TOWARDS THE DEVELOPMENT OF SPECIES-SPECIFIC FISH PRODUCTION MODELS FOR SMALL RESERVOIRS IN SOUTHERN AFRICA

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ABSTRACT

The fish populations in small southern African reservoirs are largely unexploited and there is potential for fisheries development. However, the development of sustainable fisheries requires reliable estimates of potential yield or production. Empirical models that have been developed to predict fish production only apply to large water bodies and only predict total fish production, not the production of individual species. Small reservoirs generally have few commercially important species and therefore species-specific fish production models are an alternative approach. The small reservoirs of the Eastern Cape are dominated by the moggel (*Labeo umbratus*). The principal objectives of this thesis were to gain an understanding of the ecology of small reservoirs and the function of moggel in these systems. This information was used to design a research approach to rapidly develop species-specific models for small reservoirs in southern Africa.

The limnology of two small reservoirs was compared. During the study period the reservoirs were turbid and showed a warm, monomictic pattern of thermal stratification. Anthropogenic pressure in the reservoir catchments appeared to be the overriding factor increasing the nutrient input to the reservoirs and consequently, influencing the biomass of algae in the reservoirs.

The feeding biology of moggel in Katriver and Laing reservoirs was examined. Moggel are detrivorous and successfully digested diatoms. The slower growth rate of moggel in Katriver reservoir was attributed to the poorer nutritional value of the diet as a consequence of the lower concentration of diatoms in the detrital aggregate.

The reproductive characteristics of moggel were examined in four reservoirs. Moggel were able to reproduce successfully in the reservoirs. This could be attributed to their r-selected reproductive strategy, with a high fecundity and an extended spawning season and their ability to spawn in a floodplain environment. Differences in recruitment success between years were found to be a consequence of the timing and duration of seasonal rains. The number of mature females in a population and the availability of suitable spawning habitat influenced recruitment success.

The life history of the moggel in five reservoirs was compared. Growth appeared to be related to food availability, while mortality was lower in the populations where food was abundant and there were less predatory species. Size and age at maturity were not affected by environmental factors, but were dependent on growth and mortality.

Three contrasting methods were used to estimate moggel gillnet selectivity. The Sechin, direct fyke net method and length-structured model all yielded similar results and correction factors obtained from the selectivity study were applied to the gillnet data to estimate the fish population size and structure in each reservoir.

Using information from the life history and selectivity studies, the biomass and production of five moggel populations was estimated and related to abiotic and biotic factors in the reservoirs and their catchments. Moggel biomass and production was dependent on the biomass of algae, which was dependent on morphoedaphic characteristics of the reservoirs. Small, shallow reservoirs with a reasonable amount of human habitation in their catchments would sustain the highest algal biomass and provided they had adequate spawning habitat would also have the highest moggel biomass and production.

The future research requirements for small reservoir fisheries are outlined and include a three-year program to develop a species-specific production model for any of the dominant species.

CHAPTER 1

Introduction

African inland fisheries production has been estimated at just under 2 million tonnes per annum (FAO, 2000), although large amounts of under-reporting suggests that actual catches may be under-estimated by up to 50% (Coates, 1995). While most of the reported catch is recorded from large lakes, reservoirs, rivers and floodplains, the highest under-reporting occurs in small water bodies, for which Bernacsek (1986) estimated catches at between 1 million and 2.3 million tonnes. Small water bodies, as defined by Marshall and Maes (1994), are reservoirs and lakes less than 10 km^2 (1 000 ha), ponds, canals and rivers less than 100 km long and small seasonal floodplains. In southern Africa alone, the total number of small water bodies is estimated between 50 000 and 100 000 (Verheust, 1998), of which most are reservoirs. The large number, uneven distribution and often-remote locations of these water bodies complicate the development and management of small reservoir fisheries, and in Africa, fisheries managers have historically focused their attention on large water bodies (Jackson and Ssentongo*,* 1988). For this reason there is very little information available for African small water bodies and techniques used to obtain estimates of population size and potential yield. This makes management of fish resources difficult. In addition to many unregistered reservoirs, there are approximately 3 100 registered small reservoirs in South Africa, with a total surface area of 84 439 hectares (South African Department of Water Affairs and Forestry, Reservoir Database). Unlike further north in Africa, these reservoirs are completely unexploited. The only traditional freshwater fisheries in South Africa are those in the Pongola Floodplain in northern Kwazulu-Natal and the Orange River in the Northern Cape (Andrew *et al.*, 2000). The majority of small reservoirs in South Africa are under the control of the state and since most are situated in rural areas, these fisheries resources provide an opportunity for poverty alleviation (Andrew *et al.*, 2001).

For rural communities to have sustained benefits from small reservoirs, it is necessary to obtain estimates of potential fish yield. However, due to the lack of fishing in South Africa's small reservoirs, there has been no monitoring and estimates of yield are not available. Therefore, estimates of fish production are necessary to assess the potential of small reservoir fisheries. Estimates of fish production require reliable estimates of population numbers, biomass, size structure, growth and mortality (Allen, 1971) and this involves intensive and extended sampling programmes (Kaunda, 1995; Mattson and Kaunda, 1997). Due to the large number and remote locations of many small water bodies, such a sampling programme would be prohibitively expensive, particularly since each water body is likely to only support a small fishery. Consequently, Marshall and Maes (1994), Mattson (1997) and Kaunda (1995) have argued that the development of empirical models that use easily measurable morphometric and/or limnological characteristics to estimate fish production in small water bodies are pivotal for guiding and developing sustainable fisheries in these impoundments.

To address the issue of rural fisheries development in South Africa, Rhodes University established the Rural Fisheries Programme (RFP) in 1997 as a collaborative effort between the Department of Ichthyology and Fisheries Science and the Institute of Social and Economic Research. The objectives of the RFP were: i) to identify a range of suitable freshwater systems in rural areas of the Eastern Cape for the development of experimental fisheries, ii) to promote and facilitate the development of sustainable freshwater fisheries in consultation with interested communities, iii) to contribute towards an improved quality of life through ensuring greater food security and income generating opportunities for rural people, iv) and to develop guidelines for the future expansion of freshwater fisheries in the Eastern Cape.

Empirical modelling to predict fish yield and production in inland waters has been a focus of scientific research for decades (Rawson, 1952; Ryder, 1965; Jenkens and Morais, 1971; Henderson and Welcomme, 1974; Melack, 1976; Ogelsby, 1977; Hanson and Legget, 1982; Downing *et al.*, 1990; Quiros, 1990; Nissanka *et al.*, 2000). However, most models have been developed for larger water bodies. Small reservoirs do not conform to these models for a number of reasons. These include the higher catchability of fish in small water bodies (Ogelsby, 1977), greater fluctuations in temperature, oxygen concentration, turbidity and water level (Mattson, 1997), relatively greater light penetration (Marshall and Maes, 1994) and higher exchange of nutrients from the substratum to the water column due to a large surface to volume ratio (Howard-Williams and Ganf, 1981). To date, a suitable model to predict fish production in small reservoirs has eluded researchers, and fisheries managers have relied on life history studies on growth, size at sexual maturity and mortality to assess and manage such fisheries.

Besides not being applicable for small reservoirs, traditional empirical models are generally developed using information available in the published literature. Since field and laboratory techniques are not standardised, this approach introduces considerable error and bias, which no doubt affects the robustness of such models. Ideally, parameter estimates used to develop a model for a particular region should be representative of the variety of environmental conditions present in that region. The development of an empirical model suitable for all large water bodies should incorporate equal numbers of sites from all continents and represent the variety of environmental conditions present on each.

A potential solution to these problems is the development of species-specific empirical models. This would first require a detailed ecological study of the species in the environment for which the model is being developed. Instead of selecting sites throughout the region to which the model is to be applied, sites representative of environmental conditions that influence the production of the species should be selected throughout the species' distribution. Once sites are selected, standardised field and laboratory methods should be used to develop the fish production model for the species. Once models have been developed for all dominant species, their application would allow one to predict which species are likely to dominate in any given reservoir.

Since small reservoirs are generally characterised by a low number of species (Marshall and Maes, 1994), not many species-specific empirical models would be required in order to assess total fish production. In addition, the influence of species interactions can easily be included in the models. Small reservoirs are suited to obtain fish population estimates using depletion models (Leslie and Davis, 1939; De Lury, 1947) or mark-recapture studies (Koch and Schoonbee, 1980; Mitchell and Jordaan, 1985; Kaunda, 1995; Schoonbee *et al.,* 1995), and age, growth and mortality estimates for each species. The small size of these systems makes research easier and studies can be conducted concurrently on a number of small water bodies using standardised techniques and a single method to calculate fish production.

Since small reservoirs are widely distributed in South Africa (Davies and Day, 1998), study sites can be selected on the basis of their environmental characteristics. Once species-specific empirical models have been developed for the dominant species in small reservoirs, an estimate of total fish production could theoretically be made after measuring a few simple parameters.

Another criticism of traditional empirical models is their inability to predict fish production per species (Cochrane and Robarts, 1986). The species-specific approach could solve this problem and be used to predict changes in the overall production in response to environmental disturbances.

The development of species-specific empirical models for small reservoirs requires an initial understanding of the forces driving fish production in these systems. This requires a detailed understanding of the ecology of the small reservoir environment and its interactions with the species.

In the Eastern Cape Province in South Africa, fish populations in small water bodies are dominated by the cyprinids, *Labeo umbratus* (A. Smith, 1841) and *Cyprinus carpio* (Linnaeus, 1758)*,* the cichlid, *Oreochromis mossambicus* (Peters, 1852) and the clariid catfish, *Clarias gariepinus* (Burchell, 1822). *L. umbratus* was found to be dominant in terms of numbers and biomass and was therefore selected for this study.

The moggel, *L. umbratus*, is a riverine fish that is widely distributed throughout South Africa (Skelton, 1993) and has adapted extremely well to reservoirs, where it occurs in high densities (Gaigher, 1984). It attains a length of 500 mm TL and a weight of just under 3 kg (Skelton, 1993). It has been recognised as a commercially important species in Mentz, Kalkfontein (Merron and Tomasson, 1984) and Bloemhof reservoirs (De Villiers, Free State Nature Conservation, pers. comm.), and has recently been the focus of rural fisheries projects in the Eastern Cape (Andrew *et al.,* 2000).

Thesis outline

The principal objectives of this thesis were to gain an understanding of the ecology of moggel and the small reservoir ecosystem to contribute towards the development of empirical models to predict fish production in small reservoirs. To achieve these objectives, this thesis has been divided into nine chapters. Each chapter addresses either a step to estimate the production of *L. umbratus* in selected reservoirs, or to gain an overall understanding of the ecology of small reservoirs. Chapter 2 describes the process of site selection and describes each study area, the sampling strategy and the general methods used in this study. Chapter 3 attempts to develop an understanding of the influence of morphometry, altitude and anthropogenic characteristics on limnological processes, chlorophyll ‘a’ concentration and zooplankton biomass in reservoirs. Chapter 4 describes the growth of *L. umbratus* and relates it to the trophic differences in two reservoirs. In Chapter 5, the reproductive success of *L. umbratus* in four reservoirs is compared and related to environmental factors before and after spawning. Chapter 6 examines variations in the life history of *L. umbratus* populations and relates the observed differences to environmental conditions. In Chapter 7, gillnet selectivity of *L. umbratus* is estimated and the potential of fyke nets as a sampling gear in small reservoirs is evaluated. In Chapter 8, population, growth and mortality estimates are used to estimate the production of *L. umbratus* in five reservoirs. These production estimates are then related to a number of environmental characteristics that were found to influence food availability, growth, reproduction and mortality in the previous chapters. In Chapter 9, the ecology of moggel in small reservoirs is discussed in the context of developing empirical models for small water bodies and future research initiatives are suggested.

CHAPTER 1

Introduction

African inland fisheries production has been estimated at just under 2 million tonnes per annum (FAO, 2000), although large amounts of under-reporting suggests that actual catches may be under-estimated by up to 50% (Coates, 1995). While most of the reported catch is recorded from large lakes, reservoirs, rivers and floodplains, the highest under-reporting occurs in small water bodies, for which Bernacsek (1986) estimated catches at between 1 million and 2.3 million tonnes. Small water bodies, as defined by Marshall and Maes (1994), are reservoirs and lakes less than 10 km^2 (1 000 ha), ponds, canals and rivers less than 100 km long and small seasonal floodplains. In southern Africa alone, the total number of small water bodies is estimated between 50 000 and 100 000 (Verheust, 1998), of which most are reservoirs. The large number, uneven distribution and often-remote locations of these water bodies complicate the development and management of small reservoir fisheries, and in Africa, fisheries managers have historically focused their attention on large water bodies (Jackson and Ssentongo, 1988). For this reason there is very little information available for African small water bodies and techniques used to obtain estimates of population size and potential yield. This makes management of fish resources difficult. In addition to many unregistered reservoirs, there are approximately 3 100 registered small reservoirs in South Africa, with a total surface area of 84 439 hectares (South African Department of Water Affairs and Forestry, Reservoir Database). Unlike further north in Africa, these reservoirs are completely unexploited. The only traditional freshwater fisheries in South Africa are those in the Pongola Floodplain in northern Kwazulu-Natal and the Orange River in the Northern Cape (Andrew *et al.*, 2000). The majority of small reservoirs in South Africa are under the control of the state and since most are situated in rural areas, these fisheries resources provide an opportunity for poverty alleviation (Andrew *et al.*, 2001).

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CHAPTER 2

Study area and general materials and methods

An ideal sampling programme should incorporate sites throughout the distribution of the species and include all suites of environmental conditions in which the species occurs. Representative sites at the extremes, and within the biogeographical distribution of the species, should therefore be selected. More specifically, sites should be selected on the basis of their environmental characteristics, ensuring that the broad range of parameters that have previously been shown to influence fish production are incorporated into the sampling programme. This site selection procedure should ensure that the model predictions are sufficiently robust by incorporating sites with the lowest and highest estimates of fish production. The number of sites chosen should be dictated by the variety of habitats in which the species occurs to ensure that the model has a sufficient statistical power.

In reality, however, the perfect sampling programme is seldom possible. Financial, logistical, social, institutional and time constraints will prevent a researcher from sampling an adequate number of the most appropriate water bodies. The researcher is, therefore, often left with a sampling programme that is driven by short term, goal-oriented funding, most often driven by social needs. Core funding for this study was provided to sample two water bodies of my choice in the Eastern Cape Province between November 1998 and October 2000. Additional funding was later provided for the development of community fishing projects in Sinqemeni and Ndlambe reservoirs between June 1999 and May 2001, and Dimbaza Reservoir between February 2000 and January 2002. These reservoirs were therefore also incorporated into the study. A requirement of the funding organisations was that the programme establishes community-based fisheries in the five reservoirs. It was decided that a biological assessment for a period of at least one year should first be conducted to determine suitable management strategies for each fishery.

Study area

All five reservoirs are situated in the Eastern Cape interior (Fig. 2.1). The climate of the greater portion of the Eastern Cape is mild in winter with occasional frost and warm summers. Differences in temperature may be modified by altitude, which peaks at over 2 000 m in the mountainous and escarpment areas (Kopke, 1988). Mean annual rainfall varies between 200 – 1 500 mm in the west to 600 to >1500mm in the east. Mean annual evaporation ranges between 1 500 – 2 000 mm and <1 200 – 1 400 mm in the two areas respectively, with an overall trend of increasing evaporation from north to south (Midgley *et al.*, 1994).

Geologically, most of the Eastern Cape rock formations are sedimentary and the most common rock types include sandstone, mudstone, limestone, conglomerate and tillite (Rust, 1988).

Although 75% of the land cover is natural bush (shrubland, lowland fynbos, unimproved grassland, thicket and bushland), the Eastern Cape has the highest percentage of degraded, unimproved grassland in the country (Fairbanks *et al.,* 2000). In the eastern half of the Eastern Cape, over 20% of the land is under agriculture (mostly subsistence farming) (CSIR, 2001). As a consequence, over 20% of river catchments are degraded, mostly as a result of poor farming practices (CSIR, 2001).

Urban influences are most apparent in the Swartkops and Buffalo River catchments, which serve the Port Elizabeth and East London metropoles, respectively. The remainder of the Eastern Cape has high residential development, particularly in the rural areas (CSIR, 2001).

Choice of sampling sites

Factors that potentially influence biological production in reservoirs include morphometry (Straškraba, 1980), temperature (Schlesinger and Reiger, 1982; Van Schalkwyk and Walmsley, 1984), chemical composition and nutrient status of the water (Wetzel, 1983). Selecting two reservoirs with different morphometric, temperature, chemical and nutrient characteristics would provide little information on how each factor influenced fish production since the factors could be interrelated. Morphometric dimensions of all registered reservoirs are available in South Africa and this allowed for the selection of two reservoirs with similar morphometric characteristics. After selecting two reservoirs of similar size and shape, the influence of water temperature (if the reservoirs were situated at different altitudes) and the chemical and nutrient characteristics on fish production can be assessed. Katriver and Laing reservoirs had similar morphometric characteristics, different elevations and differing anthropogenic influences in their catchments (Table 2.1) and were therefore selected for the study. Sinqemeni, Ndlambe and Dimbaza were considerably smaller, situated at different elevations and had varying anthropogenic impact in their catchments (Table 2.1).

The five reservoirs ranged in size from 9 to 214 ha, with a mean depth of between 1.9 and 12.2 m at full supply level (Table 2.1). The catchment size of the reservoirs ranged from ± 20 km^2 to 913 km^2 (Table 2.1). The reservoirs were situated in a fairly narrow range of altitudes (100 to 740 m), but no moggel occur in small reservoirs above 1 000 m in the Eastern Cape (pers. obs). Mean annual rainfall in the area of the reservoirs ranges between 500 – 700 mm, while mean annual evaporation ranges between 1 400 – 1 700 mm. As with most of the Eastern Cape, the bedrock of the catchments of all five reservoirs was sedimentary rock with soil type characterised as either sandy or clayey loams (Table 2.1).

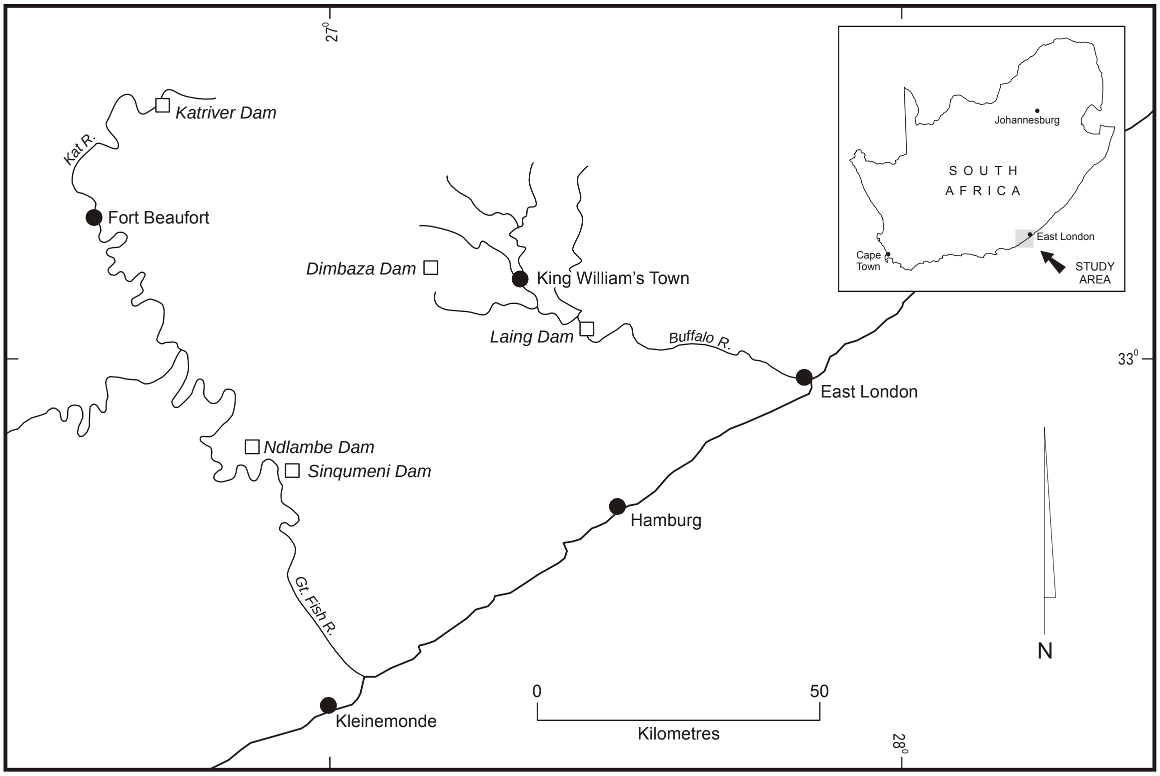

Figure 2.1. Map showing the location of the five reservoirs selected for the study.

The anthropogenic characteristics of the reservoir catchments varied widely. Population density ranged from 90.4 to 529.9 km^{-2} and the density of houses between 18.8 and 124.9 km^{-2} (Table 2.2). In terms of agriculture and industry, the density of farmers and manufacturers ranged from 0.7 to 2.3 km^{-2} and 0.3 to 55.1 km^{-2} respectively (Table 2.2). Katriver, Sinqemeni and Ndlambe reservoirs are situated in rural areas, with subsistence livestock farming dominating land use in the catchments. Due to the peri-urban situation of Laing and Dimbaza reservoirs, the land use in their catchments is broad and includes commercial and subsistence farming, industry. In addition these reservoirs are used as a domestic water supply (Table 2.2).

Table 2.1. Environmental parameters of Katriver, Laing, Sinqemeni, Ndlambe and Dimbaza reservoirs situated in the Eastern Cape Province, South Africa.

	Katriver	Laing	Sinqemeni	Ndlambe	Dimbaza
Geographical Coordinates	-32°5666'E, 26°7500'S	-32°.9667'E, 27°.4833'S	-33°1121'E 26°5800'S	-33°1018'E 26°5453'S	-32°8500'E 27°2333'S
Altitude (m) [1]	750	310	100	100	350
Catchment size (km^2) [1]	258	913	± 20	± 20	± 35
Utilisation[1]	Irrigation	Potable supply, Industry	Human and livestock supply	Human and livestock supply	Industry and livestock
Surface area at FSL* (ha)	214[1]	211[1]	9.3	16.2	46.2
Mean depth (m)	12.2	10.4	3.2	3.0	1.9
Maximum depth (m)	48.0	30.0	7.5	8.6	3.9
Catchment geology[2]	Sedimentary	Sedimentary	Sedimentary	Sedimentary	Sedimentary
Catchment soils[2]	Sandy loams	Clayey loams	Clayey loams	Clayey loams	Sandy loams
Mean annual rainfall[2]	600-700mm	600-700mm	500-600mm	500-600mm	600-700mm
Mean annual evaporation[2]	1500-1600mm	1400-1500mm	1500-1600mm	1500-1600mm	1400- 1500mm

Superscript indicates reference: 1 = Noble and Hemens (1978); 2 = Midgley *et al.* (1994). * FSL = Full supply level

Table 2.2. Selected anthropogenic catchment characteristics for Katriver, Laing, Sinqemeni, Ndlambe and Dimbaza reservoirs situated in the Eastern Cape Province, South Africa. (Data obtained from the Municipal Demarcation Board)

Catchment characteristics	Katriver	Laing	Sinqemeni	Ndlambe	Dimbaza
Number of houses	4847	36126	1185	1185	4371
Density of houses ($no.km^{-2}$)	18.8	39.6	47.4	47.4	124.9
Population	23314	172718	5484	5484	18545
Population density ($no.km^{-2}$)	90.4	189.2	219.4	219.4	529.9
Number of farmers	600	634	29	29	45
Density of farmers ($no.km^{-2}$)	2.3	0.7	1.1	1.1	1.3
Number of manufacturers	89	4275	8	8	1930
Density of manufacturers ($no.km^{-2}$)	0.3	4.7	0.3	0.3	55.1
Number of households without flush toilets	4542	20830	1167	1167	2060
Density of households without flush toilets ($no.km^{-2}$)	17.6	22.8	46.7	46.7	58.9

Five species of fish, viz. moggel (*L. umbratus*), carp (*C. carpio*), river goby (*Glossogobius callidus* (Smith, 1937)), chubbyhead barb (*Barbus anoplus* (Weber, 1897)) and longfin eel (*Anguilla mossambicus* (Peters, 1852)) were present in all reservoirs (Table 2.3). Sharptooth catfish (*C. gariepinus*) occurred in the Katriver and Laing, and largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) was present in Katriver and Dimbaza reservoirs (Table 2.3). Bluegill (*Lepomis machrochirus* (Rafinesque, 1819)) was found in Dimbaza Reservoir. The mozambique tilapia (*O. mossambicus*) was present in the Ndlambe and Laing reservoirs, and flathead (*Mugil cephalus* (Linnaeus, 1758)) and freshwater (*Myxus capensis* (Valenciennes, 1836)) mullet were introduced into Katriver Reservoir in 1988 (Table 2.3).

Table 2.3. Fish species recorded in the five reservoirs during the sampling period

Reservoir Species	Katriver	Laing	Sinqemeni	Ndlambe	Dimbaza
Labeo umbratus	*	*	*	*	*
Cyprinus carpio	*	*	*	*	*
Clarias gariepinus	*	*			
Oreochromis mossambicus		*		*	
Anguilla mossambicus	*	*	*	*	*
Micropterus salmoides	*				*
Barbus anoplus	*	*	*	*	*
Glossogobius callidus	*	*	*	*	*
Lepomis macrochirus					*
Mugil cephalus	*				
Myxus capensis	*				

Establishment of fisheries

Hand-line fishing occurred in all reservoirs prior to the study and in Laing Reservoir, two throw-net fishermen operated sporadically (± once per week). Although no moggel were ever observed in the catches of the hand-line fishermen, the throw-net fishermen captured an average of 2.1 ± 2.3 *L. umbratus* per fishing trip. After the biological surveys had continued for about one year, experimental community-based fisheries were initiated. Fishermen were given gillnets and were required to keep accurate records of their catches. The number of gillnets, their size and mesh were determined after examination of the catches from the first year. A mesh size of either 75 or 100 mm was selected depending on which mesh yielded the greatest number of fish. In Katriver Reservoir, fishermen were given six gillnets (see detailed description below), each 40 m in length with a mesh size of 75 mm. Fishing commenced in November 1999 and despite low catches, fishing continued for the rest of the survey period (Table 2.4). In December 1999, a similar fishery was initiated in Laing Reservoir. Fishermen were given similar gear, but fishing was discontinued in August 2000 (Table 2.4). Fisheries were initiated in Sinqemeni and Ndlambe reservoirs in May 2000. Fishermen were given one 40 m net with a mesh size of 100 mm. In Sinqemeni Reservoir, large numbers of fish were captured and fishing continued to the end of the study (Table 2.4). Fishing in Ndlambe Reservoir was more sporadic, with catches remaining relatively constant throughout the sampling period (Table 2.4). The Dimbaza Reservoir fishery was initiated in July 2001. Fishermen were given three gillnets of 40 m with a mesh size of 75 mm, and although fishing did not occur often, catches were high (Table 2.4).

Table 2.4. Catches of the experimental gillnet fisheries in the five reservoirs. Catch per unit effort (CPUE) expressed as number of fish per 10 m of net per night.

Reservoir	Dates of fishing records	Total days fished	Total catch (Number)	CPUE (no./net/night)
Katriver	Nov 1999 – Oct 2000	144	160	0.1 ± 0.1
Laing	Dec 1999 – Aug 2000	82	1257	1.57 ± 2.0
Sinqemeni	May 2000 – Oct 2001	217	4933	6.2 ± 3.0
Ndlambe	May 2000 – Oct 2001	32	896	7.1 ± 2.3
Dimbaza	July 2001 – Jan 2002	20	3194	9.1 ± 3.9

Water quality

Mean surface water temperature ranged from 20.3 - 22.1°C and there were no significant differences between reservoirs (Table 2.5). High turbidity (61.0 -151.2 FTU) was observed in all reservoirs, though Dimbaza and Ndlambe reservoirs were significantly more turbid (Table 2.5). All reservoirs were marginally alkaline and water conductivity ranged between 113 and 1126 µS.m^{-1}. The mean chlorophyll ‘a’ concentration in the reservoirs varied between 1.4 and 18.6 µg.l^{-1} (Table 2.5) and according to the definitions by Walmsley (1984), Katriver Reservoir could be classified as oligotrophic and the remainder as eutrophic.

Table 2.5. Average annual water quality parameters for Katriver, Laing, Sinqemeni, Ndlambe and Dimbaza reservoirs in the Eastern Cape Province, South Africa, between November 1998 and January 2002.

	Katriver	Laing	Sinqemeni	Ndlambe	Dimbaza
Temperature (°C)	20.48 ±5.2	20.30 ±4.2	21.87 ±5.4	22.05 ±5.2	21.09 ±6.1
Conductivity (mS.cm^{-1})	11.3 ±4.7	51.3 ±4.6	112.6 ±6.7	107.9 ±8.4	45.0 ±7.8
Turbidity (FTU’s)	65.89 ±15.7	74.07 ±9.2	61.0 ±0.4	147.0 ±13.4	151.2 ±44.1
pH	7.1 – 8.1	7.2 – 9.4	7.0 – 8.4	7.0 – 8.0	7.9 – 8.8
Chlorophyll ‘a’ (µg.l^{-1})	1.4 ±2.9	8.4 ±15.4	16.6 ±15.4	15.7 ±16.8	18.6 ±17.7

Field collection methods

Fish biology

Samples of *L. umbratus* were collected monthly from the Katriver and Laing reservoirs between November 1998 and October 2000, quarterly in the Ndlambe and Sinqemeni reservoirs between June 1999 and April 2001, and quarterly in Dimbaza Reservoir between February 2000 and January 2002. The fish were caught using gillnets, seine nets and fyke nets. The number of gillnets deployed and seine net sites chosen was dependent on the size of the reservoir and are summarised in Table 2.6. Fyke nets were used exclusively in Dimbaza Reservoir during the gillnet selectivity experiment and a description of this gear is given in Chapter 7. The catch records of the experimental gillnet fisheries were also used in the study.

Table 2.6. Sources of biological data used in this study.

Reservoir	Source	Frequency	No. gillnets set per trip	No. seine net pulls per trip
Katriver (Nov 1998 – Oct 2000)	Gillnets, seine nets	Monthly	6	6
Laing (Nov 1998 – Oct 2000)	Gillnets, seine nets	Monthly	6	6
Sinqemeni (Jun 1999 – May 2001)	Gillnets, seine nets	Quarterly	3	3
Ndlambe (Jun 1999 – May 2001)	Gillnets, seine nets	Quarterly	3	3
Dimbaza (Feb 2000 – Nov 2001)	Gillnets, seine nets, fyke nets	Quarterly	4	4

Gillnets

Gillnets were made of 6 ply, multifilament, green, nylon netting with manufacturer quoted stretched mesh sizes of 44, 60, 75, 100 and 144 mm. All nets were hung at a 50% height : width ratio. Actual wet stretched mesh sizes are shown in Table 2.7. Each net was 50 m x 2 m and consisted of five randomly distributed ten-metre mesh panels with each net containing all five mesh sizes. Each reservoir was divided into various zones, based on substrate type, the steepness of the bank, and riverine or lacusterine nature. The shoreline of each zone was divided into 50-metre sections and numbered. The choice of sites sampled within each zone on every sampling trip was made using a random number table. A larger number of sampling sites were selected in the larger reservoirs, and at least one net was set in each of the zones. Each gillnet was surface set, parallel to the shore along the 3 m depth contour. This technique delivered the most consistent catches in a preliminary study, conducted in September and October 1998, in which nets were surface and bottom set at various depths. Gillnets were set between 16h00 and 19h00 and retrieved the following morning between 06h00 and 09h00. For effort comparison, soak time was recorded.

Table 2.7. Manufacturer-quoted stretched mesh size (MQS) and mean wet mesh size of the experimental gillnets.

MQS	Mean mesh size ±SD
44	49.6 ± 0.1
60	66.5 ± 0.1
75	85.3 ± 0.1
100	106.7 ± 2.2
144	150.4 ± 2.6

All fish captured in the gillnets were weighed to the nearest gram and measured to the nearest millimetre fork length (FL). Fish were dissected, sexed and the gonads were weighed and categorised according to the five developmental stages (Table 2.8) described by Booth and Weyl (2000). Gonad samples were preserved in 5% formalin. Eviscerated mass of each fish was then measured to the nearest gram. Lappilar otoliths were removed and stored in labelled gelatin capsules to prevent breakage.

Table 2.8. Macroscopic criteria used to stage gonadal development in *Labeo umbratus* in various Eastern Cape dams. (After Weyl and Booth, 1999).

