning times for all the fishes is during the summer months. Some of the species will only breed during the summer and are flood-dependent, but some species are more adaptable, also breeding during other seasons (non-flood-dependent). Most of the flood-dependent fish are from non-guarding reproductive guilds. These fish are better suited to environments characterised by abiotic harshness including wide and unpredictable variations in water temperature, pH and oxygen levels (Bruton & Merron 1990). The majority of species, such as *Brycinus imberi*, *Schilbe intermedius* and *Synodontis zambezensis*, have high fecundities and small eggs (Merron & Weldrick 1994).

The majority of fish species in the Phongolo floodplain can be classified as opportunistic generalists with wide trophic niches including small omnivores, piscivores, insectivores, predator/scavengers, molluscivores, macrophytophages and detritivores.

The flood-dependent fish include the Mormyridae, Characidae, Mochokidae, and *Labeo* species. The flood-independent fish include the Cichlidae, Gobiidae, Anguillidae and Cyprinodontidae. Within the flood-dependent spawners, there are facultative spawners (*S. intermedius*, *Hydrocynus vittatus* and *Clarias gariepinus*), and obligate spawners (*S. zambezensis*, *Marcusenius macrolepidotus*, *Petrocephalus catostoma* and *Labeo* spp.). However, some of these species do spawn in response to heavy rainfall, and in the absence of flooding for a long duration. Certain species (e.g. *S. intermedius*) may change their breeding strategy in response to other environmental parameters such as rainfall, temperature and photoperiod. The eels breed in the marine environment, the killifish deposit eggs in ephemeral pools and the tilapias make nests and then care for their young (guarders).

Table 5. Checklist and characteristics of fish species present in the water bodies of the Phongolo floodplain (after Skelton 1993).

Species	AL	Feeding guild	Breeding guild	Preferred habitat type	BS
Anguillidae					
Anguilla spp.		Omnivore	Non-guarder	Rocky pools in rivers & lakes	
Mormyridae					
Marcusenius macrolepidotus	150	Insectivore	Non-guarder	Rivers & lakes with low conductivity	X
Petrocephalus catostoma	110	Insectivore	Non-guarder	Rivers & lakes with low conductivity	X
Characidae					
Brycinus imberi	180	Insectivore	Non-guarder	Unturbid rivers & lakes with little vegetation	X
Hydrocynus vittatus	500	Piscivore	Non-guarder	Unturbid rivers & lakes with little vegetation	X
Micralestes acutidens	55	Omnivore	Non-guarder	Unturbid rivers & lakes with little vegetation	X
Cyprinidae					
Labeo congoro	415	Detritivore	Non-guarder	Fast-flowing river channels	X
L. cylindricus	70	Detritivore	Non-guarder	Fast-flowing river channels	X
L. molybdinus	380	Detritivore	Non-guarder	Deep river pools	
L. rosae	210	Detritivore	Non-guarder	Sandy stretches in river channels & lakes	X
Barbus afrohamiltoni	175	Omnivore	Non-guarder	Slow-flowing river channels & lakes	X
B. annectens	75	Omnivore	Non-guarder	Slow-flowing river & well vegetated lakes	
B. pallidus	40	Omnivore	Non-guarder	Slow-flowing river channels in marginal vegetation	
B. paludinosus	150	Omnivore	Non-guarder	Rivers & lakes	
B. radiatus	120	Omnivore	Non-guarder	Unturbid river channels & well-vegetated lakes	X
B. toppini	35	Omnivore	Non-guarder	Rivers & lakes	X
B. trimaculatus	150	Omnivore	Non-guarder	Slow-flowing river channels & lakes	
B. unitaeniatus	140	Omnivore	Non-guarder	Unturbid river channels & lakes	X
B. viviparus	70	Omnivore	Non-guarder	Slow-flowing river channels & well-vegetated lakes	X
Opsaridium zambezense	150	Omnivore	Non-guarder	Unturbid, fast-flowing river channels	X
Cyprinus carpio		Omnivore	Non-guarder	River channels & lakes with soft sediments	
Mesobola brevianalis	65	Omnivore	Non-guarder	Fast-flowing river channels & open water lakes	
Schilbeidae					
Schilbe intermedius	300	Omnivore	Non-guarder	Fast-flowing river channels & vegetated lakes	X
Clariidae					
Clarias gariepinus	1 400	Predator / Scavenger	Non-guarder	Rivers & lakes	
C. ngamensis	730	Molluscivore	Non-guarder	Slow-flowing river channels & well-vegetated lakes	X
Mochokidae					
Chiloglanis paratus	85	Omnivore	Non-guarder	Fast-flowing rapids in river	X
C. swierstrai	70	Macrophytophage	Non-guarder	Shallow sandy and rocky reaches of river	X
Synodontis zambezensis	430	Omnivore	Non-guarder	Slow-flowing river channels & well-vegetated lakes	X
Cichlidae					
Oreochromis mossambicus	200	Microphytophage	Guarder	Rivers & lakes	
Pseudocrenilabrus philander	40	Predator / Scavenger	Guarder	Well-vegetated rivers & lakes	X
Tilapia rendalli	80	Macrophytophage	Guarder	River & well-vegetated lakes	
T. sparrmanii	80	Omnivore	Guarder	River & unturbid lakes	
Syngnathidae					
Microphis fluviatilis	210	Omnivore	Guarder	Slow-flowing river channels & marginal vegetation	
Cyprinodontidae					
Nothobranchius orthonotus	100	Insectivore	Non-guarder	Temporary isolated rainpools	
Gobiidae					
Awaous aenofuscus	260	Omnivore	Non-guarder	River channels with sandy bottoms	
Glossogobius callidus	120	Predator / Scavenger	Non-guarder	Rivers & lakes	
G. giuris	400	Piscivore	Non-guarder	Deep river channels & lakes	
Redigobius dewaali	42	Omnivore	Non-guarder	Unturbid, well-vegetated river channels & lakes	
Elopidae					
Megalops cyprinoides	500	Omnivore	Non-guarder	Rivers & lakes	

(Where AL = Average length (mm SL), BS = Boundary species).

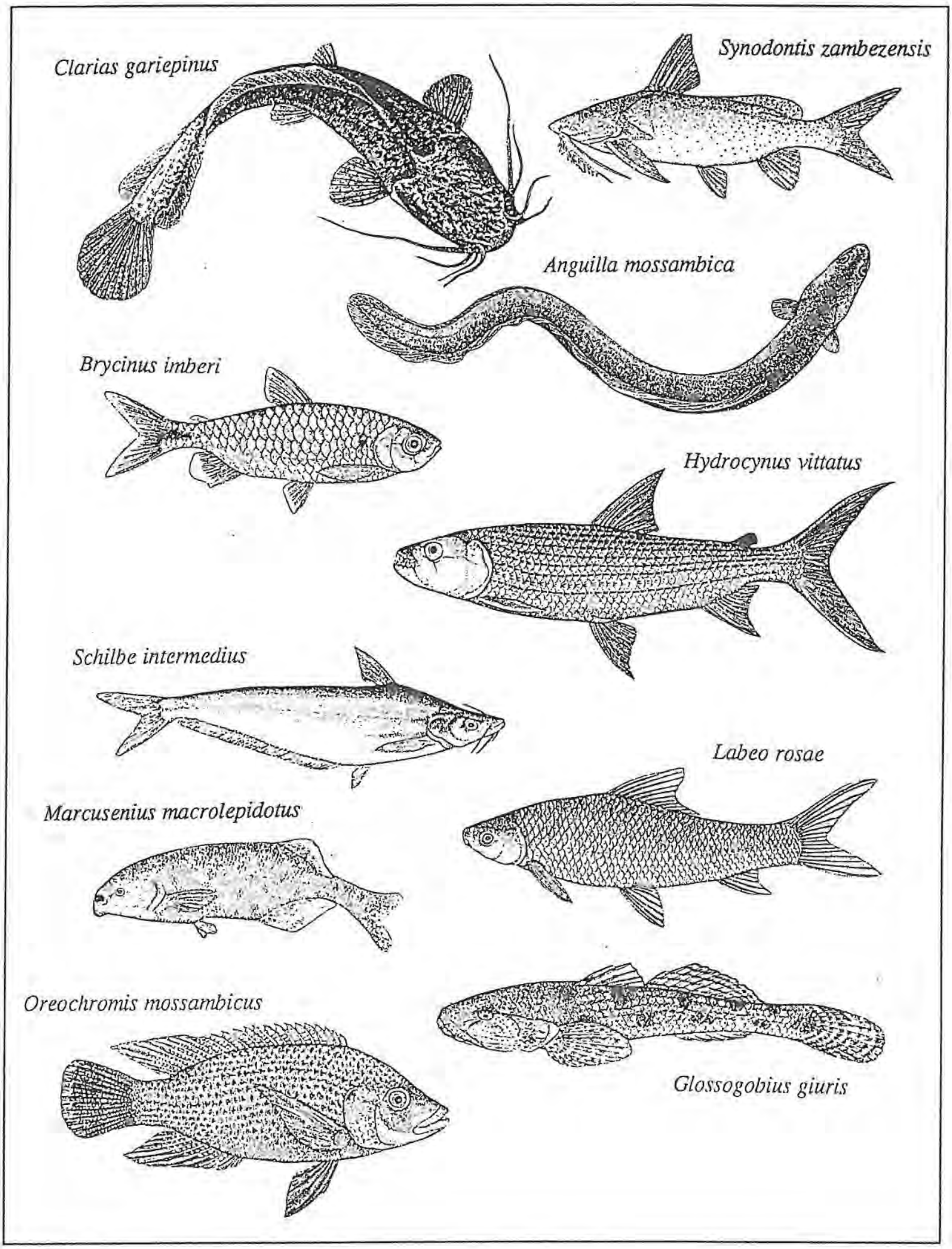

Figure 6. Some of the fish species important in the subsistence fishery of the Phongolo floodplain. These fishes are not drawn to scale. (Drawings by Dave Voorvelt).

The mormyrids (*M. macrolepidotus* and *P. catostoma*) are relatively rare on the floodplain and inhabit only a few lakes. They cannot survive the high conductivities as a result of increasing salinities during periods of dry-down. It is possible that the high conductivities interfere with their electrolocation abilities (Heeg & Kok 1988). The tigerfish (*H. vittatus*) is fairly common throughout the floodplain, but is more numerous in less turbid lakes with few aquatic macrophytes since it is an open water predator. There are several cyprinids in the Phongolo floodplain, in various habitat types, all of which are utilised by the local people and are harvested in the subsistence fishery. The preferred cyprinids are the labeos (*Labeo congoro* and *L. rosae)* as these attain a larger size than the barbs. The labeos are found mostly in the river channels and are flood-dependent, relying on summer flood releases to spawn. The sharptooth catfish (*C. gariepinus*) is a generalist and inhabits most niches on the floodplain. It is one of the dominant species occurring during periods of dry-down as it is able to withstand desiccation and is tolerant of poor water quality. The blunttooth catfish (*C. ngamensis*) is more specialised. It is a specialised feeder, feeding primarily on freshwater mussels. When the water quality deteriorates, this results in a depletion of the mussel populations which affects the feeding of the catfish. The *Chiloglanis* species are found only in fast-flowing areas of the rivers, and are susceptible to low flow conditions in the river. The *Anguilla* species in the Phongolo system are all reliant on summer water releases for the mass migrations of their elvers upstream. Their migration is inhibited by the dam wall. The Mozambique tilapia (*O. mossambicus*) is also a generalist, dominant during periods of dry-down due to its tolerance of poor water quality. The other cichlids are more specialised. The more specialist feeders, *S. zambezensis* (feeding on invertebrates) and *Glossogobius giuris* (a specialist piscivore) occur in relatively low numbers on the floodplain (Heeg *et al* 1980).

Table 5 indicates the general distributions of fishes within habitats on the floodplain. These distributions do not necessarily apply the whole year and depend on numerous factors including the flood cycle. For example, during the drier winter months, some of the lakes tend to dry out completely, and some partially due to seepage and evaporation. The river is also affected by the desiccation process, becoming a very slow-flowing, shallow, sandy stream. Therefore, it can be expected that under these conditions, most of the floodplain fishes will be restricted to the larger, deeper lakes, and those surviving in the low level lakes will be specialised in some way, or be tolerant of a wide range of harsh environmental conditions.

During normal summer floods the whole floodplain system is inundated to form a continuous water system with many of the lakes joining together to form a larger water body for a limited period of time. Fish movements into and out of lakes and the river can then occur, resulting in the redistribution of certain communities (Kok 1980). These kinds of movements have previously been observed in other floodplains in Africa (Donnelly 1966, Carey 1967, Williams 1971, Bell-Cross 1971, Welcomme 1974, Kenmuir 1976, van der Waal 1976), and are imperative for breeding to occur.

It has been hypothesised that the size and occurrence of floods determines species composition and abundance within certain habitats (Moses 1987). Flood-independent species are benefitted by long, dry periods and flood-dependent species are benefitted by stable wet periods. Eurytopic species survive fluctuating conditions better, and the presence of refuge areas prevents species extinctions and allows for mobile, generalist species to be more successful. Floods allow the re-distribution of fish species on the floodplain, especially between refuges and previously inhospitable water bodies.

The biology and ecology of three fish species important in the subsistence fishery were determined. These were *B. imberi*, *S. intermedius* and *S. zambezensis* (Merron & Weldrick 1994). The results indicated that *B. imberi* were in peak reproductive condition during the summer months from December to February. *B. imberi* were found to be facultative flood-dependent spawners, which in the absence of flood releases respond to environmental cues, such as an increase in water temperature (Merron & Weldrick 1994). *S. intermedius* was also found to be in peak reproductive condition during the summer months, as well as *S. zambezensis* although no known large-scale spawning of this species occurred during the 1993-1994 summer season. This was indicated by the resorption of gonads. There was no large scale water release during this period. All these species were found to have relatively high growth rates and all were opportunistic feeders (Merron & Weldrick 1994). It was found by Kok (1980) that several of the large fish species follow a similar trend. Of the studies carried out on the larger fish of the floodplain, it was found, that while most species are opportunistic in their feeding, each showed a degree of specialisation (Heeg & Kok 1988). It is likely that many of the smaller, unstudied fishes on the floodplain follow similar trends.

