THE BIOPHYSICAL DYNAMICS OF THE LOWER SHIRE RIVER FLOODPLAIN FISHERIES IN MALAWI

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by

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To my family – Linda, Tayamika and Davison

‘……what is common to many aquatic environments is our lack of understanding of the detailed nature and functioning of the relevant ecosystems…’

Charles (2001: p. 34)

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ABSTRACT

Fishes of African floodplains typically comprise populations having short life cycles, relatively few age groups, more generalised feeding behaviour, and which experience spawning success that is strongly influenced by abiotic factors such as hydrological regime of the river, climatic seasonality and habitat characteristics. In addition, African river-floodplain ecosystems do not have appropriate predictive models for estimating yield in these ecosystems. While most predictive models developed to date for floodplain fisheries have taken into account morpho-edaphic factors, they have generally excluded climatic factors as a mega-determinant of the variability of floodplain fisheries.

The principle aim of this thesis has been to develop a predictive management model that incorporates data on essential biological aspects of the target species, characteristics of the habitat as well as overall climatic factors, and thus allow for adaptive management of the fisheries in a continuously fluctuating floodplain environment. Lower Shire Floodplain (34 ^{0} 45’ – 35 ^{0} E and 16 ^{0} 00’-17 ^{0} 15’ S) in Malawi, one of the major rivers-floodplains in the Zambezi Basin, was used to test this type of model. The major hypothesis tested in this study was that “the dynamics of the fishery of Lower Shire Floodplain are driven by and adapted to the seasonal, but predictable, hydro-climatic regime of the floodplain”. The specific objectives were: to describe the floodplain’s climate and hydrological pattern; to develop a quantitative characterisation of the major habitats of the Lower Shire Floodplain; to assess the fishery in terms of size, gear utilisation, gear selectivity and yield; to assess the biological parameters of the target species, necessary for the management of the fishery; to analyse how water fluctuation in the floodplain affects the recruitment and life history of the two target species; and to develop of a predictive hydro-climatic model to benefit the management of the fisheries.

The climate of the floodplain was characterised by low (765 ± 198 mm) and fairly variable (C_v = 27%) rainfall, which largely occurred between December and January. The area was generally humid (mean RH 68%), with mild to hot (25- 33ºC) and variable monthly mean diurnal (12ºC) temperature. Four quarterly hydro-climatic seasons were identified and comprised: Quarter 1 (Jul-Sep) characterised by hot, dry

weather with a low flood regime; Quarter 2 (Oct-Dec) hot, windy, wet weather with low-but-rising flood regime; Quarter 3 (Jan-Mar) hot humid, wet weather with the flood regime at peak; and Quarter 4 (Apr-Jun) humid and cool weather with receding flood regime. The annual hydrograph of the floodplain was represented by four categories of flood regime as: low (Jul-Sept), low-but-rising (Oct-Dec), peak (Jan-Mar), and falling (Apr-Jun). The floodplain experienced a water deficit of 95.1 mm.year^{-1}, and it was hypothesised that ground water recharge maintained water in the floodplain the rest of the year.

Three major habitats were identified in the floodplain. The river-floodplain, characterised by deep fast-flowing water, sandy substrate and little emergent vegetation; the permanently connected lagoons, were shallow ($\leq$ 2 m) with sandy-mud bottom and slow flowing water; and the seasonally connected lagoons had slow-flowing stagnant water, with comparatively more emergent and floating vegetation. Physicochemical characteristics of the habitats varied significantly with hydro-climatic seasons (one-way ANOVA, $p \leq 0.05$), indicating the influence of flood regime, which joined the habitats in a non-equilibrial spatial distribution. Consequently, during receding and low flood regimes river-floodplain and permanently connected lagoons exhibited similar characteristics while all three habitats had similar characteristics during the rising and peak flood regimes. It was, therefore, concluded that in floodplains, habitats shift horizontally and vertically according to the water level.

Gill nets, cast nets, long line, and fish traps accounted for 99% of the total count of gears, and hence considered the major fishing sectors. Two principal species in the floodplain were the catfish *Clarias gariepinus* and the cichlid *Oreochromis mossambicus*. Length-at-maximum-selectivity (ϕ) and length-at-50%-sexual-maturity (L_{m50}) for each of the two species showed that although they were selected into the four fishing sectors at lengths above maturity, maximum selectivity into the long line occurred at a length before maturity for *O. mossambicus*. In addition, the width of the gamma selectivity function (σ) indicated that a considerable proportion of juveniles of the two species were also selected. Therefore, it was decided that management for the floodplain be centred on controlling over-fishing and preserving the spawner

stock, by banning seine and mosquito nets, and closing river-floodplain and permanently connected lagoons to fishing during the low flood regime. There were significant seasonal variations in CPUE, lowest in the low flood, and highest during the peak flood regime.

Sectioned otoliths were used to determine the age and growth of the two principal species in the floodplain. Marginal zone analysis revealed that annulus formation in all the species occurred during the period of low air and water temperatures, high evaporation and receding water levels, hence a high rate of desiccation and negative water budget. For *O. mossambicus,* maximum age reached was 6 years while in *C. gariepinus* it was 9 years. The 3-parameter von Bertalanffy growth model adequately described growth as $l_t = 177.6\left(1-e^{-0.44(t+1.43)}\right)$ mm TL for *O. mossambicus* and $l_t = 502.9\left(1-e^{-0.31(t+1.92)}\right)$ mm TL for *C. gariepinus*. Female *O. mossambicus* reached 50%-sexual-maturity at 109 mm SL, while males matured at 105 mm, and both male and female *C. gariepinus* reached Lm_{50} at 249 mm SL. The breeding seasons of both *O. mossambicus* and *Clarias gariepinus* were between September and March, with modal peaks in January and November, respectively. The annual total mortality rates (Z) were 0.62 ± 0.18 yr^{-1} for *O. mossambicus* and 0.93 ± 0.47 yr^{-1} for *C. gariepinus*. The mean empirical estimates of natural mortality (M) were 0.46 yr^{-1} for *O. mossambicus* and 0.50 $year^{-1}$ for *C. gariepinus*, and fishing mortality (F) was calculated as 0.16 yr^{-1} for *O. mossambicus* and 0.43 yr^{-1} for *C. gariepinus*. The overall exploitation level (Z/K) was 1.41 for *O. mossambicus* and 3.01 for *C. gariepinus*. Given that the Z/K ratio was >1, it was asserted that both *O. mossambicus* and *C. gariepinus* were mortality-dominated and fairly heavily exploited. However, potential for sustainable exploitation existed since both species showed signs of resilience due short longevity and high rate of natural mortality.

Given the limitation of simple exponential models of fish mortality and growth under the situation of seasonal fluctuation of water levels, a simple predictive hydro-climatic-fisheries model was developed. The model predicted the life-history and production parameters fairly accurately ($0.53 \leq r^2 \geq 0.98$, $p \leq 0.05$), and showed that environmental and biological events in the floodplain significantly ($0.43 \leq r^2 \geq 0.91$, $p \leq 0.05$) followed the periodic function of time (day-of-the-year), hence, strongly seasonal. In addition, the flood-pulse preceded all the major biological events, with predicted phase lags established at 55.6° for peak flood, 157.2°, 260.1°, 334.6° and 341.4° for condition factor for *O. mossambicus*, recruitment, spawning period for *O. mossambicus* and *C. gariepinus*, respectively. Therefore, it was recommended that water obstruction on the Shire River must ensure sufficient water flow during the peak flood and spawning period to allow flooding and inundation of the floodplain in order to create habitat favourable for spawning and feeding as well as improve recruitment.

Chapter 1

General Introduction

The aim of fisheries management is to obtain the maximum (or optimum) sustained yield of fish from a water body without depleting the capital (standing stock or biomass) (Lowe-McConnell 1987), thereby promoting sustainable economic and social well-being of the harvesting fisheries (Hilborn & Walter 1992). While the fertile floodplains of the Nile formed nuclei for early civilisation in Africa (Welcomme 1985), the importance for their aquatic life was only recognised by science just over a century ago (Forbes 1895, cited in Bayley 1991).

Unlike lake fish populations where the environment is stable, in floodplain fisheries the populations are heavily influenced by abiotic environmental factors such as flooding (Welcomme 2001). For proper management of floodplain fisheries, the extent and duration of flooding must, therefore, be taken into account (Botnariuc 1968, Welcomme 1985). Also, the floodplain cannot be considered in isolation but must be treated as an integral part of a larger system (Welcomme 1979, Botnariuc 1967 cited by Welcomme 1985, Bayley 1981 & 1991, Payne 1986). In addition to knowledge of the physical dynamics of a floodplain, proper management of the system’s fisheries also requires an understanding of the biology, life history and distribution of the target species (King 1995).

Since riparian communities have generally exploited river-floodplain fisheries in Africa for centuries, it is important to develop scientifically sound quantitative methods and models that allow for adaptive management. Ultimately, these methods must embrace the new vision for management, which focuses on science-based decision-making tools, while allowing the local riparian communities the responsibility to utilise and manage the fisheries sustainably (Welcomme 2001). Such management incorporates response of the stock to changes in abiotic variables such as climate and hydrology, as well as natural mortality and fishing mortality. Thus, before contemplating the adoption of suitable models in the Lower Shire Floodplain in Malawi, the nature and dynamics of the floodplain and its fisheries must be understood and taken into account.

African river-floodplain fisheries

Seventeen major floodplains have been recorded in Africa, covering an estimated area of 196,000 km^2 at peak floods (Welcomme 1985). Yields in tropical African floodplains have been reported to be lower (154.4±198.7 $kg.ha^{-1}.yr^{-1}$) than those in the temperate region (205.0±300.3 $kg.ha^{-1}.yr^{-1}$) (Welcomme 1985). No specific explanation has been put forward regarding the apparent low productivity of African floodplains. There have been major attempts in the past by Blanc *et al*. (1955, cited by Welcomme 1985), Welcomme (1972 & 1985), Jackson (1961 & 1963), Bell-Cross (1968), Carey (1971), Chapman *et al.* (1971), University of Michigan (1971), Kapetsky (1974), Willoughby & Tweddle (1978), Bruton & Jackson (1983) and Merron (1991) to study the floodplains of Niger, Nile, Okavango and Kafue. However, only minor studies have been carried out in the Zaire, Shire and the Zambezi, such that data on catch and biology of the fish are scanty. In essence, since 1985, little has been published on tropical African floodplains. Management of most African floodplain fisheries has, therefore, not been guided by scientific knowledge. The fact that there are bound to be differences in floodplains depending on the systems, and that the available information on other African floodplain fisheries may not be satisfactory for Malawi to develop a management strategy for the Lower Shire Floodplain, points to the need to understand the pattern in which the floodplain operates.

Location and characteristics of the Shire River and the Lower Shire Floodplain System

The Shire River is the only outlet from Lake Malawi (35º15'E and 14º25'S) from which it meanders southwards for a distance of approximately 700 km to its confluence with the Zambezi River (35º20'E and 17º50'S). About 95% of the Shire River is situated in Malawi and the rest in Mozambique. The Shire is generally divided into three sections, the upper, middle and lower sections (Pike 1972, Cantrell 1977, Tweddle *et al*. 1979) (Figure 1.1).

The Upper Shire is the stretch from the outlet from Lake Malawi and Lake Malombe (35º10' -35º15'E and 14º26'-14º42'S). The Shire River flows from the southern tip of the south-east arm of Lake Malawi at approximately 468 meters above sea level (m.a.s.l.), across a submerged sand bar, 4 km north of Mangochi town (Figure 1.2a). Fifteen kilometres from Lake Malawi the Shire River flows into Lake Malombe (29 km long and 14.5 km wide) (Pike 1972). The section is characterised by low-lying sand banks.

The Middle Shire stretches from the outlet from Lake Malombe to Kapichila Falls, where the Kapichila hydroelectric dam is situated (34º50'-35º10'E and 14º40'-15º29'S). The river flows from Lake Malombe southeast, then south into Liwonde National Park for about 30 km up to the Liwonde Barrage (Pike 1972) (Figure 1.2b). This forms the first section of the Middle Shire. This portion of the river has low banks and two major tributaries, the Likuzi and the Kavunguti Rivers. During the rainy season this section of the Middle Shire breaks its levees to form Likuzi and Kavunguti swamps. The second section of the Middle Shire is approximately 50 km long, stretching from the Liwonde Barrage to Matope Bridge. The river meanders over a fairly flat terrain with a number of small rapids. In this section there is only one major tributary, the Rivi Rivi. The third section of the Middle Shire stretches for a distance of approximately 80 km, between Matope Bridge and Kapichila Falls (Pike 1972) (Figure 1.2c). This section of the Shire drops into a gorge, characterised by 10 rapids and 5 falls (Tweddle & Willoughby 1979), and falls by approximately 384 m in altitude (Pike 1972). The two major tributaries in this section are the Wamkurumadzi and the Khongodzi.

The Lower Shire extends from the Kapichila Falls to the end of Ndindi Marsh on the border with Mozambique (34º50'-35º17'E and 15º29'-17º05'S). Its boundaries are well defined by dominant physical features. To the east it is bordered by the intensely eroded Thyolo Mountains; to the north by the Kapichila Falls; to the west, by low-lying hills that include the southern-most end of the Kirk Range; and in the southwest by the Matandwe and Namalombo hills extending south from Bangula. Here, the floodplain system is characterised mainly by the Elephant, Eastern and Ndindi Marshes.

The Kapichila Falls marks the boundary between the Middle Shire and Lower Shire. The Kapichila Falls and the Middle Shire rapids and falls are recognised as environmental and ecological barriers to the upstream migration of the Lower Zambezi fauna (Tweddle & Willoughby 1979). The Lower Shire falls in altitude from about 107 m.a.s.l. at Chikwawa to 61 m.a.s.l. at Nsanje, where the Shire enters Mozambique (SVADD 1975). The river meanders in this section, frequently changing course through the Lower Shire Floodplain, forming oxbow lakes, lagoons and islands (Figure 1.2d).

Below the Kapichila Falls, the Shire is dominated by the Elephant, Eastern and Ndindi Marshes and flows to its confluence with the Lower Zambezi River for a distance of 200 km. The Elephant, Eastern and Ndindi marshes occur at approximately 60 m.a.s.l. The Elephant Marsh extends from southeast of SUCOMA Sugar Estates (34º45'-35º12'E and 15º59'-16º40'S) to Chiromo (Shire/Ruo confluence) covering a total area of 473–500 km^2. The Eastern Marsh (35º09'-35º20'E and 17˚45'S) situated below the Shire/Ruo confluence, on the Mozambique side of the river, covers an area of approximately 200 km^2. The Ndindi Marshes (35˚16'E-17˚55'S) stretch to the border with and into Mozambique, covering an estimated area of 150 km^2 on the Malawi side, and an estimated 200 km^2 on the Mozambique side (see Figure 2.1, Chapter 2).

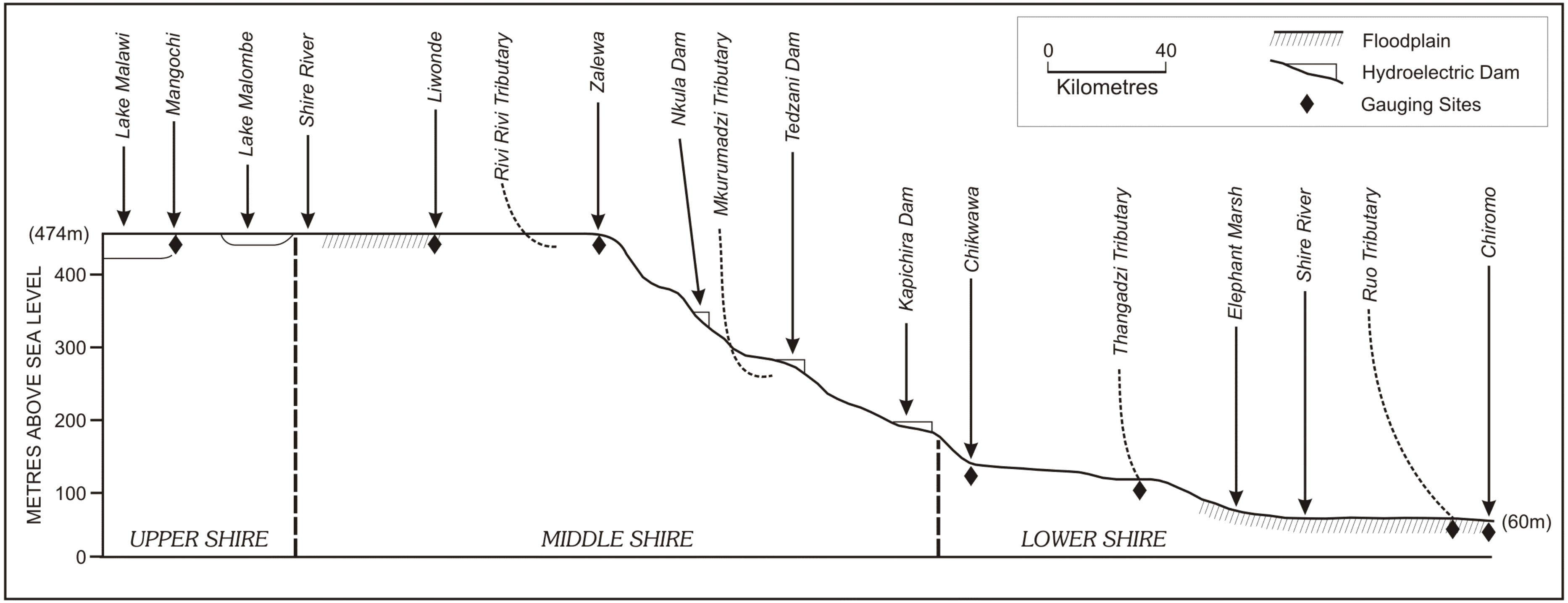


Figure 1.1. The Profile of the Shire River from the source in Lake Malawi to the Lower Shire Floodplain, showing the upper, middle and lower sections, major tributaries, gauging stations, hydroelectric dams and floodplains.

Figure 1.2 Aerial and ground pictures of various sections of the Shire River showing (a) the source of the Shire at the south-east arm of Lake Malawi (upper Shire), (b) the Liwonde barrage (middle Shire) with the barrage gates closed, (c) the border between middle and lower Shire, showing the section where the river drops in altitude through a series of falls and rapids, (d) the lower Shire section, showing the meandering and swamps.

From the border with Mozambique, the Shire (or Chire as it is known in Mozambique) forms a series of lakes and swamps, covering an estimated area of 350 km^2. The Shire River finally flows into the confluence with the Zambezi River near Mutarara.

The Lower Shire Floodplain, one of the seventeen major floodplains in Africa, directly benefits an estimated 1 million people in riparian communities in Malawi and Mozambique,. It covers an estimated area of 1100 km^2 of which approximately 650-700 km^2 are in Malawi and 400-450 km^2 are in Mozambique. The floodplain is the source of approximately 11% of Malawi's fish catch (Malawi Department of Fisheries 1989; Bulirani *et al.* 1999), 70% of irrigation water for the country's sugar plantations, and grazing land for about 80% of the country's livestock production (Kalowekamo 2000). Hydroelectric power stations on the Shire River supply all Malawi's electricity, while about 75% of the population along the Lower Shire Valley are engaged in fishing (Kashau & Chimatiro 1997, Chimatiro & Mwale 1998).

The increase in the number of uses, such as irrigation and hydroelectricity generation is putting pressure on many of the world's river floodplains (Welcomme 1985, Bayley 1991). The Shire River in Malawi is no exception. The construction of Liwonde barrage in 1965; the three hydroelectric dams (Nkula 1966, Tedzani 1972 and Kapichila 1999) (Hastings 1973, Karua pers. Comm.), a 75% increase of urban water demand, and siltation of up to 1 metre.year^{-1} in the Shire River (Sibande 2001) has put pressure on the fisheries resources of the Lower Shire Floodplain. This is happening at the same time as the fisheries of the floodplains face increasing fishing effort and infestation of water hyacinth *(Eichhornia crassipes)* (Harley 1991, Terry 1991, Tweddle *et al.* 1994, Chimatiro & Mwale 1998). Since the sustainable utilisation and management of the floodplain is a high priority of the Government of Malawi (Malawi Government 1997, 2001), there is a need to develop appropriate methods for predicting the impact of climatic, hydrological and anthropogenic changes on the fisheries, as well as a need to develop methods for the rapid assessment of the status of the fisheries.

General characteristics of river-floodplain fisheries

A number of factors, which characterise the complexity of river-floodplains, have been identified (Bonetto et al. 1969, Lowe-McConnell 1979, Welcomme 1979, 1985, 2001, Bayley 1981, Goulding 1981, Holland *et al.* 1983, Payne 1986, Kolding 1994, Hoggarth *et al.* 1999, Kvist & Nebel 2001). Firstly, as a result of high natural mortality, selection pressure tends to favour species with high fecundity, rapid development and growth. Consequently, the populations contain relatively few year classes, life cycles are short and generation turnover is fast. Secondly, the marked seasonal variations in primary and secondary productivity requires fishes at higher trophic levels to adopt a more generalised feeding behaviour with little time or opportunity to develop complex life-history patterns. Thirdly, abiotic factors influencing the spawning success of floodplain fishes are variable (e.g. geology of the catchment area, hydrological regime of the river, climatic seasonality) (Ryder *et al*. 1974, Henderson & Welcomme 1974, Schindler 1978, Lowe-McConnell 1979). In this regard, Kolding (1994) observed that the close empirical relationship between fish production indices and lake (or river-floodplain) water levels strongly suggests that the environment, more than the fishery, is the dominant agent of change. Although a relationship between fish catch and water flow has been reported for the Lower Shire Floodplain (Ratcliff 1972, Hastings 1973, Willoughby & Tweddle 1978, Tweddle *et al.* 1979, Tweddle *et al.* 1994), no quantitative evidence has been presented to show the seasonal dynamics of this relationship in combination with the vital biological parameters (e.g. spawning, recruitment) of the key commercial species.

Management challenges and options for African river-floodplains

Apart from a general paucity of data regarding African river-floodplain ecosystems, there are no appropriate predictive models for estimating yield in these ecosystems. While it has been recognised that models of population dynamics and production derived from studies of lakes may well be applied to rivers that have a stable hydrological regime (e.g. reservoir rivers), simple exponential models of mortality and growth are generally inconsistent with the biology of floodplain fisheries because of fluctuating water levels (Welcomme 1985 & 2001). Where such exponential models are appropriate, however, their applicability has been limited by the methodological difficulties experienced by many African floodplain experts, in determining such vital rates as age, growth and mortality (May 1984, Kolding 1994, Weyl 1998).

The first attempt to adopt and develop age-based fisheries models for Malawian lakes and the Lower Shire Floodplain was made over twenty year ago (Tweddle 1975, Willoughby & Tweddle 1978) but this never materialised into the development of management strategies. Bulirani *et al.* (1999) reported that the application of precautionary reference points based on a time series of age-dependent models had not been used for the management of fish stocks in Malawi because of lack of age-based data. Only more recently (Kanyerere 2004) has progress been made in aging fish from Lake Malawi. While recognising the technical limitations of using these models to develop a sustainable management plan for floodplain fisheries, it is nonetheless, pivotal to identify ecosystem-specific (Lowe-McConnell 1958, Le Roux 1961, Hecht 1980) biological parameters for the key commercial species of the Lower Shire Floodplain, such as growth rate, length-at-maturity and spawning periodicity. These biological parameters are critical for deciding on minimum legal size for the commercially important species as well as the seasonal restrictions of fishing aimed at protecting brood stock and juveniles.

Two approaches have been used to evaluate fisheries resources in rivers and floodplains, which include (i) evaluation of the performance of the fishery (stock assessment based on a series of biological parameters, catch assessment through sampling catch and fishermen, market analysis, analysis of consumption) and (ii) estimation of the magnitude of the stock using habitat environmental quality and quantity (Welcomme 2001). These resources evaluations can be achieved by use of predictive models, and simulations based on theoretical concepts of the ecology of the fish community (Welcomme 1985).

Huet (1964) proposed the morpho-edaphic index (MEI), the model that predicted annual fish production ($kg.km^{-1}$) as a function of average width of the river, water temperature and acidity. The model was later modified and applied extensively to European rivers (Lassleben 1977, cited by Welcomme 1985, Kolbing 1978). MEI has shown that African floodplains yield much less (60 $kg.ha^{-1}$) than Asian floodplains (100 $kg.ha^{-1}$) (Welcomme

2001). Another method is known as the “Habitat Quality Index”. This method was later developed in North America to predict standing stock (Binns & Eisermann 1979, Rabern 1984) as a function of stream flow, temperature, substrate type and food index. Although each of these models takes into account a comprehensive range of parameters, their utility is limited by the limited knowledge of biological characteristics of a particular stock and its interaction with environmental parameters

Surplus production models, which are holistic and encapsulate the net effect of recruitment, growth and mortality in terms of biomass, have been employed to estimate levels of fishing effort that will maximise yield on a sustainable basis (Welcomme 2001) in river systems (MRAG 1994). Special dynamic models that simulate variation in fish growth, recruitment, mortality and fishing with flood regime have been developed specifically for floodplain fisheries (Kapetsky 1974, Welcomme & Hagborg 1977). Halls (1998) used the Welcomme & Hagborg model to develop the floodplain fisheries simulation model (FPFMODEL), which was developed to explore the effects of hydrology and hydrological modification on floodplain fisheries productivity.

Other more complex and data-demanding approaches, such as the ECOPATH approach (Polovina 1984, Christensen & Pauly 1992) have been developed and applied to aquatic ecosystem (Christensen & Pauly 1995, Moreau *et al.* 1997). However, due to paucity of data in many African fisheries, use of ECOPATH has been restricted to fisheries where data is available, such as Lake Kariba (Moreau *et al.* 1997).

Therefore, less complex but powerful empirical models have also been developed using correlations between fisheries and environmental variables like climate (Sissenwine 1984). These correlation models have been used in highly variable upwelling fisheries of West African sardinella (Freon 1991), in Lake Kariba (Kolding 1989, Marshall 1992, Kolding 1994, Karenge & Kolding 1997), and in Lake Tanganyika (Plisnier 1997). The importance of using environmental variables in correlation model of fisheries in fluctuating water bodies has been reinforced by the notion that even for the most heavily exploited populations, natural mortality rates (M) tend to be higher than the rates of fishing mortality (Kolding 1989, Marshall 1992), indicating that fishing mortality only plays a minor role in the total mortality of fish in these ecosystems. While static models have been criticised for ignoring dynamic processes and for being unable to predict structural changes under perturbation, even complicated dynamic models that explicitly account for ecological processes and simulated perturbations are regarded as having very limited predictive power (Kolding 1994).

To address the scant success of the classical models for predicting yield in floodplain fisheries, it is proposed that the development of management tools requires that floodplains be viewed holistically by considering relevant factors they interact with, in a hierarchical order (Figure 1.3). The hierarchy of factors affecting fish communities in floodplains can be separated into the following categories: (1) climate, (2) morpho-edaphic structures of the habitat, and (3) biotic components (including fish). As an ecotone (aquatic-terrestrial transitional zone) the floodplain also affects various aspects of the local ecology, by changing values of many variables such as humidity, temperature and sedimentation (Kolasa & Zalewski 1995). Particular habitats often accelerate or intensify such processes as mineralisation of organic matter and sediment build-up (Ranwell 1974). Most predictive models for floodplain fisheries to date have taken morpho-edaphic factors into account, but have ignored the climatic factors that are a mega-determinant of variability of floodplain fisheries. Therefore, the comprehensive understanding and management of the Lower Shire Floodplain fisheries can be best achieved by adopting a hierarchical order approach (Figure 1.3). Hierarchical ecosystems theory stipulates that pattern and process operate on different levels or scales, and determining cause-effect requires a hierarchical perspective, or examining all interacting components (Allen & Starr 1982, O'Neill *et al.* 1989). Hierarchical approach has been reported to be of great importance to the comprehensive study of complex ecological systems (Allen & Starr 1982, Allen & Hoekstra 1992) such as aquatic systems (Costa-Pierce 2003).

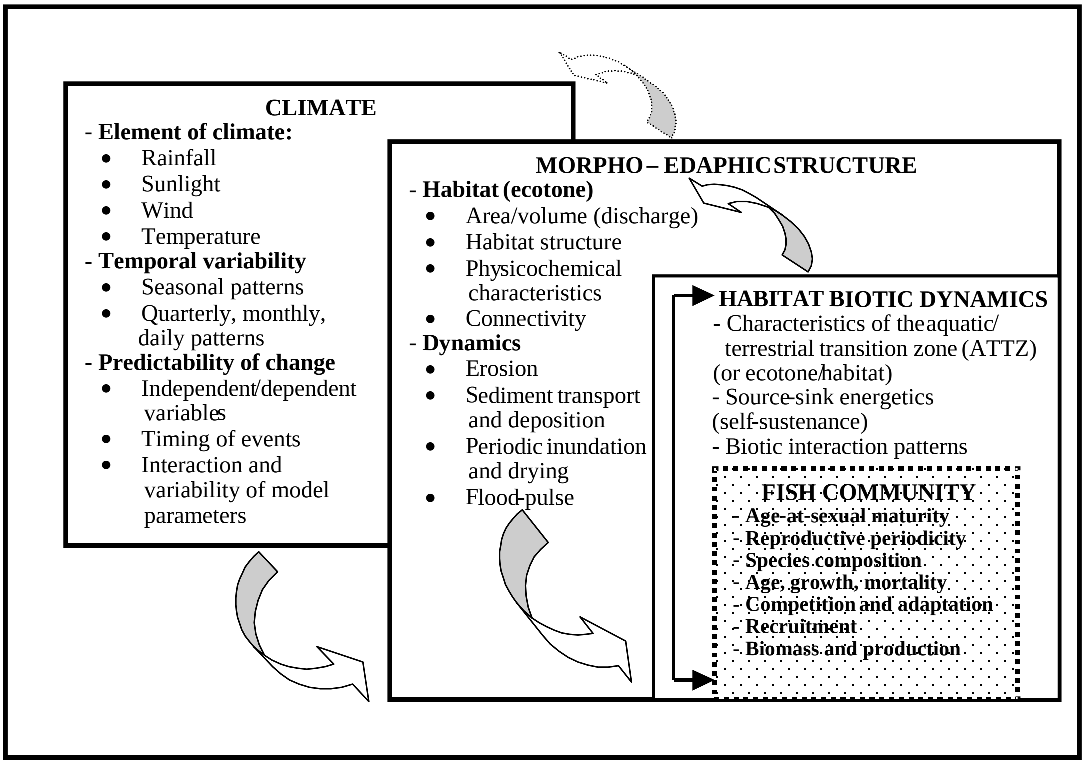


Figure 1.3 Hierarchical order of factors influencing fish production in the Lower Shire Floodplain. The arrows indicate spatial and temporal interactions, solid arrows are direct and dotted arrows are indirect interaction. The nested boxes represent the size of scale. The concept was adapted from Kolasa & Zalewski (1995)

Therefore, four stages must be followed in order to develop the management plan for the Lower Shire Floodplain. Firstly, the climate of the floodplains must be understood since climate affects the rainfall, which in return determines the hydrology of the river and floodplain. Secondly, it is necessary to have a full understanding of the hydrology of the system and the way in which it affects the commercially important fish species of the floodplain. Thirdly, an assessment of the status of the floodplain fisheries is necessary in order to determine the key indicator species and the level of fish catches in the systems, as well as their relationship with the hydrological parameters. The final stage is to decide on the best way to manage the fisheries of the floodplain, by manipulating the relationship between climate, hydrology and the various biological aspects of the key indicator species through systematic analyses and statistical modelling.

Thesis outline

The overriding hypothesis tested in this study is that “the dynamics of the fishery of the Lower Shire Floodplain are driven by and are adapted to the seasonal, but predictable, hydro-climatic regime of the floodplain”. The principle aim of this thesis was to develop a predictive model that incorporates data on essential biological aspects of the target species, characteristics of the habitat as well as overall climatic factors, to allow for the adaptive management of the fisheries in a continuously fluctuating floodplain environment. There were three major reasons for choosing this type of model for the Lower Shire Floodplain. First, despite fish being a very important source of food and livelihood for many Malawians, current fisheries management strategies are ad hoc, and have not been reviewed since their formulation over 30 years ago, despite major environmental changes (e.g. increased water obstruction, invasive weed, siltation, increased fishing effort) that have occurred in the Shire River system. Secondly, there is a lack of quantitative data regarding certain underlying ecological variabilities of the floodplain (e.g. water levels, climatic, habitat-related variables), which are necessary for developing a model for informed management of the fishery. Thirdly, vital biological data of key species necessary for the formulation of a fishery management plan for the floodplain was lacking.

The thesis is presented in eight chapters. Chapter 2 describes the climate and hydrological pattern of the floodplain. This chapter also tests the ecological theory concerning predictability of the environment namely that: “less seasonal environments tend to be more constant and predictable” (Lowe-McConnell 1987). In Chapter 3, a quantitative characterisation of the major habitats of the Lower Shire Floodplain is developed. The hypothesis tested in this chapter is that “the habitats of the floodplain are not fixed but their characteristics change seasonally according to (or are in “phase-transition” with) the hydro-climatic regime”.

Chapter 4 assesses the biological parameters of the two principal target species (*Oreochromis mossambicus* and *Clarias gariepinus*), as input parameters for the hydro-climatic fisheries model. In Chapter 5, an analysis is made of the impact of water fluctuation on the recruitment and life history of the two target species in the floodplains. The hypothesis being tested is that “recruitment in the floodplain is not random but a consequence of life history strategies adopted to ensure that the young are produced at a time of year most favourable for survival”. In Chapter 6 the fishery is assessed in terms of gear utilisation, gear selectivity and yield.

Chapter 7 considers the development of a predictive hydro-climatic fisheries model. The hypothesis being tested is that “there is a close empirical relationship between overall fish production indices and the climatic and hydrological characteristics of the floodplain”. Finally, in the concluding chapter a set of guiding principles for the management of African Floodplain fisheries and the utility of the new hydro-climatic fisheries model are considered.

Chapter 2

Climate and Hydrology of the Lower Shire River Floodplain

2.1 Introduction

Climate is the most important factor controlling watershed processes (Lotspeich 1980). Its three elements (temperature, precipitation and solar radiation) form the most important links in the hydrological cycle and are considered to drive ecosystem production (Cramer *et al.* 1999, Aber & Freuder 2000), since these provide energy and water necessary for life processes (Gordon *et al.* 1992).

Research in floodplain ecosystems is often discipline-specific, generating results that do not offer fisheries managers the opportunity to develop an integrated management plan. For example, climatologists are concerned with average and extreme variations in the state of the atmosphere over a period of time (Conrad & Pollak 1950); hydrologists are concerned with modelling water movement both above and below ground (Gordon *et al.* 1992); and fisheries biologists are interested in river and floodplains as habitat essential for the survival of fish stocks (Holcik & Bastl 1976, Welcomme 1979, Bayley 1981). However, there is a growing realisation that a holistic understanding of the climate and hydrology of the three most important African inland ecosystems (shallow lakes, floodplains and pelagic upwelling zones), which undergo climate-induced fluctuations (Sarch & Allison 2000), is an important step towards sustainable management of their fisheries (Kalk, McLachlan & Howard-Williams 1979, Marshall 1982, Lae 1992, Plisnier 1997, Kapetsky 1998, 2000, Sarch & Birkett 2000, Sarch & Allison 2000).

Before the climate and hydrology of a floodplain can be understood comprehensively, it is necessary to identify the links between the two entities. Pringle (2001) reported that the climate and the hydrology of floodplains are linked at a landscape, regional or even global level through the hydrological cycle. The river and the floodplain are linked through hydrologic connectivity (Ward 1998). Hydrologic connectivity is defined as the water-mediated transfer of matter (energy or organisms) between the river channel and the floodplain and between surface and subsurface compartments (Ward 1998, Pringle

2001). The transfer of matter can also occur within or between elements of the hydrologic cycle (Pringle 2001).

While the hydrologic cycle is the link between climate and hydrology of floodplains, the link between the river, floodplain and biota is through the concept of the “flood-pulse” (Junk *et al.* 1989). The flood-pulse is the pulsing of river discharge, which facilitates the lateral exchange of water and matter between the floodplain and river channel and aids nutrient recycling within the floodplain (Junk *et al.* 1989). Lateral exchange between the river and floodplain occurs when the river overflows its banks. The water level or discharge at which this occurs is known as “bankfull” (Leopold *et. al* 1960, Wolman & Leopold 1957, Leopold & Skibitzke 1967, Emmett 1975, Speight 1965, Harvey 1969, Pickup & Warner 1976, Williams 1978).

The flood-pulse is manifested in a number of ways. First, the hydrological regime, chemistry and nutrient status of the river-floodplain to a large extent reflect the climate and seasonality of precipitation of its upstream catchment area (Junk *et al.* 1989). Secondly, the life cycles of biota inhabiting the floodplain are related to the flood-pulse in terms of its annual timing, duration and the rate of rise and fall in water level. Consequently, floodplains are dominated by fish species that depend on seasonal colonisation of floodplain habitat (Bonetto *et al.* 1969, Welcomme 1979, Bayley 1981, Goulding 1981). Spawning of many species occurs at the beginning or during the rising flood, resulting in timely colonisation of the floodplains by juveniles for feeding and shelter (Bruton & Allanson 1974, Willoughby & Tweddle 1978[a], Bruton 1979, Holland *et al.* 1983, Welcomme 1985, Lowe-McConnell 1987, Weyl & Hecht 1998). Moreover, many floodplain fish species show seasonality in food uptake related to flood cycles (Lowe-McConnell 1964, Willoughby & Tweddle 1978[a], Goulding 1980, 1981, Junk 1982, Ribeiro 1983, Merron 1991).

A holistic understanding of the climate and hydrology of the Lower Shire Floodplain, in particular the link between the two, is important as it may provide the basis for a better understanding of the life history and biology of the fish species. Currently, neither the climate nor the hydrology of the Lower Shire Floodplain has been quantitatively described. The only previous description (SVADD 1975) is based on observations of the entire Lower Shire Valley and does not provide adequate and detailed information and data for the climate of the floodplain.

The climate of the Lower Shire Valley is characterised by two well-defined seasons; the hot-dry season from May to October, and the warm-wet season from November to April. Rains are generally low and erratic (between 650 and 750 mm per annum) with the onset dates varying significantly from year to year (SVADD 1975). In wetter years, the Lower Shire receives light rains from April to July caused by the intrusion of moist maritime air from the Indian Ocean (Lineham 1972). Mean maximum monthly temperature in October and November is 27.2^0C, while mean minimum temperatures are in the range of 13.3 and 22.8^0C, in January and late October, respectively (SVADD 1975).

The hydrology of the Shire River was dominated by the drought of 1992 and below-average rainfall over five subsequent years (1993-1998), which reduced the level of Lake Malawi to a record low of 473 m.a.s.l. This in turn reduced the daily mean flow in the Shire River to as little as 130 $m^3.sec^{-1}$ in 1997 (Sibande 2001). Since 1998 river flow has increased, remaining well above the minimum flow of 170 $m^3.sec^{-1}$ required for operation of the hydroelectric power stations (Sibande 2001).

It has been reported that flooding in the Lower Shire Floodplain is caused by the Ruo River tributary which holds back water flow of the Shire at the confluence of the two rivers. This causes the Shire to fill the Elephant Marshes (Halcrow 1954, Pike 1972, Tweddle *et al.* 1979). These observations are, however, largely qualitative and are not based on detailed analyses of critical hydrologic parameters such as monthly, seasonal or annual variation in water level, the bankfull level of the floodplain, or factors affecting the floodplain's water level. The current, mostly qualitative understanding of the floodplain's hydrology does not provide an adequate basis for the development of water and fisheries management strategies.

Assuming climatic and hydrologic events in the Lower Shire Floodplain repeat themselves each year, then a predictable seasonal pattern must emerge. Resh *et al.* (1988) reported that predictability of river flow is ecologically important since it is thought to influence the evolution of behavioural mechanisms and the timing of life-history stages in stream biota. A number of predictive models have been used in studies of climate, hydrology and general ecology. These include simple bivariate and multivariate regression models used mainly by ecologists (Rigler 1982, Fisher & Grimm 1991) or more complex periodic regressions by climatologists (Conrad & Pollak 1950, Roosen 1973), hydrologists (Cluis 1972, Toner & Keddy 1997, Caissie *et al.* 2001) and fisheries biologists (Bell *et al.* 1995). Generally, regression methods are useful because they help to determine relationships between variables and also reveal relationships whereby one variable can be predicted from others (Hann 1977, Gordon *et al.* 1992). Sustainable management of the Lower Shire Floodplain requires the development of a simple predictive model that is able to predict the dynamics of hydro-climatic events. Such a model can, for example, be based on variables that capture the timing, duration and rate of the flood-pulse in relation to key climatic parameters. Given the relationship between climate and hydrology (Junk *et al.* 1989, Ward 1998, Pringle 2001), it is hypothesised that the dynamics of the flood-pulse of the Lower Shire Floodplain can be predicted using data concerning key climatic variables.

The objective of this part of the study was to describe the climate and hydrology of the Lower Shire Floodplain and to develop a hydro-climatic predictive model for the timing, duration and rate of the flood-pulse of the floodplain. This information formed the basis for understanding the influence of the flood-pulse on spawning, feeding, growth and recruitment of the key commercial species of the floodplain.

2.2 Materials and methods

Type and source of data

The climate of the Lower Shire Floodplain was studied using daily mean values of ten major climatic elements recorded at the Makhanga Meteorological Station (Fig. 2.1), in the floodplain. The climatic elements were; precipitation (rainfall) (mm), thunder days

(days.month^{-1}), temperature (ºC), relative humidity (RH%), wind velocity (m.sec^{-1}), evaporation (E mm), evapotranspiration (ET mm), potential evapotranspiration (PE mm), cloud cover (octans), and sunshine (hour.day^{-1}). The hydrology of the Shire River was determined using daily mean water level (m) at seven gauging stations. These stations were at Mangochi (the only existing gauging station in the Upper Shire), Liwonde and Zalewa in the Middle Shire, and Chikwawa, Thangadzi, Ruo and Chiromo in the Lower Shire (Fig. 1.1). Water temperature was measured in the Shire at Chiromo daily, at a depth of 0.30 m, with a calibrated hand-held YSI model 51 B oxygen meter. The meteorological and water-gauging stations are part of the World Meteorological Organisation (WMO) network; thus, the recording procedures are accredited by and comply with the technical regulations specified by the WMO on climate (WMO 1988) and hydrology (WMO 1980). The Malawi Department of Meteorological Services and the Hydrology Division of the Malawi Ministry of Water Resources kindly provided the climate and water-level data, respectively. The climate data cover a 30-year period from 1960/61 to 1990/91, plus additional data for 1995/96 to 1999/2000 (5 years), covering the period of the field research. Daily water-level data cover the period between 1980/81 and 1999/2000) (20 years).

Climate of the Lower Shire Floodplain

Analysis of the climate data was geographic (Conrad & Pollak 1950), so that the description of the climate of the Lower Shire Floodplain would be consistent with and fits into any systematic geographic description. Other types of descriptions are agricultural (Schnelle 1955, cited by Jaagus & Ahas 2000), health (Guest *et al*. 1999), aerologic and biologic climate (Conrad & Pollak 1950). Monthly and annual averages and standard deviations were calculated for each element of the climate data according to methods of Conrad & Pollak (1950). In order to assess long-term variations in the daily climate variables, the coefficient of variation (C_v) was calculated. Some of the data were presented in the form of graphs and charts (Ellenboek 1987) in order to show monthly variations and some data were presented in table form.

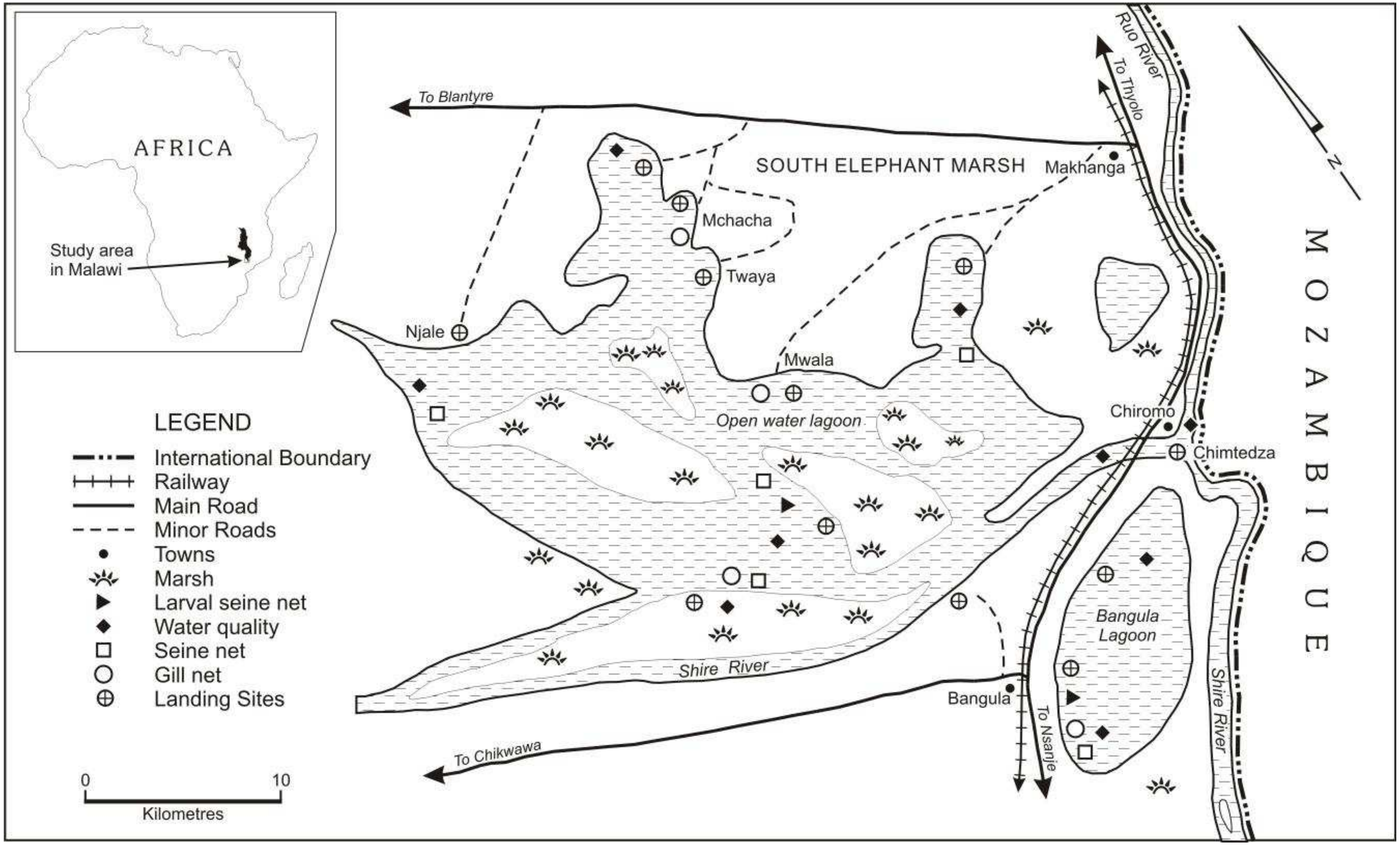


Figure 2.1 Map of the Lower Shire Floodplain, showing the southern Elephant marsh and sampling sites

In order to demarcate the calendar year into internally uniform climatic seasons that are clearly different from each other (Jaagus & Ahas 2000), “constant thresholds” (Conrad & Pollak 1950) were used to set point limits so that any mean values of the climatic variables below or above these points mark the start of another season. In this study, annual mean of daily values were used as “constant thresholds” (Ward & Brooks 1936). In this way the temperature curve was divided into parts below and above the temperature threshold. Deviations from the annual means were calculated by subtracting the annual mean from the monthly mean. Lastly, monthly relative percents were obtained by calculating the percent of the monthly mean relative to the month with the highest value above the constant threshold.

For example, using air temperature for the month of June (20.2ºC). The constant threshold of air temperature in the Lower Shire Floodplain was 25ºC; the months of highest temperature were October and November (28.4ºC). A monthly deviation from constant threshold was 20.2-25 =-4.8ºC and the relative percent was 4.8/28.4x100= 71.1%. This means that the June temperatures remain 71% below the threshold.

Hydrology of the Shire River and the Lower Shire Floodplain

(i) The flow regime or hydrograph

A water (or hydrological) year in Malawi, starts in November and ends in October. Monthly averages, standard deviations and variability (coefficient of variation, C_V) were calculated in order to determine the pattern of annual water level in the Shire River according to McMahon (1979). Records of monthly variation in water level were used to draw flow regimes or hydrographs (a graph of water level with time) by plotting mean monthly water level (m) at each gauging station against month. The section of the hydrograph where flow increases is called the “rising limb” and where flow is falling is the “falling limb”, while the portion depicting neither rising nor falling flow is called “baseflow” or estimated average minimum flow necessary to maintain the flow in the main river channel (Hawkes 1975). The baseflow index (%) was calculated according to Hamilton & Bergen (1984) as follows:

Baseflow index = $\frac{lowest\ mean\ monthly\ flow}{mean\ annual\ flow}\ x\ 100$ (Equation 2.1)

(ii) Water budget

In order to determine the factors affecting water level in the floodplain, a water budget comprised of two parts was calculated. One part assessed the water supply generated within the basin originating from components that bring in (precipitation, runoff) and take out water (evaporation). The other part indirectly assessed the net supplies to the basin as a residual of inflow and outflow into and from the floodplain. Water supply generated within the basin, after evaporation is subtracted from precipitation and runoff, is known as Net Basin Supplies Components $(NBS[C])$ and the supply from inflow and outflow is known as Net Basin Supplies Residual $(NBS[R])$ (Brinkman 1983). Thus:

$NBS[C] = P + R - E$ (Equation 2.2)

where P is over-floodplain precipitation, R is runoff into the floodplain and E is evaporation from the floodplain, and :

$NBS[R] = \Delta S + O - I \pm D$ (Equation 2.3)

where ΔS is the change in water storage (or CIS) computed from the difference in floodplain levels over a time interval, in this case the beginning and end of a month, O is the outflow, I is the inflow, and D is total monthly diversion of water from the floodplain.

(iii) Mean annual runoff (MAR)

MAR represents the difference between evaporation and precipitation (Gordon *et al.* 1992). It was calculated according to McMahon (1982) as:

MAR (mm) = $\frac{mean\ annual\ flow\left(million\ m^2\right)}{catchment\ area\left(km^2\right)}\ x\ 1000$ (Equation 2.4) where mean annual flow (MAF) is the measure of the annual water delivered from a catchment relative to its surface area. It was calculated by averaging daily flows over a 10 year period from 1980/81 to 1999/2000. Where there were missing data on discharge/flow (due to malfunctioning measuring equipment) water level data was converted to flow using a regression model: Y=a + bX, this yielded a = 2.05, b = 0.00482, $r^2 = 0.99$, SE $\pm$ 0.054 (1.3%), and was highly significant (p=0.0000).

(iv) Estimates of the Bankfull level

The level at which the river overflows its banks into the floodplain (bankfull) was established using a number of empirical methods, which included the following:

a) **Mean annual water level**: Welcomme (1985) proposed that bankfull can be established at the mean annual level. It is assumed that any level above the mean annual level will be large enough to overflow the riverbanks. Since arithmetic mean showed annual variability, the "mesor" was used instead. Bell (1999) described the mesor as a superior measure of central tendency because it corrects for the bias in the mean due to sampling times. The mesor was calculated using periodic regression according to Bell (1999).

b) **Water level with a return period of 1 – 2 years**: Return period is the average length of time, in years, between two flows of given size (Gordon *et al.* 1992). Numerous workers have proposed that bankfull discharge is that flow which occurs at a return period between 1 and 2 years (Wolman & Leopold 1957, Woodyer 1968, Williams 1978, Rowntree & Wadeson 1998).

(v) Estimating return period or recurrence interval for the Bankfull level

Return interval (T-years) is defined as the maximum mean daily flow that would be equalled or exceeded $100(1-p)$ percent of the time (Stedinger *et al.* 1993) and is described as:

$$P = \frac{1}{T} \qquad \text{(Equation 2.5)}$$

where P is the probability and T is the average recurrence time.

The water level with a return period of 1 – 2 years was identified using two methods.

a) Fitting log-normal distribution to the observed water-level distribution curve

The first method fitted a log-normal frequency distribution function to the frequency distribution curve of the maximum mean daily levels (Stedinger *et al.* 1993). The log-normal distribution function (Haan 1979) was of the form:

$$P(X) = \cdots \left(2\pi X^2 \sigma_y^2\right)^{-1/2} \exp\left[-\frac{1}{2}\left(\ln X - \mu_y\right)^2 / \sigma_y^2 \right] \quad (X > 0) \qquad \text{(Equation 2.6)}$$

where $P(X)$ is the probability density function, and μ and σ^2 are the mean and variance of the normal distribution, respectively.

The maximum mean daily water levels were ranked from smallest to largest, and then grouped into classes. The observed water levels were then assigned to the groups depending on their size. Later the frequency data were plotted on a graph where the y-axis represents the frequency and the x-axis represents class interval (see example in Fig. 2.5a). Finally, the log-normal distribution function was fitted to frequency of the maximum mean daily water levels.

b) Use of non-parametric quantile of the observed water-level distribution curve

The second method estimated return periods using a non-parametric quantile estimator (Porth *et al.* 2001) of the cumulative distribution function of the maximum mean daily water levels. The probability distribution function of the non-parametric quantile estimator was described by Stedinger (1993) as follows:

$$P = 1 - \frac{1}{T} \qquad \text{(Equation 2.7)}$$

where P and T have been described in equation 2.5. The cumulative frequency curve is generated as described above, except that under cumulative distribution, the frequencies are progressively summed up. For example, a five-year return period is the 1-1/5 = 0.80th quantile (Porth *et al.* 2001). The next stage is to check on the cumulative distribution curve, or any computer spreadsheet programme, to find the value of water level or flow corresponding to 0.80th quantile.

(vi) Seasonal analysis of climatic and hydrologic parameters

Mathematical and periodic regression techniques were used to assess and predict the seasonality of hydrologic parameters of the floodplain. The following is a brief explanation of the steps in periodic regression according to Bliss (1970), Batschelet (1981), Zar (1984), Bell *et al.* (1995) and Bell (1999).

Periodic function of time (month of the year) served as the independent variable, while water level was a dependent variable. Analysis of variance (ANOVA) was used to test the best-fitting curve (Bliss 1970), assuming that residuals were independently and normally distributed, or that least squares provided an unbiased fit even if those assumptions were not met (Batschelet 1981). A predictive model was derived using three parameters (i.e. length of the cycle or fundamental period, its amplitude, and the phase lag angle) according to Bliss (1970). The length of the cycle in this case is the hydrological year (12 months), the amplitude is the minimum and maximum variation in the climatic and hydrological variables, and the phase angle is the time at which the hydrologic parameters are at peak. This is expressed in a cosine regression format as:

$$Y = b + m(\cos(RX + \partial)) \qquad \text{(Equation 2.8)}$$

where: RX is the angular transformed independent X variable (Month of year: MOY), b is an intercept, m is the slope, and ∂ is the phase lag. Transformation of $\mathbf{X}$ variable into circular variables (RMOY) was done by multiplying MOY (0-12) by 2π/12 to obtain an equivalent radian measure. Equation 2.8 can be written in equivalent Fourier-regression format (Baschelet 1981) as:

$$Y = \beta_0 + \beta_1 \sin(RX) + \beta_2 \cos(RX) \qquad \text{(Equation 2.9)}$$

where β_1 and β_2 are coefficients, and β_0 is a mean (mesor), equivalent to an intercept in a non-periodic regression. In an azimuthal system, where an angle α is measured in a clockwise direction from the positive Y-axis as on a compass (Bell *et al.* 1995 Bell 1999), location of peak (P) hydrological parameter, can be determined by visual inspection of plots, or else by algebra provided by Batschelet (1981), where the position of the peak (P_p) is ∂ units, in degrees, after the nominal zero of the cycle (t_o),

$$P_p = t_o + \partial \qquad \text{(Equation 2.10)}$$

$$\partial' = \arctan\left(\beta_1 / \beta_2\right) \qquad \text{(Equation 2.11)}$$

$$\partial = \partial' + QC \qquad \text{(Equation 2.12)}$$

where QC is a "quadrant correction factor" to be added to ∂'. That is QC = 0º if (β_1, β_2) are (++) (first quadrant), QC = 180º if (+-) (second quadrant) or (--) (third quadrant) and QC = 360º if (-+) (fourth quadrant).

The amplitude (A) is the maximum positive or negative departure of predicted Y (hydrological parameter) from the mesor, such that the maximum is $\beta_0 + A$, the minimum is $\beta_0 - A$, and the entire range is $Y_{\max} - Y_{\min} = 2A$. Where the coefficients β_1 and β_2 (for sin and cos) are two sides of a right triangle then A is the hypotenuse and can be calculated using Pythagoras' theorem as:

$$A = \sqrt{\left(\beta_1^2 + \beta_2^2\right)} \qquad \text{(Equation 2.13)}$$

(vii) Conceptual hydro-climatic model

Regression analysis was performed to identify the relationship between climatic and hydrological parameters in the floodplain, with the aid of computer software StatisticaTH (StatSoft, Inc. 1999). Water-level data from the Shire River at Chiromo gauging station (the only outlet for the floodplain) and climate data from Makhanga Meteorological Station were used for modelling the relationship between climate and hydrology in the floodplain.

Independent variables

In the model, eight climatic parameters (relative humidity, rainfall, air temperature, evaporation, wind speed, sunshine, thunder days and cloud cover) were independent variables. These parameters were selected to reflect water input (rainfall, relative humidity, thunder days), output (evaporation), and factors influencing the water budget (air temperature, wind, clouds) of the floodplain.

Dependent variables

Seven hydrologic parameters i.e. water temperature, mean water level, minimum water level, sum of water fluctuation (*SWF*), river stage (*RS*), level-above-bankfull (*Lv-BF*), and slope of change in water level (Slope), were dependent variables. These parameters were selected to reflect the water level, timing of flood, duration of inundation and rate of rise and fall of the flood regime. The following is a brief description of the calculation of the hydrological parameters:

Water level (daily mean) (meters) was obtained from the gauging station records. The bankfull was established using the method outlined above. Sum of water fluctuation (*SWF*) (m) as a measure of daily differences in water level is the sum of the differences between daily water level and a benchmark level (Heiler *et al.* 1995), in this case the bankfull level:

$$SWF = \sum_{i=1}^{n} \left(x_i - x_j \right) \qquad \text{(Equation 2.14)}$$

where i is the monthly mean daily water level, and j is the bankfull level. River stage (*RS*) is the number of days in the month when the water level is above the bankfull level, and it is an indication of the duration that the floodplain is inundated. Slope is the rate at which the water level is changing (rising or falling).

2.3 Results

2.3.1 Climatic conditions of the Lower Shire Floodplain

General climate

Table 2.1 and Figure 2.2 summarises data that generally describe the climate of the Lower Shire Floodplain. The floodplain is generally a low-rainfall area (765 ± 198 mm), fairly variable (C_v = 27%), with the largest amount of rainfall occurring between December and January (Figure 2.3). The area is generally humid (mean RH 68%), mild to hot (25 - 33ºC) variable mean monthly diurnal (12ºC) temperature (Table 2.1 and Appendix 1). Evaporation and potential evapotranspiration levels were generally higher than rainfall, more especially in October when wind speed, sunshine and air temperature were highest (Figure 2.2 and Appendix 1), indicating a relationship between evaporation, air temperature and wind speed. Wind speed increases from July (2.6 m.sec^{-1}) to reach a peak in October (5.5 m.sec^{-1}) and then tapers off in November at the beginning of the rainy season. Apart from enhancing evaporation, wind also brings rain to the floodplain between May and July (locally known as “Chiperoni”), as maritime winds from the southern Mozambican Channel blow through the southern Zambezi Valley.

Hydro-climatic seasons

Flood regime and weather data were used to divide the year into hydro-climatic seasons. Four quarterly hydro-climatic seasons, distinct from each other, were identified (Table 2.2).

i) Quarterly season 1 (Qrt1) (July - September)

This season is characterised by hot (20-25ºC), dry weather (4.5-17.5 mm) with a low flood regime (4.3 m). During this quarter, rainfall levels are the lowest, below 10% of the constant threshold of 63.7 mm.month^{-1}, while temperatures are above 80% of the constant threshold of 28.4ºC per month.

Table 2.1 Summary of the climatic elements of the Lower Shire Floodplain

Climate element	Characteristics
Rainfall (mm)	• Mean annual ±SD of 765±198 mm with a coefficient of variation of 27% • Rainfall due to inter-tropical convergence zone (ITCZ) and maritime moist air from south Mozambique • Rainy season from Nov. to Mar. (47% of rain in Dec. and Jan.)
Relative humidity (%)	Monthly daily mean relative humidity ranges from 76 to 79% (Jan. to Apr.) and 51 to 73% (May to Feb.)
Surface air temperature (ºC)	• Hottest months are Oct. and Nov. (28.4 ± 6.8ºC); coldest months are June and July (20.2 ± 6.6ºC) • Daily mean 25 ± 6.8ºC; daily minimum 20 ± 3.3ºC; daily maximum 33 ± 2.8ºC • Monthly mean diurnal 12 ± 3.3ºC
Evaporation (E) (mm)	• Mean annual 2203.6 mm • Highest in Oct. (314.9 mm) when the sunshine (9.4 hours) and wind (5.5 $m.sec^{-1}$) are highest
Evapotranspiration (ET) (mm)	• Mean annual 1836.1 mm • Highest in Oct. (217.6 mm) when sunshine (9.4 hours) and wind speed (5.5 $m.sec^{-1}$) and air temperature (28.4 ºC) are highest
Potential Evapotranspiration (PE) (mm)	• Mean annual 2345.2 mm • Highest values in Oct. (268.2 mm) when wind speed (5.5 $m.sec^{-1}$) and air temperature are highest (28.4 ºC)
Sunshine (hours)	• Mean annual 8.1 hours (range: 7.1 – 9.4); highest in Oct. (9.4±1.0 hours)
Cloud cover (octas)	• Mean annual 4.1 octas (range: 2.1-5.9); highest Jan. (5.9±0.42 octas)
Thunder (days)	• Mean annual 78 days (range:0-111.2); highest number in Dec. (18±7.6 days)
Wind ($m.sec^{-1}$)	• Falling pressure over southern Mozambique causes north-easterly winds, while rising pressure causes south-easterly winds and brings low cloud with drizzle known as “Chiperoni” in Jun-Jul. • Mean monthly speed 3.3 $m.sec^{-1}$ (range: 2.4 - 5.5) highest in Oct. (5.5±1.07 $m.sec^{-1}$)

Table 2.2 Hydro-climatic seasons for the Lower Shire Floodplain. The values are deviation from constant threshold (Δ) and relative change from constant threshold (%Δ), for selected climatic (1961-91) and hydrologic (1980 – 2000) elements. Water temperature values are for the period (1999/2000)

Hydro-climatic season (Quarterly)	Month	Rainfall (mm)		Relative Humidity (%)		Air temperature (ºC)		Evaporation (mm)		Wind (m.sec^{-1})		Water level (m)		Water temperature (ºC)	
		Δ	%Δ	Δ	%Δ	Δ	%Δ	Δ	%Δ	Δ	%Δ	Δ	%Δ	Δ	%Δ
Quarter 3 Peak flood, rainy, hot, humid	January	119.4	100	9.4	98.7	2.0	95.1	-7.4	56.0	-0.7	47.3	0.77	91.0	2.6	98.3
	February	33.8	53.3	10.4	100	1.7	94.0	-32.3	48.0	-0.9	43.6	1.31	100	3.0	100
	March	48.0	61.0	9.4	98.7	1.1	91.9	-22.6	51.1	-0.9	43.6	0.86	92.5	2.6	98.5
Quarter 4 Humid, cool, receding flood	April	-24.6	21.4	7.4	96.2	-0.2	87.3	-38.9	46.0	-0.7	47.3	0.57	87.7	1.7	95.0
	May	-49.3	7.9	4.4	92.4	-2.7	78.5	-50.8	42.2	-0.9	43.6	-0.07	77.0	-0.6	87.2
	June	-47.0	9.1	3.4	91.1	-4.8	71.1	-71.1	35.7	-0.9	43.6	-0.31	73.0	-2.0	82.1
Quarter 1 Hot, dry, low flood	July	-46.2	9.6	1.4	88.6	-4.8	71.1	-61.2	38.9	-0.7	47.3	-0.29	73.2	-3.5	76.7
	August	-54.6	5.0	-6.6	78.5	-2.6	78.9	-11.2	54.7	0.2	63.6	-0.37	71.9	-4.4	73.6
	September	-59.2	2.5	-14.6	68.4	0.7	90.5	55.9	76.1	1.4	85.5	-0.61	68.0	-3.5	76.7
Quarter 2 Hot, windy, rainy, low/rising flood	October	-42.2	11.7	-17.6	64.6	3.4	100	131.3	100	2.2	100	-0.53	69.4	-0.9	86.1
	November	4.6	37.3	-9.6	74.7	3.4	100	84.6	85.2	1.5	87.3	-1.0	61.5	2.1	96.7
	December	117.4	98.9	2.4	89.9	2.4	96.5	24.1	66.0	0.2	61.8	-0.34	72.5	2.8	99.2
Constant threshold		63.7		68.6		25.0		183.6		3.3		4.68		24.8	

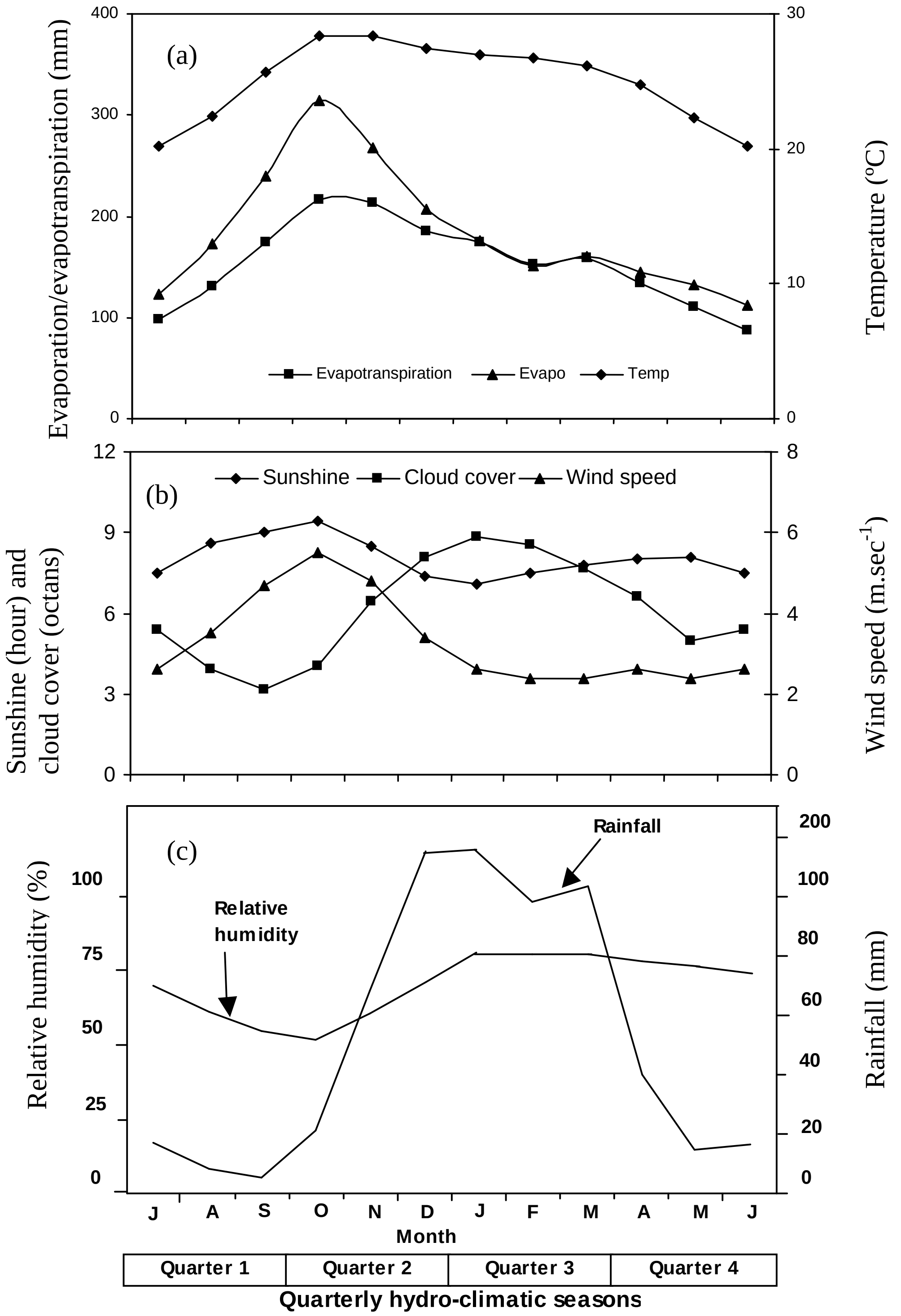


Figure 2.2 Mean monthly temperature, evaporation, evapotranspiration (a) sunshine, cloud cover and wind speed (b), and relative humidity and rainfall (c) at Makhanga, Lower Shire Floodplain.

ii) Quarterly season 2 (Qrt2) (October – December)

Characterised by hot (27-28ºC), windy (3.4-5.5 m.sec^{-1}), wet weather (21.5-181.1 mm) with low but rising flood regime (4.1 m). Rainfall has started, air temperature, wind speed and evaporation are at their highest.

iii) Quarterly season 3 (Qrt3) (January - March)

This is a season identified by hot (26-27ºC), humid (78-79%RH) and wet (97.8-183.1 mm) weather with the peak flood regime (5.7 m). Rainfall, relative humidity, flood regime, air temperature and water temperature are 100% of the constant thresholds. Evaporation and wind are at their lowest levels.

(iv) Quarterly season 4 (Qrt4) (April – June)

This season is characterised by humid (73-78%RH) and cool weather (20-24ºC) with a receding flood regime (4.7 m), and water temperatures above 80% of the constant threshold of 25ºC per month. Although it is hot and dry, evaporation levels are below 60% of thresholds (183.6 mm per month), probably because of high humidity and low wind speed.

2.3.2 Hydrology

(i) General characteristics

The three sections of the Shire River have unique characteristics that result in different flow and runoff patterns. The annual hydrograph of the Upper Shire River at the source (Mangochi gauging station) shows the lowest mean annual water level in December, which rises steadily to peak in April (Fig. 2.3). The Upper Shire River has the highest baseflow (74%) (Table 2.3), which might be caused by the buffering effect of Lake Malawi on the flow of the river. The annual hydrographs at gauging sites in the Middle Shire River show peaks in February and August (Fig. 2.3). The peak in February is probably caused by inflow of water from the catchment as result of local rainfall, while the one in August could be due to the rise in water level in Lake Malawi, which is experienced at the Mangochi site in April. The time lag of four to five months is probably due to the distance over which the water mass moves and Lake Malombe, which acts as a water sump.

Annual hydrographs of the Lower Shire River at Chikwawa, just below Kapichira Falls, shows the lowest mean annual water level in December with peaks in February and March (Figure 2.3). The water level declines from March, but maintains a stable level of approximately 2 m up to August, then declines to an annual minimum of 1.7 m in December. The Shire River at Chiromo has a low flood regime between July and September and peak flood between January and March. Thangadzi River, one of the numerous small tributaries of the Shire, shows a typical hydrograph of small Lower Shire tributaries, which experience flash floods, with low baseflow (9%) (Table 2.3) and almost dry riverbeds during parts of the year. The Ruo is the largest and single most important tributary of the Shire River. It has a fairly stable level because of having its source in Mulanje Mountain; the lowest being in November, 6.12 m and highest in February (7.53 m).

Generally, mean annual river flow is a reflection of the size of the catchment; the larger the catchment the larger the mean annual flows, and visa versa (Table 2.3). Mean annual runoff (MAR) is also a reflection of the size of the catchment area; generally MAR increases as the catchment area decreases. This trend can be seen in the various sections of the Shire River, where smaller catchment areas in Ruo and Thangadzi tributaries have the largest MAR 435.7 mm and 596 mm, respectively (Table 2.3).

(ii) Annual hydrograph of the Lower Shire Floodplain

Rainfall and water level

The relationship between rainfall at Makhanga and water level in the Shire measured at Chiromo, for the 4-year period (July 1996 to June 2000) can be seen in Figure 2.4. Water level in the Shire at Chiromo and rainfall at Makhanga represent the hydrological and rainfall status of the floodplain, respectively. Generally, water level is highest during the rainy months and lowest during low-rainfall months. The annual hydrograph representing the flood regime in the Lower Shire Floodplain fits into four flood regime categories that correspond to the quarterly hydro-climatic seasons. These four categories are: low (July to September), low-but-rising (October to December), peak (January to March), and falling or receding (April to June) (Fig.2.5).