Stage	Development	Macroscopic appearance
I	Juvenile	Not possible to visibly distinguish sex. Gonad appears as a translucent, gelatinous strip.
II	Resting	Ovaries white or slightly yellowish. Oocytes are macroscopically distinguishable. Testis are discernable as thin, white bands.
III	Developing	Ovaries enlarged, oocytes readily visible and yellow. Testis broadened, distended and cream in colour.
IV	Ripe	Oocytes of maximum size. Reddish, hydrated and extruded under abdominal pressure. Testis swollen to maximum size. Sperm extruded under abdominal pressure.
V	Spent	Ovaries flaccid and sac-like with few vitellogenic oocytes visible. Testes reduced in size and dirty grey in colour.

Seine net

The seine net was 30 m long, 2 m deep and fitted with a cod end. It was made of knotless green mesh with a stretched mesh size of 10 mm. Sites with drowned trees, submerged vegetation, a rocky substrate or steep slopes were excluded since they prevented effective seine netting. The sampling sites for each survey were chosen randomly from all suitable seine-netting sites using a random number table. More sampling sites were chosen in the larger reservoirs. Each fish captured was weighed to the nearest 0.1 g and measured to the nearest millimetre FL.

CHAPTER 3

The biomass of phytoplankton and zooplankton and its relationship with altitude, geology and anthropogenic factors in two Eastern Cape reservoirs

INTRODUCTION

Phytoplankton and zooplankton are important primary and secondary producers in reservoirs, with their biomass forming the basis of the food chain for primary and secondary consumer fish species (Uku and Mavuti, 1994; Allanson *et al.*, 1990). Environmental factors recognised to influence phytoplankton biomass include temperature (Brylinsky and Mann, 1973; Van Schalkwyk and Walmsley, 1984), turbidity and water chemistry (Brylinsky and Mann, 1973; Wetzel, 1983). Zooplankton biomass is influenced by the biomass of phytoplankton (food availability), water retention time, temperature and turbidity (Campbell *et al.,* 1998).

In reservoirs, the average surface water temperature is influenced by latitude, altitude and turbidity (Brylinsky and Mann, 1973; Van Schalkwyk and Walmsley, 1984). Turbidity, in turn, is directly related to the degree of soil erosion in the catchment and influenced by natural factors such as rainfall, wind and catchment geology and anthropogenic activities such as overgrazing, non-contour ploughing and removal of riparian vegetation (Davies and Day, 1998). The chemical properties of reservoir water are generally determined by climate, geology and anthropogenic conditions of the catchment (Davies and Day, 1998). The biomass of phytoplankton and zooplankton in a reservoir is therefore intricately linked to the natural and anthropogenic characteristics of its catchment.

Although many reservoirs have been constructed in South Africa to compensate for unpredictable seasonal rainfall and the lack of permanent water bodies (Davies and Day, 1998), there is a lack of limnological information pertaining to them (Hart, 2001). In the Eastern Cape, basic limnological information is only available for the Laing, Bridle Drift and Nahoon reservoirs (Tow, 1981). Selkirk and Hart (1984) conducted a study examining eutrophication of reservoirs in the Buffalo River, while the water chemistry of ten reservoirs in the former Transkei have been studied (Du Preez, 1985).

Since the Eastern Cape region has a relatively uniform geology and similar rainfall, evaporation and vegetation characteristics, this chapter aims to gain an understanding of the effects of these parameters on water turbidity and chemistry in the region. Besides the influence of geology, rainfall, evaporation and vegetation, differences in altitude and human activities in the catchment of reservoirs could influence algal and zooplankton biomass. To test this, the limnology of a "high" altitude reservoir with negligible anthropogenic pressure was compared to a "low" altitude reservoir with a high anthropogenic pressure.

MATERIALS AND METHODS

Study sites

The location of the Katriver and the Laing reservoirs are shown in Figure 2.1. The Katriver was impounded in 1969 to provide water for citrus farming in the nearby Katriver Valley, while the Buffalo River was impounded by the Laing Dam in 1950 to provide water for industrial and domestic use in King Williams Town. The two reservoirs are similar in volume, surface area and mean depth (Table 2.1). The geology of the small Katriver Reservoir catchment (258 km^2) is similar to the larger catchment (913 km^2) of the Laing Reservoir (Midgley *et al.,* 1994). Despite the differences in the altitude of the two reservoirs, the annual rainfall and evaporation rate in the catchments are similar.

Human activity in the Katriver Reservoir catchment is restricted mainly to subsistence farming (Table 2.2). The catchment of Laing Reservoir has twice the population density, almost fifty times more industrial manufacturers and over four times the number of households without flush toilets in comparison to the Katriver Reservoir catchment (Table 2.2). These factors have caused excessive nutrient loading and have led to the proliferation of the introduced water hyacinth (*Eichornia crassipes*) (M. Hill, Department of Entomology, Rhodes University, Grahamstown, pers. comm.).

The two reservoirs were sampled monthly between November 1999 and October 2000. Vertical profiles of water temperature and dissolved oxygen were measured at a deep offshore station near the reservoir wall using a hand-held oxygen meter (Oxygaurd handy MKIII). Direct turbidity and conductivity measurements were made near the major inflow, middle reaches and near the wall of each reservoir, using a Hanna 93703 turbidimeter and a Hanna HI 933300 conductivity meter respectively. Water chemistry datum and reservoir water level were obtained from the Department of Water Affairs and Forestry. Monthly rainfall datum was obtained from the South African Weather Bureau.

Chlorophyll ‘a’ concentration was determined at one-metre intervals from the surface to a depth of 5 m. Due to unavailability of a field fluorometer, water samples were stored on ice in a black-lined cooler box and frozen for a maximum of six months at –30°C. While the degradation of chlorophyll ‘a’ over time and the poor filtration efficiency of chlorophyll ‘a’ after freezing is recognised, the standardised method used for both reservoirs ensured that comparisons between the systems are still valid. In the laboratory, samples were defrosted in black containers and filtered (GF/F filters) with a vacuum pump. Chlorophyll ‘a’ was extracted in 90% acetone for 24 hours in the dark and concentrations were determined flourometrically (Turner 10AU flourometer), before and after acidification with 4N HCl (Holm-Hansen and Riemann, 1978).

Zooplankton was collected using vertical hauls with a conical plankton net, with a mouth opening of 55 cm and a mesh aperture of 100 µm. Floating algal colonies were decanted (Seaman *et al.,* 1981) and zooplankton preserved in 5% formalin. In the laboratory, the species composition was assessed after mixing the sample thoroughly and subsampling fractions of between 1/10 and 1/50 with a fulsum splitter. Zooplankton was identified to genus level, where possible using the keys of Day *et al.* (1999). Each whole sample was then filtered through pre-weighed gf6 glass fibre filter papers and dried to a constant mass at 70°C (Seaman *et al.*, 1981). The filter was then reweighed and the biomass of zooplankton.m^{-3} of water calculated.

Littoral benthic invertebrates were collected monthly in muddy substrata using a Peterson Grab. Three sediment samples were collected at a depth of 0.5 m in three different sites from near the wall to the upper reaches of each reservoir and immediately preserved in 5% formalin. In the laboratory, approximately 3 litres of salt-water solution (± 50 g.l^{-1}) was added to each sample to increase the floatation of the benthic organisms (Wetzel and Likens, 2000). The sample was stirred and the supernatant sieved through a 0.4 mm sieve. To ensure that all zoobenthos was collected, this process was repeated three times for each sample. The material was examined under a dissecting microscope and all zoobenthos was removed and stored in 5% formalin. Zoobenthic organisms were identified to family level, where possible, using the keys of Davies and Day (1998).

A Shapiro-Wilk Test was used to test if the water temperature, turbidity and water chemistry values were normally distributed. Data not normally distributed were log-transformed. Differences in water quality parameters between reservoirs were then tested using a t-test. Differences in the concentration of cholorophyll 'a' and the abundance of zoobenthic organisms between reservoirs was tested using the Mann-Whitney U test, while differences in the density of zooplankton in the water column was tested using a t-test after a natural logarithm-transformation. A regression analysis was used (with chlorophyll 'a' as the dependent variable) to ascertain influential environmental characteristics.

RESULTS

The high monthly rainfall at Laing Reservoir in comparison to the Katriver Reservoir (Figure 3.1) was reflected in the reservoir levels. Laing Reservoir was almost at full supply level throughout the year. In the winter of 2000, a broken sluice gate in the Katriver Reservoir resulted in a steady decline in the water level (Figure 3.1). Laing Reservoir overflowed in late-December, mid-March and late-March, while the Katriver Reservoir overflowed in mid-March.

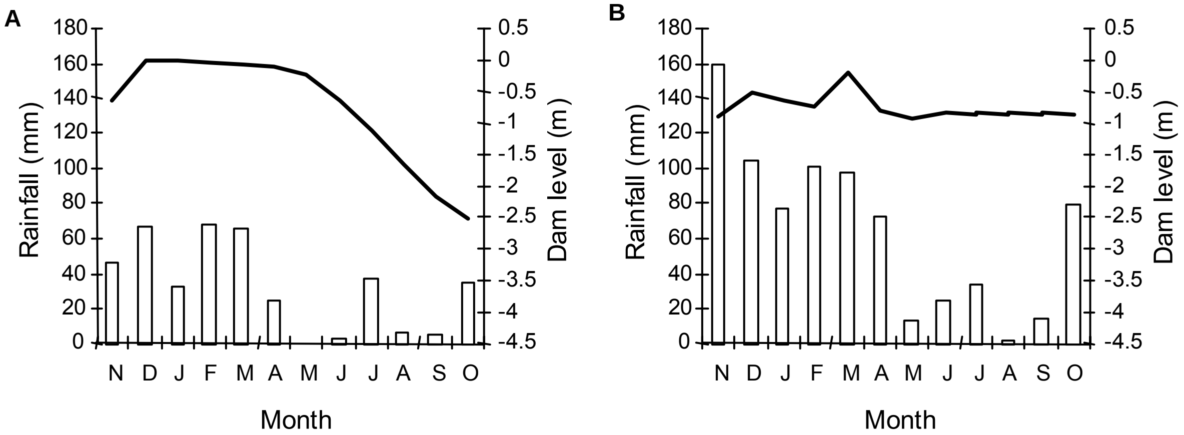

Figure 3.1. Mean monthly rainfall (bars) and reservoir level (line) of Katriver (A) and Laing (B) reservoirs (November 1999 to October 2000).

Both reservoirs (Figure 3.2) showed a typical warm monomictic pattern of thermal stratification and there was no significant difference in the mean monthly temperature at three depths between the reservoirs (p=0.86) (Table 3.1).

Both reservoirs were turbid throughout the study period (Table 3.1). Turbidity in Laing Reservoir was highest in summer and lowest in spring (Figure 3.2). No major fluctuations were observed in turbidity in Katriver Reservoir (Figure 3.2). The mean turbidity of Katriver Reservoir was not significantly different (p=0.30) from that of Laing Reservoir (Table 3.1).

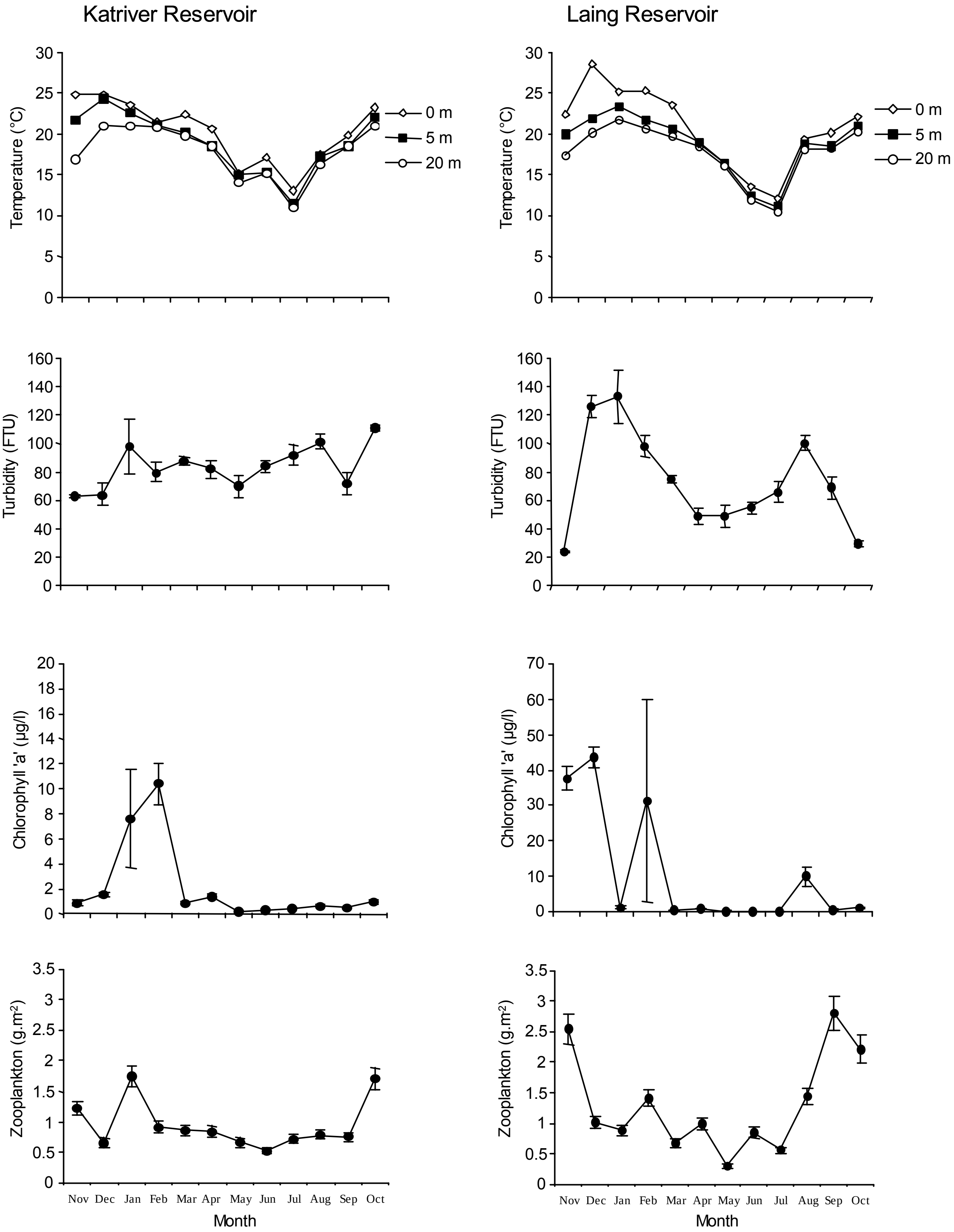

Figure 3.2. Monthly variation (± standard deviation) in temperature, turbidity, chlorophyll ‘a’ concentration and zooplankton biomass in the Katriver and Laing reservoirs sampled between November 1999 and October 2000.

Table 3.1. Mean water quality parameters (± standard deviation) from the Katriver and Laing reservoirs sampled between November 1998 and October 2000.

	Katriver Reservoir	Laing Reservoir
Mean monthly temperature (°C)	20.5 ± 5.2	20.3 ± 4.2
Mean monthly conductivity ($mS.m^{-1}$)	11.3 ± 4.7	51.3 ± 4.6
Mean monthly turbidity (FTU's)	65.9 ± 20.1	74.1 ± 28.0
pH range	7.1-8.1	7.2-9.4
Mean monthly chlorophyll *a* ($mg.m^{-3}$)	1.4 ± 2.9	8.4 ± 15.4
Trophic status	Oligotrophic	Eutrophic

The conductivity of the Laing Reservoir water was significantly higher ($p<0.01$) than the Katriver Reservoir (Table 3.1) and consequently the concentration of cations and anions were significantly higher in the former (Table 3.2). The order of cation and anion dominance in the Katriver Reservoir was similar to average river water (Wetzel, 1983), except for sodium, which normally has a higher equivalent molecular weight per volume than magnesium. The water in Laing Reservoir was, however, considerably different to average river water as result of the high sodium and chloride concentrations. The water from both reservoirs was marginally alkaline (Table 3.1), and according to the degrees of hardness proposed by Sawyer and McCarthy (1967), Katriver Reservoir water was soft, while Laing Reservoir water was moderately hard (Table 3.2). While there was little evidence of phosphorous and nitrogen enrichment in Katriver Reservoir, significantly higher levels of nitrates suggested enrichment in Laing Reservoir (Table 3.2). The source of enrichment is most likely commercial farming which occurs higher in the catchment and domestic waste which is derived from the settlements on the banks of the Buffalo River just upstream from the reservoir.

Although the mean chlorophyll 'a' concentration in Laing Reservoir was 8.4 $\mu g.l^{-1}$ (range 0.06 – 47.22 $\mu g.l^{-1}$), compared with 1.4$\mu g.l^{-1}$ (range 0.11 – 20.49 $\mu g.l^{-1}$) in Katriver Reservoir, they were not significantly different ($p=0.75$). Generally chlorophyll 'a' values were highest in the summer months in both reservoirs (Figure 3.2). The sudden drop in chlorophyll 'a' concentration in Laing Reservoir in January was ascribed to phytoplankton washout when the reservoir flooded in late December. Of all the water parameters tested, there was a significant relationship between chlorophyll ‘a’ and temperature in Katriver Reservoir ($p<0.05$), and temperature ($p=0.03$) and silica ($p<0.01$) in Laing Reservoir (Table 3.3). Silica was inversely proportional to the concentration of chlorophyll ‘a’ in both reservoirs.

Table 3.2. Conductivity, pH and dissolved constituents determined between November 1998 and October 2000 in the Katriver and Laing reservoirs.

	Katriver	Equivalent molecular weights	Laing	Equivalent molecular weights	p value
Electrical conductivity ($mS.m^{-1}$)	11.3 ± 4.7		51.3.± 4.6		p< 0.01
pH (pH units)	7.2 – 8.4		7.2 – 9.4		
Na^+ ($mg.l^{-1}$)	10.4 ± 0.6	0.45	54.4 ± 14.1	2.37	p< 0.01
Mg^{2+} ($mg.l^{-1}$)	4.1 ± 0.2	0.34	10.3 ± 2.8	0.85	p< 0.01
Ca^{2+} ($mg.l^{-1}$)	9.2 ± 0.6	0.46	17.4 ± 4.0	0.87	p< 0.01
K^+ ($mg.l^{-1}$)	1.6 ± 0.2	0.04	3.1 ± 0.6	0.08	p< 0.01
Si^+ ($mg.l^{-1}$)	7.7 ± 0.3		6.8 ± 1.6		p< 0.01
Total ($CaCO_3$) alkalinity ($mg.l^{-1}$)	46.8 ± 2.6	0.94	92.0 ± 19.2	1.84	p< 0.01
SO_4^{2-} ($mg.l^{-1}$)	12.8 ± 3.6	0.27	23.0 ± 5.2	0.48	p< 0.01
Cl^- ($mg.l^{-1}$)	12.1 ± 1.6	0.34	69.5 ± 20.0	1.96	p< 0.01
F^- ($mg.l^{-1}$)	0.15 ± 0.02		0.21 ±0.04		p< 0.01
$PO^{3+}{}_4 - P$ ($mg.l^{-1}$)	0.04 ± 0.02		0.11 ± 0.37		p = 0.18
$NH^+{}_4 - N$ ($mg.l^{-1}$)	0.03 ± 0.02		0.05 ±0.07		p= 0.02
$NO^-{}_3 + NO^-{}_2 - N$ ($mg.l^{-1}$)	0.19 ± 0.12		1.08 ± 0.61		p< 0.01

The zooplankton species observed in Katriver and Laing reservoirs included three cladocerans; *Daphnia barbata*, *Daphnia pulex* and *Moina micrura*, three copepods; *Lovenula falcifera, Metadiaptomus meridianus* and *Metadiaptomus purcelli* (Laing Reservoir only), unidentified rotifers and a large predatory *Chaoborus* species. Although mean zooplankton biomass was not significantly different ($p=0.37$) it was higher in the Laing reservoir (1.30 ± 0.8 $g.m^{-1}$) than in the Katriver reservoir (0.95 ± 0.4 $g.m^{-1}$). Zooplankton biomass peaked in the warm summer months (Figure 3.2).

Table 3.3. Statistical relationships between selected water quality parameters and chlorophyll ‘a’ in the Katriver and Laing reservoirs sampled between November 1999 and October 2000. A total of 12 data points were used in each regression.

	Katriver			Laing		
	p	F	r^2	p	F	r^2
Temperature (°C)	0.31	1.17	0.10	0.03*	6.00	0.38
Conductivity ($\mu S.m^{-1}$)	0.40	0.77	0.07	0.94	0.01	0.01
Turbidity (FTU)	0.09	3.63	0.27	0.45	0.61	0.06
Si^+ ($mg.l^{-1}$)	0.05	4.77	0.32	0.01*	13.07	0.57
Total ($CaCO_3$) alkalinity ($mg.l^{-1}$)	0.13	2.76	0.22	0.55	0.38	0.04
PO_4 – P ($mg.l^{-1}$)	0.32	1.10	0.10	0.56	0.36	0.04
NH_4 – N ($mg.l^{-1}$)	0.03*	6.16	0.38	0.93	0.01	0.01
$NO_3 + NO_2$ – N ($mg.l^{-1}$)	0.71	0.15	0.02	0.62	0.26	0.03

* indicates a significant relationship at the 0.05% level

The density of zoobenthos in the muddy littoral zones of Katriver Reservoir (56 – 2 065 organisms.m^{-2}) and Laing Reservoir (37 – 1 726 organisms.m^{-2}) was extremely variable but not significantly different (p=0.59). The composition of the benthic fauna was similar between the reservoirs (Figure 3.3), with insect larvae, most notably the Chironomidae, dominating the littoral zones in both reservoirs. Cyclopoid copepods were encountered in Laing (16.4%) and Katriver reservoirs (4.4%). These were most likely attached to benthic macrophytes, which were present in the benthic grab samples. While a large number of leeches (Hirudinea) were encountered in Katriver Reservoir, none were found in Laing Reservoir.

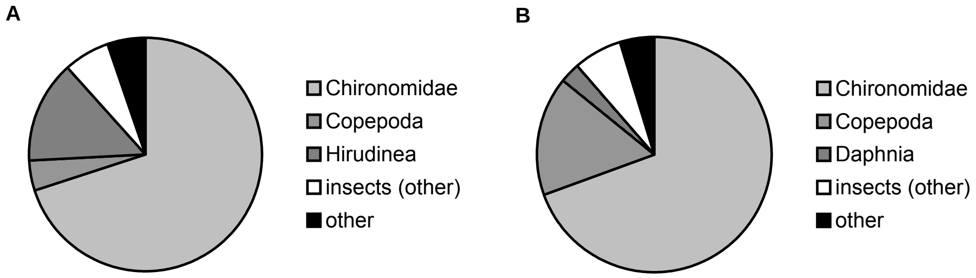

Figure 3.3. Composition of the littoral benthic fauna in the Katriver (A) and Laing (B) reservoirs sampled between November 1999 and October 2000).

DISCUSSION

On evaluating Straškraba's (1980) global surface water temperature prediction model in South African impoundments, Van Schalkwyk and Walmsley (1984) suggested that reservoir surface water temperature was influenced by impoundment morphometry, turbidity and altitude. While the morphometry of the two reservoirs was remarkably similar (Table 2.1), and the turbidity of the reservoirs was not significantly different, the 450 m difference between the reservoirs suggested that the mean temperature in the high altitude Katriver Reservoir should be lower. This was, however, not the case and the similarity in temperature between the reservoirs suggests that this parameter is unlikely to have been the underlying reason for the observed differences in chlorophyll 'a' concentration or zooplankton biomass.

Water turbidity of reservoirs is generally attributed to geology, topography, climate (Hart, 2001) and human activities such as overgrazing and poor land-use and management (Hart, 1999). Sedimentary rock, such as that found in the catchments of the reservoirs is highly susceptible to erosion (Rooseboom, 1978). In addition, the high levels of subsistence agriculture and overgrazing in the catchment of both reservoirs also increases erosion and suggests that these factors also have a major influence on the turbidity of the water. Since most of the Eastern Cape rock formations are sedimentary (Rust, 1988) and the Eastern

Cape has the highest rural populations of any province in the country (CSIR, 2001), most reservoirs are expected to be turbid. Walmsley and Bruwer (1980) examined the water transparency characteristics of South African impoundments and showed that most of the highly turbid impoundments were situated in the Eastern Cape, Free State and Gauteng Province. Du Preez's (1985) work in the Eastern Cape supports this finding.

The most important effect of high abiotic turbidity levels is a reduction of the photic zone in the aquatic environment (Walmsley and Bruwer, 1980). This results in a decrease in primary production and has a cascading effect through the food chain, affecting other organisms. An increase in abiotic turbidity should result in a decrease in chlorophyll 'a' in both reservoirs, which in turn could lead to a reduction in zooplankton biomass by limiting food availability (Allanson *et al.*, 1990) and disrupting zooplankton-feeding mechanisms (Hart, 1988). Since the water turbidity was similar in the reservoirs, the algae and zooplankton were affected equally by this parameter and it is therefore not considered a cause for the differences in their biomass between the reservoirs.

Fish production can also be significantly influenced by turbidity. In Vanderkloof Reservoir, Tomasson and Allanson (1983) and Merron and Tomasson (1984) indicated that an increase in turbidity ultimately resulted in decreased growth and production of the larger cyprinid species due to a decrease in food availability. However, some recent evidence suggests that the sharptooth catfish, *C. gariepinus*, which is present in both reservoirs, is adapted to feeding in low visibility conditions and may grow faster and be more productive in turbid environments (Potts, unpublished data). In the case of moggel production, the influence of turbidity can only be assessed after comparing the populations in reservoirs with contrasting water turbidity.

High turbidity has been noted to decrease the potential for eutrophication (Wamsley and Bruwer, 1980). This may be particularly important in Laing

Reservoir due to its nitrogen enrichment. A consequence of eutrophication is an increase in algal biomass and a change in algal species composition (Welcomme, 2001). However, until the feeding biology of moggel is understood, the influence of eutrophication on the production of these fish is unknown.

Surface waters acquire specific chemical characteristics as a result of physical and chemical weathering processes of geological formations, chemical reactions with the atmosphere and from anthropogenic sources (Faust and Aly, 1981). The cationic and anionic order of “average river water” is Ca^{2+}>Mg^{2+}> Na^{+}>K^{+}, and CO_3^{2-} > Cl^{-} > SO_4^{2-} respectively (Wetzel, 1983). While the water in Katriver Reservoir was similar to average river water, sodium and chloride ions dominated in the Laing Reservoir. The natural source of both sodium and chloride in fresh water is igneous rock (Faust and Aly, 1981), rain, snow and other forms of precipitation (Davies and Day, 1998). Anthropogenic sources of sodium and chloride include domestic effluents and particularly high concentrations of sodium are found in synthetic detergents (Wetzel, 1983). In general, reservoirs in catchments dominated by sedimentary rocks have low nutrient and salt concentrations (Davies and Day, 1998). These reservoirs are known as ‘precipitation dominated’ and their waters are soft, pure and unbuffered with sodium and chloride being the dominant ions (Davies and Day, 1998). The similar geological formations in the catchment of both reservoirs and the hardness of the Laing Reservoir water suggest that the dominance of sodium and chloride in this reservoir cannot be explained by catchment geology. The difference in concentrations of these ions between reservoirs therefore suggests that anthropogenic activities in the catchment of Laing Reservoir are the dominant factor influencing the ion concentration. Unfortunately, the biological implications of a different ionic dominance and a significantly higher concentration of ions are not currently understood (Day and King, 1995). However, conductivity has been used extensively as an indicator of fish production in large lakes and reservoirs (Ogelsby, 1977; Henderson and

Welcomme, 1974; MRAG, 1995), suggesting that this variable is of biological significance.

Nitrogen and phosphorus are seldom abundant in natural standing waters (Davies and Day, 1998). Elevated levels of nitrogen and phosphorus can normally be attributed to domestic, agricultural and industrial pollution (Davies and Day, 1998). The significantly higher concentration of nitrogen in Laing Reservoir is a clear indication that there are major anthropogenic influences in the Laing Reservoir catchment. The presence of high concentrations of nutrients stimulates plant growth (Davies and Day, 1998) and the difference in plant nutrient concentrations between the reservoirs is probably the factor most responsible for differences in the phytoplankton and zooplankton biomass. This is also reflected by the prolific presence of water hyacinth (*Eichornia crassipes*) in Laing Reservoir.

The only parameter that was significantly correlated with chlorophyll ‘a’ concentration within both reservoirs was water temperature, suggesting that increased temperatures in summer promoted algal growth in the reservoirs. The inverse relationship between chlorophyll ‘a’ and silica within the reservoirs is understandable since diatoms absorb it, mostly as orthosilicate (Delince, 1992). An increase in algal biomass enhances food availability for primary consumers such as zooplankton, zoobenthos as well as detritivorous and herbivorous fish, and would therefore result in increased fish growth production.

Zooplankton biomass is influenced by factors such as phytoplankton biomass, water retention time, temperature and turbidity (Campbell *et al.,* 1998). Since water retention time, temperature and turbidity were similar in the two reservoirs, the higher zooplankton biomass in the Laing Reservoir is likely to be a consequence of the higher phytoplankton biomass. Seaman *et al.* (1981) reported mean zooplankton biomass values between 0.38 and 5.32 $g.m^{-2}$ in eleven reservoirs in the former Transvaal Province and found a linear relationship between chlorophyll ‘a’ and zooplankton biomass. The relationship between chlorophyll ‘a’ and zooplankton biomass in the Katriver and Laing reservoirs fall within the 95% confidence levels of this regression (Seaman *et al.*, 1981), suggesting that the zooplankton biomass was dependent on phytoplankton biomass in both reservoirs.

The similar density of zoobenthos in the two systems was surprising and may indicate that these organisms utilise an alternative food source (e.g. detritus) in Katriver Reservoir. An increase in nutrients in waters subject to organic pollution often results in a decrease in species richness and the dominance of tolerant species (Davies and Day, 1998). The low zoobenthic species diversity and dominance of chironomids in both reservoirs is a clear indication of nutrient enrichment.

CONCLUSION

Water temperature was not influenced by the difference in altitude and had an equal effect on algal biomass of algae in both reservoirs. The reservoirs were both turbid as a consequence of erosion, which was caused by the weathering of sedimentary rock and exacerbated by human activities (improper land-use practices and overgrazing) in the catchments. As with temperature, the similar turbidity in the reservoirs had a comparable influence on light penetration and on the algal biomass. Due to the uniform geological formations and high rural population density, such conditions are expected in reservoirs throughout the Eastern Cape. The dominance of sodium and chloride in the water of the reservoirs was caused by the deficiency of other ions in the catchment bedrock and was further exacerbated by the increased input of these ions from anthropogenic sources. The increased concentration of nutrients was through human activities in the catchment, and is considered to be the main cause of the increased phytoplankton and zooplankton biomass in Laing Reservoir. Although understanding the processes influencing food availability for fish is important, a description of the diet of moggel is crucial to understand the relationships between trophic levels in the small reservoir ecosystem.

CHAPTER 4

The effect of reservoir trophic status on feeding and growth of *Labeo umbratus*

INTRODUCTION

Fish production is directly influenced by growth, which in turn is dependent largely on food availability, feeding rate and the nutritional value of the ingested food (Welcomme, 2001). Food availability may be influenced by changes in the trophic status of a water body (Treasurer and Owen, 1991; Bayne *et al*., 1991; Bayne *et al*., 1992; Liu *et al*. 1994) and it is therefore not surprising that fish production has been linked to primary production (Boyd, 1979; Goodyear *et al.,* 1972; Melack, 1976). In southern Africa, both Tomasson and Allanson (1983) and Merron and Tómasson (1984) noted that a depression of the trophic resource base in Lake Le Roux resulted in a cascading effect through the food web, resulting in decreased growth and production of larger cyprinid species. Marshall (1978) and Cochrane (1985) have also reported that an increase in the trophic resource base, through eutrophication, resulted in increased fish production in Lake Chivero and Hartebeespoort Reservoir, respectively. To understand how fish growth is influenced by changes in trophic status it is essential to examine their feeding biology. Unfortunately no feeding studies were conducted on the fish from Hartebeespoort Reservoir and Lake Chivero, but theoretically, depending on the feeding guild of the species, an increase in primary production may directly (in the case of a primary consumer) or indirectly (in the case of a secondary consumer) increase food availability and the nutritional value of the food, ultimately resulting in increased growth.

The only previous feeding study on moggel was undertaken in Baberspan by Schoonbee (1969), who described it as an indiscriminate feeder, with plant material, detritus and cladocera as the most important food items. Based on this information, Skelton (2001) described the moggel as a detritivore.