As shown with these species above, the river-floodplain biota has high annual growth and mortality rates (Pianka 1970), tending towards an altricial life-history style (Bruton 1989). They have evolved life-history strategies enabling them to colonise large areas rapidly. This enables them to persist as different areas become accessible and optimal for their survival with variations in the annual flood regime (Bayley 1995). The specialist fish have little possibility of niche shifts along the dietary axis. However, they are efficient resource utilisers, e.g. the *Labeo* species are morphologically adapted to gather up loose particulate matter from the substrate, *H. vittatus* is a fast swimmer with efficient sight for hunting, and *M. macrolepidotus* and *P. catostoma* are efficient searchers, with the use of their electrolocation capabilities. The generalists on the other hand are able to exploit the available food resources wherever, and whenever it becomes energetically feasible for them to do so (Heeg & Kok 1980). This suggests that competition is an important factor affecting the community structures within the floodplain.

CHAPTER 5. CAN A MODEL BE DEVELOPED FOR THE PHONGOLO FLOODPLAIN?

The following sections are an attempt to develop an ecological model for the Phongolo floodplain. The sections cannot be interpreted individually, as they are all interrelated, emphasising the importance of a holistic approach to management.

In order to simplify the complexity of the ecosystem, for the purpose of the model, each lake has been divided subjectively into littoral and limnetic zones (Fig. 7). This division was based primarily on the method of fish capture, which was indirectly related to lake characteristics. Seine netting, rotenone application and electrofishing were carried out in the shallow periphery of the lakes (littoral zone) and gill netting was carried out in the deeper middle of the lakes (limnetic zone). The littoral zone, on the periphery of the lake, can be characterised by the presence of extensive rooted aquatic vegetation. The limnetic zone, in the middle of the lake, is deeper than the littoral zone and has little aquatic vegetation.

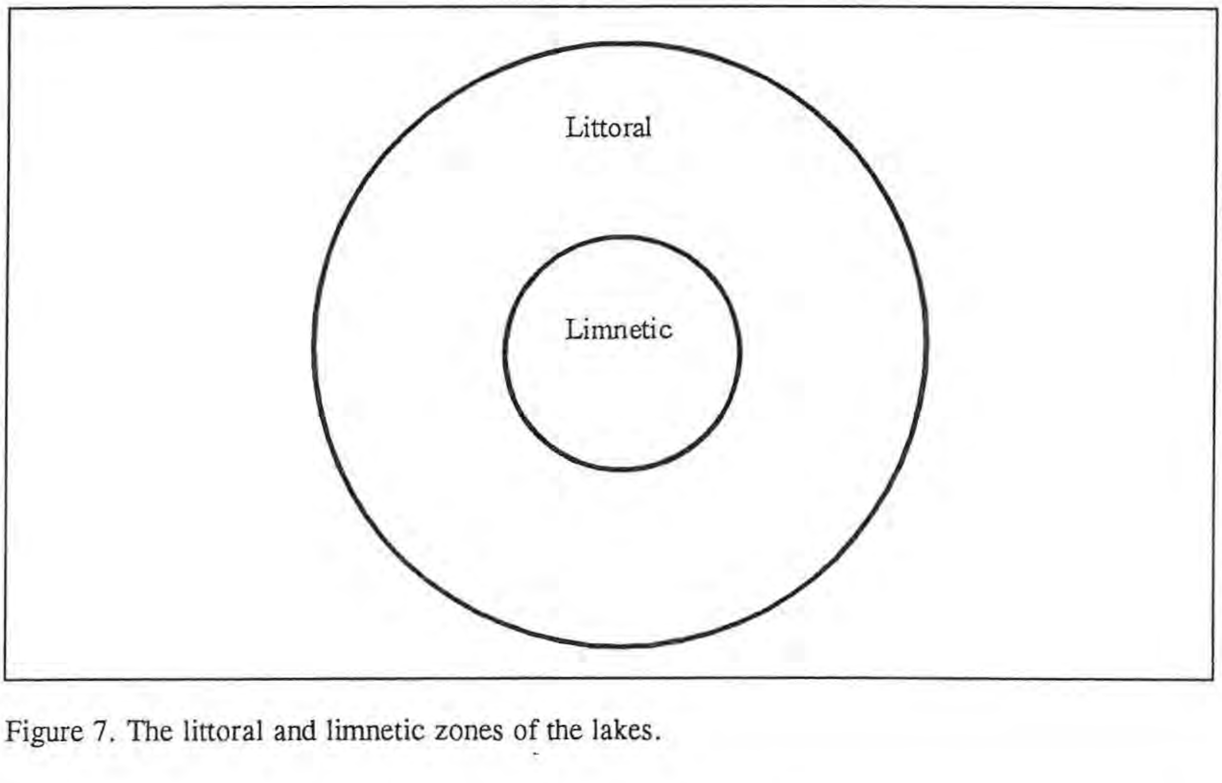

Figure 7. The littoral and limnetic zones of the lakes.

The 'moving littoral' zone, defined by Junk *et al* (1989) as the inshore zone from the water's edge to a few metres depth fluctuates and moves as flooding and drawdown occur. As a result of this movement, high turnover rates of organic matter and nutrients are predicted to occur (Bayley 1995).

Species richness, distribution and relative abundance of fishes

The species richness, distribution and relative abundance of fishes in each of these zones for each lake was determined. This information was necessary to provide an accurate community classification, and to provide estimates of the potential yields of fish for the entire floodplain.

Determining the species richness, distribution and relative abundance of fish is the first step in the development of the model: determining what fish are where, and how many. This information for each for the lakes is fundamental to the determination of accurate potential yields, and to the classification of fish communities. From the data, resource managers can predict the potential percentage species compositions of fishes at each of the lakes. The demography of the small fishes has not previously been determined, so this is important in the understanding of the ecosystem.

The smaller fishes were collected in the littoral zone of each site to determine species richness, distribution and relative abundance of fishes. The species compositions in this zone have not previously been quantified, but are equally important in the subsistence fishery and the ecosystem as the larger commercial fishes. The Margalef Species Richness Index was used to determine the species richness of the sites between sampling periods.

A total of 60 645 specimens representing 35 species in 10 families with a combined mass of 355.19 kg was collected using seine nets, rotenone and electrofishing in the Phongolo Floodplain between December 1993 and April 1995. Of the fishes that were collected, 24 species reached an average adult size of <150 mm SL. In an attempt to distinguish between the smaller fish species and the larger species collected mainly in gill nets, the results are presented as species <150 mm SL. This also includes the juvenile fishes of some of the larger species. Of the smaller fishes, 13 can be considered as common, occurring in more than 19 out of the 24 sites sampled (Table 6). Numerically, the most abundant species included *Oreochromis mossambicus*, *Glossogobius callidus*, *Barbus toppini*, *B. paludinosus* and *Tilapia rendalli* (Table 6). The difference in numbers of fishes collected in the different sites was influenced by the amount of sampling effort and the biological productivity of the site.

The highest species diversity was recorded in the Sutu River (27 species) followed by the Phongolo River (26 species) (Table 6). This was followed by Lake Banzi (23 species), Lake Tete (21 species), Lake Nhlanjana (21 species), Lake Mzinyeni (20 species), Lake Sokhunti (20 species), Lake Mhlolo (19 species), Lake Khangazini (19 species), Lake Ngodo (18 species), Lake Sokhunti (15 species) and Lake Shalala (17 species). There were two water bodies with 16 species recorded: the Mlambongwenya River and Lake Mandlankunzi. The rest of the water bodies had 15 or fewer species present. These numbers of species are the total, over the entire sampling period, but this value varied between sampling periods with fluctuating water levels. No significant difference was found between sampling periods ($p < 0.001$).

The percentage species composition and biomass for each of the lakes sampled has been included in Table 6. The highest percentages have been highlighted.

Many of the species were scarce in the collections and several were only collected once or twice over the six surveys. For example, *Opsaridium zambezense* and *Barbus pallidus* were only recorded once in the Sutu River. *Microphis fluviatilis* was recorded only in the Sutu River, and *Nothobranchius orthonotus* only in the isolated ephemeral pool (Emathamini Enkulu) in Ndumo Game Reserve on the Balamhlanga vlei. *Anguilla* spp. were only found in four sites along the floodplain, including the Phongolo River, where they were most abundant. Juvenile anguillids were recorded in the Phongolo River, Lakes Mzinyeni and Nhlanjana. *Anguilla marmorata* adults were caught in Lake Mayazela when it was rotenoned. Both species of mormyrids, *M. macrolepidotus* and *P. catostoma*, occurred together consistently in Lakes Nhlanjana and Banzi and the Phongolo River.

The characins were relatively widespread throughout the floodplain, *B. imberi* was the most common species in Sokhunti lake. *M. acutidens* appears to have the most widespread distribution, occurring at 12 sites, most commonly in the Phongolo River and Lake Tete. *H. vittatus* juveniles were found mostly in water with a low turbidity. The cyprinid *L. rosae* was the most common juvenile labeo recorded, occurring in nine sites. The other *Labeo* species were relatively uncommon on the floodplain. Of the barbs, *B. toppini* and *B. paludinosus* were the most common, occurring at the majority of sites sampled. *B. trimaculatus* and *B. radiatus* were also relatively common. *C. gariepinus* juveniles were found at 12 sites after the August 1994 flood release. Both *Chiloglanis paratus* and *C. swierstrai* were restricted to the Phongolo and Sutu rivers, but were relatively

Table 6. The relative abundance and biomass (%) of fish caught at each site over the entire sampling period in the littoral zone. The abbreviations for the sites are in Fig. 3, Appendix 1.

Species	No. sites	Pho		May		Nhl		Mkh		Mzi		Mla		Ntu		Nsi	
		No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass
No. of spp		26		10		21		11		20		16		13		9	
Anguilla spp.	5	1.1	4.1	0.5	**76.3**	0.1	2.5			0.1	0.1						
M. macrolepidotus	2					0.1	0.8										
P. catostoma	4	0.1	0.1			0.1	1.0										
B. imberi	16	0.6	2.3			0.4	5.4			6.2	**25.8**	4.4	11.0				
H. vittatus	6	0.1	1.9							0.1	0.3						
M. acutidens	14	**28.3**	3.9			0.5	0.4			0.7	0.3	**24.6**	**13.9**	0.5	0.1		
L. cylindricus	5	0.9	3.8														
L. rosae	13	0.1	7.4							0.7	4.9	0.2	6.8	0.1	0.1		
B. afrohamiltoni	14	0.1	0.1	2.7	0.2	0.1	0.2					0.2	0.5				
B. annectens	17					6.2	2.1	15.9	10.5	0.2	0.1	**12.1**	9.3	0.9	0.2	1.1	0.7
B. pallidus	1																
B. paludinosus	22	6.9	2.5	0.5	0.1	8.9	8.1	**35.3**	**23.6**	2.2	0.1	5.0	4.7	**18.5**	**63.3**	6.7	**15.3**
B. radiatus	14	0.6	0.2			0.1	0.1			6.4	2.4	3.9	2.8	0.6	0.1		
B. toppini	22	1.5	0.1	**35.9**	1.0	**34.7**	**14.3**	12.5	9.3	0.2	0.1	8.9	2.5	**30.5**	0.3	**15.2**	0.9
B. trimaculatus	18	5.5	1.4			1.6	2.1	0.2	0.2	**19.7**	1.6	**12.2**	**12.5**	2.6	0.3		
B. unitaeniatus	2	0.1	0.1	0.5	0.1												
B. viviparus	10	0.2	0.1			0.1	0.1	0.2	0.1			0.3	1.4				
O. zambezense	1																
C. carpio	7																
M. brevianalis	16	6.6	0.3	16.7	0.6	15.3	3.5	0.1	0.1	0.4	0.1	0.9	0.4			10.3	2.1
S. intermedius	9	0.1	1.6			1.0	**14.6**			0.2	2.9						
C. gariepinus	20	1.0	**17.4**					1.1	11.5	0.3	7.4	0.2	2.2	3.8	**17.9**	2.1	8.8
C. paratus	2	0.9	0.5														
C. swierstrai	2	1.3	0.2														
S. zambezensis	3	0.1	0.5														
O. mossambicus	23	**15.2**	**38.5**	**28.0**	**19.2**	7.2	**30.1**	**32.2**	**37.8**	**18.7**	15.9	**13.2**	**21.2**	8.0	4.0	**53.4**	**60.5**
P. philander	20	1.5	0.4			2.3	1.6	1.1	4.8	2.3	1.2	1.9	1.8	**29.9**	**11.7**	6.0	7.8
T. rendalli	21	6.7	**8.2**			0.8	2.5	1.0	1.8	6.5	11.0	2.5	3.5	0.7	0.1	0.3	0.2
T. sparrmanii	14	0.2	0.1			0.1	0.4			2.6	3.0			2.6	2.5		
M. fluviatilis	1																
N. orthonotus	1																
A. aeneofuscus	1																
G. callidus	23	**18.7**	4.0	14.9	1.0	**19.4**	7.7	0.4	0.3	**22.3**	**19.7**	9.5	5.5	1.3	0.4	4.9	3.7
G. giuris	12	0.7	0.3	0.3	1.6	0.1	2.3			1.4	2.5						
R. dewaali	12					0.9	0.2			9.3	0.6						
TOTAL	24	7971	55.6 kg	389	10.4 kg	3198	7.4 kg	3096	2.6 kg	2537	6.7 kg	2691	4.8 kg	875	3.8 kg	283	0.2 kg

Table 6 cont.