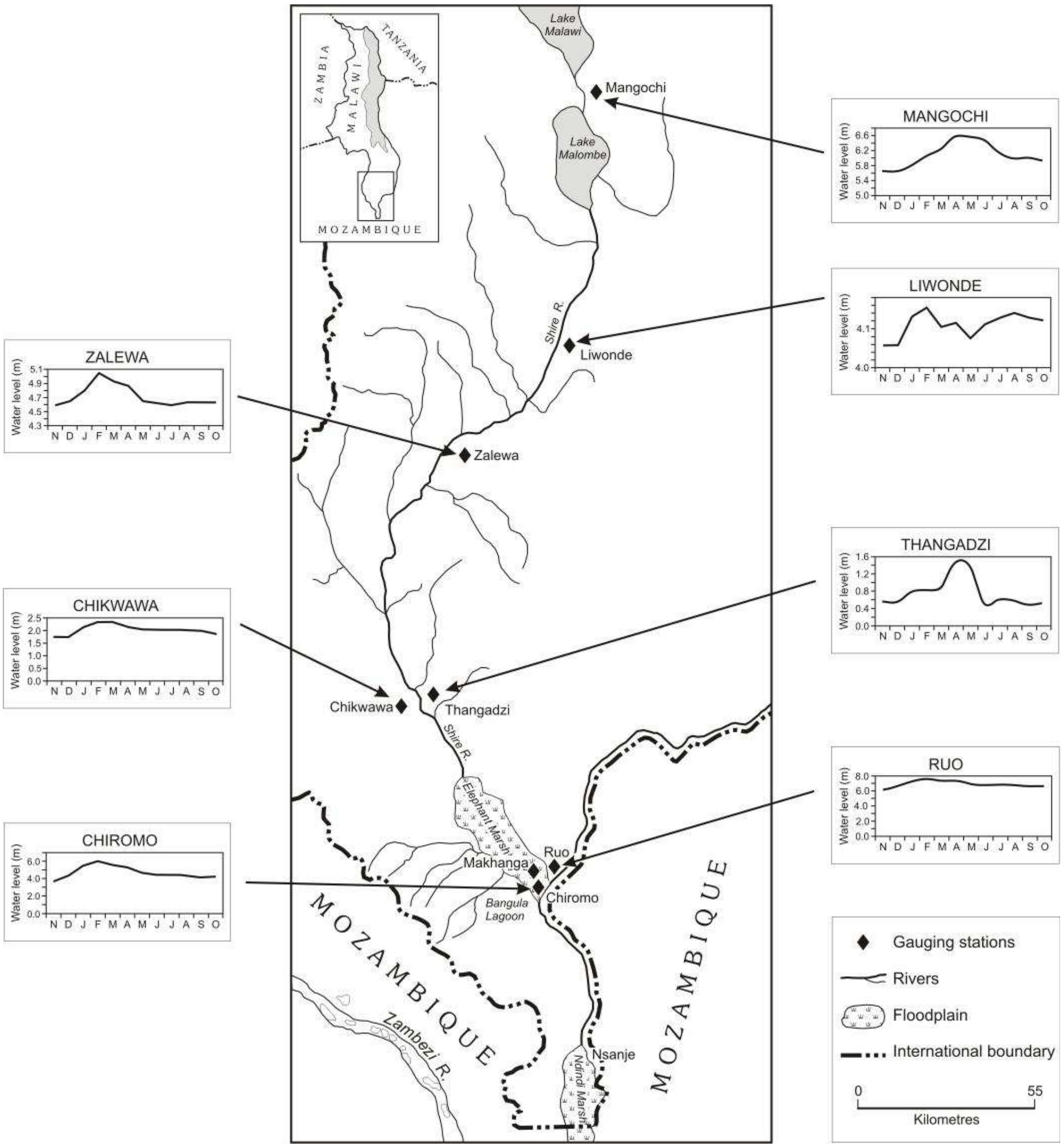


Figure 2.3 Map of southern Malawi showing the Shire River System, selected sample gauging sites and their annual hydrographs

(iii) Water balance

Bankfull water level was empirically established to be within the range of 4.7 to 5.15 m (or 549.79 - 643.15 $m^3.s^{-1}$) (average of 4.87 m or 584 $m^3.s^{-1}$) with a return interval of between 1.4 and 2 years (Table 2.4). Therefore, flooding is likely to occur in the Lower Shire Floodplain if the water level exceeds 4.7 metres (549.79 $m^3.s^{-1}$) ($p < 0.01$). This is the critical minimum water level, which is only equalled or exceeded between January and April (4.8 m) in the Shire River at Chiromo (Fig. 2.4). Overall Net Basin Supplies Components (NBS[C]) shows that the Lower Shire Floodplain loses more water than it gains from rainfall. Annual evaporation (2,203.6 mm) is far greater than precipitation (764.5 mm) and runoff (1301.7 mm), resulting in an annual water deficit of -137.4 mm (Table 2.5). However, there are monthly variations. For example, from December to April, the floodplain's water budget is positive because of the rainy season, as well as in June due to "Chiperoni" rains brought by maritime winds from the Mozambique Channel. Heaviest water losses are experienced between September and November when both rainfall and runoff are low (Table 2.5).

Three patterns emerge from Table 2.5 regarding the floodplain's water budget. First, during the months of high rainfall (December to March), precipitation drives the monthly net basin supplies (NBS), resulting in a positive water budget. Secondly, during months of low rainfall (April to July) when flood regime is receding/low, runoff drives the NBS, resulting in a low but positive water budget. This means that although rainfall is low, evaporation is not excessively high. Therefore, water supply in the floodplain remained higher than the amount lost through evaporation. Thirdly, during the transition between the hot-dry and hot-wet months (August to November) when flood regime is low but rising, evaporation drives the *NBS*, resulting in a negative water budget. As for the role of inflow and outflow in the floodplain's water budget, it is necessary to focus on the change in water storage (CIS) (Table 2.5), because CIS represents the net basin supplies computed from residual of the water balance (*NBS*[*R*]) after taking into account the outflow and inflow as well as the monthly change in floodplain water level.

Table 2.3 Characteristics of streamflow in selected sections of the Shire River and its tributaries (1980/81 – 1999/2000)

River section	**Gauging station**	**Catchment area (km^2)**	**Mean annual flow (m^3.sec^{-1})**	**Mean annual runoff (mm)**	**Baseflow index (%)**	**Mean maximum water level (m)**	**Mean minimum water level (m)**	**Max: min ratio (max/min)**	**C$_v$ (mean annual level)**
Upper Shire	Mangochi	126,500	830.9	207.145	74	6.551	5.523	1.2	0.08
Middle Shire	Liwonde	130,200	400.3	96.9	53	4.32	3.928	1.1	0.03
	Zalewa	133,769	553.9	130.6	52	5.463	4.55	1.2	0.07
Lower Shire	Chikwawa	138,600	510.6	116.6	56	2.983	1.2315	2.42	0.21
	Chiromo	149,500	509.1	107.6	59	6.421	3.5035	1.83	0.20
	Ruo River	748	10.3	435.7	30	8.199	5.95	1.38	0.12
	Thangadzi River	45.5	0.86	596.1	9	1.518	0.444	3.42	0.75

Table 2.4 Empirically calculated bankfull for the Lower Shire Floodplain.

Bankfull level (m)	**Discharge (m^3.sec^{-1})**	**Return interval (years)**	**Method**
4.7	549.02	1.4	Periodic regression
4.765	562.51	1.5	Flow duration curve
4.85	580.14	1.5	Percentile 0.33
5.15	642.39	2	Percentile 0.5

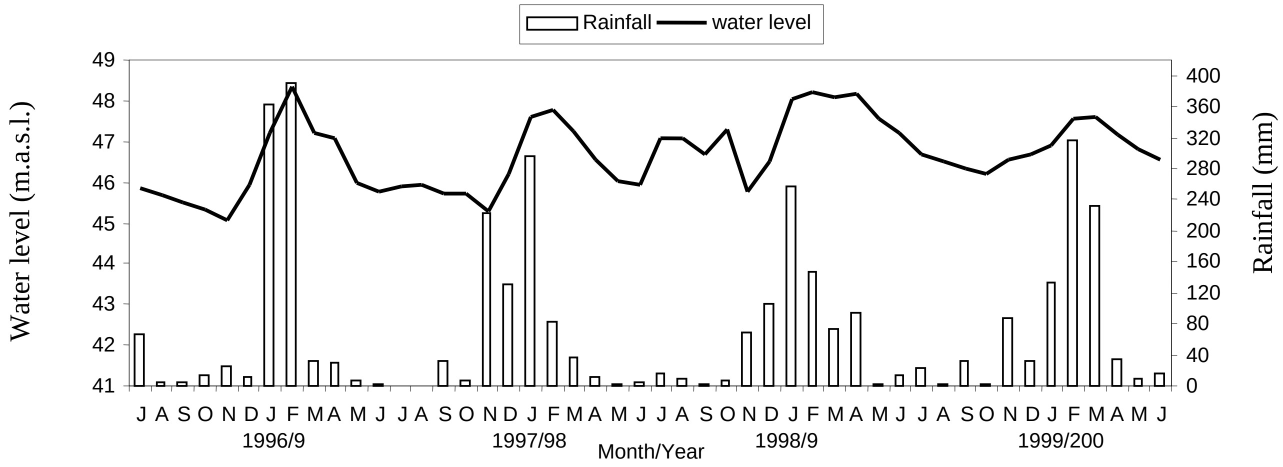


Figure 2.4 Mean monthly rainfall (mm) at Makhanga and water level (meters above sea level – m.a.s.l.) on Shire River at Chiromo, Lower Shire Floodplain, from July 1996 to June 2000.

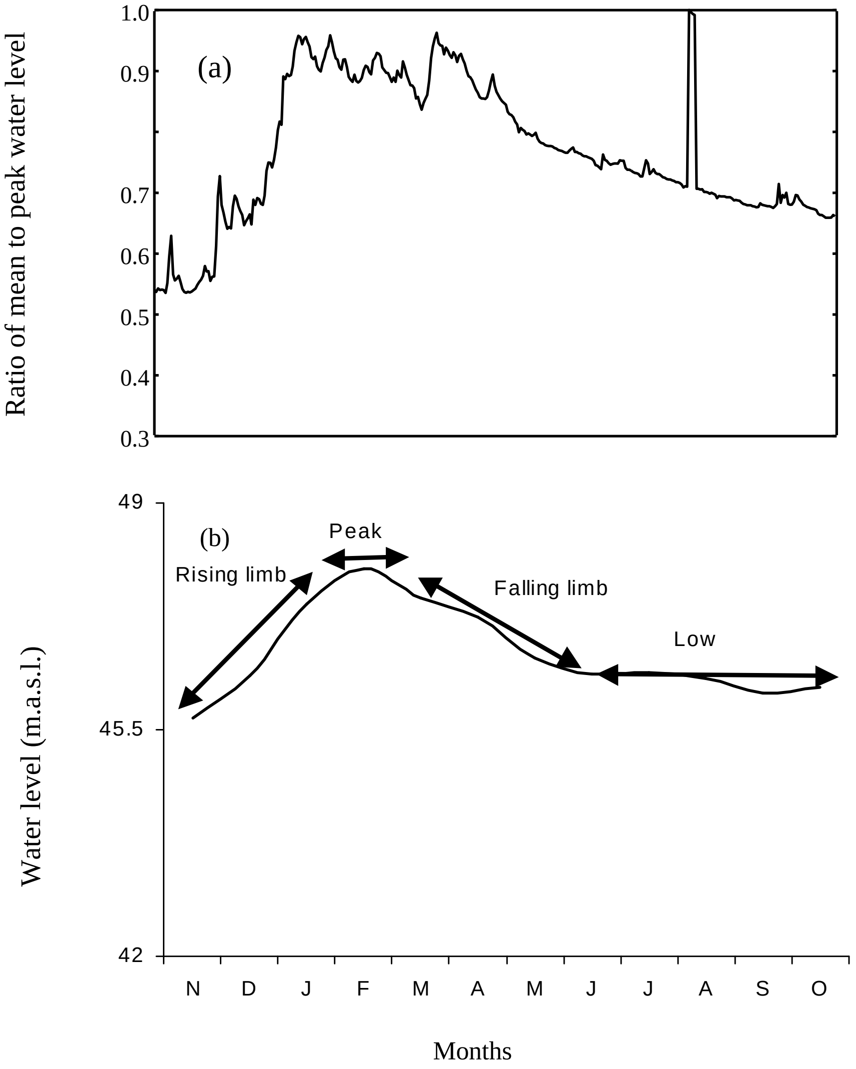


Figure 2.5 The flood regime in the Lower Shire Floodplain: (a) ratio of mean monthly water level to peak level (flood-curve) and (b) typical hydrograph of the floodplain. Graphs based on 1980/81-1999/2000 records from Chiromo.

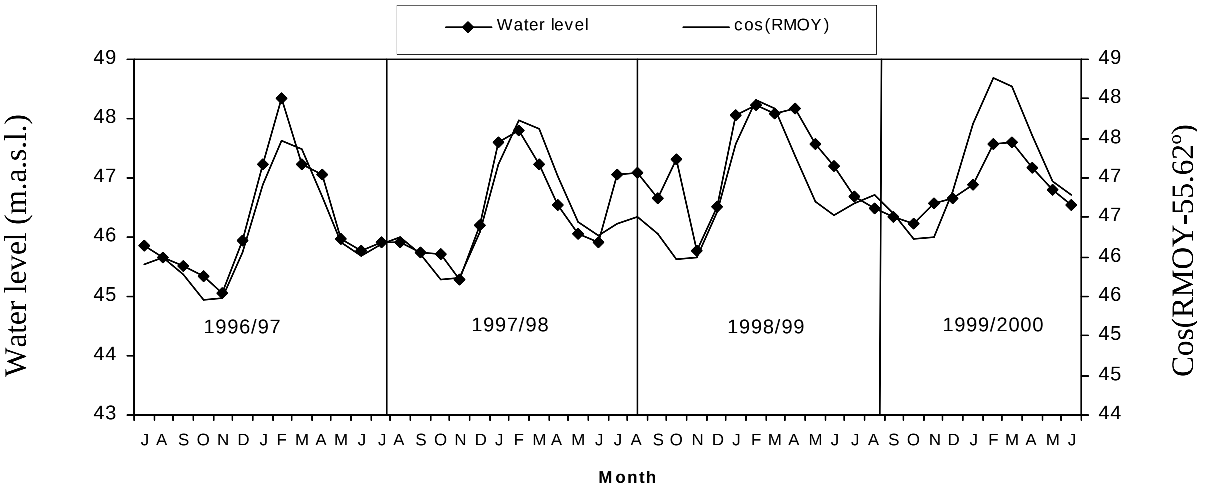


Figure 2.6 Seasonal cyclic trends of the Shire River at Chiromo with respect to monthly water level, for the 4-year period (1996-2000), fitted with a cosine curve. See Equation 2.8 for the regression equation of the cosine curve.

Table 2.5 Monthly mean ± standard deviation of the water budget component in the Lower Shire Floodplain (mm). Net basin supplies derived from the estimates of its components (NBS[C]) and Change in water storage (CIS), Equations 2.2 and 2.3.

Month	**Precipitation**	**Runoff**	**Evaporation**	**NBS-C**	**CIS**
Jan	183.1 ± 75.6	137.9 ± 16.2	176.2 ± 12.6	144.8 ± 63.2	1011.5 ± 417.7
Feb	97.5 ± 85.4	158.4 ± 13.5	151.3 ± 11.3	104.6 ± 74.3	517.1 ± 510.1
Mar	111.7 ± 75.9	151.8 ± 10.9	161 ± 12.7	102.5 ± 63.4	-116.5 ± 650.9
Apr	39.1 ± 34.8	134.8 ± 14.8	144.7 ± 16.3	29.3 ± 18.7	-404.9 ± 708.5
May	14.4 ± 13.1	111.9 ± 12.9	132.8 ± 16.1	-6.5 ± 2.9	-518.2 ± 714.3
Jun	16.7 ± 14.5	101.5 ± 10.8	112.5 ± 15.5	5.7 ± 0.9	-243.3 ± 586.9
Jul	17.5 ± 14.9	98.9 ± 11.1	122.4 ± 58.8	-6.1 ± 4.8	-54.6 ± 481.4
Aug	9.1 ± 7.9	90.2 ± 14.8	172.4 ± 56.2	-73.1 ± 48.2	-196.9 ± 191.9
Sep	4.5 ± 6.9	80.1 ± 11.4	239.5 ± 57.6	-154.1 ± 50.6	-218.9 ± 275.4
Oct	21.5 ± 30.9	77.3 ± 11.7	314.9 ± 53.7	-135.6 ± 22.7	-80.4 ± 450.7
Nov	68.3 ± 34.9	64.3 ± 13.4	268.2 ± 53.6	67.1 ± 18.5	-297.5 ± 335.7
Dec	181.1 ± 65.2	93.7 ± 13.2	207.7 ± 54.5	-137.4 ± 10.8	644.9 ± 95.7
Annual total	764.5	1301.7	2203.6	-137.4	42.3

In Equation 2.3, outflow (*O*) and inflow (*I*) from and into the floodplain are assumed to balance because mean annual water discharge at Chikwawa (inlet to the floodplain) and Chiromo (outlet from the floodplain) are almost equal (range: 507 – 510 $m^3.sec^{-1}$) (Table 2.3). Total diversion (*D*) over the year is assumed negligible because there are no major diversions in the floodplain. This establishes *NBS-R* as equal to the difference in water levels in the floodplain ($NBS[R] = \Delta S$). Overall, there is an annual positive water balance (42.3 mm) generated by *NBS*[*R*]. This means that more water appears to be retained in the floodplain than the amount flowing out (Table 2.5), although monthly variations do occur. From December to February, during a rising/high flood regime, more water is generated by *NBS* than is let out by between 50 and 100% (Table 2.5). Generally, between March and November, the reduction in *NBS* is greater than the amount of water kept in the floodplain by >100%. Putting together the factors that affect the water supply to the floodplain (e.g. *NBS*[*C*], *NBS*[*R*]) shows a water deficit of 95.1 mm per year. Yet if there is a net loss, how does the floodplain maintain water throughout the year? This question is addressed in the next section.

(iv) Seasonal changes in water levels

A summary of the relationship between water level and seasons is reflected in the periodic regression models in Table 2.6. The Correlation between water level ($0.44 \le r^2 \ge 0.90$) and the month of the year (MOY) were significant ($0.0000 \le p \ge 0.05$). Seasonal cyclic trends in water level in the floodplain, based on the level in the Shire River at Chiromo, can be seen in Figure 2.6. Water levels in all the study sites on the Shire River and its tributaries vary seasonally. The variations are strongly positive ($0.44 \le r^2 \ge 0.90$); significant ($0.0000 \le p \ge 0.05$); and in phase with each other (Table 2.6).

(v) Inter-sectional relationship of water level in the Shire River with the floodplain

Forward stepwise multiple regression of water level (m) of the Shire River at Chiromo (the dependent variable) and water levels at the other gauging stations (independent variable) revealed that only the levels at Mangochi, Zalewa and in the Ruo River had a significant impact ($r^2 = 0.84$; $p < 0.01$) on the level in the Shire River at Chiromo, and hence the floodplain. The following regression model can best describe the relationship:

$$\begin{array}{llllll} \mathrm{CH} = & -\,4.126 & +\,1.451\mathrm{RU} & -\,0.304\mathrm{MH} & +\,0.315\mathrm{ZW} & -\,0.339\mathrm{CK} \\ & p=0.0003 & p=0.0000 & p=0.059 & p=0.095 & p=0.302 \quad (r^2 = 0.84;\ p<0.001) \end{array}$$

where CH = on Shire River at Chiromo, RU= Ruo (Lower Shire), MH = Mangochi (Upper Shire), ZW = Zalewa (Middle Shire), CK = Chikwawa (Lower Shire).

Figure 2.7 shows bivariate regression lines for individual sites. Judged from the coefficient of determination ($r^2 = 0.90$; $p < 0.001$), the Ruo River exerts the greatest impact on the water level of the Shire River at Chiromo, and hence the level in the Lower Shire Floodplain.

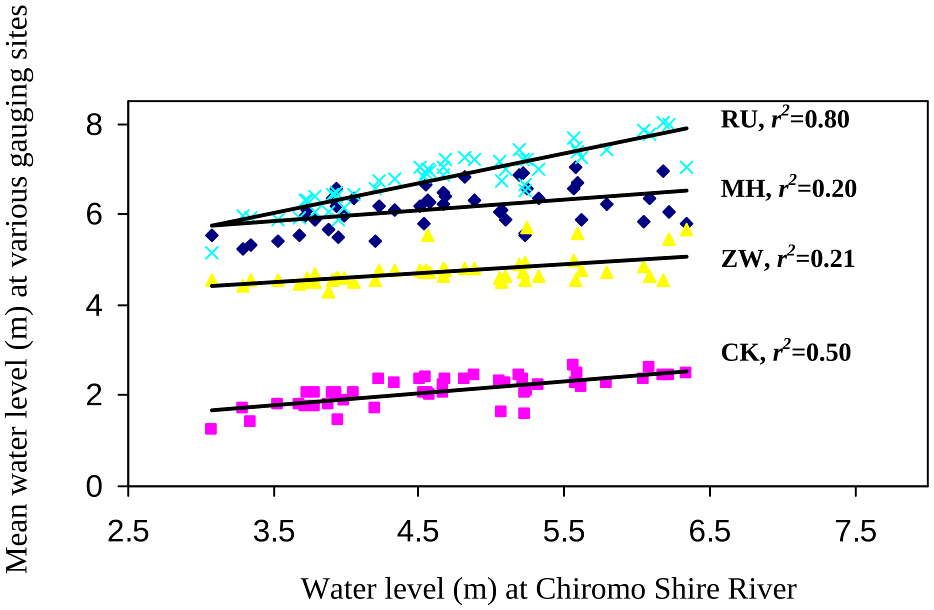


Figure 2.7 The relationship between water levels of the Lower Shire Floodplain and Ruo River (RU), Shire River at Mangochi (MH), Zalewa (ZW) and Chikwawa (CK). The water level in the Lower Shire Floodplain is based on the level at Chiromo. Solid lines are regression lines: r^2 = coefficient of determination.

Table 2.6 Relationship between water level (m) and seasons (MOY) in the various sections of the Shire River and its tributaries. The peak and amplitudes are calculated from Equation (3.10 – 13), r^2 = coefficient of determination, *p*=level of significance, Int = intercept

Sections and tributaries of Shire River	Parameter	Predictive equation	Amplitude	Peak	r^2	*p*
Upper Shire	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 6.07 + 0.346\sin(RMOY) - 0.215\cos(RMOY)$ $p = 0.0000$ $p = 0.0012$	0.82 m	3rd May	0.90	0.0000
Middle Shire	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY) + \beta_3\sin(HMOY) + \beta_4\cos(HMOY)$ $= 4.07 + 0.004\sin(RMOY) - 0.007\cos(RMOY) + 0.0319\sin(RHMOY) + 0.0121\cos(RHMOY)$ $p = 0.0067$ $p = 0.1936$	0.07 m	11th March	0.71	0.0437
Middle Shire	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 4.71 + 0.1247\sin(RMOY) + 0.125\cos(RMOY)$ $p = 0.0099$ $p = 0.0098$	0.1767	15th February	0.70	0.0043
Lower Shire	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 2.02 + 0.189\sin(RMOY) + 0.044\cos(RMOY)$ $p = 0.0082$ $p = 0.454$	0.39	19th March	0.57	0.0220
Lower Shire Floodplain	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 4.677 + 0.671\sin(RMOY) + 0.46\cos(RMOY)$ $p = 0.0028$ $p = 0.021$	1.63 m	26th February	0.73	0.0028
Ruo River	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 6.811 + 0.431\sin(RMOY) + 0.216\cos(RMOY)$ $p = 0.0021$ $p = 0.0623$	0.96 m	5th March	0.72	0.0035
Thangadzi River	Mean level	$Y = Int + \beta_1\sin(RMOY) + \beta_2\cos(MOY)$ $= 0.85 + 0.191\sin(RMOY) + 0.032\cos(RMOY)$ $p = 0.0035$ $p = 0.527$	0.48 m	23rd March	0.64	0.0105

Note: $RMOY = MOY(2\pi/12)$ (i.e., MOY transformed to radians of year)

2.4 Discussion

Local climate of the Lower Shire River and its influence on the floodplain

The climate of the floodplain seems to be influenced internally by the topography, altitude and floodplain itself, and externally by maritime pressure belts in the Indian Ocean. Situated at an altitude of about 70 meters above sea level (m.a.s.l.) the floodplain generally has high average temperatures. This is the case because there is a general decrease in temperature with increasing altitude of about 0.55 ºC for every 100 meters at night and increasing about 0.92ºC for every 100 m during the hot part of the day (Torrance 1972).

Topography influences the climate because the floodplain lies in a valley bordered by hills that act as a funnel, fanning any air masses that pass through the valley. Bordering the floodplain are Thyolo Escarpment on the east, the Kirk Range and Matandwe hills on the west and the Namalombo hills in the southwest (SVADD 1975). As a result, maritime air masses that enter the Zambezi valley are fanned outward along the Shire River (Lineham 1972). These air masses have two effects, either they bring rain (May- July) (Lineham 1972) or coupled with high air temperatures, they increase the rate of evaporation from the floodplains (Appendix 1). Locally, the floodplain acts as a temperature reservoir, due to the low diurnal water temperature range (Table 2.7).

Table 2.7 Maximum and minimum air and water temperatures in the Lower Shire Floodplain.

Month	**Air temperature (ºC)**			**Water temperature (ºC)**		
	Min.	max.	Δ	Min.	Max.	Δ
January	15	28	13	26	30	4
February	16	29	13	25	30	5
March	19	35	16	26	29	3
April	21	36	15	26	29	3
May	23	34	11	22	28	6
June	23	32	9	20	27	7
July	24	34	10	19	23	4
August	23	34	11	18	24	6
September	23	33	10	19	24	5
October	21	32	11	22	27	5
November	17	30	13	25	30	5
December	17	28	11	26	29	3

Despite its relatively small size, it is possible that cool air from the floodplain moves over the heated land during the day (floodplain breeze) and at night cool air from the land moves over the floodplain. Such air exchange between day and night has also been reported to reduce diurnal temperature fluctuations in Lake Malawi (Torrance 1972).

Proposed classification of the climate for the Lower Shire Floodplain:

(i) Koppen classification System

A widely used method for classifying climate is the Koppen system (McKnight 1990). The method uses easily acquired statistics on mean monthly values of temperature and precipitation (Gordon *et al.* 1992). The nomenclature for labelling each climate type uses a combination of letters according to Chapman *et al.* (1985) (Table 2.8). Based on this system, the climate of the Lower Shire Floodplain can be classified as "tropical hot-rainy" or "Awa", where:

"*A*" = a tropical rainy climate with no month cooler than 18ºC (Table 2.8),
"*w*" = winter drought (i.e. winter is the period of least rainfall) (Table 2.8), and
"*a*" = warmer summer temperatures (Table 2.8).

Table 2.8 Description of letters and nomenclature of the Koppen climate system, adapted from Chapman *et al.* (1985). [1]The first letter refers to the general category of climate.[2]The second letter refers to the season of least rainfall.[3]The third letter fine-tunes the description of summer temperatures (Gordon *et al.* (1992).

First letter[1]	**Description**	**Second letter[2]**	**Description**	**Third letter [3]**	**Description**
A	Tropical rainy climate, with no month cooler than 18ºC	“s”	Summer drought	“a”	Warmer than “b”
B	Arid climates, where evaporation exceeds rainfall (classification by rainfall)	“S”	Semi-arid	“h”	Hot
		“W”	Arid	“k”	Cold
				“H”	Highland climate
C	Humid warm climate, with temperatures in the cooler months less than 18ºC but more than -3 ºC	“w”	Winter drought	“b”	Warmer than “c”
D	Humid cool climate, with the coldest month below -3ºC and the warmest above 10ºC	“f”	Rain all year round		
E	Tundra climates, with the warmest month below 10ºC	“m”	Monsoon-type rains		

(ii) Hydro-climatic seasons

The climate of the Lower Shire is characterised by high temperatures, with two well-defined seasons: a hot-dry season from May to October and a warm-wet season from November to April (SVDD 1975). This description of seasonal characteristics of the climate fits well with the ("*Awa*") classification proposed above. However, both the description and classification are not sufficient aids on which to base water management of the floodplain, because they leave out distinct features of the flood regime that shape the climate of the floodplain. By adopting a hydro-climatic approach, the two seasons have been further divided into four. The hot-dry season has two parts: April to June that is humid and cool with a receding flood regime (Table 2.2). It is only the second half of the season that qualifies for "hot-dry" with a low flood regime. The warm-wet season is also subdivided into two periods, both of them hot-wet. However, October to December is further characterised by strong winds and rising flood regime, while January to March is a hot-wet-humid season with peak flood regime.

This new hydro-climatic season classification is relevant for the management of the floodplain's water and fisheries because it has been demonstrated that climate is linked to the dynamics of the floodplain hydrology. Furthermore, this link provides the basis for future research on climate change because the dynamics of the floodplain water and biota can be used as reference points for changes that might occur due to a rise in temperature or changes in any of the climatic parameters.

This is the reason why hydro-climatology has recently become a prominent field of research. This has been due to the realisation that, from a hydrological perspective, regional variations in precipitation and potential evaporation tend to be mutually reinforcing since low precipitation is usually associated with increased potential evaporation (Fowler 1999). Furthermore, the seasonal variables of the hydrological cycles (e.g. annual runoff, flood and flow) are largely determined by mean annual rainfall (Zhang *et al.* 2001).

Impact of climate and water supply on the water budget of the floodplain

Hydrological characteristics of a river are primarily a reflection of the size and climate of the catchment (Pike 1972, Welcomme 1985, Gordon *et al.* 1992, Knighton & Nanson 2001). It is important to note that while there is a direct relationship between rainfall and water level in the floodplain, the relationship is not significant ($p > 0.05$), yet the relationship was significant with the slope of change in water level ($p < 0.05$) (Table 2.10). This means that although rainfall brings water to the floodplain, the quantity of rain does not immediately result in a rise in water level, rather it is the rate of change in the level that is most affected. This is understandable since the quantity of water reaching the river (runoff) is the difference between rainfall and evaporation (Chow 1964, Gordon *et al.* 1992, Brinkmann 2000). Ecologically, this is very important. Young *et al.* (2000) reported that changes to the incidence of flood, flow variabilities and rates of change of flow were more important than reduction in discharge in providing important cues to fish for life-cycle events such as spawning and migration.

It is also interesting to note the inverse relationship between air temperature, wind speed, evaporation, evapotranspiration, potential-evapotranspiration and water level (Table 2.9). This indicates that an increase in any one of these climatic parameters leads to a significant ($p < 0.05$) reduction in water level in the floodplain. The relationship is more complex than it appears, since evaporation occurs even during months of high rainfall (Table 2.2).

Table 2.9 The correlation coefficient (r) between mean monthly hydrologic and climatic parameters in the Lower Shire Floodplain, and between catchment areas (Km^2) and flow parameters (runoff, mean annual flow and baseflow) of the three sections of the Shire River and tributaries. The relationship between parameters is linear unless otherwise specified as P = power relationship, RH (%) =(%) relative humidity, PE=potential evaporation, E=Evaporation, ET=evapotranspiration, , *=significant at $p<0.05$.

Hydrologic parameters	**Climatic parameters**										**Catchment area (km^2)**
	RH (%)	**Rainfall (mm)**	**Air temperature (ºC)**	**PE (mm)**	**E (mm)**	**ET (mm)**	**Thunder (days)**	**Wind (m.sec^{-1})**	**Sunshine (hrs)**	**Cloud cover (octas)**	
Water temperature (ºC)	0.54	0.79	0.66	0.48	0.07	0.44	0.85	-0.22	-0.44	0.88	
Mean water level (m)	0.81	0.45	0.10	-0.11	-0.49	-0.18	0.34	-0.69	-0.56	0.68	
Mean minimum water level (m)	0.78	0.25	-0.08	-0.28	-0.60	-0.35	0.15	-0.73	-0.54	0.55	
Sum of daily water fluctuation (***SWF***) (m)	0.60	0.17	-0.03	-0.16	-0.45	-0.22	0.09	-0.55	-0.31	0.42	
River stage (days)	0.53	0.01	-0.28	-0.37	-0.55	-0.41	-0.13	-0.58*	-0.28	0.20	
Level above bankfull	0.87	0.42	-0.01	-0.22	-0.59*	-0.29	0.29	-0.77*	-0.62*	0.67*	
Slope of change of level	0.06	0.79 *	0.44	0.44	0.27	0.45	0.77*	0.12	-0.39	0.51	
Mean annual runoff (mm)											0.92 *
Mean annual flow (m^3.sec^{-1})											0.99 (P)*
Baseflow (%)											0.91 (P)*

Table 2.10 Comparison of climatic parameters in selected floodplains in Southern Africa.

Floodplain	**Rainfall (mm)**	**Evapotranspiration (mm)**	**Temperature (ºC)**		**Reference**
			Water	Air	
Shire	765	1836	18-30	15-36	This study
Kafue	762	1650	15-32	20.5-37	Tait (1967)
Okavango	650	1800	9-38	7.0-35.5	Wilson & Dincer (1976)

Compared to the Kafue and Okavango floodplains which receive more or less a similar quantity of rainfall, and have similar general climatic status (Ellenbroek 1987; Merron 1991), the Lower Shire Floodplain experiences far greater evapotranspiration than the other two, and also has a relatively narrow diurnal temperature variation (Table 2.10). This could be caused by the invasion of the Shire valley by the maritime winds that accelerate evaporation as well as air and heat exchange between the water and land. The insignificant contribution of rainfall to the water budget of tropical floodplains has been recognised by Welcomme (1985), which leads to either an overall water budget deficit or, with a few exceptions, to a just balanced budget (e.g. Okavango). Due to methodological difficulties few studies have been carried out in tropical African floodplains, hence few studies are cited in this chapter (Table 2.10). However, using a net basin supplies (***NBS***) approach it has been possible to isolate the impacts of precipitation, runoff and evaporation. The *NBS* approach has been widely used in assessing water budgets of the North American Great Lakes (Brinkmann 1983, 2000).

Three major results have emerged from the *NBS* water-budget analysis of the Lower Shire Floodplain. Firstly, during months of high precipitation, rainfall accounts for the greatest supply of water to the floodplain; during months of low rainfall runoff is important, and during the hot-dry and hot-rainy periods evaporation has the greatest impact and hence, drives the *NBS*[*C*]. It was shown that the Lower Shire Floodplain has an overall annual negative water budget of -137.4 mm.year^{-1}. It is important to note that the floodplain experiences the highest water loss through evaporation between October and November, once rains have started (Figure 2.2). A similar scenario was reported in the North American Great Lakes by Brinkmann (2000), which he attributed to strong winds during the rainy season that led to even greater evaporation during such wet seasons. Secondly, the floodplain's overall water inflow and outflow (*NBS*[*R*]) results in a net positive water budget of 42.3 mm.year^{-1}, despite the fact that the difference between water inflow and outflow is negligible (i.e. mean annual inflow is 510.6 m^3.sec^{-1} and outflow is 509.1 m^3.sec^{-1}) (Table 2.3). This points to the fact that there is a net rise in water level in the floodplain despite the volume of outflow cancelling that of inflow. Similarly, the Okavango Delta experiences high evaporation with outflow (2% of the inflow), which almost balanced inflow (Wilson & Dincer 1976, Welcomme 1985, Merron 1991). Thirdly, summing estimates of $NBS[C]$ and $NBS[R]$ results in a net water budget deficit of -95.1 mm.year^{-1}.

Although one might, therefore, expect the floodplain to dry up completely every year, this does not happen. This might be explained by understanding the hydrological cycle. In the hydrological cycle, a large proportion of the water that falls to the ground in form of rainfall evaporates directly (evaporation) or through plants (evapotranspiration), and this process of water loss depends on solar energy (hours of sunshine per day) (Davis & DeWiest 1966). The difference between rainfall water and the amount that is retained on the surface of the soil is called “runoff”. Part of the water which continues to infiltrate below the surface soil (subsurface water) might flow laterally into the streams, then into the ground-water table and eventually reach the stream channel to provide the baseflow (Hawkes 1975; Hamilton & Bergen 1984) (Equation 2.1). Alternatively, some subsurface water may remain above the water table in the zone of unsaturated flow; or might even move farther below the water table to become “ground water” in the zone known as the “phreatic zone” (Davis & DeWiest 1966).

The water level in the floodplain may likely be maintained by the recharge from the groundwater or the phreatic zone. Welcomme (1985) suggested that permanent pools and lagoons (in the floodplain) must either be filled annually to a depth greater than the loss by evaporation, or receive inflow from groundwater. The possibility that the Lower Shire Floodplain receives an amount of water exceeding evaporation does not seem feasible, since evaporation is high during the period of high rainfall. Therefore, this leaves recharge by groundwater as the most plausible option. The likely recharge from groundwater is reflected in a high estimated baseflow of 59% (Table 2.3). This volume enables the floodplain to have water throughout the year. Determination of the status of groundwater in the floodplain is beyond the scope of this work, but such information would make an important contribution to a better understanding and ultimately, management of the floodplain.

Seasonal predictability of the flood regime

Seasonal predictability of flow is one of the most important ecological and economic factors in river floodplain fisheries and water management (Welcomme 1985, Resh *et al.* 1988, Gordon *et al.* 1992, Young *et al.* 2000). Predictable river flow is important ecologically because flow influences evolution and timing of life-history cycles in river and floodplain biota (Lowe-McConnell 1964,1987, 1979, 1985, Bayley 1981, Junk 1982, Holland *et al.* 1983, Resh *et al* (1988) (see Chapters 4 and 5).

Annual hydrographs of the various sample gauging station on the Shire River depicted variability of factors that contribute water to the river (such as rainfall and baseflow). Furthermore, it has been shown that the flood regime in the Shire River and the Lower Shire Floodplain is seasonal, as confirmed by the harmonic analysis and periodic regression that showed a positive ($0.44 \leq r^2 \geq 0.90$) and significant ($0.0000 \leq p \geq 0.05$) variation (Table 2.6). Therefore, it can be concluded that the water level and flood regime of the Shire River and the Lower Shire Floodplain is highly predictable at a confidence level of 95%.

This finding fulfils one of the most important attributes of river ecology "predictability". It confirms the theory which states that "if data show that a seasonal pattern repeats itself nearly the same way each year, then the pattern is predictable" (Resh *et al.* 1988). Seasonality in river flows is a natural pattern which, in the absence of anthropogenic influence, is normally broken or altered by natural changes in seasonal events, such as rainfall (Welcomme 1985, 1986, Petts & Foster 1985, Junk *et al.* 1989, Bayley 1991). In practice, it means that the predictability of the flood regime of the Lower Shire Floodplain will remain as it is now as long as there are no major changes in the climate, or alteration of the river flow by construction of dams or irrigation channels.

Effect of hydrological characteristics of the catchment on the flood regime

Inter-sectional differences in the quantity of water that the upper, middle and lower sections of the Shire River contribute to the floodplain flood regime became clear when difference between gauging stations were analysed. On the basis of forward stepwise multiple regression analysis, the data showed that the stations closer to the floodplain (e.g. Ruo and Chikwawa) have more significant impact $(0.50 \leq r^2 \geq 0.80,\ p < 0.01)$ on water level in the floodplain than those farther away (e.g. Zalewa and Mangochi) $(0.20 \leq r^2 \geq 0.27,\ p < 0.01)$ (Fig. 2.7).

Working in semi-arid zone rivers, Knighton & Nanson (2001) reported that inter-station differences in hydrological characteristics of the rivers were related to distance and area, and that variations could be explained by the distance from the river source. There are similarities between Knighton & Nanson’s (2001) observation and the inter-sectional difference recorded here. It appears that inter-sectional differences in terms of contribution to water level in the floodplain are related to (a) the location of the section in relation to the floodplain, and (b) the duration or distance that the water travels. This is confirmed by the significant relationship found between water level in the floodplain and the river sections of the Shire River as follows: Ruo (r^2 = 0.80) > Chikwawa (r^2 = 0.50) > Zalewa (r^2 = 0.27 > Mangochi (r^2 = 0.20), in the order of proximity to or distance away from the floodplain (Fig. 2.7).

Such inter-sectional variation of hydrological characteristics with area (location) and duration of travel have been called “scale-dependent” events (Knighton & Nanson 2001). A synopsis of scale theory is provided below as a prelude to a better definition of the hydrological characteristics of the three sections of the Shire River as they relate to the floodplain. This will improve the understanding of the predictions of the flood regime and suggestions for management of the floodplain.

“Scale” has been defined as temporal (duration) and spatial (area) dimensions at which phenomena are observed (Peterson & Parker 1998). “Scale Theory” is one of several emerging ecological theories that have been proposed to explain observed patterns which might be the result of numerous processes with different origins and scales in space and time (Wiens 1989, Peterson & Parker 1998). In many ecological studies, scales of observation are set *a priori* (e.g. water level at one site). However, moving up and down the scales, dominant patterns and processes may change and as a result, important aspects of the system can be easily overlooked (Peterson & Parker 1998, Rietkerk *et al.* 2002). It has been recently recognised that quantitative interactions between different sub-components of ecosystems can only be adequately described by observing phenomena at scale both above and below the focal level (Rietkerk 2002). Therefore, it seems plausible that the hydrological characteristics of the Lower Shire Floodplain can be best explained through scale theory.

First, the spatial aspect of scale can be explained by the relationship between the catchment area (km^2) and the discharge characteristics of the various sections of the Shire River. Baseflow (%) and mean annual flow ($m^3.sec^{-1}$) varies significantly as a power function of catchment area (i.e. $y=ax^c$), while mean annual runoff (mm) varies significantly as a linear function of catchment area (i.e. y=a+cx) (Table 2.9). Thus, on one hand, the quantity of water flowing from the catchment (runoff) into the river increases with decreasing catchment area. On the other hand, the quantity of mean annual flow and baseflow increases at a much higher rate with increasing catchment area. A similar type of relationship has been observed in several large rivers from all continents (McMahon 1982, Gordon *et al.* 1992, Knighton & Nanson 2001).

Secondly, the temporal aspect of scale can be explained by the inter-sectional variation in water level, where the water levels at stations closer to the floodplain (e.g. Ruo and Chikwawa) have significant impact ($0.50 \leq r^2 \geq 0.80$, $p<0.01$) on water level in the floodplain than those farther away (e.g. Zalewa and Mangochi) $(0.20 \leq r^2 \geq 0.27,\ p < 0.01)$ (Figures 2.7 and 2.8). This indicates that although flooding in the floodplain might be caused by locally generated runoff, the water level in the floodplain is likely to depend on inputs from Lake Malawi as well as catchment areas in the middle and lower sections of the river.

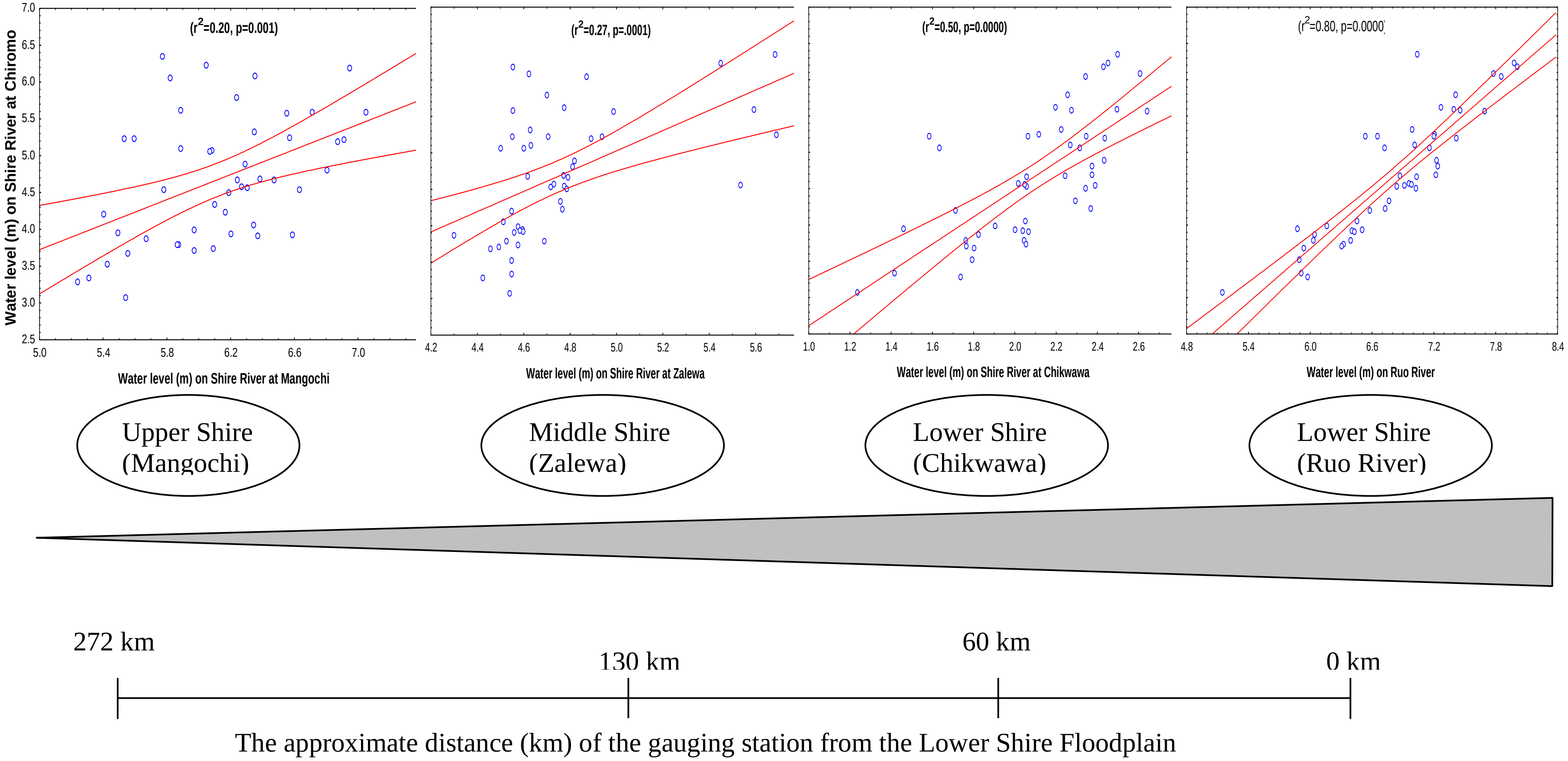


Figure 2.8 Correlation of water levels (m) between selected gauging stations and the Lower Shire Floodplain. The water level in the floodplain is based on the level in the Shire River at Chiromo. The dark triangle is a graphic illustration of the increasing correlation between the gauging stations at Mangochi, Zalewa, Chikwawa and Ruo with the Lower Shire Floodplain.

However, the farther away from the floodplain the section of the river is, the less is the impact. This could be explained by transmission losses as the distance from the source increases. The transmission losses were first reported by (Pike 1972), who noted a time lag (four months) between high water levels in Lake Malawi at Mangochi (April/May) and the Shire River at Liwonde (August). It is likely that the flood wave gets attenuated (Shaw 1988, Knight & Shiomo 1996) by the time it reaches the Lower Shire Floodplain. Similar observations on flood-wave attenuation with distance from source were reported for the Okavango Delta (McCarthy et al. 1998), Niger Delta (Welcomme 1985) and the Kafue floodplains (Ellenbroek 1987).

2.5 Conclusion

The Government of Malawi is planning construction of more barrages and dams on the Shire River for the generation of electricity and irrigation (Ministry of Water Resources 2003). Planners need to ensure that current river flow regime is maintained in order to avoid serial discontinuity (Ward & Stanford1983) as well as maintaining the hydrologic connectivity (Junk *et al.* 1989, Ward & Stanford 1995, Heiler *et al*. 1995, Pringle 2001). Serial discontinuity defines the effect a dam has on a river by disrupting the continuum and causing upstream-downstream shifts in biotic and abiotic parameters and processes (Hauer & Stanford 1982, Stanford *et al.* 1988, Ward & Stanford 1983).

Since the bankfull water level of the Lower Shire Floodplain was established empirically to be within the range of 4.7 to 5.15 m (or 549.79-643.15 $m^3.s^{-1}$) (Table 2.4), water regulation on the river should allow these levels to be maintained, especially between December and March (the normal flooding season). This will allow hydrologic-connectivity between the river and the floodplain to provide breeding cues for fish (Rowntree & Wadeson 1998) and create favourable habitat in the floodplain for feeding as well as enhancing recruitment success (Chapter 5 and 6).

The scale-dependence of inter-sectional variations in water level is important for the management of the Shire River particularly as regards fisheries in the floodplain. First, sections of the river and tributaries with smaller catchment areas are prone to flash floods that reach the floodplain with minimal transmission losses, while flow in large catchment areas takes more time to reach the floodplain. Therefore, the smaller catchments are more sensitive to any form of river regulation, such as the construction of dams. For example, dam construction on the Ruo would be detrimental to the floodplain because it would alter the flood-pulse of the Ruo and consequently that of the floodplain. Secondly, the effect of catchment proximity to the floodplain means that alteration of flow in river sections nearer to the floodplain will cause significant changes in the hydrology of the floodplain. This is coupled to flow variability in the catchments of lower sections, which are relatively unstable (C_v 0.20 – 0.75) (Table 2.3). Therefore, construction of dams on the Lower Shire as proposed by the Minstry of Water Resources, would have significant changes from the norm and hence, serious consequences for the fisheries and livelihood of the riparian communities of the Lower Shire Floodplain, and requires careful planning.

The knowledge of climate and hydrology of the Lower Shire Floodplain generated in this study sheds light on the impact of climate and the river flow on the flood regime of the floodplain. This knowledge forms a strong basis for the understanding of the characteristics and dynamics of the habitats of the floodplain, the life history cycles and strategies of the fish and ultimately the management of the floodplain fisheries.

Chapter 3

Characterisation of habitats in the Lower Shire Floodplain

3.1 Introduction

Seasonal changes in water flow make floodplain systems complex, dynamic and diverse habitats. This is mainly caused by the process of sediment deposition, which forms bars, levees, swales, ox-bow lakes, and backwaters, each with different small-scale habitats having dynamic physico-chemical and nutrient conditions (Lorenz 1997, Ward *et al*. 1999, Schramm *et al*. 2000). Habitats of river-floodplain systems are primarily defined by the periodic inundation of the system, which is influenced by the seasonal and cyclic pattern of rainfall, runoff, groundwater recharge, local and regional climate as well as river discharge or flow. River flow has been deemed the "maestro that orchestrates the pattern and processes of the river" (Graf 1988) and is extremely important in terms of the distribution of biota (Mulholland 1981, Welcomme 1986, Junk *et al.* 1989, Bayley 1991, Fisher & Grimm 1991). The seasonal flood regime imposes constant but repetitious habitat instability (Odum 1967). Therefore, effective management strategies for floodplain fisheries are best developed after a thorough consideration of the characteristics of the habitats that make up the ecosystem.

To better describe the Lower Shire Floodplain, Tweddle & Willoughby (1979) separated the system into three major habitats viz. riverine, lagoon, and marsh. The riverine habitat comprises the main channels of the Shire River and its tributary the Ruo River, the banks of which are dominated by grasses of the genus *Echinochloa*. Lagoons are large open water bodies usually less than 4 m deep, containing dense beds of mainly *Ceratophyllum* and *Nymphaea*, separated by small channels and subjected to low flow rates (Tweddle & Willoughby 1979). The marsh ecosystem comprises areas permanently covered in shallow, standing waters (≤2 m deep) with rooted plants of mainly *Echinochloa*; the fringes become dry during low flood, and inundated at peak flood (Howard-Williams 1973). Given that these classifications are largely descriptive and based mainly on water depth, the distinction, for example, between marsh and lagoon is not very clear. Earlier efforts to characterise the Lower Shire Floodplain using physico-chemical features indicated a tendency for the marshes to lose and gain certain chemicals at particular times of the year (Hastings 1973, Howard-Williams 1973, Hall *et al*. 1977). However, these figures were based on two months of data and gave an inadequate picture of true annual “profit” and “loss” (Hastings 1973). The qualitative description of the habitats provided by Tweddle & Willoughby (1979) and Howard-Williams (1973) is not sufficiently robust considering the fact that there is a significant seasonal water level fluctuation (Chapter 2). Therefore, there is a need for a more acceptable, quantitatively and statistically robust measure of habitat type for fisheries managers to fully understand the effect of water fluctuation and habitat on the key commercially important fish species of the Lower Shire Floodplain.

The nutrient and water exchange between land in the catchment and the floodplain itself influences the characteristics of the floodplain habitat. The “flood-pulse” concept or the pulsing of river discharge (Junk *et al*. 1989) has been used to explain this exchange of energy and matter. In this regard, Junk *et al.* (1989) observed that the floodplain is an “aquatic/terrestrial transition zone” (ATTZ), with the inshore edge of the aquatic environment being termed “moving littoral”. Given that phosphorus and nitrogen are biolimiting nutrients (Welcomme 2001) both on land (Sanchez 1976) and in water (Wetzel 1975), by comparing the levels of these elements in the terrestrial and aquatic zones of the ATTZ, it should be possible to determine the pattern and extent of energy and matter exchange.

The quantitative characterisation of habitats or classification (Barnes 1984) can be achieved by dividing the whole physical and chemical data set into increasingly select groups, or by starting with a particular data set and combining and recombining them to form successively larger groups (Pielou 1977). A number of methods for classifying stream habitats have been developed. These include discriminate and cluster analysis, where membership in a group can be predicted from a set of variables (Gordon *et al*. 1992). These variables might be actual measurements, similarity/dissimilarity indices or ordination scores from a principal component analysis. Minchin (1987) proposed another technique, viz. multidimensional scaling (MDS) and Clarke & Warwick (1997) have packaged multidimensional scaling (MDS) and principal component analysis (PCA) into a computer programme called Primer Software. However, these classification methods are only correlative and suggestive of cause-and-effect relationships and can be only as complete as the list of independent variables included (Fisher & Grimm 1991). For example, if the model explains 60-90% of the variance, then a substantial fraction (10-40%) remains unexplained. Therefore, some workers have used more direct measurements of ecosystem attributes. For example, Momen & Zehr (1998) used lake water chemistry and terrestrial characteristics together with univariate ANOVA and multivariate descriptive discriminant Analysis (DDA) statistics to classify watersheds.

Assuming that the flood-pulse will determine physical and chemical properties of the soils, sediment and water, which in return will allow differentiation into distinct habitats, then it is hypothesised that the habitats of the floodplain are not fixed but their characteristics change seasonally according to (or are in “phase-transition”) with the hydro-climatic regime. Therefore, there is a need to develop a simple but robust quantitative classification tool for floodplain habitats. The aim of this study was to determine the physico-chemical characteristics of the Lower Shire Floodplain, and then use this information to quantitatively define the area’s different habitats that will allow further analysis on fish production and yield.

3.2 Materials and Methods

Sampling sites

The study was carried out in representative sites of the floodplain’s three major habitats (see Figure 2.1 and Figure 3.1). Special focus was put on dividing the three major habitats according to their degree of connectivity to the river-channel, and then devising a set of quantitative indicators, and finally a set of response and predictor variables to synchronise the classification with the hydro-climatic seasons developed in Chapter 2. In the analysis throughout this portion of work, the three habitats are the main river channel and the immediate floodplain; referred to as river floodplains (RF), permanently connected floodplain lagoons (PCL), and seasonally connected floodplain lagoons (SCL).

Figure 3.1 Photographs showing typical habitats of the Lower Shire Floodplain (a) main river channel, (b) river-floodplain, note the extraordinarily wide river-channel, (c) seasonally connected lagoon during peak flood, showing decomposing marshes and sudds, (d) seasonally connected lagoon during low water level, note the heavy weed infestation, especially water hyacinth, (e) permanently connected lagoon, the arrow marks the connection with the main river channel.

Three stations were established per sampling sites, from which two samples were collected once every month. Samples representing the riverine floodplain were collected at Chiromo, including the Shire/Ruo confluence. Samples from permanently connected floodplain lagoons were collected at Mwala and Twaya lagoons. Samples representing a seasonally connected floodplain lagoon were collected at Bangula and Njale lagoons.

Water level, flow, depth and substrate characteristics

A record of daily water level of the Shire River at the Chiromo gauging station, for the period from July 1999 to June 2000, was obtained from the Hydrological Division of the Malawi Ministry of Water Reosurces. Vegetative cover in the habitats was identified as emergent, submerged or floating according to Howard-Williams (1973), and its frequency measured according to a ranking scale of 0 to 3 (0 = absent, 1 = rare, 2 = common, 3 = abundant). Depth was measured using a line marked at 10 cm interval and weighted at the bottom with a heavy piece of metal. Bottom sediments, collected using an Eckman sediment sampler, were assessed for texture by “hand texturing” as gravel, sand and mud, according to the methods of Folk (1980). Soil samples were sent to the Malawi Geological Survey Laboratory for analysis of nitrogen, phosphorus, potassium, sodium, carbon and silicon. Water current was ranked on a scale of 0 to 4 (0 = no current, 1 = visible but low flow, 2 = fast flow with little water perturbation, 3 = fast with water perturbation, 4 = white water) according to Rosenberger & Chapman (1999).

Water quality

Water quality parameters were measured monthly at the sample sites in the three major habitats, for a period of nineteen months, from November 1998 to June 2000, however, only those samples from July 1999 to June 2000 were in the analysis in this chapter. Water samples were collected 0.3 meters below the surface. Temperature, conductivity, dissolved oxygen (DO), hydrogen ion concentration (pH), hardness, alkalinity, total dissolved solids, phosphorus and nitrate were measured according to methods outlined in Strickland & Parson (1972) and Golterman *et al.* (1978). DO and temperature were measured with a calibrated hand-held YSI model 51B oxygen meter. Conductivity and pH were measured using hand held meters, calibrated daily. Water transparency was measured by secchi-disc visibility according to Golterman *et al.* (1978). Estimates of total phosphorus were made from 100-ml water samples by adding Hach's reagent AccuVac and reading the colour change on a DREL/2010 Portable Aquaculture Laboratory. Nitrate was likewise measured by adding Hach's reagent NI 15. Total alkalinity (as $CaCO_3$) was determined by drop-count titration of a 100-ml water sample with sulphuric acid after adding phenolphthalein as an indicator. Total hardness (as $CaCO_3$) was determined by drop-count titration of a 100 ml water sample with EDTA.

Seasons, statistics and classification

The year was divided into four quarterly hydro-climatic seasons (see Chapter 2). Qrt1 (July-September) is characterised by hot, dry weather with a low flood regime, Qrt2 (October-December) is a hot, windy, wet period with a low but rising flood regime, Qrt3 (January-March) has hot-humid, wet weather with the flood regime at peak, and Qrt4 (April-June) has humid and cool weather with a receding flood regime. Data (mean± 95% confidence intervals) from each habitat were summarised and arranged with respect to the quarterly hydro-climatic seasons.

Statistical analyses were carried out with the aid of StatisticaTH computer software. Differences in the physico-chemical parameters among the various habitats and over different quarterly seasons were tested with a non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) (Zar 1984). Data sets for the quarterly seasons were combined to test for overall differences in mean values of physico-chemical parameters among the three habitats. Where significant differences were found, values were compared using a non-parametric Mann-Whitney U-test. The relationship between various physico-chemical and habitat parameters was assessed using forward stepwise multiple regression analysis. In this type of regression analysis redundant predictors are removed to yield a final model that accounts for most of the variance (Roy 1958, 1967).

Differences in the physico-chemical characteristics of the habits over quarterly seasons were used to determine the characteristics of the habitat using similarities, hierarchical clustering (CLUSTER) and multidimensional scaling (MDS). Analysis of similarities

(ANOSIM) (Clarke 1993) was undertaken to statistically determine distinctions between habitats. The tests were performed using the Primer Software (Clarke & Warwick 1994). The parameters were divided into three groups: (i) hydrological (e.g. water level), (ii) water quality and (iii) habitat structure (e.g. substrate type, vegetation), and spread over the hydro-climatic seasons.

3.3 Results

Physical characteristics of the habitats

Table 3.1 shows the general physical characteristics of the different sampling sites. The river-floodplain was characterised by deep fast-flowing water, sandy substrate and little emergent vegetation. The permanently connected lagoons were shallow ($\leq$ 2 m) with sandy-mud bottom and slow flowing water, while the seasonally connected lagoons had slow-flowing or stagnant water, with comparatively more emergent and floating vegetation.

Table 3.1 Summary of the physical characteristics of the sample habitats in the Lower Shire Floodplain. Habitat type: RF = riverine floodplain, SCL = seasonally connected lagoons, PCL = permanently connected lagoons. Depth in meters is mean ± SD. For frequency of occurrence of emergent, submergent and floating vegetation, ranking scale is 0 = absent, 1 = rare, 2 = common, 3 = abundant. For water flow, ranking scale is 0 = no current, 1 = visible but low flow, 2 = fast flow with little water perturbations, 3 = fast with water perturbation, 4 = white water.

Sample site	**Habitat**	**Mean depth (m)**	**Substrate**	**Emergent vegetation**	**Submerged vegetation**	**Floating vegetation**	**Water flow**
Chiromo	RF	5.93 ± 3.35	**Sandy**	1	0	0	3
Bangula lagoon	SCL	3.8 ± 0.67	Muddy-sand	3	3	3	0-1
Mwala lagoon	PCL	2.2 ± 0.45	Sandy-mud	3	2	2	1-2
Twaya lagoon	PCL	2.5 ± 0.32	Muddy	3	2	2	1-2
Njale lagoon	SCL	3.0 ± 0.91	Muddy-sand	3	2	2	1-2

Nutrient characteristics of the soil and sediment

Table 3.2 shows the variations in nutrients in the aquatic/terrestrial transition zone (ATTZ). Potassium (K^+) concentration was significantly higher (one-way ANOVA, $p<0.05$) in the water (6.40 ± 1.35 $mg.l^{-1}$) and sediment-water interface (12.40 ± 4.3 $mg.l^{-1}$) than in the soils (1.80 ± 0.65$mg.l^{-1}$), sediments (1.60 ± 0.70 $mg.l^{-1}$), and decomposing organic matter (1.40 ± 0.52 mg.l^{-1}). A similar trend was observed for sodium (Na^{+}). Nitrogen was significantly lower (one-way ANOVA, $p<0.05$) in the farm soil (1.0 ± 0.37 mg.l^{-1}) than in the marsh sediments (3.0 ± 0.84 mg.l^{-1}) and decomposed marsh (4.0 ± 0.72 mg.l^{-1}). Phosphate ranged from 1.7 to 1.9 mg.l^{-1} in the marsh sediments and sediment-water interface of the lagoon and marshes, respectively, but only occurred as a trace in the farm soil and water. Carbon and silicate were recorded in the soils but not in the water. Silicate levels were significantly greater (one-way ANOVA, $p<0.05$) in the farm soil (525.4 ± 71.2 mg.l^{-1}) than in the decomposing marsh (268.0 ± 53.5 mg.l^{-1}) and its sediments (330.3 ± 64.3 mg.l^{-1}).

Table 3.2 Chemical characteristics of the aquatic/terrestrial transition zone (ATTZ) in the Lower Shire Floodplain during the rising flood (November). Data is presented as mean concentration ± Standard Deviation (SD).

Chemical parameter	**Soil**			**Water**		
	Farm soil	**Marsh sediments**	**Decomposing marsh**	**Main channel**	**Floodplain pools**	**Sediment-water interface**
Potassium (K) (mg.l^{-1})	1.80±0.65	1.60±0.70	1.40±0.52	6.40±1.35	7.00±2.02	12.40±4.3
Sodium (Na) (mg.l^{-1})	2.70±0.75	1.20±0.61	0.90±0.47	15.00±4.2	15.00±5.5	50.00±15.8
Nitrogen (mg.l^{-1})	1.0±0.37	3.0±0.84	4.0±0.72	0.00	0.00	0.00
P_2O_5 (mg.l^{-1})	Trace	1.7±0.61	Trace	Trace	Trace	1.9±0.47
C (mg.l^{-1})	12.8±4.8	Trace	Trace	Trace	Trace	Trace
SiO_2 (mg.l^{-1})	525.4±71.2	330.3±64.3	268.0±53.5	Trace	Trace	Trace

Physico-chemical characteristics of the habitats

Figure 3.2 shows the daily mean water level (m) above the arbitrary datum on the Shire River at Chiromo and the mean daily water temperature (°C) in the three sample habitats. Temperature was lowest in Qrt1 during which the water level was receding. In Qrt2, when water level was lowest, temperature was still rising. During Qrt3 both water level and temperature were at peak, while during Qrt4, both the water level and temperature were dropping. However, the mean daily water temperatures in the three habitat types were not significantly different (one-way ANOVA, $p>0.05$).

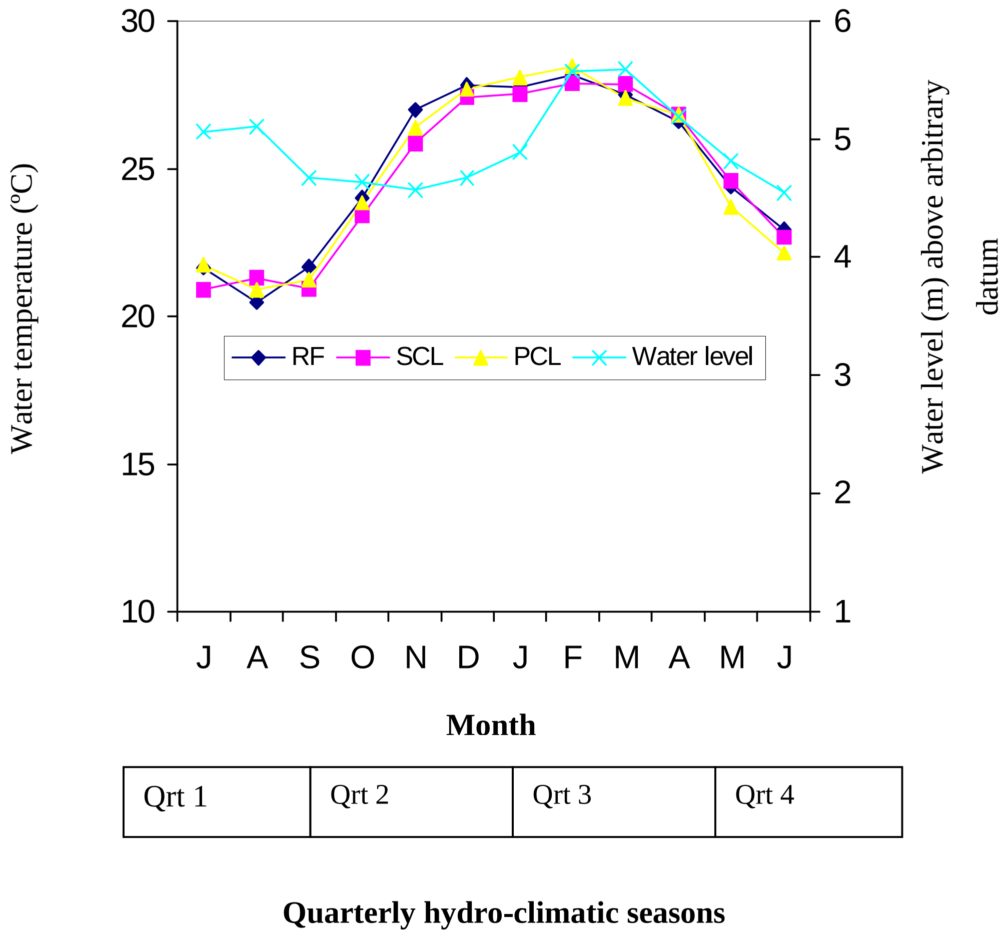


Figure 3.2 Mean daily water temperature (ºC) in the river floodplain (RF), seasonally connected lagoons (SCL) and permanently connected lagoons (PCL); and daily mean water level (m) in the Shire River at Chiromo, from July 1999 to June 2000. Qrt1-Qrt4 denote quarterly hydro-climatic seasons.

Figures 3.3-3.5 show the mean water depth, conductivity, and total dissolved solids (TDS), respectively, in the three habitats. In all major habitats, water depth varied significantly between quarterly seasons (one-way ANOVA, p<0.05). Water depth was greatest during Qrt3 (peak flood phase) and lowest during Qrt2 (low-rising flood phase) in all habitats (Fig. 3.2 and Table 3.3). Within habitats, water depth also varied significantly between quarterly seasons (one-way ANOVA, p<0.05) (Fig. 3.3 and Table

3.3). Alkalinity was lowest during Qrt3 in all habitats; hardness was highest during Qrt2 in seasonally connected and permanently connected lagoons, and during Qrt3 in the river-floodplain; phosphate was lowest during Qrt4 in all habitats (Table 3.3).

Table 3.3 Seasonal variations in physico-chemical parameters of the water in river floodplain (RF), seasonally connected lagoons (SCL) and permanently connected lagoons (PCL) of the Lower Shire Floodplain. Data presented as means ± 95% confidence intervals. Qrt1- Qrt4 are quarterly hydro-climatic seasons.

Parameter	**Habitat**	**Quarterly Hydro-climatic seasons**			
		Qrt1	**Qrt2**	**Qrt3**	**Qrt4**
Water depth (m)	RF	5.24 ± 3.52	2.32 ± 1.73	5.93 ± 2.46	4.44± 3.39
	SCL	3.8 ± 0.39	2.5 ± 0.0	4.25 ± 1.47	3.8 ± 0.0
	PCL	0.8 ± 0.22	0.5 ± 0.21	2.2 ± 0.68	1.2 ± 0.41
Total dissolved solid (mg.l^{-1})	RF	96.5 ± 2.47	120 ± 34.3	139.5 ± 7.7	121.8± 15.41
	SCL	736.5 ± 657.57	1350 ± 0.0	203.5 ± 108.78	1160 ± 0.0
	PCL	102.83 ± 2.65	132 ± 56.85	132.83 ± 3.37	155.67 ± 13.1
Conductivity (µS.cm^{-1})	RF	195.83 ± 3.6	274.6 ± 0.99	278.5 ± 14.94	242.6 ± 30.92
	SCL	937 ± 264.6	2690 ± 0.0	407.5 ± 218.54	531.33 ± 232.29
	PCL	204.33 ± 7.62	227 ± 41.22	265.33 ± 6.63	310.83 ± 26.42
Water transparency (Secchi disk visibility) (cm)	RF	27.83 ± 4.89	33 ± 13.19	17.2 ± 9.1	19.2 ± 9.51
	SCL	24 ± 0.0	13 ± 0.0	40 ± 58.8	50 ± 0.0
	PCL	23.5 ± 2.07	24 ± 3.0	17.25 ± 3.43	24 ± 2.26
pH	RF	7.83 ± 0.21	7.718 ± 0.01	7.54 ± 0.13	6.83 ± 0.33
	SCL	7.9 ± 0.2	8.1 ± 0.0	6.955 ± 0.03	7.02 ± 1.1
	PCL	7.7 ± 0.2	7.58 ± 0.43	6.83 ± 0.1	7.41 ± 0.43
Alkalinity (mg.l^{-1})	RF	149.33 ± 48.06	115.2 ± 33.18	86.8 ± 30.43	97.2 ± 37.92
	SCL	248 ± 23.84	280 ± 0.0	68 ± 0.0	148 ± 0.0
	PCL	137 ± 9.85	136.67 ± 17.29	117.33 ± 11.16	184.67± 116.99
Hardness (mg.l^{-1})	RF	194.67 ± 47.02	130.4 ± 19.62	164.67 ± 20.54	135 ± 40.95
	SCL	303.33 ± 20.27	319.5 ± 63.74	202 ± 0.0	116 ± 0.0
	PCL	158.33 ± 33.73	243.25 ± 135.48	169.33 ± 14.55	138 ± 24.48
Phosphate (mg.l^{-1})	RF	1.61± 1.01	0.7 ± 0.36	0.81 ± 0.29	0.49 ± 0.35
	SCL	3.31 ± 2.46	1.29 ± 1.06	1.2 ± 0.0	0.12 ± 0.0
	PCL	1.08 ± 0.53	1.73 ± 0.62	1.22 ± 0.8	0.27 ± 0.11
Nitrate (mg.l^{-1})	RF	1.1 ± 0.78	0.178 ± 0.16	0.39 ± 0.19	5.79 ± 2.9
	SCL	3.83 ± 6.06	1.12 ± 0.03	0.96 ± 0.0	0.86 ± 0.0
	PCL	3.34 ± 1.2	0.89 ± 0.31	0.35 ± 0.32	6.54 ± 1.54
Dissolved oxygen (DO) (mg.l^{-1})	RF	7.99 ± 0.87	6.5 ± 0.95	7.88 ± 2.25	6.57 ± 0.46
	SCL	3.81 ± 0.66	7.46 ± 4.8	1.99 ± 0.45	2.64 ± 1.05
	PCL	3.96 ± 0.82	3.94 ± 1.13	1.33 ± 0.64	3.07 ± 2.1
Temperature (°C)	RF	24.34 ± 0.48	28.75 ± 0.75	30.25 ± 0.82	21.86 ± 0.47
	SCL	23.03 ± 0.8	28.4 ± 1.0	29.23± 0.73	23.75 ± 1.83
	PCL	22.81 ± 0.78	24.48 ± 0.76	30.24 ± 0.42	22.32 ± 1.15

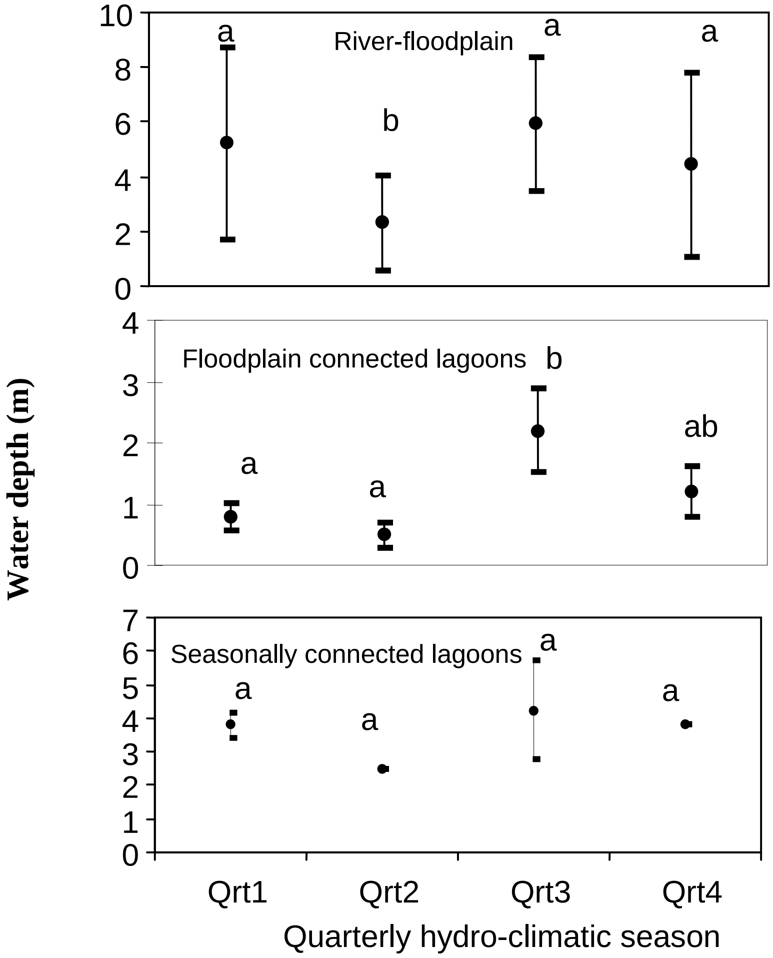


Figure 3.3 Mean water depth (in meters ±95% confidence interval) for sample sites in the river-floodplains, permanently connected lagoons and seasonally connected lagoons in the Lower Shire Floodplain, during four quarterly hydro-climatic (Qrt) seasons from November 1998 to June 2000. Qrt1 = Jul-Sept, Qrt2 = Oct- Dec, Qrt3 = Jan- Mar, Qrt4 = Apr-Jun. Different letters denote differences at $p<0.05$ level of significance (Kruskal-Wallis one-way ANOVA on ranks; and Mann-Whitney U-test).