While detritus is a general term used to define non-living particulate material in aquatic ecosystems (Yossa and Araujo-Lima, 1998), detritivorous fish generally feed on detrital aggregate. This is a mixture of organic matter, consisting of dead material, which is rich in lignin and cellulose, and small amounts of living micro-invertebrates, algae, fungi and bacteria (Bowen *et al.,* 1984). Although detrital aggregates consumed by fish in different habitats are mixtures of similar components, their relative quantity and nutritional value may vary greatly (Bowen 1979). These differences are reflected in highly variable growth rates (Lowe-McConnel, 1975; Bowen, 1979; Persson, 1983; Mundahl and Wissing, 1987). The protein content of detrital aggregate has most often been used as a measure of nutritional quality (Bowen, 1979). In Lake Sibaya, protein content was proportional to the diatom concentration in the detrital aggregate (Bowen, 1979). Therefore, the enhanced primary production of eutrophic systems could increase the proportion of diatoms in detrital aggregate, thus improving its nutritional quality and consequently resulting in enhanced fish growth.

It was hypothesised that moggel inhabiting eutrophic systems will exhibit faster growth than in oligotrophic systems, as a direct result of an increase in the nutritional quality of the available detrital aggregate. To test this hypothesis, the growth and feeding biology of moggel in a eutrophic and an oligotrophic system were compared.

MATERIALS AND METHODS

Study sites

The Katriver and the Laing reservoirs were selected for this study and their environmental characteristics are described in Chapter 2.

General sampling

Water temperature, pH, turbidity, conductivity, oxygen and chlorophyll ‘a’ concentration were recorded at representative, randomly selected sites in each reservoir on a monthly basis using the methods described in Chapter 3. These results are summarised in Table 3.1.

Fish were sampled monthly using the methods described in Chapter 2. Fish captured in gillnets were only considered for gut analysis if they were collected within one hour of setting the gear. The fork length (mm) and mass (g) of each fish was measured. The entire alimentary canal was removed within one hour after capture and preserved in 10% formalin. The lappilar otoliths were removed from all fish and stored in gelatine capsules for age determination.

Gut analysis

In the laboratory, the alimentary canal was carefully unravelled and measured. The contents of the first and last five percent of the alimentary canal were removed by rinsing with a known volume of water (20 ml). The volume of each sample was then calculated by subtraction after measuring the new total volume. The samples were thoroughly mixed and five (±0.1 ml) sub-samples placed on a graduated microscope slide (1 mm^2) and examined using a compound microscope (magnification 40 x). The contents of five randomly selected squares were described by classifying the food items into the following broad categories; algae (diatoms, green or blue-green), sand, detritus and other. The proportion of each food category in each graduation was estimated as a percent of the total contents.

The percent volume contribution of each food category in juveniles and adults was calculated, root-root-transformed and subjected to a Bray-Curtis (1957) similarity analysis for comparison. Percent similarity in volumetric contribution of each food category for fish from the two reservoirs was illustrated by way of dendograms and tested for differences using an analysis of similarity (ANOSIM) permutation test (Clark, 1993; Clark and Warwick, 1994).

Algal digestibility

Algae were categorised into three categories, viz. diatoms, blue-green algae or green algae, and the number of whole and broken algal cells recorded. Algal cells were considered to be broken if the cell wall was ruptured or the cytoplasm was absent. It was assumed that the contents had been or would be digested. The percent broken algal cells was calculated in the foregut and hindgut, arcsin transformed and compared between reservoirs using ANOVA.

Nutritional value of the diets

In January, April, July and September 1999, the alimentary canals of 20 fish were collected in the field, stored on ice and transported back to the laboratory in black containers to inhibit post-mortality photosynthesis. The foregut contents were removed and rinsed in water. The water was removed by vacuum filtering (0.5 atm) using membrane filters with a pore size of 0.45 µm. The samples were pooled, oven dried at 105°C and subjected to a micro Kjeldahl analysis (N x 6.25). The analysis was conducted in triplicate and differences in the mean protein content of moggel diets between reservoirs were assessed with a t-test. While the nutritional importance of carbohydrates and lipids in the diet of moggel was recognised, these analyses were not possible due to the small size of the samples and the cost of the analysis.

Detrital aggregate (including detritus, algae and bacteria) was collected seasonally at three randomly selected sites each month from the muddy and sandy substrates in each reservoir using a custom-built core sampler constructed from 100 mm diameter PVC pipe. Only the top 1 cm layer of each sample was oven dried at 105°C, and subject to a protein content analysis using the micro Kjeldahl method. The analysis was conducted in triplicate and differences in the mean protein content of moggel diets between reservoirs were assessed using the monthly data using a t-test.

Age and growth

The most suitable method of interpreting growth zones in the otoliths was assessed. Lappilae were either burned or left unburned and read whole in water and methyl-salicylate under transmitted or reflected light using a dissecting microscope. After three readings, the burned and unburned otoliths were either sectioned longitudinally or transversely through the nucleus with a double bladed, diamond-edged saw. The sections were mounted onto glass slides with DPX mountant, and read three times using the same methods. The most consistent readings were obtained using whole, unburned otoliths immersed in methyl-salicylate BP, read under reflected light, prompting the use of this method to age all fish sampled.

The number of translucent zones was counted on three occasions using transmitted light. If the three readings were the same, the age estimate was accepted. If they differed, the otolith was rejected. To validate the periodicity of ring formation, the outer margin of the otoliths were examined. The composition of the outer margin (either opaque or translucent) was noted and expressed as a percent of the monthly sample. The von Bertalanffy (Ricker, 1975) growth model was fitted to the length-at-age data using a downhill simplex search (Nelder and Mead, 1965), a nonlinear minimisation routine to obtain model parameter estimates. Model fits were obtained by minimising the negative normal log-likelihood of the observed and predicted lengths at age. To compare the model fits, a non-parametric one-sample runs test for residual randomness and the Bartlett's test for their homoscedascity (Hughes, 1986) were applied. In addition, variance estimates were calculated using the (conditioned) parametric bootstrap resampling method (Efron, 1982) with 1 000 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). A likelihood ratio test (Cerrato, 1990) was used to compare the model parameters between the two systems.

RESULTS

The fish ranged from 82 to 314 mm FL and 47 to 413 mm FL in the Katriver and Laing reservoirs, respectively (Figure 4.1).

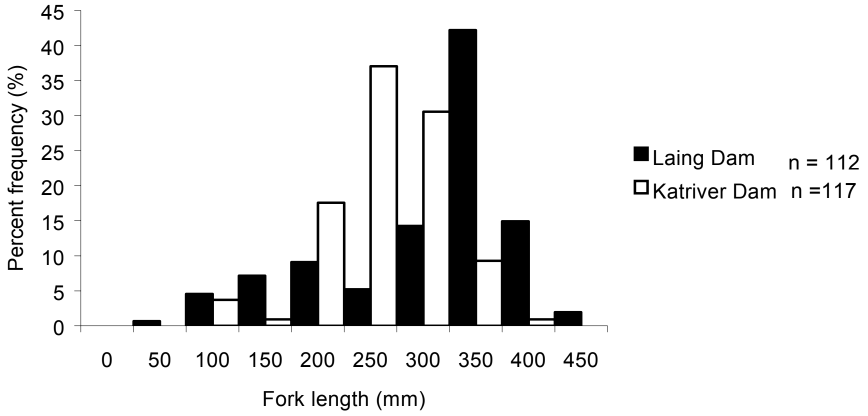

Figure 4.1. Length frequency distribution of *Labeo umbratus* from Katriver and Laing reservoirs between November 1998 and October 1999.

Gut analysis

Forty-seven percent of the 117 fish foreguts from Katriver Reservoir were empty, while 18% of the foreguts of the 112 fish from Laing Reservoir were empty (χ^2 = 13.8, df=1, p<0.001). The diets of juvenile and adult moggel from both reservoirs comprised three main constituents; sand, detritus and algae (Figure 4.2). In the Laing Reservoir, the diet of juveniles and adults had a similarity index of 99.6% (Figure 4.3). In Katriver Reservoir, juveniles consumed less detritus and more sand than the adults and consequently had a lower similarity index of 93.9% (Figure 4.3). When combined, the diets of juvenile and adult moggel had a similarity index of 90.9% between the two reservoirs. Due to the high similarity (99.6%) between the diets of the juvenile and adult fish, samples were pooled per reservoir to compare seasonal dietary differences.

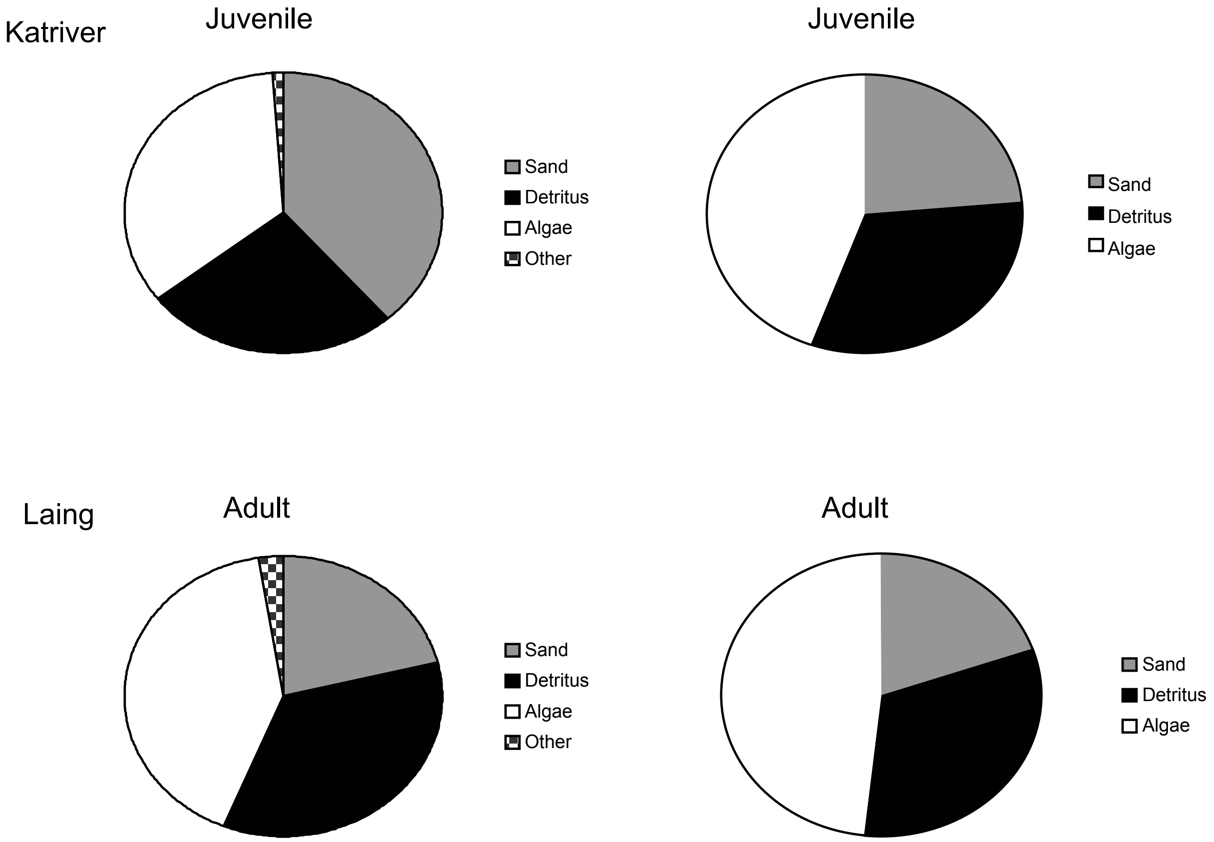

Figure 4.2. The volume estimate of major prey categories in the foreguts of juvenile and adult *Labeo umbratus* from Katriver and Laing reservoirs between November 1998 and October 1999.

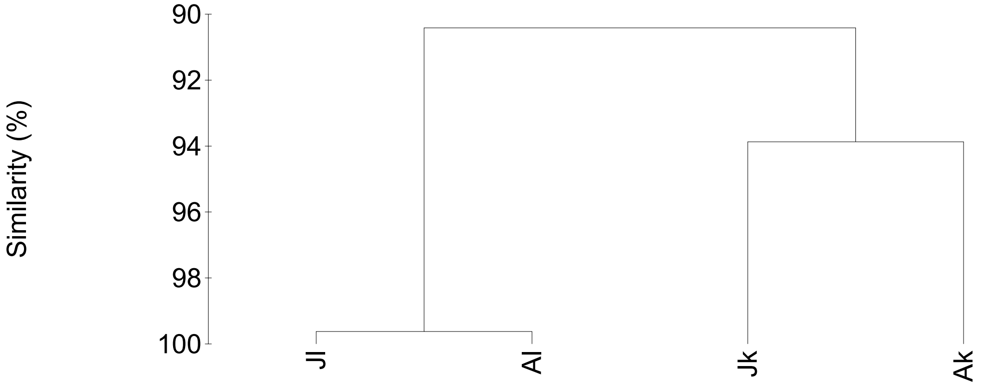

Figure 4.3. Similarity dendogram of the diet of juvenile and adult *Labeo umbratus* in Katriver and Laing reservoirs. (Jl = Laing juveniles, Al = Laing adults, Jk = Katriver juveniles, Ak = Katriver adults).

Detritus and algae dominated the diet of moggel in both reservoirs (Figure 4.4). The highest and lowest proportion of algae in the diets of the fish in both reservoirs was recorded in summer and winter respectively (Figure 4.4). Except in spring, the diet in Laing Reservoir had a higher proportion of algae than in Katriver Reservoir (Figure 4.4). The proportion of sand in the diet ranged from 8.9% to 39.1% (Figure 4.4). Seasonal differences in the diets of Laing Reservoir moggel were small, with a similarity index of 91.7% (Figure 4.5). In Katriver Reservoir, the diet of moggel had a similarity index of 90.3% between autumn and winter, while the similarity index between diets in spring and summer was 90.1% (Figure 4.5).

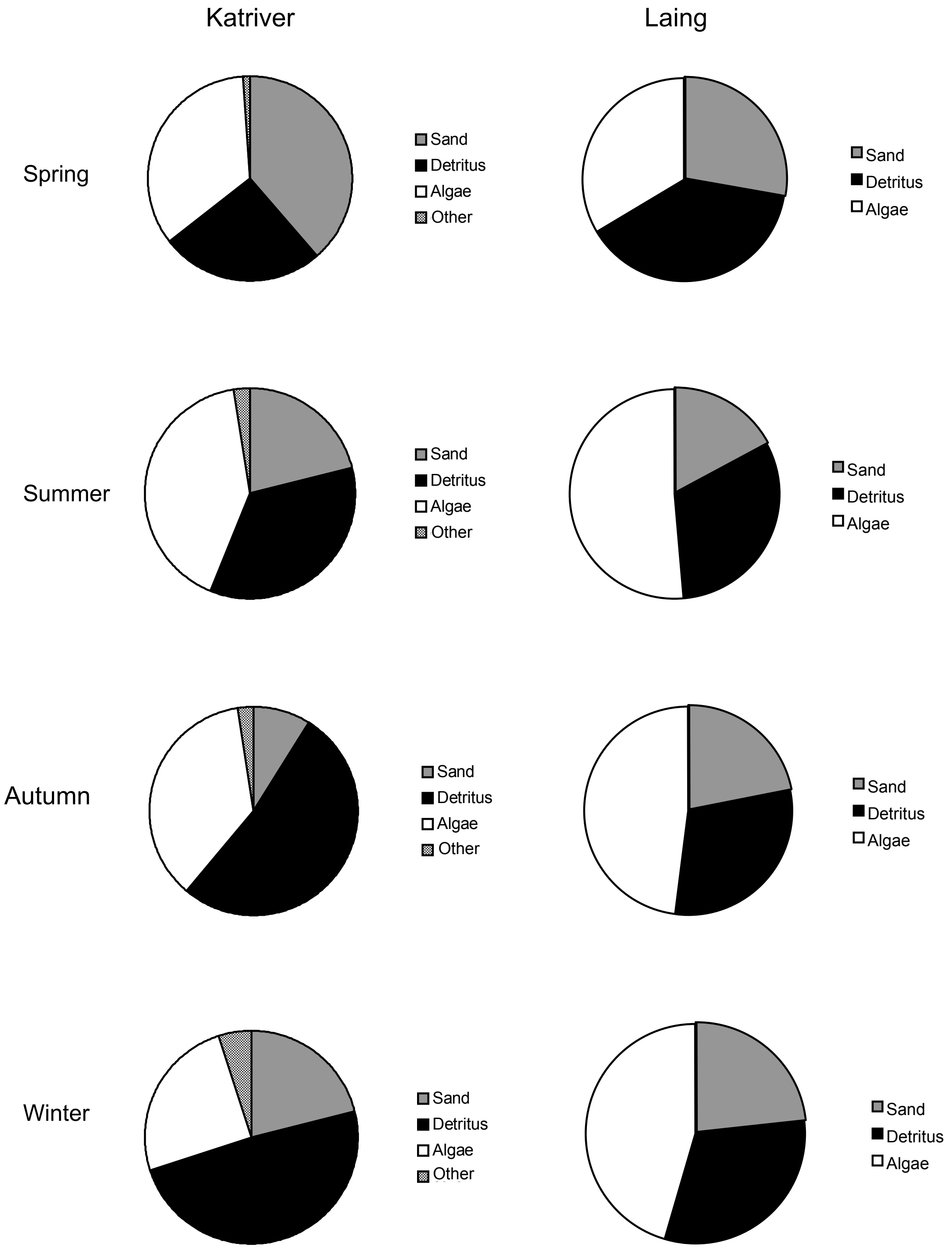

Figure 4.4. The seasonal volume estimate of major prey categories in the foreguts of *Labeo umbratus* sampled from Katriver and Laing reservoirs between November 1998 and October 1999.

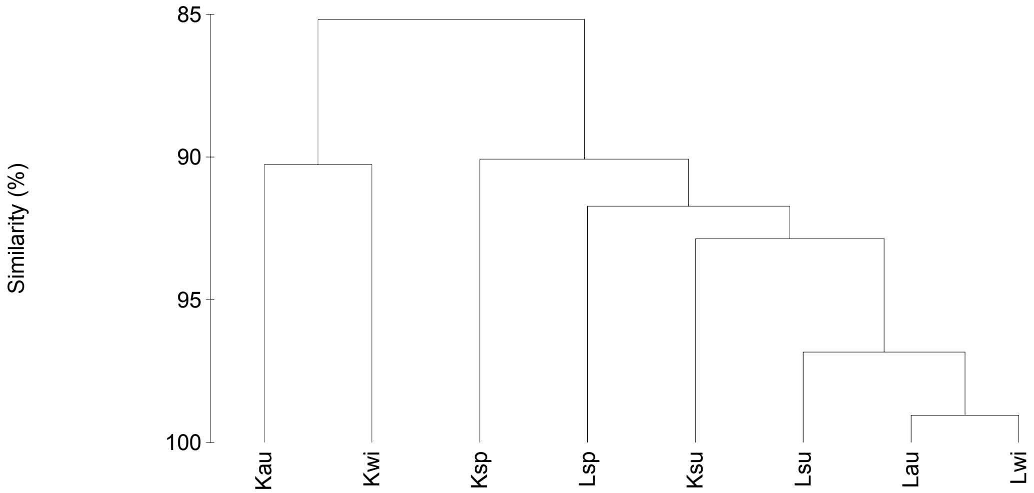

Figure 4.5. Seasonal diet similarity dendogram of *Labeo umbratus* (combined size classes) in Katriver and Laing reservoir. (Kau = Katriver Reservoir autumn, Ksu = Katriver Reservoir summer, Kwi = Katriver Reservoir winter, Ksp = Katriver Reservoir spring, Lsp = Laing Reservoir spring, Lwi = Laing Reservoir winter, Lsu = Laing Reservoir summer, Lau = Laing Reservoir autumn).

Nutritional value of the diets

The protein content of the foregut contents ranged from 14.9 - 19.8% and 18.0 - 23.1% in the Katriver and Laing reservoirs, respectively (Figure 4.6). The mean protein content of the diet in Katriver Reservoir (17.9% ± 3.6 SD) was significantly lower ($p<0.001$) than in Laing Reservoir (20.9 ± 4.1 SD). The protein content of the moggel diets was generally higher in the warmer months than in the colder months (Figure 4.6). This trend was reflected in the protein content of the detrital aggregate (Figure 4.7), which ranged from 10.3 - 19.9% and 14.4 - 21.2% in the Katriver and Laing reservoirs, respectively. The protein content of the diet of moggel was consistently higher than the protein content of the detrital aggregate.

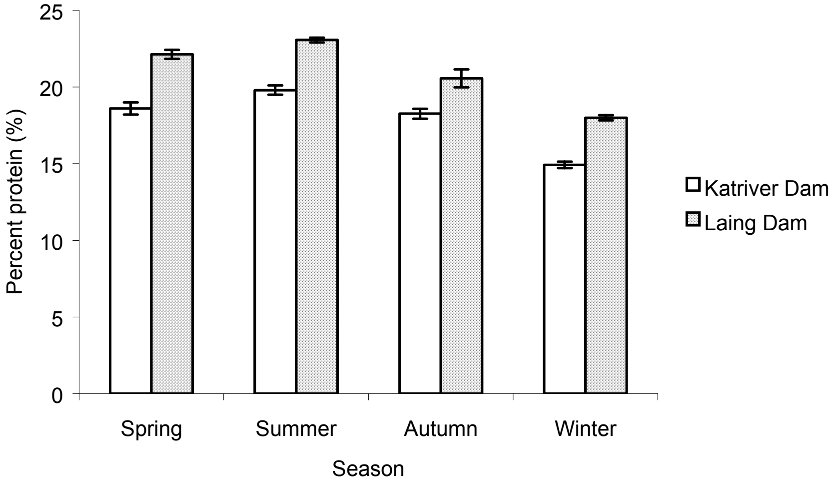

Figure 4.6. The percent protein composition (± standard deviation) of the diet of *Labeo umbratus* in Katriver and Laing reservoirs.

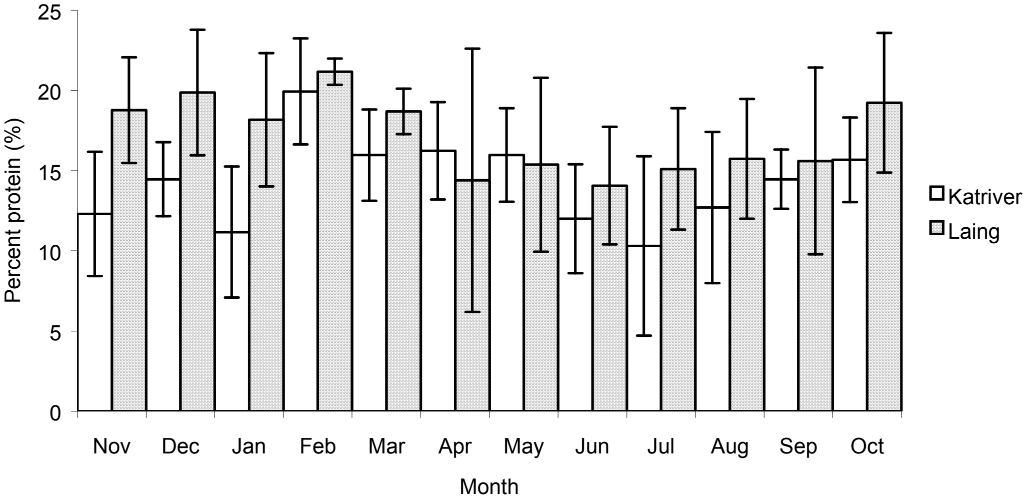

Figure 4.7. Mean percent protein (± standard deviation) of detrital aggregate in Katriver and Laing reservoirs.

Algal digestibility

Diatoms were 'digested' more readily than blue-green algae (Figure 4.8). The digestion of blue-green algae by moggel was low (14%) in Katriver Reservoir and almost negligible (1.2%) in Laing Reservoir (Figure 4.8). While ‘digested’ diatoms were observed in the foreguts, a higher percent was ‘digested’ in the hindgut (Figure 4.8). A higher proportion of diatoms were ‘digested’ by the fish in the Laing Reservoir (43.5%) than in the Katriver Reservoir (39.5%) (Figure 4.8).

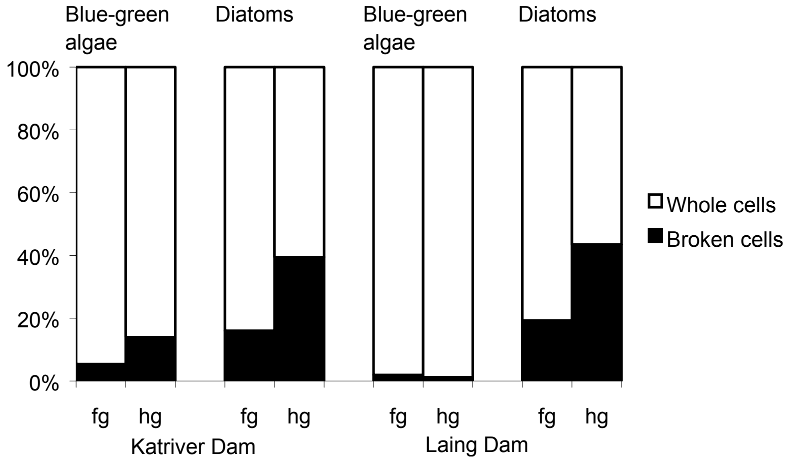

Figure 4.8. The percent broken diatoms and blue-green algae in the foregut and hindgut of *Labeo umbratus* from Katriver and Laing reservoirs (fg=foregut, hg=hindgut).

Age and growth

The marginal zone analysis indicated that a single opaque and translucent zone was deposited each year (Figure 4.9). One opaque ring was therefore interpreted as representative of one year’s growth.

The residuals were both random and homoscedastic by age in Laing Reservoir and random, but not homoscedastic by age in Katriver Reservoir (Figure 4.10). The growth of *L. umbratus* in the Katriver and Laing reservoirs was best described by the Von Bertalanffy growth model: $l_t = 392.3\ (1-e^{-0.20(t-1.43)})$ and $l_t = 372.9\ (1-e^{-0.33(t-0.17)})$, respectively (Figure 4.11). The von Bertalanffy parameters and their coefficients of variation are presented in Table 4.1.

Brody’s growth coefficient (k) was significantly higher for fish from Laing Reservoir ($p = 0.02$), while maximum length (L_∞) was similar ($p = 0.34$).

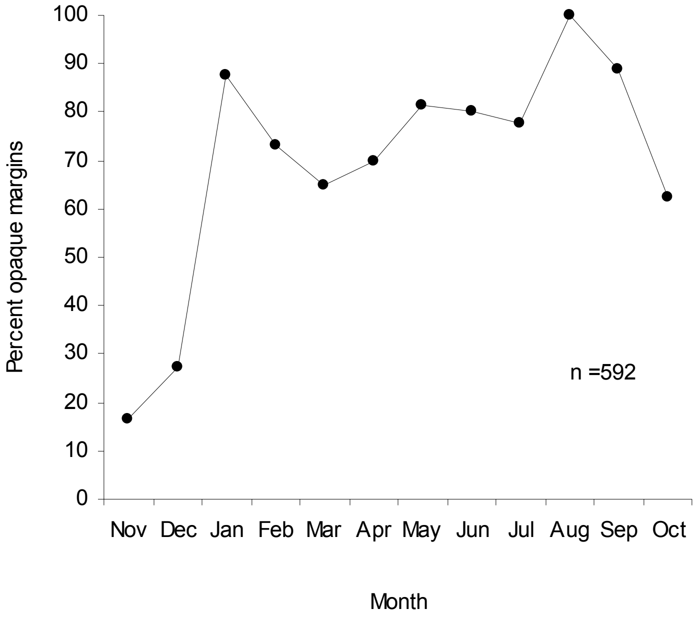

Figure 4.9. Percentage of *Labeo umbratus* otoliths with an opaque margin sampled monthly from Katriver and Laing reservoirs.

Table 4.1. The von Bertalanffy growth parameters and coefficient of variation of *Labeo umbratus* from Katriver and Laing reservoirs.

Growth parameter	Katriver	CV (%)	Laing	CV (%)
L_∞	392.58	5.11	372.98	3.05
k	0.20	15.89	0.33	12.85
t_0	-1.43	27.08	-0.17	124.11

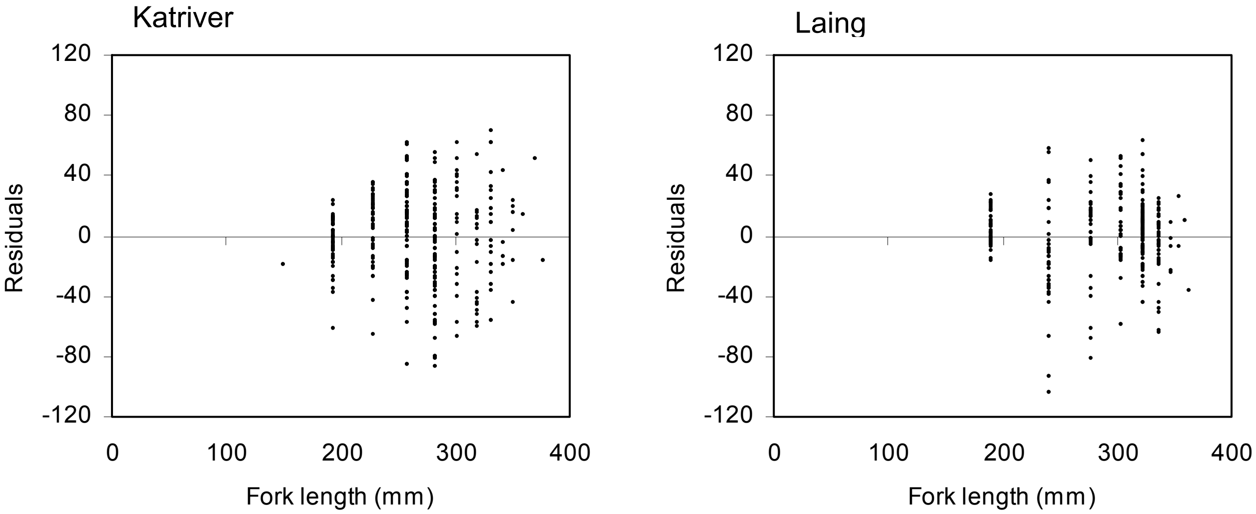

Figure 4.10. Residual plots for the von Bertalanffy growth curve in Katriver and Laing reservoirs.

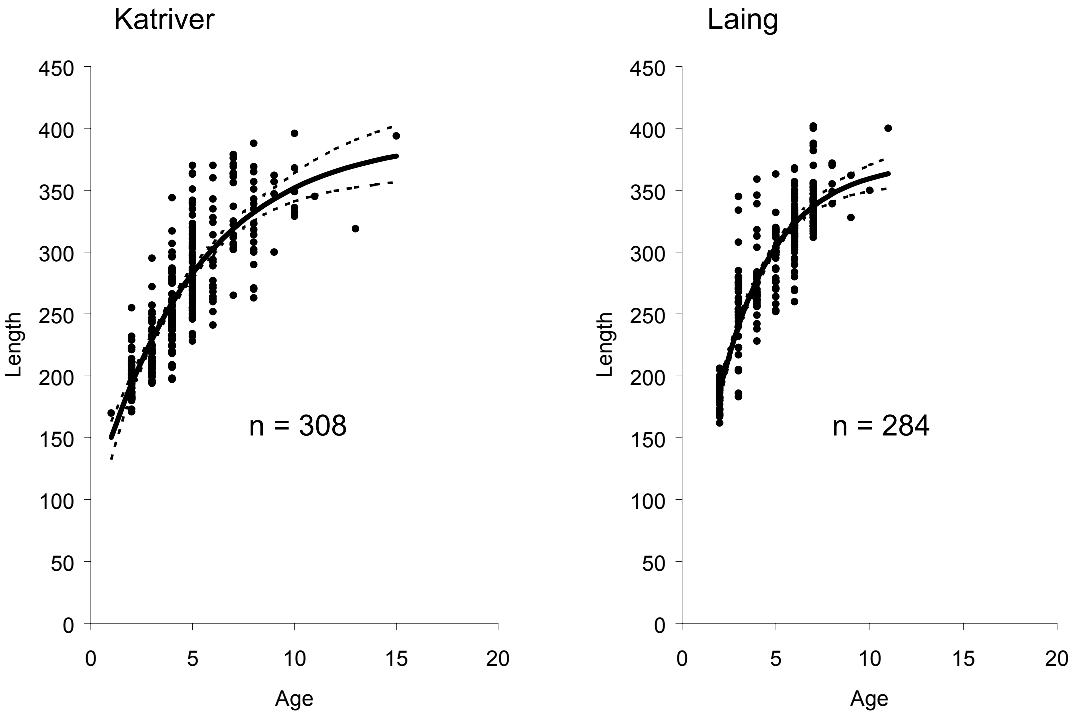

Figure 4.11. The growth of *Labeo umbratus* in Katriver and Laing reservoirs. Dotted lines are the upper and lower 95% confidence intervals from the bootstrapped predicted lengths-at-age.

