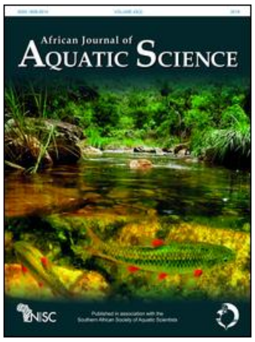

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African Journal of Aquatic Science

ISSN: 1608-5914 (Print) 1727-9364 (Online) Journal homepage: https://www.tandfonline.com/loi/taas20

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To cite this article: Warren M Potts , Anthony J Booth , Thomas Hecht & Timothy G Andrew (2005) Reproductive biology of a riverine cyprinid, *Labeo umbratus* (Teleostei: Cyprinidae), in small South African reservoirs, African Journal of Aquatic Science, 30:2, 147-155, DOI: 10.2989/16085910509503849

To link to this article: https://doi.org/10.2989/16085910509503849

Published online: 07 Jan 2010.

African Journal of Aquatic Science 2005, 30(2): 147–155
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AFRICAN JOURNAL OF AQUATIC SCIENCE
EISSN 1727–9364

Reproductive biology of a riverine cyprinid, *Labeo umbratus* (Teleostei: Cyprinidae), in small South African reservoirs

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Received 29 July 2004, accepted in revised form 16 August 2005

The reproductive and recruitment characteristics of moggel, *Labeo umbratus*, populations were examined in four small South African reservoirs. Reproduction, characterised by an extended spawning season, high fecundity, short incubation time and rapid larval development, appears to be ideally suited to the highly variable environment of small reservoirs. Evidence suggested that *L. umbratus* spawns in the reservoirs. In two reservoirs where samples were conducted monthly, GSI (gonado-somatic index) was positively correlated with both water temperature and day length, whilst the CPUE (catch per unit effort) of juveniles was not related to any environmental variable. The success of moggel spawning appeared to increase when there was early spring and consistent summer rainfall.

Keywords: fecundity, moggel, small water bodies

Introduction

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). These reservoirs often have markedly different fish faunas to the original river systems (Skelton 1993), which may reflect environmental change associated with reservoir construction. 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).

As regards a fluctuating floodplain environment, Welcomme (1985) and Merron *et al*. (1993) suggested that spawning success is dependent on the proximate hydrological regime. Egg survival and juvenile recruitment are 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).

The moggel, *Labeo umbratus*, is a riverine fish that is widely distributed throughout South Africa (Skelton 1993) and which has persisted in reservoirs where it occurs in high densities (Gaigher 1984). It attains a length of 500mm TL, a maximum weight of just under 3kg (Skelton 1993) and a maximum age of 15 years (Potts 2003). The species is commercially important in the Mentz, Kalkfontein (Merron and Tómasson 1984) and Bloemhof reservoirs (P de Villiers, pers. comm., Department of Environmental Affairs and Tourism, Free State. *L. umbratus* is the dominant species in many small reservoirs in the Eastern Cape and has recently been a focus for rural fisheries projects in this region (Andrew *et al.* 2000). In order to develop a management protocol for these rural fisheries projects, an understanding of *L. umbratus* reproduction in the small reservoir environment was necessary.

Reviews of moggel breeding behaviour have focussed predominantly on rivers or large reservoirs and little information is available for small reservoirs. Previous studies suggested that these fish are reliant on flood conditions to spawn and that spawning was preceded either by an upstream and lateral migration (Mulder 1973) or only a lateral migration (Gaigher 1984). Spawning was reported to occur 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). Spawning substrate varies from flooded vegetation (Jackson and Coetzee 1982) to rocks and gravel (Gaigher *et al*. 1975, Mitchell 1984).

The objective of this study was to describe aspects of the reproduction of *L. umbratus* in four reservoirs and to identify environmental predictors of gonadal development and juvenile recruitment. To meet these objectives, the reproductive characteristics and juvenile recruitment of moggel were compared in four small reservoirs over a period of two years.