The level of nitrate was highest during Qrt4 in both the river-floodplain and permanently connected lagoons and highest during Qrt1 in the seasonally connected lagoon. Phosphates levels ranged between 0.12 ± 0.0 mg.l^{-1} and 3.31 ± 2.46 mg.l^{-1}, with a declining trend in all habitats from Qrt2 to Qrt4. Seasonally connected lagoons had the highest level of phosphate (3.31 ± 2.46 mg.l^{-1}) during Qrt1. The permanently connected lagoons had the highest phosphate levels (1.73 ± 0.62 $mg.l^{-1}$) during Qrt2, while the river-floodplain had the highest level during Qrt1 (Table 3.3).

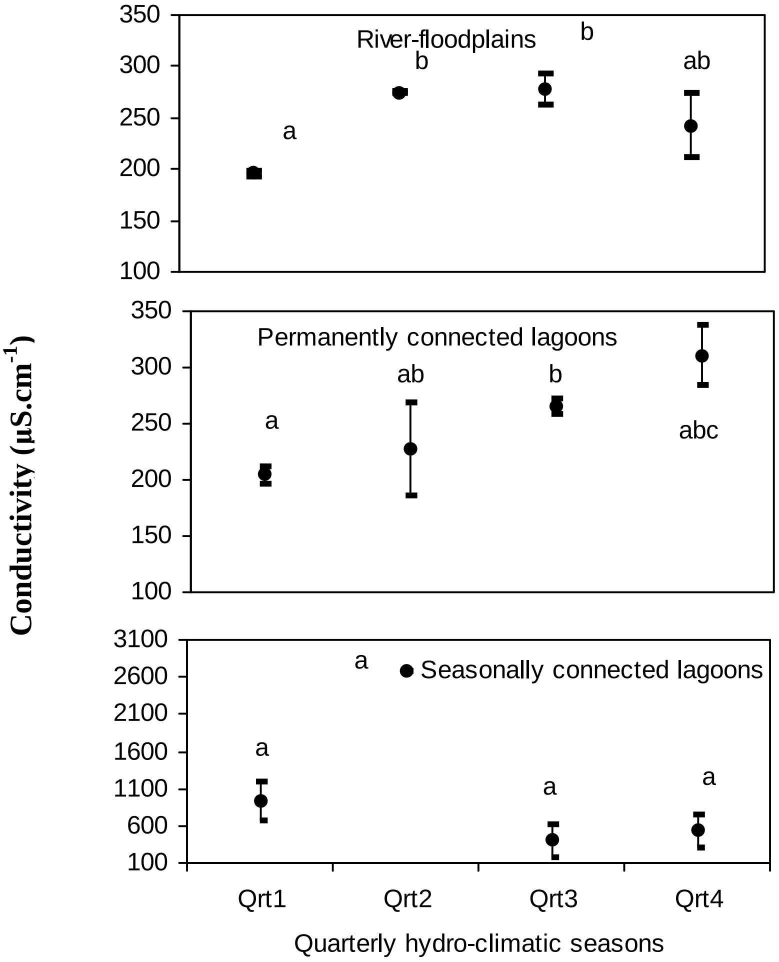


Figure 3.4 Mean conductivity ($\mu S.cm^{-1}$ ± 95% confidence interval) for sample sites in the river-floodplains, and permanently connected and seasonally connected lagoons in the Lower Shire Floodplain, during quarterly hydro-climatic (Qrt) seasons, from November 1998 to June 2000. Qrt1 = July to September, Qrt2 = October to December, Qrt3 = January to March, Qrt4 = April to June. Different letters denote differences at $p<0.05$ level of significance (Kruskal-Wallis one-way ANOVA on ranks; and Mann-Whitney U-test).

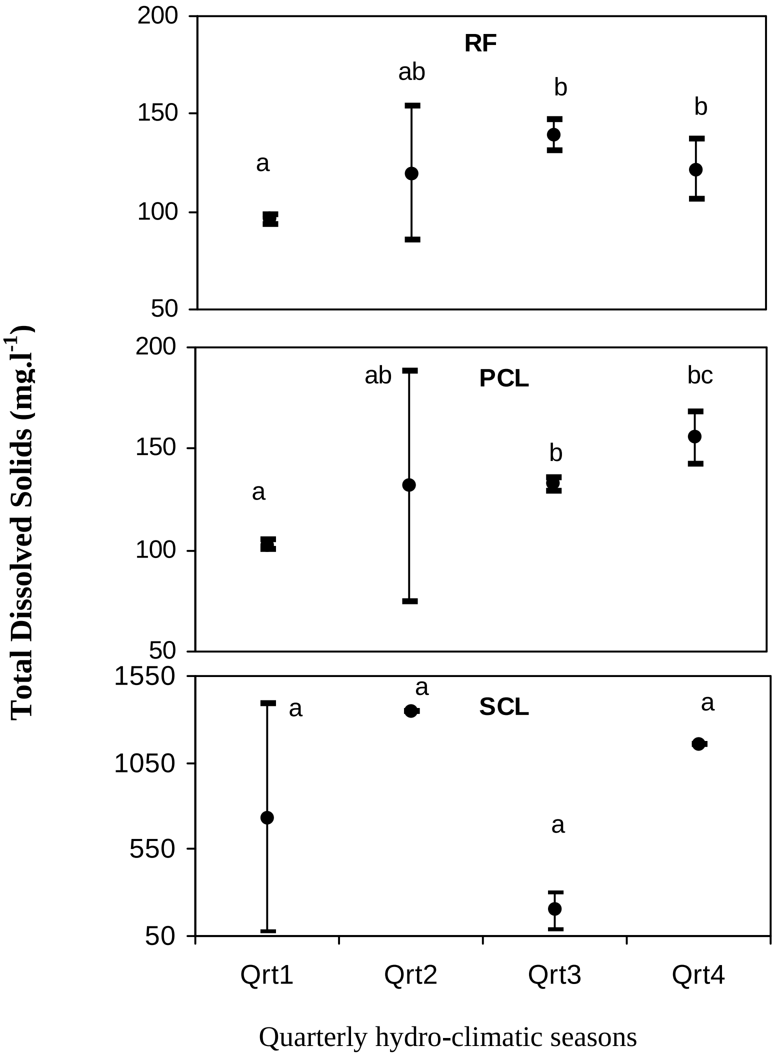


Figure 3.5 Total dissolved solid in mg.l^{-1} (mean ± 95% confidence interval) for sample sites in the river-floodplain (RF), permanently connected lagoons (PCL) and seasonally connected lagoons (SCL) in the Lower Shire Floodplain, during quarterly hydro-climatic (Qrt) seasons from November 1998 to June 2000. Qrt1 = Jul-Sept, Qrt2 = Oct-Dec, Qrt3 = Jan-Mar, Qrt4 = Apr- Jun. Different letters denote differences at p<0.05 level of significance (Kruskal-Wallis one-way ANOVA on ranks; and Mann-Whitney U-test).

Figure 3.6 shows the seasonal variation in pH, DO, water temperature and water transparency (Secchi disc visibility). In the river floodplain and permanently connected lagoon, the levels of pH, DO and water transparency varied significantly between quarterly hydro-climatic seasons (one-way ANOVA, p<0.05). DO and water temperature also varied significantly (one-way ANOVA, p<0.05) with season in all three habitats.

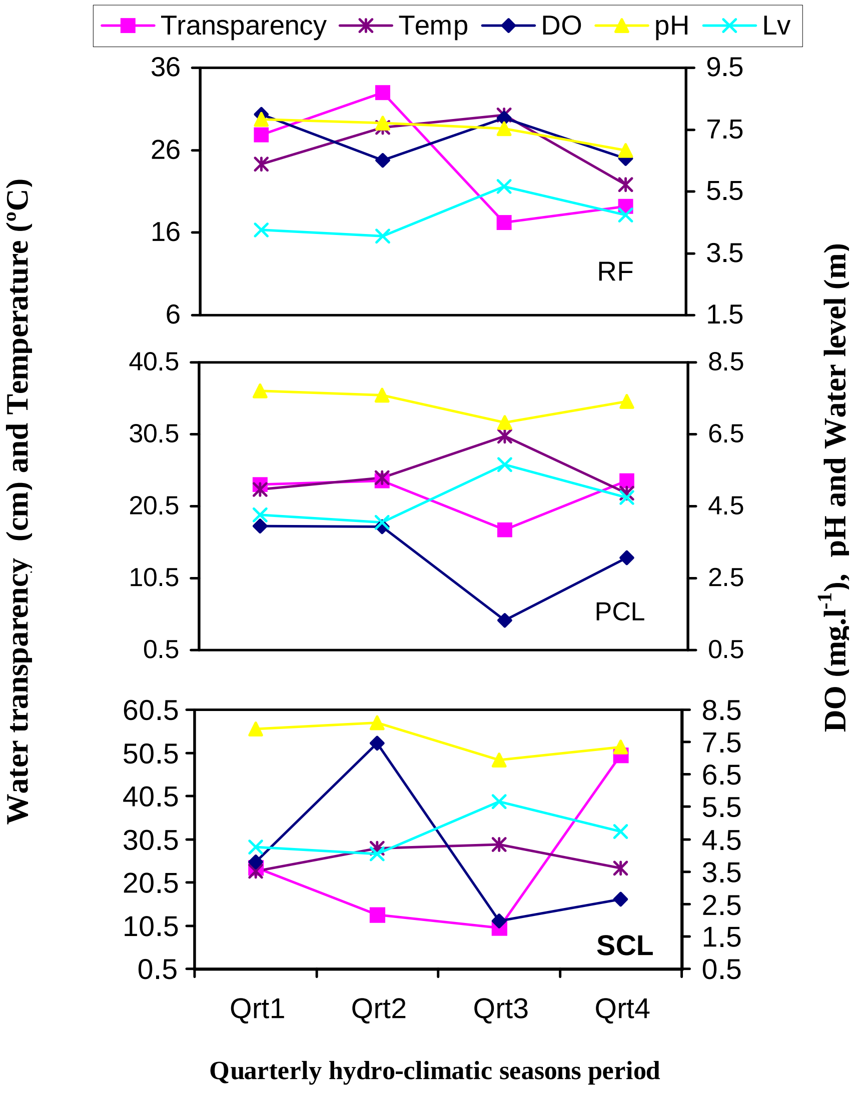


Figure 3.6 Quarterly variation in water temperature, transparency (SDV), dissolved oxygen (DO) and pH with water levels (m) in river floodplain, permanently connected lagoon and seasonally connected lagoon in the Lower Shire Floodplain, measured from November 1998 to July 2000. Qrt1-4 are hydro-climatic seasons.

The differences in physico-chemical characteristics between the three habitats of the Lower Shire Floodplain

Table 3.4 shows the results of inter-habitat comparison of pooled samples using one-way ANOVA. There were significant inter-habitat differences ($p<0.05$) in TDS, conductivity, depth, alkalinity, hardness, and DO. However, there were no significant (one-way ANOVA, $p>0.05$) inter-habitat differences in nutrient levels (phosphate and nitrate), pH, water temperature and transparency.

Table 3.4 Results of the Kruskal-Wallis, one-way analysis of variance (ANOVA) by ranks and median, and Mann-Whitney U-test for the effect of habitat (RF = river floodplain SCL = seasonally connected lagoon, PCL=permanently connected lagoon) on physico-chemical parameter in the Lower Shire Floodplain. Data is presented as p = level of significance at, ns=not significant at <5% level.

Parameter	**RF x PCL**	**RF x SCL**	**PCL x SCL**
PH	ns	ns	ns
Alkalinity (mg.l^{-1})	ns	$p<0.05$	$p<0.05$
Hardness (mg.l^{-1})	$p<0.05$	$p<0.05$	ns
Nitrate (mg.l^{-1})	ns	ns	ns
Phosphate (mg.l^{-1})	ns	ns	ns
Total dissolved solids (mg.l^{-1})	$p<0.05$	$p<0.05$	ns
Conductivity (µS.cm^{-1})	$p< 0.05$	$p<0.05$	ns
Dissolved oxygen (mg.l^{-1})	$p<0.05$	$p<0.05$	$p<0.05$
Secchi-disc visibility (cm)	ns	ns	ns
Temperature (ºC)	ns	ns	ns

Table 3.5 shows the relationship among physico-chemical parameters upon each other. Although the correlation between water level, transparency and temperature with the other water quality parameters was relatively low ($0.02 \le r^2 \ge 0.49$), the correlation was highly significant ($0.05>p<0.01$). It is important to note that there was a significant positive correlation between water level and pH (r^2 = 0.49, p = 0.0003), TDS (r^2 = 0.36, p = 0.01), and conductivity (r^2 = 0.22, p = 0.01), but an inverse relationship between water level and alkalinity, hardness, nitrate, phosphate and DO (Table 3.5).

Table 3.5 Relationship among some physical and chemical variables in the Lower Shire Floodplain. The data is presented as coefficient of determination (r^2) and percent level of significance (p)

Parameter	**Water level (m)**		**Transparency (cm)**		**Temperature (ºC)**	
	r^2	p	r^2	p	r^2	p
pH	0.49	0.0003	0.39	0.001	0.37	0.002
Alkalinity (mg.l^{-1})	-0.38	0.01	0.06	0.39	-0.08	0.29
Hardness (mg.l^{-1})	-0.29	0.21	-0.002	0.88	0.12	0.19
Nitrate (mg.l^{-1})	-0.15	0.15	0.12	0.11	-0.23	0.02
Phosphate (mg.l^{-1})	-0.11	0.18	-0.02	0.55	0.26	0.02
Total dissolved solids (mg.l^{-1})	0.36	0.01	-0.13	0.04	-0.06	0.17
Conductivity (µS.cm^{-1})	0.22	0.01	-0.003	0.77	0.18	0.01
Dissolved oxygen (mg.l^{-1})	-0.29	0.0000	0.12	0.005	-0.15	0.001

Figures 3.7 and 3.8 show the dendrogram for hierarchical clustering and multi-dimensional scaling ordination computed for three habitats based on hydrological, water quality parameters and habitat characteristics (viz. substrate, vegetation and water flow).

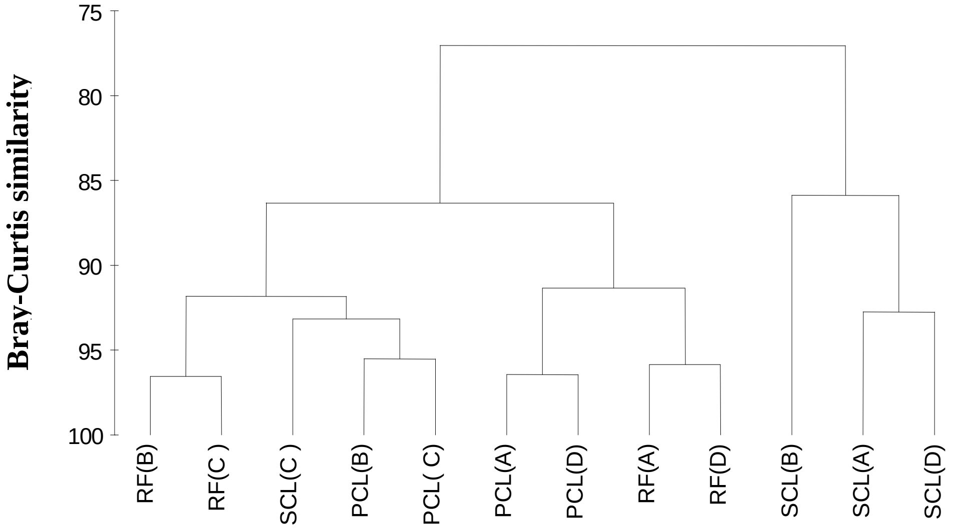


Figure 3.7 Dendrogram for hierarchical clustering of major habitats (RF = river floodplain, SCL = seasonally connected lagoons, PCL = permanently connected lagoons). A, B, C and D represent quarterly hydro-climatic seasons: A = Qrt1 (Jul-Sep), B = Qrt2 (Oct-Dec), C = Qrt3 (Jan-Mar), D = Qrt4 (Apr-Jun).

It is apparent that the three major habitats are clearly and significantly distinguishable from each other (one-way ANOSIM, $p<0.05$) (Figures 3.7 & 3.8). The habitats were defined in the context of hydro-climatic seasons. Although there were minor overlaps between permanently connected lagoons and seasonally connected lagoons, and between permanently connected lagoons and river floodplains, the three broad groups can be identified as comprising seasonally connected lagoons, permanently connected lagoons and river floodplain (Fig. 3.8).

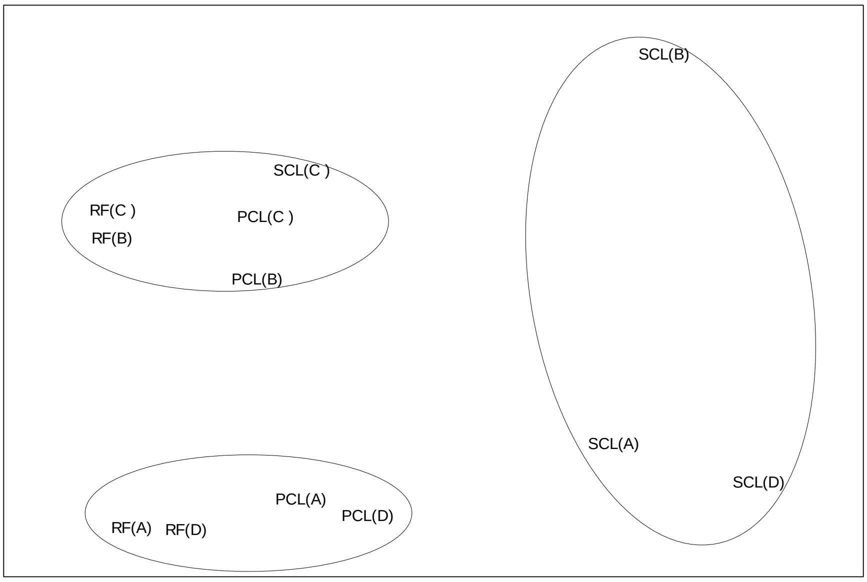


Figure 3.8 Multi-dimensional scaling (MDS) ordination of the three habitats (RF = river floodplain, SCL = seasonally connected lagoons, PCL = permanently connected lagoons in the Lower Shire Floodplain, based on fourth-power transformed physical and chemical variables and Bray-Curtis similarities (stress = 0.05). A, B, C and D represent quarterly hydro-climatic seasons: A = Qrt1 (Jul-Sep), B = Qrt2 (Oct-Dec), C = Qrt3 (Jan-Mar), D = Qrt4 (Apr-Jun).

3.4 Discussion

The three major habitats of the Lower Shire Floodplain seem to exhibit nutrient dynamics which are characteristic of the different habitats. Baldwin & Mitchell (2000) recognised the division between soil and sediment as arbitrary, since soil and sediments of the floodplain are differentiated by the period of submergence; thus, sediments are inundated and rarely exposed to the air, while soils are exposed to the air for longer periods than they are inundated. Therefore, sequential wetting and drying process influences the nutrient dynamics in the ATTZ. Findings from this study seem to support the report by Baldwin & Mitchell (2000).

While the level of sodium (Na^+) was found to be higher than potassium (K^+) in the farm soil, both cations were less concentrated in the farm soil than in water. However, Na^+

concentration (15–50 mg.l^{-1}) was greater than the K^+ concentration (6.4–12.40 mg.l^{-1}) in the water (Table 3.2). Availability of cations in the soil is governed by climatic factors, soil type and the mode of bonding to the soil particles (Maida 1985). Petts & Foster (1985) noted that potassium usually exists in much lower concentrations in river water than sodium, because the large size of the K^+ ion (Na^+ is smaller and highly soluble) gets fixed in soil minerals in layered lattice structures. Mineral with a layered lattice structure are illites and vermiculite (Pedro 1973, Mengel & Kirkby 1982); these minerals are common in soils of the Lower Shire Valley (Maida 1980, 1985), this might explain the higher concentration of Na^+ than K^+ in the water of the Lower Shire Floodplain.

Despite high concentration of silicon, carbon and nitrogen in the farm soils (Table 3.2) and the soils of the Lower Shire Valley in general (Maida 1985), the recorded levels of these elements were lower in the sediments and water of the floodplain. This could be interpreted as being a result of a complexity of exchange of energy and matter in the ATTZ. Ibańez *et al.* (2000) reported low nutrient concentrations in the pre-Amazonian floodplain in the rainy season and attributed this to an intensive recycling process and dilution caused directly by rainfall. Importantly, the efficiency of organic matter materialisation and nutrient cycling in floodplain ecosystems depends on a fine balance between aerobic and anaerobic processes (Baldwin & Mitchell 2000), as well as the presence of bio-available carbon to support metabolic activities (Gottschal 1986).

Given that the low carbon concentration in the floodplain (Table 3.2) was probably a result of drying of the sediment (during the low flood regime), there was likely a severe carbon limitation and consequently a decrease in the rate of nutrient cycling. Hence, the reduction in sediment-nutrient processing following episodic wetting-drying cycles (Baldwin & Mitchell 2000) as observed by low carbon concentration in the floodplain (Table 3.2). A higher level of phosphate in the floodplain sediments than in farm soils may indicate an internal generation of phosphate in the floodplain ecosystem. This could also be influenced by the flood regime, since large flushes of mineral N and P have been reported in re-wetted soils and sediment (Birth 1960, Starling & Ross 1988, Qui & McComb 1995) as a result of drying-induced microbial-cell lysis (Baldwin & Mitchell

2000). In addition, this condition could also be explained by the nature of soils in the floodplain, which are rich in vermiculite minerals that have a tendency to absorb large quantities of phosphate (Sanchez 1976).

The most significant effect of inundation is isolation of the soil from atmospheric oxygen, and hence the potential onset of anoxia (Faulkner & Richardson 1989). Upon inundation of floodplain soil, an initial increase in aerobic heterotrophy and nitrification activity are expected, with the potential for an increase in anaerobic conditions as the flood duration advances (Baldwin & Mitchell 2000). This process will result in a loss of N and release of P as a result of iron (Fe (III) (Maida 1978) and sulphate-reducing bacterial activity (Baldwin & Mitchell 2000).

Variation in quarterly hydro-climatic physico-chemical characteristics of the water in the three habitats is a clear indication of the influence of the flood regime. High conductivity (195–2690 $\mu S.cm^{-1}$) (Table 3.3) is an indication of high availability of dissolved nutrients in the floodplain. In fact the value is one of the highest levels recorded for southern hemisphere rivers (Table 3.6). Talling & Talling (1965) noted that in African natural freshwaters 60-80% of TDS concentration consists of bicarbonate ions, which, at pH 6-8, regulates pH by the calcium-carbonate buffering system. During Qrt3 (peak flood period) pH (6.83 – 6.95) and DO (1.33-1.99 $mg.l^{-1}$) in the seasonally connected and permanently connected lagoons were at their lowest. This may have been caused by the decomposition of recently inundated floodplain vegetation, crop residues from dry season cultivation and a high quantity of organic matter brought into the floodplain by runoff.

Higher levels of carbon may not have been recorded because of rapid rates of decomposition (Table 3.2). For example, it has been reported that most organic matter in the Amazon floodplains was completely decomposed within the first few weeks of inundation (Furch & Junk 1985, Thomaz *et al.* 1992).

Table 3.6 Comparison of physico-chemical characteristics of the Lower Shire Floodplain with other river-floodplains in Africa. Sources: 1 = Davies (1986), 2 = Petr (1970), 3 = Petr (1986), 4 = Hastings (1973), 5 = Howard-Williams (1973), 6 = This study, 7 = Coche (1974), 8= Bailey (1986), 9 = Begg (1970), 10 = Hall *et al.* (1977), 11 = Seaman *et al.* (1978)

River system	**Conductivity (μS.cm^{-1})**	**pH**	**Alkalinity (mg.l^{-1})**	**Hardness (mg.l^{-1})**	**Nitrate (mg.l^{-1})**	**Phosphate (mg.l^{-1})**	**Dissolved Oxygen (DO) (mg.l^{-1})**	**Temperature (°C)**	**Water transparency (SDV cm)**	**Source**
Kafue	30-320	6.8-8.2	25-192		23-240		1.4-8.3	15.9-26	34.63-124.07	1
Black Volta		7.7-8.6	76-90					29.8-31.7		2, 3
Shire	240	7.1- 7.8		70-80		0.1-0.45	2-11	26-30		4, 5
Shire	195-2690	6.95-8.1	68-248	116-303	0.18-3.83	0.12-3.31	1.33-7.88	21.86-30.25	13-50	6
Lake Kariba	7.44-94.7	8.4	1.49-41.7		0.01-0.017				220-537	7
Zaire River		6.4-8.2				1-18.1		23-33		8
Zambezi (Kariba)	55-75	5.5-8.35	12-33	7-35.2	0.0008-0.0015	0.005-0.37	0.96-8.35	3-23	20-537	9
Zambezi (below Shire confluence)	61-315	7.54	17-110	6-54	0.13-0.18	0.09-0.21	2.01-5.5	4-24	30-31	10
Lake Liambezi	23.8 - 27.9	-	30.9-33.6	-	0.2-0.3	0.4-1.2			10	11

The decaying of organic matter was evident by the smell of sulphide (most likely hydrogen sulphide) in the floodplain between February and March (personal observation). Similarly, in the Amazon, Junk *et al.* (1983) reported that the level of H_2S reached 1 $mg.l^{-1}$ during the month of December when detritus brought into the floodplain lakes by floodwater was decaying.

Low pH and DO in pre-Amazonian floodplains during the peak flood have been attributed to the abundant presence of aquatic macrophytes in all shallow areas and decomposition of humic compounds (Schmidt 1973, Rai & Hill 1981 & 1982, Ibańez *et al.* 2000). When aquatic plants take up bicarbonate from water of pH 6-9, they excrete hydroxyl ions into less buffered water, and decaying organic material produce humic acid, causing the pH to drop (Welzel 1975). Therefore, reduction of pH and DO in the Lower Shire Floodplain during the peak flood period (Qrt3) could have been caused by both decomposition of recently inundated organic material and presence of abundant aquatic macrophytes whose growth has been stimulated by recent rainfall and flooding.

The decline in alkalinity and hardness in all the habitats during the peak flood period (Qrt3) and subsequent reduction in pH is further evidence of the uptake of bicarbonate from the water, and a general paucity of Ca^{2+} and Mg^{2+} ions as these ions might have chelated with allochthonous and autochthonous organic matter brought in by flood waters. Free Ca^{2+} ions are said to be rare in the natural environment because of the strong propensity of Ca^{2+} for chelating with humic compounds that also adsorb and precipitate phosphates (Sanchez 1976). Low pH can be caused by a decrease in exchangeable cations because H^+ brings into the ambient solution cations such as Mg^{2+} and Ca^{2+} by exchange reactions. These cations are susceptible to leaching, as they are not strongly adsorbed by soil colloids (Maida 1985). This may best explain why phosphate concentration in all the three habitats declined from Qrt1 to Qrt3 (Table 3.3). Hastings (1973), based on recordings made only in December and January, reported that the Lower Shire Floodplain was losing chemical elements such as phosphate by gaining oxygen and nitrate. The findings in this study may offer a more complete picture and understanding of the reasons why certain chemical elements are available or absent in the floodplain ecosystem, at certain periods of the year.

Conductivity and TDS peaked in Qrt3 in the river floodplain and permanently connected lagoons, and in Qrt2 in the seasonally connected lagoons, reflecting a possible influx of ions brought in by the floods from the catchment area. High conductivity has also been reported during peak floods in the Amazon as a result of nutrient-rich runoff water from the catchment (Thomaz *et al.* 1992). Similarly, Bootsma & Hecky (1999) reported high nutrient concentrations in rivers flowing into Lake Malawi just as flow increased at the beginning of the rainy season.

It is interesting to note that both phosphate and nitrate were generally higher during Qrt4 and Qrt1 in all the three habitats. Phosphorus and nitrogen are both major primary rate-limiting elements (Wetzel 1975) also referred to as biolimiting nutrients (Welcomme 2001). Probably aided by a rise in pH, temperature and DO levels, decomposition of organic matter was enhanced during Qrt4, and hence mineralisation of the two elements may have been faster. During the process of decomposition, in general, temperature will primarily affect the rates of decay, whereas oxygen will influence the efficiency and completeness of decomposition (Wetzel 1975; Godshalk & Wetzel 1978). This could be the reason why the concentration of phosphate and nitrate increased during Qrt4, and peaked in Qrt1. Notably, fish species in the Lower Shire Floodplain are young in Qrt4 and Qrt1, as indicated by the high density of juveniles in the littoral zone (Chapter 5); and hence, fertile water during this time ensures abundant food for juvenile fish.

The high concentration of nitrate and phosphate in Qrt1 could also be a result of aerial deposition from fires, set by farmers as they clear marshland for cultivation (personal observation). Hastings (1973) also reported massive fires in the Lower Shire Floodplain, especially in the north-eastern parts. Bootsma & Hecky (1999) reported that seasonal burning of grasses in the catchment of Lake Malawi stimulates soil fertility, which in return mobilizes nitrogen and phosphorus in surface waters.

The physico-chemical characteristics of the Lower Shire Floodplain are influenced by a number of physical and chemical factors, as represented by coefficient of determination listed in Table 3.5. The inverse and direct correlations between water level and chemical elements reflect the dilution and concentration effects of floodwater on water chemistry (Egborge 1971). In this study the overall relationship was positive, except in the seasonally connected lagoons. Possibly, the mixing of water from the lagoons and the river-floodplain produces water with relatively lower conductivity. Furch (1984) also reported that the more the water of the lakes in the Amazon mixed with river water, the lower was the mean conductivity value.

Exhibition of a simultaneously negative and positive relationship between some physico-chemical parameters and the flood regime supports the hypothesis that the habitats of the floodplain are not fixed but are in “phase-transition” with the hydrological (and obviously the climate) regime (Zallen 1983; Levin & Segel 1985; Holland *et al.* 1991).

If the theory of phase transition is applicable to a particular floodplain, then the system must conform to a number of attributes. Firstly, the floodplain must exhibit fundamental changes in phase or spatial structure (Milne *et al.* 1996). This can be demonstrated by the dynamic changes in physico-chemical characteristics with hydro-climatic seasons, which define the characteristic habitats of the floodplain (see Table 3.3, Figures 3.7 and 3.8). Secondly, fundamental changes in phase must occur at a critical threshold for controlling factors (e.g. temperature, density) (Milne *et al.* 1996). The four quarterly hydro-climatic seasons affecting the Lower Shire Floodplain, were established based on “critical thresholds” (Chapter 2) of climatic and hydrologic parameters of the floodplain that influence the primary critical threshold of the flood-pulse.

As demonstrated here, the flood-pulse influences the characteristics of the habitats (Fig. 3.7 and 3.8). However, critical aspects of the flood-pulse are explained by Ward’s (1998) concept of hydrologic connectivity through which the habitats are either seasonally or permanently connected to the main-river channel. This may explain why during Qrt1&Qrt4 (receding and low flood regime) two major habitats (RF & PCL) exhibit similar characteristics (Fig. 3.7 and 3.8) and during Qrt2&Qrt3 (rising and peak flood-pulse) all three major habitats (RF, PCL&SCL) exhibit similar characteristics simply because they are joined by a high water level, in a non-equilibrial spatial distribution. This supports the observation of Junk *et al.* (1989) that floodplain habitats shift horizontally and vertically according to the water level. The strong positive correlation between water level and TDS and conductivity points to the fact that the Lower Shire Floodplain relies a great deal on an allochthonous input of nutrients for its productivity. This reliance on external input is reflected in the strong negative correlation ($r^2 = 0.13$, $p<0.05$) between TDS and transparency, further supporting the notion that the flood-pulse is the carrier of energy and matter (Junk *et al.* 1989).

Using the amount of phosphorus as one criterion for fertility, the Lower Shire Floodplain is relatively fertile compared with other river-floodplains in the southern hemisphere (Table 3.6). Lund (1965) noted that because inorganic phosphorus is utilised so rapidly and can be stored in excess of a system's immediate needs, the total amount of phosphorus present might be an index of water fertility. The high alkalinity, hardness, phosphate and nitrate concentration and transparency as reported in this study are relatively consistent with the once-off observations reported over twenty years ago by Hastings (1973) and Hall *et al.* (1977) (Table 3.6).

This study has shown that it is possible to use statistical techniques to define major floodplain habitats or ecotones. Given that the hydrological and climatic setting were common to all the habitats (Qrt1-4), and that the ANOVA analysis did not differentiate between SCL & PCL (Table 3.4) and that the multivariate regression analysis did not account for much of the variance in the models (i.e. lower regression coefficients $0.002 \leq r^2 \geq 0.49$) (Table 3.5), hierarchical approach was then used to strengthen the habitat classification methods.

The hierarchical combination into cluster and multi-dimensional scaling of the hydrological, physico-chemical and habitat structure attributes overlaid over the four hydro-climatic seasons resulted in a distinction between the three habitats (Figures 3.7 & 3.8). The univariate ANOVA and multivariate regression analyses show that water level, temperature, pH, conductivity, DO and TDS are the most important variables in determining or defining habitat characteristics (Tables 3.4 and 3.5). The various sets of the positive and negative relationships between physico-chemical variables and the habitats reflects the intricate dynamics between dilution-concentration effects (Ibańez *et al.* 2000), source-sink energetics (Forman & Moore 1992, Odum 1993) and hydrologic connectivity (Heiler *et al.* 1995, Ward 1998, Pringle 2001) brought about by the flood-pulse (Junk *et al.* 1989) during the various hydro-climatic seasons. The cluster and multi-dimensional scaling exercise also reflects the scale-dependence (Peterson & Parker 1998) of the habitats with the hydro-climatic seasons (temporal scale) and the hydrologic-connectivity to the main river channel (spatial scale).

Most importantly, the habitat classification confirms the notion that floodplains are aquatic/terrestrial transition zones (ATTZ) (Junk *et al*. 1989) or ecosystem boundaries (ecotones) (Kolasa & Zalewski 1995), in phase transition (Zallen 1983) that form a "moving littoral zone" (Junk *et al.* 1989, Bayley 1991). Ultimately the habitats of the floodplain change due to the rising and falling flood-pulse. The classification also defines the three major habitats as functional units of the ecosystems (Forman & Moore 1992), permits further investigation on fish production, yield and management with a greater degree of confidence.

3.5 Conclusion

The major habitats of the Lower Shire Floodplain have been identified, using a more acceptable, quantitatively and statistically robust measure as river-floodplain, permanently connected lagoons and seasonally connected lagoons. The classification defines these habitats as functional units, reflecting the intricate dynamics between dilution-concentration effects, source-sink energetics and hydrologic connectivity brought about by the flood-pulse, as well as the scale-dependence of the ecotones with the hydro-climatic seasons (temporal scale) and the hydrologic-connectivity to the main river channel (spatial scale). The physico-chemical variables used in this study are used routinely in water quality monitoring in aquatic ecosystems. Therefore, the methodology described here can be easily applied to tropical floodplain habitat characterisation elsewhere. The measure of habitat type developed in this study is important for fisheries managers to fully understand the effect of water fluctuation and habitat on the key commercially important fish species of the Lower Shire Floodplain.

Chapter 4

The Biology of *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain

4.1 Introduction

The absolute abundance of fish population is influenced by four major factors, viz. growth, recruitment, natural and fishing mortalities (Welcomme 2001). Therefore, management of fish stocks requires a comprehensive understanding of these factors (Pauly 1981 & 1987, Beamish & McFarlane 1987, Wooton 1990). However, age, growth rates, size at sexual maturity, reproductive periodicity and mortality rate can vary from one water body to another (Le Roux 1961, Hecht 1980, Lowe-McConnell 1982, Pauly & Munro1984, Weyl & Hecht 1998), depending on stability or instability of the environment (Welcomme 2001).

Rivers and floodplains are dynamic environments and habitats that strongly influence the life-histories of the fishes (Southwood 1977, Welcomme 2001). The most important environmental factor that influences fishes in floodplains is the flood regime (Junk 1970, Welcomme 1975, Howard-Williams & Junk 1976, Bayley 1981 & 1991, Fernando & Holcik 1991, Hanna & Schiemer 1993). For example, the timing of breeding in many floodplain fish species coincides with the peak flood to ensure maximum supply of food for the young (Lowe-McConnell 1975, Welcomme 1979, Merron & Bruton 1995). The amplitude of the flood determines the area of floodplain covered by water and subsequent nutrients released in the habitat, while the duration of the flood determines the exposure of the young fish to food-rich floodplain environments (Welcomme 2001). The Flood Pulse Concept describes the process of nutrient and energy transfer during flooding (Junk *et al.* 1989) (see also Chapter 3).

Furthermore, in tropical river floodplains, changes in population size/age structure and sexual maturity in exploited fish populations have been associated with environmental stresses and heavy fishing pressure (Bayley 1981, Welcomme 1995). From a fisheries perspective, particular elements of the reproductive strategy are of interest. Age-at-sexual maturity and seasonal timing of reproduction, coupled with mortality rate, determine how many fish survive to recruit into the fishery (Welcomme 2001).

In river systems the major factors affecting mortality rate are fishing, stranding, abiotic factors and predation, all of which vary with the flood cycle, intensifying during the drawdown and receding during the high-water period; hence mortality rate is assumed to be density-dependent (Welcomme 1979, 1985&1989; MRAG 1994).

In Chapter 2 it was shown that the flood regime in the Lower Shire Floodplain varies according to the four hydro-climatic seasons. In Chapter 3, it has been shown that the flood pulse, which influences an intricate array of dilution-concentration effects, source-sink energetics, hydrologic connectivity and physico-chemical dynamics, defines major habitats as functional units of the floodplain. It is expected that these dynamic abiotic changes would have a significant impact on the biology of fishes and the fishery itself.

The Mozambique tilapia, *Oreochromis mossambicus* (Cichlidae) and the African catfish, *Clarias gariepinus* (Clariidae) are the two most important species in the Lower Shire Floodplain fisheries and dominate the catches (Hastings 1973, Willoughby & Tweddle 1978[a], Chapter 6). For various reasons, *Clarias gariepinus* is regarded as a hardy, ecological pioneer species (Bruton 1979). It has the ability to air-breath, is well adapted to feed on a wide range of prey, is able to adapt its feeding habits depending on food availability. It is able to withstand adverse environmental conditions (Bruton & Allanson 1974, Hecht 1980, Quick & Bruton 1983, van der Waal 1985). It is also recognised as an altricial species (Bruton 1989). Some of the altricial life-history style traits include high fecundity; small (1.2mm) eggs, short incubation period (about 24 hours), no parental care. Furthermore, the larvae hatch and absorb the yolksac within 2-4 days, and exhibit a long larval stage of between 11 and 15 days (Bruton 1979).

On the other hand, *O. mossambicus* is recognized as having a precocial life-history style (Noakes & Balon 1982; Bruton 1989). It is a nest-spawning mouth-brooder; produces large eggs, which hatch after 20-22 days and develop into juveniles, which are released when they reach a length of 9-10 mm (Bruton & Bolt, 1975; Arthington

& Milton, 1986). It is an omnivore, with some preference for detritus, plant matter and diatoms (Bowen, 1979; Trewevas, 1983; Bruton & Bolt 1975; De Silva *et al.*, 1984).

Several studies have been conducted on the biology and ecology of the two species in the Lower Shire Floodplain in the past. Hastings (1973) investigated reproductive seasonality of the two species. More detailed studies on feeding and the breeding ecology of the two species were carried out by Willoughby & Tweddle (1978^a), whilst Willoughby & Tweddle (1978^b) investigated the growth of catfish using vertebrae, though their study was based on limited material and growth was not related to the changing nature of the habitat. Willoughby & Tweddle (1978^b) also attempted to age *O. mossambicus* in the Lower Shire Floodplain using scales, but did not succeed. While these studies have provided an excellent understanding of the biology of the two species, especially the feeding and breeding ecology, they do not provide a complete understanding of the relationship between their biology and the flood regime.

The principal objective of the study was to develop input parameters for a hydro-climatic fisheries model for tropical floodplains and to provide the means with which to improve management strategies for the fisheries of the Lower Shire Floodplain. Therefore, the biological studies on *O. mossambicus* and *C. gariepinus* were not geared towards providing a detailed interpretation of the life-histories of the two species per se. The purpose of investigation was rather to quantify certain parameters such as age, growth, mortality, reproductive seasonality, size-at-age/sexual maturity, as input parameters for the development of a predictive hydro-climatic fisheries model for tropical floodplains.

4.2 Materials and Methods

General

Specimens of *Oreochromis mossambicus* and *Clarias gariepinus* were collected monthly from the Lower Shire Floodplain between March 1998 and June 2000 using experimental gill nets and seine nets. Multifilament 3-ply gill net fleets were used to catch the fish. These consisted of five randomly distributed panels, 100 m length and 1 m deep, with stretched mesh sizes of 50, 65, 75, 90 and 100 mm. The nets were set between 1400 and 1600 hours and lifted between 0600 and 0800 hours the following morning. Twenty gillnetting sites were randomly selected from the three major habitats of the floodplain; four, ten and six sites from the River-floodplain = RF; Permanently connected lagoon=PCL, and Seasonally connected lagoon=SCL, respectively. The sites are shown in Figure 2.1 (Chapter 2).

Seine net samples were also taken monthly at three sites in permanently connected lagoons and three sites in the seasonally connected lagoons (Figure 2.1). The seine net was 30 m long and 2 m deep with a 13 mm mesh bag and 25 mm mesh wings. It was not possible to operate such a large seine net in the main river channel. The two gears were used on the assumption that they would catch all size classes. All fish species in each catch were identified, counted and measured for total length (TL) and standard length (SL) to the nearest 1 millimetre and weighed to nearest 0.1 gram. For *O. mossambicus* and *C. gariepinus* gonads were removed, weighed and categorised according to the five developmental stages as described in Table 4.1, and the eviscerated mass of the fish was later recorded. The sagittal and lapillar otoliths were removed, from *O. mossambicus* and *C. gariepinus*, respectively, for age estimation. All otoliths were measured for length and diameter. The other fish were preserved in formalin, later washed in water and stored in alcohol.

Age and growth

Reliability of the methods used to determine life history traits such as age is a paramount requirement for elucidating fish population age structure, mortality rate, and growth rate parameters (Pauly 1981, Carlander 1987, Beamish & McFarlane 1987, Pauly 1987). A number of methods have been used to estimate age of fish with varying success (Summerfelt & Hall 1987). These methods include length-frequency analysis, and growth rings on scales, otoliths, spines and vertebrae (Foucher & Fournier 1982, Carlander 1987, Beamish & McFarlane 1987). Otoliths are considered to be the most suitable hard tissue for age and growth estimation in tropical and subtropical areas (Hecht 1980, Samuel *et al.* 1987, Booth *et al.* 1995, Weyl & Hecht 1998).

A sample of twenty pairs of otoliths of *O. mossambicus* and ten of *C. gariepinus* were used to determine whether burning them would enhance the growth zones and make it easier to estimate age. One otolith of each pair was burnt over a methylated spirit flame until pale brown. Care was taken not to char the otoliths as this may obscure the internal structure and the margins (Booth & Meron 1996).

Table 4.1 Macroscopic criteria used to determine the stage of gonad development in *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain.

Stage	**Development**	*Macroscopic appearance*	
		Oreochromis mossambicus	*Clarias gariepinus* (modified from Bruton 1979)
1	Juvenile	Not possible to visibly distinguish sex. Gonad appears as translucent gelatinous strip.	Minute gonads set close under vertebral column, undeveloped sexual products, testes and ovaries transparent and elongate, eggs invisible to naked eye.
2	Resting	Ovaries are white or slightly yellowish. Oocytes are macroscopically distinguishable. Testes are discernible as thin white strands.	Gonads very small, transparent or white sacs under vertebral column, eggs invisible to naked eye.
3	Developing	Ovaries enlarged, oocytes readily visible and yellow. Testes are broadened, distended and cream coloured.	Ovaries enlarged and oocytes visible to naked eye, ovary wall transparent, testes swollen and white.
4	Ripe	Oocytes of maximum size, yellow to green and testis swollen to maximum size and cream coloured.	Ovaries distend the body cavity, oocytes readily visible and opaque and orange, testes enlarged and white or pinkish with white/grey proximal edging.
5	Spent	Ovaries flaccid and sac-like with few vittellogenic oocytes visible. Testes reduced in size and dirty grey in colour.	Sexual products have been discharged, ovary dark red with few remaining eggs, testes a deflated, grey white sac.

The otoliths were then embedded in clear polyester casting resin, medial side down and transversely sectioned along the dorsoventral plane through the nucleus using a double-bladed diamond-edge saw. The otolith sections (0.2-0.5 mm thick) were then mounted on microscope slides using DPX as a mountant. The burnt otoliths of both species were easier to read in all cases, whereupon all otoliths were burnt prior to ageing.

The number of opaque zones was read on two occasions with a dissecting microscope under transmitted light using variable magnification. If two readings were the same, the age estimate was accepted. If the readings were different, a third reading was done. An age estimate was accepted if two of the three readings were similar. If the three readings differed by two years, the average of the three readings was used. If the readings differed by more than two years the otolith was rejected.

Marginal zone analysis (Mannoch 1982) was used to validate the observed growth zones as annuli. Growth rings on otoliths are reflected as alternating opaque and translucent zones. The outer margins of otoliths sampled at monthly intervals were examined and the composition of the outer margin (either opaque or translucent) was expressed as a percentage of the monthly sample. A total of 233 sagital otoliths of *O. mossambicus* and 175 lapillar otoliths of *C. gariepinus* were examined.

Length-at-age was modelled using both the three-parameter von Bertalanffy and the four-parameter Schnute growth models (Ricker 1975, Schnute 1981, Punt 1993). In order to determine and fit appropriate growth models, the recommendations made by Punt (1993) were applied. A non-parametric one-sample runs test for randomness of residuals and the Bartlett's test for homoscedascity (Hughes 1986) were applied. Variance estimates were calculated using the (conditioned) parametric bootstrap technique described by Efron (1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). A Microsoft Excel spreadsheet programme (developed by Dr. A. Booth, Department of Ichthyology and Fisheries Science, Rhodes University) was used to execute the above procedure. The models were fitted using a non-linear minimisation routine (or downhill simplex method) (Punt 1993) to obtain parameter estimates for the selected growth model. A maximum likelihood ratio test was used to assess the model with the best fit; where there were no significant differences ($p \geq 0.05$) and the model with the least number of parameters was chosen. The specialised von Bertalanffy growth model is:

$$l_t = L_\infty \left(1 - e^{-k(t - t_o)}\right) \qquad \text{(Equation 4.1)}$$

where t_o is age at "zero" length; L_∞ is the predicted asymptotic length and k is the Brody growth co-efficient (Ricker 1975). The Schnute model is described by the following equation:

$$\ell(t) = \left[\ell_1 + \left(\ell_2^b - \ell_1^b\right) \frac{1 - e^{-a(t - t_1)}}{1 - e^{-a(t_2 - t_1)}} \right]^{1/b} \qquad \text{(Equation 4.2)}$$

where $\ell(t)$ is the length at age t; t_1 is the smallest age in the sample; ℓ_1 is the value of $\ell(t)$ at time $t=t_1$; ℓ_2 is the value of $\ell(t)$ at $t=t_2$; a and b are parameters.

To compare the growth performance of the two species in the Lower Shire Floodplain with populations from other floodplains in Southern Africa, phi-prime (ϕ') Pauly & Munro (1984) was used. Phi-prime is described by the function:

$$\phi' = 2 \log L_\infty + \log K \qquad \text{(Equation 4.3)}$$

where L_∞ is the predicted asymptotic length and K the Brody growth co-efficient from the von Bertalanffy growth model. Pauly and Munro's (1984) ϕ', which is a statistical correlation of K and L_∞ or W_∞, is appropriate for comparison of growth because growth is a multivariate parameter: some populations may grow faster than others at younger ages, while others may grow slower when older (Moreau 1987). Since ϕ' is the constant in the regression of log K upon log L_∞ or W_∞ and is directly related to the maximum slope of the growth curve, irrespective of growth rate and asymptotic size, it may reflect differences among populations, between years and localities (which might have been caused by environmental differences, e.g. temperature or food availability).

Sexual maturity and spawning season

Length at sexual maturity for 407 male and 375 female *O. mossambicus* and 166 male and 128 female *C. gariepinus* was determined using data collected during the peak reproductive season of both species from September 1998 to February 1999. The specimens showing little or no gonad development during these months were regarded as immature, while those with gonads in stages 3 to 4 were considered to be mature (Merron & Mann 1995). A five-stage gonad development scale was used (Table 4.1). The proportion of sexually mature fish was fitted to a non-linear logistic ogive of the form:

$$\psi = \frac{1}{1 + e^{-(L - Lm_{50})/\delta}} \qquad \text{(Equation 4.4)}$$

where ψ is the proportion of sexually mature fish by length, Lm_{50} is the mean length-at-50% sexual maturity, and δ is the width or steepness of the logistic ogive (King 1995).

The spawning season was determined by using the five-stage macroscopic gonad scale (Table 4.1) (Bruton 1979, Merron & Mann 1995), as well as by calculating the monthly gonadosomatic index (GSI) for females as follows:

$$GSI = \left[\frac{Gonad\ mass\ (g)}{Eviscerated\ mass\ (g)} \right] \times 100 \qquad \text{(Equation 4.5)}$$

GSI is the relative mass of the gonad with respect to total or somatic mass (Welcomme 1985, Wootton 1990, King 1995).

All the female fish used in the GSI analysis were greater than the expected length-at-50% sexual maturity. No males were used for the GSI analysis.

To assess whether the reproductive cycle was in any way dependent on the hydro-climatic seasonal cycle of the Lower Shire Floodplain, the GSI and the proportion of ripe females of *O. mossambicus* and *C. gariepinus* were examined in relation to the four hydro-climatic seasons (Qrt1-4, see Chapter 2). A non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) (Zar 1984) was used to assess the seasonal effects on GSI. Where significant differences were found, values were compared using a non-parametric Mann-Whitney U-test.

Mortality estimates

The estimates of the instantaneous rate of total mortality (Z) for *O. mossambicus* and *C. gariepinus* were obtained by using catch curve analysis (Ricker 1975) and the method described by Butterworth *et al.* (1989). Before constructing the catch curve the age-length keys of the aged subsamples were normalised for each length class and combined with the total length-frequency distribution of the whole catch to give the full catch age-frequency distribution (Butterworth *et al.* 1989). Both methods were applied to the transformed age-frequency data for *O. mossambicus* and *C. gariepinus* obtained from experimental seine nets and gillnet samples and from the catches of the four major artisanal gears (cast nets, gill nets, long lines, and fish traps). This approach was used to compare fishery-independent and fishery-dependent fishing mortalities in the floodplain. Z was obtained by plotting the natural logarithm of age frequency against age. The slope of the straight line fitted to points greater than the age at full recruitment to the fishery (a_r) provided an estimate of instantaneous total mortality (Z). The Butterworth *et al.* (1989) method is considered to be statistically superior to the catch curve analysis if the numbers of fish caught at any age are low. The Butterworth *et al.* (1989) mortality model is described by the equation:

$$Z = \ln\left[1 + \frac{1}{(a_r - a_f)} \right] \qquad \text{(Equation 4.6)}$$

where a_f is the mean age at full recruitment and a_r is the age of fully recruited fish sampled.

Natural mortality (M) is one of the most difficult parameters to measure. Most studies have relied upon empirical methods (Rihkter & Efanov 1977, Pauly 1980, Hoenig 1983, Gunderson & Dygert 1988). Weyl (1998) in his study of fish populations in a sub-tropical lake in Mozambique proposed estimating natural mortality (M) using an average of the following four empirical equations:

a) Pauly (1980) equation:

$$\log M = -0.006 - 0.27 \log L_{\infty} + 0.6543 \log K + 0.463 \log T \qquad \text{(Equation 4.7)}$$

where L_{∞} and K are the von Bertalanffy growth parameters and T is the mean annual water surface temperature (24.87 $^{\circ}C$) for the Lower Shire Floodplain (Chapter 3);

b) Rihkter & Efanov (1977) equation:

$$M = \frac{1.521}{a_m^{0.72}} - 0.155 \qquad \text{(Equation 4.8)}$$

where a_m is the age-at-50% maturity;

c) Gunderson & Dygert (1988) equation:

$$M = 0.03 + 1.68 \times GSI \qquad \text{(Equation 4.9)}$$

where GSI is the gonadosomatic index of ripe female fish;

d) Hoenig (1983) equation:

$$\ln Z = 1.46 \times 1.01 \times \ln\left(a_{\max}\right) \qquad \text{(Equation 4.10)}$$

where $\left(a_{\max}\right)$ is the maximum age of fish sampled.

Fishing mortality (F) was obtained by substitution into the equation $\left(F = Z - M\right)$ with the known values for Z and M.

4.4 Results

Age and growth

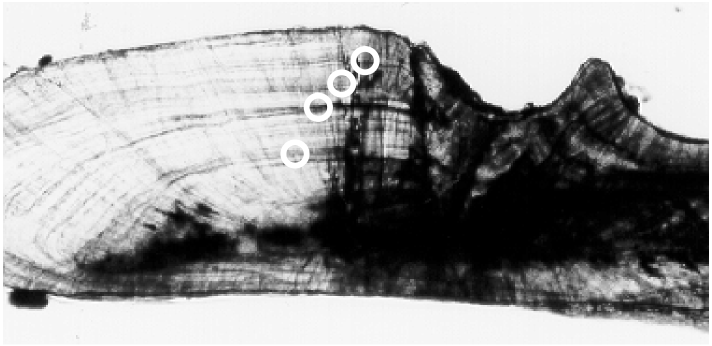
The morphometric relationships between TL, SL, weight and otolith length are summarised in Table 4.2.

Table 4.2 Morphometric relationships of *Oreochromis mossambicus* and *Clarias gariepinus* from the Lower Shire Floodplain. TL = total length, SL = standard length, Wt = weight, OL = otolith length, r^2 = coefficient of determination, p = level of significance, n = sample size.

Parameter	**Relationship**	r^2	p	n
O. mossambicus				
Wt (g)	= 0.00053 x TL (mm) $^{2.299}$	0.93	<0.001	1168
SL (mm)	= -1.541 + 0.799 x TL (mm)	0.98	<0.001	986
TL (mm)	= 29.026 x OL (mm)$^{0.962}$	0.78	<0.0001	163
C. gariepinus				
Wt (g)	= 0.000012 x TL (mm) $^{2.918}$	0.91	<0.001	128
SL (mm)	= 5.319 + 0.861 x TL (mm)	0.98	<0.001	986
TL (mm)	= 59.877 x OL (mm)$^{1.135}$	0.85	<0.0001	61

The growth zones on the otoliths of the two species are illustrated in Figure 4.1. The monthly examination of the otolith margins revealed that one translucent and one opaque zone were deposited every year, during the period May to October (Qrt4-Qrt2) for *O. mossambicus* and from May to August (Qrt4-Qrt1) for *C. gariepinus* (Fig. 4.2). One opaque zone and one translucent zone, therefore, constitute an annulus and where counted as such. Of the 233 *O. mossambicus* and 175 *C. gariepinus* otoliths examined, 8 (3.4%) and 28 (16.0%) respectively, were rejected as unreadable because of unclear rings. Length-at-age keys for *O. mossambicus* and *C. gariepinus* are presented in Tables 4.3 and 4.4. *O. mossambicus* in the Lower Shire Floodplain attain a maximum age of 6 years (Table 4.3), while *C. gariepinus* attains 9 years (Table 4.4).

a



b

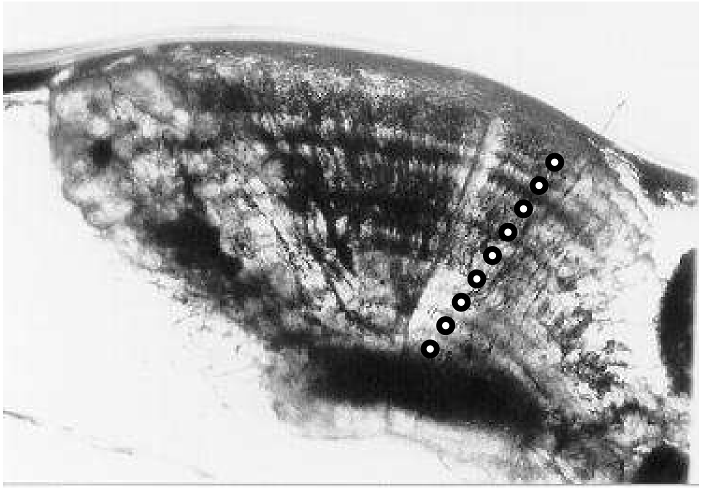


Figure 4.1 Photomicrograph of a sagittal otolith from a 184 mm TL, 4 year-old *Oreochromis mossambicus* (a) and lapillus otolith from a 550 mm TL, 9 year-old *Clarias gariepinus* (b) from the Lower Shire Floodplain.

There were no significant differences (One-way ANOVA, $p \geq 0.05$) between the growth models for males and females of both species. Length-at-age for *O. mossambicus* and *C. gariepinus* were adequately described by both the von Bertalanffy growth model (VBGM) and the Schnute model, and comparison of the two models using a maximum likelihood ratio test revealed that they did not differ significantly ($p \geq 0.05$). The von Bertalanffy model was therefore chosen for fitting the growth curve since it has the least number (3) of parameters. Furthermore, the VBGM was chosen since its parameters are commonly used in empirical estimates of natural mortality (Pauly 1980) and for ease of comparison with studies conducted on the two species in other localities.

Table 4.3 Age/length key for *Oreochromis mossambicus* from the Lower Shire Floodplain.

Size class			**Age (years)**					
(mm TL)	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
1-75	3							
76-95	19	5						
96-115	51	7	5					
116-135	29	12	8	6				
136-155	3	9	5	7	4	6		
156-175		5	6	6	3	1		
176-195			2	4	4		3	
196-215		1	2	2	4	2		
216-235					1			
236-255							1	
n	105	39	28	24	16	9	4	= 225

Table 4.4 Age/length key for *Clarias gariepinus* from the Lower Shire Floodplain.

Size class (mm TL)					**Age (years)**						
	0	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**Total**
200-220	6										
221-240	3										
241-260	1	5									
261-280		7									
281-300		3									
301-320		2	1								
321-340		6	3	2							
341-360		3	7	2	4	2					
361-380			5	5	2						
381-400			4	1	1	1	1				
401-420				6	2	4	6	3			
421-440			1	1	6	4	3	4			
441-460					2	3	1				
461-480					1	2	1		1		
481-500				2	1		1	1			
501-520							2	2			
521-540								1	1		
541-560									1		
561-580									2	1	
581-600									1		
601-620								2			
621-640										1	
n	10	26	21	19	19	16	15	13	6	2	**147**

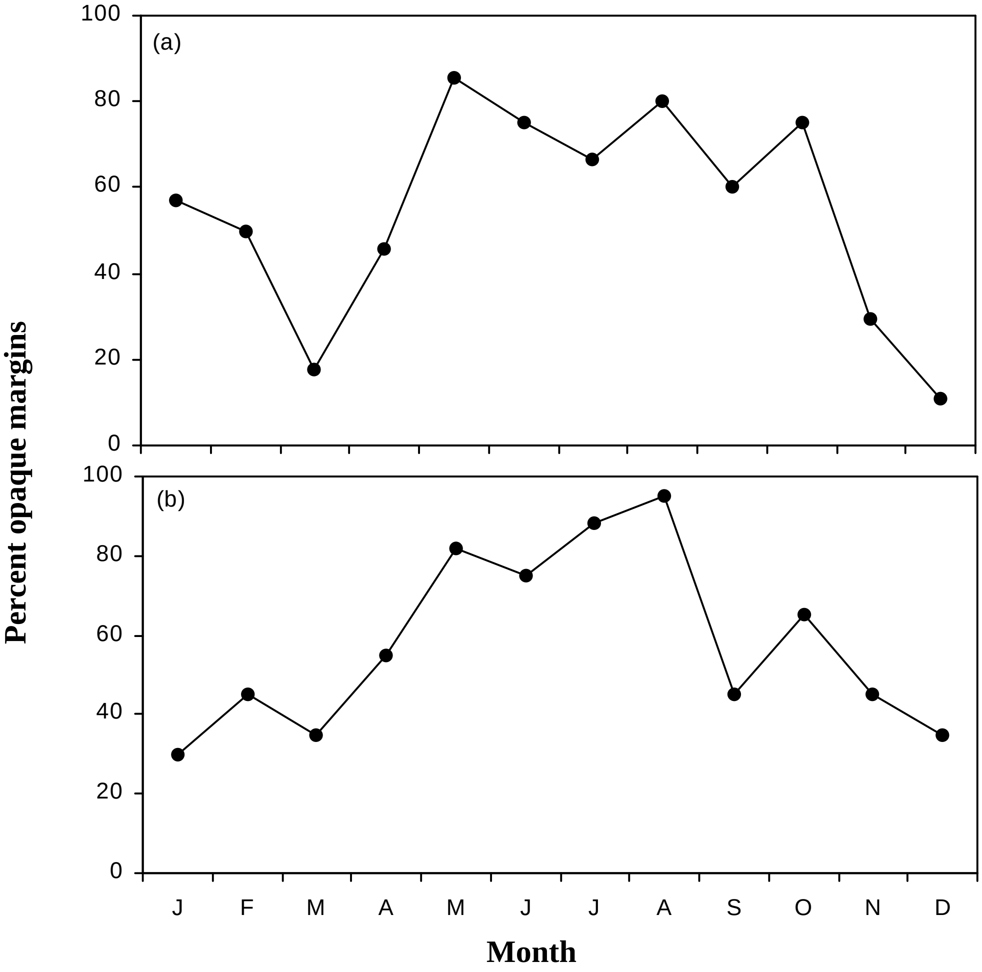


Figure 4.2 The monthly percent occurrence of an opaque outer margin on otoliths of (a) *Oreochromis mossambicus* and (b) *Clarias gariepinus* in the Lower Shire Floodplain.

The von Bertalanffy growth model parameters for the two species are summarised in Table 4.5 and growth of the two species is illustrated in Figure 4.3. Initial growth rate for both species was rapid, with asymptotic length being attained within two years by *O. mossambicus* and three years by *C. gariepinus*.

Table 4.5 The von Bertalanffy growth parameters, standard error (SE) and 95% confidence interval for *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain.

Parameter	Estimate	SE	95% confidence interval
O. mossambicus			
K	0.44 years^{-1}	0.01	(0.43, 0.44)
L_∞	177.6 mm TL	1.33	(161.7, 211.4)
t_o	-1.43	0.03	(-2.07, -0.83)
C. gariepinus			
K	0.31 years^{-1}	0.005	(0.22, 0.43)
L_∞	502.9 mm TL	1.98	(472.1, 550.5)
t_o	-1.92	0.03	(-2.51, -1.43)

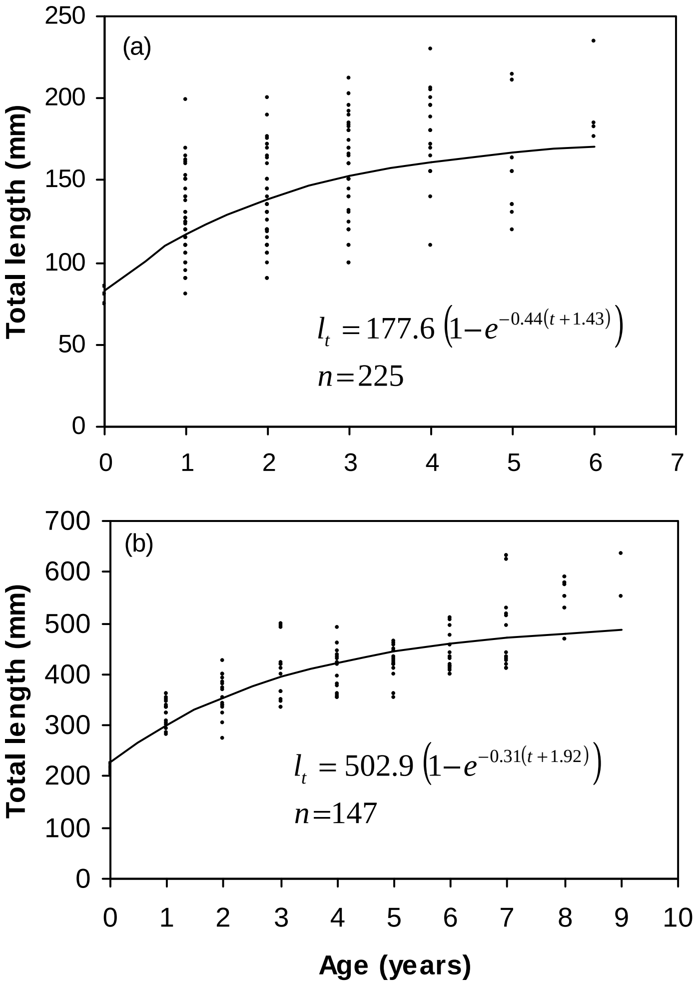


Figure 4.3 Observed and predicted length-at-age of (a) *Oreochromis mossambicus* and (b) *Clarias gariepinus*. Samples were collected between September 1998 and August 1999. The growth curves were fitted to combined sex data using the von Bertalanffy growth model with an absolute error structure.

Sexual maturity and reproductive seasonality

A total of 782 mature *O. mossambicus* were sampled of which 48% were female and 52% were male giving a sex ratio of 1 female: 1.09 males. This ratio was not significantly different from unity ($\chi^2 = 1.28$, df = 1, $p \geq 0.05$). Male *O. mossambicus* reached 50% sexual maturity (Lm_{50}) at 109 mm SL, and females at 105 mm SL (Fig. 4.4), but they were not significantly different from each other ($\chi^2 = 1.33$, df = 1, $p \geq 0.05$). Of 294 mature *C. gariepinus*, 55% were female and 45% male, giving a sex ratio of 1 male: 1.22 females, but the ratio was not significantly different from unity ($\chi^2 = 1.22$, df = 1, $p \geq 0.05$). Both male and female *C. gariepinus* reached 50% sexual maturity (Lm_{50}) at 249 mm SL (Fig. 4.4).

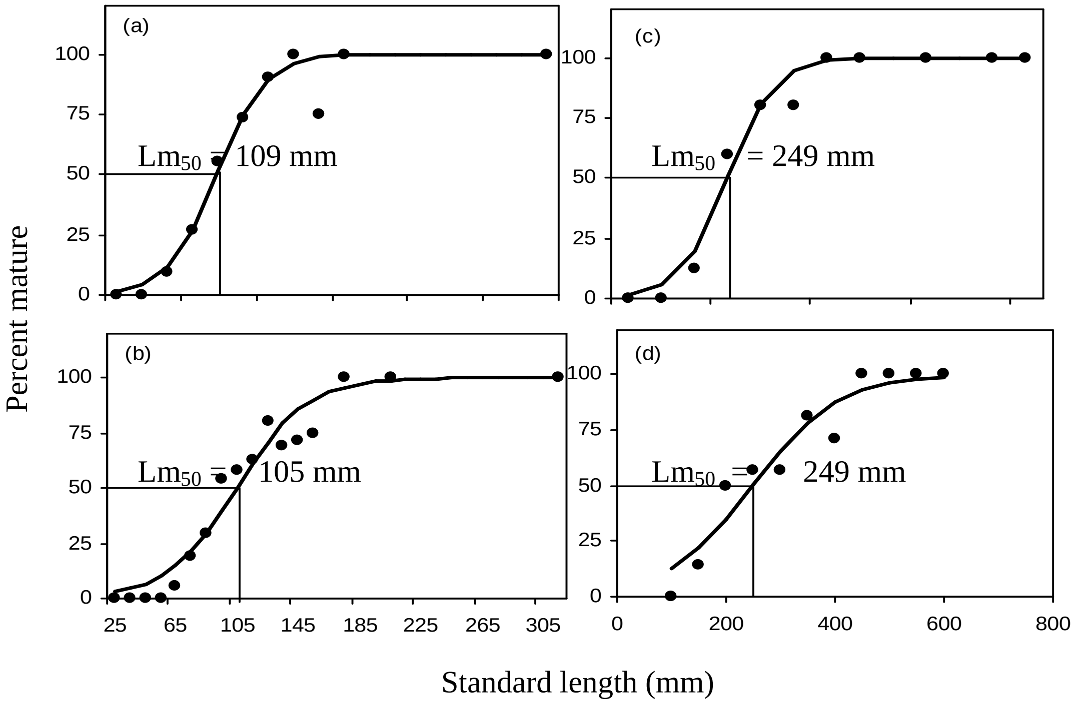


Figure 4.4 Length-at-50%-sexual maturity of (a) *Oreochromis mossambicus* males (n = 407), (b) *O. mossambicus* females (n = 375), (c) *Clarias gariepinus* males (n = 166) and (d) *C. gariepinus* females (n = 128) in the Lower Shire Floodplain.

The occurrence of developing and ripe females throughout all months, suggested that *O. mossambicus* might spawn throughout the year when conditions allow it to, although peak spawning appears to occur from October to February (Fig. 4.5). There were significant quarterly seasonal variations ($\chi^2 = 82.37$, df = 3, $p \leq 0.01$) in the proportion of mature females that were in stages 3 and 4 during the rising (Qrt2) and peak (Qrt3) flood regimes or stages 2 and 5 during low (Qrt1) and receding (Qrt4) flood regimes. This indicates the effect of the flood regime on reproductive seasonality. The GSI data also showed a significant seasonal pattern (one-way ANOVA, $p \leq 0.01$) (Fig. 4.6). The GSI values were significantly (one-way ANOVA, $p \leq 0.01$) higher during the rising (Qrt2) and peak (Qrt3) water level; while the lowest GSI values occurred during the periods of receding (Qrt4) and low (Qrt1) water level. Although there were some breeding activities in June, it can be inferred that the major breeding season of *O. mossambicus* in the Lower Shire Floodplain is between September and March, with a modal peak in January.

The occurrence of developing and ripe females also suggested that *C. gariepinus* has a protracted spawning season from September to March. Peak spawning activity, however, occurs between October and December (Fig. 4.5), during the rising water phase (Qrt2). There were significant quarterly seasonal differences ($\chi^2 = 253.33$, df = 3, $p \leq 0.01$) in the proportion of mature females that were in stages 3 and 4 (Qrt2 and Qrt3) or stages 2 and 5 (Qrt4 and Qrt1).

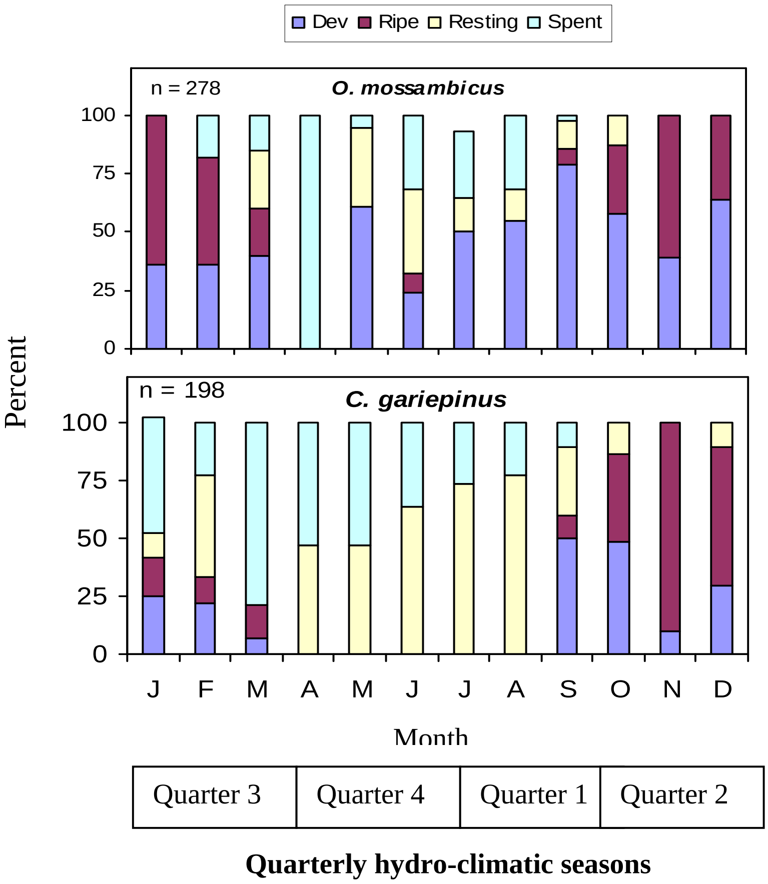


Figure 4.5 Monthly gonad maturity stages of *Oreochromis mossambicus* and *Clarias gariepinus* females from the Lower Shire Floodplain.