DISCUSSION

Despite a highly similar dietary composition (>90%) there was a significant difference in the growth rate of the fish in the two reservoirs. Although water temperature has a direct influence on fish growth (Delincē, 1992), the similar temperatures in the reservoirs suggest that the difference in growth rate cannot be ascribed to temperature (Table 2.1). The primary cause for the difference in growth rate must therefore either be food abundance or quality.

When quantifying the diet of detritivorous fishes, the measurement of food availability is inherently difficult. Measuring the volume of detritus in a reservoir is virtually impossible. The quantity of detritus can be influenced by a number of parameters, including the size and number of rivers entering a reservoir and the composition of the vegetation in the riparian zone (Pusey and Arthrington, 2003). The substantially larger catchment of the Buffalo and Yellowoods rivers (Table 2.1) could have increased the availability of detritus in Laing Reservoir, leading to the faster growth of fish in this reservoir. However, the effect of food availability on growth could not be quantified.

The nutritional value of detritus is often quantified by determining the amount of protein present in the detrital aggregate (Bowen, 1979). Diets that are low in protein are reflected by poorer condition and slower growth in detritivorous fishes (Bowen, 1979; Persson, 1983). The protein content of the detrital aggregate in Laing Reservoir was consistently higher than in Katriver Reservoir throughout the year. Calow (1975) and Bowen (1979) report a range of 0% -14% protein as a fraction of organic dry weight, while freshwater algae have a protein content of between 31.0% and 58.6% (Tacon, 1990). The protein content of detrital aggregate therefore appears to be relative to the amount of algae in it. From this it was concluded that differences in moggel growth rate could probably be attributed to the nutritional quality of their diet.

Although the protein content may provide an indication of the nutritional value of the ingested material, the digestibility of algae may have a profound effect on the amount of protein that is assimilated. In both systems, the fish ‘digested’ approximately 40% of the diatoms and an average of 8% of the blue-green algae. Similar diatom and blue-green algae digestion rates have been reported for an estuarine fish species, the Cape Stumpnose (*Rhabdosargus holubi*) (Blaber, 1974). A prerequisite for the digestion of algae is the disruption of the cell wall to expose the contents to digestive enzymes. Stomachless fishes (like cyprinids) use three methods to break down algal cell walls (Bitterlich, 1985). These include acid hydrolysis, enzymatic digestion with cellulase and mechanical breakdown. As cyprinids do not produce cellulase and have a neutral gut pH (Bitterlich, 1985), they must therefore rely on the mechanical breakdown of cell walls (Xie, 1999). The mechanical breakdown of algal cells by the pharyngeal teeth in cyprinids has been documented in silver carp, *Hypophthalmichthys molitrix* (Xie, 1999) and roach, *Rutilus rutilus* (Persson, 1983).

A factor contributing to the successful mechanical breakdown of diatoms is the composition of the cell wall. The silica-based cell wall of diatoms is brittle and facilitates mechanical breakdown, while the cell wall of blue-green algae is cellulose-based and much stronger (Reynolds, 1984; Gerking 1994). In addition, the porous nature of the frustule of diatoms (Blaber, 1974) makes them more vulnerable to digestion. Evidence of mechanical cell wall breakdown was obtained by the presence of broken diatoms in the foregut of moggel. This initial mechanical breakdown may be facilitated by mastication of the food with the pharyngeal plates during feeding (Gerking, 1994) and may be secondarily aided by the large quantity of abrasive sand in the diet.

The increase in the proportion of broken diatoms in the hindgut of moggel indicates that further ‘digestion’ takes place within the alimentary canal after the foregut. This mechanical breakdown in the alimentary canal is probably assisted through the compaction of the algal cells and sand in the alimentary canal.

Cyprinids are very capable of separating food from non-food particles using their palatal organ (Sibbing, 1988). The high proportion of sand in the diet of moggel therefore suggests that this species has adjusted its feeding strategy to specifically use sand for the mechanical breakdown of food items.

In this study, the growth of moggel appeared dependent on the abundance of diatoms in the detrital aggregate. It would therefore appear that conditions that favour the production of diatoms should also favour faster moggel growth. Like all algae, diatom production is high in shallow reservoirs due to their high surface area to volume ratios. Small reservoirs also promote algal and diatom production due to their characteristic thermal instability, which ensures a more rapid exchange of nutrients within the water column and between the water and the sediments (Marshall and Maes, 1994). The concentration of plant nutrients is normally proportional to algal and diatom production and higher concentrations of plant nutrients are normally found when there is agro-chemical or sewage effluent release in the catchment (Welcomme, 2001). However, when the nutrient concentration becomes too high, eutrophication may occur. During this process, the phytoplankton changes from a diatom/green to a blue-green dominated community (Welcomme, 2001). Since blue-green algae are indigestible to moggel, eutrophied water bodies should not promote optimal *L. umbratus* growth.

CONCLUSION

Moggel is a detritivorous species that can successfully digest diatoms. It appears that differences in growth rate of the species between the two reservoirs can be attributed to differences in the abundance of diatoms in the detrital aggregate. However, if eutrophication causes a change in the algal species composition from a diatom to a blue-green algal dominated population, the growth of moggel could be negatively influenced. Water bodies that are small, shallow and slightly enriched are therefore the most suited for optimal moggel growth.

CHAPTER 5

Reproductive strategies of the riverine cyprinid, *Labeo umbratus*, in small reservoirs

INTRODUCTION

The perpetuation of a species is dependent on successful reproduction and recruitment (Welcomme, 2001). For a species to be 'successful' within a 'foreign' environment, it requires an ancestral reproductive strategy that confers a degree of 'fitness' and an adaptation to distinctive environmental conditions (Moyle, 1986). In South Africa, the paucity of natural lentic waters has led to the construction of thousands of reservoirs on almost all river systems (Davies and Day 1998, see Chapter 1). These 'foreign' environments have considerably different fish faunas in comparison to the original river systems (Skelton, 1993). For moggel to be successful in small reservoirs, it is necessary for them to have a reproductive strategy that is suited to this unique environment. Since these fishes have only recently (in about the last 50 years) found themselves in reservoirs, their adaptation to the 'foreign' environments is unlikely. However, in many ways, the small reservoir environment is similar to a river floodplain, with large fluctuations in temperature, oxygen concentration, turbidity and water level (Mattson, 1997). Therefore, moggel may have unique preadaptations in their reproductive strategy which allows successful reproduction in small reservoirs.

For fish to successfully reproduce on floodplains, their reproductive strategies must be able to cope with the unpredictable environmental conditions. Typically, fish with r-selected reproductive traits such as early maturity, high fecundity, single broods and rapid egg and larval development are successful in unstable environments. By contrast, K–selected traits that include delayed maturity, fewer, larger offspring and multiple broods are characteristics of fish in stable environments (Mann *et al.*, 1984). The r-K continuum concept was further developed by Winemiller and Rose (1992) who analysed and compared estimates of the life history traits of North American fishes.

In a fluctuating floodplain environment, Welcomme (1985) and Merron *et al.* (1993) suggested that spawning success is dependent on the hydrological regime in the same year. Egg survival and recruitment is often lower in drier years due to density-dependent competition for food and shelter by juveniles (Welcomme, 2001). In addition, a decrease in flooding is likely to reduce nutrient inputs, which reduces primary and secondary production and food for juveniles (Kolding, 1993).

Previous reviews of moggel breeding behaviour have suggested that these fish are reliant on flood conditions to spawn. Spawning was preceded by either an upstream and lateral migration (Mulder, 1973) or only a lateral migration (Gaigher, 1984) and took place on floodplains (Jackson and Coetzee, 1982), in river channels (Gaigher *et al.,* 1975; Mitchell, 1984) and in large tributaries flowing into reservoirs (Tómasson *et al.*, 1984). The spawning substrate varied from flooded vegetation (Jackson and Coetzee, 1982) to rocks and gravel (Gaigher *et al.,* 1975; Mitchell, 1984).

Since the small reservoir is most similar to floodplains, it is hypothesised that the reproductive success of this species in small reservoirs is related to their preadaptaion to successfully spawn on floodplains. It is also hypothesised that, as with floodplains, successful reproduction is dependent on the occurrence, duration and intensity of seasonal floods. To test these hypotheses, reproductive characteristics and juvenile recruitment of moggel were compared in four small reservoirs over a period of two years.

MATERIALS AND METHODS

Study sites

The sites selected for this study were the Katriver, Laing, Ndlambe and Dimbaza reservoirs (Figure 2.1). A description of the surrounding environment and conditions found in each reservoir and its catchment is provided in Chapter 2.

Surveys were conducted monthly in Katriver and Laing reservoirs and quarterly in Ndlambe and Dimbaza reservoirs. Water quality measurements, hydrological data and climatic information were obtained as described in Chapter 2. Water level data was not available for Ndlambe and Dimbaza reservoirs, but since these are earthen dams, water level was assumed to be directly related to rainfall. Moggel samples were collected using gillnets and seine nets, using the methods outlined in Chapter 2.

All fish were measured to the nearest millimetre fork length and weighed whole to the nearest gram. Fish were dissected, sexed and the gonads were weighed, categorised according to the five developmental stages (Table 2.5) as described by Weyl and Booth (1999) and preserved in 5% formalin. The eviscerated mass of the fish was then measured to the nearest gram.

The gonado-somatic index (GSI) was used to describe temporal patterns in reproductive activity. Variable gut fullness between individuals necessitated the use of eviscerated mass, such that the gonado-somatic index of mature fish was expressed as:

$$\mathrm{GSI} = \frac{\text{Gonad Mass (g)}}{\text{Eviscerated Body Mass (g)}} \times 100$$

The fecundity of the females in a ‘ripe’ reproductive state (Table 2.5) was estimated by sub-sampling using gravimetric methods (Bagenal, 1978). Fecundity was expressed as a function of fork length as: $F_L = aL^b$, where F is fecundity and L the fork length (mm) of each fish analysed.

The total population fecundity of the four systems was calculated. The total number of eggs produced (*EP*) by fish from the smallest size at maturity (160 mm FL) in each reservoir was estimated as:

$$\mathrm{EP} = n\sum_{L}\left[SR_L \times LF_L \times \frac{1}{S_L} \times \%M_L \times Fec_L\right]$$

where n is the estimated number of fish per length (see Chapter 8 for details), SR is the sex ratio by length (see Chapter 6 for details), LF is the length frequency, S is the selectivity function by length (see Chapter 7 for details), $\%M$ is the percent maturity by length and Fec is the fecundity by length.

The proximate factor(s) influencing gonadal recrudescence were determined by analysing the relationship between various suites of predictor variables (climatic, hydrological, habitat) and the gonado-somatic index (GSI) (dependent variable) using a Pearson product-moment correlation after the data were log-transformed, to stabilise variance, where required. Since gonadal development generally occurred between May and November, GSI and environmental data from these months was used exclusively in the analysis. The relationship between CPUE of juvenile fish (3-4 cm fork length) and environmental parameters, at the assumed time of spawning (three months previously), were analysed using the methods described above to determine the ultimate/causal factors that influence spawning. Since juveniles between 3-4 cm were only captured between September and February, CPUE data from these months and environmental data between July and February were used in the analysis. Because Katriver and Laing reservoirs were sampled more frequently, only data from these reservoirs were used in this aspect of the analysis.

The potential spawning sites were evaluated by inspection of the river inlets and shoreline of the four reservoirs during low and high water periods over the two years. Rocky or gravel substrata in the rivers and grassy banks that would be inundated with an increase in water level of 20 cm above full supply level in the reservoir were considered to be potential spawning sites. These areas were mapped and expressed as a percent of the shoreline length. Potential spawning sites were not expressed in area as this was too subjective and could only be assessed during times of the highest water levels.

RESULTS

Water temperatures increased between July and December in all reservoirs (Figure 5.1 and 5.2). Rainfall began in August 1998, October 1999 and July 2000 (Figure 5.1). While there was a general increase in water level between August and November 1998 in the Katriver and Laing reservoirs, the lack of spring rainfall resulted in a lowering of the water level in both reservoirs between May and November 1999.

Gonadal development started as early as June and May in the Katriver and Laing reservoirs, respectively (Figure 5.1). Fish with ripe and running gonads were observed from October to March in the Katriver Reservoir and from August to January in Laing Reservoir (Figure 5.1). The prolonged spawning season was confirmed by the elevated GSI values recorded throughout the summer months (Figure 5.1). In Dimbaza and Ndlambe reservoirs, fish with ripe gonads were observed in spring and summer, and the GSI values suggested that recrudescence was initiated in late winter (Figure 5.2).

The Pearson product-moment analysis identified correlations between GSI and day length ($\rho = 0.86$, $p<0.01$) and water temperature ($\rho = 0.58$, $p<0.01$)(Table 5.1).

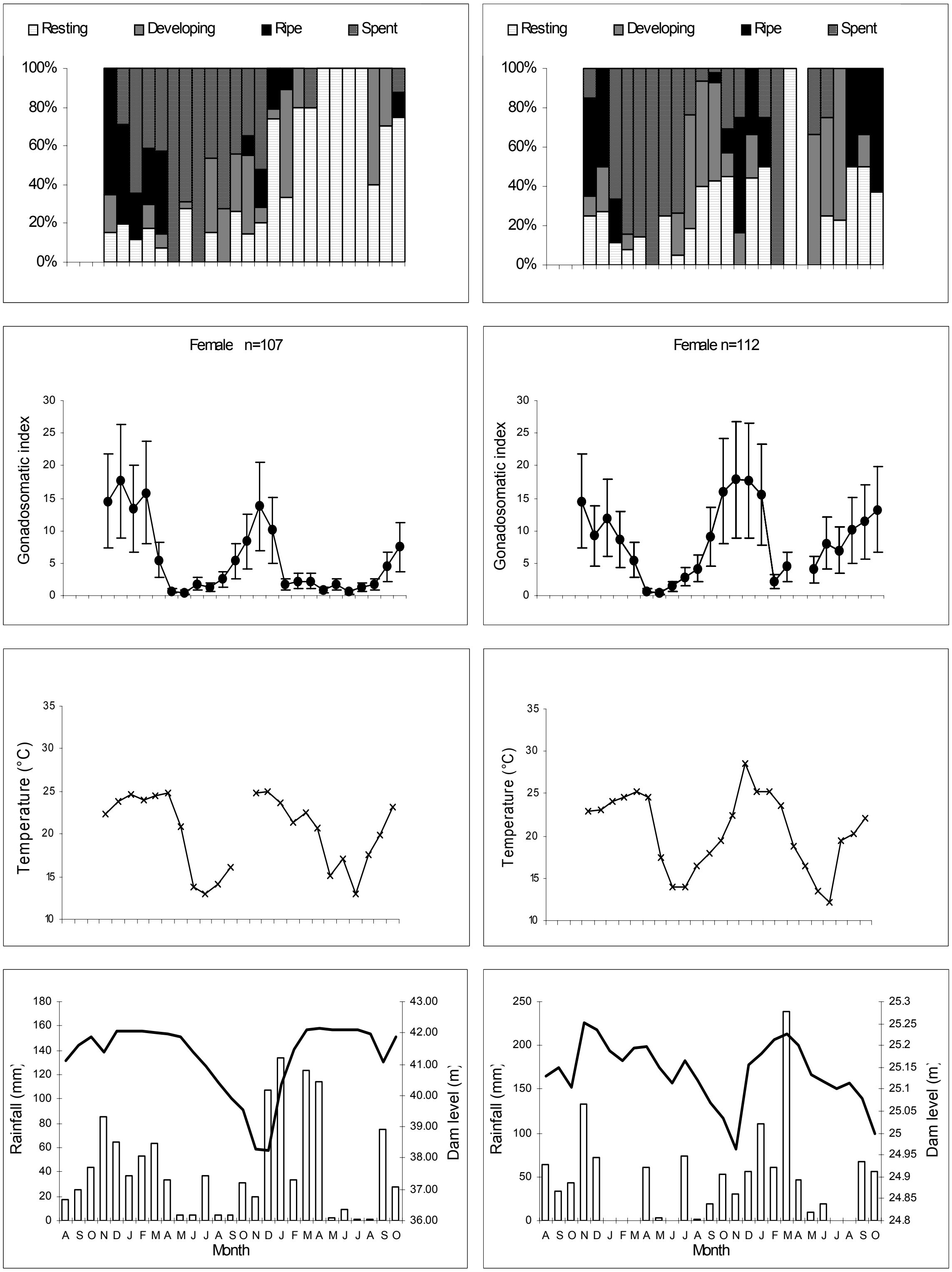

Figure 5.1. Female monthly maturity stages and gonadosomatic indices (GSI) (± standard deviation) for *Labeo umbratus* and monthly air temperature, monthly rainfall (bars) and reservoir water level (line) from Katriver and Laing reservoirs between August 1998 and October 2000.

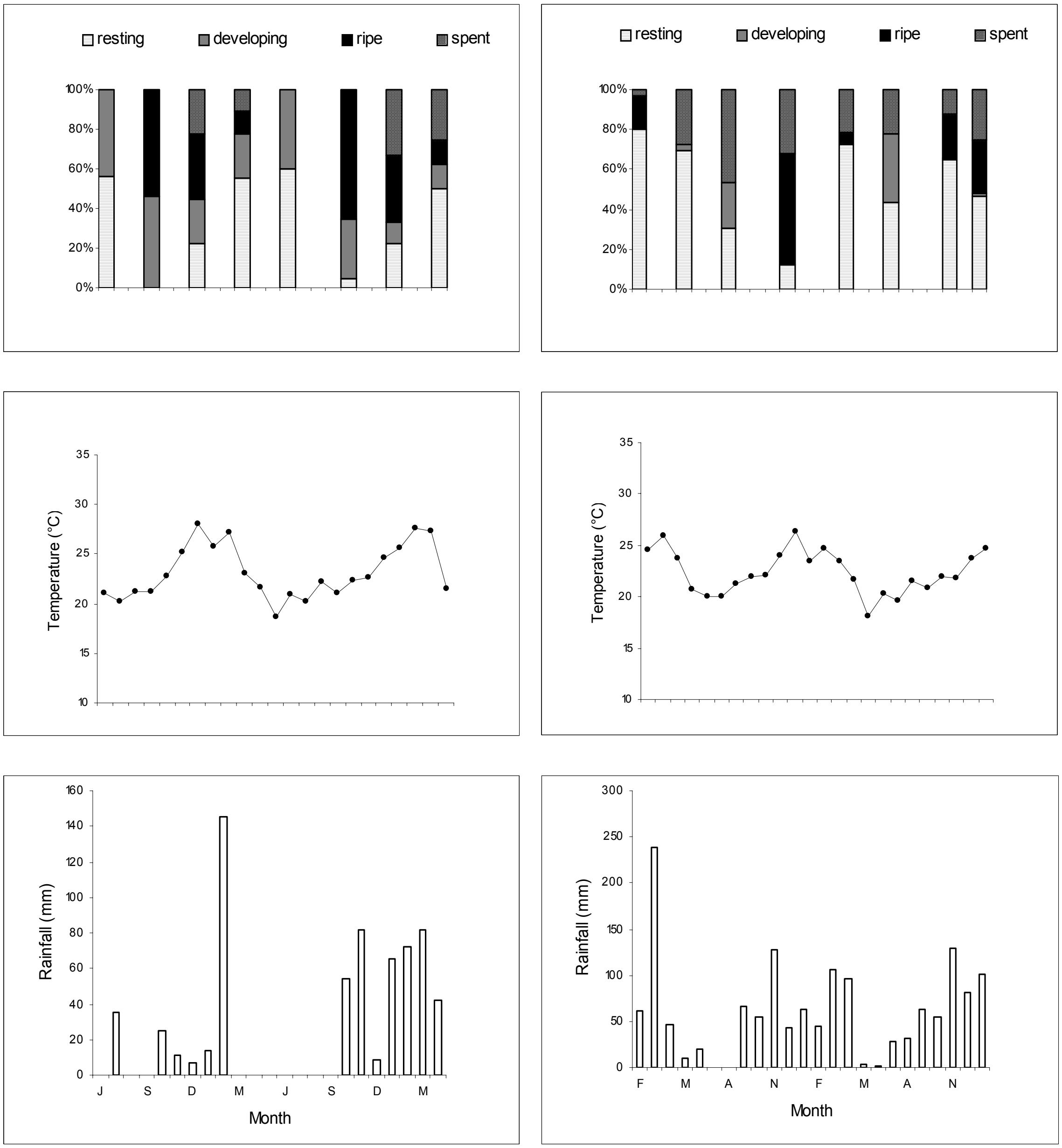

Figure 5.2. Monthly maturity stages for female *Labeo umbratus* and water temperature and monthly rainfall in Ndlambe and Dimbaza reservoirs between June 1999 and January 2002.

Table 5.1. Summary of Pearson product-moment correlation coefficients describing the relationship between the gonadosomatic and juvenile catch per unit effort of *Labeo umbratus* and environmental variables in the Katriver and Laing reservoirs (n=22).

	GSI		Juvenile CPUE	
	p	p value	*p*	p value
Rainfall	0.42	0.05	0.75	<0.01*
Water temperature	0.86	0.01*	-0.20	0.45
Water level	-0.11	0.61	-0.25	0.33
Day length	0.86	<0.01*		
Conductivity	0.09	0.69		
pH	0.31	0.15	-0.28	0.26
Nitrate	0.10	0.65	-0.37	0.15
Alkalinity	0.42	0.05	-0.32	0.21
Phosphate	-0.15	0.49	-0.17	0.50

The fecundity of moggel ranged from 36 500 to 210 000 for fish ranging between 251 and 475 mm FL respectively. The relationship between fork length and fecundity in each reservoir is shown in Figure 5.3, and the equations best describing their statistical relationships are summarised in Table 5.2.

Table 5.2. Relationship between fork length and fecundity of *Labeo umbratus* in the four reservoirs.

Reservoir	Exponential equation	r^2
Katriver Reservoir	$F = 11.853FL^{0.0068}$	0.79
Laing Reservoir	$F = 1.1136FL^{0.0127}$	0.89
Ndlambe Reservoir	$F = 8.1212FL^{0.0071}$	0.79
Dimbaza Reservoir	$F = 2.773FL^{0.0102}$	0.70

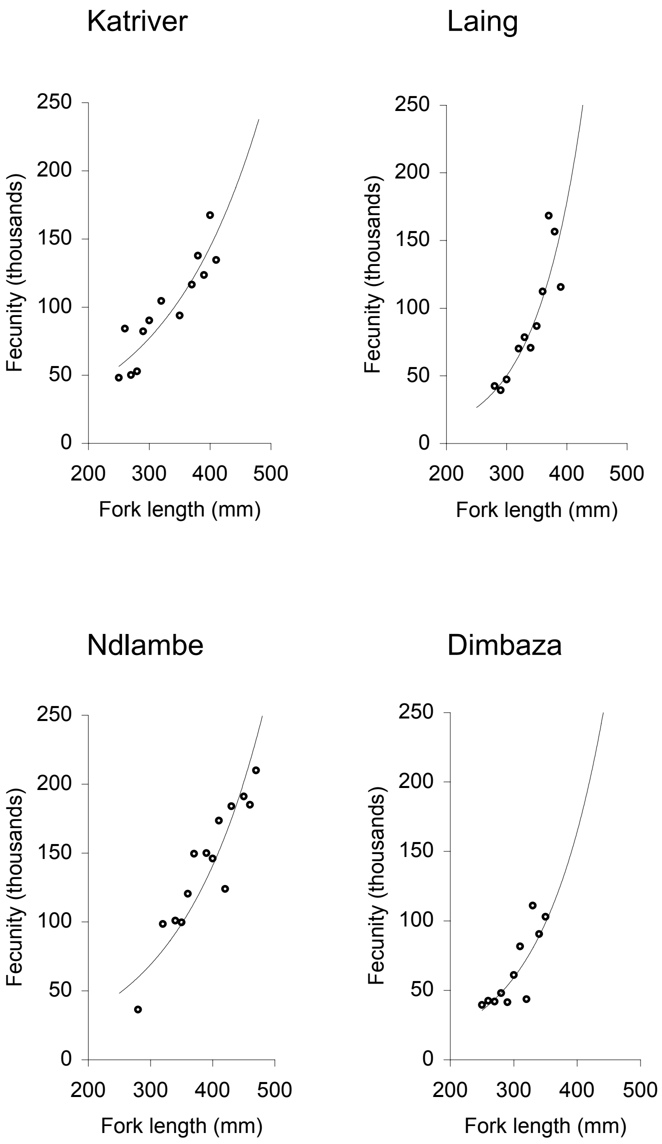

Figure 5.3. Relationship between fork length and fecundity of *Labeo umbratus* in four Eastern Cape reservoirs.

The number of eggs produced by 1 000 fish, greater than 160 mm FL, ranged between 17 and 32 million in Dimbaza and Ndlambe reservoirs, respectively (Table 5.3). The total population fecundity ranged between 40.2 million and 145.9 million eggs in Katriver and Ndlambe reservoirs, respectively (Table 5.3).

Table 5.3. Estimates of the number of eggs per thousand fish and the relative fecundity of the *Labeo umbratus* populations in the reservoirs.

	Katriver	Laing	Ndlambe	Dimbaza
Million eggs (.1000 fish^{-1})	30	25	32	17
Population estimate	1348	4928	4594	7784
Total population fecundity (million)	40.2	121.7	145.9	133.5

The Pearson correlation indicated a significant trend ($\rho = 0.75$, $p < 0.01$) between rainfall and juvenile CPUE (Table 5.1) in Katriver and Laing reservoirs (Figure 5.4.) An insignificant positive correlation was found between juvenile CPUE and rainfall in Ndlambe and Dimbaza reservoirs, where the low juvenile CPUE in 1999 was correlated to a lack of rainfall (Figure 5.5).

Juvenile fish between 3-4 cm were caught between November and February in Katriver and Laing reservoirs in both years, suggesting that successful reproduction took place between August and November. Mean CPUE of juveniles was considerably higher in 1998 than in 1999 (Table 5.4).

In the Dimbaza Reservoir, juvenile fish were caught in January, February, May and October, while juveniles in Ndlambe Reservoir were captured in September, October, December and January (Figure 5.5). The mean CPUE in both reservoirs was considerably higher in 2000 than in 1999 (Table 5.4). The highest mean juvenile CPUE, after correcting for reservoir size, was observed in Dimbaza, followed by Laing, Ndlambe and Katriver reservoirs (Table 5.4).

The substratum of the rivers flowing into the Katriver and Laing reservoirs was dominated by silt and no suitable spawning sites were identified. Dimbaza and Ndlambe reservoirs were fed by small feeder streams that only flow for a few hours after rain and would therefore not function as spawning grounds. Analysis of the shoreline data revealed that 2.5% of the shoreline of Katriver Reservoir had submerged grassy vegetation when flooded, compared with 30.5% in Laing, 42.1% in Ndlambe and 66.3% in Dimbaza Reservoir (Table 5.5).

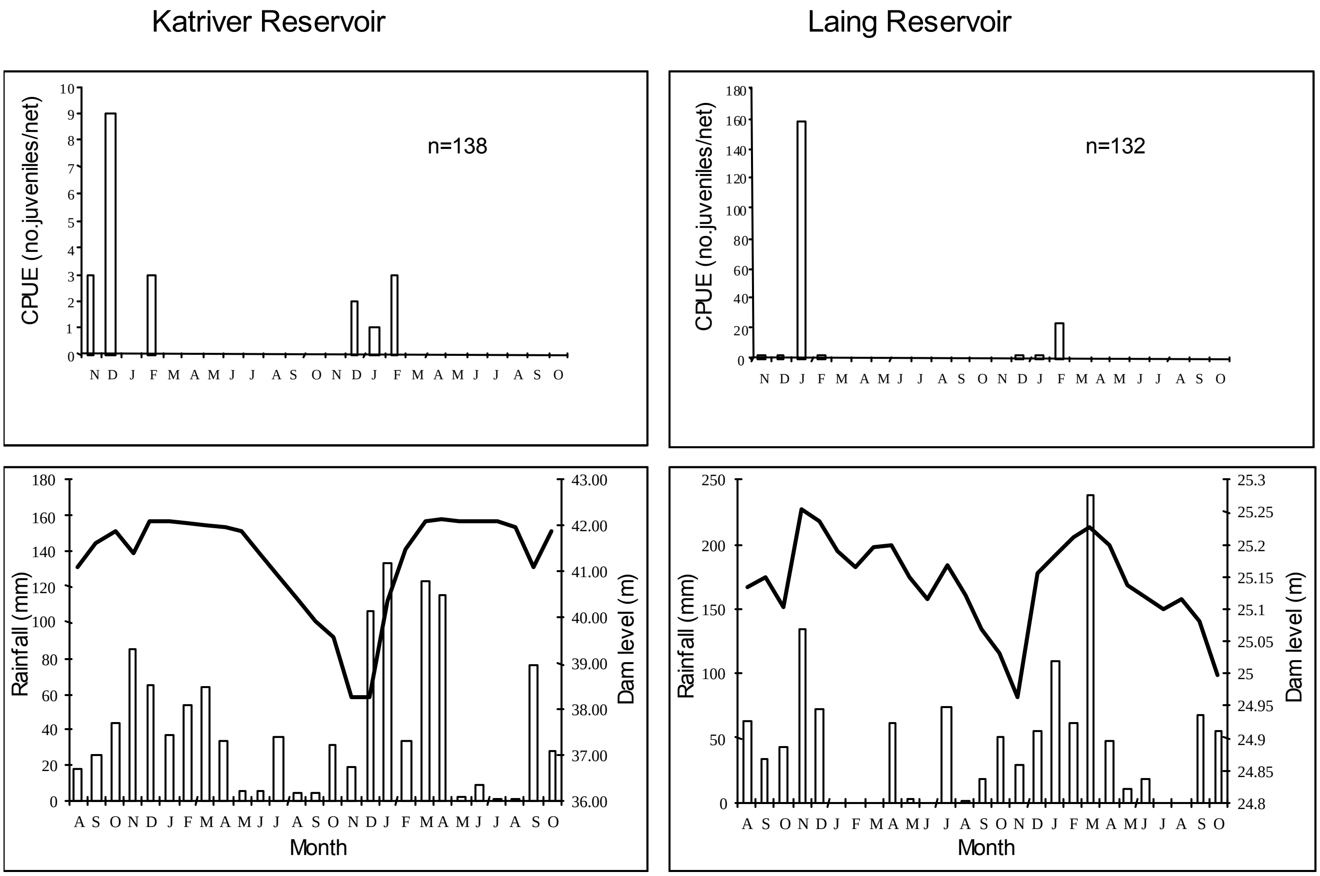

Figure 5.4. Juvenile (3-4 cm) *Labeo umbratus* seine net catch per unit effort (CPUE) (November 1998 to October 2000) and monthly mean rainfall and water level for Katriver and Laing reservoirs between August 1998 and October 2000. It was assumed that 3-4 cm juveniles hatched 3 months prior to capture.

Table 5.4. Mean seine net catch per unit effort (CPUE) of juvenile *Labeo umbratus* (3-4 cm FL) in the four reservoirs (1998 and 2000).