Methods

Study sites

The Katriver, Laing, Ndlambe and Dimbaza reservoirs are situated in the Eastern Cape interior (Figure 1). Detailed

Published online 07 Jan 2010

environmental and other data of these reservoirs are summarised in Table 1.

Five species of fish, namely moggel (*L. umbratus*), carp (*Cyprinus carpio*), river goby (*Glossogobius callidus*), chubbyhead barb (*Barbus anoplus*) and longfin eel (*Anguilla mossambica*), are present in all reservoirs. Sharptooth catfish (*Clarias gariepinus*) occur in the Katriver and Laing reservoirs, and largemouth bass (*Micropterus salmoides*) is present in the Katriver and Dimbaza reservoirs. Bluegill (*Lepomis macrochirus*) occur in the Dimbaza reservoir. Mozambique tilapia (*Oreochromis mossambicus*) is present in the Ndlambe and Laing reservoirs, and flathead (*Mugil cephalus*) and freshwater mullet (*Myxus capensis*) were introduced into the Katriver reservoir in 1988.

General sampling

Samples of *L. umbratus* were collected monthly in the Katriver and Laing reservoirs between November 1998 and October 2000, quarterly at Ndlambe between June 1999 and April 2001, and quarterly at the Dimbaza reservoir between February 2000 and January 2002.

At each sampling period, the water temperature and dissolved oxygen were measured at a deep offshore station near the reservoir wall, using a hand-held oxygen meter (Oxyguard Handy MKIII). Turbidity and conductivity measurements were made near the major inflow, in the middle reaches and near the wall of each reservoir, using a Hanna 93703 turbidimeter and a Hanna HI 933300 conductivity meter, respectively. Reservoir water level information was obtained from the Department of Water Affairs and Forestry. Water level data were not available for the Ndlambe or Dimbaza reservoirs, with their water levels assumed to be directly related to rainfall. Monthly rainfall data were obtained from the South African Weather Bureau.

Fish were sampled using gill-nets made of 6-ply, multifilament, green nylon netting with manufacturer-quoted stretched mesh sizes of 44, 60, 75, 100 and 144mm. Each 50m x 2m net consisted of five randomly distributed 10m mesh panels, with each net containing all five mesh sizes. Gill-nets were surface set, parallel to the shore, along the 3m depth contour. The nets were deployed between 16h00 and 19h00, and retrieved the following morning between 06h00 and 09h00.

Captured fish were weighed to the nearest gram and their fork lengths (FL) measured to the nearest millimetre. Fish were dissected, sexed and the gonads were weighed and categorised according to the five developmental stages described by Booth and Weyl (2000) (Table 2). Gonad samples were preserved in 5% formalin. The eviscerated mass of each fish was then measured to the nearest gram.

To estimate the CPUE of juvenile fish, we used a 30m long by 2m deep seine net, fitted with a cod-end made of knotless green mesh with a stretched mesh size of 10mm.