Species	Mti		Tet		Kha		Men		Sha		Mfe		Sok		Mhl	
	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass
No. of spp	10		21		19		14		17		7		20		19	
Anguilla spp.													0.1	3.0		
M. macrolepidotus																
P. catostoma																
B. imberi	1.8	0.9	3.4	4.2	5.8	2.4			0.1	0.1			**13.6**	**8.5**	0.5	7.8
H. vittatus													0.4	2.1	0.1	1.0
M. acutidens			0.9	0.4	0.2	0.1	0.2	0.3	0.1	0.1			1.4	0.4	0.1	0.1
L. cylindricus			0.1	0.1												
L. rosae	5.3	4.9	0.5	0.5	1.7	1.3							0.1	1.8		
B. afrohamiltoni			6.2	9.4	0.1	0.1	0.3	4.0	0.1	0.4			0.4	0.1	0.2	0.5
B. annectens			0.5	0.1	0.1	0.1	6.9	2.9	0.2	0.1	15.8	5.8	0.1	0.1	1.4	0.6
B. pallidus																
B. paludinosus	7.4	1.6	**13.4**	4.5	**28.2**	6.1	5.7	6.0	**31.7**	10.0	**16.7**	**28.6**	0.3	0.1	**57.8**	**31.0**
B. radiatus	6.1	2.6	0.1	0.1	0.1	0.1	0.2	0.4	0.1	0.1						
B. toppini	0.6	0.2	2.7	0.6	1.6	0.2	1.3	0.5	**27.1**	3.9	3.0	1.4	0.1	0.1	4.6	2.9
B. trimaculatus	**24.5**	4.2	0.2	0.1	0.3	0.1	0.3	0.7					0.1	0.1	1.9	0.7
B. unitaeniatus																
B. viviparus					0.7	0.1			0.4	0.1					0.1	0.1
O. zambezense																
C. carpio			0.4	0.4	0.6	0.1							0.1	1.4	**18.8**	**34.5**
M. brevianalis			1.5	0.2	0.1	0.1	**11.7**	4.9	7.8	1.7			0.9	0.1	0.4	0.1
S. intermedius			0.1	0.2	0.1	0.1									0.1	0.6
C. gariepinus	0.4	1.5	3.1	**25.3**	3.4	**31.4**	0.6	8.5	1.9	**50.3**			0.1	1.1	0.5	1.6
C. paratus																
C. swierstrai																
S. zambezensis																
O. mossambicus	**12.2**	**14.6**	**33.8**	**25.4**	**19.2**	**39.6**	**13.1**	**19.2**	3.8	2.6	**61.9**	**48.6**	4.9	6.6	**7.4**	**13.8**
P. philander	**28.6**	**37.6**	**14.7**	5.6	**32.8**	**17.3**	3.2	2.0	4.8	4.1	1.2	2.0	0.9	0.3	0.7	0.2
T. rendalli			2.2	**17.1**	1.8	0.3	1.3	2.2	10.4	**18.9**	1.2	10.8	**15.9**	**22.9**	0.9	0.8
T. sparrmanii	**12.2**	**31.2**	1.2	1.9					1.3	2.9			**22.1**	**44.0**	2.8	1.5
M. fluviatilis																
N. orthonotus																
A. aeneofuscus																
G. callidus	0.9	0.7	11.9	2.8	3.2	0.4	**46.8**	**46.3**	9.2	4.5	0.2	2.8	**25.5**	2.0	0.6	2.0
G. giuris			0.6	0.9					0.1	0.1			7.6	5.2		
R. dewaali			2.5	0.2	0.1	0.1	8.4	2.1	0.9	0.1			5.4	0.1	1.1	0.1
TOTAL	542	1.1 kg	4118	16.9 kg	2882	9.4 kg	632	0.7 kg	1479	3.5 kg	952	1.0 kg	2685	19.9 kg	4704	23.0 kg

Table 6 cont.

Species	Bum		Ngo		Nam		Man		Nya		Ban		Sut	
	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass
No. of spp	11		18		15		19		11		23		27	
Anguilla spp.													0.2	0.1
M. macrolepidotus											0.1	0.3		
P. catostoma											3.1	2.5	2.6	**14.6**
B. imberi			0.1	0.3	0.5	2.9	0.2	0.2	0.1	0.4	3.9	3.7	0.8	2.1
H. vittatus									0.2	5.7			0.2	2.7
M. acutidens									0.1	0.1	0.4	0.1	3.4	2.2
L. cylindricus					0.1	0.2					1.0	0.5	0.2	0.5
L. rosae	0.3	0.1					0.3	0.9	0.1	3.2	3.8	**16.9**	3.8	**18.2**
B. afrohamiltoni			0.3	1.4	1.1	4.9					3.3	3.3	0.1	0.1
B. annectens					2.1	0.9					3.0	0.3	6.9	1.9
B. pallidus													1.8	0.5
B. paludinosus	9.5	1.6	11.2	4.4	**20.2**	**11.8**	**25.1**	**13.2**			**13.3**	2.7	11.2	5.6
B. radiatus			0.5	0.2			0.9	0.4			0.2	0.1	0.2	0.2
B. toppini	0.6	0.3	6.4	0.9	9.3	6.7	12.6	1.2			**39.1**	5.1	**21.2**	4.1
B. trimaculatus	1.4	0.4	2.2	0.5	0.3	0.2	2.3	0.4			0.2	0.2	2.7	2.4
B. unitaeniatus														
B. viviparus							0.7	0.1			0.4	0.1	4.9	2.0
O. zambezense													0.1	0.2
C. carpio			0.6	0.2	0.3	0.9	1.3	6.7						
M. brevianalis			0.2	0.1			0.6	0.1					0.1	0.1
S. intermedius			**38.1**	**42.9**							3.9	8.3	0.6	3.0
C. gariepinus	0.3	0.7	2.5	**22.7**	1.3	4.9	4.9	**39.4**	0.1	**10.9**	0.4	12.9	2.1	10.3
C. paratus													0.1	0.1
C. swierstrai													**12.7**	2.6
S. zambezensis			**11.2**	**10.5**							0.1	0.3		
O. mossambicus	**18.1**	9,9	3.9	2.5	**34.2**	**50.0**	2.0	3.6	**74.2**	**58.5**	**16.7**	**37.7**	**19.1**	**20.0**
P. philander	**29.4**	7.0	6.3	3.2	15.5	**11.0**	5.5	7.5			0.3	0.1		
T. rendalli	3.6	**52.4**	0.2	0.1	12.4	2.2	1.3	7.4	5.6	**16.8**	1.2	3.3	0.3	2.7
T. sparrmanii	3.3	3.6	0.1	0.7			1.0	2.7	0.1	0.4	0.1	0.1		
M. fluviatilis													2.4	1.6
N. orthonotus														
A. aeneofuscus													0.2	0.5
G. callidus	**26.11**	**23.6**	**16.2**	7.5	2.3	3.0	**41.2**	**16.1**	**18.5**	3.5	5.2	1.3	2.0	1.2
G. giuris			0.2	1.8	0.3	0.3			0.9	0.4	0.1	0.1	0.1	0.5
R. dewaali	7.4	0.4	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1		
TOTAL	337	1.7 kg	1907	5.3 kg	1131	1.9 kg	1622	3.9 kg	7248	102.1 kg	6889	75.7 kg	1272	3.4 kg

common there.

O. mossambicus was collected at all sites except for the isolated pool (Emathamini Enkulu) in Ndumo Game Reserve. *P. philander* was also relatively common (collected from 17 sites). *T. sparrmanii* was the least common of the cichlids, occurring at only 9 sites. Of the gobies, *G. callidus* was the most common, occurring at 22 sites, followed by *R. dewaali* (9 sites).

To determine the species richness, distribution and abundance of fishes within the limnetic zone the larger fishes of the Phongolo floodplain were collected in gill nets. The demography of the larger fishes has been previously quantified for the Phongolo floodplain (Kok 1980), but in conjunction with historical data and with the data collected from the littoral zone, can now be used in the model to determine the most holistic representation of the fishery.

A total of 8 698 specimens representing at least 20 species within nine families and with a combined mass of 1 962.78 kg was collected using gill nets in the Phongolo floodplain between December 1993 and April 1995. These fishes are the larger fishes on the floodplain, and reach an average adult size of > 150 mm SL. The percentage relative abundance and biomass of fish is shown for the entire sampling period in Table 7 (the total masses indicated are in kg).

Discussion

The total fish biomass of the Phongolo floodplain was found to vary with the fluctuating water levels (Merron *et al* 1993c, 1994a, 1994b, 1994c, 1994d, 1994e, Merron & Weldrick 1995). This was also found for the Okavango Delta (Merron 1993). This is as a result of concentration and dilution effects on the fish stocks.

In general many of the smaller fish species are common but are restricted to a few suitable habitat types on the floodplain. Conversely, a few species are true generalists and are found throughout the Phongolo River and associated floodplain lakes. For example, the tilapia are generalists which are found in a wide variety of habitat types and do not rely on summer floods to spawn. *O. mossambicus* is dominant throughout the floodplain. It is a eurytopic species, able to adapt easily to harsh conditions. It is the one of the last species recorded during the dry-down of the lakes (such as Lake

Table 7. Relative abundance and biomass (%) of fish caught at each site in the limnetic zone for the entire sampling period. The abbreviations for the sites are in Fig. 3, Appendix 1.

Species	Pho		Nhl		Mzi		Tet		Kha		Sok		Mhl		Man		Nya		Ban	
	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass
M. cyprinoides					0.1	0.3											0.4	0.8		
M. macrolepidotus	1.7	0.5	9.5	6.6	7.9	6.8	0.9	0.8			0.2	0.7			1.2	1.6				
P. catostoma	1.9	0.1	10.3	2.8	1.5	0.4			0.1	0.1	0.1	0.1								
B. imberi	**31.7**	5.5	**21.2**	9.3	**42.3**	**24.2**	16.3	9.8	**31.5**	15.5	**60.2**	**47.0**	**40.4**	20.1			0.9	0.1	2.8	0.2
H. vittatus	4.7	4.1	1.1	2.8	0.2	0.7	5.2	3.9	0.7	2.1	1.0	2.5					**26.6**	**24.3**	**63.0**	**49.4**
L. congoro	4.4	**37.1**															0.5	1.1	0.8	1.3
L. cylindricus	4.2	1.4									0.1	0.2								
L. molybdinus	0.7	0.7															10.7	19.1	5.7	10.1
L. rosae	**20.5**	**35.4**	0.3	3.1	1.7	2.8	1.0	2.1	0.5	0.5	1.0	2.5								
B. afrohamiltoni	0.2	0.1	1.9	0.5	0.3	0.1	5.8	2.0	0.9	0.2	0.1	0.1	0.9	0.4						
C. carpio	0.4	0.5	**19.7**	**14.2**	0.3	1.7	1.7	4.5	2.2	1.8	0.4	0.2	0.9	0.8	11.6	**20.9**				
S. intermedius	**20.4**	4.7	12.8	7.2	**14.2**	9.3	**25.6**	**17.6**	**23.2**	12.0	**21.9**	**17.8**	13.6	9.4					4.6	1.6
C. gariepinus	1.5	6.3	6.1	**35.4**	1.3	9.8	4.5	14.3	6.2	**29.8**	0.6	2.6	4.8	**26.8**	3.5	5.5	9.3	19.0	**14.0**	**30.6**
C. ngamensis			0.3	1.5	0.4	2.7	0.3	4.3											0.1	0.1
S. zambezensis	4.6	1.1	5.3	2.4	**15.7**	6.6	6.4	4.6	5.6	3.1	3.9	4.4								
O. mossambicus	2.3	1.7	11.3	14.1	9.1	**27.6**	**27.8**	**32.9**	**27.1**	**33.8**	3.1	7.3	**25.8**	**27.1**	**23.3**	17.5	**35.0**	**31.4**	8.0	6.3
T. rendalli	0.8	0.8			0.1	0.1	2.8	1.5	1.7	0.9	0.5	1.2	4.2	5.1	**56.9**	**45.4**	11.6	2.7	0.9	0.3
T. sparrmanii							0.4	0.2	0.2	0.1	3.0	3.9			3.5	9.1	2.3	1.2	0.1	0.1
G. giuris			0.2	0.1	4.7	6.9	1.3	1.5	0.1	0.1	3.9	9.5	9.4	10.3			2.3	0.2		
TOTAL	920	263.4	642	67.1	1486	116.6	1182	83.8	1016	90.6	1031	59.2	213	19.1	86	4.3	214	147.1	824	507.0

Mfelu) and it is one of the first species recorded when the lakes become inundated (such as Lakes Nsimbi and Mthikeni). The reduction of fish species to the most eurytopic forms was found to be typical of floodplain fish communities during periods of dry-down (Merron *et al* 1993a). *Pseudocrenilabris philander* is also widespread, but found in the shallows usually amongst dense macrophytic growth, such as *Trapa natans* and *Nymphaea* sp. Unfortunately, many lakes dried out in 1994 and limited information was available to correlate plant communities and associated fish assemblages. These fishes are not flood-dependent spawners but mouthbrooders.

B. paludinosus has similar habitat requirements to *P. philander* and is abundant in shallow well-vegetated areas. *B. toppini* was found in a wider variety of habitats throughout the sampling period, suggesting that it is a generalist, flood-independent spawner.

G. callidus is another broad generalist, found in lakes during periods of dry-down when most other fish species were no longer present. It is always associated with *O. mossambicus* and seems to have a high conductivity tolerance level as it was recorded abundantly in the most saline lakes (Nyamithi and Mhlolo). *Redigobius dewaali* was abundant in relatively clear lakes but was not common during dry-down, suggesting slightly more specialised habitat requirements.

Anguillids appear to be relatively uncommon on the floodplain but their abundance is difficult to assess as they are difficult to catch. They survive in a wide variety of habitat types from superoxygenated water (such as in the rapids at the New Bridge in the Phongolo River) to oxygen-poor water during dry-down (such as Lakes Mhlolo and Mayazela).

The suckermouth catlets (*Chiloglanis paratus* and *C. swierstrai*) and labeos (*L. cylindricus*) are specialists and are restricted to a few suitable habitats on the floodplain. Both of these species are rheophilic, preferring fast-flowing water. Although these species are relatively common in their particular habitats, the actual habitat type is limited along the floodplain.