Reservoir	Juvenile CPUE (fish.net^{-1})
Katriver (1998)	5.0 ± 3.5
Katriver (1999)	2.0 ± 1.0
Laing (1998)	41.5 ± 78.3
Laing (1999)	10.0 ± 12.1
Ndlambe (1999)	39.5 ± 40.3
Ndlambe (2000)	83.0 ± 106.1
Dimbaza (2000)	65.0 ± 63.6
Dimbaza (2001)	284.5 ± 335.9

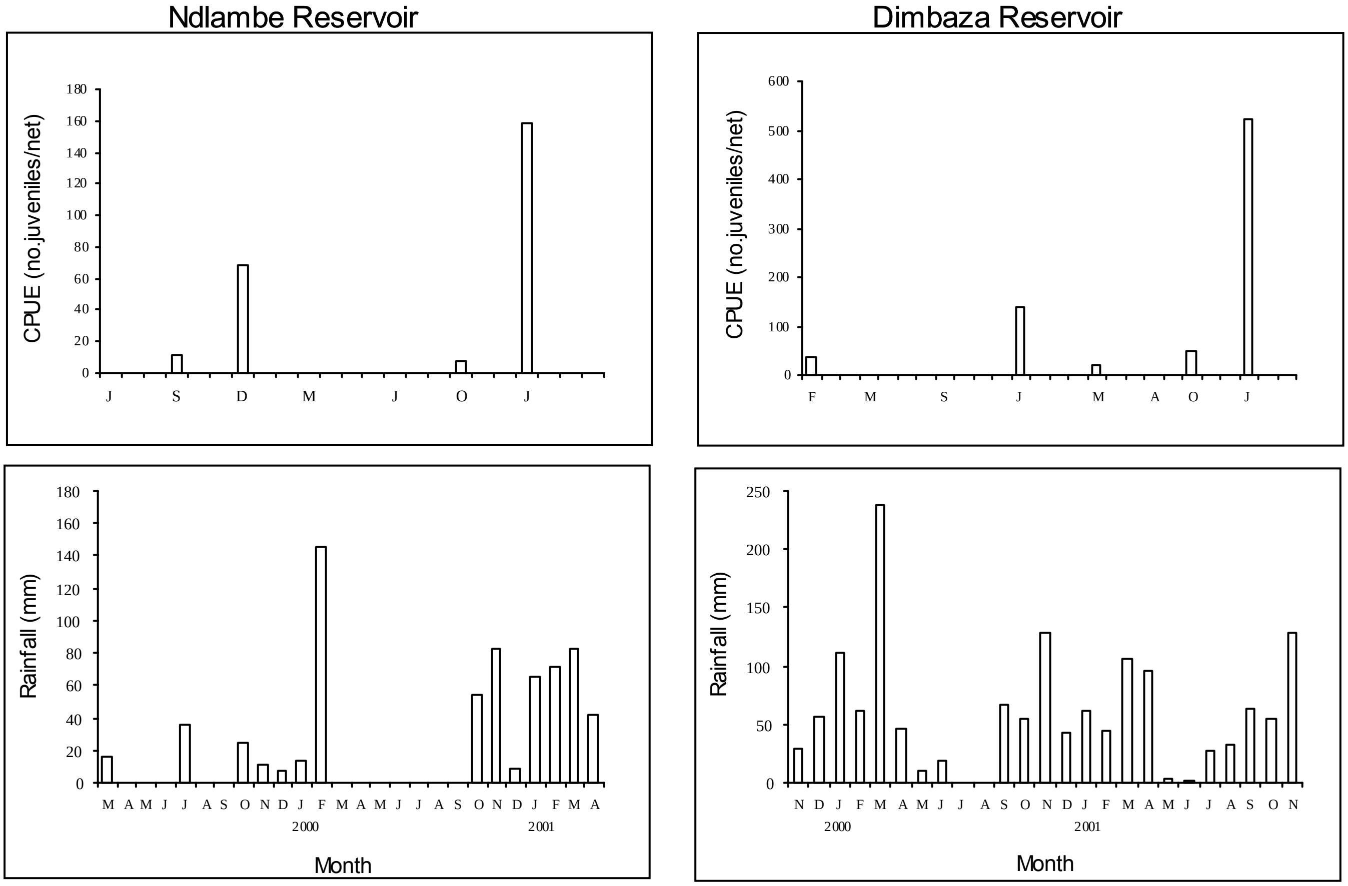

Figure 5.5. Juvenile *Labeo umbratus* (3-4 cm) seine net catch per unit effort (CPUE) in and Dimbaza Reservoir and monthly rainfall data three months previous to the catches on the assumption that 3-4 cm juveniles were born 3 months before capture.

Table 5.5. The shoreline length and suitable spawning areas for *Labeo umbratus* in the four reservoirs.

Reservoir	Katriver	Laing	Ndlambe	Dimbaza
Shoreline length (m)	16100	22100	1425	3167
Suitable spawning area (m)	400	6750	600	2100
Suitable spawning area (%)	2.5	30.5	42.1	66.3

DISCUSSION

Moggel appears to be adapted to offset the characteristic ephemeral conditions of small reservoirs with a reproductive strategy nearing the r – selected end of the continuum. This strategy includes traits such as an extended reproductive season, high fecundity, short incubation time and early larval development (Tomasson *et al.*, 1984; Gaigher *et al.,* 1975). Winemillar and Rose (1992) catagorised fish life history patterns into three adaptive strategies viz. periodic, opportunistic and equilibrium. While the moggel falls most closely into the periodic strategy, which is characterised by delayed maturity, high fecundity and synchronous spawning, its extended spawning season places it into an intermediate category.

The extended spawning season of moggel allows fish to reproduce whenever conditions are favourable and this would increase the overall likelihood of reproductive success. Due to the fluctuating conditions found in small reservoirs, optimal egg survival may only occur on a few occasions each season. Since these fish have an extended spawning season, it is unlikely that the eggs of many females would be sufficiently developed on these occasions and high fecundity is therefore necessary. In addition, an abbreviated embryogenesis (1-3 days) and rapid larval development (Gaigher *et al.,* 1975) allows moggel larvae to move away from unfavourable conditions, such as receding water or decreasing oxygen concentrations soon after spawning. Similar larval development was found in other floodplain spawners such as *L. victorianus* (Fryer and Whitehead, 1959) and *L. capensis* (Mulder, 1971).

Since moggel are capable of spawning on gravel beds in rivers (Mulder, 1973, Gaigher *et al.*, 1975, Mitchell, 1984) or on river floodplains (Jackson and Coetzee, 1982), it would appear that the species fits into the intermediate, phyto-lithophil reproductive guild proposed by Balon (1975). Spawning in the inflowing rivers of the Katriver and Laing reservoirs is unlikely to have occurred as the substratum was dominated by silt. It is also highly unlikely that the fish would have spawned in the feeder streams of Ndlambe and Dimbaza reservoirs that only flow for a few hours after heavy rains. Although the environmental characteristics of small reservoirs are often compared to large reservoirs and lakes, they are more similar to rivers and floodplains (Mattson, 1997). The level of small water bodies fluctuates more rapidly in response to rainfall than in large reservoirs and conditions become more riverine than lacusterine after heavy rains. Thus, the flooded terrestrial vegetation in small water bodies provides a typical floodplain environment, which is required by moggel to spawn. Further evidence for ‘floodplain’ spawning is the survival of large populations of moggel in Dimbaza and Ndlambe reservoirs, which do not have suitable riverine spawning habitat.

Although small reservoirs may provide suitable habitat for moggel to spawn, successful reproduction in small reservoirs is dependent on the recognition of environmental cues that allow them to spawn in conditions that will ensure maximum reproductive success (Hontela and Stacey, 1990). In previous studies, the environmental cues that stimulate gonadal recrudescence in moggel have not been adequately quantified and only illustrate possible correlations. In Katriver and Laing reservoirs, photoperiod and water temperature were found to be the most dominant proximate factors responsible for gonadal development. These factors are considered the norm for most cyprinids (de Vlaming, 1972).

Flooding has been recognised as the ultimate or causal factor regulating spawning in almost all moggel populations that have been studied (Jackson and Coetzee, 1982; Gaigher, 1984; Mitchell, 1984; Tomasson *et al.*, 1984). In this study, rainfall was identified as the most significant ultimate factor. Heavy rain causes flooding of terrestrial vegetation together with a change in water chemistry and has been identified as ultimate cues for the spawning of cyprinids (Hontela and Stacey, 1990). Similarly, Cambray (1982) also identified flooding of terrestrial vegetation in a reservoir to be the ultimate cue responsible for initiating spawning in *Barbus anopolus*, another riverine South African cyprinid.

The poor recruitment of moggel in all reservoirs in 1999 may be explained by the timing of rainfall. Generally, the highest CPUE of 3-4 cm fish was recorded between October and January, suggesting that reproduction is most successful when rainfall occurs between July and October. In 1999, the poor rainfall between August and October and dropping water levels in the reservoirs corresponded with poor recruitment (Fig 5.4 and 5.5). Gaigher (1984) and Tomasson *et al.* (1984) showed that when the spawning requirements of moggel in Wuras Reservoir and Lake Le Roux were not satisfied, the fish failed to spawn and reabsorbed their gonads. Some females in the four reservoirs in 1999 may have absorbed their gonads. In addition, the dropping water levels in 1999 probably resulted in an absence of suitable spawning sites in all of the reservoirs, which may have contributed to the partial recruitment failure.

Although heavy rain only occurred in October 2000 in the Ndlambe Reservoir, successful reproduction did occur. However, when compared with 1999, the late rainfall in 2000 was followed by substantial summer rainfall, such that the water level remained high for an extended period. Tómasson *et al.,* (1984) suggested that juvenile survival of moggel was enhanced in summer when water levels increased. Thus, the heavy rainfall may have increased juvenile survival in Ndlambe Reservoir by providing food and refuge in the submerged terrestrial vegetation. It therefore appears that early summer rainfall is essential for successful reproduction of this species and substantial post-spawning rainfall is required to increase juvenile survival. This was most clearly demonstrated in Dimbaza Reservoir in 2000, where the high level of recruitment was related to early and consistent rainfall.

A number of factors may have been responsible for the differences in recruitment between reservoirs. These include the number of adult fish, the number of eggs, differences in juvenile mortality and availability of spawning habitat. Since the abundance of adult moggel was considerably higher and juvenile CPUE was approximately 20 times higher in Dimbaza than in Katriver Reservoir, it appears that there is a relationship between the number of adults and successful reproduction. It may be assumed that a high abundance of adults would result in increased population fecundity and, therefore, increased reproductive success. However, since there were a low number of larger, highly fecund females in Dimbaza Reservoir, the total fecundity was only about three times higher than Katriver Reservoir (Table 5.4). The higher reproductive success in Dimbaza Reservoir is therefore not only a result of higher egg production. Considering the major environmental fluctuations in small reservoirs and the protracted spawning season, it may be more advantageous to have more small, reproductively active females with fewer eggs, than fewer, large females with many eggs. Although the overall number of eggs may be the same, a population whose spawners are dominated by large fish may not always have individuals in a ripe spawning condition when environmental conditions are suitable for egg and larval survival. This may result in reduced spawning success.

CONCLUSION

Moggel can be categorised into the phyto-lithophyl reproductive guild. Their reproductive strategy, including an extended spawning season, high fecundity, short incubation time and rapid larval development, appears to be ideally suited for highly variable small reservoirs. The primary factors influencing gonadal recrudescence are photoperiod and temperature, while rainfall and its associated effects appears to initiate spawning. While the success of moggel spawning in small reservoirs is dependent on early spring and consistent summer rainfall, it is also related to the number of reproductively active adults and dependent on the availability of suitable spawning habitat.

CHAPTER 6

The influence of environmental factors on the life history and fishery potential of *Labeo umbratus* in small reservoirs in the Eastern Cape, South Africa

INTRODUCTION

An empirical model that uses morphometric and/or limnological characteristics to predict fish production in small reservoirs has eluded researchers (Kaunda, 1995; Mattson, 1997; Marshall and Maes, 1994). Consequently, fisheries managers have relied on life history studies such as growth, size at sexual maturity and mortality to assess fishery potential. Fortunately, most small reservoirs in southern Africa are species poor (Marshall and Maes, 1994) which can solve this problem by developing species-specific, empirical models for the most prevalent species. Since fish of the same species may exhibit highly variable life history strategies in different environments (Beamesderfer and North, 1955; Lowe-McConnell, 1958; DeMerona *et al.,* 1988), an understanding of the effects of environmental parameters on the life history of the study species may well assist in the development of a model to estimate fish production in small reservoirs.

Several studies on fishes have shown a close relationship between growth and reproduction (Molander, 1925 (cited in Stearns and Crandall, 1984); Pitt, 1975; Grainger, 1953 (cited in Stearns and Crandall, 1984); Donaldson and Olson, 1955; Wooton, 1977). A decrease in growth rate after maturation has been observed in many species and it is proposed that the energy required to produce reproductive tissue is no longer utilised for growth (Alm, 1959; Roff, 1983; Deacon and Keast, 1987). Theoretically, individuals who produce more eggs in an unstable environment are likely to have higher reproductive success and since there is a general increase in fecundity with body size in fishes (Bagenal 1978), delayed maturity should be favoured to maximise egg production. However, individuals that delay maturity increase the risk of being exposed to limited food resources (Roff, 1982), predators (Baltz and Moyle, 1982) or fishing (Spangler *et al.,* 1977), which may result in death. Fish in water bodies with abundant food and no predators should grow faster and exhibit delayed maturity.

It is hypothesised that moggel in small reservoirs with abundant food and few predators will have a higher growth rate, a greater age and larger size at maturity and a lower mortality rate than those in small reservoirs with less food and many predators. To test this hypothesis, the growth, reproduction and mortality of moggel was compared in the five small water bodies.

MATERIALS AND METHODS

Moggel were collected monthly from Katriver and Laing reservoirs, and quarterly in Sinqemeni, Ndlambe and Dimbaza reservoirs using gillnets (described in Chapter 2). In addition, monthly catch records were obtained from the experimental gillnet fisheries (Chapter 2). The laboratory methods used are described in Chapter 2. Moggel were aged using the methods described in Chapter 4. A likelihood ratio test (Cerrato, 1990) was used to compare growth model parameters of fish in the five systems. Since populations with different growth parameters may have a similar growth performance, the parameter $\omega = \mathrm{k}\mathrm{L}_{\infty}$ (Gallucci and Quinn, 1979) was calculated to compare growth.

The population structure in each reservoir was determined from the surveys prior to the establishment of experimental fisheries in each reservoir. The sex ratio of moggel in each reservoir was determined for the survey catches before the initiation of the experimental fisheries and tested for unity using a chi-square test.

Length- and age-at-50%-sexual maturity for *L. umbratus* was determined using the macroscopic staging information (Table 2.8). All fish in stages I and II were considered immature, while fish in stages III and above were considered mature. Fish were separated into 10 mm length classes and into 1-year age classes. The proportion of sexually mature fish (PM_i), by length (L_i) and age was fitted with a logistic ogive of the form:

$$PM_i = \frac{1}{1 + e^{-(li - l_{50})/\delta}}$$

where: PM_I = proportion of mature fish in the i^{th} length class

l_i = i^{th} length (or age) class

l_{50} = mean length (or age)-at-50%-maturity

δ = width of the logistic ogive (this describes the rate at which the population changes from 0% to 100% mature)

Maximum likelihood estimates of the parameters were obtained by minimising a binomial likelihood. The parameters were compared using a likelihood ratio test (Cerrato, 1990). Age at maturity was only calculated from the fish that were aged, rather than converting the lengths of all fish to age using the von Bertalanffy equation describing the fish growth.

The instantaneous rate of total mortality (Z) for *L. umbratus* over 160 mm FL (minimum size captured in the gillnets) was estimated using a catch curve analysis (Ricker, 1975). Length frequency distributions from the gillnet catches before the initiation of the fisheries were corrected for selectivity (see Chapter 7) and converted to age frequency distributions by means of a normalised age-length key (Butterworth *et al.,* 1989).

The relationship between various suites of predictor variables (climatic, hydrological, habitat) and fish growth, length- and age-at-50%-maturity and mortality (dependent variables) was analysed using a Pearson product-moment correlation after the data were log-transformed, to stabilise variance, where required.

RESULTS

Water quality parameters for the five reservoirs are presented in Table 2.5.

The moggel populations in each reservoir had different size structures (Figure 6.1), with all populations dominated by females in the larger length classes (Figure 6.1). The mean female and male fork length of the fish in the five reservoirs is summarised in Table 6.1.

The female:male sex ratio of the five populations ranged from 1.0:0.4 to 1.0:1.6 (Table 6.1). In the Laing Reservoir (χ^2 = 7.6, df = 1, $p < 0.05$) and the Ndlambe Reservoirs (χ^2 = 7.8, df = 1, $p < 0.05$), males dominated the moggel populations and were significantly different from unity. In the Sinqemeni (χ^2 = 1.4, df = 1, $p > 0.05$) and the Katriver (χ^2 = 0.14, df = 1, $p > 0.05$) reservoirs, the sex ratio was close to 1:1 and differences were not significantly different from unity. Female moggel dominated the populations of Dimbaza Reservoir (χ^2 = 53.0, df = 1, $p < 0.05$), and were significantly different from unity.

Table 6.1. The mean female and male length and sex ratio of *Labeo umbratus* prior to experimental gillnet fishing in five small Eastern Cape reservoirs.

Reservoir	Mean female fork length (mm)	Mean male fork length (mm)	Mature fish (n)	%Males	%Females	Sex ratio (F:M)	χ^2
Katriver	279 ± 57.3	264 ± 42.3	448	44.3	55.7	1.0 : 1.0	0.14
Laing	313 ± 45.6	307 ± 51.5	540	55.9	44.1	1.0 : 1.3*	7.6
Sinqemeni	390 ± 71.1	360 ± 50.6	176	45.5	54.5	1.0 : 0.8	1.4
Ndlambe	333 ± 80.4	325 ± 82.8	128	62.5	37.5	1.0 : 1.6*	7.8
Dimbaza	291 ± 34.1	253 ± 20.1	267	27.4	72.6	1.0 : 0.4*	53.0

* indicates significant difference from unity

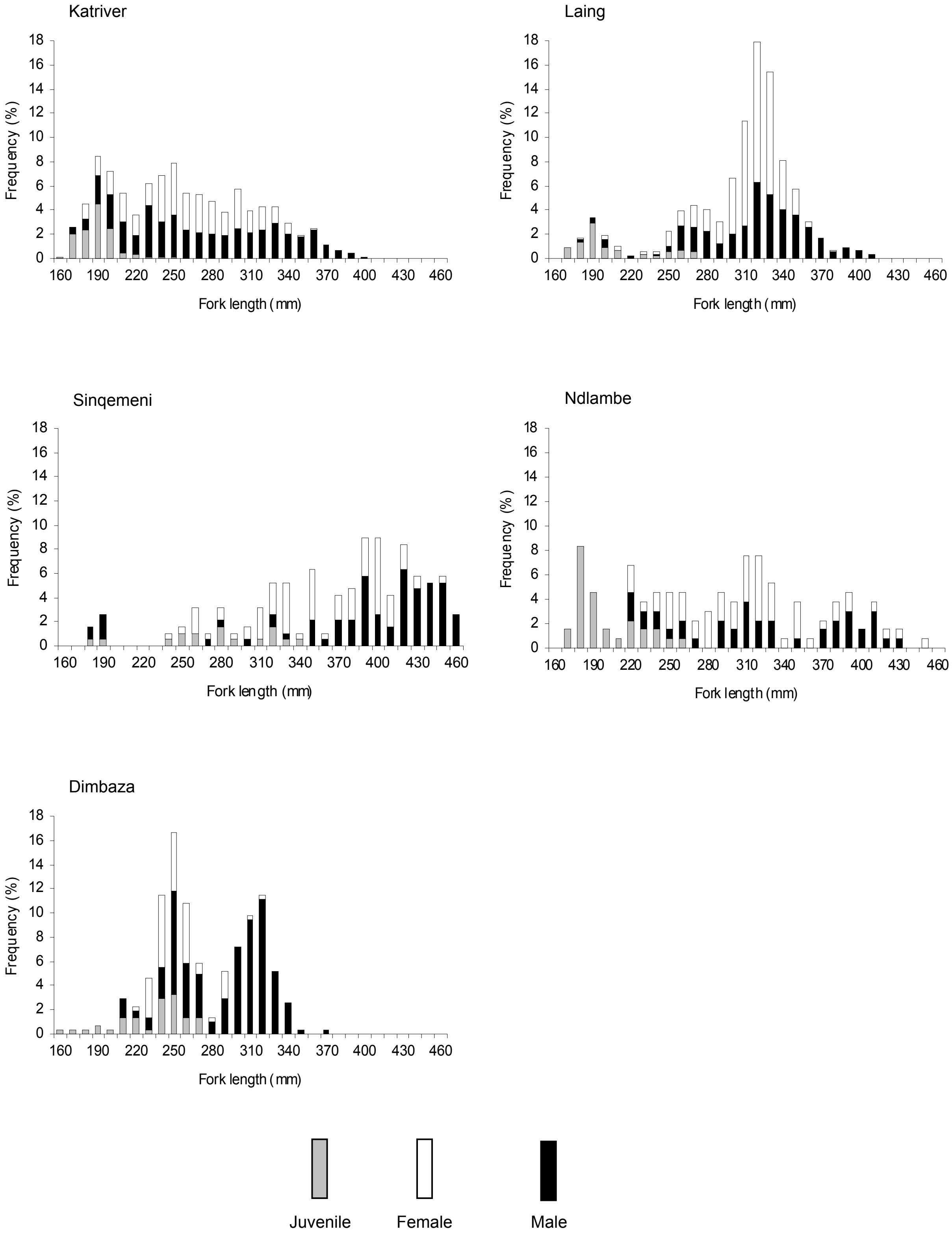

Figure 6.1. Length frequency histogram of juvenile, male and female *L. umbratus* in five Eastern Cape reservoirs.

Size at maturity

Length-at-50%-maturity (L_{50}) for females ranged from 229 mm to 274 mm in the five populations and the maturation pattern is described by the logistic curves in Figure 6.2. Inter-population comparisons of the female L_{50} showed significant differences (Table 6.2). Females in the Laing Reservoir matured at a significantly larger size (274 mm FL) than the other populations. In the Katriver and the Sinqumeni reservoirs, the female L_{50} estimates differed only by a few millimetres. Females in Ndlambe and Dimbaza reservoirs (Table 6.2) matured at a significantly smaller size than in the other reservoirs.

The length-at-50%-maturity of males ranged from 234 mm to 283 mm and the rates of maturation are described by the logistic curves in Figure 6.2. Males in Sinqemeni attained sexual maturity at a significantly larger size than in the other reservoirs. The L_{50} of males in Laing Reservoir was second highest and significantly different from all other populations. The L_{50} of males from Katriver and Ndlambe reservoirs were different by only a few millimetres, while males in Dimbaza had a significantly lower L_{50} than the males in the other populations (Table 6.2).

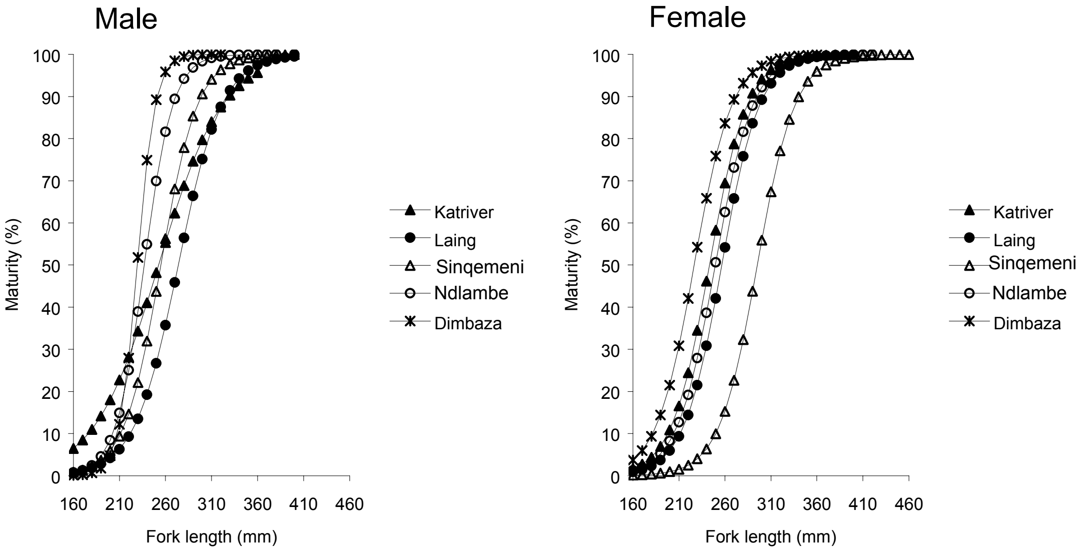

Figure 6.2. Length at sexual maturity of male and female *Labeo umbratus* in five small Eastern Cape reservoirs.

Age and growth

Marginal zone analysis (see Chapter 3) indicated that a single annulus was deposited each year. On the assumption that the zone formation was similar in fish from all reservoirs, the von Bertalanffy growth parameters of *L. umbratus* in each of the five reservoirs is shown in Table 6.3. The estimated asymptotic length of moggel in the Sinqumeni and Ndlambe reservoirs was significantly higher than in the other reservoirs ($p<0.01$)(Table 6.3). The estimated growth coefficient (k) in the Laing ($p = 0.02$) and Sinqemeni reservoirs ($p = 0.04$) was significantly higher than in Katriver Reservoir ($p=0.09$)(Table 6.3). The growth performance index (ω) showed that fish in Sinqemeni grew the fastest, followed by Laing, Ndlambe, Katriver and Dimbaza reservoirs, respectively (Table 6.3).

Table 6.2. Parameters of the logistic curves describing sexual maturity of *Labeo umbratus* in five small Eastern Cape reservoirs.

Reservoir	Females		Males	
	L_{50}	delta	L_{50}	delta
Katriver	253^{a}	34.7^{d}	243^{h}	20.9^{l}
Laing	274^{b}	23.6^{e}	261^{i}	16.0^{m}
Sinqemeni	255^{a}	19.9^{ef}	283^{j}	41.7^{n}
Ndlambe	236^{c}	15.5^{f}	249^{h}	16.4^{lm}
Dimbaza	229^{c}	9.8^{g}	234^{k}	10.8^{o}

Values with the same superscript in each column are not significantly different at the 5% level.

Table 6.3. The von Bertalanffy, growth parameters, the associated coefficients of variation and ω values describing growth of *Labeo umbratus* in five small reservoirs in the Eastern Cape.

Reservoir	L_{∞}	CV (%)	K	CV (%)	t_0	CV (%)	n	omega (ω)
Katriver	392.3^{a}	5.11	0.20^{d}	15.89	-1.43	27.08	308	78.5
Laing	372.9^{a}	3.05	0.33^{e}	12.85	-0.17	124.11	284	123.1
Sinqemeni	430.4^{b}	4.23	0.29^{e}	14:00	0.22	116.65	129	124.8
Ndlambe	439.5^{b}	5.58	0.26^{de}	15.28	-0.03	491.73	108	114.3
Dimbaza	358.0^{a}	4.34	0.21^{de}	13.08	-2.23	98.51	92	75.2

Values with the same superscript in each column are not significantly different at the 5% level.

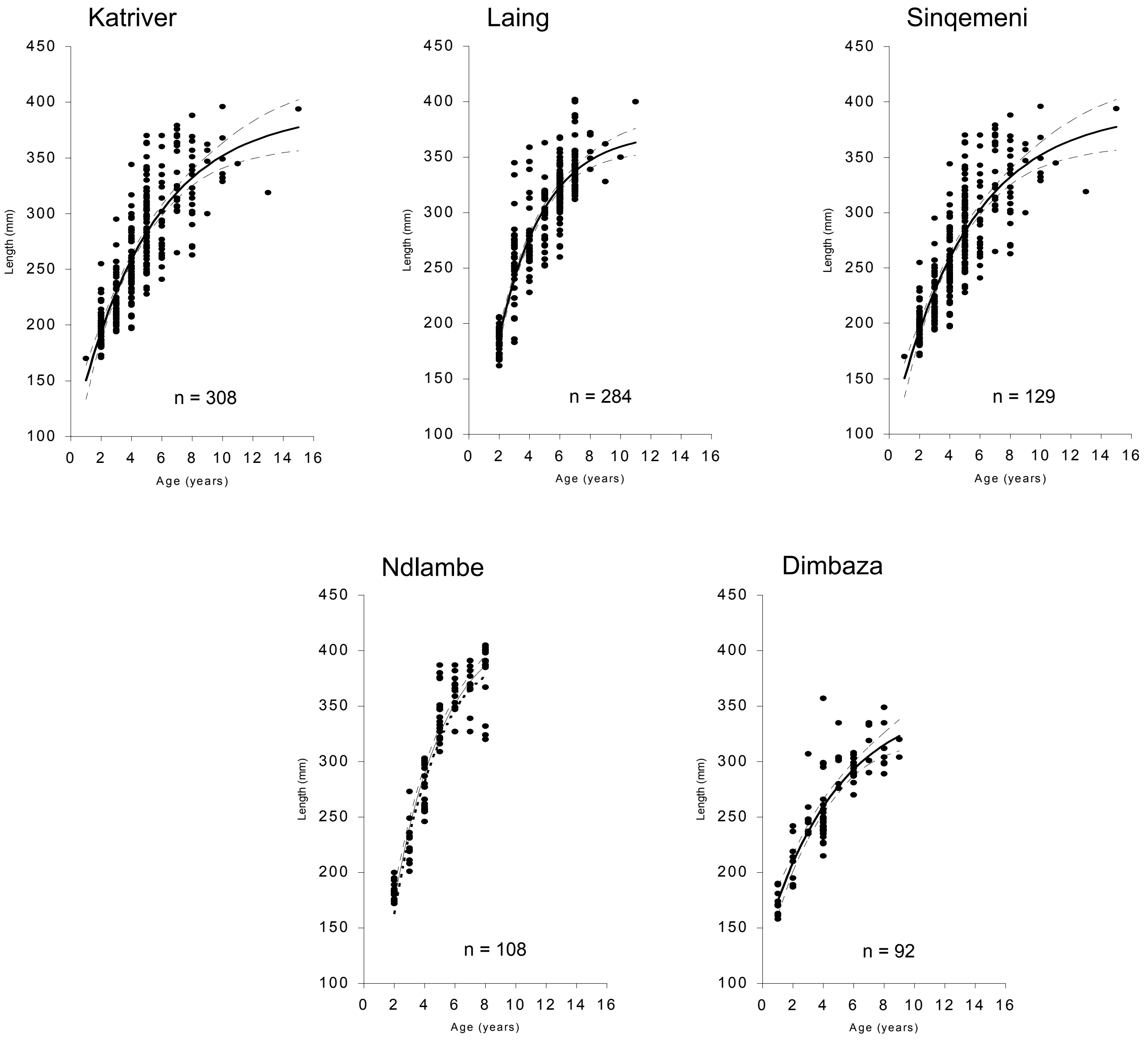

Figure 6.3. The growth of *Labeo umbratus* in five Eastern Cape reservoirs. Dotted lines are the upper and lower 95% confidence intervals from the bootstrapped predicted lengths-at-age.

Age at maturity

Maturation patterns are described by the logistic curves presented in Figure 6.4. Age-at-50%-maturity (A_{50}) of males in the five reservoirs ranged from 4.4 to 5.1 years and was significantly different in all populations. The highest age-at-maturity was observed in Ndlambe Reservoir (5.1 years) and the lowest in Katriver Reservoir (4.4 years)(Table 6.4). The A_{50} of females in the five reservoirs ranged between 3.4 and 5.2 years and was also significantly different between all populations. Females in the Sinqemeni Reservoir had the highest A_{50} (5.2 years) and the lowest (3.4 years) was recorded in Dimbaza Reservoir (Table 6.4).

Table 6.4. Parameters of the logistic curves describing sexual maturity of *Labeo umbratus* in five small Eastern Cape reservoirs.

Reservoirs	Male		Female	
	A_{50} (years)	delta	A_{50} (years)	delta
Katriver	4.4^{a}	1.5^{f}	4.3^{k}	0.8^{p}
Laing	4.8^{b}	1.1^{g}	4.8^{l}	0.6^{q}
Sinqemeni	4.9^{c}	0.7^{h}	5.2^{m}	0.9^{r}
Ndlambe	5.1^{d}	0.5^{i}	3.7^{n}	0.8^{pr}
Dimbaza	4.6^{e}	0.3^{j}	3.4^{o}	0.5^{s}

Values with the same superscript in a column are not significantly different at the 5% level.

Mortality

Total mortality (Z) estimates were highest in the Katriver Reservoir, followed by the Laing, Dimbaza, Ndlambe and Sinqemeni reservoirs (Table 6.5).

Table 6.5. Estimates of mean total mortality (Z) of *Labeo umbratus* in five small Eastern Cape reservoirs calculated from catch curve analysis (Ricker, 1975).

Reservoir	Mortality (Z)
Katriver	0.40
Laing	0.25
Sinqemeni	0.14
Ndlambe	0.21
Dimbaza	0.22

Correlation analysis

Except for a positive correlation between turbidity and age-at-50%-maturity of males, no additional correlations were found between any environmental variables and growth, length-at-50%-maturity or age-at-50%-maturity of females or males. There was a negative significant correlation between mortality and algal biomass (chlorophyll ‘a’) and a positive significant correlation between mortality and the number of predatory species in the reservoir (Table 6.6).