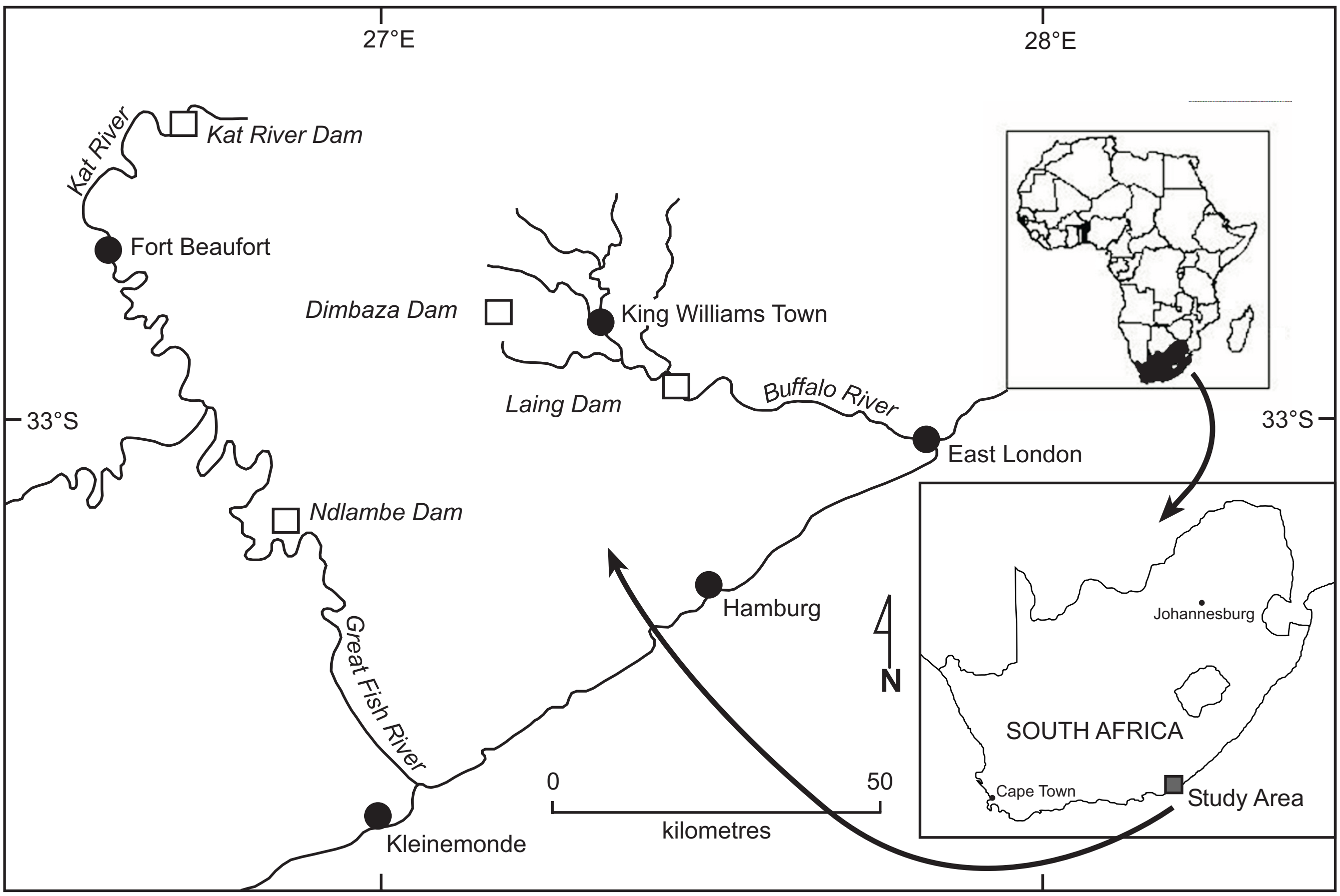

Figure 1: Map showing the location of the four study reservoirs in the Eastern Cape, South Africa

The sampling sites for each survey were chosen randomly from all suitable seining sites, excluding those with drowned trees, submerged vegetation, a rocky substrate or steep slopes, since these prevented effective sampling. The number of sites chosen was dependent on the size of the reservoir. Each juvenile captured was weighed to the nearest 0.1g and measured to the nearest millimetre FL.

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

$$GSI = \frac{\text{Gonad mass (g)}}{\text{Eviscerated body mass (g)}} X100$$

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

We estimated the total population fecundity (TPF) of *L. umbratus* in the four reservoirs as:

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

where POP_2 is the estimated number of fish in the population above the smallest size at maturity, 160mm FL (Potts 2003), SR is the sex ratio by length, LF_L is the length frequency, S_L is the selectivity function by length, $\%M_L$ is the percent maturity by length (Potts 2003) and Fec_L is the fecundity at length L.