The mormyrids (*P. catostoma* and *M. macrolepidotus*) are habitat specialists and are relatively uncommon throughout the floodplain. These fish were not found in lakes with high salinities as it is possible that the conductivity of the water affects their electrolocation (Heeg & Kok 1988). Thus, if the lakes are not flushed out regularly with flood releases, it possible that these species will disappear due to a concentration of salts and minerals in the water resulting in an increase in conductivity. These species are also both flood-dependent spawners but no juveniles of either species were collected for the duration of the sampling period.

The biomass of fishes per volume of water is the highest in Lakes Banzi and Nyamithi (Ndumo Game Reserve) compared to any other lakes on the floodplain. The former lakes are not fished and appear to be more productive than the other lakes, partially as a result of fertilisation by hippopotami, which transfer nutrients from the land to the water. Lakes Banzi and Nyamithi are not affected to the same extent as the lakes outside the reserve by untimely water releases from the Pongolapoort Dam, due to their comparatively large sizes and pristine condition. The lakes outside Ndumo Game Reserve are affected by factors such as increasing turbidity as a result of improper farming activities and erosion which can affect the overall harvestable biomass of fishes. It is possible that the biomass values are distorted for the rotenone stations at Lakes Mayazela and Mfelu as these lakes were in the final stages of dry-down, and fish were more concentrated, resulting in a higher biomass per volume ratio than normal.

The major factor determining the distribution and abundance of fishes in the Phongolo floodplain appears to be habitat preference, with the physical characteristics of the environment playing a major role. Several species are restricted in range, and species richness is highest in the riverine habitats. The permanence of the water, and the nature of its flow properties and nutrient content, are important ecological factors influencing community structure of fishes in the Phongolo floodplain.

The high species richness and diversity in the riverine sites could be attributed to the wide range of microhabitats and food resources occurring which would allow fish to occupy niches within these microhabitats. It was found by Merron (1991) for the Okavango River floodplain, and Chapman & Chapman (1993) for the Sokoto River floodplain, that the fish faunas were most diverse in the riverine habitats. The primary reason for this could be the heterogeneity of habitats and the better water quality in riverine areas compared to lacustrine areas (Schiemer & Zalewski 1992). It was also found that the number of juvenile species present correlated significantly with the diversity of shoreline habitats at the mean retention level. This would indicate the importance of maintaining the shoreline, by maintaining the condition of the levees, minimising deforestation and encroachment of agriculture and cattle, and ensuring a water level sufficient for maintaining a range of microhabitats (Merron & Weldrick 1994).

As previously mentioned, the fishes feed on a wide range of foods. One of the main ecological roles of Phongolo fishes is to convert the nutrients at the base of the food chain, i.e. plants, detritus or epiphytes, into food for higher trophic levels such as man, piscivorous birds and crocodiles. The three important energy pathways include a grazing pathway, which has living plant material as its basis; a detritus pathway based on dead plant and animal material, often of allochthonous origin; an epiphyte pathway, based on algae and invertebrates that are attached to plant stems; and a piscivorous pathway based on other fish species. These pathways would account for the relatively high species diversity throughout the floodplain.

The relative abundance and biomass of fish in the different habitats gives an indication of habitat niches and trophic levels. But, as the floodplain ecosystem is a dynamic one and constantly fluctuating, the composition and mass of fish species are likely to change. In order to assess the fishery as accurately as possible, these values have been used as an average in an attempt to provide potential yields for the fishery and a community classification of all the fishes in particular habitats.

Williams (1964) found that area is the primary habitat parameter that is most commonly correlated with species richness. This was substantiated by Halyk & Balon (1983) with the proposal that an increased area is associated with an increase in number of habitat niches, resulting in an exponential increase in species number. It is possible that the riverine habitats have the highest species richness, as most of these habitats occupy relatively large areas. But several of the lakes on the Phongolo floodplain have a large area, and a relatively low species richness. This is due to several other factors such as water quality and amount and type of macrophytic growth. Therefore, although area is the fundamental parameter correlated with species richness, the other environmental variables which are affected by water fluctuation, should also be taken into account. Kushlan (1976) suggested that the seasonal fluctuation of water level is the most critical environmental factor affecting a fish community.

Several species on the Phongolo floodplain occur in most habitat types. A possible reason for this is that the fish perceive the floodplain as a continuous habitat, instead of isolated habitats, through regular temporary events such as seasonal flooding (Mahon & Balon 1977). Through these events, floodplain ecosystems can be viewed as chaotic systems. Chaotic systems are characterised by a high degree of non-equilibrium that maintain self-organising processes. These processes are maintained by a continuous exchange of matter and energy in the environment (Bruton 1989).

The change in water quality has been found by Larimer *et al* (1959) to affect invertebrates in North American floodplains. On the Phongolo floodplain deteriorating water quality conditions could result in increased competition for food resources by fishes. The species richness decreased during dry-down (Merron *et al* 1994b, 1994c) as a result of the desiccation of the substrate and resultant changes in the dissolved salts and gases in the remaining water. The deteriorating water quality is also affected by soil erosion. The primary reason for soil erosion is habitat degradation through over-utilisation of the resources by a concentrated and increasing human and livestock population surrounding the floodplains. Similar effects have been found to affect the long-term production of fishes in the Okavango Delta (van der Waal 1991). Large- scale soil erosion results in increased sedimentation and decreased water quality of important refuge areas such as the river. When sedimentation occurs, shallow, unstable sandbanks are formed, widening the river and covering the reedbeds. During flood releases, the shallower river cannot carry the same volume of water, and cuts into the banks. This results in further erosion of the system as several of the banks have been deforested.

The long-term affects of destabilisation and siltation of the river bed may seriously impact the fish production potential of the system through a decrease in species richness and relative abundance (from an ecological perspective), and thus a decrease in availability of fresh, high quality protein for the local people (from a fisheries perspective).

The data on the total fish biomass at each site are important for the estimation of the potential yields. The information on distribution and species richness is important for the community classifications of the fishes.

Potential yields of the fishes

The potential yields of fishes need to be calculated to compare with the actual harvest of the subsistence fishery, in order to manage the fishery sustainably (Oglesby 1985). The potential yields are based on the biomass of fish collected at each site throughout the sampling period.

The biomasses for the small fishes in the littoral zone have been determined to estimate the potential yields for the littoral zones of the floodplain. These have not previously been determined, as yields have been based primarily on gill net catches. The potential yields of the littoral zones will give a more realistic estimation of the total potential yield of the fishery.

The biomass estimates for the lakes were based on seine net and rotenone samples. All samples up to and including August 1994 were combined, as several lakes were dry prior to this period. The calculated biomass was the highest for Banzi at 299.8 kg.ha^{-1}, followed by Nyamithi at 183.1 kg.ha^{-1} (Table 8). Both these lakes are within Ndumo Game Reserve and appear to have a higher productivity than the other floodplain lakes. The biomass in Lake Mayazela (163.6 kg.ha^{-1}) is relatively high but this lake was almost dry when sampled and the use of rotenone ensured a total catch. Therefore, this ratio is an overestimate due to fish stocks being more concentrated than in the fuller lakes. Lake Khangazini, Mkhonjeni pools and Lake Ngodo had the highest standing stocks outside the game reserve at 69.6 kg.ha^{-1}, 67.8 kg.ha^{-1} and 58.4 kg.ha $^{-1}$ respectively. Lake Khangazini is relatively shallow with a high surface area and as a result dries out relatively quickly. Mkhonjeni pools are annual rainpools, fed by the irrigation canal on the Balamhlanga vlei and have a high concentration of fish (as the pools are very eutrophic and rich in nutrients and are not extensively fished). Lake Ngodo is a relatively small lake with a concentrated fish population. The Phongolo River had an average biomass of 64.1 kg.ha^{-1}. Lakes Mengu at 46.3 kg.ha $^{-1}$, Sokhunti at 46.0 kg.ha $^{-1}$, Mandlankunzi at 42.6 kg.ha^{-1} and Shalala at 40.2 kg.ha^{-1} were all above 40 kg.ha^{-1}, the average biomass estimated for wetlands according to Welcomme (1979). The remainder of the lakes had a biomass less than 40 kg.ha^{-1} (Table 8).

The average biomass in the littoral zone, based on all samples, was 59.9 kg.ha^{-1}. The average biomass on the floodplain excluding the game reserve was 43.7 kg.ha^{-1}. The biomass for the game reserve was much higher at 241.5 kg.ha^{-1}. The potential yields have been calculated at one third of the standing stocks (Lagler *et al* 1971). From the potential yields calculated for each site, an annual yield for the total area can be calculated.

Table 8. Calculated fish biomass and potential yields from all littoral samples collected (kg.ha^{-1}). The abbreviations for the sites are in Fig. 3, Appendix 1:

Sites	A	B	C	D	Average	Yield
Dam				0.2	0.2	0.1
Pho	47.4	152.3	39.8	16.8	64.1	21.4
May	163.6				163.6	54.5
Mzi	28.4	11.9	9.7	22.6	18.1	6.0
Mla		27.1		8.83	17.9	5.9
Ntu	8.3	8.7	1.9	81.1	25.0	8.3
Mkh		25.9		109.6	67.8	22.6
Nhl	33.3	19.3	2.6	55.8	27.8	9.3
Tet	58.3	25.1	21.7	23.3	32.1	10.7
Nsi	3.1				3.1	1.0
Mti	25.7	8.8		78.4	37.6	12.5
Kha	53.0	11.1	1.7	212.7	69.6	23.2
Men	30.0	99.4	9.4		46.3	15.4
Sha	6.5	70.1		43.9	40.2	13.4
Sok	35.0	35.5	26.6	86.9	46.0	15.3
Mhl	4.3	49.6	4.0	15.9	18.5	6.2
Man	3.3	88.6		35.9	42.6	14.2
Bum	12.1	17.8		78.4	36.1	12.0
Ngo	23.8	37.8		113.7	58.4	19.5
Nam	12.0	18.6	9.5	20.6	15.2	5.1
Nya	384.0	120.3	65.1	163.9	183.1	61.0
Ban	522.1	184.6		192.6	299.8	99.9
Sut		36.4		2.8	19.6	6.5

(Where A = Up to and including August 1994, B = November 1994, C = February 1995, D = April 1995)

The highest average biomasses in the limnetic zone for the sampling period were recorded in Lakes Banzi (464.9 kg.ha^{-1}) and Nyamithi (126.9 kg.ha^{-1}, Table 9). Both these lakes are within Ndumo Game Reserve. On the floodplain, the highest average biomass was recorded for Lake Khangazini (83.0 kg.ha^{-1}, Table 9). This lake was not surveyed during each sampling period as it had almost completely dried out, resulting in difficult gill netting conditions, and a concentration of fish during dry-down. Lake Khangazini was followed by the stilling pool below the dam wall (63.8 kg.ha^{-1}) and the Phongolo River (56.8 kg.ha^{-1}). Lake Mzinyeni had the next highest average biomass of 54.1 kg. ha^{-1}. The remaining lakes had average biomass of less than 40.0 kg.ha^{-1} (Table 9).

Table 9. Total biomass for each site in the limnetic zone for the entire sampling period (kg.ha^{-1}). The abbreviations for the sites are in Fig. 3, Appendix 1.

Site	Survey											
	A	B	C	D	E	F	G	H	I	J	AVE	PY
Sti	54.4	148.4	108.5	47.5	95.4	54.9	52.4	24.4	52.3	0.2	63.8	21.3
Pho	35.9	20.2	27.1	79.6	54.4	37.7	39.4	0.6	206.2	42.4	56.8	18.9
Mzi	30.7	9.1	64.9	57.8	123.1		90.9	45.5	23.9	40.8	54.1	18.0*
Nhl	35.9	14.3	31.8	56.6	2.8	79.7	114.1	5.8	25.4	5.6	37.2	12.4*
Tet	48.9	44.2	15.5	61.1	20.3	95.0	29.4	21.2	14.2	18.2	36.8	12.3*
Kha		19.7	38.4			196.2	4.9				83.0	27.7*
Sok	32.8	133.6	22.8	88.8	12.9	21.9	42.5	10.1	20.5	3.7	39.0	13.0*
Mhl	66.8	14.4				27.0	14.6	6.2	0.1	3.2	19.9	6.3*
Nya	51.9	334.9	56.1	127.2	309.9	85.4	77.1	44.5	102.6	80.1	126.9	42.3#
Ban	518.0	213.7	283.4	208.9	1587.8		299.8	183.1		324.0	464.9	154.9#

(Where A = December 1993, B = February 1994, C = April 1994, D = June 1994, E = August preflood 1994, F = August postflood 1994, G = November 1994, H = February preflood 1995, I = February postflood 1995, J = April 1995, AVE = average biomass , PY = potential yield).

The average biomass for the fished floodplain lakes* which were gill netted was 45.0 kg.ha^{-1} , compared to those within Ndumo Game Reserve# at 295.9 kg.ha^{-1} (Table 9).

When the area of inundation within the littoral and limnetic zones is calculated, the potential biomass for that area can be estimated. The percentage areas for the lakes have been based on the fluctuating water levels throughout the entire sampling period, and are an average, from drought conditions to flooding conditions. These areas are shown in Table 10 . The potential yields were calculated in kg.y^{-1}.

The total potential yields were not calculated for the Phongolo River as the area sampled was low relative to the area of the river, so the result would be inaccurate. This is not crucial as no fishing is permitted in the river in an attempt to conserve it as a refuge area for the rest of the floodplain (Holtzhausen *pers comm* 1995).

The total potential yield was again highest in the unfished lakes within Ndumo Game Reserve, at 27 180.7 kg.y^{-1} for Banzi Lake, and 8 032.7 kg.y^{-1} for Nyamithi Lake. The potential yields outside the reserve ranged from 348.2 kg.y^{-1} at Lake Mhlolo to 1 346.1 kg.y^{-1} at Lake Sokhunti.

Within the littoral area outside the reserve, the potential yield ranged from 15.8 kg.y^{-1} to 1 561.4 kg.y^{-1}. Within the limnetic area outside the reserve, the potential yield ranged from 59.9 kg.y^{-1} to 1 082.9 kg.y^{-1}.