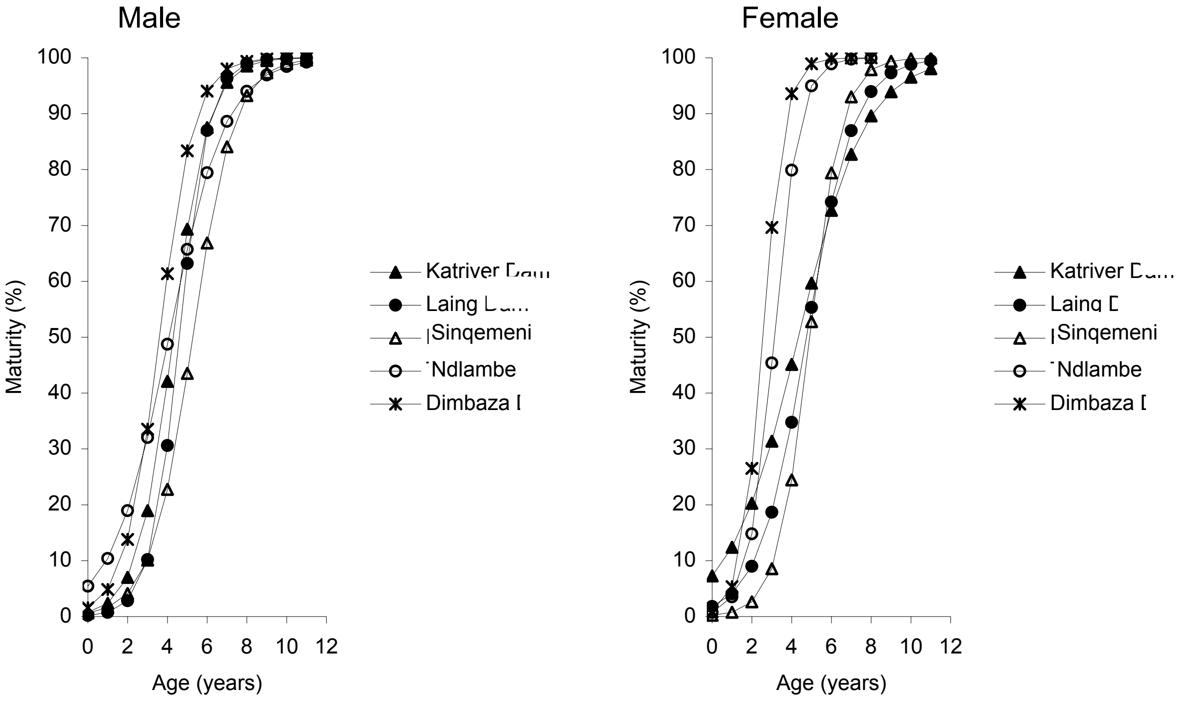

Figure 6.4. Age of sexual maturity of male and female *Labeo umbratus* in five Eastern Cape reservoirs.

Table 6.6. Pearson product-moment correlations between selected environmental parameters and life history traits of *Labeo umbratus* in five small Eastern Cape reservoirs.

	Growth ω		Mortality Z		L_{50} male		L_{50} female		A_{50} male		A_{50} female	
	ρ	p	ρ	p	ρ	p	ρ	p	ρ	p	ρ	p
Water temperature	0.35	0.57	0.70	0.19	0.32	0.60	-0.54	0.35	-0.26	0.67	0.16	0.79
Chlorophyll ‘a’	0.21	0.74	-0.89	0.04*	0.58	0.30	-0.19	0.77	0.41	0.50	0.53	0.36
Turbidity	-0.32	0.60	0.24	0.39	-0.64	0.24	-0.83	0.81	-0.96	0.01*	-0.81	0.99
Conductivity	0.74	0.16	0.86	0.06	0.63	0.26	-0.14	0.82	0.05	0.94	0.44	0.45
Fish density	-0.23	0.71	-0.62	0.26	-0.20	0.74	-0.81	0.10	-0.72	0.17	-0.40	0.51
Surface area	-0.20	0.75	-0.68	0.20	-0.21	0.74	0.66	0.23	0.42	0.48	-0.01	0.99
Mean depth	-0.96	0.88	-0.64	0.24	-0.06	0.92	0.71	0.18	0.57	0.32	0.16	0.80
Number of predator species	-0.70	0.19	0.91	0.03*	-0.55	0.34	0.19	0.76	0.06	0.93	-0.34	0.57

* indicates significant correlation at the 5% level

DISCUSSION

The diversity of environmental conditions recorded in the reservoirs studied is characteristic of small water bodies in Africa (Mattson, 1997; Marshall and Maes, 1994). Despite the variation in moggel growth and size- and age-at-maturity, the differences were not related to environmental conditions. However, the low statistical power may have contributed to the lack of correlation between life history parameters and environmental conditions.

The growth of moggel in other reservoirs (Gariep, ω = 126.2, Boskop, ω = 113.8) (Hamman, 1981; Koch, 1975) was similar to the fastest growth recorded in this study (Table 6.3). Thus, the growth rate in the Sinqemeni and Laing reservoirs is probably in the upper range, while the growth rate in the Katriver and Dimbaza reservoirs is the lowest recorded for the species. Since there were no significant differences between mean surface water temperature in the five reservoirs, growth is unlikely to have been influenced by this environmental parameter.

In Chapter 4, it was demonstrated that differences in the nutritional value of food in Katriver and Laing reservoirs resulted in a significant difference in growth. The higher growth rate of fish was attributed to the abundance of diatoms and high phytoplankton biomass (Chapter 3) in the reservoir (Chapter 4). However, when examining the relationship between moggel growth and chlorophyll ‘a’ in the five reservoirs, no trend was observed. The slow growth of fish in the Dimbaza Reservoir was unexpected since the chlorophyll ‘a’ concentration was high in this reservoir. When excluding the data from this reservoir, a significant, positive correlation was observed between moggel growth and chlorophyll ‘a’ (ρ=0.95, p=0.047). In the highly eutrophic Dimbaza Reservoir, it is possible that the algal species composition has moved from a diatom dominated to a blue green algae dominated community. Since blue green algae are poorly digested compared to diatoms (Chapter 4), this would explain the decrease in the growth of moggel in this reservoir.

There were considerable differences in mortality between the moggel populations in the reservoirs. This could be attributed to predation and food abundance, since moggel mortality was directly related to the number of predatory species (Chapter 2), and negatively related to the chlorophyll ‘a’ concentration (algal biomass).

While the observed differences in length- and age-at-maturity between the populations were smaller than observed in tilapias (De Silva, 1986; Noakes and Balon, 1982), there was an overall decrease in length- and age-at-maturity with decreasing growth (Figure 6.5). This trend was particularly apparent in the slower growing fish from the Katriver and Dimbaza reservoirs. Although the confidence intervals of these regressions are broad due to the low sample size, these results do show overall trends.

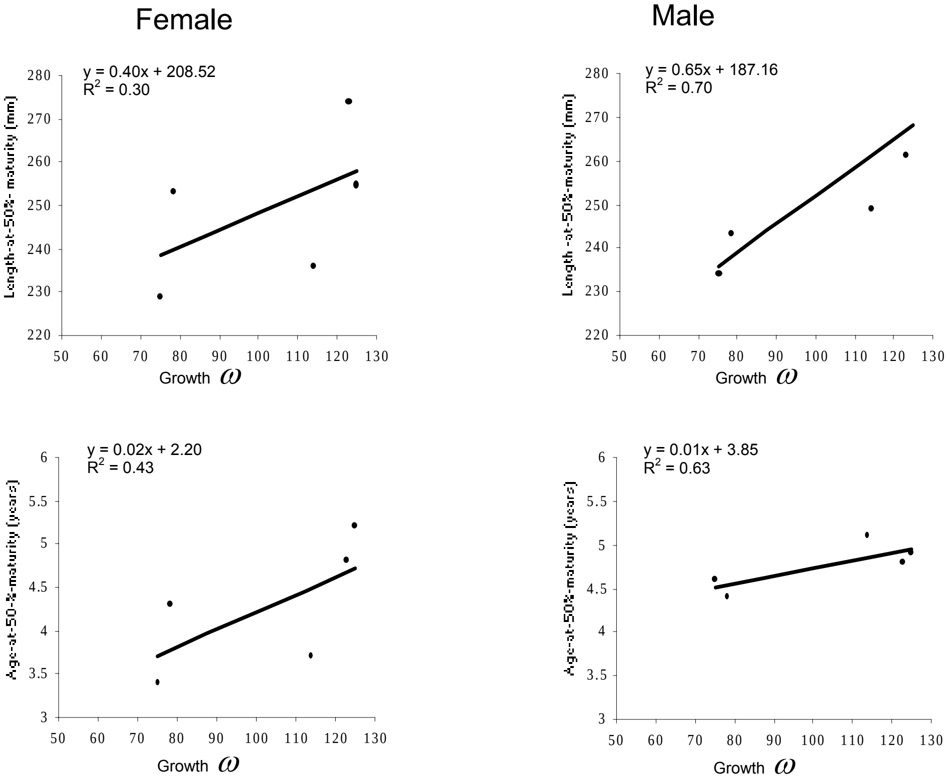

Figure 6.5. Relationship between the growth and maturity of *Labeo umbratus* in five Eastern Cape reservoirs.

Alm (1959) suggested that slower growth in fish with a repeated spawning cycle results in a smaller size at maturity. A reduction in growth rate has also been observed to increase the age-at-maturity and decrease the size-at-maturity of witch flounder (*Glyptocephalus cynoglossus*) (Molander, 1925, cited by Stearns and Crandall, 1984), increase the age-at-maturity and not influence the size-at-maturity of Actic charr (*Salvelinus alpinus*) (Grainger, 1953), and increase both the age- and size-at-maturity of Atlantic cod (*Gadus morhua*) (Pinhorn, 1969, cited by Stearns and Crandall, 1984). Stearns and Crandall (1984) argued that selection pressure operates on age- and size-at-maturity simultaneously and not individually, and consequently results in an age-size maturation trajectory. They described four types of trajectories, each corresponding to specific demographic conditions. The J-shaped trajectory should emerge when a species is subject to slower growth and high adult mortality. This trajectory is characterised by populations displaying early maturity at a small size in response to slower growth and later maturity at a larger size in response to faster growth (Stearns and Crandall, 1984). The slow growth (Figure 6.3, Table 6.4) and high adult mortality

(Table 6.5) of moggel in Katriver Reservoir indicates that the J-shaped trajectory may be followed and this was confirmed by a decrease in size- and age-at-maturity. In addition, the largest size- and age-at-maturity was observed in Sinqemeni Reservoir, where the fish had the highest growth and lowest mortality rates. Similar trends have been observed in two populations of pumpkinseed (*Lepomis gibbosus*), where slower growth was associated with a decrease in the size- and age-at-maturity (Deacon and Keast, 1987). The decrease in size- and age-at-maturity of moggel in the Dimbaza and Katriver reservoirs can therefore be attributed to a combination of reduced growth and increased mortality. Reduced growth was caused by a poor food resource in the Katriver Reservoir and probably by intraspecific competition due to the high density of fish in Dimbaza Reservoir. The high mortality in both reservoirs was probably the result of the presence of largemouth bass (*Micropterus salmoides*) (Chapter 2).

Differences in growth, mortality, length- and age-at-maturity, lifespan (this study) and reproductive success (Chapter 5) were observed in the moggel populations in the five reservoirs. The combined influences of these traits determine the structure of a population (Nikolskii, 1969) and it was therefore not surprising that there was much variation in the population structure of moggel in the reservoirs. Despite the variation in population structure, a dominance of females in the large size classes was observed in all reservoirs. This has also been observed in other moggel populations (Gaigher *et al.,* 1975; Hamman, 1981; Gaigher, 1984). The competitive advantage of this would be to increase the number of eggs produced by the population. The characteristically ephemeral conditions of small water bodies make high population fecundity advantageous since larval and juvenile mortality can be extremely high. Another method of ensuring the survival of eggs and larvae during times of environmental perturbation is mouth brooding, which is used by several tilapia species that dominate many small water bodies in Africa (Mattson, 1997). Here, the smaller number of eggs produced is offset by the high degree of parental care and subsequent lower mortality when exposed to environmental fluctuations.

The extended spawning season of moggel (Chapter 5, Mulder, 1973; Gaigher, 1984) also counteracts the variable conditions encountered in small water bodies. The extended spawning season allows fish to spawn throughout the wet season, when conditions are favourable. This prevents recruitment failure, which could occur if all mature fish in the population spawned at the same time just before an unfavourable environmental change.

The sex ratio of a species may vary between populations and reflects its relationship with the environment (Nikolskii, 1969). Changes in the quantity and quality of food are the most common cause for an alteration in the sex ratio (Nikolskii, 1969). The sex ratio of the moggel populations in this study was more variable (female:male ratio between 1.0:0.4 to 1.0:1.6) than observed in other populations (female:male ratio between 1.0:0.7 to 1.0:1.1) (Gőldner, 1967 Mulder, 1973; Gaigher *et al*., 1975, Gaigher, 1984). The wide variations in sex ratio recorded here are not unique (Nikolskii, 1969). It can be postulated that in reservoirs with reduced food availability, the high-energy requirements of mature female fish for reproduction should increase their mortality (Mann, 1980). It was noted that the opposite trend occurred in Katriver Reservoir, where moggel food was considered to be of lower nutritional quality (Chapter 4) and Dimbaza Reservoir, where a high population density is thought to have increased intraspecific competition. A similar trend was found in *Pleuronectus flesus luscus* (Zambriborshch, 1956, cited in Nikolskii, 1969) that were exposed to conditions of low food availability in the Black Sea. Another possible explanation for the high variability in sex ratio in moggel may be the unpredictability of the small water body environment. From year to year, differences in reproductive success, food availability, growth and mortality may contribute to changes in the sex ratio. This may be particularly relevant in moggel since the feeding preferences of juveniles and adults are similar (Chapter 4).

The diversity in life history parameters suggests that some moggel populations are more suitable for harvest than others. Typically, populations with fast growth and a shorter lifespan are more likely to promote sustainable fisheries. Thus a moggel fishery in the Sinqemeni Reservoir should have the greatest potential, followed by the Laing and Ndlambe reservoirs. Due to the slow growth, long lifespan and high natural mortality of the fish in the Katriver, it is unlikely that this system could support a sustainable moggel fishery. Although growth of moggel in Dimbaza Reservoir was the slowest, this reservoir supports the largest population (Chapter 8). The slow growth in Dimbaza Reservoir is possibly attributed to intraspecific competition, due to increased reproductive success (Chapter 5), which may result in decreased somatic growth. According to surplus production theory (Quinn and Deriso, 1999), the introduction of a fishery to the Dimbaza Reservoir could increase fish production, by decreasing competition and increasing net population growth rate. Thus, the Dimbaza Reservoir was considered to have the greatest fishery potential, followed by the Sinqemeni, Laing, Ndlambe and Katriver reservoirs. However, once fisheries are established, the growth rate and the size and age of sexual maturity are likely to change considerably. This study would therefore provide useful baseline information when describing the influence of fisheries on the life history of moggel.

While many environmental factors may influence moggel life history, reservoirs with a higher algal biomass (chlorophyll ‘a’ concentration) appear to have the highest fishery potential (Chapter 2, Table 2.3). This suggests that moggel populations in small reservoirs with conditions that support a high algal biomass are likely to have a greater potential for exploitation. Small water bodies that support a high algal biomass tend to be shallow (Howard-Williams and Ganf, 1981) and nutrient enriched (Davies and Day, 1998, Chapter 3). Moggel populations occurring in small, shallow reservoirs with some nutrient enrichment probably have the greatest potential for exploitation.

CONCLUSION

A significant positive correlation between chlorophyll ‘a’ and growth was noted in four of the reservoirs. In the highly eutrophic Dimbaza Reservoir, the slow growth rate of moggel was attributed to intraspecific competition. Mortality was lower in moggel populations that were exposed to less predatory species and where food was abundant. Size- and age-at-maturity were not affected by environmental factors, but were dependent on growth and mortality. There appeared to be a relationship between the fishery potential of moggel and algal biomass and thus it is concluded that moggel in small, shallow, slightly enriched reservoirs would exhibit life history traits suitable for exploitation.

The growth and mortality estimates from this chapter provide some information for the calculation of biomass and production. However, the accurate estimation of biomass and production requires estimates of the population size and structure in each reservoir. In order to achieve this, the selectivity of the sampling gears must be calculated (Chapter 7).

CHAPTER 7

Estimating gillnet selectivity for *Labeo umbratus* and an evaluation of fyke nets as a non-destructive sampling gear in small reservoirs

INTRODUCTION

Optimal management strategies are essential for communities to have sustained benefits from directed fisheries in small reservoirs. Gillnets are arguably the most suitable gear for harvest in directed fisheries. In addition, management is simplified because of their highly selective properties. However, as a sampling gear, these selective properties must be accurately and precisely estimated to determine the most suitable mesh sizes to be used for a new fishery (De Silva and Sirisena, 1987), to evaluate potential changes in the population dynamics of a harvested species, and allow for the inclusion of a selectivity correction factor when estimating population numbers, population size structure (Millar, 2000), biomass and productivity from the catch per unit effort data (Mattson, 1997). The significance of selectivity estimation makes validation prior to application essential and it is therefore preferable to employ a number of methods.

Gear selectivity can be defined as a mathematical function that describes that proportion of fish in each size, or age, class that is retained from a population by a unit of effort using a particular fishing gear (Lagler, 1968). Estimation of selectivity is not, however, a trivial task. Direct and indirect methods have been used to estimate the selective properties of gillnets. Direct methods involve comparing catches with a known population structure (normally determined from tagging experiments) or against a non-selective gear (acoustic methods), or one with known selectivity characteristics. Unfortunately, the expense of tagging high numbers of individuals (Borgstrøm, 1989) and acoustic surveys has largely prevented their application. Indirect methods, by contrast, require no prior knowledge of population structure and a number of types with different basic approaches have been developed. Olsen (1959) developed what are known as

"Type A" selectivity curves. These methods calculate the probability of capturing various size classes of fish with one mesh size. "Type B" curves, developed by Baranov (1948), estimate the probability that fish in one size class may be captured and retained by one of a multitude of mesh sizes. Boy and Crivelli (1988) combined both "Type A" and "Type B" curves and developed a hybrid model for cyprinids. This method uses prior knowledge of the distribution of fish length with different age classes and the length distribution for each mesh size. Another simple, and widely used, method developed by Sechin (1969) uses the morphological characteristics of the harvested fish.

Since small reservoirs may have small fish populations, sampling gear that is non-destructive and suitable for determining population size and structure should be sought. Fyke nets have recently been employed in the Eastern Cape to assess the prospect of eel fisheries and their potential as a non-destructive method for sampling small reservoirs needs to be evaluated. Unlike gillnets, fyke nets are fish trapping gears and in theory, any fish larger than the mesh of the fyke net would be captured. Like with all passive gears, encounter selectivity (Rudstam *et al.,* 1984) would apply and this would reduce the likelihood of smaller fish encountering the gear. Assuming that fyke nets are non-selective during the process of capture, they provided an opportunity to test an alternative direct method to estimate gillnet selectivity.

This chapter presents two alternative methods for calculating gillnet selectivity – one direct (fyke net) and one analytical - and compares them against the conventional indirect Sechin (1969) method. In addition, the use of fyke nets as a non-destructive sampling gear in small reservoirs is evaluated.

MATERIALS AND METHODS

Age and growth, length, weight and mortality parameters were determined from gillnet data collected on quarterly sampling trips between February 2000 and November 2001 (see Chapter 6). The selectivity experiment was performed concurrently with the final quarterly sample in November 2001. Moggel samples were collected using gillnets (50 m x 2 m) constructed with green, knotted multifilament nylon (210/9). The hanging ratio of the nets was 0.5. Each gillnet consisted of five randomly positioned panels (10 m x 2 m) with stretched mesh sizes of 44 mm, 60 mm, 75 mm, 100 mm and 144 mm. Dutch-designed fyke nets with a stretched mesh size of 19 mm were deployed simultaneously (Figure7.1). On all sampling occasions one gillnet and two fyke nets were set in series and parallel to the shore at two randomly selected sites. All nets were set in water at a depth of ±2.5 m.

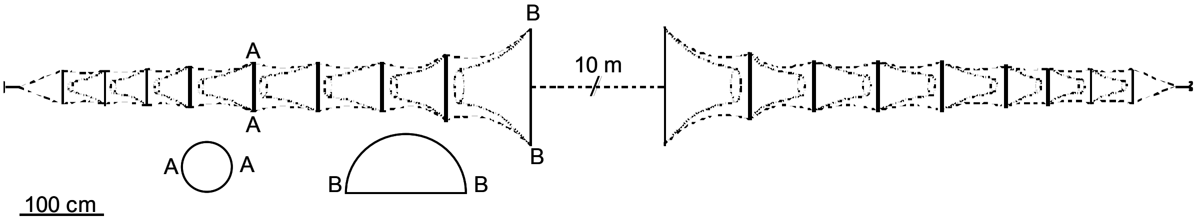

Figure 7.1. Schematic diagram of a Dutch fyke net (viewed from above).

Nets were set at 16:30 and fish retrieved at 08:30 the following morning. Fork length (to the nearest mm) and gill girth (to the nearest mm) were measured for each fish captured. Gill girth was measured using 0.55 mm diameter nylon fishing line that was stretched taut behind the operculum at the position where almost all fish in the samples were caught. Due to the fusiform shape of *L. umbratus*, few fish were wedged and no fish were tangled in the mesh.

Indirect Sechin method

The principal assumption of Sechin's (1969) indirect estimate of gillnet selectivity is that the selective properties of the gear are dependent on the morphology of the fish. This method assumes that all fish are fully selected if their maximum girth is greater, but their head girth smaller, than the mesh perimeter. If both girth and the stretched mesh are (asymptotically) normally distributed, and there is negligible tangling of fish in the nets, selection of fish at length (*L*) by gear (*i*) is discrete normally distributed such that

$$S_{i,L} = \exp\left(-\frac{1}{2(\sigma_{i,girth} + 2\sigma_{i,mesh})^2}\left(G_L - 2\overline{M}_i\right)^2\right)$$

where $\overline{M}_i$ and $\sigma_{i,mesh}$ are the mean and standard deviation of the stretched mesh of gear *i* (measured between opposing knots), $\sigma_{i,girth}$ is the girth standard deviation of the fish caught in mesh *i*, and G_L is the predicted girth behind the gills estimated by the linear regression as $G_L = \beta_0 + \beta_1 L$. Length, opposed to girth, based parameter estimates were calculated through the girth-length relationship.

Direct Fyke net method

Since gill and fyke nets are passive gears it was assumed that the net encounter rate by fish was equal. It was also assumed that a relatively unselective gear, such as a fyke net, would adequately represent the relative length frequency distribution of fish in the population.

The selectivity $\tilde{S}$ per length L of each gillnet mesh i is obtained by dividing the catch at length $N_{L,i}$ by the catch of the non-selective gear (in this case the fyke net) at length $N_{l,fyke}$ such that

$$\tilde{S}_{i,L} = \frac{N_{L,i}}{N_{L,fyke}}\ .$$

The selective properties of the gear was estimated by fitting a discrete normal distribution of the form

$$\hat{S}_{i,L} = \exp\left(-\frac{1}{2\sigma_i^2}\left(L - \mu_i\right)^2\right)$$

to the relative retained proportions by length through the minimisation of a negative normal log-likelihood of the form

$$\ln L = \frac{n}{2}\ln\left[\sum_{x}\left(\tilde{S}_{i,L} - \hat{S}_{i,L}\right)^2\right]$$

where $\tilde{S}_{i,L}$ is the normalised retained fraction for gear i at length L and $\hat{S}_{i,L}$ the predicted selectivity. The parameters that govern the size at maximum selection and variance of gillnet i are μ_i and σ_i^2, respectively.

Due to the low numbers of fish sampled in the fyke net, the number of fish per length L was replaced by the moving average $N_{L,fyke} = \left(N_{L-1,fyke} + N_{L,fyke} + N_{L+1,fyke}\right)/3$.

Indirect length-structured model

Under the assumptions that the population is closed and subject only to (age-independent) natural mortality and continuous deterministic recruitment (i.e., a steady-state situation) then it is possible to model the selective properties of a fishing gear by reconstructing a population of fish by length and comparing expected catches from this population against observed catches. The modelling framework is, therefore, length-based as the gear selection process is governed by length rather than age.

Catches

The combined expected catch, in number of fish, in length class L by a series of sequential gears (each denoted with the subscript i) can be expressed as:

$$\hat{C}_L = N_L qF \sum_{i} \psi_i S_{i,L}$$

where q is a scaling parameter to equate the observed and expected catches, F the instantaneous asymptotic rate of fishing mortality (assumed to be extremely small in this study due to the absence of harvesting), $S_{i,L}$ the relative selectivity of the gear i on fish at length L , N_L the number of fish in length-class L and ψ_i the proportional effort expended by gear i. The term “relative” selectivity is used in this context as it is assumed that the maximum selection by the gear is 1 (or

100%). The parameter ψ_i for each gear was considered equal as the same number of different meshed panels was used in the experiment.

Assuming that catching is governed by an underlying Poisson-process (Kirkwood and Walker, 1986), the parameter point estimates, selectivity and mortality, were obtained by minimising a negative Poisson log-likelihood function. Additional information pertaining to the population structure, as obtained from the fyke net catches, was added to the likelihood by assuming that the numbers at length with the population was log-normally distributed. The negative log-likelihood to be minimised is of the form

$$-\ln L = \sum_i \sum_L \left(\hat{q}_{catch} \hat{C}_{i,L} - C_L \ln \hat{q}_{catch} \hat{C}_{i,L} \right) + \frac{n}{2} \ln \left[\sum_L \ln \left(\frac{N_{L,fyke}}{\hat{q}_{fyke} \hat{N}_L} \right)^2 \right]$$

where $C_{i,L}$ and $\hat{C}_{i,L}$ are the observed and expected catches at length *L* by gear *i*, $N_{L,fyke}$ the observed fyke net numbers at length, $\hat{N}_L$ the model predicted numbers at length and $\hat{q}_{catch}$ and $\hat{q}_{fyke}$ the scaling parameters.

The maximum likelihood estimates of the scaling parameters are

$$\hat{q}_{catch} = \frac{\sum_i \sum_L C_{i,L}}{\sum_i \sum_L \hat{C}_{i,L}} \quad \text{and} \quad \hat{q}_{fyke} = \frac{\sum_L N_{L,fyke}}{\sum_L \hat{N}_L}.$$

Population dynamics

The length-structured population dynamics is based on a discrete version of Deriso and Parma's (1988) model as proposed by Quinn *et al.* (1998). This reparameterisation, despite not being a closed analytic solution, is advantageous because it is general; it adds additional flexibility to the specification of the selectivity, growth and variance functions in the modelling process at the expense of limited additional computational overhead.

Suppose that recruitment of N_r individuals occurs at age r and that the length x of each individual is considered to be a discrete variable. By assuming that the distribution of lengths x for age r is a discrete normal N_D with mean μ_r and variance σ_r^2 then probability density function (PDF) is $f_r(x) \sim N_D(\mu_r, \sigma_r^2) = e^{-\frac{1}{2\sigma_r^2}(x-\mu_r)^2} (NC_r)^{-1}$ with the normalisation constant $NC_r = \sum_x f_r(x)$.

The abundance of age r individuals at each length is then $N_r(x) = N_r f_r(x)$. For the purposes of this study $N_r = 1$ as all catches were considered relative and scaled accordingly by the parameter q.

Abundance for the following age (a+1) is obtained through the processes of growth and mortality, with natural mortality and gear selectivity assumed to be a function of length and not age.

By assuming that gillnet selectivity is additive, the selection by a fleet of gillnets for length x is calculated as a sum of discrete normal distributions as $S_x = \sum_i S_{i,x}$.

For a given PDF $f_a(x)$ at the start of age a, the relative distribution of lengths after mortality occurs, or at the end of year a, is $p_{a,Z}(x) = f_a(x)\exp^{-Z_{a,x}}$ where $Z_{a,x} = M_x + F_{a,x}$ is total mortality that is comprised of both a natural mortality M_x and the partially recruited fishing mortality $F_{a,x}$ component. It is assumed that fishing mortality is separable into its fishing mortality and selectivity components such that $F_{a,x} = F_a S_x$.

The absolute number of individuals at length x after mortality and the PDF for lengths after mortality is

$$N_{a,Z}(x) = N_a p_{a,Z}(x) \text{ and } f_{a,Z}(x) = p_{a,Z}(x) \Big/ \sum_x p_{a,Z}(x) .$$

To account for growth, it is assumed that an individual of length x will grow to length L in one time step according to a stochastic growth model. A commonly used growth model is the von Bertalanffy (VB) model with the stochastic error component derived by Cohen and Fishman (1980).

The deterministic VB model is of the form

$$L_a = L_\infty (1 - e^{-K(t-t_0)})$$

where L_∞, K and t_0 are the VB parameters. An equivalent recursive formulation for size at $a+1$, or L_{a+1}, with the inclusion of a stochastic error term is

$$L_{a+1} = L_\infty (1-\rho) + \rho L_a + \varepsilon_a \text{ where } \rho = \exp(-K), \text{ and } \varepsilon_a \sim N(0, \sigma^2).$$

From Cohen and Fishman (1980), the expected length increment and variance at $a+1$ for an individual at length x at age a, considering that it was recruited at age r is

$$\mu_{a+1}(x) = L_\infty (1-\rho) + \rho x \text{ and } \sigma^2_{a+1} = \sigma^2 \frac{1-\rho^{2(a-1)}}{1-\rho^2} + \sigma_r^2 \rho^{2(a-1)} .$$

The normal PDF for the length distribution after one growth increment for an individual originally of size x is

$$f_{a+1,G}(L \mid x) \sim N_D\left(\mu_{a+1}(x), \sigma^2_{a+1}\right) = \frac{e^{-\frac{1}{2\sigma^2_{a+1}}(L-\mu_{a+1}(x))^2}}{NC_{a+1}} \text{ with } NC_{a+1} = \sum_L f_{a+1,G}(L \mid x) .$$

The relative distributions of lengths at the start of age $a+1$ is then obtained from the relative distribution of lengths after mortality and growth, such that

$$p_{a+1}(L) = \sum_x f_{a+1,G}(L \mid x) p_{a,Z}(x) = \sum_x f_a(x) e^{-Z_{a,x}} e^{-\frac{1}{2\sigma^2_{a+1}}[(L-\mu_{a+1})]^2} / NC_{a+1,x} .$$

The absolute numbers at length at age $a+1$ and the corresponding PDF are then

$N_{a+1}(L) = N_a p_{a+1}(L)$ and $f_{a+1}(L) = \frac{p_{a+1}(L)}{\sum_L p_{a+1}(L)}$.

The total number of fish at age $a+1$ is $N_{a+1} = \sum_L N_{a+1}(L)$, while the total number of fish per length *x* across all ages is $N_x = \sum_a N_a(L)$.

Parameter estimation

To reduce over-parameterisation, a common problem when estimating gear selectivity, the parameters for the von Bertalanffy model (L_∞, K, t_0, σ_r^2 and σ^2) were estimated by minimising the negative normal log-likelihood of the form

$$\ln L = \sum_{i=1}^{n} \left[\ln(\sigma_{a,i}^2) + \frac{\left(L_{a,i} - \hat{L}_{a,i}\right)^2}{2\sigma_{a,i}^2} \right].$$

Estimation of parameter variability for all models

To facilitate the comparison of the variability estimates, the asymptotic standard errors of each parameter θ were obtained from the inverse Hessian. This was considered suitable as an inspection of the likelihood profiles for each parameter showed that they were approximately normally distributed.

RESULTS

A total of 204 *L. umbratus* were captured in the fyke nets; 96 in the 44 mm mesh gillnet, 136 in the 60 mm mesh gillnet and 68 in the 75 mm mesh gillnet (Table 7.2). The typically high level of selectivity by each gillnet mesh, denoted by a clearly defined unimodal distribution, is illustrated in Figure 7.2. All 204 individuals captured in the fyke net were measured and released live; no mortalities were observed. The stochastic error von Bertalanffy growth parameters are shown in Table 7.1.

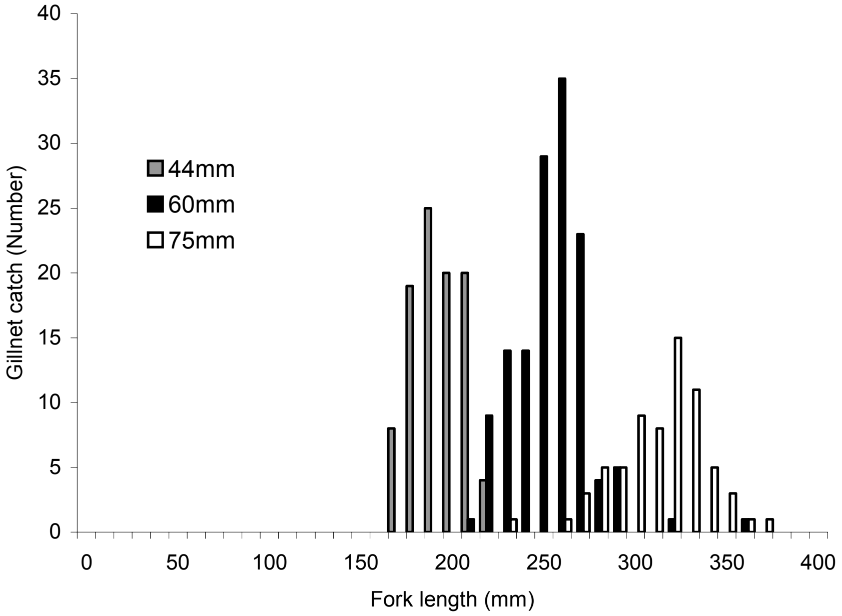

Figure 7.2. Gillnet catches of *Labeo umbratus* using three mesh sizes in Dimbaza Reservoir, Eastern Cape, South Africa.