To identify environmental correlates of gonadal development, we examined relationships between GSI and a suite of environmental variables, using a Pearson product-moment correlation after the data were log-transformed to stabilise variance. Variables tested included day length, water temperature, rainfall and water level fluctuation. It was noted that different environmental variables and gonadosomatic index followed an annual cycle. Comparisons of rainfall, water temperature, water level, day length and GSI cycles, particularly the peak phase, were conducted using periodic regression (Batchelet 1981), in which the cyclic dependent variable is modelled against the independent temporal variable, such as day of the year or month, using multiple linear regression. Significant periodicity is noted if one of the sine/cosine transformed parameters is statistically significant. After fitting the models, joint 95% confidence regions were constructed to compare the timing and variability of each phase peak. A significant difference in phase peaks was noted when there was a lack of overlap of the joint confidence regions (Draper and Guttman 1995). Because the Katriver and Laing reservoirs were sampled more frequently than the others, only data from these reservoirs were used in this aspect of the analysis.

The CPUE of fish between 3–4cm fork length was calculated. This size class was estimated to be three months of age, based on modal progression analysis of the length frequency histograms of fish from the Laing reservoir (Gayanilo and Pauly 1997). To identify environmental

Table 1: Environmental parameters of the Katriver, Laing, Ndlambe and Dimbaza reservoirs, Eastern Cape Province, South Africa

	Katriver Reservoir	Laing Reservoir	Ndlambe Reservoir	Dimbaza Reservoir
Co-ordinates	32°33'43"S 26°46'08"E	32°57'32"S 27°30'05"E	33°10'14"S 26°54'04"E	32°50'38"S 27°13'37"E
Altitude (m) [1]	750	310	100	350
Catchment size (km²) [1]	258	913	Small localised	Small localised
Utilisation[1]	Irrigation	Potable supply, industry	Human and livestock supply	industry and livestock
Surface area at full supply level (ha) [1]	214	211	16.2	46.2
Mean depth (m)	12.2	10.4	3.0	1.9
Maximum depth (m)	48.0	30.0	8.6	3.9
Catchment geology[2]	Basic/mafic lavas	Sedimentary rock	Basic/mafic lavas	Basic/mafic lavas
Catchment soils[2]	Sandy-loams	Clayey loams	Clayey loams	Sandy-loams
Mean annual rainfall[2]	600–700mm	600–700mm	500–600mm	600–700mm
Human activities in catchment	Livestock subsistence farming	Agriculture, industry, domestic	Livestock subsistence farming	Industry, domestic and livestock
Mean annual evaporation[2]	1 500–1 600mm	1 400–1 500mm	1 500–1 600mm	1 400–1 500mm
Labeo umbratus CPUE (kg/net/night)	1.9 ± 1.4	5.1 ± 4.0	18.4 ± 2.0*	28.9 ± 9.7*
Labeo umbratus CPUE (fish/net/night)	5.5 ± 4.5	11.3 ± 5.3	44.2 ± 3.5	98.9 ± 32.9*
Temperature (°C)	20.48 ± 5.2	20.30 ± 4.2	22.05 ± 5.2	21.09 ± 6.1
Conductivity ($mS.cm^{-1}$)	11.3 ± 4.7	51.3 ± 4.6	107.9 ± 8.4	45.0 ± 7.8
Turbidity (FTUs)	65.89 ± 15.7	74.07 ± 9.2	147.0 ± 13.4	151.2 ± 44.1
pH	7.1–8.1	7.2–9.4	7.0–8.0	7.9–8.8
Chlorophyll *a* ($\mu g.l^{-1}$)	1.4 ± 2.9	8.4 ± 15.4	15.7 ± 16.8	18.6 ± 17.7

1 Noble and Hemens (1978)
2 Midgley *et al.* (1994)
* indicates significant differences between reservoirs, using an ANOVA

Table 2: Macroscopic criteria used to stage gonadal development in *Labeo umbratus* in various Eastern Cape reservoirs (after Booth and Weyl 1999)

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

correlates of the relative abundance of juveniles, a Pearson product-moment correlation and periodic regression was used, as described above.

Results

Water quality parameters in the four reservoirs are summarised in Table 1. Water temperatures increased between July and December in all reservoirs and rainfall began in August 1998, October 1999 and July 2000 (Figures 2 and 3). While there were high water levels in the Katriver and Laing reservoirs by November 1998, the lack of spring rainfall resulted in a lowering of the water level in both reservoirs between May and November 1999.