As mentioned previously, based on the potential yields, an annual yield for the total area can be estimated. For the littoral zone, the estimated yield would be 14.2 kg.ha^{-1} (average) for the average area of the zone, 49.6% of 2 700 ha, which is equivalent to 19.0 tonnes per year. For the limnetic zone, the estimated yield would be 14.9 kg.ha^{-1} (average) multiplied by the average area of the zone, 50.4% of 2 700 ha, which is equivalent to 20.3 tonnes per year. Therefore, the total potential yield is calculated at 39.3 tonnes per year for the entire floodplain at MRL, provided that all the lakes were flooded.

Table 10. The potential yields (PY) for the littoral and limnetic zones for each lake. The abbreviations for the sites are in Fig. 3, Appendix 1.

Sites	Area (ha)	Littoral			Limnetic			TOTAL
		%	Area (ha)	PY (kg)	%	Area (ha)	PY (kg)	(kg)
Mzi	74.2	19	14.1	84.6	81	60.1	1081.8	1166.4
Ntu	23.5	95	21.2	176.0	5	2.3		
Mkh	1.0	65	0.7	15.8	35	0.4		
Nhl	37.9	30	11.4	106.0	70	26.5	328.6	434.6
Tet	115.9	55	63.8	682.7	45	52.2	642.1	1324.8
Kha	74.0	91	67.3	1561.4	9	6.7	185.6	1747.0
Men	32.2	28	9.0	138.6	72	23.1		
Sha	49.2	67	32.9	441.0	33	16.2		
Sok	101.0	17	17.2	263.2	83	83.8	1082.9	1346.1
Mhl	56.0	83	46.5	288.3	17	9.5	59.9	348.2
Bum	58.4	48	28.0	336.0	52	30.4		
Ngo	22.1	52	11.5	224.3	48	10.6		
Nam	63.4	62	39.9	203.5	37	23.5		
Nya	183.4	8	14.7	896.7	92	168.7	7136.0	8032.7
Ban	238.0	74	176.1	17592.4	26	61.9	9588.3	27180.7

Discussion

The biomass estimates of the smaller fish species were found to be within the range predicted by Welcomme (1979) i.e. 40 - 60 kg.ha^{-1} for African floodplains. The standing stock for Ndumo Game

Reserve was much higher as the fish stock is not exploited, and the fishes are able to grow to a much larger size than the fishes in the harvested floodplain lakes. These estimates are valuable for the prediction of sustainable yields for the Phongolo floodplain, but are a generalisation and cannot be directly applied to the management of the fishery without taking the life-history styles of the fishes into account. The estimations also do not take the dynamics of the ecosystem into account. There is a wide variation within the floodplain due to the variation in habitat types. Some of the lakes were more productive than others, resulting in some lakes having a higher standing stock than others.

The high biomass values in Ndumo Game Reserve and the Phongolo River could be a result of a number of factors. Firstly, these fishes were larger than the fishes in the floodplain lakes, and are generally caught in much larger gill net mesh sizes. Margalef (1969) proposed that a high species richness could be correlated with productivity. The fish from Ndumo Game Reserve were larger than those caught in floodplain lakes which are harvested, and these lakes were more productive than the harvested lakes. The stilling pool had a relatively high biomass due to the migration of rheophilic fish (such as the labeos) towards the incoming water (base flow) from the dam. The river generally showed a higher biomass than the utilised floodplain lakes, and served as a refuge area (from desiccation and deteriorating water quality conditions) for the fish during periods of dry-down. Only a very small percentage of the river was gill netted, so the biomass calculated could be an underestimation of the true biomass.

The general biomass, number of fish caught and fish size decreased during the winter months. This could be as a result of less food being available to the fish, resulting in less fish movement, and a weight loss. The weight loss could also be a result of relatively undeveloped gonads, as most of the fish examined are flood-dependent spawners, spawning naturally during summer.

The biomass estimates for the littoral zone (average of 42.5 $kg.ha^{-1}.y^{-1}$ excluding Ndumo Game Reserve) were slightly higher than the biomass estimates reported for the marginal fish species of Lake Kariba (33.0 $kg.ha^{-1}.y^{-1}$) (Marshall *et al* 1982), and for the limnetic zone at 45.0 $kg.ha^{1}.y^{1}$ were also higher than the production in the pelagic zone in Kariba (9 - 23 $kg.ha^{-1}.y^{-1}$). Cochrane (1987) cited unpublished estimates of standing stocks from tropical African lakes of between 80 and 800 $kg.ha^{-1}.y^{-1}$, with most below 400 $kg.ha^{-1}.y^{-1}$. The average catch from these fisheries was estimated to be 80 $kg.ha^{-1}.y^{-1}$ (Oglesby 1985). It is possible that these values are an overestimation of the biomass from African freshwater bodies. Jackson & Ssentongo (1988) cited production estimates ranging from 9.1 $kg.ha^{-1}$ in Lake Malawi to 388.9 $kg.ha^{-1}$ in Lake Kioga. Lake Bangweulu was found to have an estimated production of 32.1 $kg.ha^{-1}$ for a similar area to the Phongolo floodplain.

It was found from work carried out on several northern hemisphere freshwater bodies that nutrients have a significant positive relationship with fish standing stocks (Hanson & Legget 1982), and therefore potential yields. According to Cochrane (1987), similar relationships were found between primary production and yield in tropical lakes by Melack (1976) and Oglesby (1977). This was substantiated by Robarts (1984), who found that high nutrient concentrations in the Hartebeespoort Dam resulted in high primary production. In the absence of other limiting factors, the rate of primary production resulted in high standing stocks in the Hartebeespoort Dam (Cochrane 1987). This could explain the relatively high yields from within Ndumo Game Reserve. There are relatively high hippopotami and crocodile concentrations in the reserve which contribute to the high nutrient level in the water. This would contribute to primary production; coupled with this is the fact that the lakes within the reserve are not harvested.

It is likely that the yield in some of the lakes decreased during the dry-down phase not only due to predation (Larimer *et al* 1959) but most of the remaining fish were small (Merron *et al* 1994c). Small fishes are able to utilise the oxygenated surface film of the water more efficiently than larger fish (Tramer 1977).

Production estimates for the Kafue River floodplain (Zambia) were between 630 - 870 $kg.ha^{-1}.y^{-1}$ (Welcomme 1979), which is much higher than the production estimates for the Phongolo floodplain. The factors influencing the production in ecosystems are primarily the range of aquatic habitats available for shelter and reproduction, and secondarily, the quality and variety of potential food resources available (Gorman & Karr 1978). Most of the other floodplain ecosystems in southern Africa are much larger than the Phongolo floodplain.

It is possible that several of the well-vegetated lakes in the Phongolo floodplain had a high potential yield due to efficient primary production. Fish production in Chinese lakes was found to be strongly correlated to primary production (Liang *et al* 1981). This primary production would be a result of the amount of organic substrate present. During dry-down the amount of organic substrate becomes concentrated and nutrients accumulate resulting in an increase in primary production. The opportunist fishes would have taken advantage of the increased nutrient levels in the water. The juvenile fishes need to grow relatively quickly through the flood period to reach a sufficient size to reduce predation losses when water volume subsequently reduces as the water levels recede (Bayley 1995).

For biomass estimates from tropical floodplains, yields are only available for the river floodplain area at maximum retention level, resulting in an underestimation of the predicted optimal yields compared with those of the lakes (Bayley 1995). This is due primarily to the inadequacy of estimation methods in accounting for the highly dispersed fishing activities in these systems, which is also true for the Phongolo floodplain.

Yield is correlated with the flood level in a given year (Merron 1991). Yields were relatively high when the water level was low as a result of the concentration of fish stocks (Merron *et al* 1994c). When the water level was high, the yields are lower, as the fish are more dispersed and diluted (Merron *et al* 1994d, 1994e, Merron & Weldrick 1995).

Community classification of the fishes

A community classification is necessary for the management of the Phongolo floodplain as it is necessary to group particular habitat types and fish communities together.

Based on the relative abundance and biomass of the fish species at each of the sites, a community classification of all the fish species within different habitat types was established. The sites sampled were classified subjectively according to the following environmental characteristics: flow rate, depth of the lake or river, amount of aquatic macrophytes present, substrate type, and distance from the river. The classification of these habitats was based on a scale from 1 - 4 as indicated in Table 11.

Table 11. Environmental variables for representative sites. For codes, see Table 12. The abbreviations for the sites are in Fig. 3, Appendix 1.

Site	Flow rate ($m.s^{-1}$)	Depth (m)	Substrate type	% Macrophyte cover	Distance from river (km)
Pho	4	3	1	1	1
Mab	4	1	3	1	1
Mzi	1	3	1	1	2
Mla	2	2	2	2	1
Ntu	1	2	2	4	4
Nhl	1	3	2	2	2
Tet	1	2	1	3	2
Kha	1	1	2	3	2
Sok	1	3	1	2	2
Mhl	1	2	2	2	2
Nya	1	3	2	1	1
Ban	1	2	2	3	2
Sut	4	2	1	1	1

The particular variables which are used above fall into the categories as described in Table 12.

Table 12. Codes for the respective variables.

Variables	1	2	3	4
Flow rate ($m.s^{-1}$)	0	0 - 0.25	0.25 - 0.5	> 0.5
Average depth (m)	0 - 1	1 - 2	>2	
Substrate type	sandy	muddy	rocky	
Macrophytic cover (%)	0 - 25	25 - 50	50 - 70	75 - 100
Distance from river (km)	0 - 0.5	0.5 - 1	1 - 1.5	> 1.5

The cluster analysis of the environmental variables indicated a definite gradient from a lacustrine to a riverine environment (Merron & Weldrick 1994, Fig. 8). The flow rate was plotted both against relative plant cover and distance from the water course. These plots both showed similar community clusters. The first cluster of Lakes Sokhunti and Mzinyeni positioned closely to the second cluster of Lakes Nhlanjana, Mhlolo, Khangazini, Tete, Ntunte, Nyamithi and Banzi was characterised by typical lacustrine conditions with low flow rates, similar muddy substrate types and the presence of relatively large amounts of aquatic vegetation. The third cluster of the Mlambongwenya River showed a trend towards a more riverine environment with less aquatic vegetation and a more sandy substrate type, while the fourth cluster of the Phongolo and Sutu Rivers was clearly lotic, characterised by a high flow rate, little aquatic vegetation and a sandy or rocky substrate type.

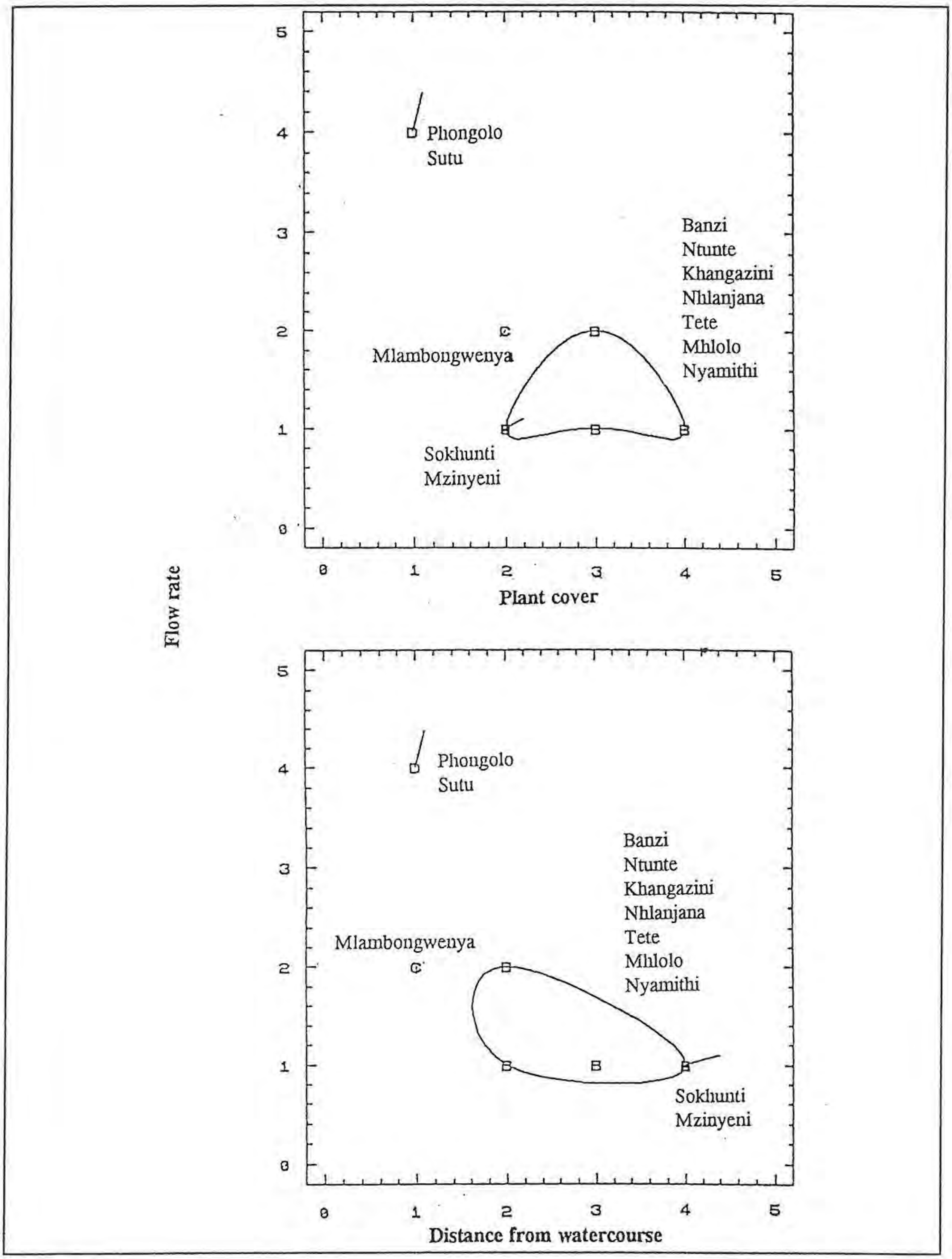

Figure 8. Cluster analysis of environmental variables for the Phongolo floodplain.