Table 7.1. Stochastic error von Bertalanffy growth parameters of *Labeo umbratus* in the Dimbaza Reservoir.

Parameter	Estimate
L_∞ *(mm)*	344.91
K *(.year^{-1})*	0.24
t_0 (years)	-1.93
σ^2	16.70
σ_r^2	11.62

Table 7.2. *Labeo umbratus* captured in gillnets (44 mm, 60 mm and 75 mm mesh) and fyke net in Dimbaza Reservoir.

Length (mm)	44mm	60mm	75mm	Fyke net
110	0	0	0	2
120	0	0	0	7
130	0	0	0	2
140	0	0	0	1
150	0	0	0	1
160	0	0	0	9
170	8	0	0	6
180	19	0	0	3
190	25	0	0	13
200	20	0	0	11
210	20	1	0	12
220	4	9	0	11
230	0	14	1	16
240	0	14	0	26
250	0	29	0	15
260	0	35	1	10
270	0	23	3	11
280	0	4	5	10
290	0	5	5	8
300	0	0	9	7
310	0	0	8	8
320	0	1	15	8
330	0	0	11	2
340	0	0	5	2
350	0	0	3	3
360	0	1	1	0
Total	96	136	68	204

Indirect Sechin method

The morphometric characteristics measured to determine gillnet selectivity using the Sechin method are shown in Table 7.3. The selectivity curves calculated for the 44, 60 and 75 mm mesh sizes were all unimodal (Figure 7.3), with the probability of catching *L. umbratus* in the 44, 60 and 75 mm mesh being highest for fish in the 180, 250 and 320 mm size classes, respectively (Figure 7.3, Table 7.4).

Table 7.3. Selected morphometric characteristics of *Labeo umbratus* in Dimbaza Reservoir.

Parameter	Estimate
Fork length (mm) vs weight (mm)	$FL=10.501e^{0.0123W}$
Gill girth (mm) vs fork length (mm)	$GG=0.53FL-4.85$

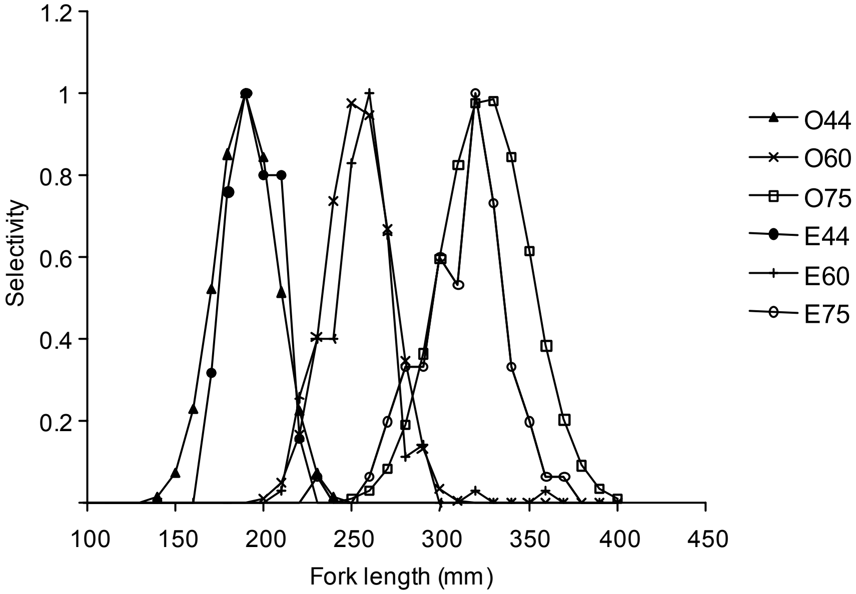

Figure 7.3. Selectivity curves for *Labeo umbratus* captured in gillnets with three mesh sizes, calculated using the indirect Sechin method (O=observed, E=expected).

Direct fyke net method

The probability of catching *L. umbratus* in the 44, 60 and 75 mm mesh sizes was highest for fish in the 190, 250 and 320 mm size classes respectively (Table 7.4) and the estimated selectivity curves are shown in Figure 7.4.

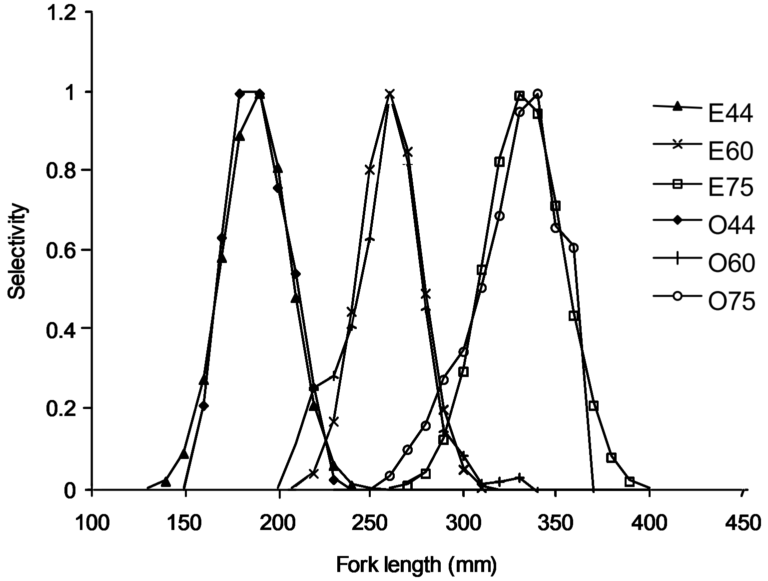

Figure 7.4. Selectivity curves for *Labeo umbratus* captured in gillnets with three mesh sizes, calculated using the direct fyke net method (O=observed, E=expected).

Indirect length-structured model

There was a strong similarity between the observed catches in the fyke net and the expected catches calculated using the length-structured model (Figure 7.5). However, the large number of fish captured in the 240 mm size class resulted in a marked deviation of the observed and expected catches. The probability of catching *L. umbratus* in the 44, 60 and 75 mm mesh was highest for fish in the 190, 250 and 320 mm size classes, respectively (Table 7.4). As with the two other methods used, this model estimated the selectivity curves to be unimodal (Figure 7.6).

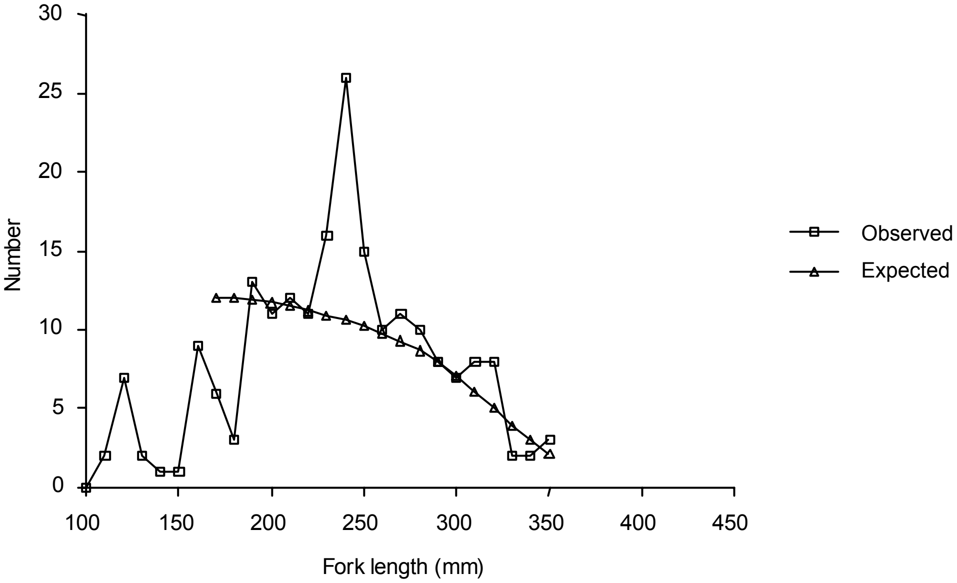

Figure 7.5. Observed fyke net catches and expected catches using the length-structured model for *Labeo umbratus* in Dimbaza Reservoir.

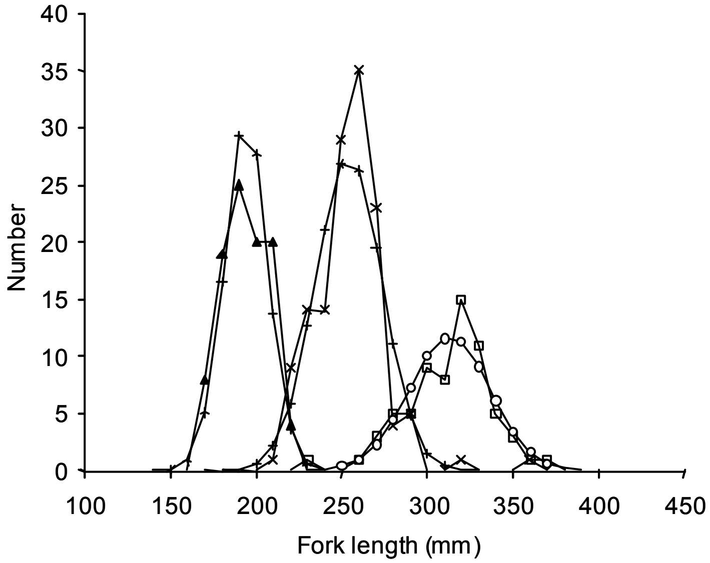

Figure 7.6. Observed and expected catches for moggel (*Labeo umbratus*) using the length-structured model (O=observed, E=expected).

Table 7.4. Gillnet selective curve parameter estimates together with their asymptotic standard errors.

	Parameter	Estimate	SE
	Indirect method		
44mm	μ	189.88	-
	σ	18.41	-
60mm	μ	254.00	-
	σ	18.81	-
75mm	μ	325.46	-
	σ	25.91	-
	Direct method		
44mm	μ	188.51	0.43
	σ	17.83	0.34
60mm	μ	260.69	0.78
	σ	16.32	0.69
75mm	μ	332.88	1.05
	σ	21.28	0.86
	Length-based model method		
44mm	μ	193.87	0.89
	σ	12.70	0.53
60mm	μ	256.04	1.25
	σ	19.92	0.72
75mm	μ	328.02	3.26
	σ	26.59	1.73

Comparison of the three methods

The three methods used to estimate gillnet selectivity yielded similar results (Figure 7.7, Table 7.4). When compared with the length frequency distribution, the observed catches were mostly within the selection range of the expected catches (Figures 7.3, 7.4, 7.6).

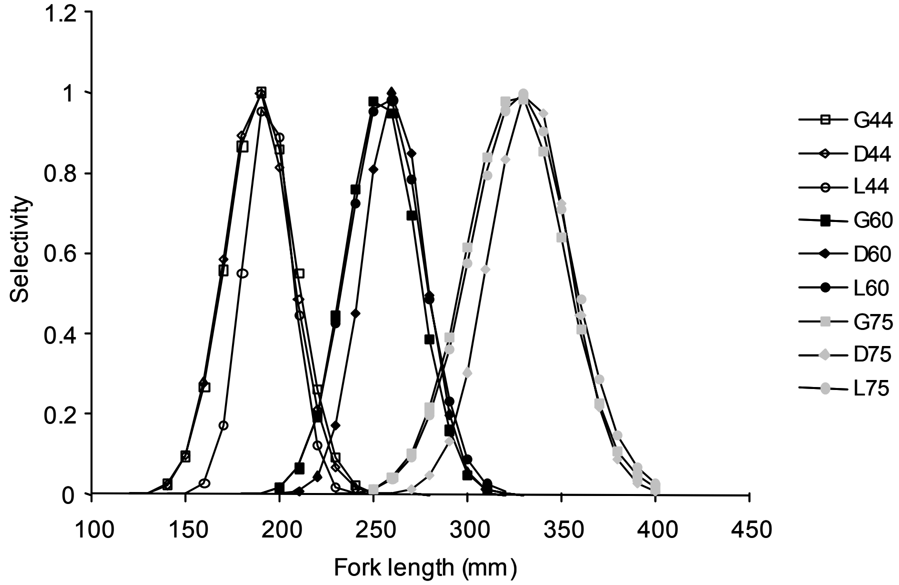

Figure 7.7. A comparison of the gillnet selectivity curves estimated for *Labeo umbratus* using the indirect Sechin method, a population matrix method and a direct fyke net method (G=girth(Sechin) method, D=direct method, M=matrix method).

DISCUSSION

The selectivity curves for moggel were easily estimated. The similar results obtained suggest that all three methods could be used for research in small reservoirs in the future. The assumption that the fyke nets were unselective for the capture fishes over 150 mm FL appears to have been validated in this experiment. Although the probability of these fish encountering the gear was not considered, fyke nets and gillnets are both passive gears. Thus provided they are deployed in the same area, it is reasonable to expect that the same part of the population is exposed to both of these gears and an equal encounter rate per square meter of net will occur. Given that similar parts of the population are exposed to the gears, then fyke nets could be very useful tools to determine gillnet mesh selectivity. This is due to their unselective nature during the capture process.

Fyke nets can also be used for an accurate, rapid, assessment of population structure. However, this will only be achieved if the nets are placed in a variety of habitats within the reservoir to account for variation in the size of fish between different habitats. The non-destructive nature of this gear also makes it suitable for estimating population numbers in small reservoirs using mark recapture methods.

One weakness of Sechin's (1969) method is the lack of consideration for fish that are captured by tangling. Fortunately the moggel's fusiform shape and lack of teeth and serrated spines resulted in only one individual captured by tangling and this method was therefore the simplest and most suitable for estimating selectivity. This method is therefore recommended for any potential commercially important species with these morphological attributes. Some of the African species suitable for this method include the Orange River mudfish, *L. capensis*, smallmouth yellowfish, *Labeobarbus aneus*, and the manyame labeo, *L. altivelis*. Some species with large or serrated spines such as the sharptooth catfish, *C. gariepinus*, common carp, *C. carpio,* and silver catfish, *Schilbe intermedius*, would be unsuitable. Since this method only relies on the length-girth relationship of the fish, the measurement of girth is not trivial. It is therefore essential that the material used to measure girth is similar to the gillnet material and that the material is stretched taut to mimic the capture process when measuring.

Direct estimates are considered to be the most reliable estimates of gear selectivity (Hamley, 1975). Although the direct fyke net method has not previously been used in gillnet selectivity studies, it yielded similar selectivity estimates to the Sechin method. Unlike other direct methods, such as acoustic surveys (Winters and Wheeler, 1989), fyke nets are passive gears and thus effort can be compared directly to gillnet effort. Another advantage of this method is that fish do not need to be excessively handled or sacrificed. While it can be argued that there is no unselective fishing gear, the trap-like nature of this gear does not increase the likelihood of capturing fish with spines and teeth by tangling. This suggests that this method may have application for any species, regardless of its morphometric characteristics. A disadvantage of the fyke net method, however, is the large number of fish required to accurately estimate the population structure. In this study, the number of fish captured in the fyke nets (204) was just sufficient to reliably estimate selectivity. This method can therefore only be used as a once-off, rapid technique in reservoirs with high fish abundance. Overall, the fyke net method provided reliable selectivity estimates and its potential as a method to determine the selectivity of other species in other gears should be explored.

The indirect, length-structured model was also suitable for estimating the gillnet selectivity of moggel. However, the requirements that the population growth must be known and that the population be closed, are seldom met. Additional parameters, such as migration, growth and recruitment, could be estimated but these would be confounding as there are too few data to provide a strong signal. Overparameterisation is also a common problem in selectivity experiments and thus careful consideration must be given at the experimental design stage to ensure that the number of variables to be estimated is not excessive.

The strengths of the length-structured model are that selectivity can be estimated without any field experimentation and it can be used to estimate fishing and natural mortality. This method may therefore provide an alternative method to estimate parameters in a multi-gear fishery. In addition, the morphology of the species has no bearing on the selectivity estimate and it can therefore be applied to any fish species. The optimal application for this method is at the investigational stage of a virgin fishery when the permutations of various management strategies using various gears are being assessed.

CONCLUSION

In fisheries research, all three methods of estimating gillnet selectivity could be relevant. The Sechin (1969) method is the most applicable when fish are unlikely to tangle in the nets, while the direct fyke net method could be suitable for species regardless of their morphometric characteristics, but only in systems where populations are found in high concentrations. Lastly, the length-structured model could be a suitable approach for any species captured by any gear – given that the requirements of accurate growth information are met. Failure would unfortunately limit its application. The potential of fyke nets to estimate fish population numbers and structure should be further explored.

Any of the three methods could be used to estimate the population structure of moggel in a reservoir. However, to limit fieldwork, the length-structured model was chosen to estimate the population structure from gillnet catches in order to calculate moggel biomass and production in the five reservoirs.

CHAPTER 8

Predictor variables for moggel (*Labeo umbratus*) biomass and production in small reservoirs

INTRODUCTION

South Africa has approximately 3 100 registered reservoirs ranging in size from 1 – 1 000 hectares, with a surface area totalling 84 439 hectares (South African Department of Water Affairs and Forestry, Reservoir Database). Within southern and eastern Africa, Lindqvist (1994) estimated the number of small reservoirs to be between 50 000 and 100 000. Given Bernacsek's (1986) estimate of the fishery potential of small reservoirs in Africa at 1 and 2.3 million tonnes, this number of reservoirs clearly could provide fishery opportunities for rural communities.

Fisheries information for small reservoirs in South Africa is not available. This is partly due to the lack of traditional harvesting of freshwater fish in South Africa (Andrew *et al.,* 2000) and to the scientific focus on larger reservoirs and lakes such as Le Roux Reservoir (Allanson and Jackson, 1983), Gariep Reservoir (Hamman, 1981), Hartebeespoort Reservoir (Cochrane and Robarts, 1986) and Lake Sibaya (Bruton and Allanson, 1974; Bruton, 1979). Since most small reservoirs are situated in poor, rural areas, the need for fisheries research and development is a priority (Andrew *et al.,* 2000). To ensure that sustainable fisheries are developed it is essential to obtain at least basic information for each reservoir. However, the collection of fishery information from the predominantly rural and widely dispersed small reservoirs is time consuming and expensive.

Empirical modelling of fish production in large inland water bodies has been a focus of scientific research for decades (Rawson, 1952; Ryder, 1965; Jenkens and Morais, 1971; Henderson and Welcomme, 1974; Melack, 1976; Ogelsby, 1977; Hanson and Legget, 1982; Downing *et al.,* 1990; Nissanka *et al.,* 2000). Since small reservoirs (<1000ha) do not conform to these models (Ogelsby, 1977), it is necessary to explore alternatives. The low number of species with fishery potential occurring in small African reservoirs (Marshall and Maes, 1994) provides an opportunity to explore empirical models that are species-specific. Identifying variables that can be used to predict fish production in unstudied systems is the first step to developing a model to predict production. The objective of this chapter is to identify easily measurable parameters that can be used to predict biomass and production of moggel in small reservoirs.

MATERIALS AND METHODS

To identify variables that could possibly predict moggel biomass and production in unexploited reservoirs, it was critical to obtain production estimates for moggel in unfished populations. Therefore, population size, structure and mortality (Chapter 6) were estimated from surveys before experimental gillnet fishing began. Samples of *L. umbratus* were collected monthly from Katriver and Laing reservoirs, and quarterly from Sinqemeni, Ndlambe and Dimbaza reservoirs, using the methods described in Chapter 2. Moggel growth was determined in Chapters 4 and 6. Only fish above 160 mm FL were considered in the biomass and production calculation since the size selectivity of seine nets and population number of the small size classes could not be estimated.

Population numbers

The removal method was employed to estimate the number of fish in each population, since the lack of suitable seine netting sites made mark-recapture experiments impossible. It was assumed that there was no immigration or emigration from the reservoirs and that the fish did not develop a resistance to capture. A boundary condition for the use of the removal method is a considerable reduction in the catch per unit effort (CPUE). This only occurred in all reservoirs after two years of sampling and one year of experimental gillnet fishing. The number of moggel over 160 mm FL was estimated using the Leslie removal method (Leslie and Davis, 1939) from gillnet catch per unit effort (CPUE) data from the fisheries surveys and the independent, experimental fisheries. The number of small fish was not estimated. While a VPA may have provided population estimates for the small fish (< 160mm FL) using the estimates of the larger fishes, the variable reproductive success observed in the reservoirs (Chapter 6) suggested that the VPA would not provide meaningful results.

Population structure

The population size structure was estimated from information collected in the fisheries surveys in the first year of study. This was done because the independent, experimental fisheries used one mesh size and removed only larger individuals. The survey gillnet catches from the first year were corrected for selectivity using the length-structured model (Chapter 7) and the proportion of fish in each length class was calculated. The population structure was calculated by multiplying the estimated population number with the proportion in each length class.

Growth and mortality

The growth and mortality of moggel was estimated using the methods described in Chapter 6.

Biomass and production

Moggel biomass (B) and production (P) for fish between 160 and 400 mm FL was calculated using the exponential (single) von Bertalanffy formulae proposed by Allen (1971):

$$\mathrm{B} = \sum_{i=160}^{400} N_L W_\infty \left(\frac{e^{-(ti+1-ti)Z}}{Z} - \frac{3e^{-(ti+1-ti)(Z+K)}}{Z+K} + \frac{3e^{-(ti+1-ti)(Z+2K)}}{Z+2K} - \frac{e^{-(ti+1-ti)(Z+3K)}}{Z+3K} \right)$$

and

$$\mathrm{P} = \sum_{\mathrm{i}} 3N_L W_\infty K \left(\frac{e^{-(ti+1-ti)(Z+K)}}{Z+K} - \frac{2e^{-(ti+1-ti)(Z+2K)}}{Z+2K} + \frac{3e^{-(ti+1-ti)(Z+3K)}}{Z+3K} \right)$$

where K is the Brody growth coefficient, N_L is the number of individuals in the L length class, W_∞ is the theoretical maximum fish weight and Z is the mean total mortality rate and $t_i = t_o - \frac{1}{k}\ln\left(1 - \frac{L_i}{L_\infty}\right)$. W_∞ in each reservoir was calculated by converting the mean L_∞ (400 mm FL) to weight by using the length-weight relationship for each system. Since the lowest L_∞ was 358 mm FL, the standardisation of L_∞ was required for comparative purposes and consequently an upper limit of 400 mm FL was set for the calculation of biomass and production.

Influence of environmental variables on production

Based on the findings of the previous chapters, a number of environmental variables were tested to determine their value as predictors of biomass and production (Table 8.1). Mean depth (Rawson, 1952), surface area (Jenkins and Morais, 1971) and catchment area (Niassanka *et al.,* 2000) have been used in empirical models and were included in the analysis. The amount of suitable spawning area was highlighted as an important factor contributing to reproductive success (Chapter 5) and was therefore also tested. Temperature (Schlesinger and Reiger, 1982) and most commonly, conductivity (Ogelsby, 1977; Henderson and Welcomme, 1974) has been used in empirical models, while turbidity has an influence on photosynthesis, which in turn may influence algal biomass (Chapter 3) and moggel growth (Chapter 4). Human activities in the catchments influence the physiochemical conditions and algal biomass in reservoirs (Chapter 3) and were therefore included in the analysis. Chlorophyll 'a' was included as it has been used in other empirical models (Melack, 1976; Ogelsby, 1977) and algal biomass has been highlighted as an important factor influencing moggel growth (Chapter 4 and 6). The number of predatory and competitor (phytoplankton feeders) species was included to assess the effect of species interactions on biomass and production.

Table 8.1. Parameters used to determine predictor variables for *Labeo umbratus* biomass and production in five small reservoirs in the Eastern Cape, South Africa.

Dependent variables	**Predictor variables**			
	Morphometric	**Physiochemical**	**Anthropogenic**	**Biological**
Biomass (kg.ha^{-1})	Mean depth (m)	Temperature (°C)	Population density (no.ha^{-1})	Chlorophyll 'a' (µg.l^{-1})
Production (kg.ha^{-1}.yr^{-1})	Surface area (ha)	Turbidity (FTU)	Density of farmers (no.ha^{-1})	Number of competitors
	Suitable spawning area (% shoreline)	Conductivity (µS/cm)	Density of manufacturers (no.ha^{-1})	Number of predatory species
	Catchment area (km^{-2})		Density of houses without flush toilets (no.ha^{-1})	

Morphometric information was obtained from the Department of Water Affairs and Forestry (DWAF) and field measurements. Water quality in all five reservoirs was measured using the methods described in Chapter 3. The anthropogenic information used in the analysis is presented in Table 2.2. Mean chlorophyll 'a' concentration in the reservoirs was calculated using the methods described in Chapter 3.

Pearson product-moment correlations for pairs of dependent (biomass and production) and independent (climatic, water quality, anthropogenic parameters) variables were obtained to investigate the relationship between each independent variable and either moggel biomass or production after the data was logarithm transformed to stabilise variance.

RESULTS

Moggel population estimates at the time of the first survey ranged from 1 348 to 7 784 fish in the five reservoirs, at densities of between 6.6 and 474.1 fish per hectare (Table 8.2).

Small fish dominated the population in Katriver and Dimbaza, while large fish dominated in Laing, Sinqemeni and Ndlambe reservoirs (Fig 8.1). There was wide variation in moggel growth with ω values ranging between 75.2 and 124.8 (Table 8.2). Mean total mortality ranged from 0.14 in Sinqemeni to 0.40 in Katriver reservoirs (Table 8.2).

Table 8.2. Population estimates and life history parameters used to estimate biomass and production of *Labeo umbratus* in five small reservoirs, Eastern Cape, South Africa.

Reservoir	Population estimate	Moggel density (no.ha^{-1})	Mortality (Z)	W∞ (g)	K	omega (ω)
Katriver	1348	6.3	0.40	1333.0	0.20	78.5
Laing	4928	23.5	0.25	1202.0	0.33	123.1
Sinqemeni	5215	474.1	0.14	961.1	0.30	124.8
Ndlambe	4594	287.1	0.21	932.6	0.26	114.3
Dimbaza	7784	169.2	0.22	1416.8	0.21	75.2

Moggel biomass estimates ranged between 1.9 kg.ha^{-1} and 1 254.6 kg.ha^{-1} (Table 8.3). Although the confidence intervals were broad due to the low sample size, moggel biomass was positively correlated to the chlorophyll ‘a’ concentration and conductivity, and negatively correlated to mean reservoir depth, surface area and the number of predatory species (Table 8.4 and Figure 8.2). Production ranged between 0.8 and 174.7 kg.ha^{-1}.year^{-1} (Table 8.3) and although the confidence intervals were broad due to the low sample size, it was correlated to the same variables as biomass (Table 8.4 and Figure 8.3). The P/B ratio ranged from 0.14 to 0.40 in the five reservoirs.

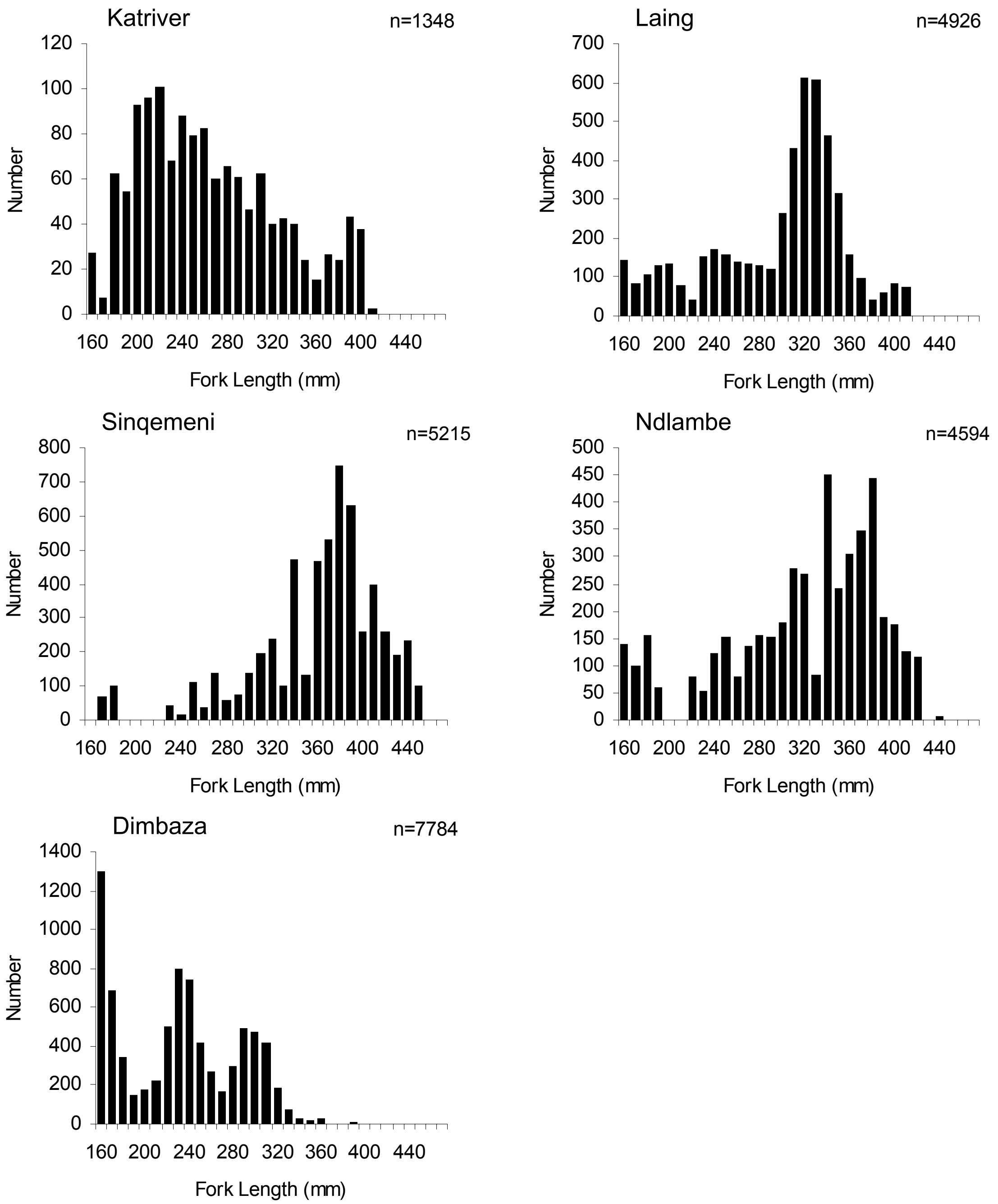

Figure 8.1. Population size structure of *Labeo umbratus* in five Eastern Cape reservoirs.

Table 8.3. Biomass, production and production-biomass ratios for *Labeo umbratus* in five small reservoirs, Eastern Cape, South Africa.

Reservoir	Biomass (kg.ha^{-1})	Production (kg.ha^{-1}.year^{-1})	P/B
Katriver	1.9	0.8	0.40
Laing	33.7	8.2	0.24
Sinqemeni	1254.6	174.7	0.14
Ndlambe	347.7	72.8	0.21
Dimbaza	214.2	46.8	0.22

Table 8.4. Results of the Pearson product-moment correlation (ρ) between environmental factors (independent variable) and *Labeo umbratus* production and biomass (dependent variable).