The GSI data for two years (Fig. 4.6) mirrored the results on gonad maturity (Fig. 4.5) and that the breeding season of *C. gariepinus* in the Lower Shire Floodplain is between October and March, with a modal peak in December and January. However, the presence of ripe ovaries in the September samples would suggest that breeding may begin earlier than October.

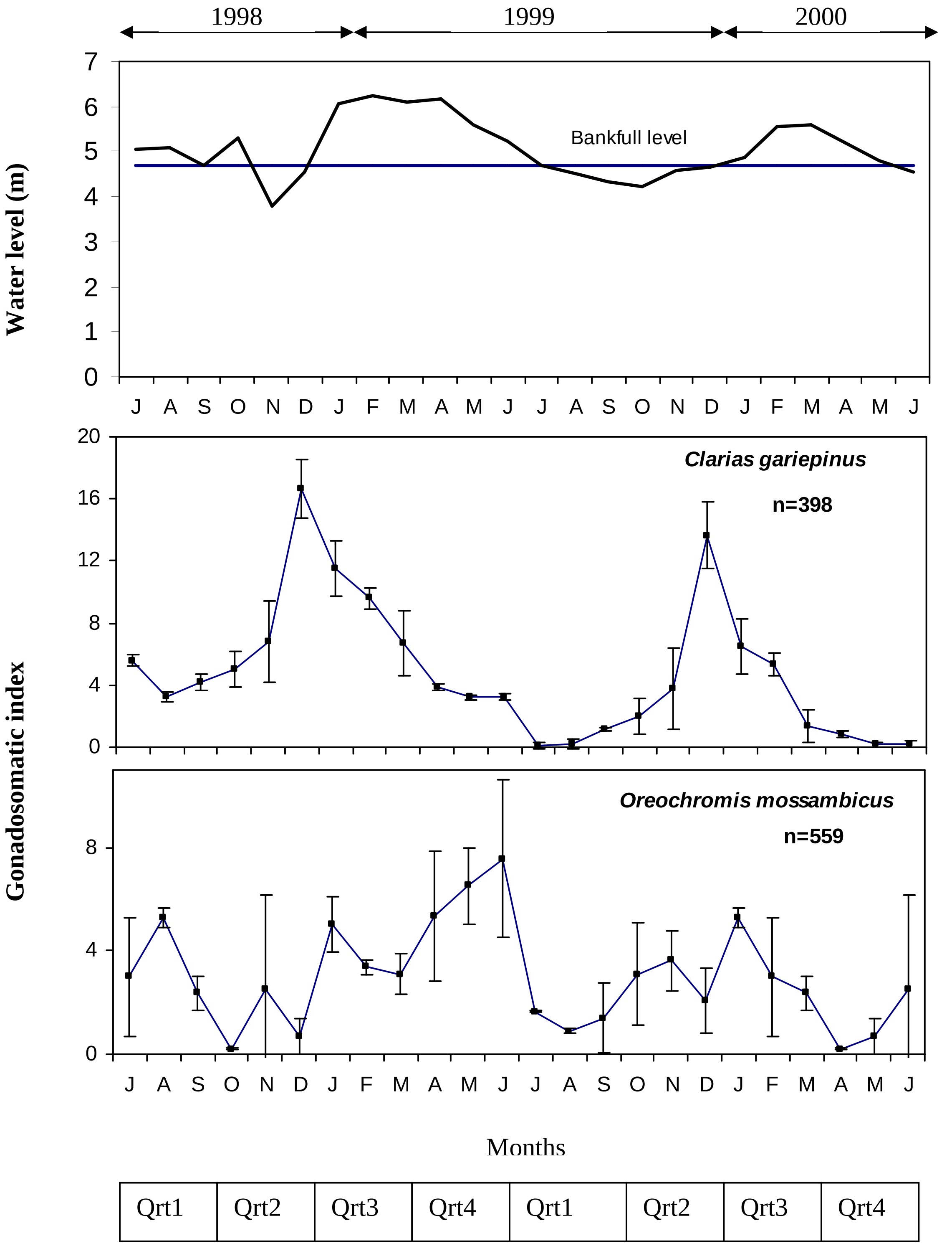


Figure 4.6 Gonadosomatic index (GSI) (±standard deviation) for female *Clarias gariepinus* and *Oreochromis mossambicus* in the Lower Shire Floodplain, in relation to changes in water level in the floodplain, from 1998 to 2000.

Mortality estimates

The age-based catch curves for *O. mossambicus* and *C. gariepinus* calculated from the experimental gill nets and seine nets, and from the artisanal cast net, gill net, long line and fish traps fisheries are shown in Figures 4.7 and 4.8. Both species are first recruited into the fisheries at 0 years of age, *O. mossambicus* was fully recruited between 0 and 3 years of age and *C. gariepinus* between 2 and 4 years of age (Fig. 4.7&4.8). Total mortality estimates for *O. mossambicus* obtained using the Butterworth *et al.* (1989) equation were on average somewhat higher (Z=0.52 for fisheries independent and 0.99 year^{-1} for fisheries dependent data) than those from the catch curve analysis (Z=0.45-0.68 year^{-1}) in both experimental gear and artisanal fisheries data (Table 4.6). An overall approximation of total mortality (Z) was obtained by first averaging Z from individual gears and then averaging all Z estimates from all gears to obtain 0.62±0.18 year^{-1} (Table 4.6).

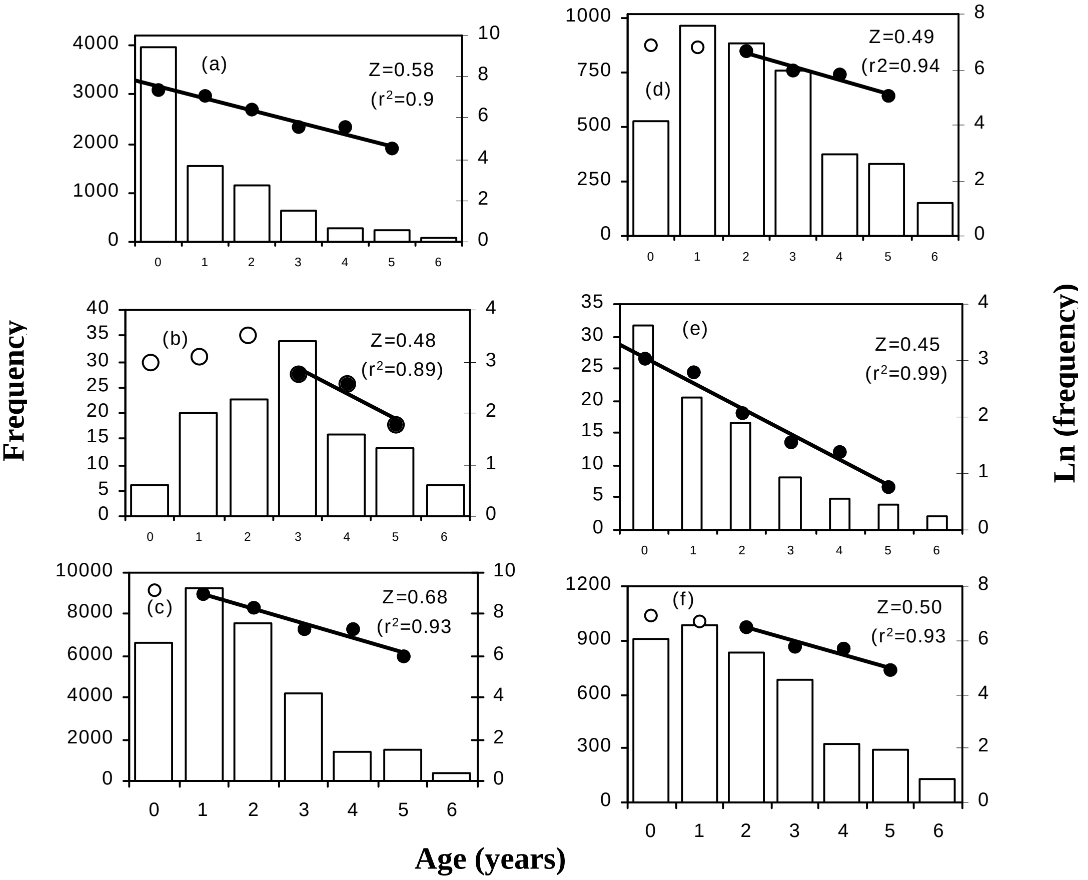


Figure 4.7 First estimates of the total annual mortality rate (Z) for *Oreochromis mossambicus* in the Lower Shire Floodplain. The Z estimates were obtained by fitting linearlised catch curves (closed circles) to age-frequency distributions (bars) obtained from (a) experimental seine nets, (b) experimental gillnet fleet, (c) artisanal castnet fishery, (d) artisanal gillnet fishery, (e) artisanal longline fishery, (f) artisanal fishtrap fishery in the Lower Shire Floodplain.

Total mortality estimates for *C. gariepinus* obtained from both the catch curve analysis and the Butterworth *et al.* (1989) methods using experimental gill net and seine net data were slightly lower (Z=0.43-1.44 year^{-1}) than those obtained for the artisanal fisheries (Z=0.46-1.98 year^{-1}) (Fig. 4.8). Although there were differences between some of the estimates, the differences were consistent in both methods, so it was decided that the first approximation of total mortality be obtained by also first averaging the Z from individual gears and then averaging all Z estimates from all gear to obtain 0.92±0.47 year^{-1} (Table 4.6). Generally, the Z values obtained using the Butterworth equation were higher than the Ricker catch curve values for both species, probably as a result of the gear catching small fish, which were not yet fully recruited, leading to lower values of mean age at full recruitment (a_f) in equation 4.6.

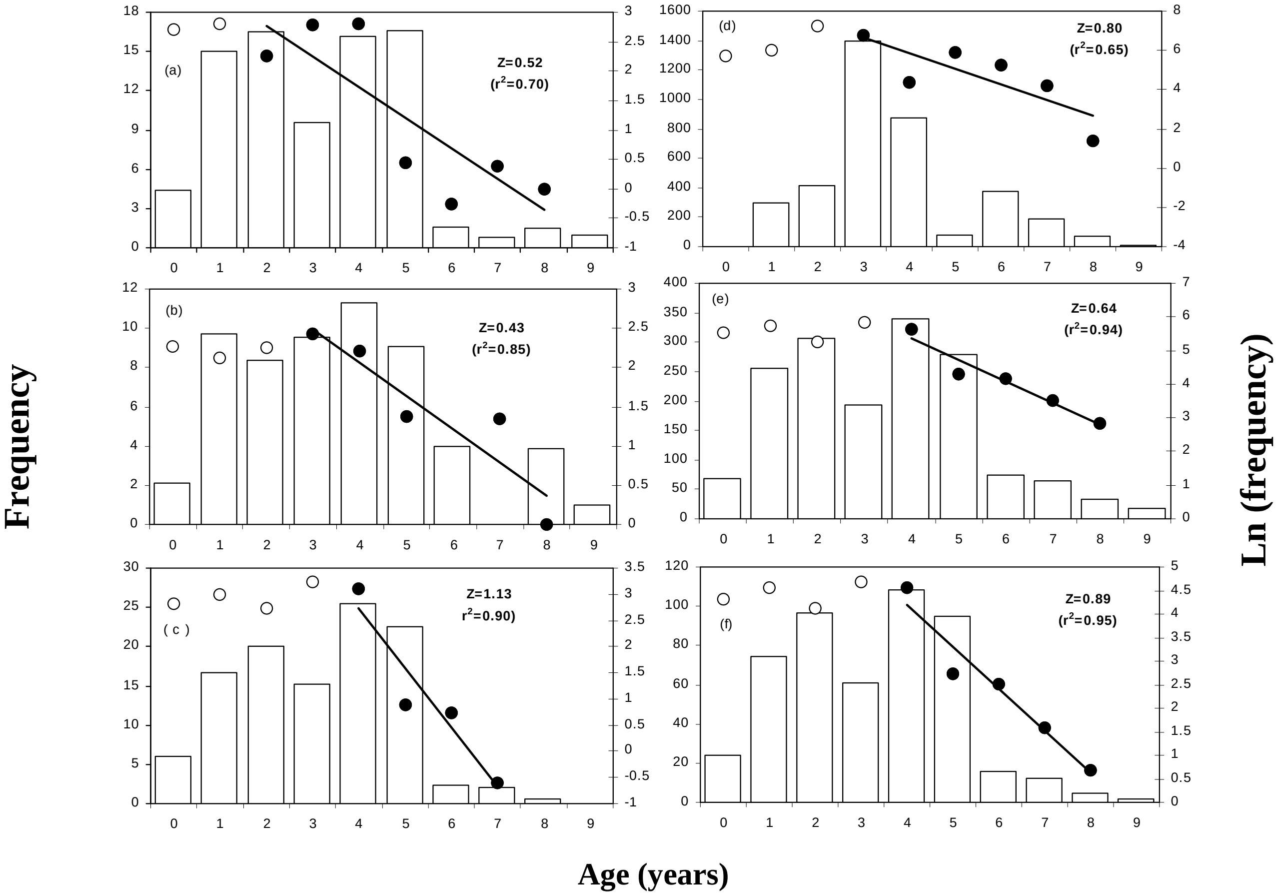


Figure 4.8 First estimates of the total annual mortality rate (Z) for *Clarias gariepinus* in the Lower Shire Floodplain. The Z estimates were obtained by fitting linearlised catch curves (closed circles) to age-frequency distributions (bars) obtained from (a) experimental seine nets, (b) experimental gillnet fleet, (c) artisanal castnet fishery, (d) artisanal gillnet fishery, (e) artisanal longline fishery, (f) artisanal fishtrap fishery in the Lower Shire Floodplain.

The four empirical estimates of natural mortality (M) obtained for *O. mossambicus* varied widely (Table 4.6). Following Weyl's (1998) rationale the average of the four estimates (0.46 year^{-1}) (Table 4.6) was taken as a first approximation of natural mortality.

Table 4.6 First estimates of the instantaneous rate of total mortality (Z) (year^{-1}) and natural mortality (M) (year^{-1}) for *Oreochromis mossambicus* and *Clarias gariepinus*. Estimates of Z were obtained from catch curves and the Butterworth *et al.* (1989) equation using age frequencies from experimental gill net fleet, experimental seine nets and the artisanal castnets, gil lnets, lon gline, fish traps fisheries in the Lower Shire Floodplain. Methods used to estimate M are ^{1} = Pauly (1980), ^{2} = Rihkter & Efanov (1977), ^{3} = Hoenig (1983) and ^{4} = Gunderson & Dygert (1988).

Species/gear	**Z (Catch curve)**	**Z (Butterworth *et al.* 1989)**	**M**	**F**
O. mossambicus				
Experimental gill nets	0.48	0.99	1.35^{1}	
Experimental seine nets	0.58	0.65	1.37^{2}	
Artisanal cast nets	0.68	0.89	0.02^{3}	
Artisanal gill nets	0.49	0.44	0.03^{4}	
Artisanal long lines	0.45	0.52		
Artisanal fish traps	0.50	0.75		
Average (year^{-1})	0.62±0.18		0.46	0.16
C. gariepinus				
Experimental gill nets	0.52	0.58	0.52^{1}	
Experimental seine nets	0.43	1.44	1.35^{2}	
Artisanal cast nets	1.13	0.46	0.01^{3}	
Artisanal gill nets	0.80	1.98	0.08^{4}	
Artisanal long lines	0.64	1.06		
Artisanal fish traps	0.89	1.27		
Average (year^{-1})	0.92±0.47		0.50	0.43

Similarly, for *C. gariepinus*, the estimate of M varied widely (Table 4.6). However, the average of the four estimates resulted in M=0.50 year^{-1}, which was not very different from the Pauly estimate (0.52). Therefore, the average of the four was taken as a first approximation of natural mortality. By substitution in F=Z– M, fishing mortality (F) was calculated at 0.16 year^{-1} for *O. mossambicus* and 0.43 year^{-1} for *C. gariepinus* (Table 4.6).

4.4 Discussion

Growth

C. gariepinus has been successfully aged previously by Willoughby & Tweddle (1978^b) using vertebrae as mentioned previously. However, their attempt to age *O. mossambicus* using scales was not successful. The calculated length-at-age estimates (Fig. 4.3) showed that both *O. mossambicus* and *C. gariepinus* in the Lower Shire Floodplain grew fast during their first two years of life. Both species mature at lengths corresponding to ages of between 1 and 2 years of age and thereafter growth declines. Asymptotic length in both species was attained by more than 50% of the fish at 2-3 years after sexual maturity.

The trend of rapid growth within the first two years is typical for both *O. mossambicus* and *C. gariepinus* and this has also been observed in other populations (Bruton & Allanson 1974, Hecht 1980, Quick & Bruton 1983, van der Waal 1985). This strategy is common in fish populations found in unstable environments, such as floodplains, where rapid growth enables juvenile fish to quickly attain a size large enough to evade predators and early attainment of sexual maturity to ensure successful reproduction (Lowe-McConnell 1967, Welcomme 2001).

The high variability in growth rate and length-at-50% maturity in *O. mossambicus* is evident when the data from this study are compared to earlier studies in the Lower Shire Floodplain, as well as studies in other sub-tropical localities. Although the length-at-50%-sexual maturity (Lm_{50}) was not calculated by Willoughby & Tweddle (1978^b) they reported a size-at-first maturity for *O. mossambicus* of 135 mm (TL) (106 mm SL), compared to 58 mm SL in the current study (Table 4.7). Female *O. mossambicus* in the Lower Shire floodplain attain 50% sexual maturity at a size(105 mm SL) similar to those in Lake Sibaya (100 mm SL), but at a smaller size than those in Lake Chicamba (161 mm SL) (Table 4.7). The smallest mature females in Lake Sibaya were between 68-78 mm (SL) (Bruton & Allanson 1974), which is very similar to the size at-first-maturity as recorded in the Lower Shire Floodplain in this study. Also based on phi-prime (ϕ') values (Table 4.7) growth of *O. mossambicus* in the Lower Shire Floodplain and Lake Sibaya is similar.

Table 4.7 Length-at-50%-sexual-maturity in mm (Lm_{50}) (SL), length-at-first maturity (SL), von Bertalanffy growth parameters, index of growth performance ϕ' (phi-prime, Pauly & Munro 1984) for *Oreochromis mossambicus* in southern African water bodies. M = male, F = female, M+F = both sexes.

Locality	**Sex**	**Lm_{50}**	t_0	L_∞	K	ϕ'	**Reference**
Lower Shire	M	109					This study
	F	105					
	M+F		-0.44	177.6	0.44	4.14	
Lake Sibaya	M	120	-0.360	217	0.358	4.23	Bruton & Allanson 1974
	F	100	-1.054	217	0.240	4.05	
Lake Chicamba	M	171					Weyl & Hecht 1998
	F	161					
	M+F		-0.269	212	0.790	4.55	
		Size-at-first maturity					
Lower Shire	F	58 SL					This study
	F	106 SL					Willoughby & Tweddle 1978[b]

It is common for length at sexual maturity in cichlids to vary from place to place, depending on the ecological opportunity provided by the habitat, including food availability (Bruton & Allanson 1974, Bowen 1979, Arthington & Milton, 1986). For example, dwarf or stunted populations of tilapia species are known from numerous natural systems, such as hot springs, drought-stricken lakes, isolated pools and habitats subjected to extreme environmental conditions (Lowe-McConnell 1958, Hickling 1961, Whitehead 1962, Coe 1966, Fryer & Iles 1972, Iles 1973, Bruton & Allanson, 1974; Bowen, 1979, Legendre & Jalabert 1988). Stunting is believed to be an adaptation to harsh environments (Bruton & Allanson 1974), although the environmental factors and/or biological mechanism behind this switching condition are not yet fully understood. *O. mossambicus* displays high phenotypic plasticity; if biotic or abiotic conditions change, it has the ability to mature at a smaller or larger size so that under prevailing conditions, reproduction output and success is maximised.

The smaller size-at-maturity of *O. mossambicus* in this study could be attributed to early maturity and precocious breeding in a hydrologically unstable environment (Bruton & Allanson 1974, Bruton 1979, Weyl & Hecht 1998). However, it is also likely that the current population in the Lower Shire matured at a smaller size, compared to those reported by Willoughby & Tweddle (1978^{b}) due to the increase in fishing effort (Nikolsky 1963, Iles 1973, Lowe-McConnell 1982, Kolding 1994, Welcomme 1995). This point will be elaborated later in the section.

The range in the size and age-at-first maturity has also been reported to vary widely in *C. gariepinus* (from 135 to 651 mm SL) between ages of 1 to 4 years (Bruton 1979, Merron 1991, Bruton 1996). Previous studies in the Lower Shire Floodplain reported size-at-first maturity for *C. gariepinus* at 229 mm (SL) Willoughby & Tweddle (1978^{b}), which is also greater than that reported in this study (193 mm, SL) (Table 4.8). Compared to populations in other localities, the previous and current populations of the Lower Shire Floodplain matured at smaller size than those in the Okavango Delta (229 mm SL) (Merron 1991), Lake Liambezi (238-264 SL) (van der Waal 1985), Le Roux dam (Quick & Bruton 1984) and Lake Sibaya (Bruton 1979) (Table 4.9). Quick & Bruton (1983) attributed maturity at a greater length to high food availability. Greater availability of food is also reflected in a higher length-to-mass ratio (Table 4.9).

Table 4.8 Length -at-first maturity in mm (SL), von Bertalanffy growth parameters, index of overall growth performance ϕ' (phi-prime, Pauly & Munro 1984) for *Clarias gariepinus* in African water bodies based on published data. The length -at-first maturity is standard length in mm (SL); M = male, F = female, M+F = both sexes.

Locality	**Sex**	**Size-at-first maturity**	t_0	L_∞ **(mm)**	K	ϕ'	**Reference**
Lower Shire	M	193					This study
	F	193					
	M+F		-1.92	502.9	0.31	4.89	
Le Roux Dam	M	820-920		1150	0.31	3.61	Quick & Bruton 1984
	F	>740		1020	0.45	3.67	
Okavango Delta	M	255					Merron 1991
	F	275					
Lake Sibaya	M	298		760	0.36	3.32	Bruton 1979
	F	289		670	0.49	3.34	
Lake Liambezi	M	238					Van der Waal 1985
	F	264					
	M+F				0.03	3.51	
Lower Shire	M	229		1390	0.09	3.21	Willoughby & Tweddle 1978^{b}
	F	229		790	0.17	3.5	Willoughby & Tweddle 1978^{b}
Lake Kariba	M+F			1240	0.17	2.97	Marshall 1990

Table 4.9 The average mass (g) of *C. gariepinus* 1000 mm TL from seven populations. The ratio of length to mass, as an index of condition of the fish, is derived from length-mass regressions.

Population	**Mean mass (g) at 1,000 mm TL**	**Source**
Lake Sibaya	5,539	Bruton & Allanson 1974
Lower Shire floodplain	6,811	This study
Eland River	6,971	Van der Waal 1972 (cited by Bruton 1979)
P.K. le Roux Dam	7,750	Quick & Bruton 1984
Gariep Dam	9052	Hamman 1980
Phongolo floodplains pans	9,681	Kok 1980
Lower Shire Floodplain	11,366	Willoughby & Tweddle 1978^{b}
Hardap Dam	17,078	Gaigher 1977

Notwithstanding the lower length:mass ratio, the current *C. gariepinus* population in the Lower Shire Floodplain has better growth performance (ϕ' =4.89) than the one previously reported by Willoughby & Tweddle (1978^{a}) (ϕ' =3.21-3.5) and four others in Southern Africa (Table 4.9). This may be attributed to higher temperatures (Quick & Bruton 1984) as well as less variation between the minimum and maximum ranges (18-30°C) in the Lower Shire Floodplain compared to Lake Sibaya (18.5-26.5°C) and the Okavango (9-38°C), which experiences very low winter temperatures (see Chapter 2). This would suggest that *C. gariepinus* also displays phenotypic plasticity, with the ability to adapt to a variety of environmental conditions (Bruton 1979&1996, Merron 1991).

Furthermore, the reduction in length-at-first- and 50%-sexual maturation in current populations of both *O. mossambicus* and *C. gariepinus* in the Lower Shire Floodplain might have been caused by the increase in fishing pressure exerted on the stocks which might have led to change in life-history traits of the current populations (Table 4.10), which Iles (1973) termed “a response to variations in mortality rates”. Fishing has been reported to cause changes in population structure, such as age and size composition, growth rate, age of maturity and sex ratio (Nikolsky 1963, Welcomme 1995).

Table 4.10 Comparison of the life-history traits of past and present populations of *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain.

Species/Life-history trait	Willoughby & Tweddle (1978)	This study
Oreochromis mossambicus		
Length-at-first maturity	106 mm (SL)	58 mm (SL)
Length-at-50%-sexual-maturity	-	105
Relative egg size (egg/g wet weight of ovary)	135	435
Sex ratio (male: female)	1.09:1	1.09:1
Length-at-age (first year)	-	121 mm SL
Clarias gariepinus		
Length-at-first maturity	260	218mm SL
Length-at-50%-sexual-maturity	-	249.5
Relative egg size (egg/g wet weight of ovary)	1000	995
Sex ratio (male: female)	1.09:1	1.22:1
Length-at-age (first year)	180	301 mm SL

For example, Lowe-McConnell (1982) attributed the reduction in the median maturation size of *Oreochromis niloticus* in Lake Turkana, from 28 cm to 18 cm over a period of 20 years, to the effects of intensive fishing. Similarly, significant reductions in the age-at-sexual-maturity have also been reported in heavily fished stocks elsewhere (Kolding 1994). Heavy fishing pressure in the Lower Shire Floodplain is evident by the high Z and F values (Figures 4.7&4.8 and Table 4.6). Further evidence of the change in life-history traits in response to environmental condition or fishing can be seen in the shift towards an increase in the reproduction rate, as reflected in the increase in fecundity (decreasing egg size) for *O. mossambicus* and the faster growth in the first year in both species (Table 4.10).

Influence of the flood-pulse on the reproductive biology of *O. mossambicus* and *C. gariepinus*

Reproduction in many floodplain fishes has been reported to be governed by and dependent on the flood regime (timing, amplitude, pattern and duration) (Jackson 1961, Junk 1970, Chapman *et al*. 1971, Welcomme 1975&2001, Howard-Williams & Junk 1976, Bayley 1981, 1991, Kok 1980, van der Waal 1985, Junk *et al.* 1989, Fernando & Holcik 1991, Merron 1991, Hanna & Schiemer 1993, Merron & Mann 1995). In tropical and sub-tropical rivers, fishes either migrate upstream during flood periods in order to spawn (Olatunde 1978, Kok 1980) or spawn during the peak flood without migrating (Merron 1991, Merron & Mann 1995, Welcomme 2001). In this study, the synchrony between spawning and the hydro-climatic seasons for the two principal target species has been demonstrated. Spawning in *C. gariepinus* seems to be better synchronised with the rising and peak flood regime (Fig. 4.5&4.6). Similar observations were made by Willoughby & Tweddle (1978[a]) in the Lower Shire Floodplain, as well as by Bruton (1979) in Lake Sibaya. This synchrony is thought to be caused by the simultaneous change in flood regime and the physico-chemical environment to ensure a suitable environment for the development of eggs and larvae and adequate protection and food for the juveniles (Greenwood 1957) and to ensure dispersal of the species (Jackson 1961, Fryer 1965, Lowe-McConnell 1975, Welcomme 1979). The change in the physico-chemical environment of the floodplain is reflected in the elevated temperatures and higher levels of alkalinity, conductivity, TDS and hardness in all three major habitats during the peak flood period (Qrt3) (see Chapter 3).

Although spawning in *O. mossambicus* also occurs during the rising and peak flood regimes, the data suggest that spawning can also occur during the low flood regime (Qrt4), especially in June (Fig. 4.6), similar to observations made by Willoughby & Tweddle (1978^a). This could be as a result of changes in temperature conditions. A number of environmental factors seem unique in the floodplain during the month of June. Water temperature gradient is the highest (7°C), while the air temperature gradient is the lowest (9°C) and the deviation from the constant threshold (25°C) is the highest (-4.8°C), resulting in overall highest relative temperature changes (see Chapter 2). Although the water level is generally receding during the month of June (Qrt4), the floodplain begins to experience the largest deviation from the threshold (bankfull) and least number of days of inundation. Therefore, it is likely that the high temperature gradient coupled with the reduction in water level in the floodplain constitute a "disturbance" (Pianka 1988) in the environment of *O. mossambicus*, which coupled with high mortality levels (Fig. 4.7, Table 4.6), result in catastrophic density-dependent mortality, which reduces the population to levels below the carrying capacity of the habitat. In such a "competitive vacuum" the best reproductive strategy is often to put the maximal amount of energy into reproduction and to produce as many progeny and as soon as possible (Pianka 1988).

While rising water levels provide breeding cues to both *C. gariepinus* and *O. mossambicus* in the Lower Shire Floodplain, drawdown also stimulates *O. mossambicus* to breed. Therefore, the seasonal fluctuation of the floodplain habitats provides the template for the development of the life-histories of the two major species.

Implication for fisheries management

The observed reduction in the length-at-first-sexual maturity (Table 4.10) shows that both species have adapted along the r-k continuum, through a compensatory strategy (Odum 1993). A rule of thumb is that if the Z/K ratio is <1, then the particular population is growth-dominated; if >1 then it is mortality-dominated; and if equal to 1 then mortality is balanced by growth (Etim *et al*. 1999). Given that the overall exploitation level (Z/K) was 1.41 for *O. mossambicus* and 3.01 for *C. gariepinus*, it can be asserted that both species are mortality-dominated and fairly heavily exploited, as confirmed by the level of fishing mortality (*O. mossambicus* F = 0.16; *C. gariepinus* F = 0.43). However, there is potential for sustainable exploitation of these species since they exhibit substantial phenotypic plasticity (see above) which may contribute towards their resiliency. Moreover, the short life span and the high rate of natural mortality of both species are typical characteristics of river-floodplain fishes, which are kept in a state of early succession, dominated by strong year-classes (Welcomme 1979, Junk *et al.* 1989). Welcomme (2001) reported that parameters of fish population dynamics (growth, mortality, production and biomass) are strongly related to each other and to length, such that a reduction in size is associated with increases in mortality rates, growth rate and, production and a reduction in biomass and catch per unit effort (CPUE). However, the combination of falling biomass and rising production means that yield remains stable over a large range of effort. This will be examined in detail in Chapter 6.

This chapter has helped shed light on the life-history traits of the two most commercially important species, as they relate to the hydro-climatic seasons, and has highlighted significant changes that have occurred over a 25-year period. Collectively these data are important input parameters for the development of the hydro-climatic-fisheries model for the Lower Shire Floodplain. However, before such a model is developed, there is a need to establish the impact of the flood regime on the recruitment patterns and growth of the juveniles of the two species.

Chapter 5

The Impact of the flood regime on juvenile recruitment, fish condition factor and growth of *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain

5.1 Introduction

Understanding the relationship between spawning stock and recruitment is crucial particularly in heavily exploited populations, since this ensures the continuity of the stock and the fishery (Pitcher & Hart 1982, Gulland 1983). Recruitment has also been identified as the most important factor affecting the dynamics of a floodplain fish community (Welcomme & Hagborg 1977, Halls *et al.* 2000). The failure to recognise the importance of this has often led to recruitment overfishing and eventual collapse of several stocks (Welcomme 2001).

Recruitment has been described as a response to spawner stock density, which may be controlled by biotic, or density-dependent factors or environmental perturbation, abiotic or density-independent factors (Pitcher & Hart 1982, Gulland 1983, Mann & Mills 1985, Hilborn & Walters 1992, King 1995, Halls *et al.* 2000). Although knowledge of recruitment is critical for the management of floodplain fisheries, many fisheries scientists have admitted that it is difficult to quantify the relationship (Cushing 1988, Hilborn & Walters 1992, Welcomme 2001). Many studies have shown a great deal of scatter in the stock-recruit relationship, which has been attributed to environmental perturbation that may affect one of the many stages in the recruitment process (Welcomme 2001).

The majority of stock-recruit relationships that have been documented for freshwater fish populations have been derived from stable lake environments. The relationships in tropical rivers and floodplains are less well understood (Welcomme 2001).

Many riverine systems consist of a channel-floodplain complex, where the two components are intimately interrelated and linked by an annual cycle of flood and recession (Welcomme 1995). In turn, the life cycles of the biota inhabiting the floodplain are related to the flood-pulse in terms of its annual timing, duration, and the rate of rise and fall (Junk *et al.*, 1989). Consequently, floodplains are dominated by fish species that depend on timely seasonal colonisation of floodplain habitats for spawning, feeding and shelter (Bonetto *et al.* 1969, Willoughby & Tweddle 1978[a], Welcomme 1979&1985, Bayley 1981, Goulding 1981, Lowe-McConnell 1987).

Many floodplain fish species show seasonality in food intake related to the flood cycle (Lowe-McConnell 1964, Willoughby & Tweddle 1978, Goulding 1980, 1981, Junk 1982, Ribeiro 1983). The seasonality of food intake is reflected in the condition factor of fish (Bolger & Connoly 1989), which manifests itself in seasonal growth and production. This has been reported in many floodplains world wide, such as the Phongolo floodplain (Kok 1980), the Okavango Delta (Merron 1991), the Niger floodplains (Welcomme 1986), the Piracicaba River, Amazon (Silvano & Begossi 2001), Lake Chilwa and shallow areas of Lake Malawi (Furse *et al.* 1979).

It therefore, implies that the hydrological conditions during the year of spawning or during the year prior to spawning have a strong influence upon the availability of food, feeding behaviour, growth (Welcomme 1985), condition factor (Tesch 1971) and ultimately recruitment (de Merona & Gascuel 1993, Welcomme 2001) and total catch (Welcomme 1978& 1985, Karenge & Kolding 1995). Previous studies in the Lower Shire Floodplain reported a marginally significant correlation between mean annual catch and mean annual water flow over a number of years (Tweddle *et al.* 1994). While the work by Tweddle *et al.* (1994) was very important, it only served as a first step towards understanding the dynamics of the flood regime and fish production. There is uncertainty over the components of the hydrological regime which have the most influence on recruitment and the causal mechanisms of the empirical relationship between the two (Welcomme 2001).

The flood-pulse significantly influences the characteristics of the Lower Shire Floodplain’s three major habitats (river floodplain, permanently connected lagoons, and seasonally connected lagoons) (Chapter 3) and the spawning periodicity of the two major fish species, *O. mossambicus* and *C. gariepinus* (Hastings 1973, Willoughby & Tweddle 1978[a], Chapter 4). These studies on the Lower Shire Floodplain have certainly contributed to our knowledge of the fisheries; however, some gaps still remain. For example, Bulirani *et al.* (1999) noted that the Lower Shire Floodplain fish stocks were affected by various environmental factors such as flooding, but they were not able to establish the link. Previous studies have also not focused on the impact of the flood regime on recruitment and abundance, therefore, severely limiting our capacity to predict the effects of the flood regime on the life cycle and production of the fish in this important ecosystem.

The lateral exchange between the river and floodplain occurs when the river overflows its banks at a water level or discharge known as "bankfull" (Leopold *et. al* 1960, Wolman & Leopold 1957, Speight 1965, Leopold & Skibitzke 1967, Harvey 1969, Emmett 1975, Pickup & Warner 1976, Williams 1978). However, in many river floodplain ecosystems, the exchange between the river and the floodplain is constrained by human regulation of the river flow by construction of dams, navigation, flood control, and irrigation schemes (Welcomme 1985, Bayley 1991, Bryan & Rutherford 1993). The Shire River has not escaped such modern "advances". Human intervention on the flow of the Shire River include construction of hydroelectric dams at Tedzani, Nkula and Kapichira falls, control barrier at Liwonde (Hastings 1973), a 75% increase (39,064 - 68,312 m^3) in water abstraction for urban use, siltation of up to 1 metre.$year^{-1}$ since the 1980s (Sibande 2001) and the infestation of the river and the floodplain by water hyacinth (*Eichhornia crassipes*) (Harley 1991, Terry 1991, Tweddle *et al.* 1994, Chimatiro & Mwale 1998). All these factors are likely to have some sort of impact on juvenile recruitment of the two major species (*O. mossambicus* and *C. gariepinus*) in the floodplain.

Given the influence of the flood-pulse on floodplain habitats and spawning periodicity of the two species, this part of the work examines the impact of water fluctuation on juvenile recruitment and abundance of the two target species and other species in the floodplain. The hypothesis to be tested is that juvenile recruitment in the floodplain is not a random activity, but exists as a consequence of a strategy to ensure that the young are produced at a time of year most favourable for their survival. This part of the study aims to provide a fuller understanding of the impacts of flood characteristics (timing, duration, frequency, amplitude, rate of rise/fall) on recruitment (density-independent), and assess the effects of feed availability, competition as well as predation (i.e. density-dependent) on the growth of the adults and juveniles, so that better management decision support can be provided for the Lower Shire floodplain. This is based on the assumptions that the flood-pulse increases favourable habitat and food for the spawning stock, which in return produces "healthier" juveniles which grow faster to migrate to adult feeding grounds. Due to the significant impact of fluctuating water levels on spawning periodicity of the two species in the floodplain, it was felt that the use of the traditional recruitment models (Ricker 1954; Beverton & Holt 1957) would not be appropriate because of their underlying assumptions. For example, Beverton & Holt's model assumes that recruitment approaches an asymptote at high stock densities; while Ricker's model assumes declining recruitment above some maximum level of recruitment and that mortality is a function of spawner stock density. The focus here is on determining the dynamics of juvenile recruitment periodicity, temporal length frequency distributions, condition factor and to disentangle the relative contribution of the various hydrological indices towards the growth of the juveniles before they are recruited into the fishery.

5.2 Materials and Methods

Annual flood regime and hydrology of the Lower Shire Floodplain

The Malawi Department of Water Resources kindly provided the daily water-level data. All data were recorded at Chiromo gauging station in the Lower Shire (see Figure 2.3) covering five hydrological years (1995/96 to 1999/2000). The water levels were analysed to derive the following seven hydrological indices: (i) monthly sum of water fluctuation (SWF), measured as sum of differences in daily water level and the bankfull; (ii) Cumulative sum of water fluctuation (*CSWF*) is the sum of the *SWF* values across months (iii) mean daily (maximum and minimum) water levels; (iv) mean daily water level; (v) timing of flooding measured as mean daily water level (m) above the bankfull (Lv-BF); (vi) duration of floodplain inundation or river stage (RS), measured as the number of days in the month when water level is above the bankfull and (vii) rate of change of water level (Slope), measured as daily slope. The detail of the hydrological regime of floodplain is provided in Chapter 2. These hydrological indices were later used as predictor (independent) variables in the regression analysis performed to identify the relationship between the life-history traits of the fish (dependent variables) and the flood regime.

Estimates of juvenile recruitment

As a measure of juvenile recruitment, estimates of monthly relative abundance of early juveniles were obtained using a (2m long x 0.9m deep) larval seine net with 1-mm mesh. Samples were collected monthly from six lagoon and two riverine sites in the littoral zone (<1m deep) between July 1998 and June 2000. Three of the sites were in the seasonally connected lagoons (SCL), three were in the permanently connected lagoons (PCL), and the other two were in the river floodplain (RF) (Figure 2.1, Chapter 2). Three hauls, covering a total area of 10 m^2 each, were made per site per month. All fish were counted, identified to the lowest possible taxon, weighed to the nearest 1 gram and measured to the nearest 1 millimetre total length (TL) and standard length (SL).

To effectively sample for juvenile fish in areas deeper than 1 m, three sites in each of the two lagoons (PCL and SCL) were chosen. Three hauls, covering an area of 180 m^2 each, were made at each site using a (30m long x 2m deep) seine net with 13-mm mesh. Sampling was done once a month. All *Clarias gariepinus* <150 mm TL and *Oreochromis mossambicus* <75 mm TL were weighed and measured as described above. The variation in fish abundance in relation to the four hydro-climatic seasons was assessed using these data.

Condition factor

To determine the possible effect of the flood regime on food availability and intake, as reflected by the condition of the fish, mean monthly condition factors were calculated mainly for mature *Oreochromis mossambicus* (>100 mm TL) and *Clarias gariepinus* (>200 mm TL) collected from experimental gill nest and seine nets as outlined in Chapter

4 from July 1998 to June 2000. Condition factor (CF) was calculated using the equation recommended by Bolger & Connolly (1989) and Murphy & Willis (1996), based on the assumption that the heavier fish of a given length were in better condition (Bolger & Connoly 1989):

$$Condition\ \ factor\,(K) = \frac{Fish\ \ weight\,(g)}{Fish\ \ length\,(mm)^3}\ x\,10^5 \qquad \text{(Equation 5.1)}$$

It was hypothesised that changes in monthly condition factor of fish reflects food abundance and that this would manifest itself in the monthly length-weight relationship.

Growth response of fish to water-level fluctuation

It was further hypothesised that the flood regime would in some way or other have an effect on the growth pattern of the fish and that such events may be revealed by an analysis of the growth pattern of the otoliths. To examine whether and how the flood regime affects the growth rate of the fish, sectioned sagittal otoliths of *O. mossambicus* were prepared and examined according to procedures outlined in Chapter 4. *Clarias gariepinus* was excluded from this analysis since they were not easy to handle. Otolith length (OL) and width (OW) were measured along the longitudinal and transverse axes, respectively.

Otolith sections with clearly defined annuli along a measuring plane from the medial to the lateral margin across the nucleus (Figure 5.1) were scanned under a scanning microscope using the software package Winstor SEM, and later converted to Tag Image Files (TIF). These were loaded into the Sigma Scan software using a 1-mm calibration bar. All measurements were done at a resolution of 0.001 mm. The thickness of each otolith was measured from the medial to the lateral margin across the nucleus. Annulus width (Aw) was measured as the distance between the first and the second annulus, from the beginning of the translucent zone to the end of the opaque zone along the same plane as the sectioned otolith thickness (Fig. 5.1).

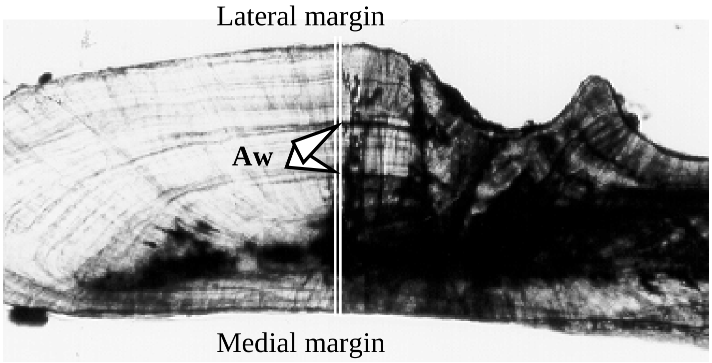


Figure 5.1 Photomicrograph of a sectioned *O. mossambicus* otolith showing the measuring plane used in the determination of the annulus width (Aw). Annulus width (Aw) = distance between the first and second annulus from the beginning of the translucent zone to the end of the next opaque zone

All readings and measurements were done twice, and the average measurement was adopted if the two differed by not more than 0.005 mm, otherwise the otolith was rejected. Comparison of growth was confined to the period between the first and second annuli (two years' growth) because the species attains asymptotic length within the first two to three years, and hence growth during the first year represents the best measurable period (Figure 4.3, Chapter 4). The annulus width and other morphometric variables of the otoliths (length and width) were used as dependent variable while hydrological indices as independent variables in a linear regression analysis, to assess the relationship between growth of the fish and flood regime.

Statistical analysis

Statistical analysis was carried out with the aid of StatisticaTH computer software (StatSoft, Inc. 1999). Values for seasonal abundances were compared using a non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) (Zar 1984). Where significant differences were found, values were compared using a non-parametric Mann-Whitney U-test. A two-step procedure was applied to the statistics of regression analysis. First, Pearson product-moment correlations (Neter *et al.* 1979, Zar 1984) for pairs of dependent (biological parameters of the fish) and independent variables (hydrological indices) were obtained in order to explore the functional relationship between various pairs of variables. Secondly, forward stepwise multiple regression analyses were conducted to determine the relationship between various suites of independent variables and a single dependent variable in order to construct best possible predictive models. In forward stepwise multiple regression analysis; redundant predictors are removed to yield a final model that accounts for most of the variance (Roy 1958, 1967). Otolith dimensions, condition factor (CF) and relative abundance acted as dependent variables while hydrological indices were used as independent variables.

5.3 Results

Hydrological indices

Figure 5.2 shows a typical hydrograph for the Lower Shire Floodplain over four hydro-climatic seasons (details in Chapter 2), and Figure 5.3 summaries the hydrological parameters of the floodplain. Water level in the floodplain is lowest in November, as reflected in the mean level as well as Sum of Water Fluctuation (SWF). The water level is at its highest between December and March, but inundation of the floodplain occurs between January and April when the water is above bankfull (Figure 5.3b). Theoretically, the floodplain is inundated for most days of the year (Figure 5.3c), but taking into account the sum of daily water level fluctuations (SWF) the floodplain is effectively only inundated between January and April (Figure 5.3b). This can be seen for May to December when mean monthly water levels are below the bankfull and designated negative, while those above bankfull are designated as positive. For example, the empirical bankfull level is 4.7 m (Chapter 2), therefore, if on day *x* of the month the level is 3.7, then this day will be designated –1 m, even if water rises to 5.7 m the following day, the SWF for the two days will be (5.7-4.7=1+(-1)=0 m). The period between August and November is critical for fish in the floodplain because the water level is progressively receding as reflected by the SWF (Figure 5.3b), posing the risk of desiccation and stranding in dry areas.

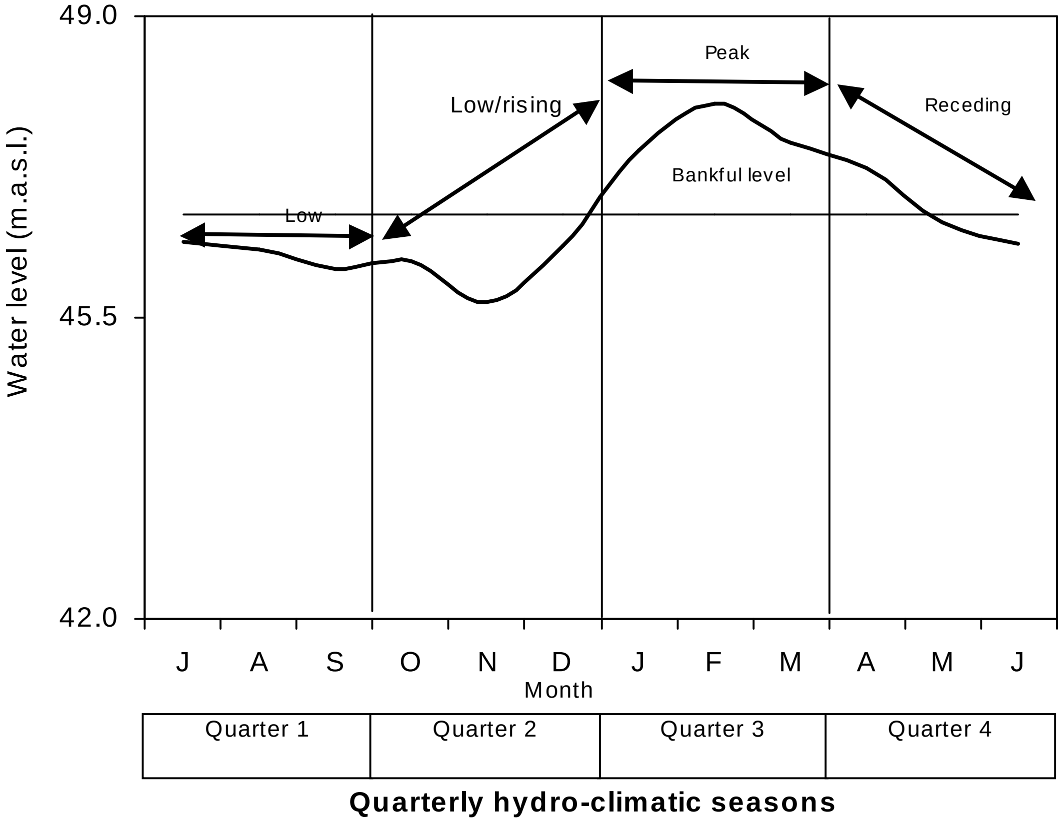


Figure 5.2 An annual hydrograph (flood regime) for the Lower Shire Floodplain. The mean monthly data is based on water levels (mean above sea level in metres) recorded at Chiromo gauging station, Lower Shire River, for the period 1995/96 to 1999/2000. Double arrows indicate the status of the flood regime; the horizontal line indicates the bankfull level.

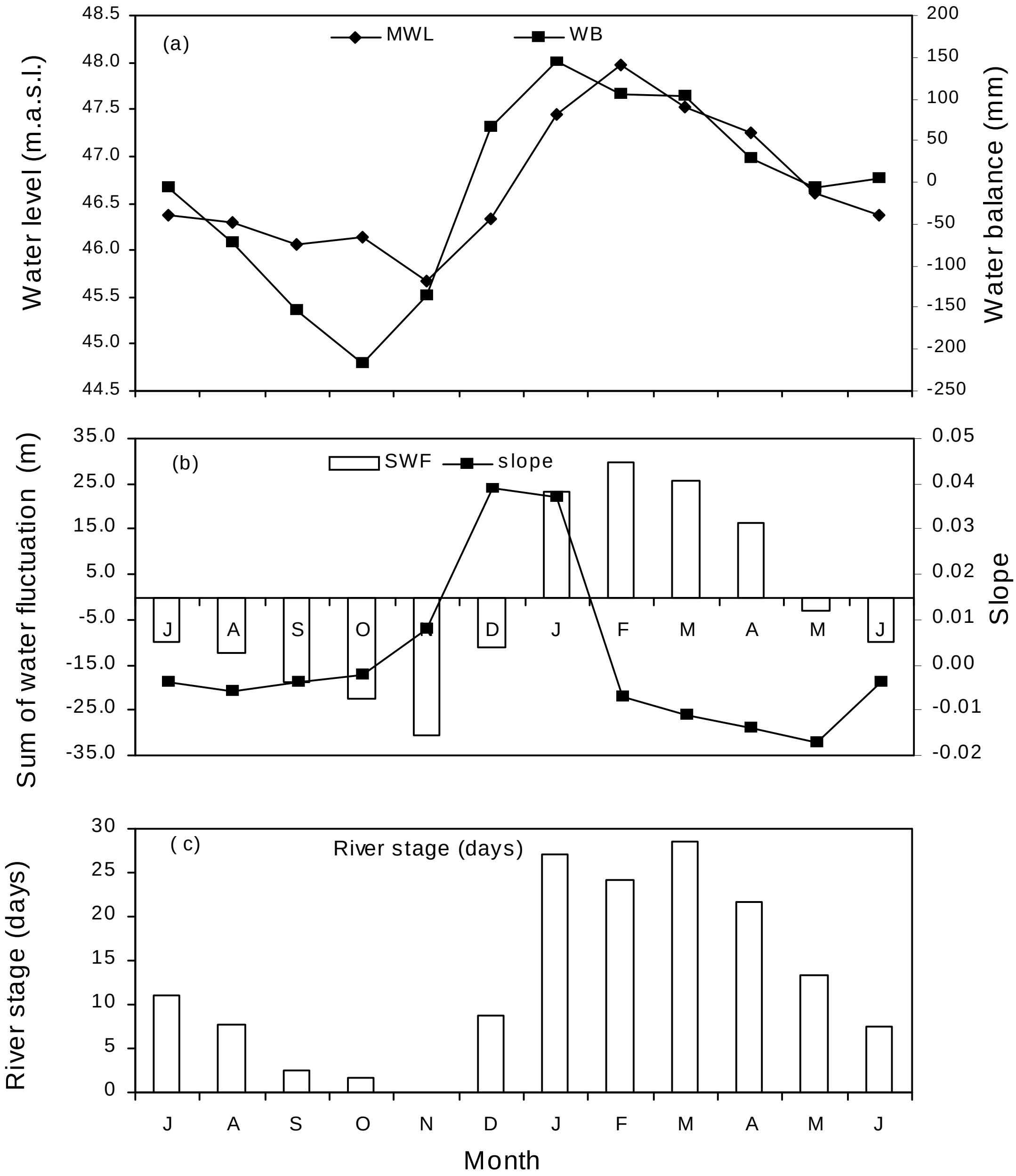


Figure 5.3 Summary of mean monthly hydrological parameters of the Lower Shire Floodplain: (a) mean water level (MWL) and water balance (WB), (b) sum of daily water fluctuation (SWF) and slope of change in water level; (c) river stage (RS) (number of days of inundation). Summary based on mean daily water recorded at Chiromo, Shire River during the period 1995/96 to 1999/2000.

Relative abundance of juvenile fish

Juvenile cichlids and clariids collected from the littoral zone with the 1-mm mesh seine were not easily identifiable to species level (hence, they were categorised as cichlids and clariids), but those captured with the 13-mm mesh net were easily identified. Estimates of mean monthly abundance (numbers.haul^{-1}) for the early juveniles collected with the 1-mesh mm net are shown in (Figure 5.4), while the estimates of mean monthly density (numbers.m^{-2}) and the length frequency distribution of early juvenile cichlids and catfish collected with the 1-mm mesh net are shown in Figures 5.5a&b and 5.6a&b, respectively.

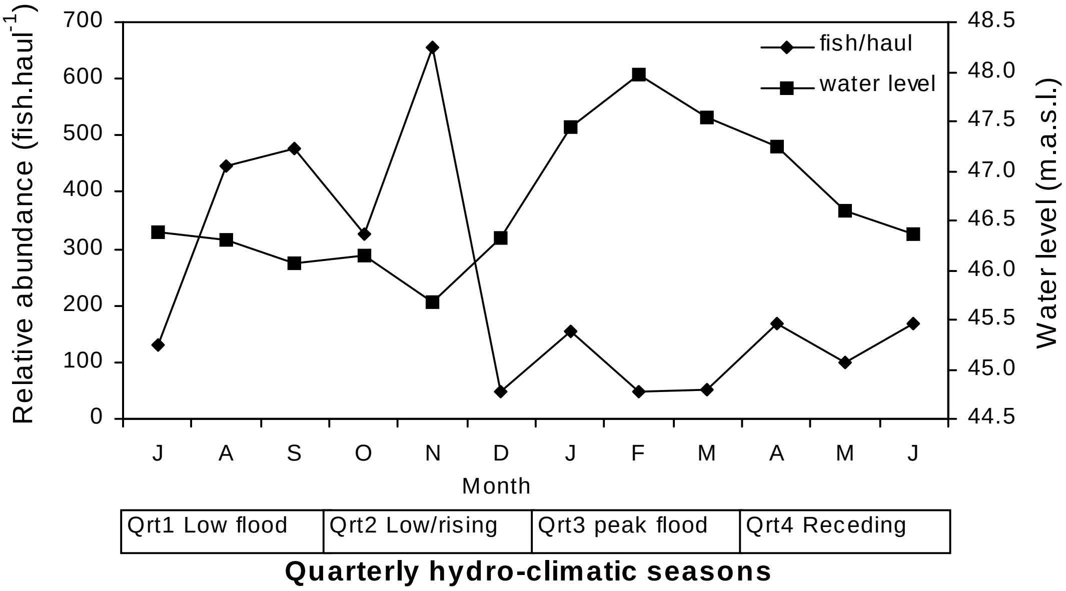


Figure 5.4 Estimate of mean monthly relative abundance of fish (mean number of fish per haul) in the littoral zone of the Lower Shire Floodplain. The fish were sampled using a 2-m long 1 mm mesh, larval seine net, between July 1998 and June 2000.

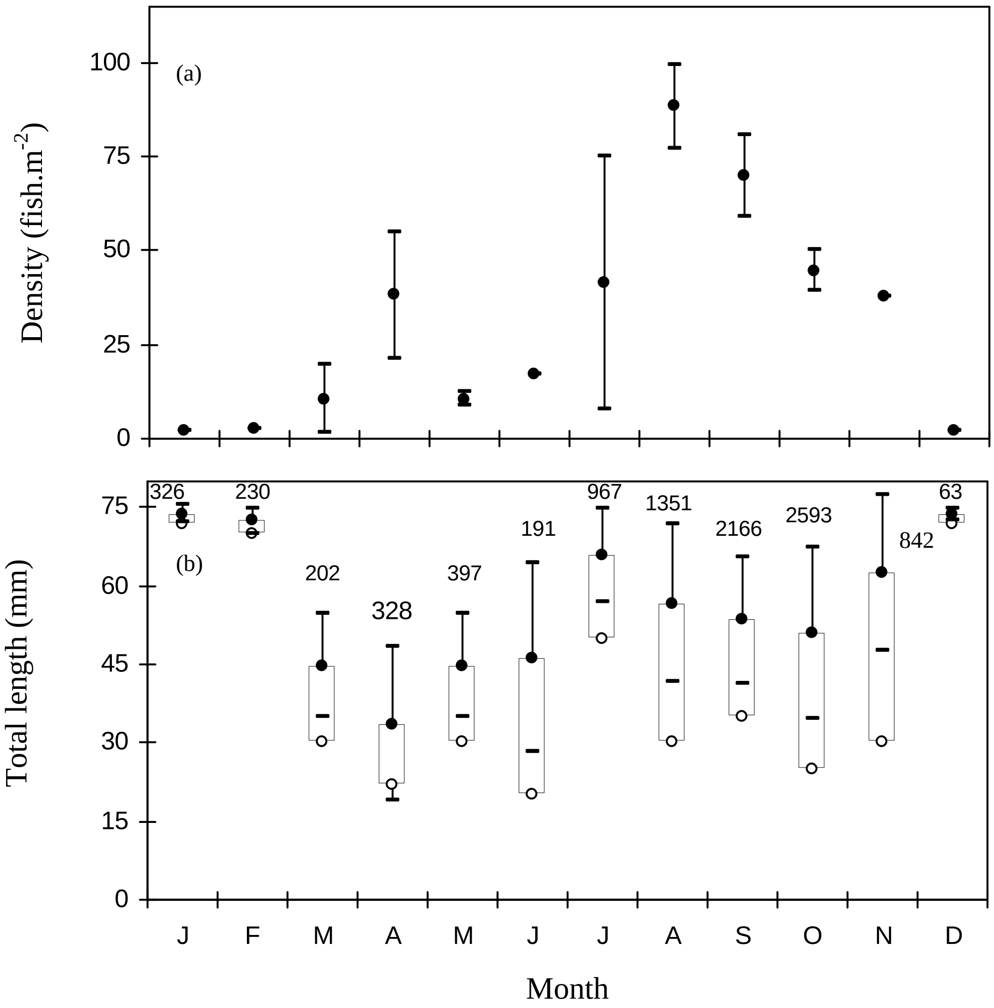


Figure 5.5 (a) Mean (± SD) monthly density (fish.m^{-2}) of early juvenile cichlids and (b) length distribution of juvenile cichlids in the littoral zone (<0.1 m) of the lagoon and riverine habitats of the Lower Shire Floodplain, collected using a 1-mm mesh seine net (2m x 0.90m), between July 1998 and June 2000. The open circles are 5th percentile, closed circles are means, the cross bars are SD, and the numbers above the SD points are the size of the sample, the boxes depict the length distribution below mean.

Since there were no significant differences in early juvenile fish densities among the sampled sites (one-way ANOVA, $p \geq 0.01$), the samples were pooled and analysed as a composite sample. However, there were significant quarterly seasonal differences in juvenile fish density (one-way ANOVA, $p \leq 0.01$). There were significant differences (one-way ANOVA, $p \leq 0.01$) in the density of early juveniles in the 1-mm seine net hauls, with the highest density recorded between August and November (Figure 5.4).

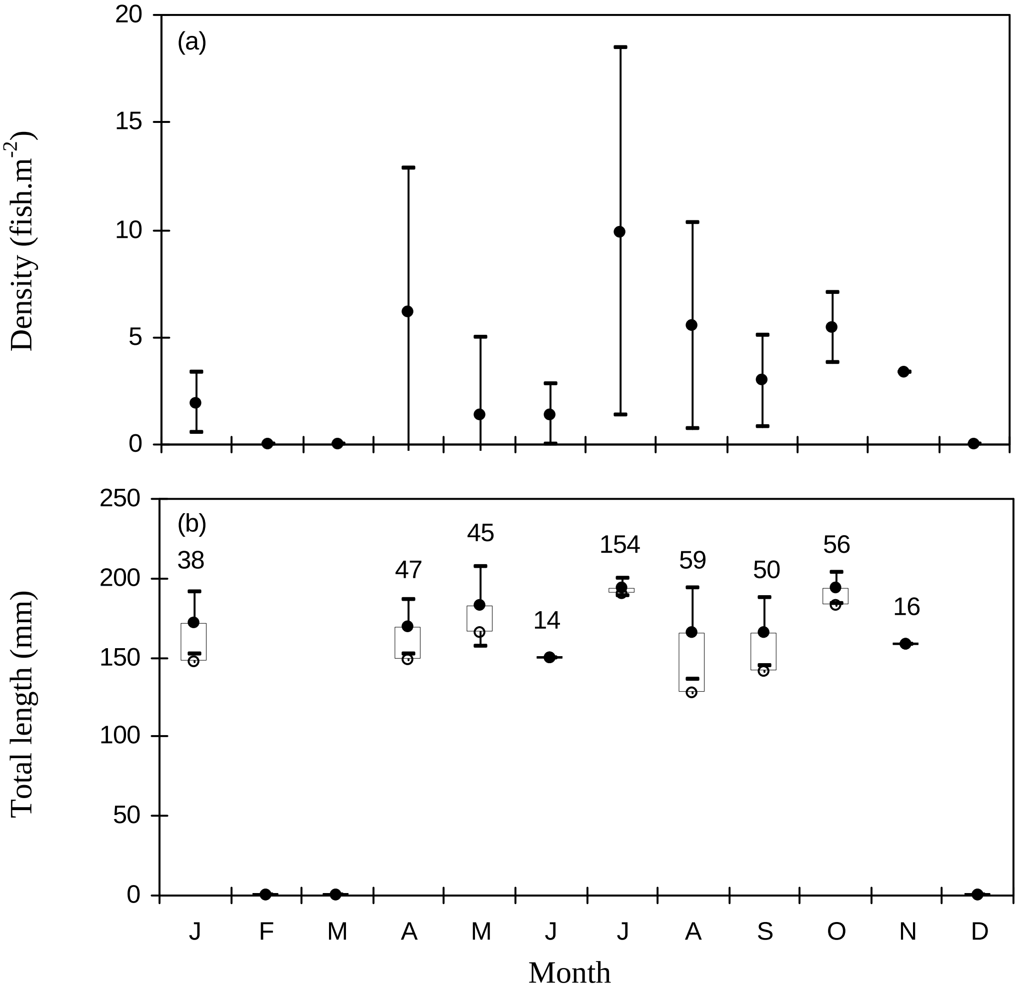


Figure 5.6 (a) Mean (± SD) monthly density (fish. m^{-2}) of early juvenile clariids and (b) length distribution of juvenile catfish in the littoral zones (<1 m) of the lagoon and riverine habitats of the Lower Shire Floodplain, collected using a 1-mm mesh seine net (2m x 0.90m), between July 1998 and June 2000. The open circles are 5th percentile, closed circles are means, the cross bars are SD, and the numbers above the SD points are the size of the sample, the boxes depict the length distribution below mean.

The monthly relative abundance of juvenile fish of various species in the littoral zone collected with the 13-mm mesh seinenet can be seen in Figure 5.7. The bulk (58.5%) of the fish assemblage constituted three cichlid species with *Oreochromis mossambicus* comprising 34.7%, *Astatotilapia calliptera* 1.7% and *Tilapia rendalli* 21.2%. Three catfish species, *Synodontis zambezensis, Clarias gariepinus* and *Schilbe intermedius,* were the second largest component making up 16.2%, while four cyprinids, *Labeo altivelis, L. congoro, Barbus paludinosus* and *B. afrohamiltoni*, constituted the third largest group at 9%. Early juvenile abundance (numbers.haul^{-1} of all species) was highest (602 – 1127 fish.m^{-2}) between the period of low and low-but-rising flood regimes in 1998 (August and November 1998) and in 1999 (July and November 1999) (184 – 353 fish.m^{-2}) (Figure 5.7).

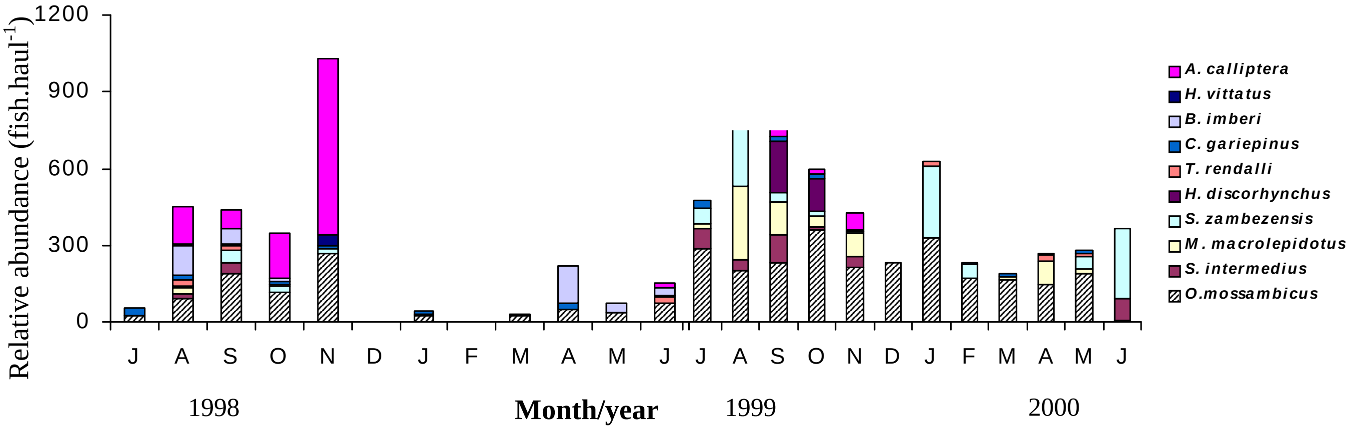


Figure 5.7 Mean monthly relative abundance of juvenile fish (mean number of fish per haul) in the littoral zone (<1 m) of the Lower Shire Floodplain, sampled from July 1998 to June 2000 using a 13-mm mesh

Although there were no significant interannual hydro-climatic seasonal differences in early juvenile density (for example Qrt1 in 1998 and Qrt1 in 1999 (Mann-Whitney rank sum test, $p \geq 0.01$), there were significant quarterly seasonal differences, Mann-Whitney rank sum test, $p \leq 0.01$). It is apparent therefore, that there is a movement of new recruits into the littoral zones of the floodplain during the period of low and low-but-rising flood regime. Juvenile *O. mossambicus* were fairly abundant throughout the year, an indication that it can breed throughout the year, while juvenile *C. gariepinus* showed clear seasonal patterns of abundance (Figure 5.7), probably a reflection of distinct breeding seasons.

The length frequency distribution for larger *O. mossambicus* (>75 mm, TL) and *C. gariepinus* (>150 mm, TL) is shown in Figure 5.8. Larger *O. mossambicus* were dominant from July to November (1998/99), the trend almost repeated itself in July to November (1999/00) (Figure 5.8), corresponding to the periods of low flood and low-but-rising flood regimes. Similarly, for *C. gariepinus* larger individuals appeared between

December and March in 1998/99 and during the same period the following year (Figure 5.8), corresponding to the period of rising and peak flood regimes. For *O. mossambicus* and *C. gariepinus*, the length frequency distributions exhibit sinusoidal patterns with peaks and troughs. In December, smaller *O. mossambicus* larger *C. gariepinus* were more abundant (Figure 5.8). This shows an apparent simultaneous movement of larger *C. gariepinus* and smaller *O. mossambicus* into the littoral zone between September and November. In some ways, this mirrors the situation shown in Figures 5.5 &5.7, where cichlid and *O. mossambicus* juveniles are most abundant between August and December.

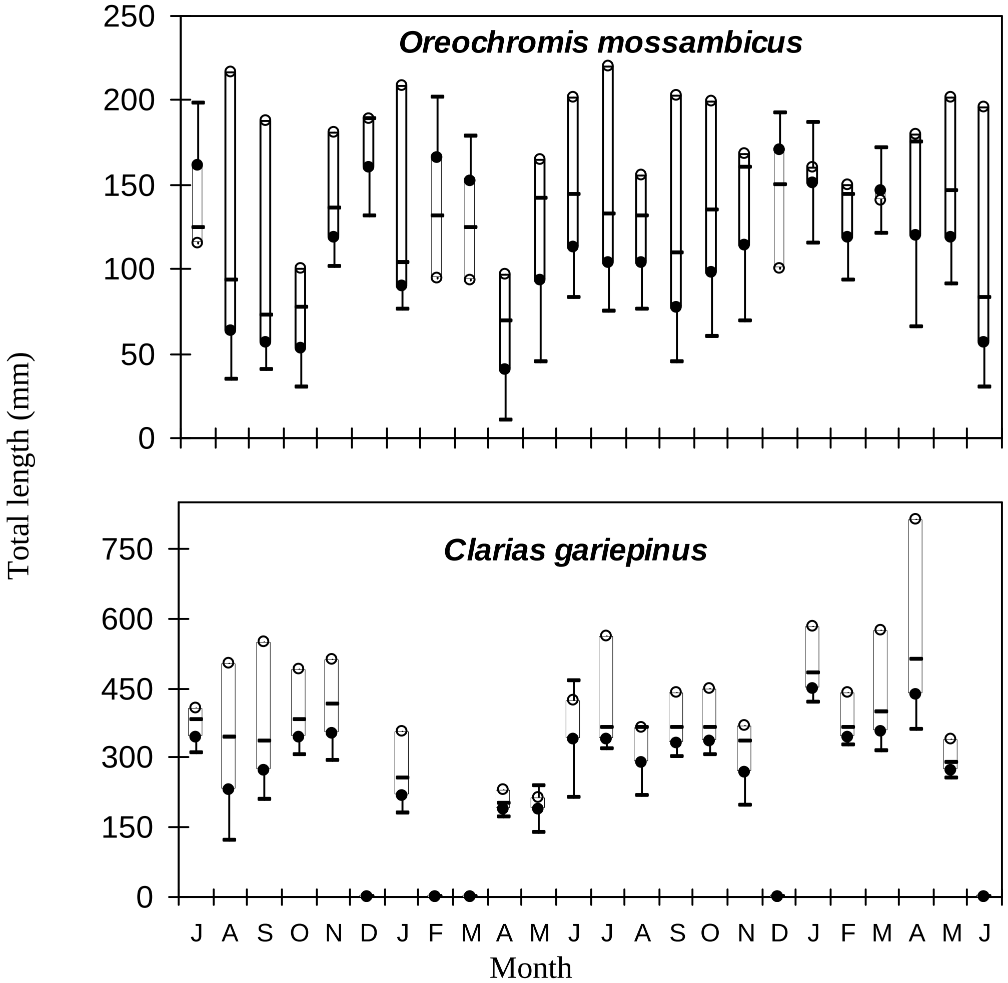


Figure 5.8 Length distribution of *Oreochromis mossambicus* and *Clarias gariepinus* in the littoral zone (<1 m) of lagoon and riverine habitats of the Lower Shire Floodplain, sampled with a 13-mm mesh seine net (30m x 2m) between July 1998 and June 2000. The closed circles indicate mean length; the error bars indicate ± SD and the open circles are set at 95th percentile. The boxes indicate lengths recorded above the mean length.

Condition factor

Figure 5.9 shows the mean monthly condition factor (CF) for *Oreochromis mossambicus* and *Clarias gariepinus*. Although there were no significant (one-way ANOVA, $p \geq 0.05$) monthly differences in CF in both species, there were significant quarterly seasonal differences between the receding (Qrt3) and low (Qrt1) flood regimes (one-way ANOVA, $p \leq 0.05$). For *O. mossambicus*, condition was lowest (1.44±0.04) during the peak flood (Qrt3) between January and March and highest during the receding flood regime (Qrt1) (2.72±1.23), April to June, with a peak in June.