The TWINSPAN ordination was carried out on each individual sampling survey both for number and mass on the combined littoral and limnetic zones. For the purpose of the modelling, these results have been pooled to show the broad trends within the floodplain ecosystem, as no significant difference within the sites between the sampling periods was found. The TWINSPAN ordination also indicated a gradient from a lacustrine to a riverine environment within the floodplain.

As sampling was performed in distinctive habitat types, the final 'groups' should reflect this and a mixture of the groups together at level five is indicative of communities with a similar species composition.

On the basis of total number, the Phongolo River and Nyamithi Lake divided off at level 1. Many of the species in the Phongolo River are rheophilic and do not occur in many other habitat types. Nyamithi Lake is the largest on the South African side of the floodplain, with its own catchment, so it could be perceived by euryhaline biota as riverine. Level 2 divided the most lacustrine environments from the most riverine environments. The more riverine lake habitats consisted of the Mzinyeni group, which all had similar sandy substrate types, with similar aquatic vegetation, and were relatively clear. Level 3 divided these lakes from Lake Sokhunti, and Lakes Mhlolo and Shalala, which were divided at level 4. Lake Sokhunti is the deepest lake on the floodplain, is clear, with a sandy substrate type and little aquatic vegetation. It is slightly more lacustrine in that it does not flood easily due to the height of the levee. Lakes Mhlolo and Shalala were divided from Sokhunti on the basis of a different species composition due to higher conductivities. The conductivity of Lake Shalala was recorded throughout the survey, and although was highly variable, was found to be relatively high and similar to that of Lake Mhlolo. These two lakes also shared similar substrate and vegetation types. Of the more lacustrine habitats, the Khangazini group remained together after level 5, as a consequence of all having similar environmental variables and thus species compositions. Lakes Nhlanjana and Ngodo were divided from this group at level four. These lakes have their own catchment areas, possibly resulting in the presence of some rheophilic fauna. At level 3, the Mlambongwenya River and the Sutu River and Banzi Lake were divided from the other groups. The Mlambongwenya River is only susceptible to flowing conditions at periods of high rainfall. The Sutu River and Banzi Lake have been divided on level 4 as they have species not occurring on the Phongolo floodplain but only on the Sutu floodplain (Fig. 9).

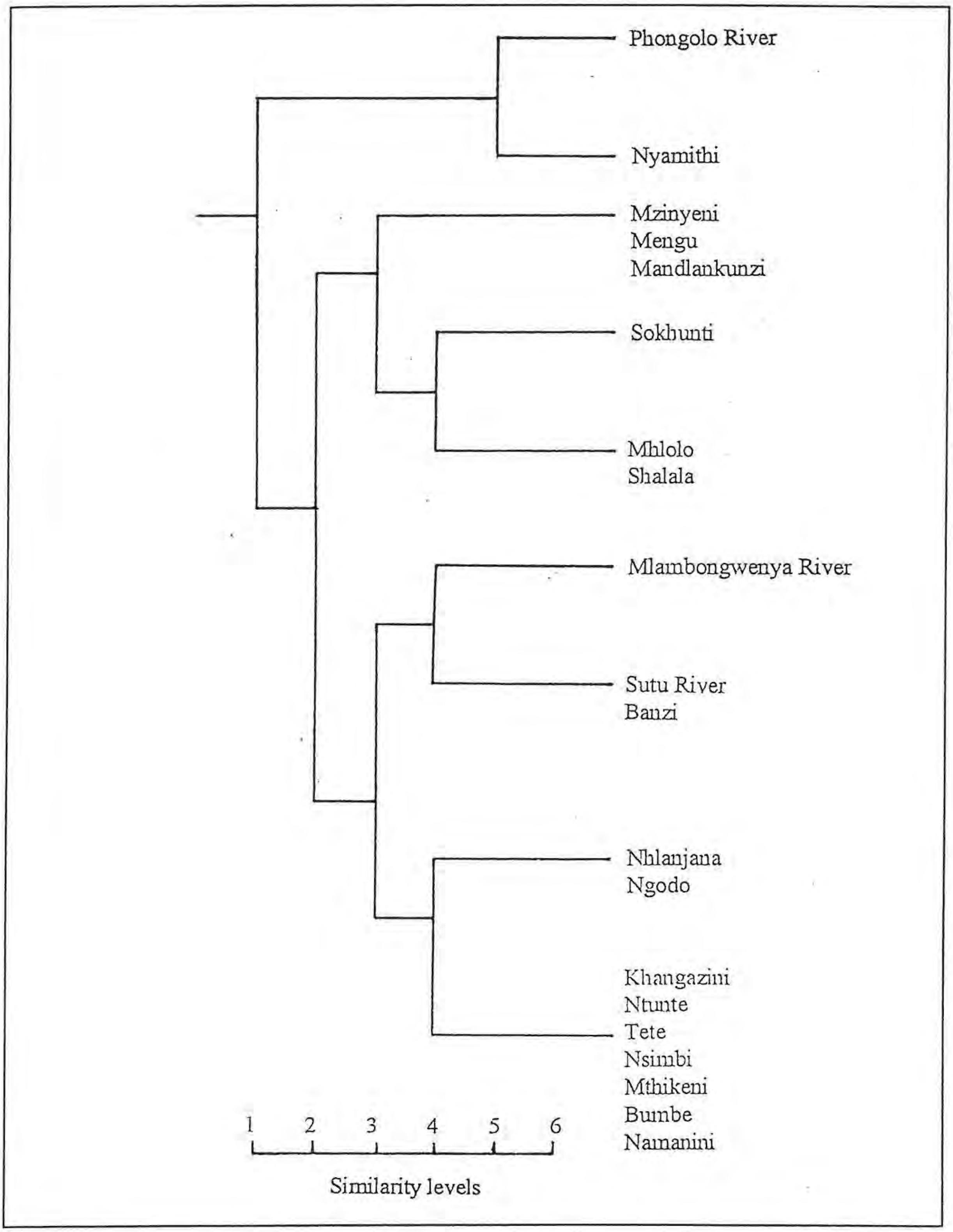

Figure 9. TWINSPAN classification of the fishes on the Phongolo floodplain based on relative abundance.

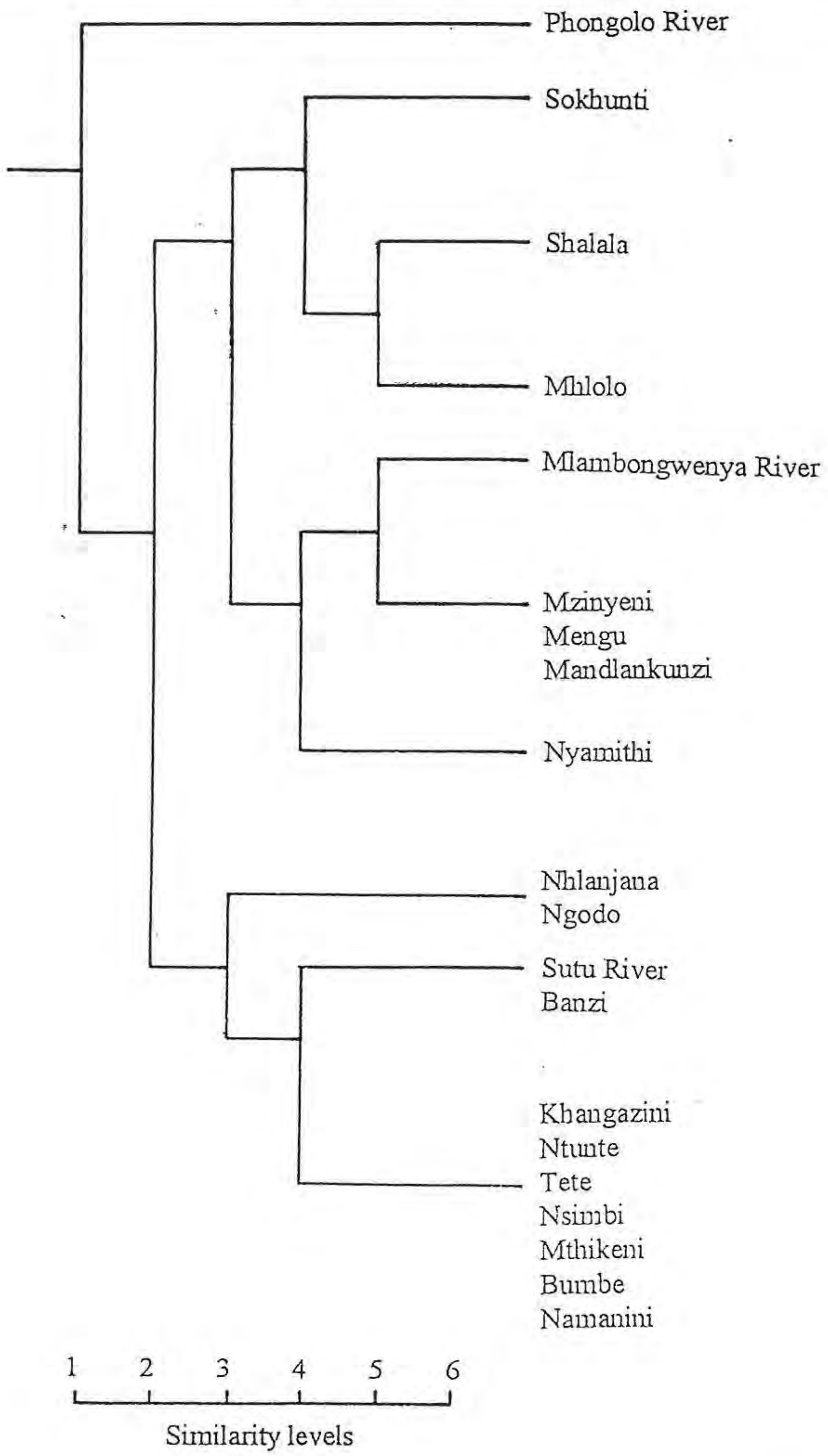

Figure 10. TWINSPAN classification of the fishes of the Phongolo floodplain based on biomass.

On the basis of total biomass, a similar trend was followed, with ten major divisions (Fig. 10).

Discussion

Cluster analysis is a synchronised way of analysing geometrically and spatially related data (Copp 1989) and was used to determine the extent to which the selected environmental variables of the floodplain correlated with the fish species present. It has been proposed that the fish communities at a specific site could be statistically predicted when environmental variables had been determined (Rodriguez & Lewis 1990). A distinct gradient from a lacustrine to a littoral environment was determined (Merron & Weldrick 1994) with water flow as a major influence on the community structure (Merron 1991).

The constancy of fish habitat communities is similar to other tropical floodplain systems. In the Parana floodplain (Amazon), the species richness and composition remained relatively constant throughout the floodplain on an annual basis (Rodriguez & Lewis 1990). For the Okavango system, the proportions of species within communities did not change, although production varied annually (Merron 1991). An annual variation of less than 22% was found in communities in the Sokoto River in Nigeria (Chapman & Chapman 1993).

The TWINSPAN classification indicated distinct fish communities in particular habitats similar to the cluster analysis based on habitat characteristics. The range of fish communities from typically riverine to lacustrine forms was similar to those identified by Kok (1980). Hyslop (1988) found species diversity decreased after dam completion on the Sokoto river, Nigeria, which was attributed to both a restriction of natural migration patterns, and a decrease in nutrient transport (Bonneto *et al.* 1989). The fish communities on the Phongolo floodplain are only affected by these factors when artificial flood releases do not co-incide with natural flood regimes.

The fact that there are distinct communities in different habitat types is important for both conservation and management. It is imperative that the restricted habitat types on the floodplain (e.g. rocky riverine areas) be protected from degradation. An isolated community living in a specialised habitat type such as the rapids at the Phongolo River Bridge could be impacted negatively if there was insufficient water to sustain the fish or their breeding cycles. If a habitat type is lost it could result in the loss of a species.

According to Yant *et al* (1984), spatial and trophic resource partitioning are the primary mechanisms which facilitate co-existence in river systems. Several investigators have suggested that differential microhabitat use of limiting resources maintains coexistence in lotic fish assemblages. Grossman *et al* (1995) argue that spatial resource partitioning may not be important for co-existence in many stream fishes. Within the Okavango Delta, the major factor determining the distribution and abundance of fishes was habitat preference (Merron 1993). The permanence of water and the nature of its flow were found to be the principal ecological variables influencing the community structure. These factors, in turn, influence other physico-chemical parameters such as substrate type, extent of macrophytic growth, dissolved oxygen concentrations, temperature, conductivity, turbidity, etc, which in turn affect the distribution of the fishes.

Within the gradient occurring in the dendrograms (Figs. 9 & 10) from riverine to lacustrine, a greater diversity of fish species was found in the more hydrologically stable riverine environments (e.g. Lakes Sokhunti, Mzinyeni, Mandlankunzi), compared with the more unstable environments (e.g. Lakes Mhlolo, Khangazini, Shalala; Tables 6 & 7). Typical species present were *H. vittatus* and *L. rosae* which is similar to the findings in the Okavango system (Merron 1991). Similar species compositions can be attributed to greater habitat heterogeneity, resulting in a wider range of available habitat types. The availability of habitat types within lakes decreases with the decreasing water level, whereas in the larger riverine habitats there is either a continual base flow which maintains the microhabitats at a constant level, or the lakes are large enough so that evaporation does not have as dramatic an effect on the water level as in the smaller, shallower lakes.

Biomass was also used in the TWINSPAN analysis to indicate the differences between number and mass in terms of management. For conservation and ecological purposes, the abundance dendrogram would be useful in the grouping of lakes, whereas for fishery purposes, the biomass dendrogram would be more useful for determing total allowable catch of various habitats.

The communities of each lake have been grouped according to species diversity within each lake. Lakes with similar environmental variables may not necessarily be grouped together as communities can differ in species diversity in several ways (Bruton 1989). This would also explain the divisions in the community classification. The diverse communities may have a wider range of available resources than the less diverse communities, they may have fish species with narrower niches, they may differ in the degree of niche overlap, and they may differ in the extent to which the available resources are exploited (Bruton 1989). On the Phongolo floodplain it is likely that in the more diverse communities there is a greater range of resources available. These communities are likely to have a spread of life-history styles from altricial, generalised species to precocial, specialised species.