	Production (kg.ha^{-1}.yr^{-1})		**Biomass (kg.ha^{-1})**	
	ρ	p	ρ	p
Biological parameters				
Production (kg.ha^{-1}.yr^{-1})			0.99	<0.01
Biomass (kg.ha^{-1})	0.99	<0.01		
Chlorophyll ‘a’ (mg.m^{-3})	0.95	0.02	0.94	0.02
Number of predatory species	-0.93	0.02	-0.93	0.02
Number of competitor species	-0.87	0.06	-0.87	>0.05
Physiochemical parameters				
Temperature (°C)	0.83	0.08	0.81	0.09
Turbidity (FTU)	0.40	0.51	0.36	0.56
Conductivity (μS.m^{-1})	0.88	<0.05	0.88	<0.05
Morphological parameters				
Surface area (ha)	-0.92	0.03	-0.90	0.04
Mean depth (m)	-0.91	0.03	-0.90	0.04
Suitable spawning area (% shoreline)	0.86	0.06	0.85	0.07
Catchment area (km^{-2})	-0.48	0.41	-0.46	0.44
Catchment characteristics				
Population density (no.ha^{-1})	0.50	0.40	0.48	0.42
Density of farmers (no.ha^{-1})	-0.63	0.25	-0.65	0.24
Density of manufacturers (no.ha^{-1})	0.20	0.75	0.18	0.78
Density of houses without flush toilets (no.ha^{-1})	0.05	0.93	0.05	0.93

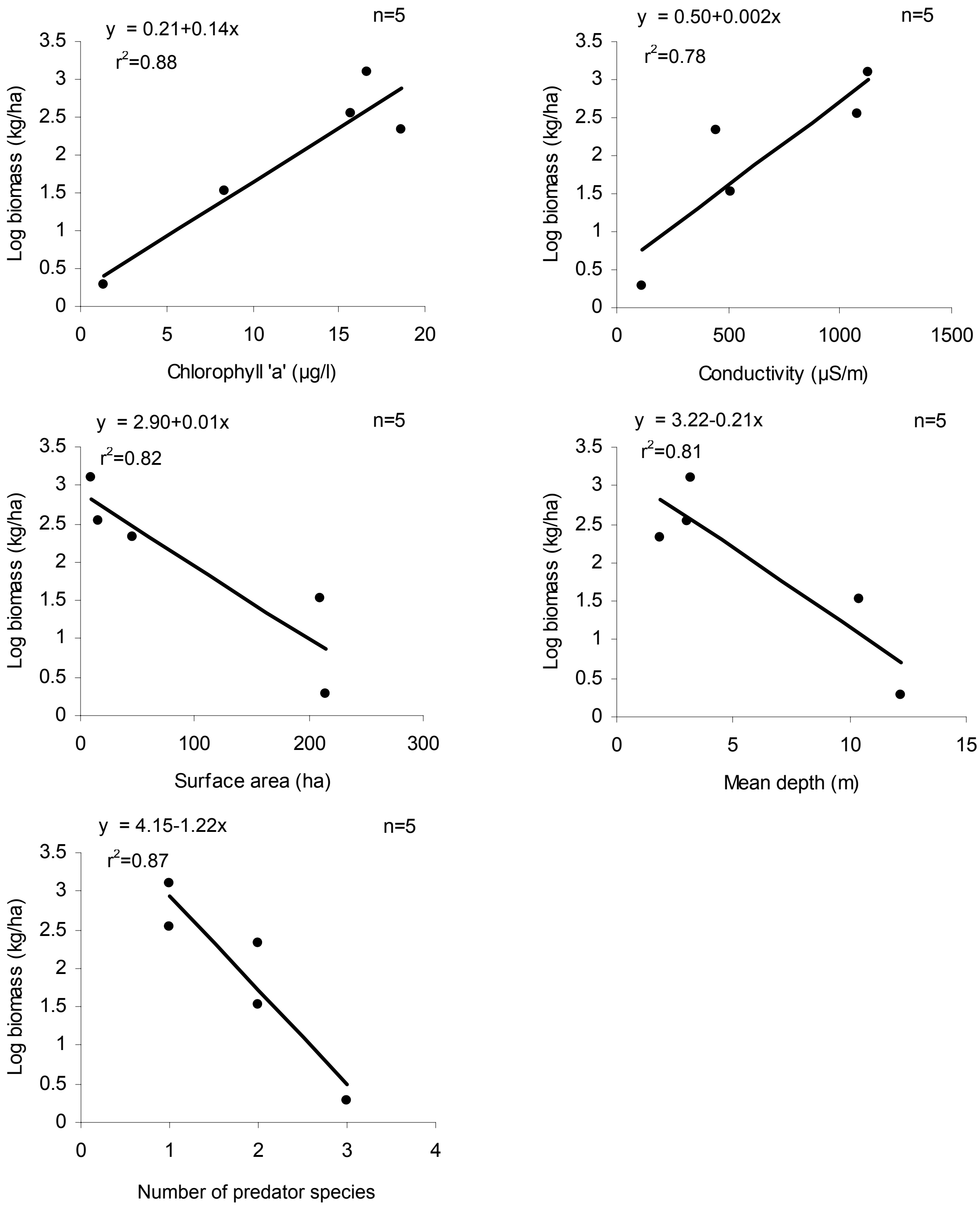

Figure 8.2. Relationship between *Labeo umbratus* biomass and selected biotic and abiotic variables in five small Eastern Cape reservoirs.

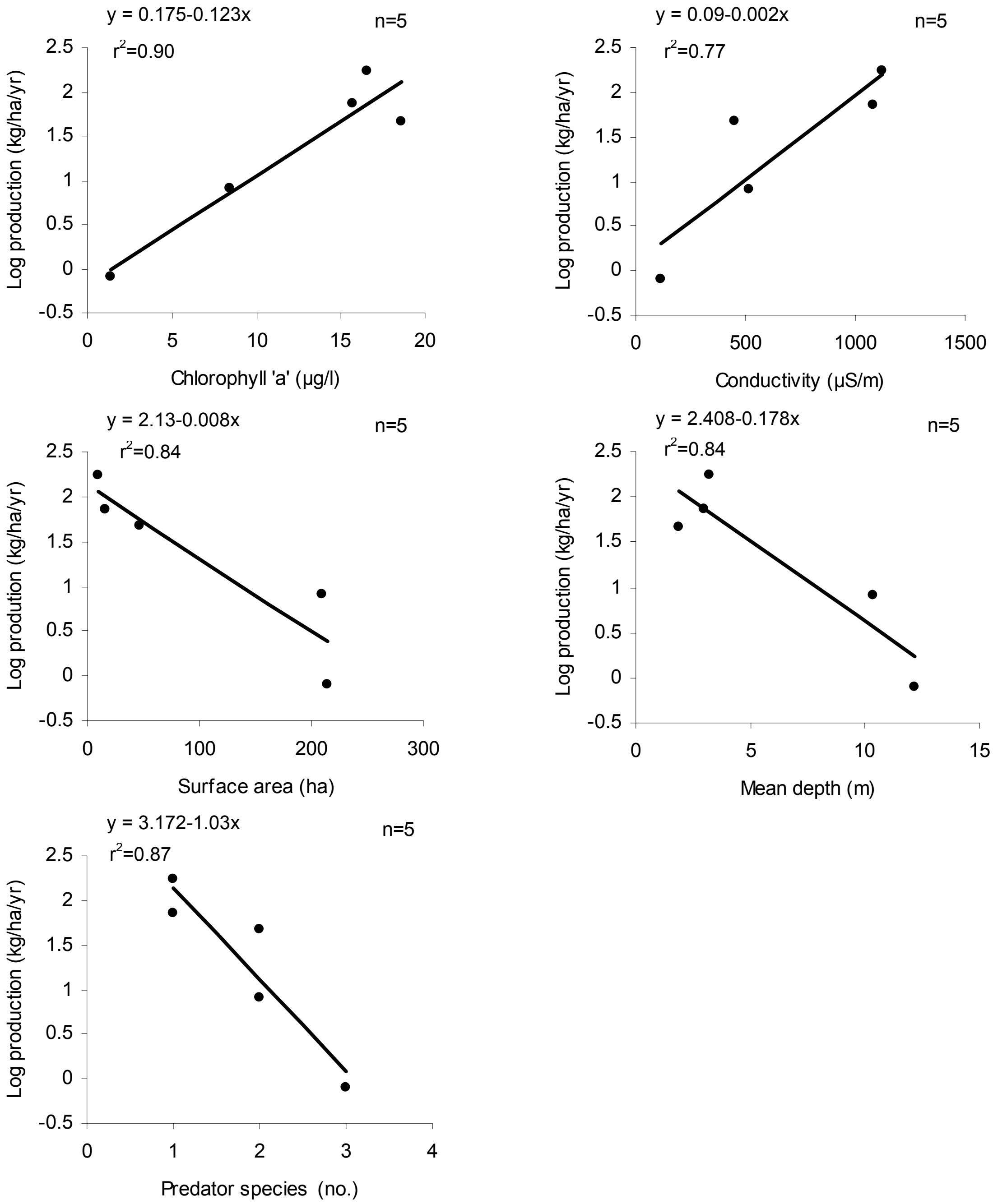

Figure 8.3. Relationship between *Labeo umbratus* production and selected biotic and abiotic variables in five small Eastern Cape reservoirs.

DISCUSSION

There was considerable variation in the biomass (1.9 – 1 254.6 kg.ha^{-1}) and production (0.8 – 174.7 kg.ha^{-1}.yr^{-1}) estimates of the five moggel populations. This indicated that conditions in the reservoirs ranged from unsuitable to very suitable for this species. Other estimates of biomass and production for a number of cyprinid species in small reservoirs ranged from 3.3 – 248.0 kg.ha^{-1}and 2.0 – 107.6kg.ha^{-1}.yr^{-1} respectively (Downing and Plante, 1993) (Table 8.5). This study therefore shows two extreme cases, one below (Katriver Reservoir) and one above (Sinqemeni Reservoir) the previous highest and lowest biomass and production recorded. This scale of the variation has not previously been observed for one species in small reservoirs. The greatest variation in the biomass and production has been found in the European perch (*Perca fluviatuilis*), which only ranged from 7.7 to 37.0 kg.ha^{-1} and 2.4 to 22.2kg.ha^{-1}.yr^{-1} respectively (Downing and Plante, 1993) (Table 8.5). The only other study of this type in small African water bodies focused on the biomass and production of the cichlid, *Oreochromis shiranus* in two small reservoirs in Malawi. While the biomass estimates were lower, production estimates were considerably higher (Mattson and Kaunda, 1997) (Table 8.5) due to the high estimates of natural mortality in excess of 2.yr^{-1}.

Since estimates of biomass and production were not obtained for fish smaller than 160 mm FL in this study, the actual production estimates may be considerably higher than recorded as juvenile fishes are generally considered to be the most productive component of the population (Balon, 1974; Chadwick, 1976). While small fish may have influenced the production estimates, the lack of consideration of fish larger than 400 mm FL may have resulted in an underestimate of biomass, particularly in Sinqemeni and Ndlambe reservoirs, which were dominated by larger fish.

The P/B ratios for moggel in these reservoirs were low as P/B ratios for most species range between 0.48 and 3.4 (Welcomme, 2001). The P/B ratio is regarded an indicator of fishery potential (Welcomme, 2001) and thus the results in this study suggest that Katriver Reservoir should have the highest and Sinqemeni Reservoir the lowest fishery potential. This was not the case and the use of the P/B ratio as an indicator of fishery potential may well not apply for these unexploited populations. According to surplus production theory (Quinn and Deriso, 1999), the introduction of a fishery would increase the P/B ratio of high-density populations, by decreasing intraspecific competition. An increase in the P/B ratio of moggel in Sinqemeni, Ndlambe and Dimbaza reservoirs would be more reflective of their fishery potential.

Table 8.5. Production ($kg.ha^{-1}.yr^{-1}$), Biomass ($kg.ha^{-1}$) and Production: Biomass ratio (P/B) of selected fish populations. Data sources below.

Lake or Reservoir	Size (ha)	Family	Species	Production ($kg.ha^{-1}.yr^{-1}$)	Biomass ($kg.ha^{-1}$)	P/B
Alinen Mustajärvi[1]	1	Percidae	*Perca fluviatilis*	15.9	37.0	0.43
Bojärn[1]	10	Percidae	*Perca fluviatilis*	16.6	29.4	0.56
Haukilampi[1]	2	Percidae	*Perca fluviatilis*	5.9	7.7	0.77
Horkkajärvi[1]	1	Percidae	*Perca fluviatilis*	5.3	21.0	0.25
Iso-Mustajärvi[1]	3	Percidae	*Perca fluviatilis*	22.2	28.7	0.77
Karhujärvi[1]	1	Percidae	*Perca fluviatilis*	2.4	8.5	0.28
Kuitäjärvi[1]	45	Percidae	*Perca fluviatilis*	11.2	18.7	0.60
Vitlampa[1]	3	Percidae	*Perca fluviatilis*	9.8	20.2	0.49
Demenets[1]	7	Cyprinidae	*Tinca tinca*	2.0	3.3	0.61
Demenets[1]	7	Cyprinidae	*Rutilus rutilus*	107.9	248.0	0.44
Demenets[1]	7	Cyprinidae	*Scardinius erthrophtalmus*	8.6	15.7	0.55
Kiutäjärvi[1]	45	Cyprinidae	*Rutilus rutilus*	4.3	13.1	0.33
Katriver[2]	214	Cyprinidae	*Labeo umbratus*	0.8	1.9	0.40
Laing[2]	210	Cyprinidae	*Labeo umbratus*	8.2	33.7	0.24
Sinqemeni[2]	9.3	Cyprinidae	*Labeo umbratus*	174.7	1254.6	0.14
Ndlambe[2]	16.2	Cyprinidae	*Labeo umbratus*	72.8	347.7	0.21
Dimbaza[2]	46.2	Cyprinidae	*Labeo umbratus*	46.8	214.2	0.22
Chisombezi[3]	2.2	Cichlidae	*Oreochromis shiranus*	208.5	42.0	4.96
Mbvoniha[3]	3.6	Cichlidae	*Oreochromis shiranus*	436.0	53.0	8.23

Superscript: 1 = Downing and Plante, 1993; 2 = This study; 3 = Mattson and Kaunda, 1997.

In unexploited systems, it appears that a better indication of fishery potential could be obtained by assessing the relative abundance and population structure of the fish. However, this, as with the P/B ratio, requires exhaustive sampling and consequently simpler, cheaper methods are being sought. Despite the low statistical power (n = 5), this study highlighted a number of environmental variables that can be used as predictors of moggel biomass and production. Biomass and production were positively correlated to chlorophyll ‘a’ concentration (algal biomass) and water conductivity, and negatively correlated to mean reservoir depth, surface area and the number of predator fish species.

Relationships between fish yield and phytoplankton has been shown by a number of investigators (Melack, 1976; Ogelsby, 1977; Jones and Hoyer, 1982; Biró and Vörös, 1988; Downing *et al.*, 1990; Gomes *et al.*, 2002). In Chapter 4 it was shown that growth appeared to be dependent on the biomass of diatoms and thus the relationship between fish production and chlorophyll ‘a’ concentration is not unexpected. It was also concluded (Chapter 4) that blue-green algae were considerably less digestible than diatoms. Since algal communities generally change from diatom/green algae dominated to blue- green algae dominated in response to eutrophication (Welcomme, 2001), there is likely to be an upper critical point where moggel production is no longer correlated with chlorophyll ‘a’. The use of chlorophyll ‘a’ as a predictor of production, while sounding simple, is not practical. The concentration of chlorophyll ‘a’ fluctuates seasonally and diurnally, and may be severely reduced after flooding (Chapter 3). Its use as a predictor of fish production would therefore require an appropriate, intensive sampling programme, which would limit its application.

Conductivity may be a useful alternative as a predictor of moggel production as it is an indicator of nutrient status of the water, which in turn influences the productivity of phytoplankton and the rest of the food web (Welcomme, 2001). In addition, water conductivity fluctuated considerably less than chlorophyll ‘a’ concentration in these reservoirs (Table 3.1) and could therefore be used as a more reliable predictor of production. Conductivity has been used extensively in fish production models (Ogelsby, 1977; Henderson and Welcomme, 1974; MRAG, 1995) and would be widely accepted as a suitable predictor of moggel production.

There was a significant relationship between mean depth and fish production. This is not surprising as mean depth has been used in most empirical fish production models (Rawson, 1952; Ryder, 1965; Hayes and Anthony, 1964; Hanson and Legget, 1982; Jenkens, 1982; Prepas, 1983). Generally, shallow reservoirs are considered more productive than deep ones (Marshall and Maes, 1994; Brylinsky and Mann, 1983). In addition, these systems have high surface to volume ratios, which increases photosynthesis and algal biomass (Vollenweider, 1976 and Chapter 3). Mean depth is a simple and easily measured variable and is thus considered a suitable predictor variable for moggel biomass and production.

Jenkins and Morais (1971) suggested that there is a correlation between surface area of the water body and fish production. Smaller systems are generally more productive, mostly due to their large surface area to volume ratios, thermal instability and rapid exchange of nutrients between sediments and water (Marshall and Maes, 1994). This trend appeared to apply even within these ‘small’ (<1 000 ha) reservoirs and since this variable is easily measured, it also appears to be a good predictor of moggel biomass and production.

The number of predator species in the reservoir was also correlated with biomass and production. While the negative relationship between biomass and predators was expected, surplus production theory suggests that production would be higher when predation increases. This trend, while not apparent from the biomass and production estimates, was visible in the P/B ratios, as reservoirs with the most predatory species (Katriver, Laing and Dimbaza) had the highest P/B ratios. The use of this variable as a predictor of biomass and production is not, however, considered appropriate, since the abundance of predators was not considered.

The results from Chapter 3 suggested that eutrophication in Eastern Cape reservoirs is caused primarily by anthropogenic factors. Cultural eutrophication is known to be an important factor influencing fisheries in large lakes and reservoirs (Colby *et al.*, 1972; Leach *et al.*, 1977; Marshall, 1978; Bninska, 1985; Cochrane, 1985; Wolter *et al.*, 2000). A normal consequence of eutrophication is the disappearance of predators and an overall reduction in the number of species (Colby *et al.*, 1972; Bninska, 1985). The absence of predators and the increase in plant production results in an increase in herbivorous and phytoplanktivorous species (Bninska, 1985). In southern Africa, Marshall (1978) and Cochrane (1985) reported a decrease in the number of species and an increase in fish production in Lake Chivero and Hartebeespoort Reservoir, respectively. Although the process of eutrophication should be more rapid, its effects on fish populations have not been documented in small reservoirs. However, in southern Africa, the species composition in small reservoirs is unlikely to change since these waters are dominated by a few tolerant species (Marshall and Maes, 1994). In this study, increased algal biomass in these reservoirs resulted in an increase in moggel production and since they readily digests diatoms (Chapter 4), the trends found in large systems appear to apply to small reservoirs.

A logical extension to these results is the construction of a model by correlating fish production against environmental variables. A forward or backward step-multiple regression or a canonical analysis would be suitable at this stage. The number of cases in such analysis must be considerably higher than the number of variables. In this study, there are only 5 estimates of production (cases) and many environmental variables (n = 14). Since the validity of the results would be questionable and the risk of a type 1 error would be great, no attempt was made to produce a model from these results.

CONCLUSION

Moggel biomass and production estimates ranged widely in the five reservoirs. The P/B ratios were not a good indicator of fishery potential in unexploited systems, but chlorophyll ‘a’ concentration, conductivity, mean reservoir depth and surface area can be used to predict moggel biomass and production. Of these variables, conductivity, mean depth and surface area are the most suitable. This study suggested that smaller (< 50 ha), shallow (< 3 m) reservoirs with a high conductivity (> 50 $mS.m^{-1}$) would have the highest moggel biomass and production.

CHAPTER 9

General discussion with proposed steps for future fisheries research in small water bodies

The calculation of fish biomass and production was relatively simple and required estimates of the population structure and size, growth patterns and mortality rates. Despite the simplicity of determining variables that predict fish biomass and production in small reservoirs, an understanding of the ecological processes that govern these factors is far more complicated. Traditionally, fisheries biologists have largely confined their area of study exclusively to the reservoir or lake itself (Rigler, 1982). This approach defines the system narrowly and a broader limnological approach that includes conditions in the catchment is preferred. Small reservoirs in particular, are greatly influenced by environmental conditions in the catchment and small changes may have a considerable impact. Therefore, the initial approach of this study was to gain an understanding of the limnology of small reservoirs (Chapter 3). The flowchart (Figure 9.1) represents the complex abiotic, biotic and anthropogenic interactions between the catchment, moggel and the small reservoir environment.

The major factor influencing the biomass of algae was the concentration of nutrients (Chapter 3), which is influenced by catchment geology and anthropogenic activities. Catchment geology influences the physiochemical properties of the reservoir (Fig 9.1) and, in general, reservoirs with catchments that consist of well-weathered rock are nutrient poor and support a low algal biomass. The rock composition also influences nutrient concentration, and generally, igneous rock is nutrient poor compared with calcareous rocks (King and Garling, 1986). Human settlements, particularly those without sanitation, increase the amount of nutrients (often a limiting factor in reservoirs) that flow into the reservoir. Commercial farmers generally use fertiliser and these nutrients can significantly increase algal biomass when they enter the reservoir (Davies and

Day, 1998). In the reservoirs studied (Chapter 3), the major factor increasing the nutrient concentration was human activities. In South Africa, most small reservoirs are situated in rural areas and thus the major source of nutrients is likely to be domestic livestock and human waste.

Another factor influencing algal biomass is turbidity (Figure 9.1). The small reservoirs in this study had a high abiotic turbidity as a result of geological and anthropogenic factors, which included overgrazing and non-contour ploughing (Chapter 3). The geology of the Eastern Cape in particular is susceptible to erosion and poor farming practices have exacerbated this. High turbidity limits light penetration to all algae except those that are situated close to the surface and may cause a reduction in algal biomass.

The altitude of the reservoir may have a significant impact on algal biomass (Figure 9.1). Although the reservoirs in this study differed in altitude by up to 640 m, there were no significant differences in temperature. Temperature is a significant factor influencing the growth rates of algae (Raymont, 1980) as it regulates the rate of chemical reactions and functioning of aquatic ecosystems (Wetzel, 1983). In most South African reservoirs, the highest algal biomass coincided with the highest water temperatures (Walmsley, 1984 and Chapter 3). Reservoirs that are situated at low altitudes and latitudes should be the warmest (Chapter 3) and therefore sustain a higher algal biomass.

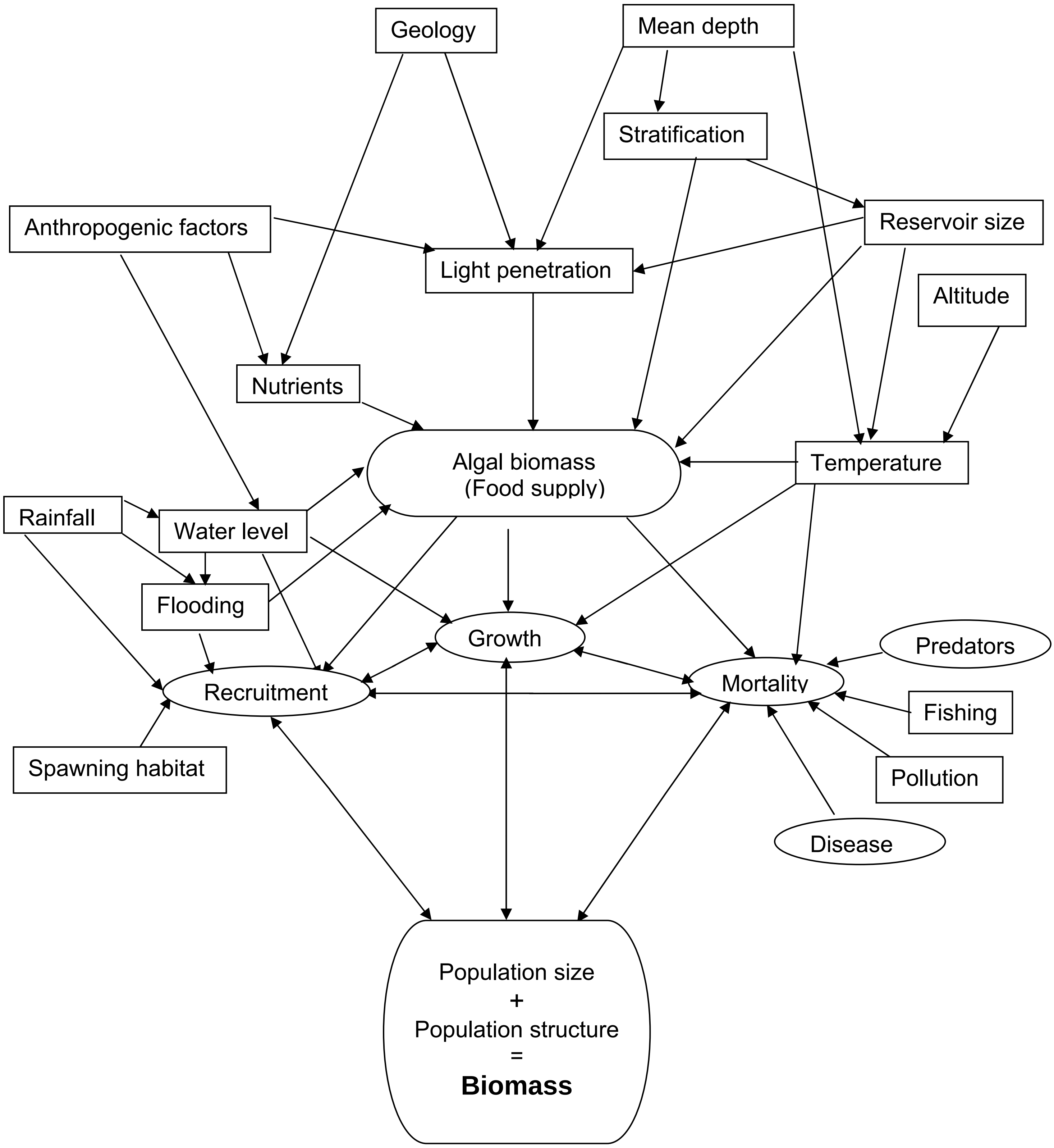

Figure 9.1. Relationships between moggel biomass and environmental factors in small reservoirs.

The temperature profile of a reservoir can also have a considerable impact on algal biomass. The profile is largely dependent on the size and shape of the reservoir. Generally, South African reservoirs, such as those in this study, exhibit a warm monomictic pattern of stratification. This pattern is characterised by a warm surface-mixing layer, the epilimnion, which is separated from cooler water by a thermocline. Algae move horizontally and vertically with the currents of this mixing layer and if the depth of the euphotic zone is shallower than the depth of the epilimnion, then much of the algae will spend time in low light conditions. Growth will therefore decrease and the reservoir would not support a high algal biomass. Since the thermocline is deeper in larger reservoirs (Sterner, 1990) and in those with a large fetch (Gorham and Boyce, 1989), the epilimnion in smaller reservoirs is likely to be shallow and maintain algae in the euphotic zone. Shallow reservoirs have a high light availability due to their larger surface area to volume ratios (Marshall and Maes, 1994) and thus smaller, shallower reservoirs are able to sustain a higher algal biomass.

Flooding has a direct and usually negative impact on algal biomass (Figure 9.1), as large volumes of phytoplankton are lost to the systems when they overflow (Chapter 3). Small reservoirs are more likely to flood and overflow than large reservoirs, resulting in large fluctuations in algal biomass.

Since moggel are riverine fish, it was also essential to understand their ecological function in the ‘foreign’ small reservoir environment. The feeding study (Chapter 4) was the first comprehensive study on this fish and confirmed that it is a detritivorous species. Moggel were able to digest diatoms and their growth was dependent on the abundance of benthic diatoms in the detrital aggregate, which was in turn directly related to algal biomass (Chapter 4 and 6). The diet of moggel is remarkably similar to that of *O. mossambicus* (Bowen, 1979) and in reservoirs where both species are present (Ndlambe and Laing), interspecific competition for resources may occur.

Although many small reservoirs provide suitable environments for algae and promote moggel growth, the survival of the populations is dependent on their ability to reproduce. In order to survive in the ‘foreign’ environment, moggel must have an ancestral strategy, with adaptations that allow it to reproduce in small reservoirs. Moggel have been observed to spawn in inundated grassy floodplains in rivers after heavy rain (Jackson and Coetzee, 1982). Similar conditions are often found in small reservoirs after heavy summer rains. Thus, the rise in water level and inundation of grassy banks in the reservoirs provided a similar ultimate cue to that in rivers and spawning was initiated. The characteristic high fecundity, long reproductive season, and rapid embryogenesis and larval development allowed for successful reproduction in small reservoirs (Chapter 5).
A related species *Labeobarbus kimberlysensis* has a markedly different spawning strategy. These fish spawn in river channels on rocky substrates (Jackson and Coetzee, 1982) and not surprisingly, seldom occur in small reservoirs that do not have major tributaries. Similarly, other labeos, such as *Labeo cylindricus* are dependent on large tributaries in large reservoirs for reproduction (Booth and Weyl, in press). These fish are found in small reservoirs, but only those with large, steady inflowing streams (Hecht, pers. comm.).

Successful moggel recruitment in small reservoirs was dependent on initial flooding conditions, followed by stable water levels (Chapter 5), during which the juveniles had access to abundant food and could shelter in the inundated vegetation. Recruitment also appeared to be related to the number of mature females, the amount of suitable spawning habitat available and the abundance of food (Chapter 5).

There were differences in the life history of the populations in the various reservoirs (Chapter 6). Although differences in age and size at maturity were not as great as in some *Oreochromis* species, the age and size at maturity of moggel was reduced when the growth rate was high and the rate of mortality was low (Chapter 6). Moggel growth appeared to be related to algal biomass (Chapter 4 and 6) and mortality was correlated to the number of predator species and the biomass of algae in the reservoir (Chapter 6).

There are very few estimates of fish biomass and production in African small reservoirs. However, the variation in this study alone was greater than in all previous studies on cyprinids (Table 8.4). The biomass and production estimates in Sinqemeni Reservoir were exceptionally high. The biomass of algae was high in this reservoir and there were no species competing for food resources (Chapter 2). With the exception of a few *Anguilla mossambicus*, there were no predators in the system. Almost 50% of the shoreline was suitable for moggel spawning (Chapter 5). In contrast, Katriver Reservoir had an extremely low algal biomass and moggel in this reservoir had to compete with the introduced flathead (*Mugil cephalus*) and freshwater (*Myxus capensis*) mullet for food resources. Three species of predators occur in Katriver Reservoir and one (*C. gariepinus*) was abundant (pers. obs.). Only 2.5% of the shoreline was suitable for moggel spawning. This would probably have resulted in high concentrations of eggs and juveniles in a confined space, leading to increased mortality through predation and competition for resources (Chapter 5).

A number of variables were identified that could be used to predict biomass and production of moggel in small water bodies (Chapter 8). It was not surprising that algal biomass was identified as a predictor, since this variable appeared to directly influence a variety of aspects of the ecology of this species (Chapter 4 and 6). Water conductivity, mean reservoir depth and surface area were also identified as predictor variables. Though these factors do not necessarily directly influence moggel, they determine algal biomass (Chapter 3 and 8), which in turn influences fish biomass and production. In reservoirs where estimates of algal biomass are not available, the mean depth, surface area and water conductivity may provide an indication of algal biomass and thereby fish biomass and production. It is interesting that all the predictor variables mentioned above have been used in empirical models for large systems. This implies that the ecological function of small water bodies is quite similar to those of large systems. It also suggests that these predictors may apply to other fish species and this study may have provided more than just an understanding of the ecological function of moggel in small reservoirs.

A logical extension to this study would be the development of a model to predict moggel biomass and production in small reservoirs. This study has identified food availability (algal biomass) as the major factor influencing moggel biomass and production in small reservoirs. The next step in the development of an empirical model would be the selection of suitable small reservoirs throughout the distribution of this species. These reservoirs should range from having an extremely low to an extremely high algal biomass. The reservoirs in this study were representative of these conditions but the low number of systems sampled and the consequent lack of statistical power for the development of a model suggests that more reservoirs should be selected. Future research in this field should therefore focus on obtaining biomass and production estimates for moggel in other small reservoirs. However, since the reservoirs in this study were fairly uniform in temperature (Chapter 2) and most had constant water levels, future reservoirs should be selected with these factors in mind.

It should be stressed that future research would only be comparable to this work if standardised field, laboratory and mathematical methods are employed. This is an important consideration as the lack of consistency in the methods used to obtain production estimates for current empirical models is a major weakness. However, the following changes to the current methods are recommended. To reduce sampling mortality, the number of fish in the population could be estimated using mark-recapture studies (Koch and Schoonbee, 1980; Mitchell and Jordaan, 1985; Kaunda, 1995; Schoonbee *et al.,* 1995) rather than depletion methods. While seine nets are the generally accepted gear in such studies, they cannot be used in many habitats. Fyke nets, however, can be used in a wide variety of habitats and are suitable for mark-recapture studies (Chapter 7). In addition, the trap-like nature of this gear indicates that it may have application in selectivity studies and be useful when estimating the population structure (Chapter 7).

To conclude, small reservoirs allow rapid appraisal of their fish resources and a three-year, intensive sampling programme would suffice to develop a model for any species. A protocol to achieve this is outlined below.

The first six months should be used to become familiar with all literature on the ecology of the species and identify all small reservoirs within its distribution. Twenty-four reservoirs with a range of depth and sizes should be selected. This number would ensure better statistical power and be logistically feasible. Initial site visits to the reservoirs would be used to confirm the presence of the species and measure key environmental indicators, such as chlorophyll ‘a’, conductivity and potential spawning habitat. If the reservoirs are suitable and represent the wide range of conditions found within the distribution of the species, sampling can begin.

Four reservoirs should be sampled each month. This would allow 12 reservoirs to be sampled quarterly (seasonally) for one year and the remaining 12 reservoirs to be sampled quarterly in the next year. The sampling programme should consist of gillnetting, samples from which will be used to estimate life history parameters (see methods in Chapter 6) and population structure (see methods in Chapter 7 and 8), and a mark-recapture study (using seine nets and/or fyke nets) to estimate the population number. In addition, the physiochemical properties and chlorophyll ‘a’ concentration should be measured in each reservoir on a quarterly basis (see methods in Chapter 3).

The last six months should be dedicated to the calculation of biomass and production (see methods in Chapter 8) and to the development of a model using the information from the twenty-four reservoirs. Using this protocol, production models for all the dominant species could be developed in a short space of time and this would greatly assist the development of sustainable fisheries in small reservoirs.

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