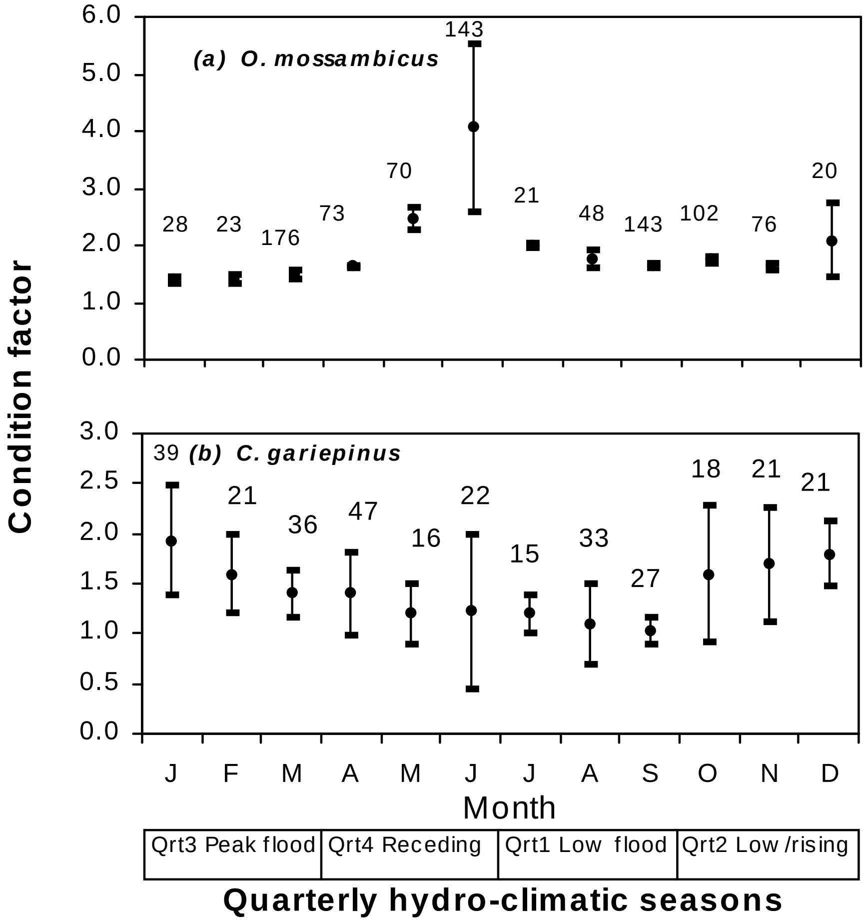


Figure 5.9 Mean monthly condition factor ±95% confidence intervals for *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain between August 1998 and July 1999. The number of fish sampled is presented above the confidence bar.

The monthly condition of *C. gariepinus* was a reverse mirror image of the pattern for *O. mossambicus*. It was lowest (1.27±0.12) during the receding flood regime (Qrt4), and highest (1.8±0.11) during the low-but-rising (Qrt2) and peak flood regimes (1.6±0.27) (Qrt3), but the two seasons were not significantly different from each other (one-way ANOVA, $p \geq 0.05$).

The relationships between the hydrological indices and fish condition factor and juvenile abundance using Pearson product-moment correlations are shown in Table 5.1. Relative changes in water level as measured by daily water fluctuation in the form of cumulative sum of daily fluctuation (CSWF) and the rate of change in water level (slope) were highly correlated with the biological parameters of fish ($0.64 \leq r^2 \geq 0.85$, $p \leq 0.05$), while absolute changes in water level (or timing of flooding) in terms of daily mean, maximum and minimum levels, as well as bankfull level (Lv-BF), was highly correlated with juvenile abundance ($0.59 \leq r^2 \geq 0.71$, $p \leq 0.05$). However, the relationship between the density of juvenile *O. mossambicus* and *C. gariepinus* with water fluctuation (CSWF) and the rate of change of water level were the reverse (Table 5.1), indicating that densities were highest during the low flood regime and visa versa, just as it was shown in Figure 5.4. The rate of change in water level mainly affected the condition factor of *C. gariepinus*, while absolute change in water level (daily mean level) had a significant effect on the density of juveniles of all species, especially catfish (Table 5.1).

The relationships between hydrological indices (HI) and CF and juvenile abundance using the forward-stepwise multiple-regression analyses in which the hydrological indices were independent and life cycle parameters were dependent variable, are summarised in Table 5.2. While the timing of the flood regime, reflected in the absolute change in water level, had a direct and significant effect on the condition factor of *C. gariepinus* ($r^2 = 0.69$, $p \leq 0.001$), it had an inverse but no significant effect ($r^2 = 0.08$, $p \geq 0.05$) on the condition factor of *O. mossambicus* (Table 5.2). Although the monthly water fluctuation, depicted as sum of daily water fluctuation (SWF), had no significant effect on early juvenile density of all species, the relationship was inverse ($r^2 = 0.20$, $p \geq 0.05$)

indicating that densities were highest during the low flood regime and visa versa as in Figure 5.4.

Table 5.1 Summary of Pearson product-moment correlation coefficients for pairs of dependent and independent variables. Dependent variables are fish biological parameters. Independent variables are hydrological indices. The data is presented as CF = Condition factor, Juvenile density (fish.m^{-2}), Mean = mean monthly water level, Max = maximum daily water level, Min = minimum daily water level, SWF = sum of daily water fluctuation (m), CSWF = cumulative sum of daily water fluctuation, RS = river stage (days), Lv-BF = level above bankfull.

Dependent variables (Biological factors of Fish)	**Independent variables (hydrological indices)**							
	Mean	Max.	Min.	SWF	CSWF	RS	Lv-BF	Slope
CF of *C. gariepinus*	0.36	0.49	0.17	0.23	-0.75**	0.15	0.31	0.65*
CF of *O. mossambicus*	-0.31	-0.42	-0.21	-0.47	0.21	-0.44	-0.22	-0.13
Juvenile abundance (mean number of fish.haul^{-1}) (all species)	-0.68**	-0.63*	-0.60*	-0.45	0.01	-0.49	-0.71***	-0.08
Juvenile density (mean number of fish.m^{-2}) (Cichlids)	-0.64*	-0.59*	-0.60*	-0.46	-0.18	-0.50	-0.68**	0.01
Juvenile density (mean number of fish.m^{-2}) (catfish)	-0.50	-0.54	-0.40	-0.28	0.49	-0.19	-0.54	-0.16

Table 5.2 The relationship between hydrological indices of the floodplain and condition factor (CF), and juvenile density (fish.m^{-2}) of *Oreochromis mossambicus* and *Clarias gariepinus*. Data is presented as CF-Om = condition factor for *O. mossambicus*, CF-Cg = condition factor for *C. gariepinus*, Lv = mean monthly water level (m), SWF = sum of daily water fluctuation (m), Fish.m^{-2} = juvenile density, r^2 = coefficient of determination, and p = level of significance (ns=not significant; * = 0.05; ** = 0.01; *** = 0.001). The models were obtained through forward stepwise multiple regression analysis.

Relationship	r^2	***P***
O. mossambicus CF-Om = 4.16 – 0.46Lv	0.08	0.380 ns
C. gariepinus CF-Cg = -1.50 + 0.52Lv	0.69	0.0008***
Juvenile density Fish.m^{-2} = 377.45 – 14.06SWF	0.20	0.145 ns

Seasonal growth patterns

The relationships between fish length and otolith dimensions of *O. mossambicus* are shown in Table 5.3 and the relationship between hydrological indices and seasonal growth patterns is shown in Figure 5.10. Total length of the fish accounted for most of the variation in otolith length, otolith width, otolith thickness and annulus width ($0.35 \leq r^2 \geq 0.78$, $p \leq 0.001$) (Table 5.3). Although total length of the fish did not account for much of the variation in annulus width ($r^2 = 0.35$), the relationship was very significant ($p \leq 0.0001$) (Table 5.3).

Table 5.3 Morphometric relationship of otolith dimensions and total length of *O. mossambicus* sampled from the Lower Shire Floodplain. TL = total length, OL = otolith length along the longitudinal axis, OD = otolith diameter along the transverse axis, OT = otolith thickness from the medial to the lateral margin, Aw = annulus width from the first to the second annulus, beginning at the translucent zone to the end of the next opaque zone. r^2 = coefficient of determination, *p* = level of significance (ns=not significant; * = 0.05; ** = 0.01; *** = 0.001).

Relationship	r^2	***P***	**n**
O. mossambicus			
TL (mm) = (29.026) * OL (mm)$^{0.962}$	0.78	<0.0001***	163
TL (mm) = (40.161) * OW (mm)$^{1.043}$	0.78	<0.001***	167
TL (mm) = (143.689) * OT (mm)$^{0.842}$	0.68	<0.001***	187
TL (mm) = (240.62) * Aw (mm)$^{0.278}$	0.35	<0.0001***	176

A summary of the relationships between individual hydrological indices and age of the fish (independent variables) and annulus width of *O. mossambicus* (dependent variable), using Pearson product-moment correlations, are shown in Table 5.4. Although the relationship was significant ($P \leq 0.05$), however, the independent variables did not account for much of the variation in annulus width ($0.03 \leq r^2 \geq 0.09$), pointing to the fact that there might be other factors being responsible for changes in annulus width, which were not captured in this study. There was a more significant trend towards annulus width increment in younger fish than older individuals ($r^2 = 0.09$, $p \leq 0.001$) (Table 5.4).

Table 5.4 Summary of the relationship between of water level parameters and annulus width in otoliths of *O. mossambicus*. Water level parameters are: SWF = Sum of water fluctuation; RS = River stage (period of inundation in days; Lv-BF = Level-above-bankfull. r^2 = coefficient of determination, *p* = level of significance (ns=not significant; * = 0.05; ** = 0.01; *** = 0.001).

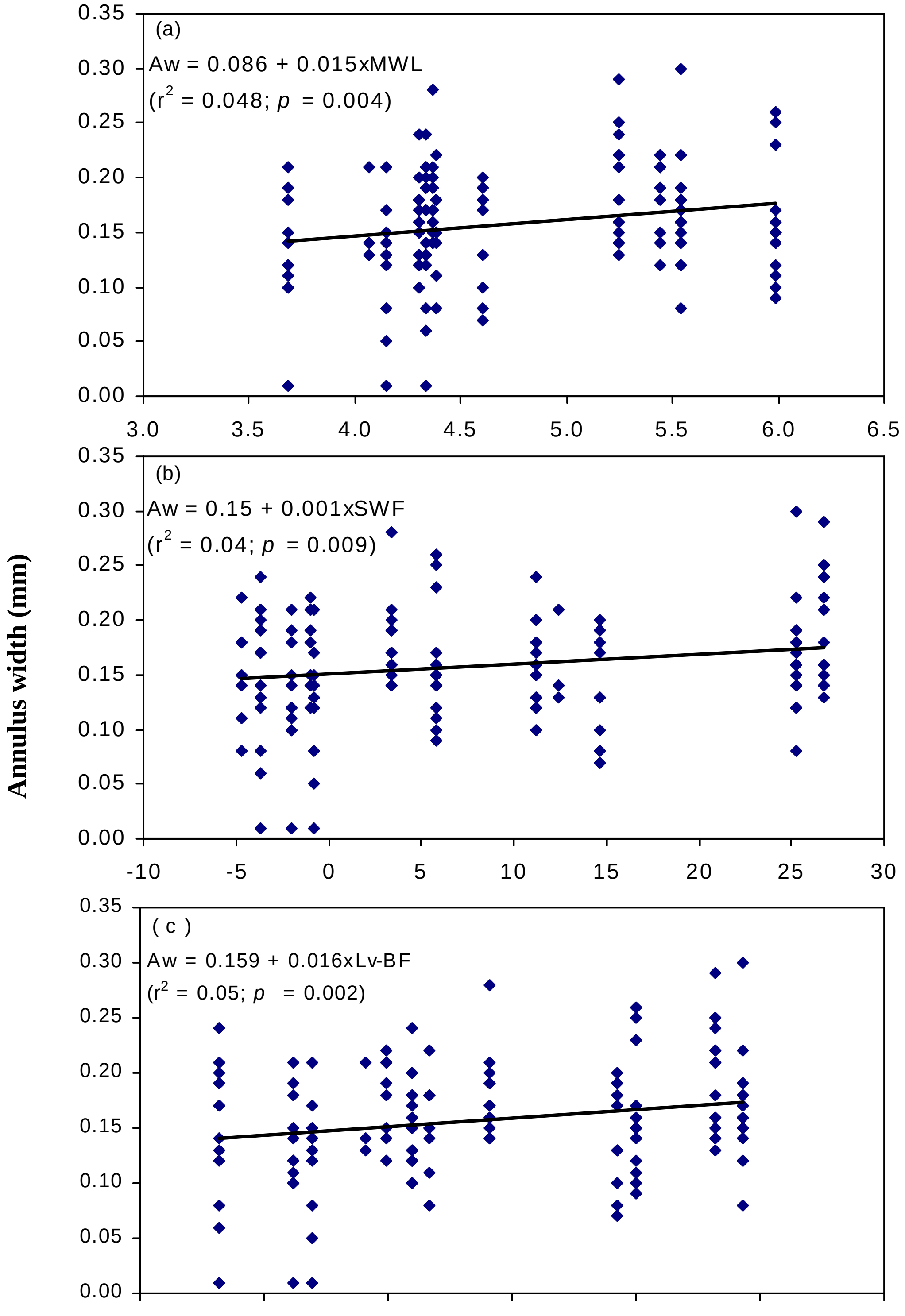
Parameter of water level	r^2	***p***
Mean water level (m)***	0.05	0.004
SWF***	0.04	0.009
RS*	0.03	0.04
Lv-BF***	0.05	0.002
Age***	0.09	0.00009

All the independent variables tested together through forward stepwise multiple-regression, identified the mean monthly water level (MWL), sum of daily water fluctuation (SWF) and mean monthly water level above the bankfull (Lv-BF) as accounting for most of the variation in annulus width (Figure 5.10).

Although the three hydrological indices (MWL, SWF, Lv-BF) did not account for much of the variation in annulus width ($0.04 \leq r^2 \geq 0.05$), these relationships were very significant ($p \leq 0.01$) (Figure 5.10). Thus, the following linear regression models could describe the response of annulus width of *O. mossambicus* to changes in hydrological indices:

a) Annulus width (mm) = 0.086 + (0.015 x MWL), (r^2 = 0.048; *p* = 0.004)
b) Annulus width (mm) = 0.15 + (0.001 x SWF), (r^2 = 0.04; *p* = 0.009)
c) Annulus width (mm) = 0.159 + (0.016 x Lv-BF), (r^2 = 0.05; *p* = 0.002)

where : MWL = mean monthly water level (m),
SWF = sum of daily water fluctuation (m),
Lv-BF = mean monthly water level above the bankfull (m)



Water level (m)

Figure 5.10 The relationship between annulus width (Aw) (mm) in *Oreochromis mossambicus* and (a) daily mean water level (MWL) (m); (b) sum of daily water fluctuation (SWF) (m) and water level fluctuation above the bankfull (Lv-BF) (m) in the Lower Shire Floodplain. The solid lines are regression lines.

The response of annulus growth in *O. mossambicus* to changes in daily mean water level and duration of inundation of the floodplain is shown in Figure 5.11. The increase in annulus width was greatest when the water level was just above the bankfull (but below 5.5 m) and after about 23 days of floodplain inundation (see dotted line in Figure 5.11).

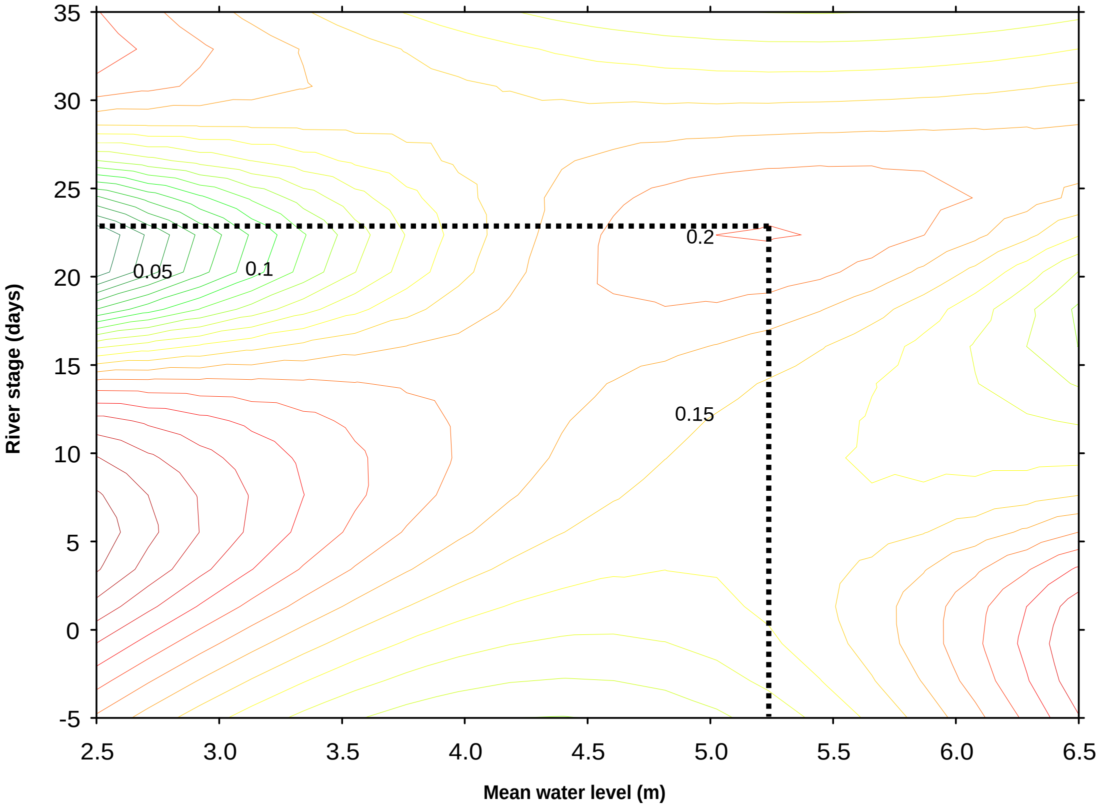


Figure 5.11 Contour plot representing the relationship between annulus width (mm) of sectioned *O. mossambicus* otolith (between the first and second annulus) and daily mean water level and river stage (days). ($r^2 = 0.06$, $p = 0.007$). 0.05-0.20 denotes annulus width (Aw) in mm.

5.4 Discussion

The seasonal dynamics of water fluctuation in floodplains and their effects on food availability, growth, reproduction, juvenile development and eventual recruitment into the floodplain fisheries has been the subject of numerous scientific studies (Lowe-McConnell 1975&1987, Welcomme 1985&2001, MRAG 1994, Halls *et al.* 1999 &2000). It has been demonstrated that fish condition factor, growth and juvenile recruitment in the Lower Shire Floodplain is associated with the flood regime. To fully understand some of these complicated associations, juvenile recruitment, growth and condition factor must be carefully examined in relation to the impact, which the flood timing, rate of fluctuation and inundation of the floodplain have on food availability, survival from predators and growth.

Effect of the flood-pulse on fish condition

The relationship between flood regime and condition of the fish becomes apparent when one examines the seasonality of dietary items and feeding intensity of the fish in relation to the flood regime and duration of inundation. The condition of *O. mossambicus* was highest during the receding flood between April and June, and lowest during peak flood regime. This clearly mirrors Willoughby & Tweddle's (1978[a]) observation that maximum food intake of *O. mossambicus* in the Lower Shire Floodplain was between April and June. Since feeding rate has been shown to be directly proportional to temperature for several fish species, including tilapia (Davis & Warren 1971, Caulton 1978) one would expect that *O. mossambicus* in the Lower Shire Floodplain would have been feeding more intensely from, say August during which time, temperature in the system is increasing. However, intensive feeding by *O. mossambicus* started in April (Willoughby & Tweddle 1978[a]) as temperature was going down from 24.8ºC in April to 20.2ºC in June, during the receding flood regime (Chapter 3). It is well known that feeding intensity of *O. mossambicus* is reduced below 20ºC (Chervinski 1982). Given the higher feeding intensity, which is also reflected by the high condition factor, during the period of receding flood between April and June, it would imply that a factor or factors other than temperature were affecting feeding rate.

It has been reported that intensity of feeding in juvenile *O. mossambicus* in Lake Sibaya was significantly affected by lake level. At high lake level it was less than half that found during low lake level period, while the protein content of benthic detrital aggregates showed a strong inverse correlation with depth (Bowen 1979, Bowen & Allanson 1982). In Lake Chicamba, Weyl (1998) reported an increase in the condition factor for *O. mossambicus* during the summer drawdown period, and in part, ascribed this to the persistence of detritus during that period. During the falling flood (Qrt4) and low flood (Qrt1) regimes in the Lower Shire Floodplain, there was a rise in both phosphate and nitrate (Chapter 3). The increase in these two primary rate-limiting elements (Wetzel 1975) would lead to increased productivity during this period. The high feeding intensity of *O. mossambicus* (reflected by the high condition factor) during this time could be one of the most important adaptations of *O. mossambicus* to the fluctuating environment of the floodplain. The fish takes advantage of the period of abundant food resources during the receding flood regime to accumulate sufficient fat and body mass in order to survive the period of scarcity during the low flood regime.

Willoughby & Tweddle (1978[a]) recorded that fish was the principal diet of *C. gariepinus* in the Lower Shire Floodplain, just before the flood peak. The highest condition for *C. gariepinus* was recorded during the low-but-rising flood and early part of the peak flood regime (Figure 5.9), which corresponds to the period of high relative abundance of juvenile fish (Figure 5.4). Similarly, in Lake Sibaya (Bruton 1979) and in the Okavango Delta (Merron 1991) maximum food intake by *C. gariepinus* was also recorded during the period of low water level.

The predominance of fish in the diet of *C. gariepinus* during the receding flood regime, when juvenile fish abundance is high could be explained by the “optimal foraging theory” (Stephens & Krebs 1986). The theory stipulates that all things being equal, a predator should feed preferentially in patches with the highest density of prey. This is likely the case since abundance and density of prey increased around September (Figure 5.4), at the start of spawning season (Chapter 4) coupled with the concentration of prey in pools with rapidly declining water level in the floodplain (Figure 5.3).

During the high flood regime (Qrt3) in the Lower Shire Floodplain (see Chapter 2), *C. gariepinus* changes its diet from mainly fish to filamentous algae, detritus and insect (Willoughby & Tweddle 1978[a]), further supporting the “optimal foraging theory”. A similar shift in the diet of *C. gariepinus* during high flood regime was reported in Lake Sibaya (Bruton 1979). This shift in diet during the peak flood could be due to increasing water level and a subsequent dilution effect of prey in the floodplain making them more illusive to predators.

The decline in the condition of *C. gariepinus* (Figure 5.9) could be a result of a reduction in feeding intensity during the peak flood and a shift to algae and detritus (Willoughby & Tweddle 1978[a]), which have a lower nutritional value (Bowen 1979). This has also been observed in the Amazon floodforest, where fishes were most ecologically separated in terms of feeding, during the period of high water (Goulding 1980). This could be explained by the ecological theory of “optimisation of energy use” (Odum 1993). The theory states that the lower the abundance of food, the larger the habitat area to forage and the greater the range of food items taken. Therefore, in line with the “optimisation of energy use” theory, the fish switch from being feeding generalists to feeding specialists with increasing food abundance, and vice versa when it declines (Werner & Hall 1979). In rivers many species appear more flexible, shifting food items according to availability (Welcomme 2001).

There have been two schools of thought regarding the shift between specialist and generalist feeding in fluctuating environments. Some authors consider that specialised trophic behaviour confers a competitive advantage during low water when food resources are scarce; while others suggest that the competitive advantage arises at times of abundance (Welcomme 2001). The high feeding intensity of *C. gariepinus* (reflected by high condition) during the low-but-rising flood regime could be one of the most important adaptations to the fluctuating environment of the floodplain. *C. gariepinus* takes advantage of the period of abundant juvenile fish prey, to rapidly build up condition, in order to reproduce successfully during the peak flood regime.

The seasonal nature of the feeding cycles as shown here has been recorded in many other systems (Lowe-McConnell 1964, Goulding 1980&1981, Ribeiro 1983, Welcomme 1985). The findings of this study also supports the general notion that highwater (when food availability exceeds demand) is the feeding and growing period for many fish (Lowe-McConnell 1987, Welcomme 2001). In addition, the periods of low food intake (as reflected in the lower condition) coincide with low or falling water levels. This is clearly shown in *C. gariepinus*, which had a low condition factor during the receding flood regime (Figure 5.9). However, the opposite was observed for *O. mossambicus*, which showed a higher condition during the receding flood regime (Figure 5.9). Welcomme (1986, citing Daget 1957) similarly, reported that in the Central Niger Delta *Tilapia zilili* gained, while *Brycinus leuscus* (a piscivore) lost condition during the falling flood.

Effect of the flood-pulse on juvenile recruitment

Adaptation to conditions or opportunities that ensure greater survival of the offspring (Reynolds 1983, Welcomme 1985) such as water temperature, food availability and habitat preferenda (Bruton 1979) are thought to be some of the factors affecting abundance or movement of juvenile fish into the littoral zones of floodplains. Early juvenile density of all species was recorded to be highest between August and November in 1998 (602 – 1127 fish.m^{-2}) and between and July and November in 1999 (184 – 353 fish.m^{-2}) (Figure 5.7), which in both years corresponded to the low flood (Qrt1) and low-but-rising flood (Qrt2) regimes. Since the cycle repeated itself over two years, it is likely that it represents a typical recruitment cycle in the Lower Shire Floodplain.

The peak-breeding season for *O. mossambicus* was in November, during the low-but-rising flood (Qrt2) regime (Chapter 5). Early juvenile cichlids (25±10 mm TL) abundance was highest in March and larger *O. mossambicus* (55± 10 mm TL) were most abundant in August (Qrt1), during the low flood regime (Figure 5.5). Similar observations on the timing of recruitment was reported in Lake Sibaya (Bruton & Boltt 1975, Bowen & Allanson 1982), Lake Victoria (Welcomme 1964) and Lake McIlwaine (Caulton 1975) where *O. mossambicus* juveniles were reported to be common in the littoral zones during low water level where they converged to feed.

While the peak-breeding season for *C. gariepinus* was from October to December during the rising flood (Qrt2) regime (Chapter 4), juvenile (150±25 mm TL) started becoming more abundant in January. However, their density was highest (10±5 fish.m^{-2}) in July

(Qrt1) during the low flood regime (Figure 5.6), at which stage they were 190± 5 mm TL. The time lag between peak breeding (Nov/Dec) and first emergence of the juveniles (January) in the littoral zone might be explained by Bruton's (1979) observation in Lake Sibaya where juvenile *C. gariepinus* were reported to move into deeper waters soon after spawning and later migrated into and inhabited the shallow, inshore, newly inundated areas where food was abundant.

This timing of the emergence of juveniles of the two species into the littoral zone could also be explained by the "predator-prey wave" theory (Savill & Hogeweg 1999), which states that piscivorous predators such as *C. gariepinus*, generally take prey of specific size. Hence, prey species are relatively safe from predation once they are above that critical size. Lowe-McConnell (1987) noted that predation probably provides a powerful selection pressure for rapid growth in prey species. It would appear that commencement of predation on fish by juvenile *C. gariepinus* is crucial for their fitness and competitiveness. Bruton (1979) reported that fish became important in the diet of juvenile *C. gariepinus* when they were $\geq$50 mm TL. Therefore, it might be the case that soon after spawning, juvenile *O. mossambicus* might be growing rapidly between October (50±15 mm TL) and February (70± 5 mm TL) (Figure 5.5b) in order to avoid predation. Furthermore, the occurrence of high density of juvenile *O. mossambicus* in August, a month earlier than *C. gariepinus* (July), could also be an adaptation for optimal survival by ensuring that there is abundant prey (cichlids) for the *C. gariepinus* by the time they migrate into the littoral zone.

It is proposed that the spawning of both species during the rising (Qrt2) and peak flood regimes (Qrt3) (Chapter 4), may be an adaptation to ensure that juveniles colonise recently inundated floodplain to take advantage of the rising flood-pulse and subsequent abundance of habitat and food resources. Elsewhere, it has been reported that flooding which brings an influx of nutrients into recently inundated vegetated areas, provides cover for the spawning fishes as well as a favourable food-rich environment for the juveniles (Lowe-McConnell 1979, Bruton 1979, Bruton & Jackson 1983). Decaying vegetation during the high water level further enriches the detritus, which is a primary food for *O. mossambicus* (De Moore *et al.* 1986, Weyl 1998) and a significant proportion of the diet of *C. gariepinus* in the Lower Shire Floodplain (Willoughby & Tweddle 1978[a]).

While newly inundated floodplain swamp and marsh vegetation might provide refuge for the juveniles (Werner *et al.* 1983, Ogutu-Ohwayo 1993, Chapman *et al.* 1996, Weyl & Hecht 1998, Rosenberger & Chapman 1999), in the Lower Shire Floodplain these habitats become inundated (Howard-Williams 1973) and the lagoons completely connected with the main river channel during the period of peak flood. Therefore, the rising river waters may enable such predators as tigerfish (*Hydrocynus vittatus)* and *C. gariepinus* to invade the floodplains, hence the low relative abundance of juveniles during the peak flood regime (Figure 5.4). This supports the observation in Lake Sibaya where *O. mossambicus* juveniles were common in the littoral zone for only a few hours after dark in order to avoid predation by *C. gariepinus* (Bowen & Allanson 1982). Similar observations were made in the Okavango Delta (Merron 1991). In view of the relatively low proportion of fish in the diet of *C. gariepinus* in the Lower Shire Floodplain during the peak flood (Willoughby & Tweddle 1978[a]). The explanation above may not be an adequate one to explain the lower abundance of juvenile cichlids (Figure 5.5) during this time. Therefore, the dilution effect and greater rate of dispersion during high water level (Figure 5.3) seems a more plausible explanation for lower abundance of juvenile fish during peak flood (Figure 5.4).

Effect of the flood-pulse on growth of juvenile fish

Gauldie & Nelson (1990) reported that growth checks on hard structures such as scales, otoliths and spines are formed as a response to one or more environmental variables that reduce metabolic rate and result in a slowing of the growth rate. Although the period of annulus formation has been reported to be variable in fishes of tropical and sub-tropical waters (Kapetsky 1974, Booth *et al.* 1995, Booth & and Merron 1996, Pannella 1974, Hecht 1980), there is a strong indication that the formation of a single opaque zone in otoliths occurs at the end of winter, when either temperature or water level are low (Weyl & Hecht 1998).

The findings of this study revealed that one translucent and one opaque zone were deposited every year in the otoliths of *O. mossambicus* and *C. gariepinus*. The opaque zone was deposited during May (Qrt4) in *O. mossambicus* and during August (Qrt1) in *C. gariepinus* (Chapter 4, Figure 4.2). In both cases the period of deposition coincides with periods of low mean, water temperature 22°C (20-27°C) in June and 21°C (19-23°C) in August and receding water levels 4.5 m (4.5-4.6 m) (Chapter 2). It is important to note that the lowest minimum water temperatures and lowest air temperature range (9°C) were recorded in June. Similarly, in Lake Chicamba the opaque zone in *O. mossambicus* was deposited during winter drawdowns (Weyl 1998).

There was a significant increment of annulus width in younger fish (r^2=0.09, p≤0.001) than older ones (Table 5.4). Similar observations have also been made elsewhere (Dudley 1979, Booth & Merron 1996, Weyl 1998). This growth pattern is known as negative Lee's phenomenon (Ricker 1969). Notwithstanding Lee's phenomenon, the possibility that inter-annual annulus width is correlated with flooding conditions should not be ignored (Weyl 1998).

The direct (0.04≤r^2≥0.05) and significant (p≤0.01) relationships between annulus width and hydrological indices (Figure 5.10) as well as the allometric relationship between fish length and otolith dimension (Table 5.3) makes it possible to relate annulus width with growth of the fish. The direct relationship between increase in annulus width in *O. mossambicus* and the timing of flood and the duration of inundation of the floodplain may be a consequence of increased availability of food and foraging area in the floodplain. This is illustrated by the increase in annulus width during years of water levels above the bankfull (>4.5 m) and longer inundation of the floodplain (20-25 days) (Figure 5.11). However, a decrease in annulus width was reported during years of low water levels (<4.5 m) or excessively high water levels (>5.5 m), coupled with longer periods of inundation of the floodplain (>25 days) (Figure 5.11).

The link between the period of rising water level (when food is abundant) and the increase in annulus width is illustrated by the high condition for *O. mossambicus* over the same period (Figure 5.9). Similar observations on fish growth rate were made in Bangladesh Floodplains, where much of the year's growth was achieved at the end of the flood season and the beginning of the drawdown period, during which nutrient levels were highest (Halls *et al.* 1999).

5.5 Conclusion

The study has demonstrated that in addition to the rise and fall of the flood regime, the timing and duration of inundation influences the availability of food as well as seasonality of food intake and growth in both *O. mossambicus* and *C. gariepinus* in the Lower Shire Floodplains. It is apparent that the flood-pulse precedes food availability, intensity of food intake, growth and juvenile recruitment of the two major species in the floodplain. The seasonality of the flood regime seems to be the major factor that drives recruitment. Therefore, by understanding the seasonal pattern of the flood regime, fisheries managers are likely to be in a better position to explain the seasonal variation in fish yield in tropical floodplains, including the Lower Shire. Contrary to the notion that seemingly random retention of ecologically similar but different species occurs in floodplains pools which become isolated as the floods recede (Lowe-McConnell 1987), it seems likely that movement of juvenile fish, and indeed recruitment, is a non-random process that is governed by an intricate process of the timing of the flood regime and duration of inundation of the floodplain. Periodic and optimal inundation of the floodplain can only be achieved if the Shire River is allowed to overflow the threshold level (bankfull) and discharge water into the floodplains uninterrupted, otherwise seasonal enrichment and availability of food, spawning and subsequently recruitment will be interrupted. This study has demonstrated the importance of the flood regime on condition, growth and recruitment, and further emphasises the need for developing a hydro-climatic fisheries model to predict production and to manage the fisheries of the Lower Shire Floodplain.

Chapter 6

The Lower Shire Floodplain Fisheries

6.1 Introduction

The Lower Shire Floodplain directly benefits an estimated one million people living in riparian communities in Malawi and Mozambique. It is one of Africa's most important floodplains, covering an estimated area of 1,100 km^2 of which 650-700 km^2 are in Malawi and 400-450 km^2 in Mozambique. Fish production from the Malawi section of the floodplain was estimated at 1,000 tonnes per annum (p.a.) in the 1940s, 7,000 tonnes p.a. in the early 1970s (Ratcliffe 1972) and an average 5,629 tonnes p.a. between 1976 and 1998 (Bulirani *et al.* 1999). About 75% of the population in the floodplain fish for their livelihood (Kashau & Chimatiro 1997, Chimatiro & Mwale 1998).

Relatively extensive research and development work was conducted on the floodplain fisheries in the 1970s (Ratcliffe 1972, Hastings 1972, 1973, 1976, Tweddle *et al.* 1978, 1979, Tweddle & Willoughby 1979, Willoughby & Tweddle 1978^a, 1978^b, Willoughby & Walker 1978). Since then, no comprehensive fisheries survey has been conducted in the floodplain and hence the current status of the fishery remains uncertain.

The first attempt to quantify fishing effort in the Lower Shire Floodplain was a survey conducted in 1968 (Ratcliffe 1972) and follow-up in 1975 (Willoughby & Walker 1978). The 1975 survey reported a total of 2,823 fishermen, using gil lnets (60%), fish traps (22%), long lines (18%) and cast nets (9%) (Willoughby & Walker 1978). Analysing catch and effort data for 1976-1993, Tweddle *et al.* (1994) showed that the numbers of fishermen and fishing gears had remained constant, while yield had apparently levelled at 6,000 tonnes p.a.

Poor knowledge of the floodplain fisheries is reflected in the erratic nature of reported landings between 1980 and 1994 (Tweddle *et al.* 1994; Bulirani *et al.* 1999; Weyl *et al.* 2000). Tweddle *et al.* (1994) suggested that the erratic records was a result of poor data collection by fisheries staff, while Bulirani *et al.* (1999) thought it was due to reduced effort. However, riparian communities of the floodplain have ascribed the reduced catches to irregular water levels, an increasing number of fishers and infestation by water hyacinth (Chimatiro & Mwale 1998).

Apart from the poor statistics, the management of the floodplain fisheries is complicated by the diversity of the ichthyofauna and the different gears used by fishermen. Hastings (1973) proposed to establish selectivity indices for the different gears as a first step towards regulating fishing effort in the floodplain fisheries. However, due to methodological problems and insufficient funding, a management strategy could not be developed. To date the only regulatory measure in place is a minimum legal mesh size for gill nets of 51 mm (Bulirani *et al*. 1999). However, this mesh size was set on an ad-hoc basis, without due consideration of current levels of fishing or the biology of target species.

Management of floodplain fisheries is further complicated by the influence of the magnitude and frequency of flooding on catches (Welcomme 1979, Bayley 1981, 1991, Payne 1986, Junk *et al.* 1989; Welcomme 2001). This constraint has been recognised previously for the Lower Shire Floodplain (Tweddle *et al.* 1994, Bulirani *et al.* 1999). An initial attempt was undertaken by Tweddle *et al.* (1994) to establish an empirical relationship between mean annual water level and total catch. Overall there was a significantly high correlation (r = 0.737, $p \leq 0.01$) between water level and fish catch over a number of years, although in certain years the relationship was insignificant. Given that the Lower Shire Floodplain has a distinct hydro-climatic seasonal cycle (Chapter 2), it seems likely that the conclusions of Tweddle *et al.* (1994) did not take into account the intra-annual seasonal relationship between water flow and catch. The sustainable utilisation and management of the floodplain is a high national priority for Malawi (Malawi Government 1997), therefore, there is a need to quantitatively determine the status of effort and catch and to develop appropriate methods for predicting the impacts of changes in climatic, hydrological and anthropogenic factors on the fisheries.

A number of fisheries assessment methods are available. These include frame or inventory surveys (Bazigos 1974), catch cards (Claytor & O'Neil 1991), angler diary (Anderson & Thompson 1991), fisheries patrols (Claytor & O'Neil 1991), roving creel surveys (Malvestuto 1983), access point surveys (Malvestuto 1983) and aerial surveys (Bazigos 1974, McNeish & Trial 1991). The access point method is popular due to easiness of design and calculation (Pollock *et al.* 1994).

Presently statistical data on artisanal fisheries in Malawi are collected using methods developed by Bazigos (1972 & 1974). For the Lower Shire Floodplain, the method was revised by Willoughby & Walker (1978) and is still used now. The method is briefly described below. The floodplain was divided into eight minor strata based on topographical and biological features by Willoughby & Walker (1978). Total catch and fishing effort for each stratum are estimated by combining data obtained in a monthly catch assessment survey (CAS) and an annual frame survey, respectively. However, it has become evident that the CAS, in its current form, is not suitable for monitoring the fisheries of the floodplain (Alimoso 1988, 1994). In particular, the method does not take into account the uneven distribution of fishing gears, while the number of canoes, as a measure of effort may also not reflect true effort. However, no alternative method has been put in place.

The aim of this study was to quantitatively assess catch and effort of the major gears types of the Lower Shire Floodplain and to relate this to prevailing hydro-climatic seasons. Specifically, the study attempted to estimate total catch, assess selectivity of the gears, develop protocol to estimate total catch in the Lower Shire Floodplain and use these data together with the hydrological data (Chapter 2) and the biological data of the two dominant species (Chapter 4) to develop an understanding of the dynamics of the Lower Shire Floodplain.

6.2 Materials and Methods

Frame survey of fishers, fishing crafts and gears

Total effort in the floodplain was determined during a frame survey conducted in all eight minor strata of the Lower Shire Floodplain ($34^0$45’-35^0E and $16^0$00’-$17^0$15’S) (Figure 6.1) between 12 and 23 July 1999. The strata codes are according to those used by the Malawi Department of Fisheries (Table 6.1).

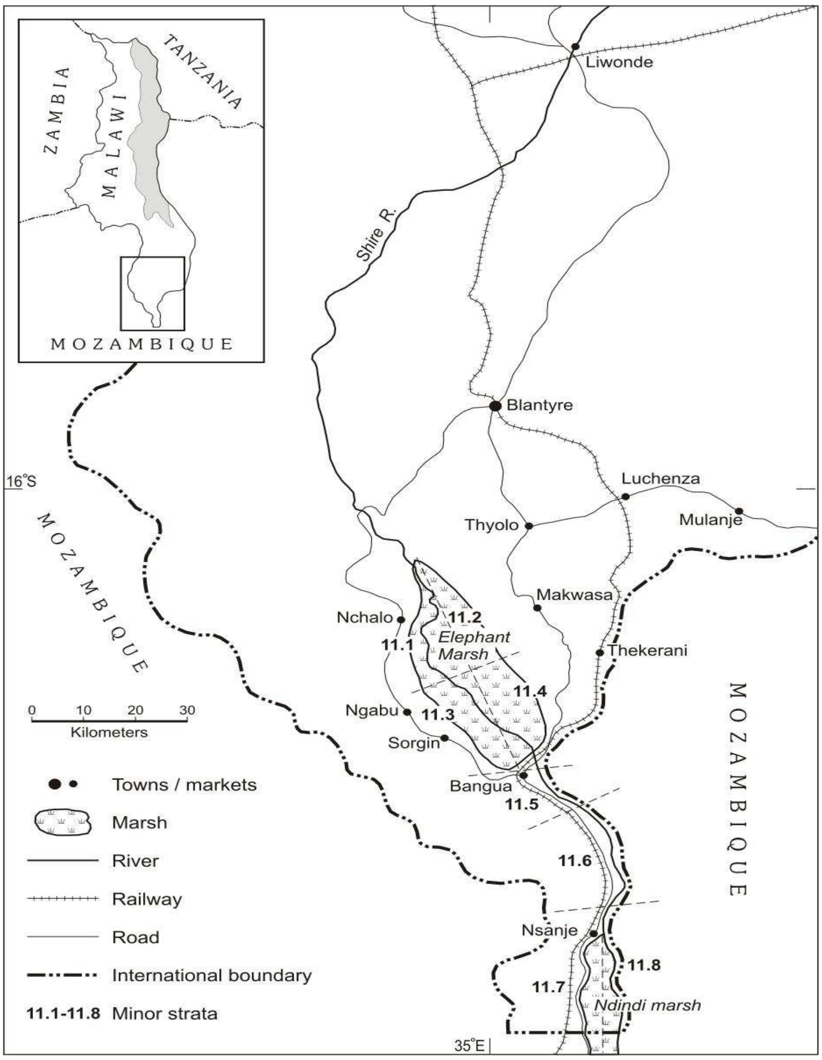


Figure 6.1 The eight minor strata (11.1-11.8) for fisheries statistics monitoring of the Lower Shire Floodplain

The frame survey was conducted by counting all fishers, fishing craft and gears in all the eight minor strata. Two enumerators were assigned to each stratum and completed their portion of the survey within two days to reduce the risk of double counting gears and crafts if fishers migrated to other areas. Every landing site was visited and fishers were interviewed using a questionnaire (Appendix 2). The dimensions of fishing gears were measured and recorded. This included the stretch mesh size of gill nets, cast nets and seine nets and also the numbers of fish traps used per fisher, the number of hooks and hook size per long lines and hand lines.

Table 6.1 Location of the eight minor strata (11.1-11.8) for fisheries statistics of the Lower Shire Floodplain.

Stratum code	Location of the stratum
11.1	North-western Elephant Marsh
11.2	North-eastern Elephant Marsh
11.3	South-western Elephant Marsh
11.4	South-eastern Elephant Marsh
11.5	Bangula Lagoon
11.6	Shire River between Elephant and Ndindi Marsh
11.7	Western Ndindi Marsh
11.8	Eastern Ndindi Marsh

Catch and effort survey

Considering the size of the Lower Shire Floodplain and time and budgetary constraints, it was not possible to conduct an intensive catch and effort survey in all eight minor strata; hence, three strata (11.3-South-western Elephant Marsh, 11.4-South-eastern Elephant Marsh and 11.5-Bangula Lagoon) (Figure 6.1) were chosen as sites for an intensive daily catch and effort survey. In total the three sampling strata covered approximately 310 km^2, representing 52% of the total area of the floodplain on the Malawi side. The area accounted for approximately 61% of the total numbers of fishers and gears in the floodplain. The sample strata also represented the three key floodplain habitats: viz. river-floodplain (RF), permanently connected lagoon (PCL) and seasonally connected lagoon (SCL) (see Chapter 3). Sampling sites around Chiromo and Mwala lagoon in stratum 11.3 represented the RF and the PCL, respectively, while Twaya and Njale Lagoons in stratum 11.4 represented PCL and SCL, respectively and Bangula Lagoon in stratum 11.5 was a seasonally connected lagoon. Furthermore, the strata represent ideal sites to study the impact of the flood regime on catches since it was shown that the water level in this area was significantly responsive to flooding (see Chapter 2). Since the sample strata were large enough and covered a large proportion of the fishers, it was assumed that the data from the daily catch and effort survey were sufficient enough to represent the whole floodplain. Therefore, the mean catch and effort data from these sample strata were used to calculate the total catch for the whole floodplain.

Random selections (Hayne 1991, Pollock et al. 1994) of eight major landing sites were randomly selected: two in stratum 11.3, four in 11.4 and two in 11.5. The number of sample sites was relative to the size of the stratum, more in larger and fewer in smaller strata. The landing sites were selected from the 1997's annual frame survey (AFS) (Malawi Department of Fisheries, unpublished data for 1997 AFS). This was done because Hayne (1991) recommended that for sample sites to be statistically sound, they must be selected from a current and complete list of all available accessible sites. The survey was conducted over a 28-month period between July 1998 and June 2000 (making for a complete overlap of 2 hydrological and fishing years).

Four fisheries enumerators working in pairs were randomly allocated to each site and visited the sampling sites on randomly selected days, with equal probability (Heggenes 1987, Hayne 1991, Pollock *et al.* 1994). Each site was randomly visited at least three days in a week. Malvestuto *et al.* (1978) recommended that about 180 days per sample site per year were statistically sufficient for estimating CPUE of anglers. Although most fishers landed their catches by around 1400 hours, to allow traders enough time to travel to markets, enumerators worked on the sites from 0600 to 1800 whether or not fishers brought in catches, to ensure equal amount of survey time per site regardless of the level of fishing. The author accompanied the enumerators on a random basis for 4 days per month throughout the 28-month sampling period.

Gear utilisation and species composition

To describe gear use and utilisation patterns, all fishers landing their catch on sampling days were interviewed using a questionnaire (Appendix 2). The total catch of each fisherman was sorted by species, weighed to the nearest 1 kg, and all fish measured for total length (TL) or fork length (FL) depending, on the species. Initial analysis of gear utilisation and catch data revealed that gill nets, cast nets, long lines, and fish traps accounted for over 85% of the total catch and that two species, *Clarias gariepinus* and *Oreochromis mossambicus* made up over 70% of the catch. Therefore, these four gear types and two species, respectively, were considered the major components of the fishery. The other types of gears and species were not included in such detailed analyses as length frequency distribution and gear selectivity. However, all gears, including seine nets and mosquito nets, and all species were included in the overall calculation of estimated total catch from the floodplain.

Estimation of fishing effort and catch rate

Procedures outlined by Pollock *et al.* (1994) were used to determine catch per unit effort (CPUE), total annual effort and annual catch for each gear. Fishing effort was calculated by multiplying the progressive count of number of days in the fishing week with the number of gears used. Unit effort was standardised to 100 m net.night^{-1} for gillnets according to Weyl (1998), 5 traps per fishing trip for traps, 90 hooks per line per fishing trip for long lines, and 1 trip per fishing day for cast nets. Mean CPUE per gear type was calculated using the following equation:

$$\overline{CPUE} = \frac{\sum_{i=1}^{n}\left(C_i \middle/ E_i \right)}{n} \qquad \text{(Equation 6.1)}$$

where C_i is the catch in numbers or kilograms on day i and E_i is the fishing effort on day i and n is number of days (Pollock *et al.* 1994).

Variations in CPUE with quarterly hydro-climatic seasons were compared using parametric one-way analysis of variance (ANOVA) when mean CPUE values were normally distributed, otherwise non-parametric Kruskal-Wallis was applied on ranks and Mann-Whitney U-test used for pair-wise comparison (Zar 1984). All tests used a 95% confidence interval in order to determine the range of estimated catch and effort values. Proportion of days fished was estimated from the creel survey data as weekly effort (days-fished), and the mean weekly effort $(\overline{wE})$ as days per gear, was calculated using the equation developed by Pollock *et al.* (1994) and modified by Weyl (1998):

$$\overline{wE} = \frac{\sum_{i=1}^{n} wE_i}{n} \qquad \text{(Equation 6.2)}$$

The estimated mean weekly effort $(\overline{wE})$ per fishery was expanded for each quarterly hydro-climatic season by multiplying the value with the number of fishing weeks per season. The annual effort by all the gears was estimated by multiplying the weekly hydro-climatic season's effort by the counts of all gears recorded in the Frame Survey. The daily fishing effort in each sampling area, over the quarterly season was estimated by expanding the frame survey gear counts by multiplying the value with the total effort on the i^{th} fishing days using the equation developed by Pollock *et al.* (1994) and modified by Weyl (1998), as follows:

$$\hat{e}_i = I_i \times T \qquad \text{(Equation 6.3)}$$

where $\hat{e}_i$ is the fishing effort for the i^{th} day, I_i is the frame survey count of the number of gears in the i^{th}-sample unit and T is the fishing day. However, in this case a fishing day was expressed in terms of one completed fishing trip since it was difficult to estimate number of hours fished. Since there were significant differences in quarterly effort (one-way ANOVA, $p \leq 0.05$), the total annual effort $(\hat{E}_{total})$ for the fishery was calculated using the equation developed by Pollock *et al.* (1994) and modified by Weyl (1998):

$$\hat{E}_{total} = \sum_{i=1}^{n} \hat{e}_i / \pi_i \qquad \text{(Equation 6.4)}$$

where π_i is the total probability that the i^{th} fishing period will be included in the sample (Pollock *et al.* 1994). The variance associated with the estimate of total quarterly effort was calculated using an equation developed by Hoening *et al.* (1993):

$$V(\hat{E}_{total}) = \frac{N^2 S^2}{n}$$

(Equation 6.5)

where N is the number of days in the quarter and S^2 is the estimated variance of the daily estimates of effort (Pollock *et al*. 1994) :

$$S^2 = \frac{1}{n_i - 1} \sum_{k=1}^{n_i} (e_{ik} - \bar{e}_i)^2 \qquad \text{(Equation 6.6)}$$

where n_i is the sample size (days), e_{ik} is effort on day k and $\bar{e}_i$ is the daily mean fishing effort.

Standard error (SE) associated with estimation of daily effort $\hat{e}_i$ was calculated according to Pollock *et al.* (1994) using the equation:

$$SE(\hat{e}_i) = \sqrt{V\,\hat{e}_i} \qquad \text{(Equation 6.7)}$$

where V is the variance associated with the estimation of daily effort.

To obtain total annual yield, annual effort was multiplied by the mean CPUE as follows:

$$C_{total} = \overline{CPUE} \times \hat{E}_{total} \qquad \text{(Equation 6.8)}$$

Gear selectivity

Individual gear sizes (e.g. mesh sizes of gill nets or hook size) could not be assessed/measured accurately due to wide variations in their dimensions. Mending of damaged gill nets and cast nets resulted in a wide range of mesh sizes, while infrequent replacement of damaged hooks and hook repairs meant that hooks of similar sizes ended up with different dimensions (width and length). For example, while the mean mesh size of gillnets was 73 mm the sizes ranged from 38 to 113 mm within single net panels, and hook sizes ranged from 9 to 18. Consequently, it was decided to determine selectivity patterns of each gear as a whole. To determine the selectivity of cast nets, gill nets, long lines and fish traps, a re-parameterised Gamma selectivity function (Punt *et al.* 1996) was fitted to the observed length frequency distribution of the two major species *Clarias gariepinus* and *Oreochromis mossambicus*. The selectivity function is described as:

$$S_j = \left(\frac{l_j}{\phi}\right)^{\frac{l}{\rho}} e^{\frac{(\phi - i_j)}{\rho}} \qquad \text{(Equation 6.9)}$$

$$\rho = \frac{\sqrt{\phi + 4\sigma_j^2 - \phi}}{2}$$

where : S_j is selectivity of the gear on fish of length j; ϕ is the length-at-maximum selectivity and σ is the width of the selectivity function. With the assumption that catches were Poisson random variables (Kirkwood & Walker 1986), expected catch-at-length proportions were fitted to the observed catch-at-length proportions using a method called SELECT (Share Each Length's Catch Total) (Millar 1995), using the maximum likelihood function developed by Kirkwood &Walker (1986) of the form:

$$L = \sum_{i}^{I}\sum_{j}^{J}\left[n_{ij}\ln\left(\mu_j S_{ij}\right) - \mu_j S_{ij}\right] \qquad \text{(Equation 6.10)}$$

where n_{ij} is the number of fish from length class *j*; S_{ij} is mean relative selectivity of the gear *i* for fish from length-class *j*; and μ_j is the relative proportion in the population from length-class *j* and it is expressed as :

$$\mu_j = \sum_{i=1}^{I} n_{ij} \Big/ \sum_{i=1}^{I} S_{ij} \qquad \text{(Equation 6.11)}$$

Substituting equation (6.11) into equation (6.10), and taking the logarithm of the likelihood, the function to be maximized becomes:

$$InL = \sum_{i}\sum_{j}\left(C_{i.j}In\hat{C}_{i.j} - \hat{C}_{i.j}\right) \qquad \text{(Equation 6.12)}$$

where $C_{i.j}$ and $\hat{C}_{i.j}$, respectively, are the observed and expected catch-at-length for gear *j*.

In addition to gear selectivity, similarities or dissimilarities in the frequency of particular species in the catches in the various habitats was assessed using hierarchical clustering (Clarke & Warwick 1997). Bray-Curtis similarity analysis for both species abundance and biomass was used. The tests were performed using the Primer Software (Clarke & Warwick 1994). A non-parametric analysis of similarities (ANOSIM) (Clarke 1993) was undertaken to determine the statistical distinction of species abundance and biomass among the various habitats.

6.3 Results

Gear utilisation

A total of 2,394 fishers and 741 assistants (crew members), 938 dugout canoes and 42 boats were counted during the frame survey (Appendix 3). There were three times as many fishermen than fishing crafts. This is because many fishermen borrow canoes or fish from the shore or fish by wading into the water. Effort was concentrated in the eastern and southern portions of Elephant Marsh, especially in minor stratum 11.4 which had the largest number of fishers, crafts and gears (Appendix 3). Table 6.2 shows the types of fishing gears used in the floodplain. Long lines, gill nets, fish traps and cast nets were the most commonly used gears, while seinenets and mosquito nets were the least common. Although driftnets were not recorded during the frame survey, the daily creel survey revealed that they were commonly used in the main river channel.

Table 6.2 Summary statistics for fishing gear dimensions as measured in the Lower Shire Floodplain between July 1998 and June 2000. Data is presented as mean values (± 95% confidence interval); n=sample size. Gill nets, mosquito nets, seine nets, reed fence and drift nets are presented as length (m); cast nets are diameter, values for fishtraps refer to numbers; values for longlines refer to number of hooks, and handlines refer to number of lines. The length of gillnets, castnets and seinenets represent a stretched panel of net.

Type of gear	**Mean length/numbers of traps and hooks (± 95% CI)**	**Average mesh or hook size (range)**	**n**
Gill nets	107.8 ± 6.3 m	76 (38-89) mm	2121
Seine nets	115.9 ± 32.9 m	40 (6-75) mm	16
Cast nets	2.7 ± 0.06 m	38 (25-76) mm	524
Mosquito nets	61.1 ± 11.6 m	0.5-0.2 mm	17
Longlines	92 ± 16.8 hooks	No. 10 (2-16)	12374
Handlines	3.2 ± 1.3 lines (1 hook/line)	No. 16 (10-18)	67
Fish traps	5.8 ± 0.4 traps	-	760
Reed fences	9.7 ± 5.3 m	-	75
Drift nets	108.5 ± 10.5 m	51 (50-75) mm	54

Of the nine commonly used gears, gill nets, cast nets, long lines and fish traps accounted for 99% of the total gear count during the frame survey. The gears were categorised as being active, semi-active or passive gears. Active gears included cast nets, hand lines, reed fences, mosquito nets and seine nets (Table 6.2).

Although scoop nets were observed, they were used so rarely (encountered only twice) that they were left out of the analysis. Scoop nets are made from a sheet of fine-meshed net with a bag, mounted flat on a Y-shaped pole. The gear is operated by fishermen standing on the edge of the river channel or in a canoe and scooping fish from the water.

Hand lines consist of either a monofilament or an 18-ply multifilament nylon line to which a single hook was attached. Commonly used hooks were Japanese No. 9-18 round-bend, spade-end, Kirby sea brand (No. 1225). A floater, usually a piece of reed, is tied to the line, and any movement of the floater is a sign of fish biting or being hooked. Sometimes a rattle is attached to alert the fisher when a fish takes the hook. When fishing in the main river channel, a platform made of poles and reeds is erected over the edge of the river, on which the fisher sits. Fishermen used an average of 3.2 (range: 1-9) lines (Table 6.2).

Drift nets are gill nets used as a semi-active gear in the main river channel only, where there is enough water current and no obstacles. One side of the net is left to float freely, while the fisherman holds the other end from a canoe and drifts downstream with the current. Regularly, the net is lifted into the canoe to remove the fish, which get entangled. Drift nets are mainly used at night. Fishermen set an average of 108.5 (range: 7-300) meters of driftnet overnight, with a mean mesh size of 51 (range: 50-75) mm (Table 6.2).

Cast nests are circular nets with a holding line in the centre of the net. Weights, usually stones, are fixed on the edge of the net such that when the net is swung and thrown, it opens, falls and covers fish over the area it lands. When the holding line is pulled, the fish get trapped, though some are entangled in the meshes. Cast nets are operated from a canoe where fishermen work in a team of two, one paddles the canoe and the other one throws the net. Figure 6.1 shows the meshsize frequency distribution of cast nets. Fishermen used cast nets with an average diameter of 2.4 (range: 3-7) meters with a mean mesh size of 38 (range: 25-76) mm.

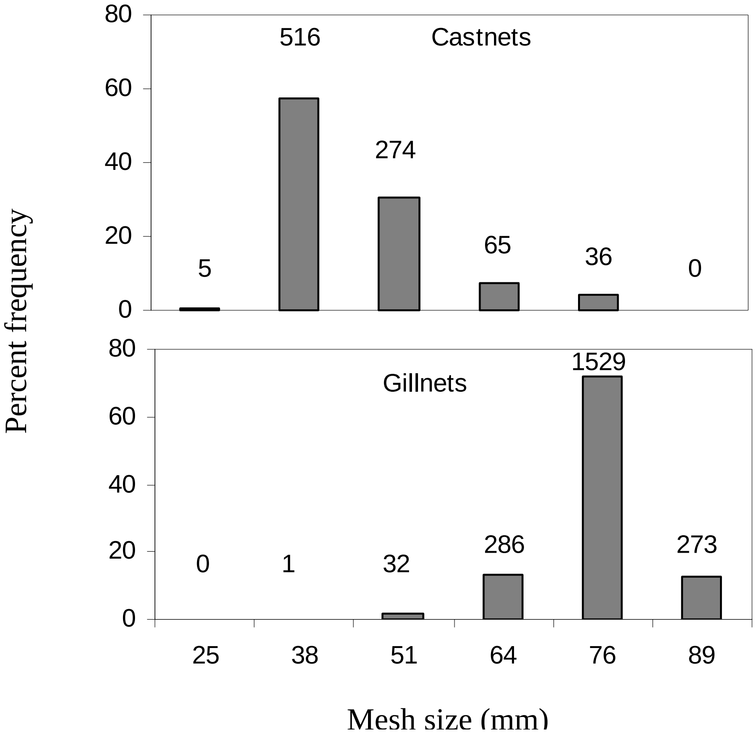


Figure 6.1 Mesh size frequency distribution for cast nets and gill nets in all eight strata of the Lower Shire Floodplain.

Reed fences are made of thin bamboo woven with palm or sisal strings into a fence. The fence is operated by standing it upright in the water and stretching it to make an enclosure. The enclosure is then folded until the space is reduced to an extent that the fish are trapped and then scooped out. The average length of reed fence was 9.7 meters (range: 7-17) (Table 6.2).

Seine nets are made from panels of multi-filament 18-ply nylon mounted on a head line with palm leaf floats and a foot line attached with stone sinkers. The head and foot ropes are attached to a pole, to which a long warp made of woven palm leaves is tied for hauling the net. The average length of seine nets was 116 (range: 100-200) metres, with a mean mesh size of 40 (range: 6-75) mm (Table 6.2). Mosquito nets are made from sheets of mosquito nets mounted in the same way as the seine nets. The average length of a mosquito net is 61.1 (range:3-100) metres (Table 6.2). Seine nets and mosquito nets are either operated on the beaches in the open lagoons or in vegetated floodplains after vegetation has been removed.

The major passive gears were long lines, gill nets and fish traps (Table 6.2). Gill nets are multi-filament 18-ply nylon, set overnight, anchored to bamboo pegs, with rock sinkers on the bottom line and palm leaf floaters on the top line. Figure 6.1 shows the mesh size frequency distribution of gillnets. Fishermen set an average of 108 (range: 25-700) meters of gill net overnight, with a mean mesh size of 76 (range: 38-89) mm (Table 6.2).

Long lines consist of an 18-ply multifilament twine mainline, on average 90 meters long, tied to a bamboo pole stuck in the bottom, with 70-90 cm ganglions of 18-ply multifilament twine spaced at an average of 1 meter apart. Similar sized hooks were used on hand lines and long lines. An average of 92 (ranges: 4-413) hooks are used per line (Table 6.2), baited mainly with earthworms, set overnight and lifted the following morning.

Funnel -valve fish traps are made from bamboo, woven with palm strings. An average of 5.8 (range: 1-24) fishtraps were set per fisher per night (Table 6.2). Fish traps are either set on the edge of the river channel or in the open lagoon anchored to a fence or barrier made of reeds or grass, which only open into the trap, that way deflecting fish into the trap. They were either unbaited or baited using cooked maize bran placed inside the traps.

Catch composition

The four major gears (gillnets, longlines, castnets, and fishtraps) accounted for 83% of total catch by mass (Table 6.3).

(i) By mass

The passive gears (gill nets, long lines, fish traps) accounted for approximately 63% (by mass) of the total catch, while 37% (by mass) was caught with active or semi-active gears (seine nets, cast nets, hand lines, reed fences, driftnets). *Clarias gariepinus* and *Oreochromis mossambicus* made up the bulk of the catch and together accounted for 93%, 88%, 72%, and 73% of the gill net, cast net, fish trap and reed fence catches, respectively (Table 6.3). Other important species were *Labeo altivelis*, *Synodontis zambezensis* and *Hydrocynus vittatus* which accounted for 28%, 34% and 21% respectively, of drift net fisheries in the main river channel, and *Distichodus mossambicus* which made up 59% of the hand line catch (Table 6.3).

(ii) By numbers

The abundance of fish species was determined by habitat type (Table 6.4). While both *O. mossambicus* and *C. gariepinus* occurred in all three habitats, they were more abundant in the seasonally connected lagoons (SCL) and less so in the river floodplain (RF). The cyprinids (*Labeo altivelis, L. cylindricus, L. congoro*), as well as *Synodontis zambezensis* and *Hydrocynus vittatus* were the most abundant species in the river-floodplain (RF), but they were remarkably rare in the seasonally connected and permanently connected lagoons (PCL).

Table 6.3 Percent (by mass) of species caught by various gears: gill nets, seine nets, long lines, hand line, cast nets, fish traps, reed fences, drift nets, and mosquito nets, sampled between March 1998 and June 2000 in the three major strata (11.3, 11.4, 11.5) of the Lower Shire Floodplain; n = number of fishers sampled.

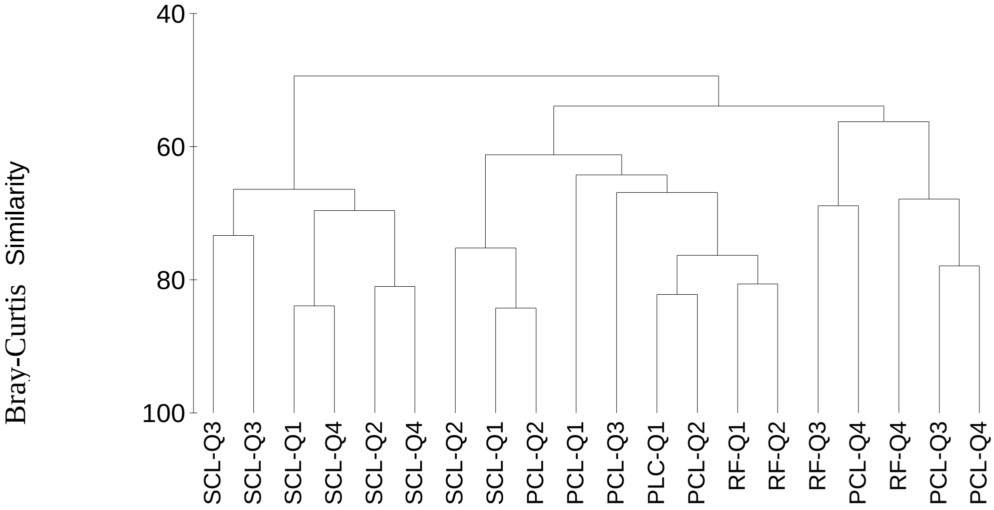
Species	**Gill nets (n=959)**	**Long lines (n=221)**	**Fish traps (n=236)**	**Seine nets (n=25)**	**Hand lines (n=40)**	**Cast nets (n=394)**	**Reed fences (n=75)**	**Drift nets (n=54)**	**Mosquit o nets (n=28)**
Cichlidae									
Oreochromis mossambicus	8.6	0.3	43.8	18.0	8.0	85.0	37.0	2.0	6.0
Tilapia rendalli	0.000	0	0.00	1.0	0	1.0	0	0	0
Astatotilapia calliptera	0.000	0.00	0	0	0	0.00	8.0	0	0.00
Clariidae									
Clarias gariepinus	68.4	92.6	23.0	23.0	18.0	3.0	36.0	0	23.0
Clarias ngamensis	0.5	0.8	0	0	0	0	0	0	0
Heterobranchus longifilis	0	0	0.00	0	1.0	0	0	0.00	0
Schilbeidae									
Schilbe intermedius	0.7	0.00	1.0	0.00	1.0	0.00	1.0	1.0	0
Mochokidae									
Synodontis zambezensis	0.4	0.1	12.0	0.00	1.0	0.00	6.0	34.0	0
Cyprinidae									
Labeo altivelis	6.4	0.3	4.0	4.0	0	7.0	1.0	28.0	0
Barbus afrohamiltoni	0.1	0	0	0	0	0.00	0.00	0	0.00
Labeo congoro	0.2	0	0	0	0	0	0	0	0
Barbus paludinosus	0	0	0	0.00	0	0	0	0	0.00
Barbus choloensis	0	0	0	0	0.00	0.00	0	0	0
Labeo cylindricus	0	0	0.00	0	0	0	0	0	0
Mormyridae									
Marcusenius macrolepidotus	7.7	0.1	5.0	2.0	0	1.0	4.0	2.0	0
Mormyrus longirostris	1.8	0	0.00	0.00	0	0.00	0	0.00	0
Hippopotamyrus ansorgii	0.2	0	0	0	0.00	0.00	0.00	0	0.00
Mormyrops anguilloides	1.8	0.00	1.0	0	12.0	0.00	2.0	7.0	0
Distichodontidae									
Distichodus shenga	0.00	0	0.00	0.00	0	0.00	0.00	0.00	0
Distichodus mossambicus	0.8	0.4	0.00	0.00	59.0	1.0	2.0	2.0	0
Characidae									
Brycinus imberi	0.1	0	0.00	0	0	0	0.00	1.0	0.00
Hydrocynus vittatus	0.2	0	0.00	0.00	0	0.00	0.00	21.0	0
Brycinus lateralis	0.00	0	0.00	0	0	0	0.00	0.00	0.00
Protopteridae									
Protopterus annectens	3.0	4.9	2.0	0.00	0	0	1.0	0	0
Malapteruridae									
Malapterurus shirensis	0.2	0	3.0	0	0	0	0.00	0	0
Others									
Unidentified fish juveniles	0.5	0	0	46.0	0	0	0	0	70.0
Total % by mass	36.8	16.98	9.5	4.04	1.7	19.4	3.6	0.9	7.1

Table 6.4 Species abundance (by numbers) in the three major habitats of the Lower Shire Floodplain. The total numbers are pooled samples from fishers of species caught by various gears: gill nets, seine nets, long lines, hand line, cast nets, fish traps, reed fences, drift nets, and mosquito nets, sampled between March 1998 and June 2000 in the three major strata (11.3, 11.4, 11.5) of the Lower Shire Floodplain.

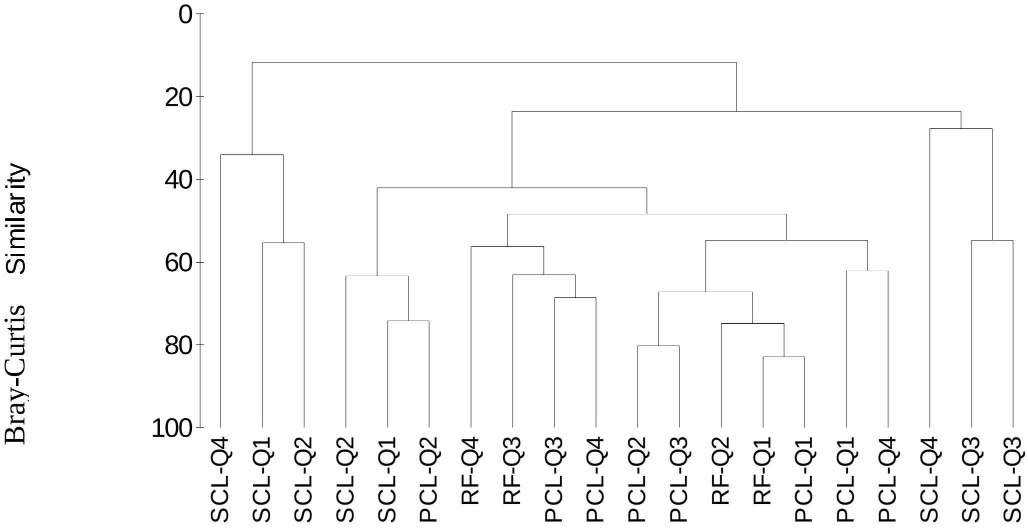
Family/Species	Habitats					
	Seasonally Connected Lagoon		Permanently Connected Lagoon		River Floodplain	
	Number of individuals	Percent abundance	Number of individuals	Percent abundance	Number of individuals	Percent abundance
Cichlidae						
Oreochromis mossambicus	28294	54	19479	37	4329	8
Tilapia rendalli	73	53	54	39	10	7
Astatotilapia calliptera	1	17	4	67	1	17
Clariidae						
Clarias gariepinus	3990	47	3076	36	1507	18
Clarias ngamensis	285	81	54	15	15	4
Heterobranchus longifilis	1	17	1	17	4	67
Schilbeidae						
Schilbe intermedius	489	31	539	34	564	35
Mochokidae						
Synodontis zambezensis	414	7	2348	39	3313	55
Cyprinidae						
Labeo altivelis	871	12	3203	43	3311	45
Barbus afrohamiltoni	24	7	186	56	125	37
Labeo congoro	0	0.00	5	7	67	93
Barbus paludinosus	0	0.00	6	100	0	0.00
Barbus choloensis	0	0.00	0	0.00	0	0.00
Labeo cylindricus	1	1	14	19	60	80
Mormyridae						
Marcusenius macrolepidotus	1932	35	2574	47	941	17
Mormyrus longirostris	93	13	295	42	312	45
Hippopotamyrus ansorgii	53	8	355	51	291	42
Mormyrops anguilloides	0	0.00	112	65	61	35
Distichodontidae						
Distichodus shenga	56	44	31	24	41	32
Distichodus mossambicus	53	7	304	41	393	52
Characidae						
Brycinus imberi	16	7	57	23	173	70
Hydrocynus vittatus	4	2	12	5	215	93
Brycinus lateralis	0	0.00	0	0.00	0	0.00
Protopteridae						
Protopterus annectens	14	21	33	49	20	30
Malapteruridae						
Malapterurus shirensis	0	0.00	0	0.00	1	100
Others						
Unidentified fish Juveniles	10	48	2	10	9	43

The hierarchical clustering of the three major habitats in the floodplain in terms of catch (by numbers and mass) is illustrated in the dendrograms in Figure 6.2a&b.

(a) Catch composition by numbers



(b) Catch composition by mass



Habitats by quarterly hydro-climatic seasons

Figure 6.2 Dendrogram of hierarchical clustering of fish catches from the major habits in the Lower Shire Floodplain, over quarterly hydro-climatic season. Q1-Q4 are hydro-climatic seasons, Q1=July-September, Q2=October to December, Q3=January to April, Q4=May to June. Habitats are represented by RF=River floodplain, PCL=Permanently connected lagoon, SCL=Seasonally connected lagoon.

Catch composition by numbers and mass were significantly different among all three habitats (one-way ANOSIM, $p \leq 0.01$). While fish abundance in the RF and the PCL were not significantly different from each other (one-way ANOSIM, $p \geq 0.05$), fish abundance in the SCL was significantly higher than those from both RF and PCL (one-way ANOSIM, $p \leq 05$). This situation is depicted by the two distinct clusters of catch composition (by numbers) in the RF and PCL habitats, on the left and SCL on the right of the dendrogram (Fig. 6.2a), regardless of the flood regime. It is apparent that the changing pattern of fish community structure in the three habitats might have been determined by the quarterly hydro-climatic seasons. For example, RF and PCL had more or less similar abundances during the peak flood (Qrt3). Regardless of the stage of the flood regime, catch composition by numbers in all sites were 30% similar (Fig. 6.2a), mainly as a consequence of the high abundance of both major species *O. mossambicus* and *C. gariepinus*. Therefore, it is apparent that the abundance of fish was determined by habitat type, although there was some overlap between habitats depending on the hydro-climatic seasons.

Fishing effort

Table 6.5 shows the mean weekly effort for all gears from the three sample strata (11.3, 11.4, and 11.5) and shows that gill nets and fish traps were the most frequently used while seine nets and mosquito nets were the least frequently used gears.

Table 6.5 Mean weekly effort (fisher days) for various gears in the three sample strata (11.3, 11.4, 11.5) of the Lower Shire Floodplain between July 1998 and June 2000. The data is presented as Mean ± 95% Confidence Interval (CI). Data on scoop net were so few that it has been excluded from the analysis.