As with the Okavango system (Merron 1991), the major factor determining the distribution and abundance of fishes on the Phongolo floodplain appears to be habitat preferences, with physical characteristics playing an important role. Fishes with limited distributions such as *H. vittatus* were found in the more stable riverine environments due to their narrow tolerance limits and specific habitat requirements. The more ubiquitous fish species such as *C. gariepinus* and *O. mossambicus* were found in most habitat types, as they have broader tolerances and more flexible habitat requirements . The species inhabiting the more stable environments would tend to a more precocial life-history strategy compared to those in the unstable environments, which tend towards a more altricial life-history (Bruton 1989). Floodplain biotas are generally characterised by r-selected species (Lowe-McConnell 1975) with their ability to respond to favourable conditions through their high fecundity, rapid growth and early maturation (altricial characteristics) (Heeg & Kok 1988). But, in the Okavango, many of the typical non-guarding fishes (e.g. *H. vittatus*) exhibiting r-selected traits are habitat specialists with narrow niche tolerances (Merron 1991). The same is true for the Phongolo floodplain, where the majority of fishes tend towards altricial life-history strategies where the organisms respond to environmental changes. Management of the fishery should therefore take the life-history strategies into consideration.

Flood manipulation using GIS

Figure 11 indicates the rivers and lakes of the Phongolo floodplain and their contour levels at 20 m intervals. Superimposed on the map are the shaded contour levels, giving an indication of the various flood levels (Fig. 11). The flood level up to 20 m is insignificant in the area that it inundates (<25% MRL). The flood level up to 40 m correlates to a flood release of approximately 100 $m^3.s^{-1}$ for a duration of 5 days (75% MRL) (based on the Department of Water Affairs & Forestry data). The flood level up to the 60 m contour level correlates to a flood of approximately 350 $m^3.s^{-1}$ for 5 days

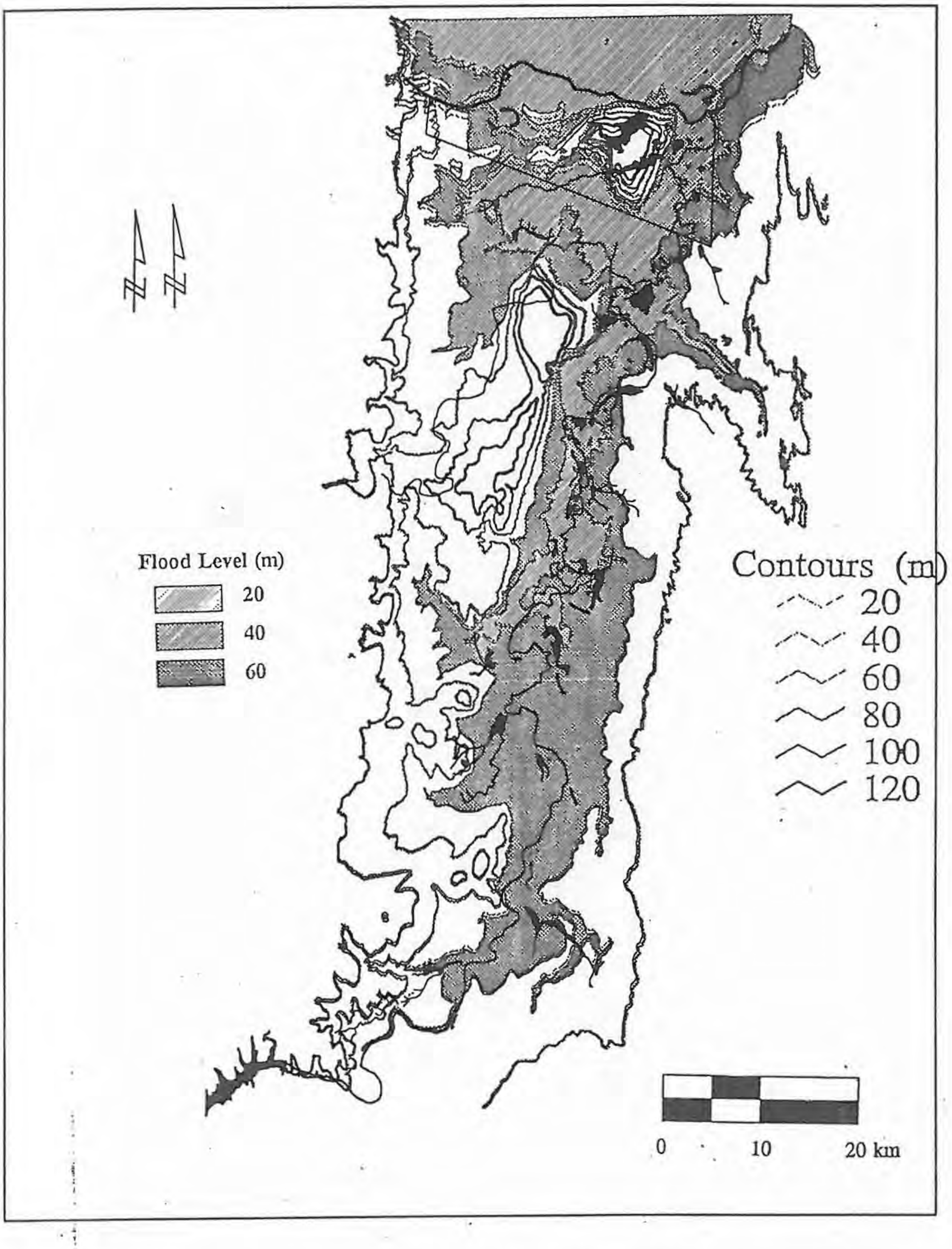

Figure 11. Flood levels of various magnitudes on the Phongolo floodplain.

(100% MRL). The latter is the approximate size of flood releases which was experienced during the surveys. Subsistence agriculture took place up to the 40 m contour line in pre-flood conditions .

Discussion

The GIS maps serve to graphically illustrate various flood release scenarios, which will ultimately aid in the management of the fishery. Flood levels using the contour lines give an indication of the extent of inundation on the floodplain, and the effect on the lakes. These maps have been based on 1:50 000 maps produced in 1985, and are therefore not 100% accurate, as the floodplain continually changes in shape, due to scouring, agriculture, sedimentation, etc. The maps do give an approximate indication of the inundation levels.

For the actual floodplain to be maintained as near to the natural conditions as possible, there should only be agricultural land above the 60 m contour line, which is above the mean retention level (MRL) of most of the lakes. This will ensure that the levees and riverine vegetation are conserved. The levees are important as a stable levee ensures a stable lake; the vegetation covering the levee attenuates water flow once the river breaks the banks and therefore prevents scouring of levees.

During flooding, the opportunity for fishes to invade the lakes should be increased with an increase in duration of the river-lake connection (Halyk & Balon 1983). This will depend on the length of time of flood release.

The GIS will aid in the recovery of the natural flood regime which is important to the natural functioning of the floodplain ecosystem. In most large river systems, the natural functions of large river floodplains have practically disappeared due to modifications that prevent regular, timely flood releases (Bayley 1995).

The duration and timing of the flood releases ties in with the flood-pulse concept (Bayley 1995) as the amount and type of allochthonous input will be affected. The rates of rise and fall of the flood waters can therefore be expected to influence fish production. Fast rates limit the time the fish can spend on the floodplain for breeding, etc., and low rates limit the extent to which the floodplain is inundated. Fish production will also be affected by the time of year that the floods are released.

The biological integrity of floodplain ecosystems is affected primarily by water sediment quality and sediment flows that shape the river channel and floodplains (Sparks 1995), which influences habitat structures, the trophic base and biotic interactions. When water is released during the winter, the floodplain is exposed when fish require access to shallow spawning areas, and then inundated when plants such as the *Cynodon* sp. lawns should be growing on the mud flats. These lawns would then be drowned in what would normally be their growing season. This also effects hippopotami which normally graze the lawns and then defaecate in the water, importing nutrients from a terrestrial ecosystem to an aquatic one. These factors have a negative influence on nutrient input into the lakes, effecting fish productivity.

For the flood releases, the amount of water (in 1980) required to maintain the floodplain at MRL was estimated at 26 x 10^6 m^3 y^{-1} (Heeg *et al* 1980). This was based on an annual evaporation rate of 2000 mm y^{-1} and rainfall of 600 mm y^{-1}. The productivity of the floodplain depends on the inundation of the whole area between levees and the adjoining high ground for a reasonable period of time. This would require a further 100 x 10^6 m^3 y^{-1}. Despite this, a relatively small flood release up to the 40 m contour line will maintain some of the ecological processes within the lakes at the northern end of the floodplain.

Application of the model

To answer the initial question : Yes, an ecological model can be developed for the Phongolo floodplain. For the purpose of resource management on the Phongolo floodplain, the model which has been developed can be applied to test the following suggestions:

Based on previous research and suggestions, water releases should be as close to the natural flood regime as possible. Once this has been established, floods of various levels can be simulated. For example, a flood of 100 $m^3.s^{-1}$ for 5 days will flood mostly the northern areas of the floodplain, resulting in most of the lakes being inundated. Most of the southern lakes will only flood at higher levels as they have higher levees.

At a flood of this level, or higher, 100% inundation will be assumed, therefore at MRL for a lake such as Sokhunti, it will be filled to 101 ha of surface area, of which on average, 17% is littoral and

83% is limnetic (Table 10). Therefore, a total potential yield for the lake can be estimated at 1 352.5 kg per annum. The typical species composition at the lake can be expected to be comprised of 25% *G. callidus*, 22% *T. sparrmanii* and 16% *T. rendalli* by number in the littoral zone (Table 6), and 60% *B. imberi* and 22% *S. intermedius* by number in the limnetic zone (Table 7).

This is just one example, but the model could be applied to any of the lakes on the floodplain. This information is useful in the maintenance of the ecological functioning of the floodplain ecosystem. For fisheries management the actual yield of the subsistence fishery needs to be calculated. There have been several attempts to determine this yield, but the fishery is widely dispersed on the floodplain and it is difficult to obtain accurate estimates. Based on calculations by van der Waal (1991), the following analysis has been derived: approximately 35% of the people fish for their own consumption on the floodplain (R. Holtzhausen *pers comm* 1995), and it is assumed that enough fish is caught for one meal each day by a fisherman. On average, approximately 600 g of fish was caught for a meal. 600 g was estimated as the average based on *isifonya* drives, hook-and-line fishing, gill netting and sack seining (Merron & Weldrick 1994). If there are 35 000 people (population estimated at 100 000) fishing for 40 days a year, 840 000 kg of fish is removed annually. The total surface area of the floodplain at MRL is 2 700 ha. The annual harvest would be 350 $kg.ha^{-1}.y^{-1}$. This is likely to be an overestimation of the actual harvest.

The potential sustainable yield has been estimated at 39.0 tonnes of fish, an annual harvest of 14.5 $kg.ha^{-1}.y^{-1}$. The total potential biomass and yield can be predicted for various flood release options, which would result in different levels of the floodplain being inundated (Table 13). These values can be broken down for the various lakes if required.

Table 13. Predicted biomass and yield values for various flood levels.

Flood level	Biomass ($tonnes.y^{-1}$)	Yield ($tonnes.y^{-1}$)
100% MRL (2 700 ha)	118.2	39.4
50% MRL (1 350 ha)	59.1	19.7
33% MRL (900 ha)	39.3	13.1
25% MRL (675 ha)	29.7	9.9

Based on the estimated harvest of 350 $kg.ha^{-1}.y^{-1}$, and the potential sustainable yield of 14.5 $kg.ha^{-1}.y^{-1}$, the subsistence fishery is not being fished sustainably. There is a 24 fold difference between estimated harvest and the potential sustainable yield, indicating that severe overfishing is occuring on the floodplain. This difference serves to illustrate the importance of determing the actual harvest for incorporation into the ecological model. Ultimately the fishery in Mocambique should also be quantified as is is likely to effect recruitment of fishes into the Phongolo floodplain waterbodies. It is likely that if fishing on the Phongolo floodplain is continued at the same effort, and fishing on the floodplain in Mocambique is increased, then the entire fishery will become depleted.

The calculated values are reliable biomass estimates of the fishery on the Phongolo floodplain as the sampling period covered both drought and flood conditions and sampling was carried out in all possible habitat types on the floodplain. But, the estimates must be viewed as flexible to take the dynamics of the floodplain into account, e.g. recruitment is not likely to be the same on an annual basis, and yield is effected by the previous flood history (Welcomme 1979). The accuaracy of the yield estimates could have been improved with replicate samples, but this was not possible due to time constraints. These biomass and yield values were calculated for one flood per year, and it is possible that the yield would decrease during drought periods and increase with more than one flood in the summer months, for example a flood in September and a flood in March of the following year. It is possible that these estimates could be used a a basis for determining sustainability of the fishery, provided that resource managers view them as flexible.

CHAPTER 6. GENERAL DISCUSSION

It is more efficient and practical to maintain necessary data for the model in a tabular format, rather than incorporating all the information into a GIS. For example, the data in Table 8 of the potential yields can be easily updated and more information can readily be incorporated.

The model is not 100% accurate, but the estimations of species compositions and potential sustainable yields together with the GIS predictions of various flood release options provide a good basis whereby management recommendations can be made.

It must be acknowledged that for the model to be operative, several assumptions were made. The most important assumptions were that lakes will always flood to mean retention level, the species potential yield is based on the average number, and the species composition is relatively stable.

On the Phongolo floodplain, not all the lakes are inundated at a particular flood release, as the levees have different levels. Several of the levees have changed substantially in the last 10 years with encroaching agriculture and increased sedimentation. If the lakes have not received water for a certain period, it is likely that they will not flood to MRL as underground aquifers will initially need to be recharged. If they do flood to the MRL, then it is likely that the model will aid in resource management. To overcome this, the duration of the flood release would have to be increased.

Although the calculated potential yields for the fishery are based on an average for the entire sampling period, and then calculated per annum, they will give a relatively good indication of the likely yields in the lakes. The reason for this is that the sampling period spanned a period of drought, during which several of the lakes were in the final stages of dry-down, and two flood releases. All the likely environmental scenarios have therefore been encountered. These potential yield values are generalisations; they should not be applied in isolation to the fishery but all the factors affecting the ecosystem should be taken into consideration.

The species composition has also been based on an average for the entire sampling period. Although the species compositions of the fish within the floodplain habitats change with the fluctuating water levels (while the lakes are at least 50% full) it is likely that the fish communities will be similar to those indicated. It is known that as the lakes become fuller, there is an increase in species diversity, which gradually decreases as the water level recedes, until during the final stages of dry-down, the dominant species are *O. mossambicus* and *C. gariepinus* (Merron *et al* 1993).

Many fisheries models are derived from an assumption that exploitation is at maximum sustainable yield level, but these models do not take the influence of community structure, life history and reproductive styles into account (Watson & Balon 1984). These are different in relatively mature ecosystems compared to those in the process of recolonisation, with the latter ecosystems comprising primarily altricial generalists compared to the more mature ecosystems which tend towards precocial specialists (Bruton 1989). This ecological model has the capacity to be flexible and to include as many variables as possible.

Many of the Phongolo fishes have a high production capacity and are likely to withstand high fishing pressures (Merron & Weldrick 1994) by altering their breeding styles. The less tolerant fish species of the continually fluctuating environment are less able to adapt to the increased fishing pressure and are more vulnerable to exploitation. This should be taken into account in the management of the fishery with the use of this model.

On the Phongolo floodplain, as with most river systems (Gore & Shields 1995), it is likely that the floodplain cannot be truly restored, but management can aim towards maximising future sustainability. Riverine ecosystems are remarkably resilient in their ability to recover from physical disturbances (Gore & Shields 1995). This has been well documented on the Phongolo floodplain, and is summarised by Merron & Weldrick (1994). If there is disturbance of the ecosystem, such as the continued disruption of the natural flood regime, the ecological integrity cannot be maintained.

Riparian zones are often degraded by erosion and encroachment. The altering of the levees and riparian vegetation to enhance agricultural productivity on the rich alluvial soils eliminates the benefits of the flood-pulse to the fisheries in the remaining environment (Spark 1995). The levees can no longer act as buffers during floods, and the lateral sediment transport will be affected, resulting in other lakes filling more rapidly, and becoming shallower. Therefore, the stability and sustained function of river-floodplain ecosystems is dependent on the maintenance of the watershed and floodplain. Each contributes to the physical and biological interactions that define the productivity of these systems (Sparks *et al* 1990). Although it has been strongly contended by Derman & Poultney (1985) that agricultural and domestic efforts far outweigh the benefits of fresh protein in the form of fish to the people of the Phongolo floodplain, it is likely that this alteration of the environment will only benefit agriculture in the short term, as it is not likely to be sustainable.

This working model should aid in the implementation of an integrated management programme, with the principal goal of sustainability. A holistic approach is fundamental, as the approach of compartmentalising the floodplain to optimise management for a particular group of animals can become contentious and controversial (Sparks 1995). Ecosystem management should aim to maintain or recover the biological integrity of the ecosystem (Sparks 1995). Biological integrity can be defined as 'the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity and functional organisation comparable to that of the natural habitat' (Angermeir & Karr 1994). The Phongolo floodplain, as with most other floodplains (Merron 1993) should be managed sustainably, so that the biodiversity within the system is conserved and the essential ecological processes of flooding and draining are retained.

CHAPTER 7. CONCLUSIONS AND FUTURE RECOMMENDATIONS

This ecological model will aid in the integrated management of the Phongolo floodplain as it is practical and can be readily updated. The relative abundance, biomass and species compositions of fishes at each of the lakes and the community classification of fishes within the habitats on the Phongolo floodplain give an accurate description of the potential fishery for the purpose of management. The potential yields of the fishes within the lakes are valuable estimates which can be compared to the actual harvests from the subsistence fishery. The subsistence fishery can then be modified to ensure the sustainability of the fish resource. The community classification can be used to group lakes with similar habitats and fish communities together. The GIS can be used to graphically illustrate various flood release scenarios. When all aspects of the model are used, the most beneficial water release scenario for the fishery can be determined. Other important parameters should also be incorporated into the model: the actual harvest from the subsistence fishery has not previously been accurately estimated. This information is crucial to the efficient management of the fishery to ensure sustainability. Natural mortality in the floodplain fishery should be incorporated into the model as it is an important factor, ultimately affecting the harvestable resource of the fishery. Agriculture, township development, water supply, vegetation, soils, water usage, etc. should be incorporated into the GIS. These variables are ultimately affected by flood releases from the Pongolapoort Dam. Actual flood levels should be determined to replace those estimated using contours which will enhance the accuracy of the model. The biology and ecology of all of the small fish species collected should be determined, which will further contribute to an the understanding of the ecosystem.

The fishery is not the only consideration on the Phongolo floodplain as there are several utilisers of the resources. Agricultural, social and economic information can also be efficiently incorporated into the model, thus facilitating a more holistic approach to the management of the floodplain. The incorporation of this information into the existing model will provide a more accurate basis for the integrated management of the Phongolo floodplain.

The model (summarised in Fig. 12), although developed for the Phongolo floodplain in particular, has applications for several other floodplain ecosystems, provided that the assumptions made are noted. The principles governing most southern African ecosystems are the same, with several utilisers of the limited natural resources. The model could be applied to these systems in an attempt to promote sustainable utilisation, and holistic management.

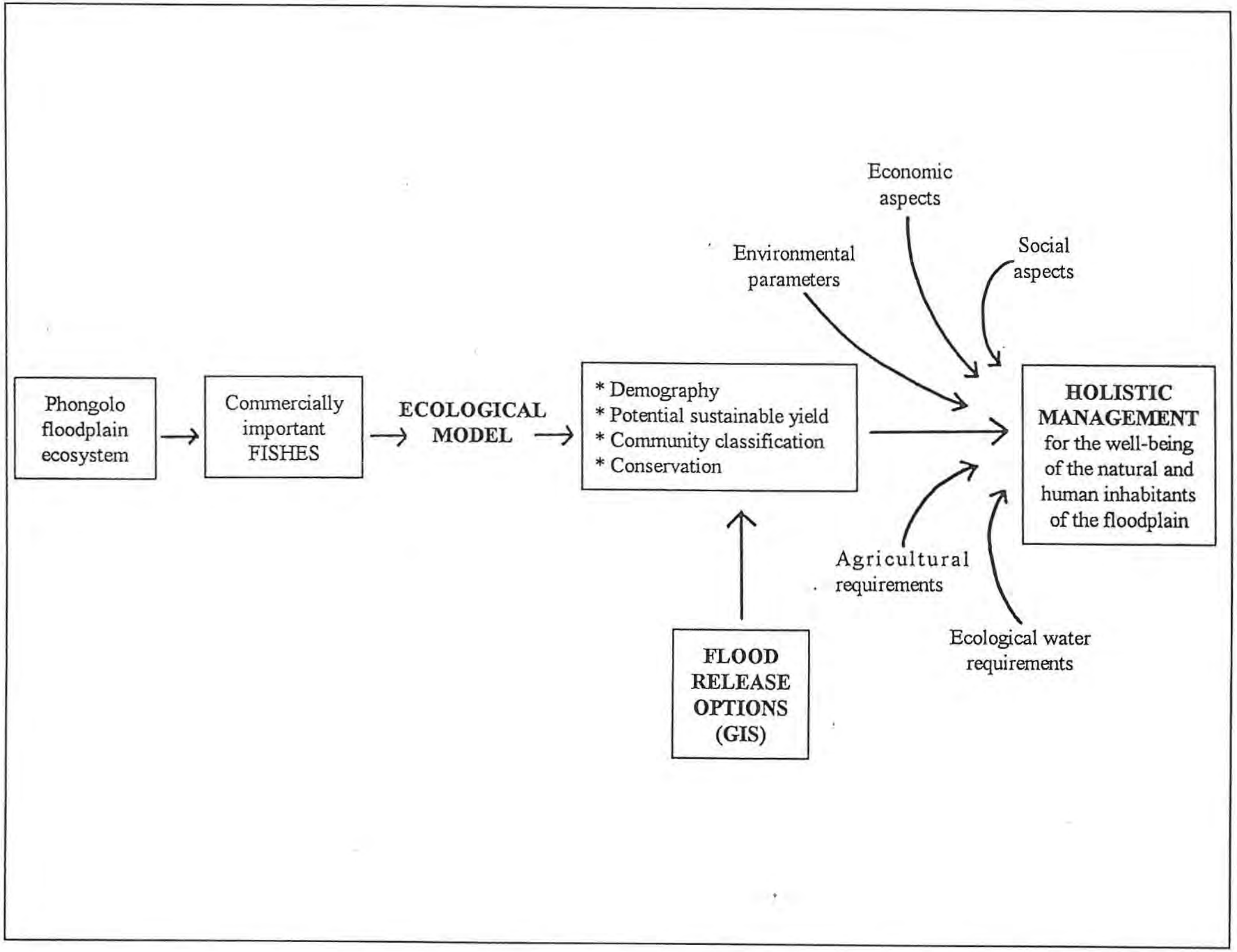

Figure 12. Flow chart illustrating the ecological model of the Phongolo floodplain.

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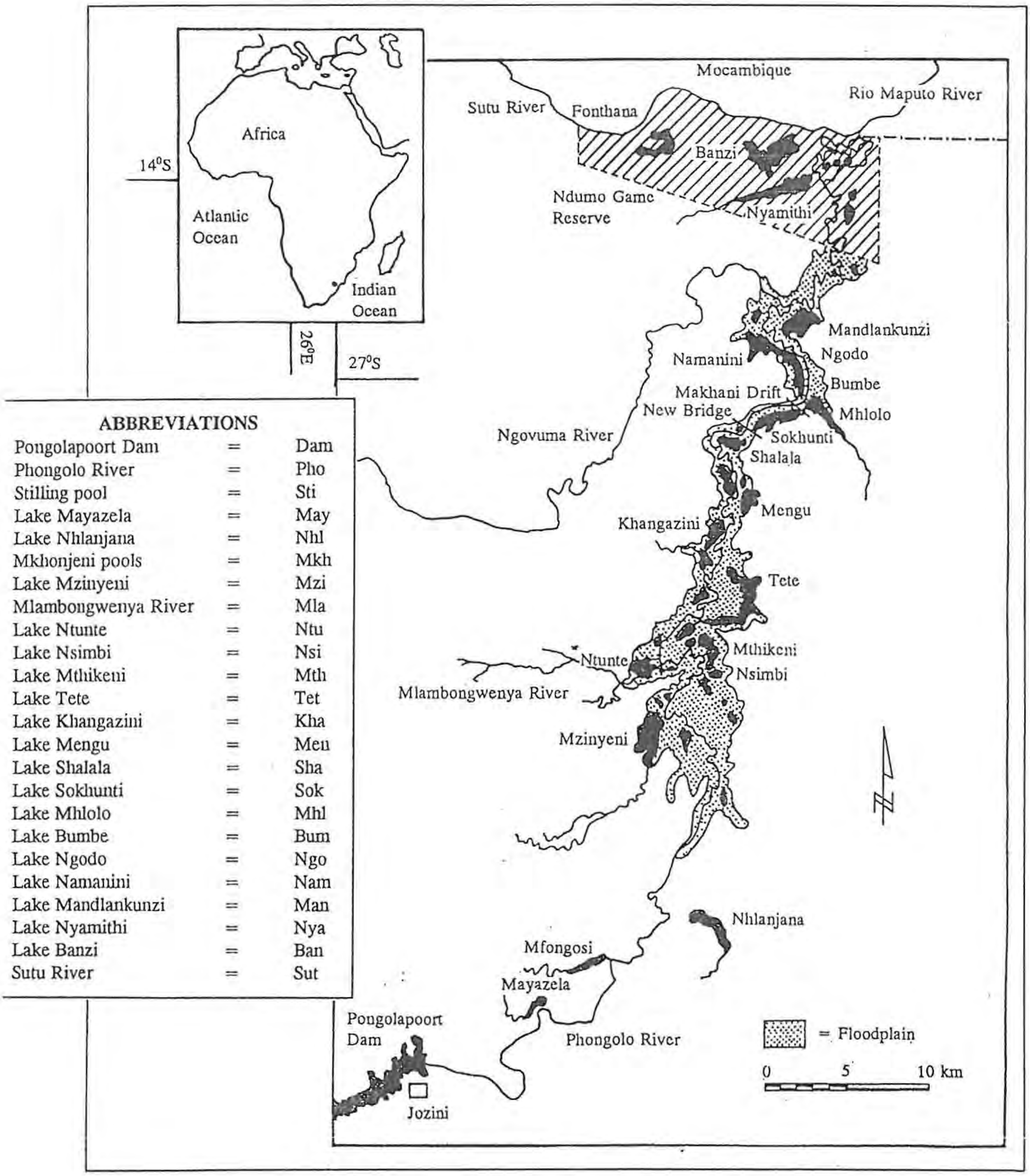
CHAPTER 9. APPENDIX 1



ABBREVIATIONS

Pongolapoort Dam	=	Dam
Phongolo River	=	Pho
Stilling pool	=	Sti
Lake Mayazela	=	May
Lake Nhlanjana	=	Nhl
Mkhonjeni pools	=	Mkh
Lake Mzinyeni	=	Mzi
Mlambongwenya River	=	Mla
Lake Ntunte	=	Ntu
Lake Nsimbi	=	Nsi
Lake Mthikeni	=	Mth
Lake Tete	=	Tet
Lake Khangazini	=	Kha
Lake Mengu	=	Men
Lake Shalala	=	Sha
Lake Sokhunti	=	Sok
Lake Mhlolo	=	Mhl
Lake Bumbe	=	Bum
Lake Ngodo	=	Ngo
Lake Namanini	=	Nam
Lake Mandlankunzi	=	Man
Lake Nyamithi	=	Nya
Lake Banzi	=	Ban
Sutu River	=	Sut

Figure 3. Map of the Phongolo floodplain (after Kok 1980, Heeg & Breen 1994).