Fishery	**Mean**	**± 95% CI**
Gill nets	6.79	0.07
Seine nets	5.48	0.75
Long lines	6.15	0.27
Hand lines	5.9	0.65
Cast nets	6.16	0.19
Fish traps	6.77	0.14
Drift nets	6.69	0.29
Mosquito nets	4.14	1.17
Reed fences	6.73	0.23

This can be expected since seining in the floodplain is dependent on season. Ideal seining conditions only occur during the low flood regime when receding water exposes the shoreline. The seasonal nature of seining and resultant variation in weekly fishing effort of seine nets and mosquito nets is also reflected in the wide confidence intervals of the CPUE of seine nets and mosquito nets (Fig. 6.4).

Gill nets were used for an average (± SD) of 6.79 ± 1.03 nights.week^{-1}, long lines 6.15 ± 2.08 days.week^{-1}, cast nets 6.15 ± 2.0 days.week^{-1} and fish traps 6.77 ± 1.13 days.week^{-1} (Table 6.5). Soak and/or fishing time was 17.4 ± 4.8 hours.night^{-1} for gillnets, 18.5 ± 13.2 hours.day^{-1} for long lines, 4.6 ± 3.35 hour.day^{-1} for cast nets, 20.0 ± 6.0 hours.day^{-1} fish traps, 5.8 ± 5.11 hours.night^{-1} for drift nets, and 7.13 ± 4.8 hours.day^{-1} for mosquito and seine nets combined. Table 6.6 shows the total estimated annual effort for the four major gears (gill nets, long lines, cast nets, fish traps) in all eight strata (11.1-11.8) of the floodplain, calculated using the data obtained during the frame survey and scaling it up using average weekly effort data from the intensive sampling survey in the three sample strata (11.3, 11.4, 11.5).

Table 6.6 Estimates of total annual effort for four major gear types in the Lower Shire Floodplain, between July 1998 and June 2000.

Fishery	**North-west Elephant Marsh**	**North-east Elephant Marsh**	**South-west Elephant Marsh**	**South-east Elephant Marsh**	**Bangula Lagoon**	**Shire River**	**West Ndindi Marsh**	**East Ndindi Marsh**
Gillnets (net-nights.yr^{-1})	25392	91790	121135	299566	54758	73560	73908	116406
Longlines (set-days.yr^{-1})	0	9797	10308	4882644	3995	113390	132288	219908
Castnets (net-days.yr^{-1})	16053	32788	35521	66507	6553	18785	16053	11271
Fishtraps (set-days.yr^{-1})	132872	927949	136637	131566	73262	282263	47403	220227

Catch rate

Figure 6.3 shows the CPUE for all species and gears in the floodplain for the two consecutive years. The data has been presented as consecutive years, and not average of the two years, in order to show the characteristic pattern of the response of CPUE to the flood pulse. Total CPUE for all species in all the nine major gears varied significantly ($p \leq 0.05$, one-way ANOVA) with quarterly hydro-climatic season (Figure 6.3). Although the magnitude of the variation differed from quarter to quarter, the trend was similar: low CPUE in Qrt1 (low flood regime) and high CPUE during Qrt3 (peak flood regime). CPUE for gill nets, seine nets and mosquito nets differed significantly from each other ($p \leq 0.05$), while the rest did not ($p \geq 0.05$) (Figure 6.4).

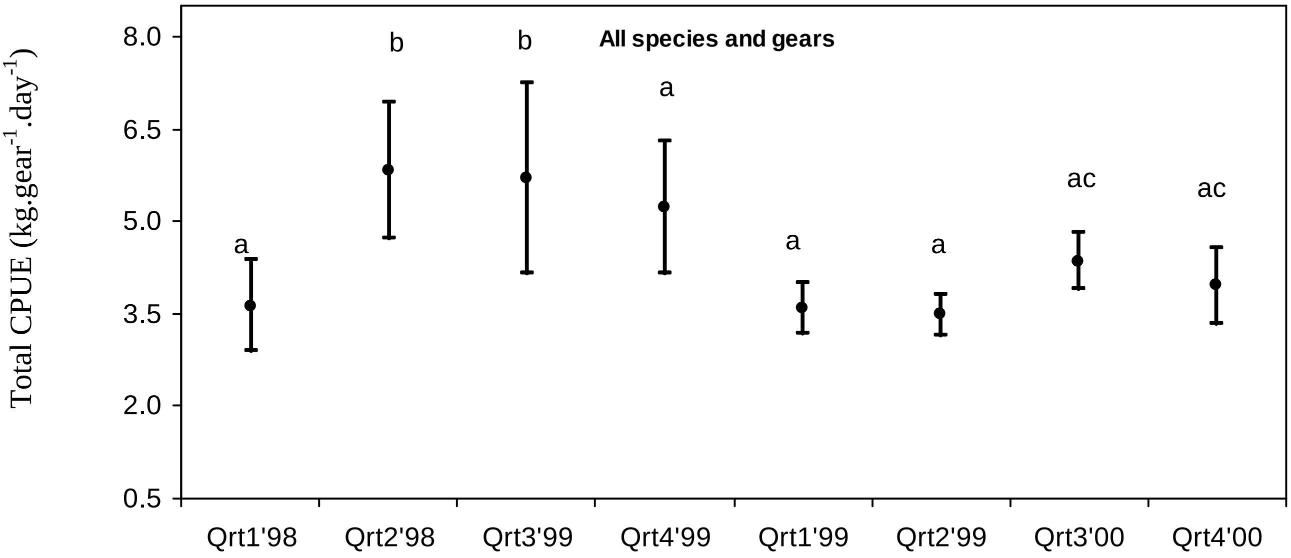


Figure 6.3 Catch per unit effort (± 95% confidence interval) for all species and gears in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison).

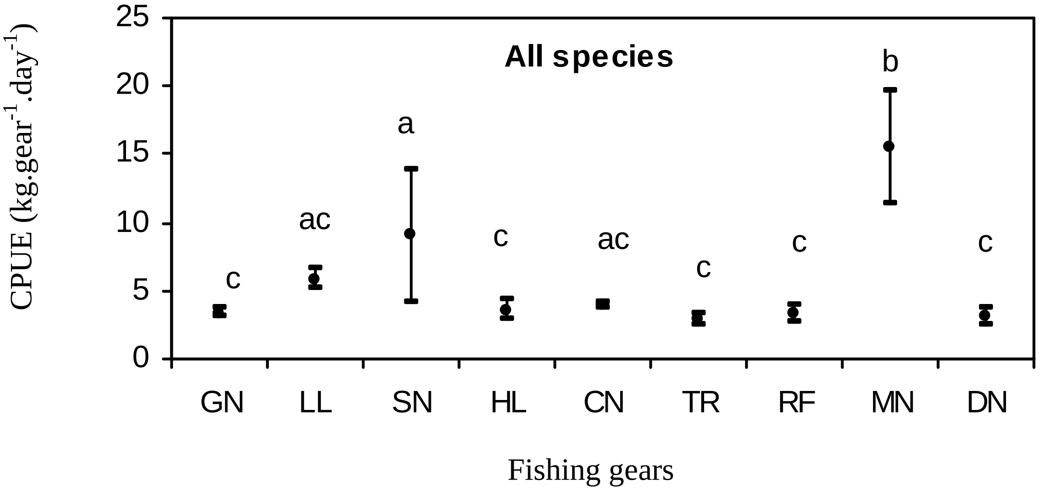


Figure 6.4 Catch per unit effort (CPUE ± 95% confidence interval) for all species by major fishing gears in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison). Abbreviations for the gears are GN=gill nets, LL=long lines, SN=seine nets, HL=hand lines, CN=cast nets, TR=fish traps, RF=reed fence, M=mosquito nets, DN=drift nets.

Figures 6.5-6.8 show CPUE for the *C. gariepinu*s and *O. mossambicus* in the various gears. The CPUE for all gears differed significantly ($p \leq 0.05$, one-way ANOVA) on a seasonal basis. The highest CPUE for fish traps, cast nets and gillnets was recorded during the peak flood regime in Qrt3. Although the long line CPUE for *O. mossambicus* did not show significant seasonal variation ($p \geq 0.05$, one-way ANOVA), that of *C. gariepinus* varied significantly with seasons ($p \leq 0.05$, one-way ANOVA) (Figure 6.7), being higher in Qrt2 (low but rising flood), and Qrt4 (receding flood). The combined gill net CPUE of *O. mossambicus* and *C. gariepinus* as well as individual CPUE of *O. mossambicus* and *C. gariepinus* was significantly higher ($p \leq 0.05$, one-way ANOVA) during Qrt2 (1998) (low but rising) than in the other seasons (Figure 6.8).

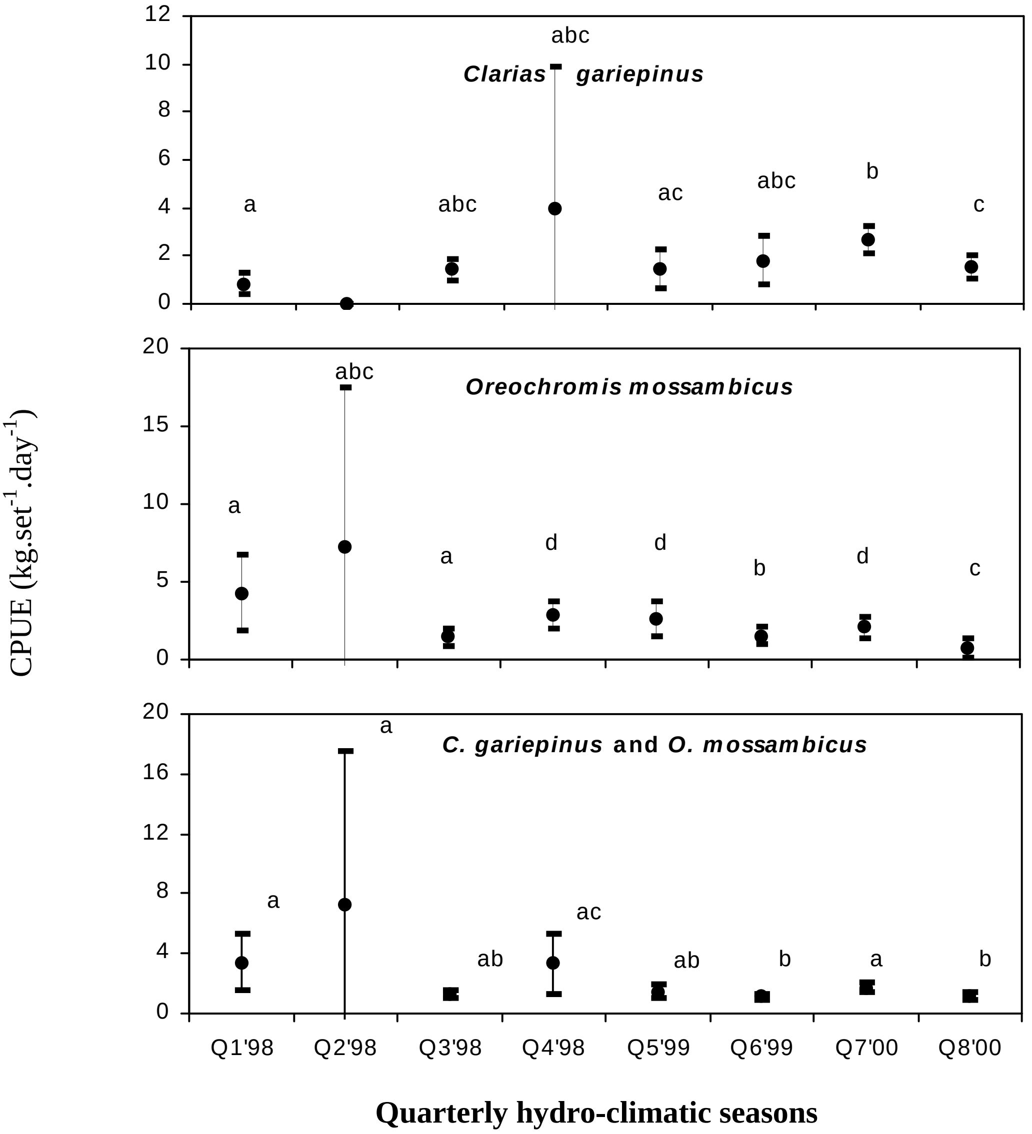


Figure 6.5 Fish trap catch per unit effort (CPUE ± 95% confidence interval) for *Clarias gariepinus* and *Oreochromis mossambicus* and the two species combined, in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison).

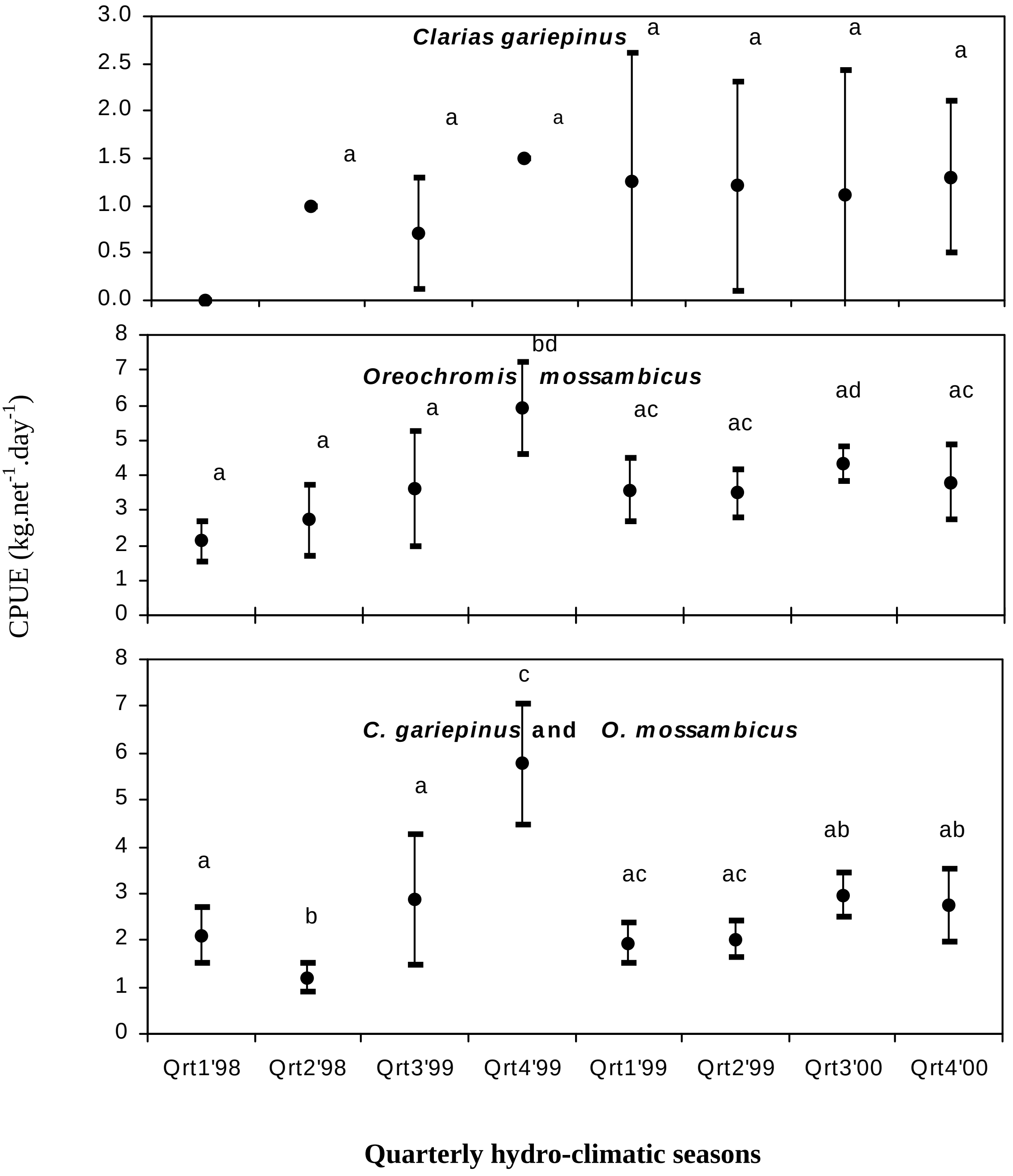


Figure 6.6 Cast net catch per unit effort (CPUE ± 95% confidence interval) for *Clarias gariepinus* and *Oreochromis mossambicus* and the two species combined, in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison).

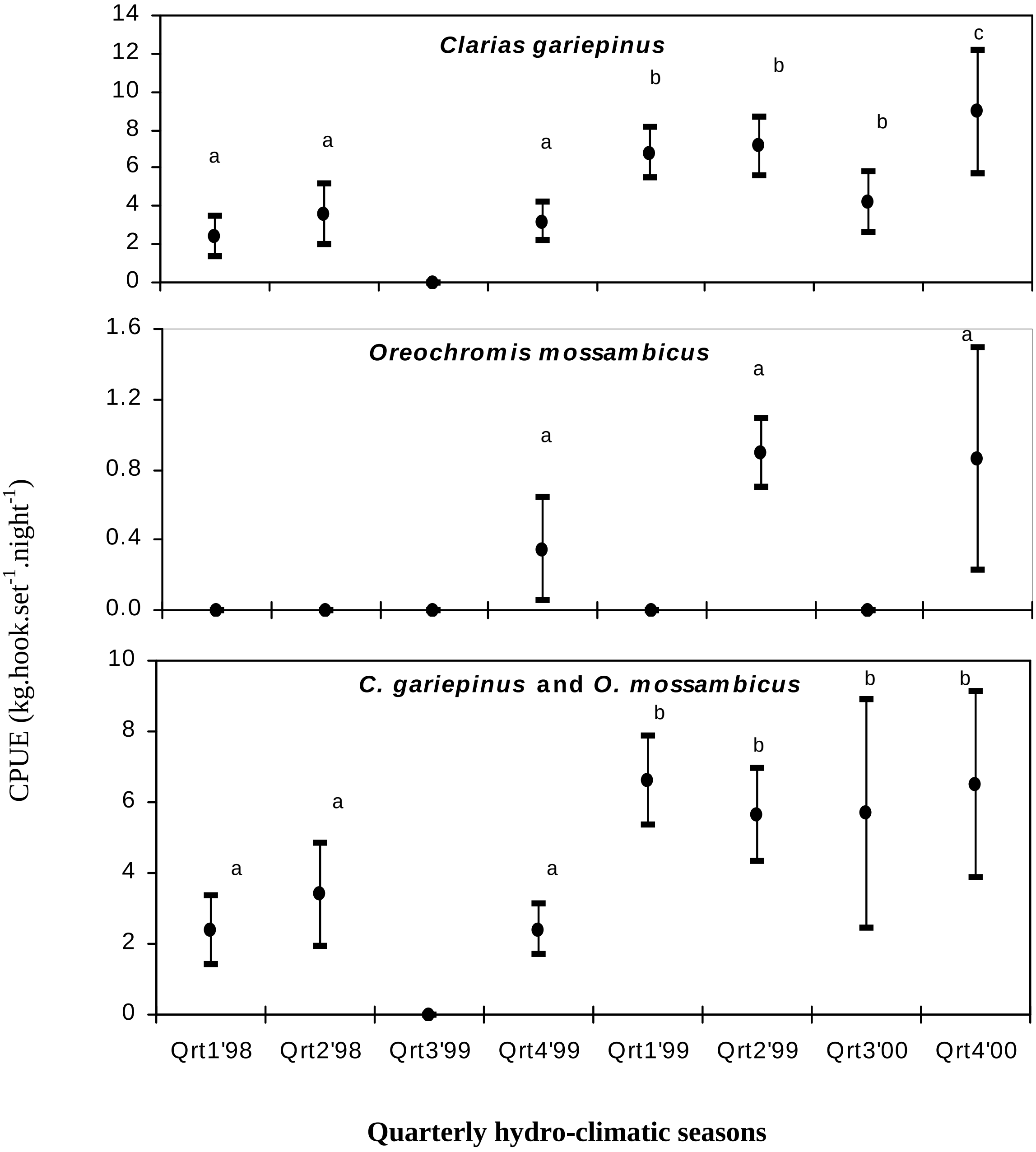


Figure 6.7 Long line catch per unit effort (CPUE ± 95% confidence interval) for *Clarias gariepinus* and *Oreochromis mossambicus* and the two species combined, in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison).

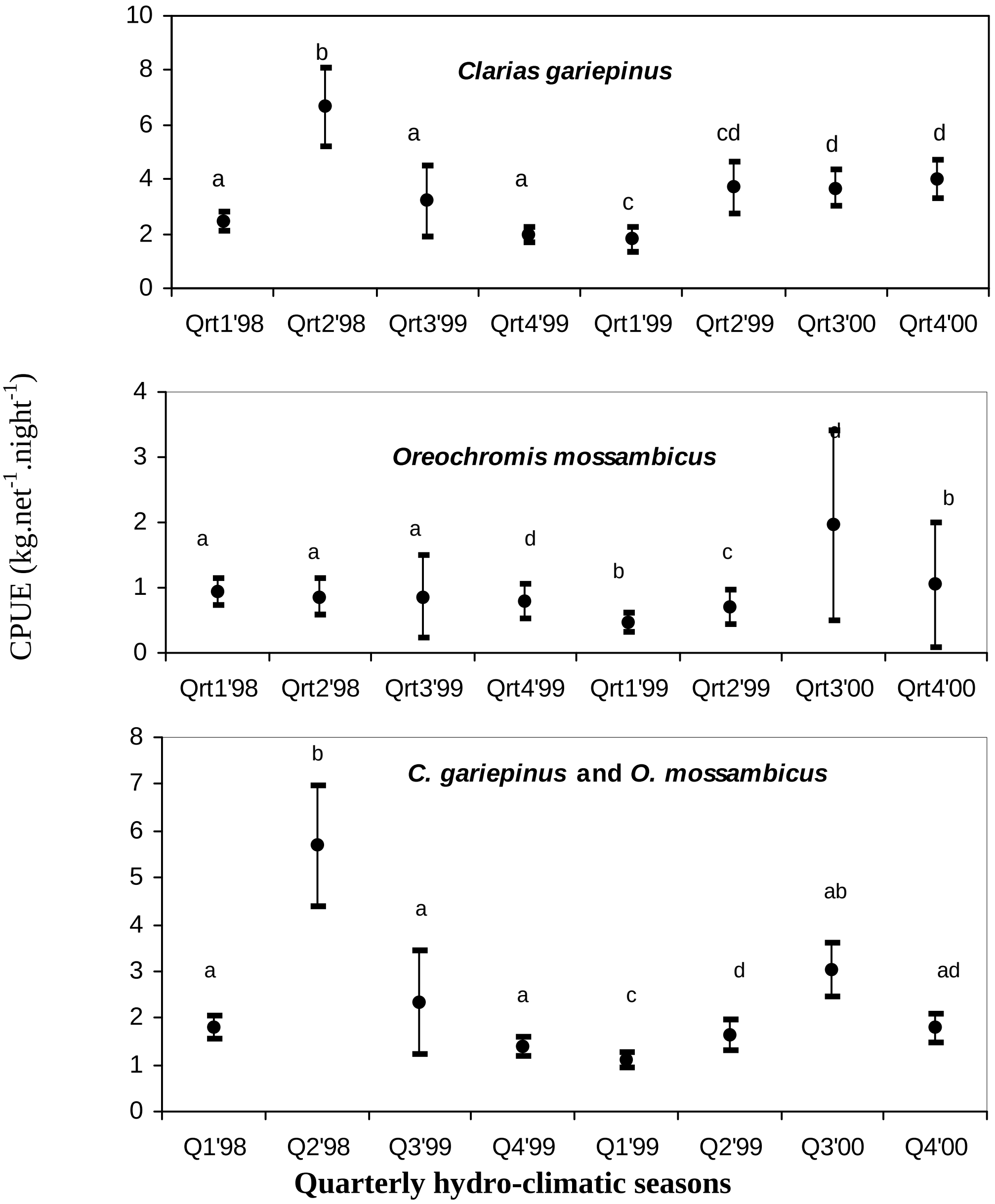


Figure 6.8 Gill net catch per unit effort (CPUE ± 95% confidence interval) for *Clarias gariepinus* and *Oreochromis mossambicus* and for the two species combined, in the Lower Shire Floodplain, from July 1998 to June 2000. Different letters denote significant differences ($p \leq 0.05$ level) (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison).

Estimate of total catch for the Lower Shire Floodplain

Catch rate and effort estimates from the sampled landing sites were used to estimate total catch for the whole floodplain. This was based on the assumptions, that the sample areas were sufficiently representative since they covered all the three major habitats of the floodplain (river floodplain, seasonally connected lagoons, permanently connected lagoons), and that the numbers of fishers sampled were sufficiently representative. The estimated total annual fish catch for all species by the major gears, and that for the two major species in the whole floodplain, are shown in Tables 6.7 and 6.8. These estimates were based on CPUE and effort calculated for one complete fishing season (1999/2000). The three sample sites (strata 11.3, 11.4, 11.5) represented about 52% of the total area and 61% of the total fishing effort of the Lower Shire Floodplain (i.e. 31% of fishers, 41% of canoes, 37% of castnets, 39% of gill nets, 40% of seine nets, 50% of reed fences and 91% of long lines). Therefore, the estimates of total effort and catches for the Lower Shire Floodplain could be calculated by scaling up the data from the intensive sampling of the quarterly CPUE and effort for each fishery sector using the total count of fishers, gears and craft determined during the frame survey.

Table 6.7 Estimates of total annual catch (kg) of all species in gill nets, long lines, cast nets, and fish traps in the Lower Shire Floodplain.

Fishery	North-west Elephant Marsh	North-east Elephant Marsh	South-west Elephant Marsh	South-east Elephant Marsh	Bangula Lagoon	Shire River	West Ndindi Marsh	East Ndindi Marsh
Gillnets	57,000	225,000	302,000	681,000	197,000	185,000	188,000	306,000
Long lines	0	700	700	341,000	9,000	8,000	16,000	0
Cast nets	62,000	127,000	138,000	256,000	23,000	73,000	62,000	44,000
Fish traps	77,000	535,000	98,000	88,000	57,000	163,000	27,000	126,000

Table 6.8 Estimated total catch (kg) of *Oreochromis mossambicus* and *Clarias gariepinus* by gillnets, long lines, cast nets, and fish traps during the 1999/2000 fishing season (July 99 – June 2000).

Species	**Gill net**	**Long line**	**Cast net**	**Fish trap**	**Total fishery**
O. mossambicus	343,000	1,000	637,000	562,000	1,543,000
C. gariepinus	1,327,000	350,000	16,000	234,000	1,927,000

<u>Gear selectivity</u>

As mentioned in section 6.2, individual gear dimensions sizes (meshes and hook size) varied greatly in all the four major gears (gill nets, cast nets, long lines and fish traps). Selectivity patterns were, therefore, calculated for each gear as a whole. The length frequency distribution of *O. mossambicus* and *C. gariepinus* in gill net, cast net, long line, and fish trap fisheries are shown in Figure 6.9. Length-at-maximum-selectivity (ϕ) and length-at-50%-sexual-maturity (L_{m50}) for each of the two species is summarised in Table 6.9. Although both species were selected by gill nets, cast nets and fish traps at lengths greater than (L_{m50}), maximum selectivity into the long lines for *O. mossambicus* occurred at a length below 50% sexual maturity (Fig. 6.9c). The width of the gamma selectivity function (σ) of 19.8 mm (Table 6.9) indicates that a small proportion of juveniles of *O. mossambicus* are also selected by the cast nets.

Table 6.9 Length-at-maximum-selectivity (ϕ) (mm); width of the gamma selectivity function (σ); mean length-at-50%-sexual maturity (L_{m50}); and width of the logistic ogive (δ) of *O. mossambicus* and *C. gariepinus* into gillnets, castnets, longlines, and fishtraps during the 1999/2000 fishing season (July 99 – June 2000).

Species	Gear selectivity								Sexual maturity			
	Gillnets		**Castnets**		**Longlines**		**Fishtraps**		Males		**Females**	
	ϕ	σ	ϕ	σ	ϕ	σ	ϕ	σ	L_{m50}	δ	L_{m50}	δ
O. mossambicus	147.8	35.35	118.4	19.8	89.8	18.3	137.0	45.77	109	19.1	105	22.73
C. gariepinus	382.6	53.39	335.8	72.1	384.2	83.0	351.6	95.22	249.2	34.98	249.6	77.84

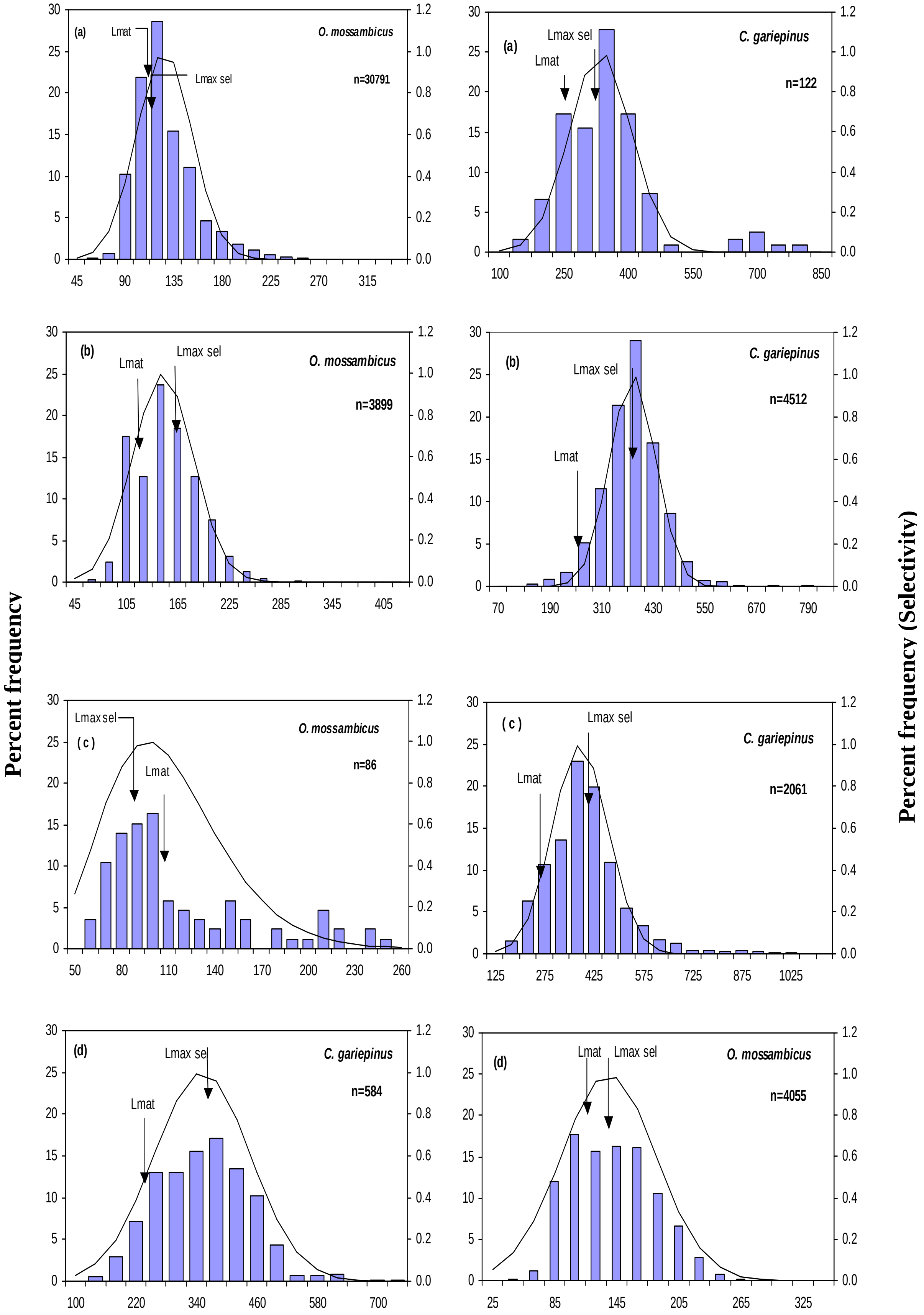


Figure 6.9 Length frequency distribution of *Oreochromis mossambicus* and *Clarias gariepinus* in (a) cast nets, (b) gill nets, (c) long lines and (d) fish traps in the Lower Shire Floodplain, fitted with gamma selectivity curve. Lmat is length-at-50%-sexual-maturity, Lmax sel is length-at-50%-selectivity; n is the sample size.

6.4 Discussion

Changes in fishing effort and selectivity

Since the earlier surveys conducted in the Lower Shire Floodplain in 1968 by Ratcliffe (1972) and in 1975 by Willoughby & Walker (1978), as well as the analysis of catch and effort data for 1976-1993 performed by Tweddle *et al.* (1994), the situation as regards important fishing gears has not changed. In this study, gill nets, fish traps, long lines and cast nets emerged as the most frequently used gears. However, there appears to have been a number of important changes. The present survey data suggest that the number of fishing crafts had decreased by 42% and the number of fishers had increased by 15%, and that the number of long lines and fish traps had increased by more than 2,000% and 800%, respectively since 1975 (Tables 6.10&6.11). Unfortunately, it is not known whether these observed differences are real or whether they are a reflection of a more structured and precise assessment of effort in comparison to the previous surveys. For this reason the comparison of CPUE between this and previous assessments should be viewed with a certain degree of circumspection.

Table 6.10 Comparison of gear counts during the frame surveys in Feb-Nov. 1975 (Willoughby & Walker 1978), 1985 (Tweddle *et al.* 1994) and July 1999 (this study). (nd = the gear may have been used by fishers, but was not recorded in the survey).

Type of effort	**Total count**		
	1975	**1985**	**1999**
Fishers	2,823	2,719	3,135
Gillnets	1,693	1,692	2,873
Seine nets	0	38	30
Castnets	254	575	608
Mosquito nets	0	0	24
Longlines	508	340	15,642
Handlines	nd	nd	62
Fishtraps	621	1,721	5,600
Fishing crafts	1,700	1,673	980

Table 6.11 Comparison of total gear counts during the frame survey in Feb-Nov. 1975 (Willoughby & Walker 1978) and July 1999 (this work), and CPUE in 1975 (Willoughby & Walker 1978) and 1999/2000 (this work). (nd = the gear may have been used by fishers, but was not recorded in the survey).

Type of gear	Number of gears used		Percent change (%)	Catch per unit effort (kg.day^{-1})		Percent change (%)
	1975	1999		1975	1999/00	
Number of gillnets	1,693	2,873	69.7	12.0	3.5	-95.8
Mesh size of gillnets (mm)						
38	0	1	100.0			
51	80	32	-60.0			
64	105	286	172.4			
76	115	1529	1229.6			
89	80	273	241.3			
102	23	0	-100.0			
Seinenets	0	30	100.0			
Castnets	254	608	139.0	14.6	4.0	-23.0
Mosquitonets	0	24	100.0			
Longlines	508	15,642	2,979	11.8	5.9	-50.0
Handlines	nd	62	100.0			
Fishtraps	621	5,600	801.8	11.7	3.0	-74.4
Fishing crafts	1,700	980	-42.4			

The decline in the number of canoes may be real, as the price of dugout canoes has soared from K110 in 1975 (Willoughby & Walker 1978) to about K9,000 during this study, such that many artisanal fisheries cannot afford them. The increase in the price of canoes is linked to the dwindling number of large trees suitable for canoe construction. Low financial resources might also be the reason for the relatively small increase in the numbers of gillnets. The number of gill nets appears to have increased by 70%. In addition, there has been a shift towards gill nets with smaller mesh sizes and a greater use of mosquito nets. For example, minimum sizes shifted from 51 mm in 1975 to 38 mm in

1999, while maximum sizes shifted from 102 mm in 1975 to 89 mm in 1999 and no mosquito nets were recorded in 1975 (Table 6.11). Current CPUE levels for gill nets, long lines, cast nets and fish traps have declined by 96%, 50%, 23% and 74%, respectively, from 1975 (Table 6.11). Mindful of the comments above, the significant decline in CPUE are probably a consequence of the increase in fishing effort over the past 20 years and concomitant changes in life history traits of the target species (Nikolsky 1963, Bayley 1981, Welcomme 1995&2001 (see Chapter 4).

In view of the suggestion above that the number of fishing crafts appear to have declined, it might be reasonable to conclude that the current protocol of the Catch Assessment Survey (CAS) implemented by the Malawi Department of Fisheries might be underestimating the fish landings of the Lower Shire Floodplain (Table 6.12).

Table 6.12 Comparison of estimates of total annual catch (tons) of all fisheries during the 1999/2000 fishing season (this study) and the official Catch Assessment Survey (CAS) by the Malawi Department of Fisheries.

Fishery	**Total annual catch (this study)**	**Total annual catch (Department of Fisheries CAS estimates)**
Gill nets	2141	839
Seine nets	67	21
Long lines	385	110
Hand lines	51	636
Cast nets	786	160
Fish traps	1171	494
Reed fences	3	8
Drift nets	9	0
Mosquito nets	45	37
Total	4656	2303

Alimoso (1988) and Tweddle *et al.* (1994) initially made the observation that the CAS was inappropriate; however, they did not offer an improved alternative CAS protocol. The protocol used in this study differs from the traditional CAS protocol in three ways. First, instead of limiting the sampling period to the beginning of the month, sample days were randomly spread over a minimum of four days per month. Secondly, fishers were randomly sampled as they landed their catch and not preselected prior to the CAS. Thirdly, the number of dugout canoes was not used as a "raising factor" (or as a basis for estimating effort). This presents serious statistical problems in that it underestimates catches from such gear as gill nets, cast nets, fish traps and seine nets since the number of canoes is dwindling (Table 6.12). Although these gears are traditionally canoe-based, it is likely that in the Lower Shire Floodplain many gill net and cast net fishers share canoes. A suggestion is made later in the discussion how the CAS protocol might be improved.

Given that there was no preference among the fishers for any particular species, target species can be defined only by selectivity of the gear used. Due to the overall pattern of gear selectivity, *C. gariepinus* and *O. mossambicus* were the mainstay of the fishery. However, these patterns varied considerably and none of the gears excluded other species (Table 6.3). Juveniles of *C. gariepinus* and *O. mossambicus* were also common in the cast nets and long lines, while gill nets selected mainly adults of the two species (Figure 6.9).

The selectivity patterns in this study confirm the notion that such patterns are an indication of the extent of the habitat occupied by different species (Hamley 1975, Heck & Crowder 1991). For example *C. gariepinus* occurs in almost any habitat but favours floodplains, and *O. mossambicus* occurs in all but fast-flowing water and thrives in standing waters (Merron 1991, Skelton 1993&2001). These species were common in gill nets, cast nets, long lines and fish traps operated in the open lagoons or along the edges of emergent vegetation in both the PCL and SCL as well as in drift nets operated in the main river channel of the RF (Tables 6.3&6.4). This might be the reason for the 30% similarity in the CPUE (by numbers of fish caught) in all the three habitats (Fig. 6.2a). *L. altivelis* and *S. zambezensis* prefer rivers and riverine habitats (Skelton 1993&2001), while *Schilbe intermedius* shoals in standing or slow flowing water with emergent or submerged vegetation (Merron 1991, Skelton 1993&2001), and indeed were caught mainly in the driftnets (Table 6.3) operated in the river-channel (Table 6.4). Bray-Curtis similarity (one-way ANISOM, $p \geq 0.05$) between RF and PCL during the Qrt3 (peak flood) and Qrt4 (receding flood) (Fig. 6.2) was shown to have been largely due to the presence of *L. altivelis, S. zambezensis* and *S. intermedius* (riverine preference species) in both habitats. In addition, this could have been due to the fact that PCL are connected to the main river channel all the year round, providing free movement of fish between PCL and the RF.

Selection of juvenile *C. gariepinus* and *O. mossambicus* in cast nets, gill nets, fish traps and long lines (Fig. 6.9) can be attributed to the preference of the juveniles of these species for the littoral zone (nursery area) in the PCL and SCL habitats (Table 6.4). In Lake Sibaya, *Oreochromis mossambicus* juveniles were reported to be common in the littoral zones only during daylight hours at low water level (Bruton & Boltt 1975, Bowen & Allanson 1982). The juveniles were also common in the littoral zone for only a few hours after dark in order to avoid predation by *C. gariepinus*, during high water levels (Bowen & Allanson 1982). Similar movements of tilapia species were reported in Lake Victoria (Welcomme 1964) and Lake McIlwaine (Caulton 1975). Likewise, juvenile *C. gariepinus* were reported to inhabit the shallow inshore areas of Lake Sibaya that had an abundant food source (Bruton 1979).

The fishery of the Lower Shire is typical of many other floodplain fisheries in Africa, being multi-gear and multi-species in nature (Welcomme 1985&2001), where the gears are targeting a wide range of ecologically diverse species (Table 6.3&6.4), through all stages of their life history (Welcomme 2001, Weyl 1998) (Table 6.9 and Fig. 6.9). The major gears (gill nets, long lines, cast nets, and fish traps) targeted all length classes of the two major species, raising fears of growth overfishing (catching recruits before they contribute to overall biomass) (Sparre & Venema 1992). This study has also shown that small-meshed gears (e.g. mosquito nets and gill nets) were gaining in popularity (Tables 6.10&6.11), raising fears of recruitment overfishing (depletion of spawners below a threshold for replenishing itself) (Hill 1992, Sparre & Venema 1992, Harley *et al.* 2000).

Effect of flood regime on catch

A significant trend (one-way ANOVA, $p \leq 05$) in the variation of CPUE with hydro-climatic seasons emerged over the two years of sampling (Fig. 6.3). CPUE was lower in Qrt1 (low flood regime) than in Qrt3 (peak flood regime). Willoughby & Walker (1978) also reported higher catches of *O. mossambicus* and *C. gariepinus* between August and December, during low and rising flood regime, and lower catches between May and July during the receding and low flood regimes. Increasing and decreasing CPUE with a respective rising and receding flood regime has also been reported in the Okavango Delta (Merron 1991), floodplains of the Niger River (Welcomme 1986) and the Piracicaba River of the Amazon (Silvano & Begossi 2001).

The seasonal variation in CPUE in the Lower Shire Floodplain supports the concept of a seasonal cycle, typical of tropical ecosystems (Welcomme 1985&1986) and Lowe-McConnell 1987, Wecomme 2001). Contrary to the notion that catches in the Lower Shire Floodplain might have levelled off as a result of constant effort (Tweddle *et al.* 1994) or declined due to reduced effort (Bulirani *et al.* 1999), this study strongly suggests that there are significant intra-annual variations in CPUE due to changes in the flood regime. It is, therefore, pivotal to relate and link CPUE to the hydro-climatic seasons to predict or calculate fish production or yield of the floodplain.

Proposed new protocol for catch assessment survey

For future surveys of the Lower Shire floodplain by the Department of Fisheries, it is recommended that gear-based (and not canoe-based) effort be used. It is evident from this study that the number of canoes in the floodplain is declining, resulting in fishers either sharing canoes or adapting the gears to suit fishing without canoes. While current CAS methods calculate total effort by scaling up the monthly effort, this study has found weekly effort to be a more realistic application due to large monthly variations in effort. Furthermore, this study has revealed that there are distinct quarterly hydro-climatic variations in CPUE. Therefore, it is necessary that the current method, used by Malawi Department of Fisheries, must be changed, in favour of the one developed in this study, where calculation of catch should be done by scaling up the weekly effort and catch to the quarterly level.

It is apparent from this study that in order to develop a management model for the fisheries of the Lower Shire Floodplain, it is important to have a thorough understanding of the dynamics of gear use and target species, including seasonal variations in effort and catch with the flood regime. However, application of these findings in the development of a management strategy for the Lower Shire Floodplain can only be realised if a predictive hydro-climatic fisheries model is developed.

Chapter 7

Development of a Predictive Hydro-Climatic Fisheries Model for the Management of the Lower Shire Floodplain

7.1 Introduction

Floodplain fisheries have more complex interactions between the environment, the fish and the fishers, than any other type of fishery, and they also exhibit high spatial and seasonal variability in habitat (Hoggarth *et al.* 1999). By concentrating only on the population dynamics of fish species without giving due attention to the complex interaction the species might have with others and the environment or ecosystem in which it exists, we risk overlooking factors that might help us explain certain parameters of population dynamics (Mann 1988). Therefore, adoption of an approach to fisheries management that recognises a continuum between population and ecosystems ecology has been proposed (Mann 1988, FAO 1999, Anon 1999, Hoggarth *et al.* 1999, Degnbol 2001). It has long been recognized that the floodplain should be seen as ecologically indivisible from and closely connected to the river and to its catchment area (Junk *et al.* 1989, Bayley 1991, Furch 1997, Welcomme 1985 & 2001, Kvist & Nebel 2001). Despite the fact that the multiple scales interaction within and among these ecologically indivisible ecosystems are linked, the ability to predict ecosystem behavior in fisheries is limited (Anon 1999).

Much progress has been made in the development of quantitative mathematical and statistical fisheries models, which have a population ecology perspective (Silvert 1981, Dickie & Kerr 1982, Kerr 1982, Rigler 1982). However, the utility of these models in floodplain fisheries management is limited by the underlying assumption that parameters under consideration are constant and the system is in a steady state.

Therefore, fisheries scientists have recognised the need to develop methods that account for the highly interactive nature of the fisheries resources. Among the new methods are ECOPATH (Polovina 1984, Christensen & Pauly 1992, 1995) and ECOSIM (Walters *et al*. 1997) approaches. ECOPATH has been widely used in the management of aquatic ecosystems (Christensen & Pauly 1995, Moreau *et al* 1997) and has proved useful in developing management strategies for Lake Kariba and Lake Turkana (Kolding 1994). Since considerable data is required in order to accurately estimate production, ecotrophic efficiency, relative food consumption and dietary composition at all trophic levels in the ecosystem, as well as fish yield (Moreau *et al* 1997), the methods have, however, not been widely adopted for management of African fisheries.

Thus, Platt *et al.* (1981) concluded that the common practice of using differential equations had led to limited success in making predictions about the consequences of perturbing ecosystems on fisheries yield. Consequently, they called for a radical re-examination of the properties of ecosystems, through five lines of inquiry: thermodynamics, input-output analysis, information theory, ataxonomic aggregations and statistical mechanisms in order to find fruitful approaches to the prediction of the functioning of ecosystems.

Statistical analyses have been used in biology as analytical tools to help uncover causal relationships (Lieth 1976) or the influence of environmental factors on key life-history traits of exploited fish stocks (Csirke 1980, Mercer 1982, Mann 1988). Using correlation models, Lieth (1976) reported that environmental parameters were reliable predictors for local, regional and global primary productivity patterns. Fisher & Grimm (1991) noted that the advantage of a multiple regression approach is that it helps identify variables that are important in shaping of running water (lotic) ecosystems. Numerous workers have used regression models to examine the relationship between floodplains and their flora and fauna (Johnson et al. 1997, Toner & Keddy 1997, Bell 1974). For example, due to the stochastic nature of the water regime, biological and chemical parameters in the Rhine floodplain, Zsuffa & Bogardi (1995) recommended the use of correlation statistical analysis in the hydrodynamic simulation between inundation variables and vegetation types and fish production.

Consequently, models that simulate variation in fish growth with flood regime have been developed specifically for floodplain fisheries in Africa (Loubens 1969, Kapetsky 1974). Welcomme (2001) reviewed a range of empirical regression models that have been used in inland fisheries, including floodplain fisheries. These include the Morpho-Edaphic Index, surplus production, dynamic pool and floodplain fisheries simulation models (PFMODEL) (Grey 1986, Montreuil *et al.* 1990, Hoggarth & Kirkwod 1996, Halls. 1998). Welcomme & Hagborg (1977) pioneered the development of a generalised model to simulate the behaviour of floodplain fisheries under different regimes of flooding and exploitation. The PFMODEL has been used to study floodplain fisheries, and recruitment of *Puntius sophore* in dry season water bodies in north-central Bangladesh (Halls *et al.* 1999 & 2001). Most of these models use hydrological and life-history parameters as inputs and show that fish production is strongly dependent on recruitment. However, influence of external abiotic factors such as climate and occurrence of different characteristics of habitats within the same floodplain make it necessary for these models to be adapted to local hydro-climatic conditions of the floodplains.

Although a relationship between fish catch and water flow has been reported for the Lower Shire Floodplain (Ratcliff 1972, Hastings 1973, Tweddle *et al.* 1979, Tweddle *et al.* 1994), no quantitative evidence has been presented to show the seasonal dynamics of this relationship in combination with the life-history parameters of the key commercial species. This study has demonstrated that besides the flood regime, other environmental factors (e.g. climate and habitat characteristics) (Chapter 2 and 3) are equally important and do have an impact on the breeding (Chapter 4), juvenile recruitment and growth (Chapter 5), as well as fish catches (Chapter 6) in the floodplain. However, the combined effect of the hydro-climatic and habitat characteristics on the biological and production traits of the fish is not known. In order to find this “missing link”, this part of the work seeks to develop a new predictive hydro-climatic-fisheries model. The aim is to develop a simple model that would predict the effects of various hydrological, climatic and habitat scenarios on the fisheries of the floodplain. Special focus was given to determining the relationship between life-history aspects of the two major fish species (*O. mossambicus* and *C. gariepinus*) and the abiotic factors of climate, hydrology and habitat. Finally, the aim was to identify the key regulatory mechanisms of the life-history traits of these species and provide an essential adaptive management tool for the fisheries.

7.2 Materials and methods

Overview of the structure and functional make-up of the model

The model was based on the conceptual hierarchical framework of the floodplain fisheries ecosystems (Figure 1.3, Chapter 1). The hierarchy of factors interacting with and affecting fish communities in a floodplain were broken into (1) climatic, (2) habitat and (3) hydrological. The model relationships were derived from existing information and findings from this study. The relationship between climate, flood regime, habitat characteristics as well as biological and production parameters of the fish in the Lower shire Floodplain has been demonstrated (Chapters 2, 3, 4, 5 and 6).

It is well established that climate has an impact on watershed processes, the hydrological cycle and subsequent influence on ecosystem production of the floodplain through the flood pulse (Lotspeich 1980, Junk *et al.* 1989, Gordon *et al.* 1992, Cramer *et al.* 1999, Aber & Freuder 2000, Pringle 2001, Sarch & Allison 2000). As an aquatic-terrestrial transitional zone, the floodplain also affects various aspects of the local ecology, by changing the values of many variables such as humidity, temperature and sedimentation (Ranwell 1974, Kolasa & Zalewski 1995).

Construction of correlation models

Determination of causal relationship between predictor (climatic, hydrological, habitat) and response variables (spawning periodicity, seasonal condition factor, recruitment) was done using multiple regression analysis according to Lieth (1975, 1976) and Fong *et al.* (1997). The analysis was based on the notion of variable-focused ecosystems analysis (Downing 1991), where a few characteristics of ecosystems that are considered to be of great theoretical or practical interest are identified through a rigorous correlation analysis with biological variables of interest. Sets of climatic, hydrological (Chapter 2) and habitat (Chapter 3) characteristics were paired with the following biological variables: spawning periodicity (Chapter 4), condition factor, recruitment (Chapter 5) of the two fish species (*O. mossambicus* and *C. gariepinus*), and catches of all exploited species in the Lower

Shire Floodplain (Chapter 6) in order to determine the relationship or relationships between them.

Juxtaposition of data and theory

Statistical analyses were followed by synthesis. The correlations among predictor and response variables were used to explore possible relationships and assess how far the correlations confirmed or refined the hypothesis about interaction between the floodplain fishes and ecosystems. A comparison of parameters that were identifiable as characterising the biological variables of the two major species were combined in a theoretical framework to provide some quantitative description of the structure and function of the fish population ecology.

Predictor variables: climatic

Daily mean values for eight climatic parameters, recorded at the Makhanga Meteorological Station in the Lower Shire Floodplain (Chapter 2, see Table 7.1), were used. These parameters reflect the water budget as input (rainfall, thunder days, cloud cover), output (evaporation, potential evaporation, evapotranspiration, sunshine) and regulatory mechanism of water gain and loss (relative humidity, air temperature, wind speed). The Malawi Department of Meteorological Services provided climate data covering the period 1960/61 to 1989/90 and 1995/96 to 1999/2000 (35 years).

Predictor variables: hydrological

Daily values for eight hydrological parameters, recorded at Chiromo Gauging Station in the Lower Shire Floodplain (Chapter 2, see Table 7.1) were used to calculate the hydrological variables. These were the absolute change in water level (daily mean and minimum water level), the rate of change in water level (*Slope*, sum of daily water fluctuation, *SWF*, and cumulative sum of daily water fluctuation, *CSWF*), timing of flooding (level-above-bankfull, *Lv-BF*), and duration of inundation (river stage or *RS*). The Hydrology Division of the Malawi Department of Water Resources kindly provided data covering the period between 1980/81 and 1999/2000).

Predictor variables: habitat characteristics

Mean monthly values of selected habitat characteristics (Table 7.1) were used from Chapter 3.

Dependent (response) variables

Biological variables (GSI and condition factor) of two species (*O. mossambicus* and *C. gariepinus*) as well as production indices (juvenile recruitment-fish.m^{-2}, fish catches-CPUE) were used as response variables (Table 7.1). Due to the seasonal fluctuation of water levels in the floodplain, CPUE was used as a measure of density because of the dilution/concentration effects of varying water levels. Biological factors and indices of recruitment and catch were obtained from Chapters 4, 5 and 6, respectively.

Table 7.1 Parameters used for the development of the predictive hydro-climatic fishery model. The climate and hydrology data are daily mean values; the habitat, biological and production characteristics are monthly mean values

Response variables	**Predictor variables**		
Biological & Production (Chapters 4, 5 & 6)	**Climatic (daily mean) (Chapter 2)**	**Hydrologic (daily mean) (Chapter 2)**	**Habitat (Chapter 3)**
Gonadosomatic index (GSI)	Rainfall (mm)	Water level (m)	Water depth (m)
Condition factor (CF)	Relative humidity (%)	Water level above bankfull (m)	Total dissolved solids (mg.l^{-1})
Relative abundance of juveniles (fish.m^{-2})	Surface air temperature (ºC)	Water temperature (ºC)	Conductivity (µS.cm^{-1})
Relative density (CPUE) (kg.day^{-1}.gear^{-1})	Evaporation (E) (mm)	Slope of daily water fluctuation	Water transparency (Secchi disk visibility) (cm)
	Evapotranspiration (ET) (mm)	Sum of daily water fluctuation (m)	pH
	Potential evapotranspiration (PE) (mm)	River stage (days)	Alkalinity (mg.l^{-1})
	Sunshine (hours)		Hardness (mg.l^{-1})
	Cloud cover (octas)		Phosphate (mg.l^{-1})
	Thunder (days)		Nitrate (mg.l^{-1})
	Wind (m.sec^{-1})		Dissolved oxygen (DO) (mg.l^{-1})
			Water temperature (°C)

Statistical analyses

Regression analysis was used to estimate the correlation between dependent (biological and production parameters) and independent (climatic, hydrological and habitat parameters) variables using StatisticaTH computer software. The basic model followed that outlined by Neter *et al.* (1979):

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \cdots + \beta_{p-1} X_{i,p-1} \qquad \text{(Equation 7.1)}$$

where Y_i is the response in the $i\,th$ observation, $X_{i1}, X_{i2}, X_{i,p-1}$ are values of the independent variables in the $i\,th$ observation, $\beta_0, \beta_1, \cdots, \beta_{p-1}$ are parameters and i ranges from 1 to n.

The analysis consisted of the following two stages. Firstly, Pearson product-moment correlations (Zar 1984) for pairs of dependent and independent variables were obtained in order to explore the relationship between various pairs of dependent and independent variables. Secondly, forward stepwise multiple regression analysis was conducted to determine the relationship between various suites of independent variables and a single dependent variable in order to arrive at a set of useful variables (Shumway & Stoffer 1999) to be used to construct various predictive models. In this type of regression analysis redundant predictors are removed to yield a final model that accounts for most of the variance (Roy 1958, 1967). In both regression analyses, analysis of variance (ANOVA) was used to test the best-fitting curve (Bliss 1970, Zar 1984), assuming that residuals were independently and normally distributed, or that least squares provided an unbiased fit even if those assumptions were not met (Batschelet 1981).

Sensitivity analysis

There are two methods of establishing the credibility of a model. Firstly, sensitivity analysis is conducted, and secondly model validation comparisons are performed (Kastner-Maresh & Mooney 1994, Fong *et al.* 1997). Sensitivity analysis is the process of making systematic and incremental changes in the portion of the model individually and comparing the results against another simulation in which all model variables are identical except for the single sensitivity test parameter (Miller *et al.* 1973, Fong *et al.* 1997). The process identifies the model parameters, structure, empirically derived inputs information and initial conditions that cause the greatest change in the model predictions (Miller 1979). The validation process of a model is similar to the normal scientific process where hypotheses are subjected to more rigorous tests (Popper 1962, cited by

Fong *et al.* 1997). Thus a numerical model is nothing more than a series of hypotheses set into mathematical terms and in validation experiments, the model is altered to simulate various conditions that reflect different natural systems with independent databases and predictions are compared to field observations (Caswell 1976, Fong *et al.* 1997). In this study, sensitivity analysis was used to test the credibility of the model.

The sensitivity analysis was conducted in three stages using modified procedures as outlined by Fong *et al.* (1997). First, the predictive models were tested for sensitivity to low levels (baseline) of the three sets of predictor variables (climatic, hydrologic, habitat characteristics) (Table 7.2). Second, the predictive models were run under conditions where the three sets of predictor variables were reduced by 10% from the baseline levels. Third, the predictive models were run under conditions where the three sets of predictor variables were increased by 10% from the maximum levels (Table 7.2).

Table 7.2 Values of baseline, +10% and –10% of predictor variables used in the sensitivity analyses. Climate data are daily means; water levels and water quality are monthly mean values.

Predictor variable	**Baseline**	**10% below baseline**	**10% above maximum**
Rainfall (mm)	4.5	4.05	201.4
Relative humidity (%)	51	45.9	86.9
Air temperature (ºC)	20.2	18.18	31.24
Water level (m)	3.68	3.31	6.58
Wind speed (m.sec^{-1})	2.4	2.0	6.05
Cloud cover (hours)	2.1	1.89	6.49
Thunder days (days)	0	0	19.8
CSWF (m) (monthly)	-6.69	-6.02	97.03
Level above bankfull (m)	-1.18	-1.06	1.02
Water temperature (ºC)	20.7	18.59	30.89
pH	6.83	6.15	8.91
Dissolved oxygen (mg.l^{-1})	1.33	1.2	8.79

The baseline conditions were assumed to be the minimum levels (average monthly minimum) of the three independent variables, while quantification of sensitivity to reduced and increased climatic, hydrologic and habitat conditions by 10% below baseline or 10% above maximum was assumed to simulate situations under reduced or increased water levels as well as extreme climatic conditions, as these in return will affect physicochemical characteristics of the habitat. In all three scenarios of sensitivity analyses, predictor variables were modelled with a sinusoidal curve using periodic regression in order to take into account the seasonal variation of these predictor variables (Fong *et al.* 1997).

In order to assess the overall changes of response variables, as a result of the sensitivity to either 10% above or below the baseline, over the entire year, a measure of relative change (%) modified from (Fong *et al.* 1997) was used as follows:

$$relative\ change\ (\%) = \frac{(P_x - simulatedP_x)}{simulatedP_x}\ x\ 100 \qquad \text{(Equation 7.2)}$$

where $simulatedP_x$ is an average of monthly predicted levels of biological or production x in the simulated model, and P_x is the average of monthly observed levels of biological or production x when the model parameters were by either increased or reduced by 10%. Although the relative change calculated in this way does not show the seasonal pattern, it is a quick management tool since none of the models shifted the timing and seasonal pattern, but rather the mean (b) and amplitude (m).

Seasonal analysis of biological and production parameters

Mathematical and periodic regression techniques were used to assess and predict the seasonality of biological and production parameters of the fish, as well as the hydrological, climatic and habitat characteristics. This was based on the assumption that if observed quantity of (*Y*) (i.e. early juvenile density) is presumed to be dependent on cyclic (temporal) variable (*X*) (e.g. time of the year e.g. months), then where temporal waves of recruitment exist, diffusion or dispersal will always cause a positive net flux of juveniles from the peaks to the troughs of the waves. Intuitively, the variation of recruitment over months will be some function of the rate of change of the recruitment, the wave amplitude and frequency. Working with competitive exclusion in populations, Savill & Hogeweg (1999) used the following equation that captured the local spatial behaviour of oscillatory dynamics:

$$r(x,t) = \bar{r} + A_r \cos(kx - \omega t) \qquad \text{(Equation 7.3)}$$

where $\bar{r}$ is the mean value of r, A_r the amplitude of the oscillations, k the wave number, ω the temporal frequency, x and t are special and temporal variables. Savill & Hogeweg (1999)'s equation can be substituted by a simpler cosine regression according to Bliss (1970) and Bell *et al.* (1995) as follows:

$$Y = M + A\cos([R't_i] - \partial) \qquad \text{(Equation 7.4)}$$

where Y is the dependent variable, M is the intercept, A is the amplitude (or slope), $R't_i$ is the angular transformation of independent time variable (time of the year) and ∂ is the phase lag. The angular transformation, amplitude and phase lag were calculated according to methods outlined in Bell *et al.* (1995) (see details in Chapter 2) as follows:

$$Y = b + m(\cos(RX + \partial)) \qquad \text{(Equation 7.5)}$$

where RX is the angular transformed independent X variable (month of year: MOY), b is an intercept (or predicted mean), m is the slope (or amplitude), and ∂ is the phase lag. Transformation of **X** variable into circular variables (RMOY) was done by multiplying MOY (0-12) by 2π/12 to obtain an equivalent radian measure (Bell 1999). The results of the analyses were presented as polar plot (azimuthal references, with angle) of periodic regression of water level and biological variables.

7.3 Results

Correlations

Table 7.3 shows the relationship between climatic variables and biological and production parameters of fish in the floodplain. Relative humidity, evapotranspiration, wind speed, cloud cover and sunshine were highly correlated with production parameters (juvenile recruitment and relative abundance (CPUE)) ($0.64 \leq r^2 \geq 0.77$, $p \leq 0.05$), while rainfall, air temperature, cloud cover and thunder days were highly correlated with biological parameters (GSI and CF) ($0.60 \leq r^2 \geq 0.85$, $p \leq 0.05$). Since cloud cover may sometimes be a sign of thunder-storm, hence rainfall, cloud cover and thunder days do affect the fish in a similar manner. Similarly, sunshine increases evaporation, which is enhanced by wind speed, which in turn lowers the relative humidity, hence the negative correlation between production parameters and relative humidity (Table 7.3).

The relationships between hydrological variables and biological and production parameters are shown in Table 7.4. Rate of change in water level as measured in daily water fluctuation *SWF*, cumulative sum of daily fluctuation (*CSWF*) and *Slope*, were highly correlated with biological parameters of fish ($0.64 \leq r^2 \geq 0.85$, $p \leq 0.05$), while absolute change in water level in terms of daily mean, maximum and minimum levels, as well as timing of flooding (measured as level of water above the bankfull level (Lv-BF)), was highly correlated with production parameters ($0.59 \leq r^2 \geq 0.71$, $p \leq 0.05$). The significant effect of the rate of change in water level on the biological parameters (GSI, CF), might signify the importance of relative change, as opposed to absolute change, in water level as a cue for breeding in fish.

Table 7.5 shows data depicting the relationship between habitat characteristics and biological and production parameters for the fish. Water temperature and nitrate levels were highly correlated with biological variables ($0.62 \leq r^2 \geq 0.74$, $p \leq 0.05$), while DO, water temperature, TDS, conductivity, pH and alkalinity were highly correlated with production parameters ($0.58 \leq r^2 \geq 0.80$, $p \leq 0.05$). The correlation between juvenile density and TDS, conductivity, pH and alkalinity was positive, indicating a direct relationship between inputs of ions in the floodplain with the emergence of juvenile fish. However, the correlation between CPUE and both DO and pH was negative, but positive with water temperature. Apart from indicating that abundance of fish was highest at the time of low DO and pH, the data also confirms the basic ecological inverse relationship between water temperature and DO.

Table 7.3 Summary of Pearson product-moment correlation coefficients for pairs of dependent and independent variables. Dependent variables are fish biological and production indices. Independent variables are climatic elements. The data is presented as GSI =gonadosomatic index, CF = Condition factor, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}) RH = relative humidity (%), Rain = rainfall (mm), Air Temp = air temperature (ºC), PE = potential evaporation (mm), ET = evaporation (mm), ETP = evapotranspiration (mm), WSpd = wind speed (m.sec^{-1}), Sun = sunshine (hours), cloud = cloud cover (hours), Thunder = thunder days (days),

Dependent variables (Fish biological/production)	**Independent variables** (climatic)									
	RH	Rain	Air Temp	PE	ET	ETP	WSpd	Sun	Cloud	Thunder
GSI of *C. gariepinus*	0.19	0.85***	0.57	0.51	0.24	0.49	0.05	-0.40	0.65*	0.87***
GSI of *O. mossambicus*	0.05	0.60*	0.51	0.51	0.33	0.50	0.15	-0.25	0.51	0.66**
CF of *C. gariepinus*	0.32	0.85***	0.67***	0.57	0.21	0.54	-0.04	-0.39	0.74**	0.88***
CF of *O. mossambicus*	0.06	-0.33	-0.64*	-0.62*	-0.41	-0.60*	-0.25	-0.20	-0.25	-0.41
Juveniles abundance (fish.haul^{-1}) (all species)	-0.73**	-0.37	0.27	0.42	0.62*	0.46	0.74**	0.67**	-0.46	-0.15
Juvenile abundance (fish.haul^{-1}) (Cichlids)	-0.64*	-0.23	0.35	0.49	0.63*	0.52	0.70**	0.55	0.29	0.02
Juvenile abundance (fish.haul^{-1}) (catfish)	-0.77**	0.49	0.08	0.23	0.50	0.27	0.67*	0.72**	-0.71**	-0.42
CPUE (density) (kg.gear^{-1}.day^{-1})	0.69**	0.46	0.07	-0.13	-0.40	-0.15	-0.57	-0.52	0.58*	0.38

Table 7.4 Summary of Pearson product-moment correlation coefficients for pairs of dependent and independent variables. Dependent variables are fish biological and production indices. Independent variables are hydrologic parameters. The data is presented as GSI =gonadosomatic index, CF = Condition factor, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}) SWF = sum of daily water fluctuation (m), CSWF = cumulative sum of daily water fluctuation, RS = river stage (days), Lv-BF = level above bankfull, Lv-1 = water level in current year, Lv-2 = level a year before, Lv-3 = level two years before.

Dependent variables (Fish biological/production)	**Independent variables (hydrologic)**										
	Mean	Max.	Min.	SWF	CSWF	RS	Lv-BF	Slope	Lv-1	Lv-2	Lv-3
GSI of *C. gariepinus*	0.11	0.24	-0.07	-0.13	-0.80**	-0.22	0.05	0.85***	-0.38	-0.35	-0.35
GSI of *O. mossambicus*	0.15	0.18	0.06	-0.15	-0.64*	-0.38	0.08	0.62*	-0.32	-0.32	-0.32
CF of *C. gariepinus*	0.36	0.49	0.17	0.23	-0.75**	0.15	0.31	0.65*	-0.05	-0.05	-0.05
CF of *O. mossambicus*	-0.31	-0.42	-0.21	-0.47	0.21	-0.44	-0.22	-0.13	-0.11	-0.11	-0.11
Juvenile abundance (fish.haul^{-1}) (all species)	-0.68**	-0.63*	-0.60*	-0.45	0.01	-0.49	-0.71***	-0.08	-0.46	-0.46	-0.46
Juvenile abundance (fish.haul^{-1}) (Cichlids)	-0.64*	-0.59*	-0.60*	-0.46	-0.18	-0.50	-0.68**	0.01	-0.49	-0.49	-0.49
Juvenile abundance (fish.haul^{-1}) (catfish)	-0.50	-0.54	-0.40	-0.28	0.49	-0.19	-0.54	-0.16	-0.32	-0.32	0.32
CPUE (density) (kg.gear^{-1}.day^{-1})	-0.50	0.54	0.39	0.12	-0.44	0.03	0.56	0.14	0.52	0.52	0.52

Table 7.5 Summary of Pearson product-moment correlation coefficients for pairs of dependent and independent variables. Dependent variables are fish biological and production indices. Independent variables are habitat physicochemical parameters. The data is presented as GSI =gonadosomatic index, CF = Condition factor, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}), DO = dissolved oxygen (mg.l^{-1}), Wtemp = water temperature (ºC), TDS = total dissolved solids (mg.l^{-1}), cond = conductivity (Sµ.cm^{-1}), SDV = water transparency (cm), Alk = alkalinity, Hard = hardnes, Phos = phosphorus, Nitr = nitrate. The asterisks denote the level of significance, wher * = 5%, ** = 1%, *** = <0.01%.

Dependent variables (Fish biological/production)	**Independent variables (habitat physicochemical)**										
	DO	Wtemp	Depth	TDS	Cond	SDV	pH	Alk	Hard	Phos	Nitr
GSI of *C. gariepinus*	0.09	0.62*	-0.22	-0.16	-0.01	-0.14	0.08	-0.21	0.31	0.14	-0.40
GSI of *O. mossambicus*	-0.29	0.46	0.13	-0.08	0.22	-0.30	0.27	-0.11	0.13	-0.13	-0.47
CF of *C. gariepinus*	-0.02	0.74**	0.17	-0.12	0.01	-0.17	-0.08	-0.40	0.20	0.08	-0.69**
CF of *O. mossambicus*	-0.15	-0.34	-0.36	0.02	-0.13	0.18	-0.002	-0.26	-0.27	-0.35	0.55
Juvenile abundance (fish.haul^{-1}) (all species)	0.19	-0.24	-0.25	0.58*	0.85***	-0.39	0.64*	0.75***	0.55	0.23	0.13
Juvenile abundance (fish.haul^{-1}) (Cichlids)	0.08	-0.06	-0.24	0.64*	0.91***	-0.38	0.63*	0.75**	0.58	0.15	-0.03
Juvenile abundance (fish.haul^{-1}) (catfish)	0.60*	-0.61	-0.24	-0.05	0.07	-0.21	0.49	0.21	0.08	0.24	0.18
CPUE (density) (kg.gear^{-1}.day^{-1})	-0.80**	0.63*	0.09	0.14	-0.06	0.004	-0.65*	-0.24	-0.28	-0.47	0.14

Predictive Hydro-climatic-fisheries model

Table 7.6 shows the predictive models for the biological dynamics of the floodplain in which hydro-climatic and habitat factors are predictor variables. The relationships identified in the Pearson product-moments correlations in Table 7.3-7.5 also emerge in the predictive models. Generally, the model predicted the biological and production parameters fairly accurately ($0.53 \leq r^2 \geq 0.98$, $p \leq 0.05$). However, the model appeared to predict production parameters more accurately ($0.75 \leq r^2 \geq 0.98$, $p \leq 0.01$) than biological parameters ($0.53 \leq r^2 \geq 0.98$, $p \leq 0.05$). Climate has a significant impact on the biological and production parameters of the fish ($0.13 \leq r^2 \geq 0.75$, $p \leq 0.001$). Flood timing and duration of floodplain inundation had significant effects ($0.04 \leq r^2 \geq 0.85$, $p \leq 0.001$) on the fish, likewise, nutrient and physico-chemical status of the habitat also had a significant impact ($0.02 \leq r^2 \geq 0.41$, $p \leq 0.001$) on the fish. It is important to note that water level in the floodplain during the previous year as well as its seasonal effect (cos(RMOY)) had some impact on fish catches (CPUE) (Table 7.6).

Sensitivity analysis of the models

Table 7.7 show the results of the sensitivity analysis. Applying baseline conditions increased the condition factor (CF) of *O. mossambicus* by 92.8% and the CPUE by 35.1%. Further reduction of the baseline condition by 10% reduced the predicted recruitment to 72.8% while increasing CPUE by 13.5%. A 10% increase of maximum levels of the three predictor variables resulted in failed spawning in *C. gariepinus* and a reduction by 29.5% in *O. mossambicus*, CF reduced to 41.6% in *C. gariepinus* but increased by 2.1% in *O. mossambicus*, respectively, with subsequent failure in recruitment and reduction in CPUE to 42%.

Table 7.6 Relationship between biological and production factors of fish ad climatic, hydrological and habitat characteristics of the Lower Shire Floodplain. The data is presented as GSI =gonadosomatic index, CF = Condition factor, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}), DO = dissolved oxygen (mg.l^{-1}), Wtemp = water temperature (ºC), TDS = total dissolved solids (mg.l^{-1}), cond = conductivity (Sµ.cm^{-1}), SDV = water transparency (cm), Alk = alkalinity, Hard = hardnes, Phos = phosphorus , Nitr = nitrate, RH = relative humidity (%), Rain = rainfall (mm), Air Temp = air temperature (ºC), PE = potential evaporation (mm), ET = evaporation (mm), ETP = evapotranspiration (mm), WSpd = wind speed (m.sec^{-1}), Sun = sunshine (hours), cloud = cloud cover (hours), Thunder = thunder days (days). The peak and amplitudes are calculated from Equation 8.3), r^2 = coefficient of determination, *p*=level of significance. The asterisks denote the level of significance, wher * = 5%, ** = 1%, *** = <0.01%.

Parameter	**Predictive equation**	r^2	*p*
GSI of *C. gariepinus*	$Y = 40.57 + 0.54\text{Thunder} + 61.2\text{Slope} + 0.11\text{SDV} + 0.76\text{DO} + 0.56\text{nitr} + 0.001\text{TDS} – 5.09\text{pH} – 2.5\text{Lv}_{-2}$ $r^2 = 0.75^{***}$ $r^2 = 0.07^{***}$ $r^2 = 0.20^{*}$	0.90	0.0001
GSI of *O. mossambicus*	$Y = -41.99 + 0.001\text{Rain} + 5.41\text{pH} – 0.96\text{Phos} + 2.28\text{Lv-BF} + 0.21\ \text{Wtemp}$ $r^2 = 0.44^{**}$ $r^2 = 0.41^{*}$	0.85	0.03
CF of *C. gariepinus*	$Y = 0.93 + 0.003\text{Rain} - 0.05\text{nitr}$ $r^2 = 0.73^{***}$ $r^2 = 0.10^{*}$	0.83	0.0003
CF of *O. mossambicus*	$Y = 6.33 - 0.15\text{Airtemp} – 0.07\text{RS} + 0.70\sin(\text{RMOY}) +0.36\text{Phos} – 0.0002\text{Cond} + 0.01\text{SDV}$ $r^2 = 0.41^{*}$ $r^2 = 0.41^{**}$ $r^2 = 0.09^{*}$	0.98	0.0007
Juvenile abundance (fish.haul^{-1}) (all species)	$Y = 1998.44 + 0.33\text{Cond} – 26.94\text{RH} + 31.38\text{nitr} + 148.27\text{Lv-BF} – 3.79\text{SDV}$ $r^2 = 0.66^{***}$ $r^2 = 0.25^{***}$ $r^2 = 0.04^{*}$	0.98	0.00003
Juvenile abundance (fish.haul^{-1}) (Cichlids)	$Y = -327.13 + 0.29\text{Cond} + 103.6\text{WindSpd} – 13.73\text{nitr} – 25.78\text{Phos}$ $r^2 = 0.82^{***}$ $r^2 = 0.13^{***}$	0.98	0.00005
Juvenile abundance (fish.haul^{-1}) (catfish)	$Y = 123.53 + 23.73\text{WindSpd} – 6.94\text{Wtemp} + 22.37\text{Lv-BF}$ $r^2 = 0.45^{**}$ $r^2 = 0.22^{*}$	0.75	0.008
CPUE (density) (kg.gear^{-1}.day^{-1})	$Y = 7.84 – 0.18\text{DO} + 0.01\text{Rain} + 0.07\text{nitr} – 0.79\text{pH} – 0.84\text{Lv-BF} – 0.41\cos(\text{RMOY}) + 0.40\text{Lv}_{-2}$ $r^2 = 0.45^{**}$ $r^2 = 0.22^{*}$	0.98	0.002

Note : RMOY = MOY(2π/12) (i.e., MOY transformed to radians of year

The sensitivity analysis showed that *C. gariepinus* is likely to be more sensitive to changes in environmental factors, especially reduction in water level and other predictor variables than *O. mossambicus*. While CPUE appeared to be less sensitive to changes in environmental factors, especially reduction in water level and other predictor variables, than recruitment, both these parameters were detrimentally affected by a 10% increase of the level of predictor variables above maximum. Clearly, increasing (+10% of maximum) and decreasing (baseline or –10%) water level and climatic conditions seems to be detrimental to the biological parameters of the two fish species.

Table 7.7 Sensitivity analysis for biological and production parameters with changes in climatic, hydrologic and habitat characteristics in the Lower Shire Floodplain. The levels are monthly averages. Observed levels are mean ± standard deviation (SD) Numbers in parentheses are relative percentages of the modelled parameter relative to the observed parameters. Baseline levels are based on monthly minimum values for climatic, hydrologic and habitat characteristics. GSI-CG = gonadosomatic index for *Clarias gariepinus*, GSI-OM = gonadosomatic index for *Oreochromis mossambicus*, CF-CG = condition factor for *Clarias gariepinus*, CF-OM = condition factor for *Oreochromis mossambicus*, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}),

Parameter of change	**GSI-CG**	**GSI-OM**	**CF-CG**	**CF-OM**	**Recruitment (fish.haul^{-1})**	**CPUE (kg.gear^{-1}.day^{-1})**
Observed level	2.95 ±0.88	2.24 ±1.13	1.02 ±0.42	1.95 ±0.24	274.64 ±205.57	3.93 ±1.41
Modelled level	2.57 (12.9)	2.14 (4.5)	1.02 (0)	1.88 (3.6)	371.13 (-35.1)	3.95 (-0.5)
Baseline level	0.81 (72.5)	1.31 (41.5)	0.82 (19.03)	3.76 (-62.5)	-171.52 (162.5)	5.31 (-35.1)
Level 10% below baseline	4.87 (-65.1)	-4.48 (300)	0.84 (17.74)	4.10 (-110.3)	74.83 (72.8)	4.46 (-13.5)
Level 10% above maximum	-1.68 (156.9)	1.58 (29.5)	1.43 (-40.48)	1.99 (-2.1)	-529.83 (292.9)	2.28 (42.0)

Seasonality of biological and production parameters of the fish

The periodic regression models for both depended and independent variables used in the model are shown in Table 7.8. It is clear that climatic parameters as well as habitat are significantly seasonal ($0.77 \leq r^2 \geq 0.85$, $p \leq 0.0001$) and ($0.51 \leq r^2 \geq 0.75$, $0.04 \geq p \leq 0.001$), respectively (Table 7.9). Periodic regression models of water level and biological parameters are shown in Table 7.9. The models show amplitude and phase lag. The amplitude (i.e. a form of standard deviation in normal statistics) is the maximum positive or negative departure of predicted Y from the mesor (a form of average in normal statistics). The phase lag is the position of the peak in degrees (°), and when these degrees are transformed to month-of-the-year (MOY), the output is the time of year (month) when peak or maximum occurrence of the variable (e.g. GSI) is recorded. Significant seasonal variation is evident in juvenile recruitment (r^2 = 0.55, $p \leq 0.05$), GSI ($0.45 \leq r^2 \geq 0.63$, $\leq p \leq 0.01$) and condition factors ($0.32 \leq r^2 \geq 0.76$, $0.10 \leq p \leq 0.01$) of both species (Table 7.9).

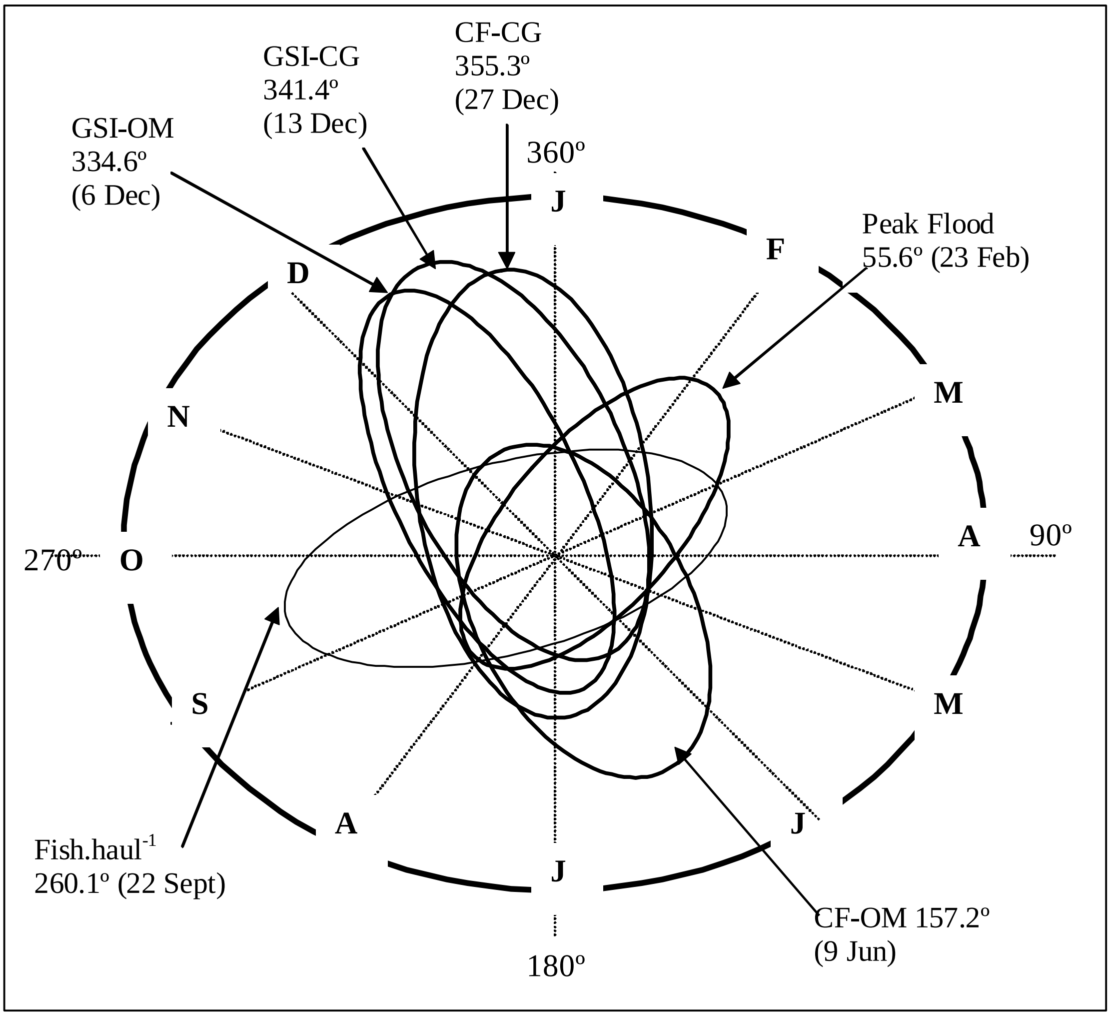
Table 7.8 Seasonal and cycling climatical, hydrological, habitat, biological and production characteristics of events in the Lower Shire Floodplain. GSI-CG = gonadosomatic index for *Clarias gariepinus*, GSI-OM = gonadosomatic index for *Oreochromis mossambicus*, CF-CG = condition factor for *Clarias gariepinus*, CF-OM = condition factor for *Oreochromis mossambicus*, CPUE = catch per unit effort (kg.gear^{-1}.day^{-1}). RMOY = Radian Month of the year. r^2 = coefficient of determination, p=level of significance.

Parameter	**Predictive model**	r^2	p
Water level (m)	Y = 4.8 + 0.81sin(RMOY) + 0.09cos(RMOY)	0.75	0.0002
Air temperature (°C)	Y = 24.97 – 1.67sin(RMOY) + 3.33cos(RMOY)	0.85	0.0002
Relative humidity (%)	Y = 68.58 + 11.15sin(RMOY) + 4.47cos(RMOY)	0.84	0.0003
Rainfall (mm)	Y = 63.71 + 4.29sin(RMOY) + 77.51cos(RMOY)	0.77	0.001
Cloud cover (hours)	Y = 4.06 + 0.68sin(RMOY) + 1.42cos(RMOY)	0.83	0.0003
Water temperature (°C)	Y = 25.03 + 1.14sin(RMOY) + 3.51cos(RMOY)	0.94	0.00001
pH	Y = 7.45 – 0.52sin(RMOY) – 0.14cos(RMOY)	0.83	0.0003
Dissolved oxygen (mg.l^{-1})	Y = 4.76 – 2.05sin(RMOY) – 1.04cos(RMOY)	0.51	0.04
GSI for *C. gariepinus*	Y = 2.95 – 1.36sin(RMOY) + 4.05cos(RMOY)	0.63	0.01
GSI for *O. mossambicus*	Y = – 2.24 – 0.55sin(RMOY) + 1.16cos(RMOY)	0.45	0.06
CF for *C. gariepinus*	Y = 1.02 – 0.03sin(RMOY) + 0.32cos(RMOY)	0.72	0.003
CF for *O. mossambicus*	Y = 1.95 + 0.22sin(RMOY) – 0.52cos(RMOY)	0.32	0.17
Recruitment (fish.haul^{-1})	Y = 274.64 – 294.11sin(RMOY) – 66.42cos(RMOY)	0.43	0.08
CPUE (kg.gear^{-1}.day^{-1})	Y = 3.93 + 0.57sin(RMOY) + 0.37cos(RMOY)	0.63	0.01

Table 7.9 Seasonal and cyclic relationship between water level (m), spawning seasons, juvenile recruitment, Condition Factor of *Oreochromis mossambicus* and *Clarias gariepinus* with sequential months of the year in the Lower Shire Floodplain. Peak (phase lag), amplitudes and time of the year the peak occurs are calculated from cosine regression of the form given in Equation 6, r^2 = coefficient of determination, p = level of significance, (ns=not significant; * = 0.05; ** = 0.01; *** = 0.001).

Parameter	**Amplitude**	**Phase lag**	**Peak time of the year**	**Quarterly season**	r^2	p
Water level (m.a.s.l.)	0.81	55.6°	23 Feb	Mid-Qrt3	0.67	0.0025
CF – *Oreochromis mossambicus*	0.56	157.2°	9 June	Late-Qrt4	0.32	0.1761
Recruitment (fish.haul^{-1})	201.3	260.1°	22 Sept	Late-Qrt1	0.55	0.0272
GSI – *Oreochromis mossambicus*	1.29	334.6°	6 Dec	Late-Qrt2	0.45	0.066
GSI – *Clarias gariepinus*	4.27	341.4°	13 Dec	Late-Qrt2	0.63	0.0116
CF – *Clarias gariepinus*	0.35	355.3°	27 Dec	Late-Qrt2	0.76	0.0006

Figure 7.1 shows a polar plot (azimuthal references, with angle) of the phase lag (peaks) of biological variables from Table 7.9. The date of peak occurrence of an event (e.g. recruitment) is represented by the angle (α) (read clockwise), and the ellipse representing the regression lines (or fitted Y). It is clear from Figure 7.1 that the peak flood is predicted to take place or occur on 23 rd February (middle of Qrt3), and the peak in the condition factor of *O. mossambicus* was predicted to occur on 9 th June (end of Qrt4).



β₁sin(RMOY)

Figure 7.1 Polar plot of periodic regression of flood regime, spawning seasons (Gonadosomatic index), juvenile recruitment, and seasonal fitness (condition factor) of *Oreochromis mossambicus* and *Clarias gariepinus* in the Lower Shire Floodplain. Recruitment is relative abundance for juveniles in the littoral zones for the period July 1998-June 2000. The large circle represents one year with 12 month of the year (MOY) marked J-D (January to December). Angular presentation of MOY, and lag-phase are marked on the graph. Lag-phase is the angle of the date of peak of event calculated by periodic regression (Table 7.4), both lag-phase and precise date are presented in the graph, regression lines are shown as circles inside the annual circle.

Subsequently, the peak spawning seasons (as measured by GSI) of *O. mossambicus* and *C. gariepinus* are predicted to occur on 6 th December and 13 th December (end of Qrt2), respectively (Table 7.9). The peak condition factor of *C. gariepinus* was also predicted to occur in December at the end of Qrt2 (Table 7.9 and Fig. 7.1). The predicted format of events is the same as those observed during this study (Chapters 3 – 6). For example, GSI for *O. mossambicus* peaks between October and February, while that of *C. gariepinus* occurs between October and December (Fig. 4.5, Chapter 4. The polar plot simply confirms the notion that the flood-pulse drives the life-history clock in the floodplain, so to speak. (Note: The use of specific dates in this interpretation of the polar plot only serves to illustrate the capabilities of the model in predicting the sequence of events in the 4 quarterly hydro-climatic seasons).

7.4 Discussion

General trends

Although climatic, hydrological and habitat parameters were individually significantly correlated with biological and production indices of the fish, the best predictive models emerged where a combination of the three predictor (independent) variables were used. The parameters from the forward stepwise multiple regression models indicate the direction of the effect of each of the predictor variables. The negative coefficient for the predictor variable generally indicates negative effect on the dependent variable while a positive coefficient indicates a positive effect on dependent variable. For example, the longer the inundation of the floodplain (RS), the higher the probability that condition factor for *O. mossambicus* will be low, conversely, the earlier the beginning of the rainfall, the greater the probability of *C. gariepinus* improving its condition (Table 7.6).

Spawning periodicity

The strong and positive correlation between spawning periodicity (based on the monthly GSI) with rainfall and timing of the flood for both *C. gariepinus* and *O. mossambicus* (Tables 7.3-7.6) signifies the complex link among climate, hydrology and biology of the fish in the Lower Shire Floodplain. Apart from bringing water into the floodplain, local rainfall and the commencement of flooding may also act as spawning cues for both species. Young *et al.* (2000) called this the “biological trigger” or “spawning flows”.

Bruton (1979) reported that in Lake Sibaya, the stimulus for spawning of *C. gariepinus* appeared to be associated with a rise in water level and inundation of marginal areas, either as a result of direct rainfall or the inflow of water from an upstream source. In order for *O. mossambicus* to breed, temperatures of at least 20ºC must be attained. However, other factors such as rainy season and accessibility of certain spawning grounds with a rise in water level also seem to play a releasing role (Huet 1970, Bardach *et al*. 1972, Balarin & Hatton 1979, Pullin & Lowe-McConnell 1982).

Lowe-McConnell (1987) reported that spawning in river fish species, whose young feed on floodplains, may be stimulated by either local rains or by floods coming downriver from rain in the drainage basin. Young *et al.* (2000) reported that a change in water depth and flow *per se* were not limiting factors for spawning in golden perch *Macquaria ambigua*, but rather the timing of the season of flow, the rate and duration of change of water depth as well as the bankfull flow events which ensured adequate access by juveniles to the rich food resources of the floodplain. Therefore, rainfall and timing of the flood may constitute the "spawning flows" for the *O. mossambicus* and *C. gariepinus* in the Lower Shire Floodplain.

Condition factor

The inverse relationship between the duration of inundation of the floodplain and the condition factor of *O. mossambicus* (r^2=0.41, $p \leq 0.001$) and the direct relationship between rainfall and CF of *C. gariepinus* (r^2=0.73, $p \leq 0.001$) (Table 7.6) confirms the findings of Willoughby & Tweddle (1978[a]) and those in Chapter 4 of this study. Willoughby & Tweddle (1978[a]) reported that *O. mossambicus* feeds intensively from April (during the receding flood-pulse) while *C. gariepinus* begins intensive feeding in November (during the low/but rising flood-pulse).

The direct relationship between the condition factor of *C. gariepinus* and rainfall is probably a result of the apparent increase in feed intake due to the higher availability of food during the rising flood-pulse (Bayley 1991). However, the inverse relationship between duration of floodplain inundation and condition of *O. mossambicus* could be a consequence of increased input of nutrient and organic matter from the aquatic/terrestrial transition zone (ATTZ) to floodplain backwaters during the retreat of the flood-pulse (Bayley 1991). This is apparent in the positive and direct correlation between condition of *O. mossambicus* and phosphorus (Table 7.6). A similar improvement in condition of *O. mossambicus* was reported in Lake Chicamba as being partly due to persistence of detritus during the summer drawdown (Weyl 1998). Decaying vegetation is reported to enrich the detritus, which is the primary food for *O. mossambicus* (De Moore *et al.* 1986, Bowen 1979, Bowen & Allanson 1982).

Juvenile recruitment

The direct and significant correlation between conductivity, nitrate and the timing of the flood ($0.04 \leq r^2 \geq 0.66$, $0.04 \leq p \geq 0.001$) and juvenile abundance for all species signifies the synchrony between nutrient-enrichment of the habitat and the timing of movement of juveniles to the littoral areas of the floodplain. The increase in nutrient loading with the advancing flood pulse in the Lower Shire Floodplain was demonstrated in this study (Chapter 3). Conductivity and total dissolved solids (TDS) progressively increased from low flood regime to highest levels during the peak flood regime, indicating an influx of nutrients and organic matter from the catchment into the floodplain (Chapter 3). Similarly, Junk *et al.* (1983) observed an increase in detritus loading in the Amazon floodplain lakes during peak flood, brought in by floodwater.

It is important to note the significant inverse relationship between juvenile abubndance for all species and relative humidity (RH) ($r^2 = 0.25$, $p \leq 0.001$), as well as the significant direct relationship with wind speed for cichlid and *C. gariepinus* juveniles ($0.13 \leq r^2 \geq 0.45$, $0.01 \leq p \geq 0.001$). This correlation is in line with observations in the floodplain, where high wind speed corresponds to the time of low relative humidity and no rainfall (Chapter 2) and high juvenile abundance (Chapter 5) (September – November).

In Lake Sibaya, *O. mossambicus* juveniles were reported to move to the littoral zone during low water levels to feed (Bowen & Allanson 1982), and juveniles of *C. gariepinus* were found in newly inundated areas when food abundance was high and when there were no permanent population of predators (Bruton (1979). Therefore, the model confirms what has been reported elsewhere that movement of juvenile fish is governed by water temperature, food availability and habitat preference (Bruton 1979, Reynolds 1983, Welcomme 1985).

Fish density

The direct relationship between the onset of rainfall and CPUE (as an indicator of relative density in fluctuating systems) indicates that catches are generally higher during the rainy season. However, the inverse relationship with the timing of the flood (Table 7.6) suggests that CPUE would also increase with receding water level. This model prediction is similar to the observations made in Chapter 6. Interestingly, CPUE was shown to be positively influenced by the flood of the previous year (Table 7.6). Correlations between catches and floods of previous years have also been reported elsewhere (Welcomme 1975, 1985, 2001; Krykhtin 1975).

The relationships between hydrological indices (timing of flood, duration of inundation, water level) and CPUE in the Lower Shire Floodplain are complex and differ between habitats. The results suggest that CPUE is significantly related to water level of the same year and one year before ($0.40 \leq r^2 \geq 0.60$) ($0.0000 \leq p \leq 0.05$), during the period between the end of the low flood and the peak flood regimes (September to February) (Table 7.10). The period of stronger relationship is shorter in the river floodplain (RF, 3 months) and seasonally connected lagoons (SCL, 4 months) but longer in the permanently connected lagoons (PCL, 5 months). CPUE is inversely related to the water level of the previous year ($0.24 \leq r^2 \geq 0.28$, $p \leq 0.05$) in the RF and SCL; but directly related ($r^2 = 0.47$, $p \leq 0.05$) in the PCL.

Overall, it can be concluded that prolonged flooding may upset the ecosystem in the SCL where fish are adapted to shorter periods of flooding and shallower water depths. On the other hand, prolonged flooding may delay the migration of fish to the river; hence prolong their stay in the permanently connected lagoons. In general, the model concurs with the conclusion by Welcomme & Hagborg (1977) who found that (a) fish can be exploited under various combinations of high and low water regimes, and (b) the most important measure for increasing yield is the retention of the maximum possible water level during the dry season.

Table 7.10 Relationship between mean monthly CPUE (kg/gear/day) and water level (m) in the Lower Shire Floodplain. In the table, n=number of days of sampling, r^2 = coefficient of determination, p = level of significance. C=CPUE, L_0 = water level of the same year, L_2 = water level of previous year before. Models were obtained using forward stepwise regression analysis.

Habitat	Predictive equation	Period of significant relationship (months)	n	r^2	*P*
Seasonally connected lagoon	$C = 0.57L_0 - 0.24L_2 - 27.22$ P=0.0251 p=0.2978	31 August – 6 January (4)	101	0.40	0.046
River floodplain	$C = 0.61L_0 - 0.28L_2 - 27.22$ P=0.0000 p=0.0331	13 September – 31 December (3)	123	0.48	0.000
Permanently connected lagoon	$C = 0.80L_0 + 0.47L_2 - 48.18$ P=0.0007 p=0.0221	6 September – 5 February (5)	100	0.65	0.001

The complex relationship between predictor variables and fish catches in the predictive model may suggest the that the flood-pulse determines the occurrence, life cycle, and abundance of primary and secondary producers whose abundance affect the level of exploitation and regeneration of the nutrient pool (Welcomme 1979, 1985, 2001, Lowe-McConnell 1987, Junk *et al.* 1989). Lowe-McConnell (1987) reported that seasonality in fish communities in most tropical river ecosystems is caused by changes in rainfall, water level regimes, wind-induced upwelling, and the consequent seasonal changes in habitat, which lead to qualitative and quantitative changes in available food. Furthermore, the extent and duration of flooding varies greatly from year to year. Abiotic factors such as those associated with the flood regime (stranding, deoxygenation), interact with the intense predation, leading to great fluctuations in numbers of particular fish species from year to year (Lowe-McConnell 1987).

Sensitivity analysis of the predictive models

All the results of the predictive models concerning gonadosomatic index (GSI) and the condition factor (CF) for both *C. gariepinus* and *O. mossambicus* were within the range of the standard deviation of the means (Table 7.7), although the variations were very wide during certain months. Therefore, it may be concluded that the models predicted the actual situation fairly well. The incorporation of climatic, hydrological and habitat factors into the model may likely have helped achieve this high level of accuracy. The level of accuracy might also be an indication of the accuracy with which the biological parameters (Chapters 4&5) were estimated; and that the life-history parameters may be a true reflection of the response to the abiotic factors of climate, hydrology and habitat. Fong e*t al.* (1997) reported that if the predictions are mostly influenced by sectors of the model that are well understood, then the model is considered more reliable. Therefore, the output of the models for seasonality of spawning and condition factor of both species in the floodplain may be considered as reliable and robust predictions.

Tested under the lowest levels of the predictor variables (baseline) the model predicted a lower spawning rate for *C. gariepinus* (72.5% of the observed GSI value) (Table 7.7 and Figure 7.2). A further reduction of baseline conditions by 10% resulted in an increase in GSI for *C. gariepinus*. However, a 10% increase in; say water level, above the maximum level, resulted in spawning failure for *C. gariepinus*. While both species could tolerate baseline environmental conditions, *O. mossambicus* was more sensitive to a 10% reduction and *C. gariepinus* appeared to be more sensitive to a 10% increase above baseline condition. Therefore, *C. gariepinus* runs a risk of spawning failure under both extreme low and high levels of environmental conditions, such as water level and temperature, but the impact on *O. mossambicus* would appear to be less.

Water temperature, rainfall, bankfull level and pH emerged as strong predictor variables in the GSI model of *O. mossambicus* (Table 7.7). The pH levels under all simulation levels (Table 7.2) never came close to the lethal pH 4 (Swingle 1961). However, it seems likely that the temperature of 18.9ºC, under baseline simulation conditions, (Table 7.2) was below the optimum temperature (20ºC) for breeding of *O. mossambicus* (Huet 1970, Bardach *et al*. 1972, Balarin & Hatton 1979). This is in sharp contrast to the notion that in tropical regions temperature is rarely a limiting factor for breeding (Jalabert & Zohar 1982).

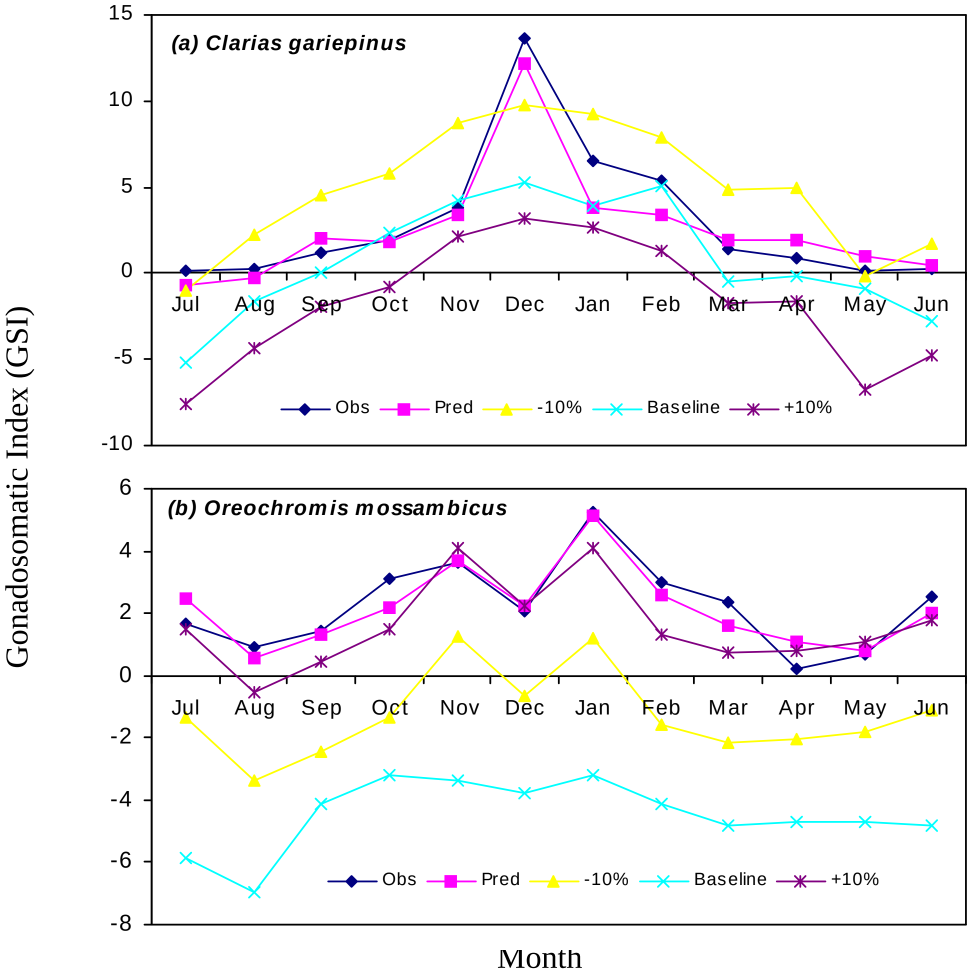


Figure 7.2 Model simulations and sensitivity analysis of the hydro-climatic-fisheries model for Gonadosomatic Index (GSI) in (a) *Clarias gariepinus* and (b) *Oreochromis mossambicus* in the Lower Shire Floodplain. Obs = observed data, Pred = predicted, -10% = simulation using predictor variables at 10% less than baseline level, +10% = simulation using predictor variables at 10% more than maximum level of predictor variables, Baseline = simulation using minimum level of predictor variables.

The model predicted that *C. gariepinus* under baseline simulated environmental conditions (for example temperature) still achieved a 72.5% spawning rate. This could be due to the probability that the lowest water temperature in the Lower Shire (18.9ºC) was still slightly above the minimum spawning temperature of (18ºC) for *C. gariepinus* (Bruton 1979). Furthermore, the Lower Shire Floodplain receives a minimum rainfall of 4.05 mm (Chapter 2). Hence simulation of minimum rainfall under baseline conditions meant that the minimum rainfall in the Lower Shire Floodplain was greater than what Bruton (1979) reported as the minimum (<1mm per month) for spawning of *C. gariepinus* in Lake Sibaya. Simulation under extremely high levels of water and temperature may have resulted in a decline of spawning because water temperature might have been too high (assumed to be >30ºC) and an all-year round rainfall may have led to continuous inundation of the floodplain. These conditions are unlikely to create the necessary stimulus for gametogensis and spawning as suggested by Bruton (1979).

The outputs of the models for condition factor also fitted the observed condition in *O. mossambicus (*Figure 7.3) fairly well. While the condition of *C. gariepinus* declined when simulated at environmental baseline and 10% below the baseline conditions, the condition factor of *O. mossambicus* almost doubled under similar conditions. The condition factor of both species rose when the model was tested under extremely high levels of predictor variables, for example, water level of 10% above the maximum. This can be explained by the seasonal variance in feed intake by *C. gariepinus* and less seasonal variance in the feed intake by *O. mossambicus*, and the type of diet items the species feed on.

Willoughby & Tweddle (1978[a]) reported that *C. gariepinus* has the tendency to feed more actively during periods of high water level. This is reflected in the significant relationship ($r^2 = 0.85$, $p \leq 0.001$) between the condition of *C. gariepinus* and rainfall (Table 7.3). Therefore, it is likely that *C. gariepinus* will suffer food deficiency during reduced water levels. Conversely, with the tendency to intensively feed during the receding and low water level (Willoughby & Tweddle 1978[a], Bowen & Allanson 1982) and being a predominantly detritivore, *O. mossambicus* may still thrive under simulated reduced water levels. This might explain the significant inverse relationship ($r^2 = 0.41$, $p \leq 0.001$) between the condition of *O. mossambicus* and duration of floodplain inundation (Table 7.6). Similarly, the period of low water level (June to August) coincides with low air temperatures (Chapter 2) and intensive feeding by *O. mossambicus* (Willoughby & Tweddle 1978[a]), hence the inverse relationship between the condition of *O. mossambicus* and air temperature ($r^2 = 0.41$, $p \leq 0.001$) (Table 7.6). Therefore, it might be concluded from the model, that the condition factor of *O. mossambicus* is less affected by adverse or unfavourable environmental conditions in the floodplain, and hence more resilient.

Although the model overestimated juvenile recruitment (371.13 fish.haul^{-1}), the values were within the observed limits (± SD) of (274.64±205.57 fish.haul^{-1}) (Table 7.7 and Figure 7.4). Predicted juvenile recruitment appears quite sensitive to a reduction or an increase in predictor parameters, particularly nutrient levels (nitrates and phosphorus) and temperature. This suggests that both species have adapted their reproductive strategies to ensure greater survival of the offspring by synchronising juvenile recruitment with suitable conditions such as water temperature, food availability and availability of preferred habitats (Reynolds 1983, Welcomme 1985, Bruton 1979).

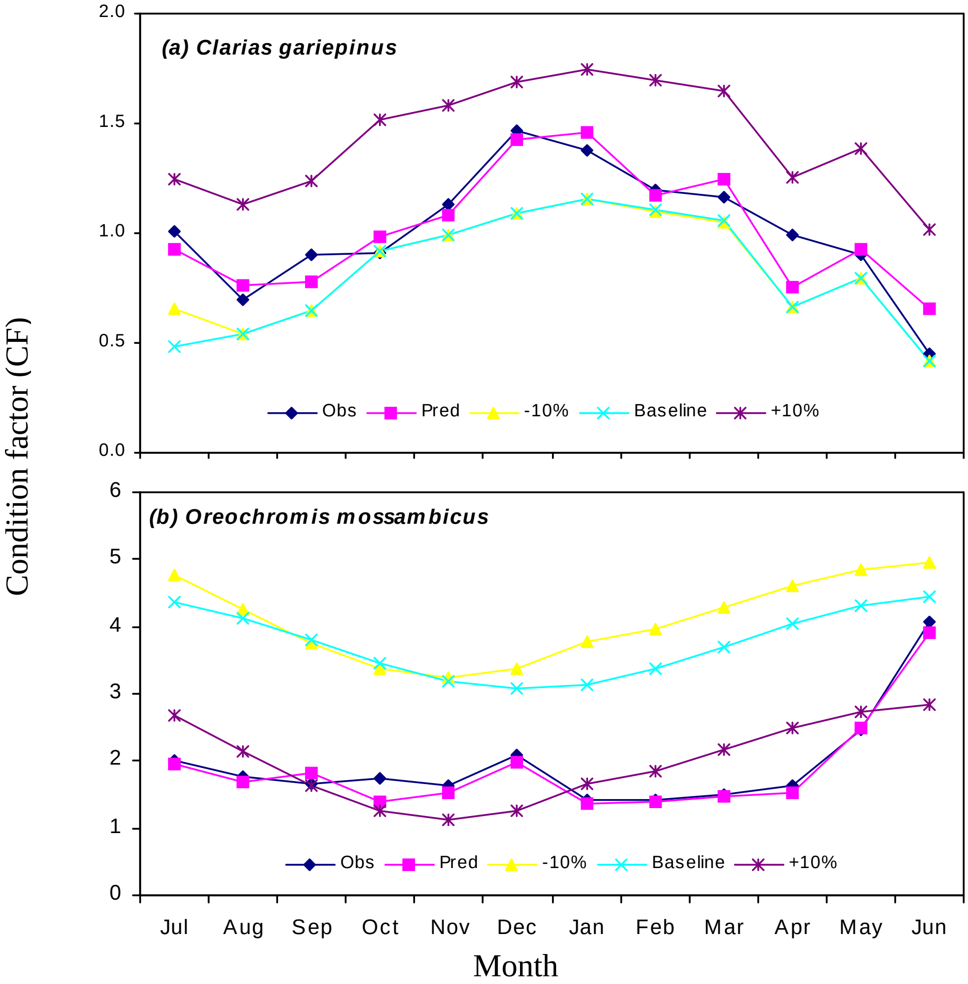


Figure 7.3 Model simulations and sensitivity analysis of hydro-climatic-fisheries predictive model for Condition factor (CF) in (a) *Clarias gariepinus* and (b) *Oreochromis mossambicus* in the Lower Shire Floodplain. Obs. = observed data, Pred = predicted, -10% = simulation using predictor variables at 10% less than baseline level, +10% = simulation using predictor variables at 10% more than maximum level of predictor variables, Baseline = simulation using minimum level of predictor variables.

The model predicted an increase in CPUE at baseline and at 10% lower than baseline conditions. However, the model predicted a 42% reduction in CPUE to only 42% at 10% increase in the predictor parameters (Table 7.7 and Figure 7.4). This sensitivity of CPUE to environmental conditions may be explained by the impact of the flood-pulse on fish production in floodplains (Junk *et al.* 1989, Bayley 1991), in a number of ways.

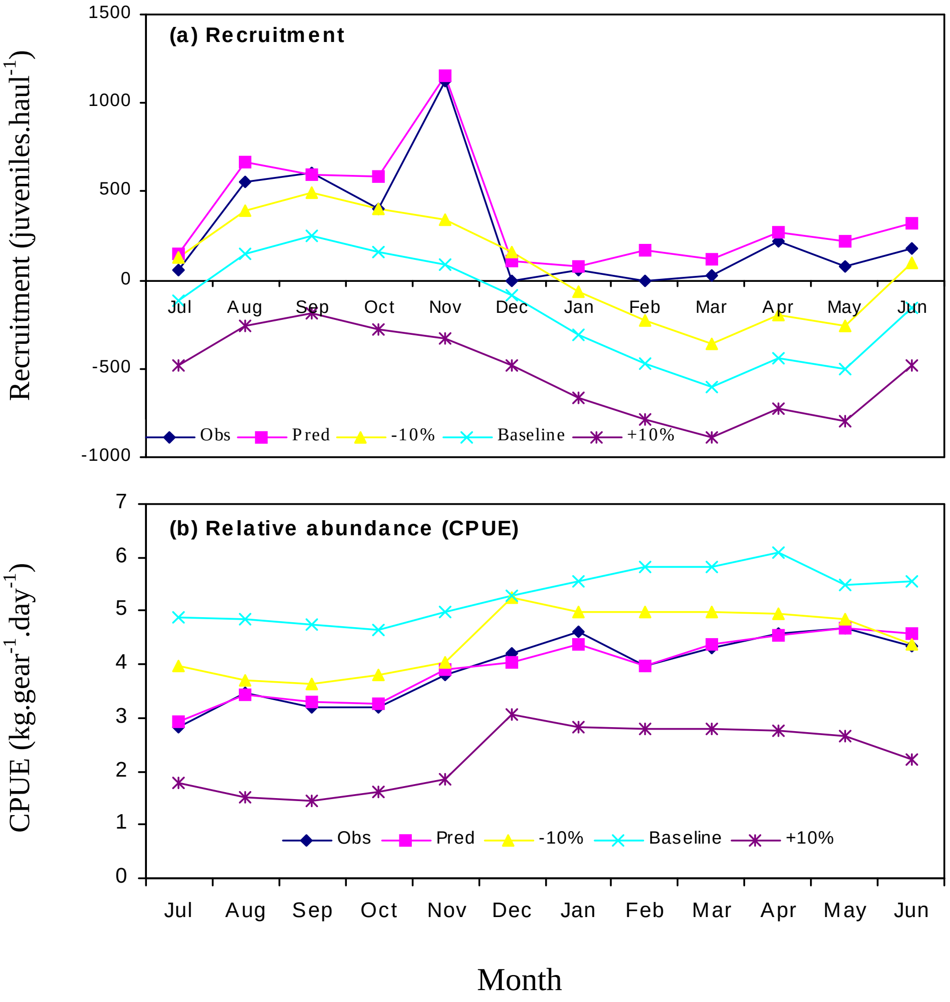


Figure 7.4 Model simulations and sensitivity analysis of hydro-climatic-fisheries predictive model for (a) recruitment and (b) CPUE in the Lower Shire Floodplain. Obs. = observed data, Pred = predicted, -10% = simulation using predictor variables at 10% less than baseline level, +10% = simulation using predictor variables at 10% more than maximum level of predictor variables, Baseline = simulation using minimum level of predictor variables.

Restricted water flow occurring through river obstruction may lead to occurrence of “serial discontinuity” (Ward & Stanford 1983), a situation where water does not overflow into the floodplain. In addition, rapid drawdown may strand or leave aquatic fauna vulnerable to predators (Bayley 1991). Furthermore, protracted periods of low water can limit the production of higher aquatic fauna as suggested by the fish production model of Welcomme & Hagborg (1977). On the other hand, too much water entering the floodplain, either through heavy rainfall or prolonged opening of dam gates, as apparently happens in the Zambezi River at Cabora Bassa (Beilfuss 1999), may not be beneficial to the fish. Junk *et al.* (1989) suggested that a situation of constant high water level might in fact reduce fish production. Prolonged high water level changes the floodplain into a stable environment, such as exists in lakes or reservoirs, in which very little of the nutrients and organic matter held in the detritus are recycled (Bayley 1991).

Seasonal oscillation of biological and production parameters

Seasonality of fish production in floodplains has been widely reported (Willoughby & Tweddle 1978^{a}, Welcomme 1985, 2001, Lowe-McConnell 1987, Merron 1991, Junk 1997, Hoggarth *et al.* 1999, Halls *et al.* 1999, Kvist & Nebel 2001, Kvist *et al.* 2001, Silvano & Begossi 2001). When environmental conditions fluctuate seasonally, subsequent fluctuation in fish populations is brought about by seasonal migrations, spawning and natural mortality (Lowe-McConnell 1987).

Since seasonality is an important element in fluctuating floodplain ecosystems, it is imperative for fisheries ecologists to predict seasonal environmental and ecological events in order to formulate fisheries management strategies. The seasonal nature of CPUE emerged in the predictive model of CPUE as the cos(RMOY) (Table 7.6).

Bell *et al.* (1995) reported that seasonality is the cause rather than variation in reproductive output and fishery yields, hence, when assessing the relationship between spawning and recruitment, seasonal variation should be taken into account. While Lowe-McConnell (1987) reported that seasonality in rivers is caused by changes in abiotic factors such as water level, this study has statistically proved this concept. It is clear that not only do climatic, hydrological, habitat, biological and production events in the floodplain significantly ($0.32 \leq r^2 \geq 0.94$, $0.05 \leq p \leq 0.05$) revolve around a periodic function of time (month of the year) or season (Tables 7.8 and 7.9), but that the flood-pulse indeed precedes all the major biological and production events (Figure 7.1). Naturally, life cycle patterns of *O. mossambicus* and *C. gariepinus* in the Lower Shire Floodplain are temporally linked to the flood regime in a “continuous oscillatory system” (Savill & Hogeweg 1999). Therefore, any alteration to the flood cycle may likely result in major changes in the cycle of biological events of the fish, including recruitment.

Fisheries management implications

The study has four major implications for the management of fisheries in the floodplain. Firstly, four major environmental predictors have been identified and they can be used to predict the biological and production indices of the two most important species in the Lower Shire Floodplain. These were climatic, hydrological, habitat, and seasonal variables. More importantly, it has been demonstrated that at the onset of flooding, the rate at which the hydrograph changes as well as the length of the period that the floodplain is inundated are critical variables affecting the biological and production indices of the two fish specie in the floodplain. Secondly, issues of seasonality, or time of the year, also have tremendous impact on some of the biological and production factors. The flood pulse has been isolated and has been statistically demonstrated to be the driving force behind major biological cycles of the fish. Changes to the hydrograph of the Shire River may result in major alterations in the biological cycle of the species that might affect the fisheries and livelihood of the riparian communities in the Lower Shire Floodplain.

Thirdly, the use of forward stepwise multiple regression analysis has helped to produce a set of simple models, which provide guidelines for the management of the floodplain. A similar statistical tool has been reported to be useful in hydrometeorology (Wilby et al. 2004). Furthermore, these models have few variables and are easy to measure.

Fourthly, although the model is yet to be tested over a longer period of time, (hence the results may need to be treated with caution), the study has formed the basis for quantitative predictive modelling for the floodplain. The strong correlation between biological and production parameters with the hydro-climatic seasons as well as habitat parameters, takes the fisheries-flood pulse relationship to another level. A strong quantitative relationship has been established between climate and seasonality and biological/production variations of the fish in the floodplain. Given the high level of predictability of this model, it is possible that many tropical river floodplains may conform to it, with minor on-site modifications.

Chapter 8

General discussion with management considerations for the hydro-climatically fluctuating fishery in the Lower Shire Floodplain

Introduction

From the procedures outlined throughout the thesis, it is clear that management decision support can be obtained using different methods. To decide upon floodplain management objectives, managers ought to customise the information management to gain the best out of available data. Obviously, the more data generated from the ecosystem under investigation, the greater the probability that a better management plan will be developed for the fisheries. However, massive data requirement entails high cost, which many African national agencies, under heavy budgetary constraints, can ill afford. Floodplain fisheries research in Africa has in recent times received little funding, if any at all, hence management advice has been derived from limited data. It is, therefore, important to prudently define the most cost-effective and appropriate approach to generate information required to manage these important ecosystems.

The generalised ecosystems conceptual model of the Lower Shire Floodplain fisheries comprises four major sub-systems of climate, hydrology, habitat and the fish (Figure 8.1). The hydrology is driven by the climate and the seasonal effects, hence the need for a hydro-climatic seasonal approach to management of the floodplain. The habitat modifies the hydrological effects mainly through the physico-chemical characteristics of the water. These physical elements then affect the fish through the impact on feeding, breeding, growth, recruitment and production. The well-being or condition of the fish has an impact on the capacity of the fish to breed, add new recruits to the fish stock and finally to increase in the biomass of the floodplain. Therefore, development of a floodplain fisheries management plan should encompass investigations of all these sub-systems.

FAO (1997) defined fisheries management as the integrated process of information gathering, analysis, planning, consultation, decision-making, allocation of resources and formulation and implementation, with enforcement of regulations or rules which govern fisheries activities in order to ensure the continued productivity of the resources and accomplishment of other fisheries objectives. Welcomme (2001) summarises fisheries management as decisions and actions affecting the magnitude and composition of fishery resources and the distribution of benefits from its products, based on natural scientific (resources-based) and socio-economic (society-based) approaches. He further advocates the "modern management" approach, which seeks to reconcile the two views as tools to reach a balanced decision on the resources with the participation of all stakeholders in the fishery.

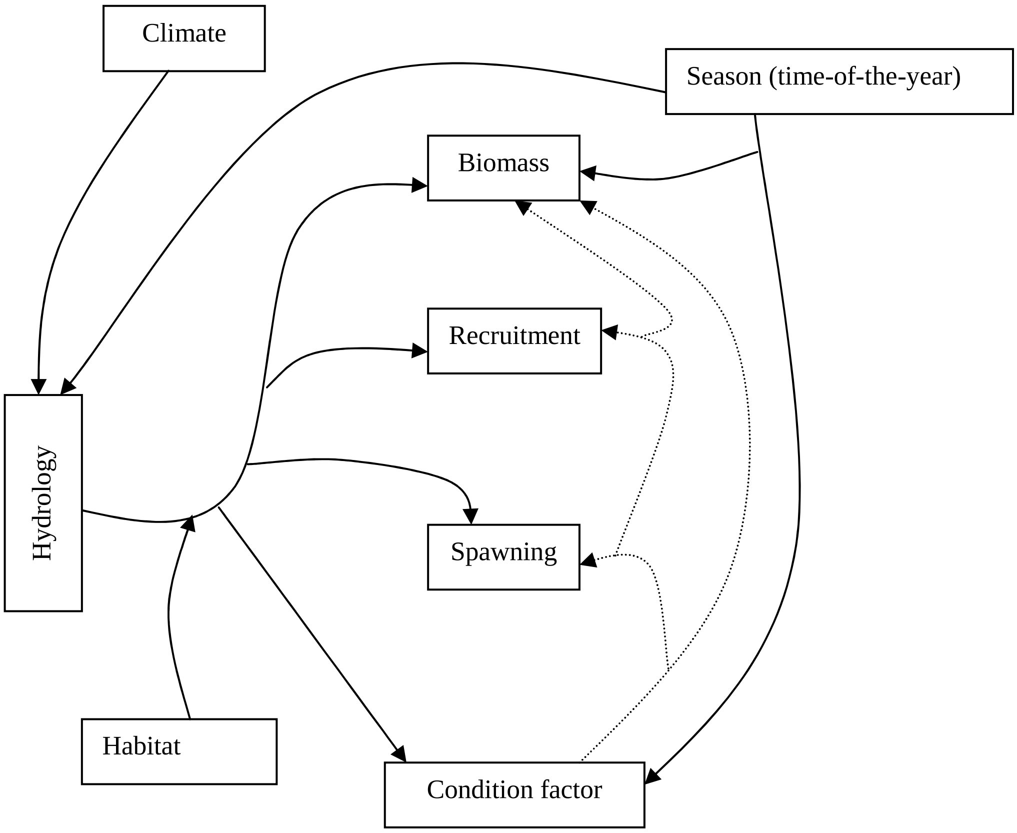


Figure 8.1 Generalised conceptual model of the Lower Shire Floodplain, showing the cause-effect pattern of climate, hydrology, habitat characteristics and the biological and production parameters of the fish. Solid lines indicate direct influences and broken lone indicate indirect influences. The model has been derived from the forward stepwise multiple regression analysis of the dependency of fish biological and production factors on climate, hydrological and habitat variable (Chapter 7).

The conceptual model for the management of the Lower Shire Floodplain Fisheries (Figure 8.2) shows that for the "modern management" approach to work, there is a need to develop an effective management protocol for decision-makers. This entails identifying the measurable ingredients or factors in the "critical decision points" (CDP), denoted by the rectangular boxes in Figure 8.1, or elements of ecosystem. Wilson *et al.* (1994) recommended that management needs to focus on the stable parameters of fisheries systems, namely habitat and biological processes. Welcomme

(2001) adds that changes required in the use of particular gears, can however, be useful. This study has also identified the need to consider climatic and seasonal (spatial and temporal) factors. Welcomme's (2001) management approach requires adoption of a hierarchical approach as suggested by Hoggarth *et al.* (1999), which highlights roles and needs to be filled by different stakeholders in order to develop an effective management protocol for floodplain fisheries.

Figure 8.2 shows an improved version of the hierarchical model in Figure 1.3 (Chapter 1). It summaries the processes that are necessary for the development of a management plan for the floodplain fisheries. It is clear from the chart that management of floodplain fisheries involves collection of information necessary for the preparation of the plan, and operationalising the plan by implementing it with the stakeholders. Although the chart puts stakeholders low in the hierarchy, it is ultimately these stakeholders with whom a decision must be made on whether or not and how to manage the floodplains. A number of steps should be taken to identify the critical decision points, which will constitute the focus for information collection. Many public agencies in Africa, such as Departments of Fisheries, often experience funding problems. This implies that critical assessments of data requirements must be made in order to identify information gaps so that only that information, which is critical, is collected. The next stage is to initiate the floodplain assessment, following the five lines of inquiry (Fig. 8.2).

This study suggests that the first step is to undertake a full hydrological analysis in order to obtain an insight into the flood regime of not only the floodplain itself, but more importantly, the rivers which make up the floodplain (Chapter 2). This should provide information on the hydrograph of the river, timing of the flood regime, duration of inundation as well as the annual water balance of the floodplain ecosystem. Secondly, the climate of the floodplain must be understood. The climate data must be assessed and analysed to determine patterns for rainfall, relative humidity, temperature, wind speed, evaporation and sunshine.

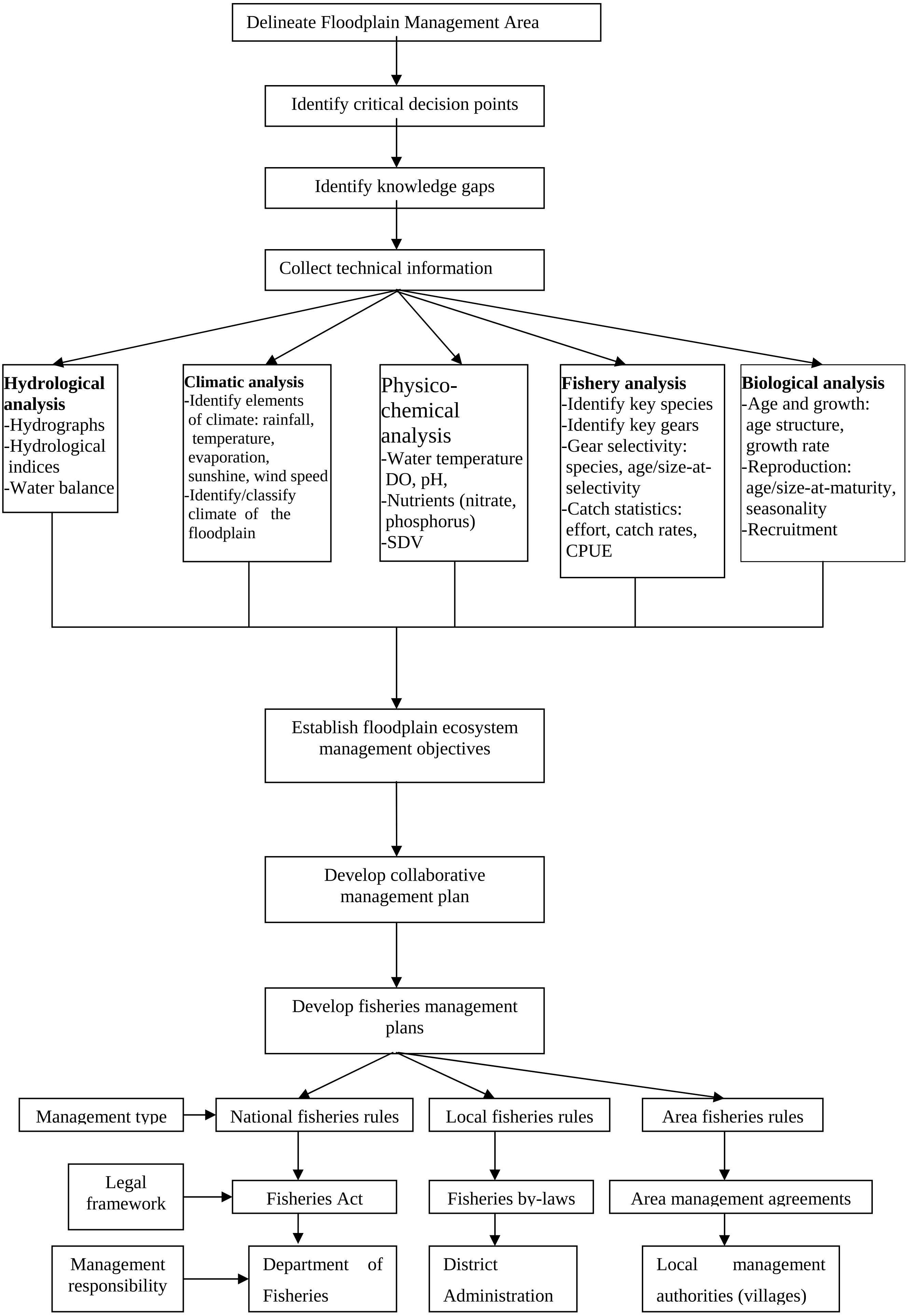


Figure 8.2. Proposed conceptual model for a fisheries management plan of the Lower Shire Floodplain.

Usually, data on hydrology and climate may be obtained from relevant public agencies in the countries. Interesting and valuable hydro-climatic seasonal patterns emerge when hydrological and climatic indices are analysed (Chapter 2). Hydro-climatic seasons are more relevant to floodplain fisheries management than normal seasons, because they offer opportunity for managers to be able to explain biological and production patterns from a hydro-climatic perspective.

Thirdly, the physico-chemical characteristics of the habitat must be assessed quantitatively. Choice of parameters to be assessed depends on availability of equipment and the need to obtain a picture on variation of nutrient levels, temperature and dissolved solids (Chapter 3). This type of data must be collected and analysed in synchrony with the hydro-climatic seasons. By this time, one has a full knowledge of the operational and dynamics of the physical environment of the floodplain.

Fourthly, a concerted effort is needed to collect primary fisheries statistics, such as the types of gears and crafts being used, the species being targeted, levels of catch and effort and gear selectivity patterns. This data can later be used to determine the age or size-at-selectivity.

Lastly, a comprehensive biological study of the representative species on which the management plan will focus, should be undertaken in order to unravel their life-histories (Chapter 4). Particular focus should be on age-at-sexual maturity, growth rate, and reproductive biology, including seasonality. Insights should also be obtained on the indices of recruitment, juvenile growth and well-being (condition) of the fish (Chapter 6). By comparing the size/age-at-sexual maturity with age-at-selectivity, the sustainability of each fishery may be assessed. Such biological data can also later be used as inputs for modelling the fisheries. The choice of conceptual, empirical or theoretical models depends on the type of decision and interventions to be made on the management of the resource. Conceptual models help to highlight the critical decision points of the whole ecosystem, while empirical models may be used by managers to make decisions based on the cause-effect outputs obtained in the simulations of physical factors of the ecosystem and biological/production parameters of the fish.

A series of procedures, which aim to define the management objectives and to operationalise the plans then have to be followed. A floodplain ecosystems management plan might include integrated watershed management, habitat rehabilitation as well as fisheries management. A floodplain has a wide range of stakeholders. Depending on their interests, a collaborative management plan might be essential in order to ensure that complimentary and conflicting objectives are reconciled. A fisheries management plan may cover the whole river basin, catchments or larger sections of the floodplain or portions of a floodplain, and these are guided by the national fisheries Acts, district by-laws or area management rules which may be managed by local management authorities or villages, respectively (Fig. 8.2).

Research activities carried out over the past three decades (Ratcliff 1972, Hastings 1973, Willoughby & Tweddle 1978[ab], Tweddle *et al.* 1979, Tweddle *et al.* 1994) provided valuable sources of data. However, an inherent problem of the Lower Shire Floodplain fisheries in Malawi is that the past research did not generate comprehensive biological data, and no quantitative evidence has been presented to show the seasonal dynamics of the relationship between fish catches and the hydrology of the floodplain.

This thesis has attempted to address these shortcomings to make a contribution towards the development of a suitable management tool for floodplain fisheries and for the Lower Shire Floodplain in particular. The hydro-climatic fisheries model that was developed in this study can be used to predict the impact of climate, hydrology and habitat parameters on the biological and production indices of the fish. In addition, it can facilitate the prediction of spatial sequencing of abiotic factors of the ecosystem and biotic elements of the fish in the floodplain. The model is simple but provides a statistically robust tool that can be integrated with existing floodplain fisheries resources assessment methods. The model developed in this study is the first step towards the development of a fisheries management protocol for the Lower Shire Floodplain. However, with a little more work and inputs it could be refined and adopted for the analysis, monitoring, as well as management of the fisheries resources of the entire Lower Zambezi Basin Floodplain.

Management of seasonally fluctuating African floodplain fisheries

The hydro-climatic fisheries model developed in this study predicts that CPUE will increase as water level recedes. Furthermore, the longer the floodplain is inundated, the greater the probability that catches will be higher in the following year (Chapter 7). This implies that for the fisheries to be effectively managed, the strategy must centre on the hydrological management of the Shire River. The models predicted the seasonal nature of the GSI, CF, juvenile recruitment and fish catches fairly accurately. This emphasises the importance of using climatic, hydrological and habitat parameters as variables in the development of predictive fisheries models for floodplains. Accurate estimation of biological parameters (Chapters 4&5) is of course also essential in order for the life-history trends to be a true reflection of the response of the fish to the abiotic factors of climate, hydrology and habitat of the floodplain ecosystem.

In order to avoid spurious models, independent variables should be carefully selected prior to model fitting on the basis of meaningful ecological hypothesis (Welcomme 2001). In addition to a careful selection of predictor variables, this study used rigorous mathematical and statistical techniques. Furthermore, robust statistical tools, such as forward stepwise multiple regression analysis, were used to eliminate the redundant predictors and yield a final model that accounted for most of the variance.

Obviously, effective hydrological management of the Shire River requires considerable information and knowledge about the climate, natural resources utilisation activities in the catchment (e.g. agriculture), as well as current and planned activities to regulate the river. Sufficient information has been collated in this study, which might allow us to embark on a further theoretical modelling exercise. This could be undertaken by integrating this model with the FPFMODEL of Welcomme & Hagborg (1977) and Halls *et al.* (1999) to test various hydrological and climatic scenarios. No doubt as more tropical floodplain-river systems become modified by hydrological engineering, this type of simulation model will become increasingly pertinent to multi-sectoral planning management (Welcomme 2001).

Management considerations for the key species in the Lower Shire Floodplain

The life-history traits of particular species in a freshwater fishery can vary from area to area and tend to be ecosystem-specific (Chapter 4). Quantification of these traits (e.g. age, growth rate, size at sexual maturity, reproductive periodicity and mortality rate) must form the basis for sound management of the fisheries of a particular floodplain. Despite the conclusion that *O. mossambicus* and *C. gariepinus* show signs of over-exploitation, there seems to be potential for the sustainable exploitation of the resources. Several biological characteristics of these species show their resilience to exploitation. Firstly, being relatively short-lived and with a high rate of natural mortality (Chapter 4), the populations exhibited traits typical of floodplain fishes (Welcomme 1979, Junk *et al.* 1989, Bayley 1991). Secondly, the annual seasonal floods periodically increase spawning and nursing grounds, thereby expanding the carrying capacity of the floodplain for both species (Chapters 2 and 5). Thirdly, protracted spawning (Chapter 4) appears to improve the recruitment potential for both *O. mossambicus* and *C. gariepinus* (Chapter 5), while fast growth may reduce the impact of fishing on larger size classes of both species (Chapter 6). However, the precocial reproductive strategy of mouth-brooding has some serious implications for the management of *O. mossambicus*. Furthermore, although age-at-50%-selectivity occurred 2 to 4 months after the age-at-50%-sexual maturity in both species, there is a need to closely monitor this since the difference between 2 and 4 months may get even narrower depending on the inter annual flood regimes.

Considerations for collaborative management of the Lower Shire Floodplain

The fishery of the Lower Shire Floodplain is open-access (Chimatiro & Mwale 1998). The challenges of open-access in fisheries management arise due to the problems of non-compliance to fisheries rule. The decision of compliance versus non-compliance behaviour by fishers is based on a calculation of the economic gain to be obtained from bypassing the regulation compared to the likelihood of detection and the severity of the sanction. Sutinen & Andersen (1985) and Anderson & Lee (1986) have argued that fishers act as rational agents and Copes (1986) noted that fishers are often creative in finding ways to bypass the regulations. Welcomme (2001) recommends that for fisheries where a substantial proportion of the fish assemblage is made up of species that reproduce and live locally, management plans need to reflect local stock status, local conditions and the needs of local stakeholder. And he advocates the "modern management" approach, which involves all stakeholders in the fishery.

A sound management strategy in the Lower Shire Floodplain can only work if the resident fishing communities comply with the regulations put in place. This requires adoption of a hierarchical approach as suggested by Hoggarth *et al.* (1999), which highlights roles and needs to be filled by different stakeholders (see Figure 8.2). The existing pressure to increase fish catches, coupled with the fact that there is no size-preference among consumers, has driven fishers to use smaller meshed gears, leading to declining catch per unit effort by over 50%, over the past two decades (Chapter 6). While fishers acknowledge a decline in catches (Table 8.1), many do not, however, attribute this directly to increased effort, but rather to a reduction in water level caused either by drought or an increase in water hyacinth infestation. The fact that the fishers did not attribute lower catches to increased effort is a typical response and is not justified at all. However, they appreciate the need to manage the fisheries and offer to form local management authorities (Table 8.2). By attributing low catches to reduced water levels, the fishers demonstrated their intuitive indigenous knowledge of the impact of the flood-pulse on fish production; and their willingness to participate in management, forms a starting point for community-based management of the floodplain fisheries (Fig. 8.2).

Given the overwhelming evidence of the effect of the flood pulse on biological and production parameters of the fish and the increasing effort over time, there is a need for a two-pronged approach to management of the fisheries of the floodplain. In an open access scenario, such as it exists in the Lower Shire Floodplain, it is notoriously difficult and a lengthy process to achieve any paradigm shift in fisher behaviour. Therefore, the first step for the sustainable utilisation of the fisheries resources would be the development of a joint management plan by the Department of Fisheries and Department of Water Resources, to manage the seasonal flow of the Shire River such that an optimal or "near optimal" hydrological regime is maintained. This would provide the basic environmental condition for successful reproduction and recruitment.

Secondly, the new plan could target the prevention of over-fishing and protection of spawner stock, by (i) setting a mesh size limitation at or near to the age-at-50%-sexual maturity, (ii) the banning of certain destructive gears and (iii) adopting a closed-areas approach. However, given that government resources for monitoring, control and surveillance are limited, it would be prudent to adopt closed area and banning of certain gear types. These would be easier to control than monitoring and controlling mesh size regulations.

Table 8.1 Problems faced by fishing communities in the Lower Shire Floodplain. The problems are ranked in the order of importance by "Score ranking" which was done by respondents ranking their problems from 1= more important to 8 = least important. In the table, n = number of respondents; 11.2-11.8 are codes of strata of the Lower Shire Floodplain (after Chimatiro & Mwale 1998).

Problem	**Stratum**					
	11.2 n=242	**11.3 n=90**	**11.5 n=92**	**11.6 n=31**	**11.7 n=190**	**11.8 n=102**
Poor catches	7	7	4	-	-	4
Water hyacinth	2	1	2	4	3	2
Large numbers of fishermen	5	-	-	-	-	8
Lack of fishing gears/crafts	1	5	3	1	3	6
Low water levels	-	3	1	-	1	3
Crocodile menace	3	2	6	-	6	5
Hippo menace	6	8	-	2	7	-

The most destructive gears are seine nets, mosquito nets and reed fences as they select juveniles of the two principal target species, *Oreochromis mossambicus* and *Clarias gariepinus* (Chapter 6). Although the number of operational seine nets (n=66), mosquito nets (n= 44) and reed fences (n=4) in the floodplain are relatively small (Chapter 6), and collectively only account for 7% of the total floodplain landings, the bulk of the catches in the seine and mosquito net fishery, are juvenile fishes: 77% of catch for seine nets (50 tons) and 70% (31 tons) of catch or mosquito nets. Between these two fisheries, a total of 81 tons of juvenile fish are harvested before they contribute towards biomass or spawner stock. Banning of these fishing gears will cause negligible loss of livelihood to the riparian community.

Another detrimental impact of the seine and mosquito net fisheries is the disturbance these gears cause to the nests of *O. mossambicus*. Assuming that all 66 seine nets (with a modal length of 100 m) and 44 mosquito nets (modal 30 m) recorded here were being used, then the area of substratum disturbed on a daily and weekly basis amounts to 7.32 $km^2.day^{-1}$ or 33 $km^2.week^{-1}$ (assuming weekly effort of 4.5 $days.week^{-1}$). It is also a common practice in the floodplain to use seine and mosquito nets to encircle vegetation in the marsh or riverbanks where fish find refuge, then progressively cut the vegetation out until all fish are trapped. Since fish use these vegetated areas as refuge and spawning and nursery habitats, the practice of cutting vegetation on the banks is detrimental, specifically to species that spawn on submerged vegetation, such as *C. gariepinus* and *Schilbe intermedius*. In addition to the direct impact of the gears on spawning grounds, bare riverbanks are prone to erosion; this results in sedimentation of spawning substrates in the floodplains. Although long lines and cast nets also target juveniles, it may not be possible to stop fishers from using them since many poor communities in riparian areas depend on these gears since they are less costly.

The “closed areas” strategy is for the following reason. Many fish species migrate from seasonally connected lagoons (SCL) into permanently connected lagoons (PCL) or the river floodplain (RF) during the receding flood-pulse; fish that do not are subjected to severe risk of mortality through desiccation and fishing. It is proposed that fishers be allowed to fish down the SCL, while the PCL be closed to fishing from June, during the dry season, to December, at the onset of the rainy season (Chapter 7). Only passive gears such as gill nets will be allowed in the RF (Chapter 6). During an aerial survey of the floodplain in November 2000, just before the flooding, a number of permanent lagoons were identified, that could be designated as closed areas. The model showed that the flooding peak in February precedes the peak in the condition of *O. mosambicus* in June and *C. gariepinus* in December (Chapter 7, Fig. 7.1). The hydro-climatic fisheries model predicted that peak spawning for *O. mosambicus* and *C. gariepinuns* occurs in December (Fig. 7.1, Chapter 4). Therefore, closing permanently connected lagoons between June and December will protect the spawner biomass and allow them to gain condition. Although closing the PCL to active fishing during the dry season may translate into a temporary loss in food and cash income, in the long run the measure might promote sustainable livelihoods to the local communities.

Table 8.2 Summary list of major key problems, causes, effects and proposed solutions mentioned by communities in the six minor strata surveyed in the Lower Shire Floodplain. Total number of respondents interviewed (n) is 749. (after Chimatiro & Mwale 1998).

Problems	**Causes or source of problem**	**Effects of problem**	**Proposed solutions to the problem**
Infestation of floodplain by Water hyacinth	▪ Drift from Zambezi River ▪ Brought by Chinese rice farmers ▪ Brought by SUCOMA Sugar Farms	▪ Reduces fish catches ▪ Reduces water level ▪ Hampers fishing and water transport	Department of Fisheries to: ▪ Control the weed; ▪ Conduct community awareness campaigns. Fishing communities to: ▪ form fisheries management committees; ▪ Manually remove the weed.
Insufficient water levels in the floodplain	▪ Deforestation ▪ Obstruction of Shire River for irrigation ▪ Drought ▪ Water absorption by water hyacinth	▪ Low fish catches	▪ Restrict amount of water used for irrigation; ▪ Afforestation ; ▪ Eradicate water hyacinth;
Lack of fishing gears and crafts for fishers	▪ Scarcity of trees for canoes ▪ Low income of fishers ▪ Theft	▪ Low fish catches ▪ Poor incomes	Provision of loans for gears and crafts by Malawi Rural Finance Company (MRFC)
Crocodile menace to fishing community	▪ Too many crocodiles	▪ Deplete fish stocks ▪ Claim human lives ▪ Damage fish gears	▪ Government to send hunters ▪ Fishermen to be allowed to kill crocodiles

An adaptive learning or co-management approach (Arthur *et al.* 2004) should now be used to create a common understanding of floodplain fisheries. Under this approach, the information, which has been generated in this study, will be shared with all the stakeholders, including the Departments of Water Resources, Meteorology, Lands and District Administration as well as the local fishing communities. This process is necessary as a precursor to the implementation of input control/management measures.

Specifically for fisheries management, the Malawi Fisheries Conservation and Management Act (1997) provides for the participation of local communities in the management of the fisheries. Based on the findings of this study, regulations to ban seine nets and mosquito nets have been formulated and included in the Malawi Fisheries Rules and Regulations. These rules will soon be reformulated into District Fisheries By-laws, under the Decentralisation Policy (1998). The District Assemblies (DA) must be encouraged to involve all stakeholders at the districts, including the Water Resources Officers. The management plan will have to be enforced jointly by the two District Assemblies (DA) sharing the Lower Shire Floodplain (Chikwawa and Nsanje), with the local fishing villagers, known as Local Management Authorities (LMA) under the Fisheries Conservation and Management Act (1997). For the LMA to enforce the rules on mesh size and closed areas restrictions, there is a need for them to enter into a legal management agreement with the DA, as provided for in the Fisheries Act.

Concluding remarks

The results presented in this thesis will hopefully contribute towards the sustainable management of the Lower Shire Floodplain fisheries. The results were achieved by establishing the critical hydrological indices for the whole Shire River and the Lower Shire Floodplain. The hydro-climatic seasonal framework formed the basis upon which the habitat characteristics, life-history traits and parameters of fish catch were developed.

Critical life-history parameters for the two target species in the Lower Shire Floodplain, *Oreochromis mossambicus* and *Clarias gariepinus*, were established, and revealed that both species exhibited typical resilient features of floodplain species (fast growth and dominated by strong 0+ year-classes). Assessment of catch and effort in the floodplain showed that the number of fishers and fishing gears has increased over the last 30 years. Coupled with the general increase in number of gears, there has been a definite shift towards smaller-meshed nets, especially mosquito nets. It has been shown that CPUE has declined over the past two decades consequently; a recommendation has been made to ban seine nets and mosquito nets in order to conserve spawner stock and improve recruitment. It has also been demonstrated that the current systems of canoe-based-effort catch assessment survey (CAS) used by the Malawi Department of Fisheries is inappropriate because of the general decline of the numbers of canoes. Therefore, a new survey protocol that is gear-based-effort has been recommended. While the current CAS calculates total effort by scaling up the monthly effort, this study has found that weekly effort is more realistic due to large monthly variations in catch and effort.

The hydro-climatic fisheries model has been developed for the floodplain, and it has shown that catches are generally higher during the rainy season as well as during the receding flood regime. Therefore, management of the floodplain fisheries can be aimed at increasing catches during peak floods or ensuring sufficient water levels in the floodplain during low flood regimes. Analysis of the seasonal and periodic hydrological events of the floodplain has revealed that the flood-pulse precedes and drives the biological clock of the major fish species in the floodplain.

Collaborative management of the flow of the Shire River must ensure maintenance of “hydrologic connectivity” whereby water level in the river remains sufficient to allow bankfull flow and inundation of the floodplain. This must be synchronised with the biological clock of the major fish species. The key function of management, especially the Department of Water resources, must be to maintain the current hydrograph of the Shire River, which allows inundation of the floodplain during the peak spawning period of fish (December to March), while maintaining the receding flood regime between April and June in order to create favourable conditions for recruitment. This will be done by ensuring that opening and closing of flow-control gates on the Shire, as well as construction of new dams, should be done in consultation with the Department of Fisheries and the fishing communities in the Lower Shire Floodplain.

REFERENCES

Aber, J.D. & Freuder, R. 2000. Variation among solar radiation data sets for the Eastern US and its effects on predictions of forest production and water yield. Clim Res. 15: 33-43.

Alimoso, S.B. 1988. A review of the present system of collecting fisheries statistics from Malawi water. *In* Report of SADCC Fisheries Statistics Workshop, Zambia – 25-29 April 1988. 77-108 p.

Alimoso, S.B. 1994. The development of an improved statistical system for the fisheries of Malawi. *In* D. Tweddle (ed.) Proc. Fisheries Research Symposium. Department of Fisheries Bulletin No. 33. Lilongwe. 12-18 p.

Allen, T.F.H. & Starr, T.B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago. 310 pp.

Anderson L.G. & Lee D.R. 1986. Optimal governing instruments, operation level, and enforcement in natural resource regulation: the case of the fishery. Ame. J. Agric. Econ. 68(3): 678–90.

Anderson, L.E. & Thompson, P.C. 1991. Development and implementation of the angler diary monitoring programme for Great Bear Lake, Northwest Territories. American Fisheries Society Symposium 12: 457-475.

Anon. 1999. Basic ecosystem principles, goals and policies. A report to the Congress by the Ecosystem Principles Advisory Panel. National Marine Fisheries Service. Silver Spring, MD. 62 pp.

Arthington, A.H., & D.A. Milton. 1986. Reproductive biology, growth and age composition of the introduced *Oreochromis mossambicus* (Cichlidae) in two reservoirs, Brisbane, Australia. Environmental Biology of Fishes 16(4): 257-266.

Arthur, R., Hartmann, W., Bhaumik, U., Prein, M., Dey, M., Saha, N. & Biswas, S.N. 2004. Fisheries and adaptive learning. Mekong River Commission. Kolkata, India. Brief No. 4. 2 pp.

Bailey, R.G. 1986. The Zaire River system. *In* B.R. Davies and K.F. Walker (eds.) Ecology of river systems. Dr. W. Junk Publishers, Dordrecht, Netherlands, 201-213 pp.

Balarin, J.D. & Hatton, J.P. 1979. Tilapia. A guide to their biology and culture in Africa. Unit of Aquatic Pathology, University of Stirling, Scotland. 174 pp.

Baldwin, D.S. & A.M. Mitchell. 2000. The effect of drying and re-flooding on the sediment and soil nutrient dynamics of lowland rover-floodplain systems: a synthesis. Regl. Rivers: Res. Mgmt. 16: 457-467.

Bardach, J.E., Ryther, J.H. & McLarney, W.O. 1972. Aquaculture-the farming and husbandry of freshwater and marine organisms. Wiley_Interscience, New York. 868 pp.

Barnes, B.V. 1984. Forest ecosystem classification and mapping in Baden-Württemberg,
West Germany. *In:* J.G. Bockheim, (ed.) Proceedings of the symposium on Forestland classification: experience, problems, perspectives; 1984 March; Madison, WI. NCR-102. Madison, WI: North Central Forest Soils Committee; Society of American Foresters; U.S. Department of Agriculture, Forest Service and Soil Conservation Service: 49-65.

Bayley, P.B. 1981. Fish yield from the Amazon in Brazil: comparison with Africa river yields and management possibilities. Trans. Am. Fish. Soc., 110:351-359.

Bayley, P.B. 1988. Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. Env. Biol. Fish 21(2) 127-142.

Bayley, P.B. 1991. The flood-pulse advantage and the restoration of the river-floodplain systems. ***Regulated Rivers*** 6: 75-86.

Bayley, P.B. and Li, H.W. 1992. Riverine fishes. Chap. 12 In: Calow & Petts (eds.) The rivers handbook Vol. 1 253-281.

Batschelet, E. 1981. Circular statistics in biology. *In* R. Gibson and J. Cohen (eds.) Mathematics in biology series. Academic Press, London. 371 pp.

Bazigos, G.P. 1972. The improvement of the Malawian fisheries statistical system. Rome, FAO, FAO.MLW/16:23 pp.

Bazigos, G.P. 1974. The design o fisheries statistical surveys – Inland waters. FAO Fish.Tech.Pap., 133: 122pp

Beamish, R.J. & McFarlane, G.A. 1987. Current trends in age determination methodology. pp. 15-42. *In* R.C. Summerfelt & G.E. Hall (eds.) Age and Growth of Fish. Iowa State University Press, Ames.

Begg, G.W. 1970. Limnological observations on Lake Kariba during 1967 with emphasis on some special features. Limnol. Oceanogr. 15: 776-788.

Beilfuss, R. 1999. Restoring the flood: a vision for the Zambezi Delta. International Crane Foundation. 5 pp

Bell, K.N.L., Pierre, P, & Brown, J.A. 1995. Seasonal, inverse cycling of length–age –at–recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* (Pisces) in Dominica, West Indies. Can. J. Fish. Aquat. Sci. 52: 1535-1545.

Bell, K.N.I. 1999. Introduction to circular and periodic variables, their statistics and periodic regression. J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown, 6140, South Africa. 13pp.

Ben-Tuvia, A. 1959. The biology of cichlid fishes of Lake Tiberias and Huleh. Bull. Res. Counc. Isr., Sect. B: Zool. 8B: 152-188.

Beverton, R.J.H. & Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II (London), 19:1-533.

Binns, NA & Eiserman, FM. 1979. Quantification of fluvial trout habitat in Wyoming. Trans. Amer. Fish. Soc. 108: 215-28.

Birth, H.F. 1960. Nitrification of soils after periods of dryness. Plant and Soil, 12: 81-96.

Bliss, C.I. 1970. Statistics in biology. Statistical methods for research in the natural sciences – Volume Two. McGraw-Hill Book Company, New York. 639 p.

Bell-Cross, G 1968. The distribution of fishes in central Africa. Fish. Res. Bull. (Zambia) (1965-66) 4: 3-20.

Bolger, T. & Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. 34, 171-182.

Bonetto, A.A., Dioni, W. & Pignalberi, C. 1969. Limnological investigations on biotic communities in the middle Parana River valley. Verh.Int.Ver.Theor.Angew.Limnol., 17:1035-50.

Bootsma, H.A. and Hecky, R.E. 1999. Water quality Report: Lake Malawi/Nyssa Biodiversity Conservation Project. SADC/GEF Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project, Senga Bay.

Booth, A.T., Merron, G.S. & Buxton, C.D. 1995. The growth of *Oreochromis andersonii* (Pisces: Cichlidae) from the Okavango Delta, Botswana, and a comparison of scale and otolith methods of ageing. Envi. Bioil. Fish. 43: 171-178.

Booth, A.T. & Merron, G.S. 1996. The age and growth of the greenhead tilapia *Oreochromis macrochir* (Pisces: Cichlidae) from the Okavango Delta, Botswana. Hydrobiologia, 321:29-34.

Botnariuc, C.A. 1967. Some characteristic features of the floodplain ecosystems of the Danube. Hydrobiologia, 8:39-49.

Bowen, S.H. 1979. A nutritional constraint in detrivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Ecological monographs, 17-31.

Bowen, S.H. 1979. A nutritional constraint in detrivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. Ecological monographs, 17-31.

Bowen, S.H. & Allanson, B.R. 1982. Behavioural and trophic plasticity of juvenile *Tilapia mossambicus* in utilisation of the unstable littoral habitat. Env. Biol. Fish.7: 357-362.

Brinkman, W.A.R. 1983. Association between net basin supplies to Lake Superior and supplies to the lower Greta Lakes. J. Great Lakes Res. 9: 32-39.

Brinkmann, W.A.R. 2000. Causes of variability in monthly Great Lakes water supplies and lake levels. Clim Res., 15:151-160.

Bryan,C.F. & D.A. Rutherford. 1993.Impacts on warm water streams: guidelines for evaluation. So. Div. Am. Fish Soc., Little Rock, Arkansas, USA. 285 pp.

Bruton, M.N. & Allanson, B.R. 1974. The growth of *Tilapia mossambicus* Peters (Pisces: Cichlidae) in Lake Sibaya, South Africa. J. Fish Biol. 6: 701-715.

Bruton, M.N. & Allanson, B.R. 1980. Growth of *Clarias gariepinus* in Lake Sibaya, South Africa. S. Afr. J.Zool. 15:7-15.

Bruton M.N. & Boltt, R.E. 1975. Aspects of the biology of *Tilapia mossambicus* Peters (Pisces: Cichlidae) in a natural freshwater (Lake Sibaya, South Africa). J. Fish Biol. 7: 423-445.

Bruton, M.N. 1979. The breeding biology and early development of Clarias gariepinus (Pisces: Clariidae) in Lake Sibaya, South Africa with a review of breeding in species of bygenus Clarias (Clarias), Trans. Zoo. Soc. Lond. 35, 1-45.

Bruton M.N. & Jackson, B.N. 1983. Fish and fisheries of wetlands. J. Limno. Soc. Sth. Afr., 9(2): 123-133.

Bruton, M.N. 1989. The ecological significance of alternative life-history styles. *In:* Bruton, M.N. (Ed.) Alternative Life-History styles of animals. Kluwer Academic Publishers, Dordrecht: 503-553.

Bruton, M.N. 1996. Alternative life-history strategies of catfishes. Aquatic Living Resources 9 (Hors serie): 35-41.

Buckland, S.T. 1984. Monte Carlo confidence intervals. Biometrics 40: 811-817.

Bulirani, A. E., M.C. Banda, Ó.K. Pálsson, O.L.F. Weyl, G.Z. Kanyerere, M.M. Manase, and R.D. Sipawe. 1999. Fish stock and fisheries of Malawian waters. Resource Report 1999. Fisheries Research Unit, Department of Fisheries, Monkey Bay. 55 pp.

Butterworth, D.S., Punt, A.E., Borchers, D.L. Pugh, J.B. & Hughes, G.S. 1989. A manual of mathematical techniques for line-fish assessment. S. Afr. Nat. Sci. Prog. Rep. 160: 1-89.

Caissie, D., El-Jabi, N. & Satish, M.G. 2001. Modelling of maximum daily water temperature in a small stream using air temperature. J. Hydrol. 251: 14-28.

Cantrell, M.A. 1977. Possible environmental changes in response to hydroelectric development of the Shire Basin (Malawi). Pp. 144-149. *In* I: The aquatic environment. Proceedings of the International Conference: Kainji Lake and River Basin Development in Africa, Ibadan, Nigeria.

Carey, T.B. 1971. Hydrological survey of the Kafue floodplains. Fish.Res.Bull., Zambia, 5: 245-95

Carlander, K.D. 1987. A history of scale age and growth studies of North American freshwater fish. pp. 3-14. *In* R.C. Summerfelt & G.E. Hall (eds.) Age and Growth of Fish. Iowa State University Press, Ames.

Caswell, H. 1976. The validation problem. 313-325 pp *In:* B. C. Patten (eds.) Systems analysis and simulation in ecology. Vol. 4. Academic Press, New York. 593 pp.

Caulton, M.S. 1975. The ability of cichlid fishes *Tilapia rendalli* Boulenger, *Tilapia sparrmanii* A. Smith and *Hemihaplochromis* (= *Psedocrenilabrus*) *philander* (M. Weber) to enter deep water. J. Fish Biol. 7: 513-517.

Caulton, M.S. 1977. The importance of habitat temperature for growth in the tropical cichlid *Tilapia rendalli* Boulenger. J. fish. Biol. 13:549-553.

Caulton, M.S. 1978. The importance of habitat temperature for growth in tropical cichlid *Tilapia rendalli* Boulenger. J. Fish Biol. 13: 99-122.

Chapman, D.W., Miller, W.H., Dudley, R.G., Scully, R.J. 1971. Ecology of fishes in the Kafue River. FI:SF/ZAM 11 Technical Report 2. 66 p, FAO, Rome.

Chapman, D., Codrington, S., Blong, R., Dragovich, D., Smith, T.L., Linacre, E., Riley, S., Short, A., Spriggs, J. & Watson, I. 1985. Understanding Our Earth. Pitman Publishing, Victoria.

Chervinski, J. 1982. Environmental physiology of tilapias. pp. 119-128 *In:* R.S.V. Pullin & R.H. Lowe-McConnell (eds.) The Biology and Culture of Tilapias. ICLARM. Conf. Proc.7, 432p.

Chimatiro, S.K. & Mwale, D. 1998. A Participatory Rural Appraisal on socio-economic impact of water hyacinth on the Lower Shire Floodplains, Malawi. CAB International Report, July 1998, 101pp.

Christensen, V. & Pauly, D. 1992. ECOPATH II – a software for balancing steady state models and calculating network characteristics. Ecol. Modelling. 61: 169-185.

Christensen, V. & Pauly, D. 1995. Fish production, catches and the carrying capacity of the world oceans. NAGA, the ICLARM Q. 18(3):34-40.

Chow, V.T. 1964. Statistical and probability analysis of hydrological data. Part I. Frequency analysis. *In*: V.T. Chow (ed.) Handbook of Applied Hydrology. McGraw-Hill, New York.

Cluis, D. 1972. Relationship between stream water temperature and ambient air temperature – a simple autoregressive model for mean daily stream water temperature fluctuations. Nordic Hydrology 3(2), 6571.

Clarke, K.R. 1993. Non-parametric multivariate analyses of change in community structure. *Aust. J. Ecol.* 18:117-143.
Clarke, K.R. 1993. Non-parametric multivariate analyses of change in community structure. *Aust. J. Ecol.* 18:117-143.

Clarke, K.R. & Warwick, R.M. 1994. Primer 5 for Windows (Computer programme). Plymouth Routines in Multivariate Ecological Research. Plymouth.

Clarke, K.R. & Warwick, R.M. 1997. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth. 45 pp.

Claytor, R.R. & O'Neil, S.F. 1991. Using small creel surveys and mark-recapture experiments to interpret angling statistics. Am. Fish. Soc. Symp. 12: 195-205.Heggenes, J. 1987. Random stratified creel surveys in the three Norwegian rivers with low fishing intensity. N. Am. J. Fish. Man. 7: 363-368.

Coche, A.G. 1974. Limnological study of a tropical reservoir. (*In*) E.K. Balon and A.G. Coche (eds.) Lake Kariba: a man-made tropical ecosystem in Central Africa. Monographiae Biologicae 24, Dr. W. Junk publishers, The Hague. 75-183 pp.

Coe, M. 1966. The biology of *Tilapia grahami* in L. Magadi, Kenya. Acta Tropica, 23: 146-177.

Conrad, V. & L.W. Pollak. 1950. Methods in climatology. Second edition, revised and enlarged. Harvard University Press, Cambridge, Massachusetts, 459p.

Copes P. 1986. Critical review of the individual quota as a device in fisheries management. *Land Economics.* 62(3):278–91.

Costa-Pierce B.A. 2003. *In*: B.A. Costa-Pierce, (ed.) *Ecological Aquacultur*e. Blackwell Science, Oxford, UK. 103-124 pp.

Cramer, W. & 43 others. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. Global Change Biol. 5 (Suppl. 1): 1-15.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. *Rapp.P.-v.Réun.CIEM,* 177:307-313

Cushing, D.H. 1988. The study of stock and recruitment. pp. 105-128 *In*: J.A. Gulland (ed.), Fish population dynamics: the implications for management, Chichester, John Wiley and Sons Ltd., 422 p.

Davies, B.R. 1986. The Zambezi river system. pp. 225-267 *In* B.R. Davies & K.F. Walker (eds.) Ecology of river systems. Dr. W. Junk Publishers, Dordrecht.

Davis, S.N. & DeWiest, R.J.M. 1966. Hydrogeology. John Wiley & Sons. New York.

Davis, G.E. & Warren, G.E. 1971. Estimation of food consumption. Pp. 227-248. *In* W.E. Ricker (ed.) Methods for assessment of fish production in freshwater. IBP Handbook No. 3. Blackwell Scientific Publ., Oxford.

De Moor, F.C., Wilkinson, R.C. & Herbst, H.M. 1986. Food and feeding habits of *Oreochromis mossambicus* (Peters) in hypertrophic Hardebeespoort Dam, South Africa. S. Afr. J. Zool. 21: 170-176.

Degnbol, P. 2001. The knowledge base for fisheries management in developing countries - Alternative Approaches and Methods. Report to Nansen Programme Seminar on Alternative methods for Fisheries Assessments in Development 24-25/1 2001, Bergen Norway. 8 pp.

Downing, J.A. 1991. Comparing apples and oranges: methodological problems in comparative ecosystem analysis. p. 24-45 *In:* J.J. Cole (ed.), Comparative analyses of ecosystems: patterns, mechanisms, and theories. Springer-Verlag, New York.

De Silva, S.S. 1986. Reproductive biology of *Oreochromis mossambicus* populations of man-made lakes in Sri Lanka: a comparative study. Aquacult. Fish. Manag. 17: 31-47.

Dickie, L.M. & Kerr, S.R. 1982. Alternative approaches to fisheries management. Pp. 18-23. *In* M.C. Mercer (ed.) Multispecies approaches to fisheries management advice. Can. Spec. Publi. Fish. Aquat. Sci. 59.

Dudley, R.G. 1979. Changes in the growth and size distribution of *Sarotherodon macrochir* and *Sarotherodon andersonii* from the Kafue floodplain, Zambia, since construction of the Kafue Gorge Dam. J. Fish Biol. 14: 205-223.

Efron, B. 1982. The jacknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, 92 pp.

Egborge, A.B.M. 1971. The chemical hydrology of the River Oshun, Western State, Nigeria. Freshwat. Biol. 1: 257-271.

Emmett, W.W. 1975. The channel and waters of the Upper Salmon River are, Idaho, *U.S. Geol. Surv. Prof.,* 870-A, 116 pp.

Ellenboek 1987) Ellenbroek, G.A. 1987. Ecology and productivity of an African wetland system. The Kafue Flats, Zambia. Dr. W. Junk Publishers, Dordrecht, the Netherlands, 267 p.

Etim, L., Lebo, P.E., & King, R.P. 1999. The dynamics of an exploited population of a siluroid catfish (*Scilbe intermedius* Reupell 1832) in the Cross River, Nigeria. Fish. Res. 40: 295-307.

FAO. 1997. FAO Technical guidelines for responsible fisheries. Fisheries Management, Food and Agriculture Organisation, Rome. No. 4: 82 pp.

FAO. 1999. Management guidelines for Asian floodplain river fisheries: Part 1. A spatial hierarchy and adaptive strategy for co-management; Part 2. Summary for DFID research. FAO *Fisheries Technical Paper Nos* 384/1; 384/2.FAO, Rome. 117 pp

Fowler, A. 1999. Potential climate change impacts on water resources in the Auckland region (New Zealand). Clim Res 11:221-245.

Fréon, P., C. Mullon and G. Pichon, 1992. CLIMPROD: Experimental interactive software for choosing and fitting surplus production models including environmental variables. *FAO Computerized Information Series (Fisheries)* No. 5. Rome, FAO, 82 p. (with programs on diskette)

Fryer, G., 1965 Predation and its effects on migration and speciation in African fishes: a comment with further comments by P.H. Greenwood, a reply by P.B.N. Jackson and a footnote and postscript by G. Fryer. Proc.Zool. Soc.Lond., 144:301–22

Faulkner, S.P. & C.J. Richardson. 1989. Physical and chemical characterisation of freshwater wetland soils. *(In)* D.A. Hammer (eds.) Constructed wetlands for Wastewater Treatment: Municipal, Industrial and Agricultural. Lewis Publishers, Michigan. 41-72 p.

Fernando, C.H. & J. Holcik, 1991. Fish in Reservoirs. Int. Rev. ges. Hydrobiol. 76:149-167.

Fisher, S.G. Grimm, N.B. 1991. Stream and disturbance: Are cross-ecosystem comparisons useful? pp. 196-221. (*In*) J. Cole, G.Lovett, and S. Findlay (eds.) Comparative analyses of ecosystems: patterns, mechanisms and theories. Springer-Verlag, New York.

Folk, R.L. 1980. Petrology of sedimentary rocks. Hemphill publishing, Austin, Texas.

Fong, P., Jacobson, M.E., Mescher, M.C., Lirman, D. & Harwell, M.C. 1997. Investigating the management potential of a seagrass model through sensitivity analysis and experiments. Ecological Applications, 7(1) 300-315.

Forman, R.T.T. & Moore, P.N. 1992. Theoretical Foundations for Understanding Boundaries in Landscape Mosaics *In:* Hansen, A.J. and Castri, F (eds.) Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows Springer-Verlag, New York 452 pp.

Foucher, R.P. & Fournier, D. 1982. Derivation of Pacific cod age composition using length-frequency analysis. N. Amer. J. Fish. Mgmt. 2: 276-284.

Furch, K. & Junk, W.J. 1985. Dissolved carbon in a floodplain lake of the Amazon and in the river channel. Mitt. Geol. Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd. 58: 285-298.

Furse, M.T., Kirk, R.C., Morgan, P.R. & Tweddle, D. 1979. Fishes: Distribution and biology in relation to changes. pp. 175-208. *In:* M. Kalk, M.J. McLachlan & C. Howard-Williams (eds.) Lake Chilwa – Studies of Change in a Tropical Ecosystem. Monographiae Biologicae 35. Dr. W. Junk Publishers, The Hague.

Fryer, G. & Iles, T.D. 1972. The Cichlid Fishes of the Great Lakes of Africa. Oliver & Boyd, Edinburgh, 641 pp.

Furch, K. 1984. Water chemistry of the Amazon basin: The distribution of chemical elements among freshwaters. pp. 167-99. *In*: Sioli, H. (Ed.) *The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and its Basin,* W. Junk, Dordrecht,

Furch, K. 1997. Chemistry of várzea and igapó soils and nutrient inventory of their flood plain forests. Pp. 47-67. *In*: Junk, W.J. (ed.) The Central Amazon Floodplain: Ecology of a Pulsing System.- Ecological Studies, Vol.126, Springer Verlag, Berlin.

Godshalk, G.L. & Wetzel, R. 1978. Decomposition in the littoral zone of lakes. (*In)* R.E. Good, D.F. Whigham and R.L. Simpson. Freshwater wetlands. Ecological processes and management potential. Proceedings of a conference held at Rutgers University, New Brunswick, N.J. Academic Press Inc. New York. 131-151 pp.

Gordon, N.D., McMahon, TA. & Finlayson, B.L. 1992. Stream hydrology: Ina introduction for ecologists. John Wiley & Sons, West Sussex, England. 526 p.

Goulding, M. 1980. The fishes and forest. Explorations in Amazonian natural history. Berkley, Los Angeles, University of California Press, 280 p.

Goulding,M. 1981. Man and fisheries on an Amazonian frontier. W. Junk, The Hague, 137 p.

Golternman, H.L., Clymo, R.S. & Omnstad, M.A.M. 1978. Methods for physical and chemical analysis of fresh waters, IBP Handbook No. 8, Blackwell, Oxford 214pp.

Graf, W.L. 1988. Fluvial processes in dryland rivers. Springer-Verlag, Berlin.

Greenwood, P.H. 1957. The reproduction of *Clarias mossambicus* in Lake Victoria. *In:* Second symposium on African Hydrobiology and Inland Fisheries, 1956. CSA Pub. No 25: 77-78.

Grey, D.L. 1986. The development and management of the Northern Territory barramundi (*Lates calcarifer*) fishery. 375-380 pp. *In:* J.L. Maclean, I.B. Dizon & I.V. Hosillos (eds.) The proceedings of the first Asian fisheries forum, Manila, Philippines, 26-31 May 1986.

Guest, C.S., Willson, K., Woodward, A.J., Hennessy, K., Kalkstein, L.S., Skinner, C., McMichael, A.J. 1999. Climate and mortality in Australia: retrospective study, 1979-1990, and predicted impacts in five major cities in 2030. Clim Res. 13: 1-15.

Gulland, J.A. 1983. Fish stock assessment: a manual of basic methods. Chichester, U.K., Wiley Interscience, FAO/Wiley series on food and agriculture, Vol. 1:223 p.

Gunderson, D.R. & Dygert, P.H. 1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. Int. Explor. Mer., 44: 200-209.

Hall, J.B., Valente, I.M. and Davies, B.R. 1977. The Zambezi River in Mozambique: the physico-chemical status of the Middle and Lower Zambezi prior to the closure of the Cabora Bassa Dam. Freshwat.Biol., 7:187-206.

Halcrow and partners. 1954. A report on the control and development of Lake Nyasa and the Shire River. Report to Govt. of Nyasalans. 18p.

Halls, A.S. 1998. *An assessment of the impact of hydraulic engineering on floodplain fisheries and species assemblages in Bangladesh*. Ph.D. Thesis. University of London. 526 pp.

Halls, A.S., Hoggarth, D.D. & Debnath, D. (1999) Impacts of hydraulic engineering on the dynamics and production potential of floodplain fish populations in Bangladesh. *Fisheries Management and Ecology* **6**: 261-285.

Halls, A. S., Debnath, K., Kirkwood, G.P., Payne, I. A. (2000). Density-dependent recruitment of *Puntius sophore*, in floodplain water bodies in Bangladesh. *Journal of Fish Biology* **56**, 915-922.

Halls, A.S., Kirkwood, G.P., & Payne, A.I. (2001). A dynamic pool model for floodplain river fisheries. *Ecohydrology & Hydrobiology* **1** (3): 323-339.

Hamilton, K. & Bergen, E.P. 1984. Methods to estimate aquatic habitat variables. Colorado State University, Denver.

Hamley, J.M. 1975. Review of gill net selectivity. J. Fish.Res.Bd.Can. 32: 1943-1969.

Hamman, K.C.D. 1980. Post-impoundment trends in the fish populations of the Hendrik Verwoerd Dam, South Africa. Journal of the Limnological Society of Southern Africa 6(2): 101-108.

Hastings, R.E. 1972. Fisheries Research Unit, Lower Shire. Interim report 1970-1972. Malawi Fish. Bull., (4): 96 p.

Hastings, R.E. 1973. Fisheries research unit: Lower Shire. Fisheries Department, Ministry of Agriculture and natural resources, Lilongwe, Malawi.

Hann, C.T. 1977. Statistical methods in hydrology. Iowa State University Press, Ames.

Harley, K.L.S. 1991. Commonwealth Science Council survey project on exotic floating African water weeds. Unpublished Survey Report, 30 p.

Harley, S.J., Millar, R.B. & McArdle, B.H. 2000. Examining the effects of changing the minimum legal sizes used in the Hauraki Gulf snapper (*Pagrus auratus*) fishery in New Zealand. Fish. Res. 45:179-187.

Harvey, A.M. 1969. Channel capacity and adjustment of streams to hydrologic regime. . *J. Hydrol.* 8, 82-98.

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

Heggenes, J. 1987. Random stratified creel surveys in the three Norwegian rivers with low fishing intensity. N. Am. J. Fish. Man. 7: 363-368.

Henderson, H.F. & Welcomme, R.L. 1974. The relationship of yield to the morpho-edaphic index and numbers of fishermen in Africa inland fisheries. CIFA Occ.Pap. 1, 19 pp.

Heiler, G., Hein T. & Schemer, F. 1995. Hydrological connectivity and flood pulses as the central; aspects for the integrity of a river-floodplain system. Regulated Rivers: Research and Management, 11 351-361.

Hilborn, R. & Walter, C.J. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman & Hall, New York. 570 pp.

Holcik, J. & I. Bastl. 1967. Ecological effects of water level fluctuations upon the fish populations in the Danube River floodplain in Czechoslovakia. Acta Sci. Natl. Acad. Sci. Bohemoslov. Bruno. 10, 3-46.

Hawkes, H.A. 1975. River zonation and classification. pp. 312-374. *In*: B.A. Whitton (ed.) River Ecology. Blackwell Scientific, Oxford.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. US. 82: 898-903.

Hoeing, J.M., Robson, D.S., Jones, C.M. and Pollock, K.H. 1993. Scheduling counts in instantaneous and progressive count methods for estimating sport fishing effort. N.Am. J. Fish. Man. 13: 723-736.

Hoggarth, D.D. & Kirkwood, G.P. 1996. Technical interactions in tropical floodplain fisheries of south and south-east Asia. *In:* I.G. Cowx (Ed.), Stock Assessment in Inland Fisheries. Fishing News Books, Oxford, 280–292 pp.

Hoggarth, D.D., Cowan, V.J., Halls, A.S., Aeron, T.M., McGregor, J.A., Garaway, C.A., Payne, A.I. & Welcomme, R.L. 1999. Management guidelines for Asian floodplain river fisheries, Part1: A spatial hierarchical and integrated strategy for adaptive co-management, Fisheries Technical Paper No. 384/1, Rome, FAO. 63 pp.

Holland, M.M., Risser, P.G. & Naiman, R.J. (eds.) 1991. Ecotones. Chapman & Hall, New York.

Howard-Williams, C. 1973. Characteristics of water and vegetation of Elephant marsh (*In*) R.E. Hastings (eds.) Fisheries research unit: Lower Shire. Fisheries Department, Ministry of Agriculture and Natural Resources, Lilongwe, Malawi.

Howard-William, C.M. & Junk, W.J. 1976. The decomposition of aquatic macrophytes with special reference to their role in the ecosystem. Arch. Hydrobiol., 79 (4): 446-464.

Huet, M. 1964. The evaluation of fish productivity in fresh waters. The coefficient of productivity. Verh.Int.Ver.Theor.Angew.Limnol., 15:524-8.

Huet, M., 1970. Traité de pisciculture. Ed. Ch. de Wyngaert, Bruxelles, 718 p.

Hughes, G.S. 1986. Examining methods of fitting age/length data to the von Bertalanffy growth curve with a view of applying a simplified version of the Beverton and Holt Yield per Recruit model. Unpublished internal Report, University of Cape Town, 70 pp.

Ibańez, M.S.R., P.R.S. Cavalcante, J.P. Costa Neto, R. Barbieri, J.P. Pontes, S.C.C. Santana, C.L.M. Serra, N. Nakamoto, & O. Mitamura. 2000. Limnological characteristics of three aquatic systems of the pre-Amazonian floodplain, Baixada Maranhense (Maranhão, Brazil). Aquatic Ecosystem Health and Management 3: 521-531.

Jaagus, J. & Ahas, R. 2000. Space-time variations of climatic seasons and their correlation with the phonological development of nature in Estonia. Clim. Res. 15:207-219.

Jackson, P.B.N. 1961. Ecological effects of flooding by the Kariba dam on the middle Zambezi fishes. Proceedings of the First Federal Science Congress 1960, Salisbury, Rhodesia, pp. 277-284.

Jackson, P.B.N. 1963. Ecological factors affecting the distribution of freshwater fishes in tropical Africa. Ann.Cape.Prov.Mus., 2:223-8.

Jalabert, B. & Zohar, Y. 1982. Reproductive physiology in cichlid fishes, with particular reference to *Tilapia* and *Sarotherodon*. pp. 129-140. *In:* R.S.V. Pullin & R.H. Lowe-McConnell (eds.) The Biology and Culture of Tilapias. ICLARM. Conf. Proc. 7, 432p.

Johnson, S.L., Richards, C., Host, G.E. & Arthur, J.W. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. Freshwater Biol., 37:193-208.

Junk, W.J. 1970. Investigations on the ecology and production biology of the floating meadows (*Paspalo echinochloetum*) on the middle Amazon. Part 1. The floating vegetation and its ecology. Amazoniana, 2(4): 449-95.

Junk, W.J. 1982. Amazonian floodplains: their ecology, present and potential use. Rev. Hydrobiol. Trop. 15 4 285-301.

Junk, W.J, Soares, G.M. & Carvalho, F.M. 1983. Distribution of fish species in a lake of the Amazon River floodplain near Manaus (Lago Cameleao), with special reference to extreme oxygen conditions. Amazonian, 7: 397-431.

Junk, W.J., Bayley, P.B. and Sparks R.E. 1989. The flood-pulse concept in river-floodplain systems. *In* D.P. Dodge (eds.) Proceedings of the International Large River Symposium. Can. Spec. Publ. Aquat.Sci. 106, 110-127.

Junk, W.J. 1997. General aspects of floodplain ecology with special reference to Amazonian floodplain. *In:* W.J. Junk (ed.) The Central Amazon Floodplain. Ecology of a pulsing system. Springer, Berlin. 3-20 pp.

Kalk, M., McLachlan, A.J. & Howard-Williams, C. (eds.) 1979. Lake Chilwa – Studies of Change in a Tropical Ecosystem. Monographiae Biologicae 35. W. Junk Publishers, The Hague.

Kalowekamo, F. 2000. Wildlife management in the Lower Shire. Community Partnerships for Sustainable Resource Management in Malawi (COMPASS), Blantyre, Malawi, 20pp.

Kapetsky. J.M. 1974. The Kafue river floodplain: an example of pre-impoundment potential fir fish production. 497-523 pp. *In:* E.K. Balon & A.G. Coche (eds.) Lake Kariba: a man-made tropical ecosystem in Central Africa. The Hague, W.Junk,

Kapetsky. J.M. 1998. Geography and constraints on inland fishery enhancements. 37-63 pp. *In:* T. Petr (ed.) Inland Fishery Enhancements. FAO Fisheries Technical Paper No. 374, FAO, Rome.

Kapetsky, J.M. 2000. Present applications and future needs of meteorological and climatological data in inland fisheries and aquaculture. Agricultural and Forest Meteorology 103:109-117.

Karenge, L. & Kolding, J. 1995. On the relationship between hydrology and fisheries in man-made Lake Kariba, central Africa. Fish. Res. 22: 205-226.

Kashau, D. & Chimatiro, S.K. 1997. Participatory Fisheries Resource Management Project for Dinde and Elephant Marshes Nsanje. District Development Sectoral Action Plan, Nsanje District. 12 pp.

Kastner-Maresch, A.E. & Mooney, H.A. 1994. Modelling optimal plant biomass partitioning. Ecological Modelling 75/76: 5-20.

King, M. 1995. Fisheries biology, assessment and management. Fishing News Books, Blackwell Science Ltd. Oxford. 341 pp.

Kolbing, A. 1978. The European method of fish harvest prediction in fluvial systems. Environ. Biol. Fish., 5(3) 249-51.

Kolding, J. 1994. On the ecology and exploitation of fish in fluctuating tropical freshwater systems. Thesis for the partial fulfilment of the dr. scient. Degree. University of Bergen, Norway.

Kolasa, J. & Zalewski, M. 1995. Notes on ecotone attributes and functions. *In*: F. Schiemer, M. Zalewski, & J.E. Thorpe (eds.) The Importance of Aquatic-Terrestrial Ecotones for Freshwater Fish. Hydrobiologia 303: 1-7.

Kirkwood, G.P. & Walker, T.I. 1986. Gill mesh selectivity for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australia waters. Aust.J.mar.Freshwat.Res 37: 689-697.

Kok, H.M. 1980. Ecological studies of some important fish species of the Pongolo floodplain, Kwazulu, South Africa. Ph.D. thesis, University of Natal, Pietermaritzburg.

Krykhtin, K.L. 1975. Causes of periodic fluctuations in the abundance of the non-anadromous fishes of the Amur River. J.Ichthyol., 15(5):826-9.

Knighton, A.D. & Nanson, G.C. 2001. An event-based approach to the hydrology of arid zone rivers in the Channel Country of Australia. J. Hydrol. 254:102-123.

Knight, D.W. & Shiomo, K. 1996. River channel and floodplain hydraulics. pp. 139-181. *In* M.G. Anderson, Walling, D.E. & Bates, P.D. (eds.) Floodplain processes. Wiley, Chichester.

Kvist, L.P. & Nebel, G. 2001. A review of a Peruvian floodplain forest: ecosystems, inhabitants and resource use. For. Ecol. Manage. 150: 3-26.

Kvist, L.P.,Andersen, M.K., Stagegard, J., Heselsøe, M. & Llapapasca, C. 2001. Extraction from woody forest plants in floodplain community in Amazonian Peru: evaluation, choice and conservation status of resources. For. Ecol. Manage. 150: 147-174.
Lae, R. 1992. Influence de l'hydrobiologie sur l'evolution des pecheries du delta
Centrale du Niger, de 1966 a 1989. *Aquat. living Resources.,* 5:115-126.

Leopold, L.B., Wolman, M.G. & Miller, J.P. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco.

Leopold, L.B. & H.E. Skibitzke. 1967. Observations on unmeasured rivers. *Geogr. Ann.*, 49, 247-255.

Levin, S.A. & Segel, L.A. 1985. Pattern generation in space and aspect. Society for Industrial Applied Mathematics (SIAM) Review 27: 45-67.

Le Roux, P.J. 1961. Growth of *Tilapia mossambicus* Peters in some Transvaal impoundments. Hydrobiologia, 18: 165-175.

Lieth. H. 1975. The primary productivity in ecosystems: comparative analysis of global patterns. pp. 67-88. *In* W.H. van Dobben & R.H. Lowe-McConnell (eds.) Unifying concepts in ecology. Dr. W. Junk, Hague.

Lieth, H. 1976. The use of correlation models to predict primary production from precipitation or evapotranspiration. pp. 392-406. *In* O.L. Langr, L.Kappen & E.-D. Shulze (eds.) Water and plant life. Ecological Studies, Vol. 19. Springer-Verlag, Berlin.

Lineham, S. 1972. Climate 1 : Wind and weather. *In* S. Agnew and M. Stubbs (eds.) Malawi in Maps. University of London Press LTD, 26-27 pp.

Lorenze, C.M. 1997. Concept of river ecology: implications for indicator development. Regul. Rivers: Res. Mgmt. 13: 501-516.

Lotspeich, F.B. 1980. Watersheds as a natural classification system, Water Resour. Bull, 16, 581-6.

Loubens, G., 1969. Etude de certains peuplements ichtyologiques par des pêches au poison (lre note), Cah. ORSTOM (Hydrobiol.), 3(2):45–73

Lowe-McConnell, R.H. 1958. Observations on the biology of *Tilapia niloticus* Linné in East African waters. Revue Zool. Bot. Afr. 57: 130-170.

Lowe-McConnell, R.H. 1964. The fishes of the rupununi savanna district of British Guiana, Pt 1. Grouping of fish species and effects of the seasonal cycles on the fish. Journal of the Linnean Society (Zoology), 45: 103-144.

Lowe-McConnell, R.H. 1967. Some factors affecting fish populations in Amazonian waters. *In*: *Atas do simposio sobre a biota Amazonia, Conselho Nacional Pesquisas,* pp. 117-86. Consevacao de Natureza e Recursos Naturais, Rio de Janiero.

Lowe-McConnell, R.H. 1975. Fish communities in tropical freshwaters. Longman, London. 302 pp.

Lowe-McConnell, R.H. 1979. Ecological aspects of seasonality I fishes of tropical waters. Symposia of the Zoological Society of London, No. 44: 219-241.

Lowe-McConnell, R.H. 1982. Tilapia in fish communities. pp. 83-113. *In:* R.S.V. Pullin & R.H. Lowe-McConnell (eds.) The Biology and Culture of Tilapias. ICLARM. Conf. Proc. 7, 432p.

Lowe-McConnell, R.H. 1987. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge. 382p.

Lund, J.W.G. 1965. The ecology of freshwater phytoplankton. *Biol. Rev.* 40:231-293.

Maida, J.H.A. 1978. Phosphate availability indices related to phosphate fractions in selected Malawi soils. J. Sci. of Food. Agric. 29: 423-428.

Maida, J.H.A. 1980. The potassium status of Malawi soils. J. Soil. Sci. 31: 595-606.

Maida, J.H.A. 1985. Some physical and chemical properties of selected Malawi soils. Luso: J. Sci. Tech. 6(1): 1-10.

Malawi Fisheries Department. 1989. Fish landings in lakes of Malawi 1976-89. Ministry of Forestry and Natural Resources. Lilongwe, Malawi. 15 pp.

Malawi Government. 1997. Fisheries Conservation and Management Act.1997. Ministry of Forestry, Fisheries and Environmental Affairs, Lilongwe, Malawi. 38 pp.

Malawi Government. 2000. Fisheries Conservation and Management (Local Community Participation) Rules, 2000. (No. 25 Of 1997). Lilongwe, 12 pp.

Malvestuto, S.P., Davis, W.D. & W.L. Shelton. 1978. An evaluation of the roving creel survey with nonuniform probability sampling. Transaction of the American Fisheries Society, 107: 255-262.

Malvestuto, S.P. 1983. Sampling recreational fishery. *In* L.A. Nielsen, and D.L. Johnson (eds.) Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Mann, R.H.K. & Mills, C.A. 1985. Variation in the sizes of gonads, eggs and larvae of the dace, *Leuciscus leuciscus,* Enviro. Bio. Fish. 13: 277-287.

Mannoch, C.S. 1982. Aging of reef fishes in the Southeast Fisheries Centre. *In* G.R. Huntsman, W.R. Nicholas, W.W. Fox, Jr. (eds.) Proceedings of a workshop, 7-10 October 1980, St. Thomas, Virgin Island, USA. NOAA Technical Memorandum, NMFS-SEFL-80: 24-43.

Mann, K.H. 1988. Towards predictive models for coastal marine ecosystems. pp. 291-316. *In* L.R. Pomeroy & J.J. Alberts (eds.) Concept of ecosystem ecology: A comparative view. Studies in ecology vol. 67. Springer-Verlag, New York.

Marshall, B.E. 1984. Towards predicting ecology and fish yields in African reservoirs from pre-impoundment physico-chemical data. CIFA Tech. Pap. 12, 36 pp.

Marshall, B.E. 1982. The influence of river flow on pelagic sardine catches in L. Kariba. J.Fish Biol., 20:465-69.

May, R.M. 1984. The effects of spatial scale on ecological questions and answers. Pp. 1-17. *In* P.J. Edwards, R.M. May & N.R. Webb (eds.) Large-scale ecology and conservation biology. Blackwell, Oxford.

McCarthy, T.S., Bloem, A., Larkin, P.A. 1998. Observations on the hydrology and geohydrology of the Okavango Delta. SA J. Geo. 101: 101-117.

Mengel, K. & Kirkby, E.A. 1982. Principles of plant nutrition, 3rd ed. International Potash Institute, Bern, Switzerland.

Mercer, M.C. (ed.), 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59. Government Canada, Fisheries and Oceans, Ottawa, Canada.

Merron, G.S. 1991. The ecology and management of the fishes of the Okavango Delta, Botswana, with particular reference to the role of the seasonal floods. PhD Thesis. Rhodes University, Grahamstown, South Africa, 171 pp.

Merron, G.S. & M.N. Bruton. 1995. Community ecology and conservation of fishes of the Okavango Delta, Botswana. Environmental Biology of Fishes 43: 109-119

Merron, GS & Mann, BQ. 1995. The reproductive and feeding biology of *Schilbe interdedius* in the Okavango Delta, Botswana. *Hydrobiologia* 308: 121-129.

Miller, D.R., Weidhaas, D.E. & Hall, R.C. 1973. Parameter sensitivity in insect population modelling. Journal of Theoretical Biology, 42: 263-274.

Miller, R.G. 1974. The jack-knife - a review. Biometrika, 61:1–15

Millar, R.B. 1995. The functional form of hook and gillnet selection curves cannot be determined from comparative catch data alone. Can. J. Fish. Aquat. Sci. 52: 883-891.

Milne, B.T., Johnson, A.R., Keitt, T.H., Hatfield, C.A., David, J. & Hraber, P.T. 1996. Detection of critical densities associated with Piñon-Juniper woodland ecotones. Ecology, 77(3): 805-821.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetation. 69: 89-108.

McKnight, T.L. 1990. Physical Geography, 3rd Edition, Prentice-Hall, Englewood Cliff, New Jersey.

McMahon, T.A. 1979. Hydrological characteristics of arid zones. Pp. 105-123. *In* The hydrology of areas of low precipitation. Procs. Camberra Symp., IAHS Publ. 128pp.

McMahon, T.A. 1982. Hydrological characteristics of selected rivers of the world. UNESCO, Paris.

McNeish, J.D. and Trial, J.G. 1991. A cost-effective method for estimating angler effort from interval counts. Am. Fish. Soc. Symp. 12: 236-243.

Momen, B. & Zehr, J.P. 1998. Watershed classification by discriminant analysis of lakewater-chemistry and terrestrial characteristics. Ecological Applications, 8, 497-507.

Montreuil, V., Tello, S., Maco, J., Ismino, R. 1990. Maximum sustainable yield of commercial fisheries in the Department of Loreto, Peru. FISHBYTE, 8:13-14.

Moreau, J. 1987. Mathematical and biological expression of growth in fishes: Recent trends and further developments. Pp. 81-113. *In* R.C. Summerfelt & G.E. Hall (eds.) Age and Growth of Fish. Iowa State University Press, Ames.

Moreau, J., Cronberg, G., Game, I., Hustler, K., Kautsky, N., Kiibus, M., Machena, C. & Marshall, B. 1997. Biomass flows in Lake Kariba, towards an ecosystems approach. Pp. 219-230. *In*: J. Moreau (ed.) Advances in the Ecology of Lake Kariba. University of Zimbabwe Publications. Harare, Zimbabwe.

MRAG. 1994. Potential yield of South Asian small reservoir fisheries. Final Report. Fisheries Management Science Programme. Overseas Development Administration.

Mulholland, P.J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecol. Mongr. 51: 307-322.

Murphy, B.R. & Willis, D.W. 1996. Fisheries techniques. 2nd ed. Amer. Fish. Soc. Bethesda, Maryland .

Neter, J., Wasserman, W. & Whitmore, G.A. 1979. Applied statistics. Ally and Bacon, Boston.

Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London. 352 p.

Noakes, D.L.G. & Balon, E.K. 1982. Life histories of tilapias: an evolutionary perspective. Pp. 61-82. *In*: R.S.V. Pullin & R.H. Lowe-McConnell (eds.) The Biology and Culture of Tilapias. ICLARM Conf. Proc., 7. Manila, Philippines.

Odum, E.P. 1967. The strategy of ecosystem development. Science, Wash 164: 262-270

Odum, E.P. 1993. Ecology and our endangered life-support systems. 2nd ed. Sinauer associates, Inc. Massachusetts.

Ogutu-Ohwayo, R. 1993. The impact of predation by Nile perch, *Lates niloticus* L. on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. Conservation Biology 7: 701-711.

Olatunde, A.A. 1978. Sex, reproductive cycle and variations in the fecundity of the family Schilbeidae (Osteichthyes: Siluridae) in Lake Kainji, Nigeria. Hydrobiologia, 57: 125-142.

O’Neill, R.V., Johnson, A.R. & King, A.W. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology 3: 193-205.

Pannella, G. 1974. Otolith growth patterns: an aid to age determination in temperate and tropical fishes. Pp. 28-39. *In*: T.E. Bagenal (ed.) Ageing of Fishes. Unwin Brothers, London.

Pauly, D. 1980. On the interpretation between natural mortality, growth parameters and mean environmental temperature in 175 stocks of fish. J. Cons. Int. Explor. Mer., 39: 175-192.

Pauly, D. 1981. The relationship between gill surface area and growth performance in fish: a generalisation of von Bertalanffy’s theory of growth. Meeresforschung 28(4): 251-282.

Pauly, D. & Munro, J.L 1984. Once more on the comparison of growth in fish and invertebrates. ICLARM, Fishbyte, 2:21.

Pauly, D. 1987. Application of information on age and growth of fish to fishery management. Pp. 495-506. *In* R.C. Summerfelt & G.E. Hall (eds.) Age and Growth of Fish. Iowa State University Press, Ames.

Payne, A.I. 1986. The ecology of tropical lakes and rivers. John Wiley & Son, Chichester.

Pedro, G. 1973. Pedogenesis in the humid tropics and the dynamics of potassium. pp. 23-49. *In* Potassium in tropical crops and soils. Proceedings of the 10th Colloquium. International Potash Institute, Bern, Switzerland.

Peterson, D.L. & Parker, V.T. (eds.) 1998. Ecological scale: Theory and applications. Columbia University Press, New York.

Petts, G. & I. Foster. 1985. Rivers and landscape. Edward Arnold, Baltimore, Maryland USA, 274 pp.

Pianka, E.R. 1988. Evolutionary ecology. 4th ed. Harper & Row. New York.

Pike, J.G. 1972. Hydrology. *In* S. Agnew and M. Stubbs (eds.) Malawi in Maps. University of London Press LTD, 34-35 pp.

Pitcher, T.J. & Hart, P.J.B. 1982. Fisheries ecology, 1st edn.. Chapman & Hall, London.

Pickup, G. and R.F. Warner. 1976. Effects of hydrologic regime on magnitude and frequency of dominant discharge. *J. Hydrol.*, 29, 51-75.

Plisnier, P-D. 1997. Climate, limnology and fisheries changes of Lake Tanganyika, Research for the Management of the Fisheries on Lake Tanganyika (GCP/RAF/271/FIN-TD/72(En). FAO/FINNIDA, Bujumbura, Burundi.

Pringle, C.M. 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. Ecological Applications, 11 (4): 981-998.

Price, R.K 1973. Flood routing methods for British rivers. Proceedings of the Institute of Civil Engineers 55, 913-30.

Porth, L.S., Boes, D.C., Davis, R.A., Troendle, C.A. & King, R.M. 2001. Development of a technique to determine adequate sampling sizes using subsampling and return interval estimating. J. Hydrol. 251: 110-116.

Pollock, K.H., C.M. Jones, T.L. Brown. 1994. Angler survey methods and their applications in fisheries management. Amer. Fish. Soc. Spe. Publ. 25, Bethesda, Maryland. 369 pp.

Petr, T. 1986. The Volta River System. *In* B.R. Davies and K.F. Walker (eds.) Ecology of river systems. Dr. W. Junk Publishers, Dordrecht, Netherlands, 163-183 pp.

Pielou, E.C. 1977. Mathematical ecology. John Wiley, New York

Polovina, J.J. 1984. Model of a coral reef ecosystem. The ECOPATH model and its application to French Fregate Shoal. Coral Reefs, 3: 1-11.

Pullin R.S.V.& Lowe-McConnell R.H. (eds.) . 1982. The Biology and Culture of Tilapias. ICLARM. Conf. Proc. 7, 432p.

Punt, A.E. 1993. The comparative performance of production-model and ad hoc tuned VPA based feedback-control management procedures for the stock of Cape hake The use of spawner-biomass-per-recruit in the management of linefisheries. Special Publication of the Oceanographic Research Institute, Durban, 2: 80-89.

Punt, A.E., Pulfrich, A., Butterworth, D.S. & Penney, A.J. 1996. The effect of hook size on the size-specific selectivity of hottentot *Pachymetopon blochi* (Val.) and on yield-per-recruit. S.Afr.J.Mar.Sci. 17:155-172.

Qui, S. & McComb, A.J. 1995. Planktonic and microbial contributions of phosphorus release from fresh and air-dried sediments. Marine and Freshwater Research 46: 1039-1045.

Quick. A.J.R. & Bruton, M.N. 1983. Age and growth of *Clarias gariepinus* (Pisces: Clariidae) in the P.K. le Roux Dam, South Africa. S. Afr. J. Zool. 19: 37-45.

Quick, A.J.R.; Bruton, M.N. 1984. Age and growth of *Clarias gariepinus* (Pisces: Clariidae) in the P.K. le Roux Dam, South Africa. South African Journal of Zoology 19 (1): 37- 45.

Rabern, D.A. 1984. Development of Habitat based models for predicting standing crops of nine species of riverine fishes in Georgia. MSc. Thesis. University of Georgia. Athens, Georgia, 126 p.

Rai, H. & Hill, G. 1981. Physical and chemical studies of lago Tupé, a central Amazonian black water [ria Lake]. Int. Revue. ges. Hydrobiol., 66: 137-182.

Rai, H. & Hill, G. 1982. On the nature of ecological cycle of lago Janauari a central Amazonian ria/várzea Lake. Trop. Ecology, 23 (1): 1-49.

Ranwell, D.S. 1974. The salt marsh to tidal woodland transition. Hydrobiol. Bull.

Ratcliffe, C. 1972. The fishery of the Lower Shire River area, Malawi, 1972. Malawi Fish.Bull., 3: 79 pp.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W. Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. & Wissmar, R.C. 1988. The role of disturbance in steam ecology. J. N. Am. Benthol. Soc., 7:433-455.

Reynolds, L.F. 1983. Migration pattern of five fish species in the Murray-Darling River system. Aust.J.Mar.Freshwat.Res., 34:857-71.

Ribeiro, M.C.L. 1983. Ecologia das migracoes das jaraquis no Rio Negro. *In* X Congrreso Brasiliera do Zoologia, Resumos, Belo Horizonte, pp. 287-8. (Abstract in English)

Ricker, W.E. 1969. Effects of size-selectivity mortality and sampling bias on estimates of growth, mortality production and yield. J. Fish. Res. Bd. Can. 26: 479-541.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd Can. Bull. 191: 1-382.

Rietkerk, M., van de Koppel, J., Kumar, L., & Prins, L.H.H.T. (eds.), 2002. The ecology of scale. Ecological model, 149(1-2): 1-4.

Rigler, F.H. 1982. The relation between fisheries management and limnology. Trans. Am. Fish. Soc., 111:121-132.

Rihkter, W.E. & Efanov, V.A. 1977. On one of the approaches of estimating natural mortality of fish populations. Trans. Atl. NIRO, 73: 77-85.

Roosen, R.G. 1973. Worldwide variation in atmospheric transmission: 1 baseline results from Smithsonian observations. Bull. Amer., Met. Soc. 54 (4) 307-316.

Rosenberger A.E. & Chapman, L.J. 1999. Hypoxic wetland tributaries as faunal refugia from an introduced predator. Ecology of Freshwater Fish, 8: 22-34.

Rowntree, K. & Wadeson, R.. 1998. A geomorphological framework for the assessment of instream flow requirements. Aquatic Ecosystem Health and Management 1, 125 – 141.

Roy, J. (1958). Step-down procedure in multivariate analysis. *Annals of Mathematical Statistics*, *29*, 1177-1187.

Roy, J. (1967). *Some aspects of multivariate analysis.* New York: Wiley.

Ryder, R.A., Kerr, S.R., Loftus, K.H. & Regier, H.A. 1974. The morpho-edaphic index, a fish yield estimator. Review and evaluation. J. Fish. Res. Bd Can. 31: 663-688.

Samuel, M., Mathews, C.P. & Bawazeer, A.S. 1987. Age and validation of age from otoliths for warm water fishes from the Arabian Gulf. pp. 253-265. *In* R.C. Summerfelt & G.E. Hall (eds.) Age and Growth of Fish. Iowa State University Press, Ames.

Sanchez, P.A. 1976. Properties and management of soils in the tropics. John Wiley & Sons.

Sarch, M.-T. & Allison, E. H. 2000. *Fluctuations in Africa's Inland Fisheries: Well-adapted Livelihoods, Maladapted Management*. Paper presented at the Biennial Conference of the International Institute for Fisheries, Economics and Trade (IIFET). Oregon State University, Corvallis, OR.

Sarch, M.-T. & Birkett, C. M. 2000. Fishing and farming at Lake Chad: responses to Lake level fluctuations. *The Geographical Journal* 166.

Savill, N.J. & Hogeweg, P. 1999. Competition and dispersal in predator-prey waves. Theoretical Population Biology 56: 243-263.

Schmidt, G.W. 1973. Primary production of phytoplankton in three types of Amazonian waters. 2. The limnology of a tropical floodplain lake in Central Amazonia, Lago do Castanho, Amazona, Brazil. Amazoniana, 4(2): 139-203.

Shaw, E.M. 1988. Hydrology in practice, 2 nd edn. Nostrand Reinhold, Wokingham.

Schindler, J.E. 1988. Freshwater ecosystems: a perspective. Pp. 57-74. *In* L.R. Pomeroy & J.J. Alberts (eds.) Concept of ecosystem ecology. Studies in ecology vol. 67. Springer-Verlag, New York.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38: 1128-1140.

Schramm, H.L., Eggleton, M.A. & Mayo, R.M. 2000. Habitat conservation and creation: invoking the flood-pulse concept to enhance fisheries in the lower Mississippi River. *Polskie Archiwum Hydrobiologii* 47: 45-62.

Seaman, M.T., Scott, W.E., Walmsley, R.O., van der Waal, B.C.W. & Toerien, D.F. 1978. A Limnological investigation of Lake Liambezi, Caprivi, J. Limnol. Soc. Sth. Afr. 4: 129-144.

Shumway, R. H. & Stoffer, D.S. 1999. Time series analysis and its applications.

Sibande, H.R.G. 2001. Water resources. Chapter 6. State of Environment Report for Malawi. Environmental Affairs Department, Lilongwe.

Silert, W. 1981. Principles of ecosystem modelling. Pp. 651-676. *In* A.R. Longhurst (ed.) Analysis of Marine Ecosystems. Academic Press, London 741 pp.

Silvano, R.A.M. & Begossi, A. 2001. Seasonal dynamics of fishery at the Piracicaba River (Brazil). Fish. Res. 51: 69-86.

Silvert, W. 1981. Principles of ecosystem modelling. pp. 651-676. *In:* A. R. Longhurst (ed.) Analysis of Marine Ecosystems, Academic Press, London.

Sissenwine, M.P. 1984. Why do fish populations vary? pp. 59-94. *In* R.M. May (ed.) Exploitation of marine communities. Springer-Verlag, Berlin.

Skelton, P. 1993. A Complete Guide to the Freshwater Fishes of Southern Africa. Southern Book Publishers, Halfway House. 388 pp.

Skelton, P. 2001. A Complete Guide to the Freshwater Fishes of Southern Africa, 2 nd edn. Southern Book Publishers, Halfway House. 395 pp.

Speight, J.G. 1965. Flow and channel characteristics of the Angabunga River, Papua. J. Hydrol., 3, 16-36.

Southwood, T.R.E. 1977. Habitat, the template for ecological strategies. Journal of Animal Ecology, 46: 337-365.

Sparre, P. & Venema, S.C. 1992. Introduction to tropical fish stock assessment. FAO Fisheries Tech.Pap. 306/1. 376 pp.

Stanford, J.V., Hauer, F.R. & Ward, J.V. 1988. Serial discontinuity in a large river system. Verh. Int. Verein. Limnol. 23: 1114-1118.

StatSoft, INC. (1995). STATISTICA for Windows [Computer program manual]. Tulsa, OK: StatSoft, Inc., Tulsa.

Stedinger, J.R., Vogel, R.M. & Foufoula-Georgiou, E.F. 1993. Frequency analysis of extreme events. *In* D.R. Maidment (ed.) Handbook of hydrology. McGraw-Hill, New York.

SVADD. 1975. An atlas of the Lower Shire Valley, Malawi. Shire Valley Agricultural Development Project (SVADD). Blantyre. 30 pp.

Summerfelt, R.C. & Hall, G.E. 1987. The age and growth of fishes. Iowa State University Press, Ames. 433 pp.

Sutinen, J.G. & Andersen, P. 1985. The economics f fisheries law enforcement. Land Econ. 61: 387-397.

Stephens, D.W. & Krebs, J.R. 1986. Foraging Theory, Princeton University Press.

Strickland, J.D. & T.R. Parson. 1960. A manual of sea water analysis. Bull. Fish. Res. B. Can. 125: 1-185.

Swingle, H.S. 1961. Relationship of pH of pond waters to their suitability for fish culture. Proc. Pac. Sci. Congr. 9:1-4.

Tait, C.C. 1967. Kafue River and flood plain. Hydrological data. Fish. Res. Bull. Zambia 3: 26-28.

Talling, J.F and Talling, I.B. 1965. The chemical composition of African lake waters. *Int. Rev. ges. Hydrobiol. Hyrogr.* **50:** 421-463.

Thomaz, S.M., Lansac Tòha, F.A., Roberto, M.C., Esteves, F.A. & Lima, A,F. 1992. Seasonal variation of some Limnological factors of lagoa do Guaraná a várzea lake of the High Rio Paraná, State of Mato Grosso do Sul Brazil. Rev. Hydrobiol. Trop. 25 (4) : 269-276.

Terry, P.J. 1991. Water hyacinth in the Lower Shire, Malawi, and recommendations for its control. Report of a consultancy from 18 September to 5 November 1991. University of Bristol, AFRC Institute of Arable Crops Research, 64 p.

Tesch, F.W. 1971. Age and growth. 98-130 pp. *In:* W.E. Ricker (ed.) Fish Production in freshwaters. Blackwell, Oxford.

Toner, M. & Keddy, P. 1997. River hydrology and riparian wetlands: a perspective model for ecological assembly. Ecological Applications, 7(1) 236-246.

Torrance, J.D. 1972. Malawi, Rhodesia and Zambia. *In* Griffiths, J.F. (ed.): Climate of Africa, pp. 409-460. Amsterdam: Elsevier.

Trewevas, E. 1983. Tilapiine Fishes of the Genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum of Natural History, Publ. Num. 878.Comstock Publishing Associates. Ithaca, New York. 583 pp.

Tweddle, D. 1975. Age and growth of the catfish *Bagrus meridionalis* Gunther in southern Lake Malawi. J. Fish. Biol., 7:677-685.

Tweddle, D., Hastings, R.E. & Jones, T. 1978. The development of a floodplain fishery: Elephant marsh, Malawi. Pp. 341-356. *In* R.L. Welcomme (ed.) Symposium on river and floodplain fisheries in Africa. CIFA Tech.Pap./Doc. Tech.CPCA, 5: 288-95.

Tweddle, D. and N.G. Willoughby. 1979. An annotated checklist of the fish fauna of the river Shire South of Kapichila Falls. JLB Smith Inst. Ichthyol. Bull. 39: 11-22.

Tweddle, D., Lewis, D.S.C. & Willoughby, N.G.. 1979. The natural of the barrier separating the Lake Malawi and Zambezi fish faunas. JLB Smith Inst. Ichthyol. Bull. 39: 1-9pp.

Tweddle, D., R. Makwinja, and G. Sodzapanja. 1994. Catch and effort data for the fisheries of the Lower Shire River and associated marshes (1976-1993). Traditional Fisheries Assessment (MG/ODA) working paper 14.

University of Michigan. 1971. The fisheries if the Kafue River Flats, Zambia, in relation to the Kafue Gorge Dam. Report prepared for the FAO/UN acting as executing agency for the UNDP. Ann Arbor, Michigan, University of Michigan Press, FI:SF/ZAM 11: Tech. Rep. 1: 161 p.

Walters, C., Christensen, V. & Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7: 139-172.

Ward, R. DeC. & Brooks, C.F. 1936. The Climate of North America. *In* K. Geiger (ed.) Handbuch der Klimatologie, vol 2, pt. J. Berlin.

Ward, J.V. & Stanford, J.A. 1983. The intermediate-disturbance hypothesis: an explanation for biotic diversity patters in lotic ecosystems. pp 347-356. *In* T.D. Fontaine & S.M. Bartell (eds.) Dynamics of lotic ecosystems. Ann Arbor Science, Michigan.

Ward, J.V. & Stanford, J.A. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regul. Rivers: Res. Mgmt., 11: 105-119.

Ward, J. V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* **83** (3):269-278.

Ward, J.V., Tockner, K. & Schiemer, F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regul. Rivers: Res. Mgmt., 15: 125-139.

Welcomme, R.L. 1964. The habitat and habitat preference of the young of the Lake Victoria tilapia (Pisces: Cichlidae). Rev.Zol.Bot.Afr., 40 (1-2): 1-28.

Welcomme, R.L. 1972. The inland waters of Africa. Les eaux interieures d'Afrique. CIFA Tech.Pap./Doc.Tech.CPCA, (1): 117 p.

Welcomme, R.L. 1975. The fisheries ecology of Africa floodplains. CIFA Tech.Pap., 3:51 p.

Welcomme, R.L. 1976. Some general and theoretical considerations on the fish yield of African rivers. J.Fish Biol., 8: 351-64.

Welcomme, R.L. & Hagborg, D. 1977. Towards a model of floodplain fish population and its fishery. Environ.Biol.Fish., 2 (1): 7-22.

Welcomme, R.L. 1979. Fisheries ecology of floodplain river. Longman, London. 317 pp.

Welcomme, R.L. 1985. River fisheries, FAO Fish.Tech.Pap, 262, 330 pp.

Welcomme, R.L. 1986. The Niger River system. In B.R. Davies and K.F. Walker (eds.) The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, the Netherlands, 9 - 49 pp.

Welcomme, R.L. 1995. Relationships between fisheries and the integrity of river systems. *Regulated Rivers*: Research and management. 11, 121-136.

Wetzel, R.G. 1975. Limnology. W.B. Saunders Company, Pennsylvania.

Weyl, O.L.F. 1998. The Dynamics of a Subtropical Lake Fishery in Central Mozambique. Ph.D. thesis, Rhodes University, Grahamstown, South Africa. 205 pp.

Weyl, O.L.F. & Hecht, T. 1998. The biology of *Tilapia rendalli* and *Oreochromis mossambicus* (Pisces: Cichlidae) in a subtropical lake in Mozambique. S. Afr. J. Zool. 33(3) 178-188.

Weyl, O.L.F., Banda, M. Sodzapanja, G. Mwenekibombwe, L.H. Namoto, W. & Mponda O.C. 2000. Annual frame survey, September 1999. Fisheries Bulletin NO. 42. Lilongwe, Malawi. 56 pp.

Werner, E.E. & Hall, D.J. 1974. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60(2): 256-264.

Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. 1983. An experimental tests of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional ecology 3: 385-397.

Wilby, R.L., Wedgbrow, C. S. & Fox, H. R. 2004. Seasonal predictability of the summer hydrometeorology of the River Thames, UK. J. Hydrol. 295:1-16.

Williams, G.P. 1978. Bank-full discharge of rivers. Water Resources Res. 14, 1141-54.

Williams, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology. 64: 1283-91.

Willoughby, N.G. & Tweddle, D. 1978[a]. The ecology of commercially important species in the Shire valley fisheries, Malawi. *In* R.L. Welcomme (eds.) Symposium on river and floodplain fisheries in Africa. CIFA Tech.Pap./Doc. Tech.CPCA, 5: 137-52.

Willoughby, N.G. & Tweddle, D. 1978[b] . The ecology of the catfish *Clarias gariepinus* and *Clarias ngamensis* in the Shire Valley, Malawi. J. Zool., Lond., 186: 507-534.

Willoughby, N.G. & R.S. Walker. 1978. The traditional fishery of the Lower Shire valley, Malawi. *In* R.L. Welcomme (ed.) Symposium on river and floodplain fisheries in Africa. CIFA Tech.Pap./Doc. Tech.CPCA, 5: 288-95.

Willoughby, N.G. 1979. The development and management of the shire Valley fishery, Malawi, Southern Africa. *In* Proceedings of the International Conference on Kainji Lake and river basins development in Africa. Ibadan, 11-17 December 1977, Vol. 2:278-287.

WMO. 1980. Manual on stream gauging, Vol. I: Fieldwork, and Vol. II: Computation of discharge, Operational hydrology Report No. 13, WHO No. 519, Secretariat of the World Meteorological Organisation, Geneva, Switzerland.

WMO. 1988. Technical regulations. Vol. I: General Meteorological Standards and recommended practices. WHO No. 43, Secretariat of the World Meteorological Organisation, Geneva, Switzerland.

Wilson, B.H. & Dincer, T. 1976. An introduction to the hydrology and hydrography of the Okavango Delta. Botswana Society, Okavango Symposium, Gaborone.

Wilson, J.A., Acheson, J..M., Metcalfe, M.& Kleban, P. 1994. Chaos, complexity and community management of fisheries. Marine Policy 18, 291-305.

Wooton, R.J. 1990. Ecology of teleosts fishes. Chapman & Hall, London.

van der Waal, B.C.W. 1985. Aspects of the biology of larger fish species of Lake Liambezi, Caprivi, South West Africa. Madoqua, 14: 101-144.

Whitehead, R.A. 1962. The life history and breeding habits of the West African cichlid fish *Tilapia mariae* and the status of *T. meeki*. Proc. Zool. Soc. London 139: 535-543.

Wolman, M.G. and L.B. Leopold. 1957. Rivers, floodplains: Some observations on their formation, U.S. *Geol. Surv*. Prof. Pap, 282-C, 86-109.

Woodyer, K.D. 1968. Bankfull frequency in rivers. J. of Hydrol., 6: 114-142.

Young, W.J., Lam, D.C.L., Ressel, V. & Wong, I.W. 2000. Development of an environmental flows decision support system. Environmental Modelling & Software 15: 257-265.

Zallen, R. 1983. The physics of amorphous solids. John Wiley & Sons. New York.

Zhang, Y., Smith, J.A. & Baeck, M.L. (in press). The hydrology and hydrometeorology of extreme floods in the Great Plains of Eastern Nebraska. Advances in Water Resources.

Zar, J.H. 1984. Biostatistical analysis. 2-nd ed. Prentice-Hall Englewood Cliffs, N.J. 718 p.

Zhang, X., Harvey, K. D., Hogg, W. D. & Yuzyk, T. R. 2001.Trends in Canadian stream flow, Water Resour. Res., 37, 987–998.

Zsuffa, I. J. & Bogardi, J. J. 1995. Floodplain Restoration by Means of Water Regime Control**.** *Phys. Chem. Earth,* Vol. 20, No. 3-4, pp. 237-243.

Apendices

Appendix 1 Summary of 24-hour daily mean values± SD of weather data for the Lower Shire Floodplain based on records from Makhanga Station (No. 797) for the period 1960/61 – 1990/91.

Climatic parameter	**Months**												
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Mean**
Dry bulb temperature (^{o}C)	27.0 ± 6.9	26.7 ± 7.9	26.1 ± 7.8	24.8 ± 7.6	22.3 ±7.0	20.2± 6.3	20.2± 4.9	22.4± 5.0	25.7 ±5.5	28.4 ± 5.7	28.4 ± 6.8	27.4 ± 7.0	25.0
Relative humidity (%)	78 ± 0.58	79 ± 0.67	78 ± 0.38	78 ± 2.1	76 ± 1.5	73 ±2.3	72 ± 8.0	70 ± 10.0	62 ± 6.9	54 ± 10.07	51 ± 11.1	71 ± 9.8	68
Wind (m/sec)	2.6 ± 0.12	2.4 ± 0.09	2.4 ± 0.18	2.6 ± 0.11	2.4 ±0.14	2.4 ±0.09	2.6± 1.05	3.5± 1.26	4.7± 0.74	5.5 ± 1.07	4.8 ± 1.32	3.4 ± 0.81	3.3
Evaporation (mm)	176.2 ±12.6	151.3 ± 11.3	161.0 ±12.7	144.7 ±16.3	132.8 ±16.1	112.5 ±15.5	122.4 ±58.8	172.4 ±56.2	239.5 ± 57.6	314.9 ± 53.8	268.2 ± 53.6	2.7.7 ± 54.5	2203.6
Evapotranspiration (mm)	174.8 ±11.6	152.3 ± 12.0	159.0 ±11.2	134.1 ±23.7	111.0 ±23.8	86.7 ±23.5	98.0± 32.1	130.8 ±35.6	174.0 ± 40.1	217.6 ± 17.8	213.3 ± 19.0	184.5 ± 16.8	1836.1
Potential Evapotranspiration (mm)	222.0 ±44.5	207.9 ± 56.8	204.4 ±34.1	173.4 ±19.9	145.7 ±26.9	115.2 ±22.6	128.3 ±9.4	168.6 ±11.3	217.2 ± 8.5	268.2 ± 29.1	263.7 ± 37.8	231.6 ± 22.0	2345.2
Rainfall (mm)	183.1 ±75.6	97.5 ± 85.4	111.7 ±75.9	39.1 ±34.8	14.4 ±13.1	16.7 ±14.5	17.5± 14.9	9.1± 7.9	4.5 ± 6.9	21.5 ± 30.9	68.3 ± 34.9	181.1 ± 65.2	764.5
Sunshine (hours)	7.1 ± 0.35	7.5 ± 0.37	7.8 ± 0.23	8.0 ± 0.32	8.1± 0.45	7.5 ± 0.22	7.5± 0.78	8.6 ±1.03	9.0 ± 0.58	9.4 ± 1.0	8.5 ± 1.21	7.4 ± 0.82	8.1
Clouds (octas)	5.9 ± 0.42	5.7 ± 0.3	5.1 ± 0.53	4.4 ± 0.57	3.3 ± 0.59	3.6± 0.47	3.6± 0.76	2.6 ±0.88	2.1 ± 0.74	2.7 ± 1.36	4.3 ± 1.46	5.4 ± 0.85	4.1
Thunder (days)	17 ± 3.6	12 ± 4.3	10 ± 2.8	3 ± 1.5	1 ± 0.6	0	0	0	1 ± 0.7	4 ± 5.1	12 ± 7.0	18 ± 7.6	78

Source: Meteorological Services, Malawi (unpublished data)

Appendix 2 Creel survey data sheet for the Lower Shire Floodplain

Gear				**Species**	**Weight**	**Number**	**Date**		
	Length	**Mesh size**	**Time/cast**				**Location**		
Gillnet								Time in	
Seine net								Time out	
Longline							**Craft used**		
Hook-and-line							Dugout		
Castnet							Plankcanoe		
Fishtrap							Others		
Reedfence								**Days fished**	
Others								Last week	
								Last month	
Species	**TL (mm)**	**Species**	**TL (mm)**	**Species**	**TL (mm)**	**Species**	**TL (mm)**	**Species**	**TL (mm)**

Appendix 3 Frame survey of the small-scale fisheries of the Lower Shire Floodplain, July 1999

Name of Recorder:
Minor strata
Date :

Fishing site	Name of Fisher	Number of assistants	Fishing craft			Fishing gears owned								Dimensions			State of net		Fishing status	
			B	BE	D	SCN	CN	FT	GN	HL	RF	SN	MN	LL	MS	L	D	G	B	Y	N

Fishing crafts : B = boats; BE=boat with engine, D=dugout canoe; Fishing gears : SCN=seine net, CN=castnet, FT=fishtraps, GN=gillnet, HL=handline, RF=reedfence, SN=scoopnet, MN=mosquitonet, LL=longline; Dimensions: MS=mesh-size, L=length, D=depth; State of net: G=≥50% intact, B= < 50% intact; Fishing : Y=active, N=inactive.