The GSI data showed that gonadal development started as early as June and May in the Katriver and Laing reservoirs respectively (Figure 2). Fish with ripe and running gonads were observed throughout the summer months (October to March in the Katriver reservoir and from August to January in the Laing reservoir) (Figure 2). The GSI was significantly correlated to day length and water temperature (Table 3). Periodic regression showed that day length peaked at the summer solstice (21 December) (r^2 = 0.99), while water temperature lagged a month behind day length (r^2 = 0.77 for both reservoirs). Rainfall peaked in late January in both reservoirs (Kat: r^2 = 0.11; Laing: r^2 = 0.44). Water level lagged behind rainfall and peaked in the Katriver reservoir in mid March (r^2 = 0.35), and in the Laing reservoir in late April (r^2 = 0.23). The GSI appeared to be most closely correlated to day length, with the Katriver reservoir GSI peaking at the end of November (r^2 = 0.54) and the Laing reservoir GSI in mid December (r^2 = 0.66). GSI and photoperiod phase peaks were not significantly different ($P > 0.05$) (Figure 2). However, the peaks in GSI and water temperature were different ($P < 0.05$) for both populations.

In the Dimbaza and Ndlambe reservoirs, fish with ripe gonads were observed in spring and summer, and the GSI values suggested that development was initiated in late winter (Figure 3).

The fecundity of moggel ranged from 36 500 to 210 000 for fish of between 251 and 475mm FL respectively. Fecundity (*F*) was strongly related to the fork length (*FL*) (Katriver: $F = 11.853FL^{0.0068}$, r^2 = 0.79, n = 13; Laing: $F = 1.1136FL^{0.0127}$, r^2 = 0.89, n = 11; Ndlambe: $F = 8.1212FL^{0.0071}$, r^2 = 0.79, n = 14; Dimbaza: $F = 2.773FL^{0.0102}$, r^2 = 0.70, n = 11).

The number of eggs produced by 1 000 fish of greater than 160mm FL ranged from 17–32 $\times 10^6$ in the Dimbaza and Ndlambe reservoirs, respectively (Table 4). The estimate of total population fecundity of *L. umbratus* in the Dimbaza reservoir was similar in number to that in the Ndlambe reservoir, while fish in the Katriver reservoir produced less than one third of this number of eggs (Table 4). Total fecundity as a ratio of surface area was the highest in the Ndlambe reservoir and lowest in the Katriver and Laing reservoirs.

Mean CPUE of juveniles was considerably higher in 1998 than in 1999 (Table 5). No significant cyclic trend was evident for juvenile density for either reservoir (Katriver: r^2 = 0.06; Laing: r^2 = 0.13) and there was no significant correlation ($P > 0.05$) between juvenile CPUE and any environmental variable (Table 3).

In the Dimbaza reservoir, juvenile fish between 3–4cm were caught in January, February, May and October, while in the Ndlambe reservoir juveniles were captured in September, October, December and January (Figure 3). Mean CPUE in all reservoirs fluctuated between the years sampled (Table 5). Highest densities were noted in 1998 for the Katriver and Laing reservoirs, while densities were the highest in 2000 and 2001 for the Ndlambe and Dimbaza reservoirs, respectively.

Discussion

Labeo umbratus appears to be adapted to offset the characteristic dynamic conditions of small reservoirs with an r-selected reproductive strategy. This strategy includes traits such as high fecundity, short incubation time and early larval development (Gaigher *et al*. 1975, Tómasson *et al*. 1984). In addition, it appears that females maintain ripe ovaries for extended periods during the summer months. This strategy allows them to reproduce whenever conditions are most favourable (probably after rains and during rising water levels), increasing the likelihood of reproductive success.

Since moggel are capable of spawning on gravel beds in rivers (Mulder 1973, Gaigher *et al*. 1975, Mitchell 1984) or

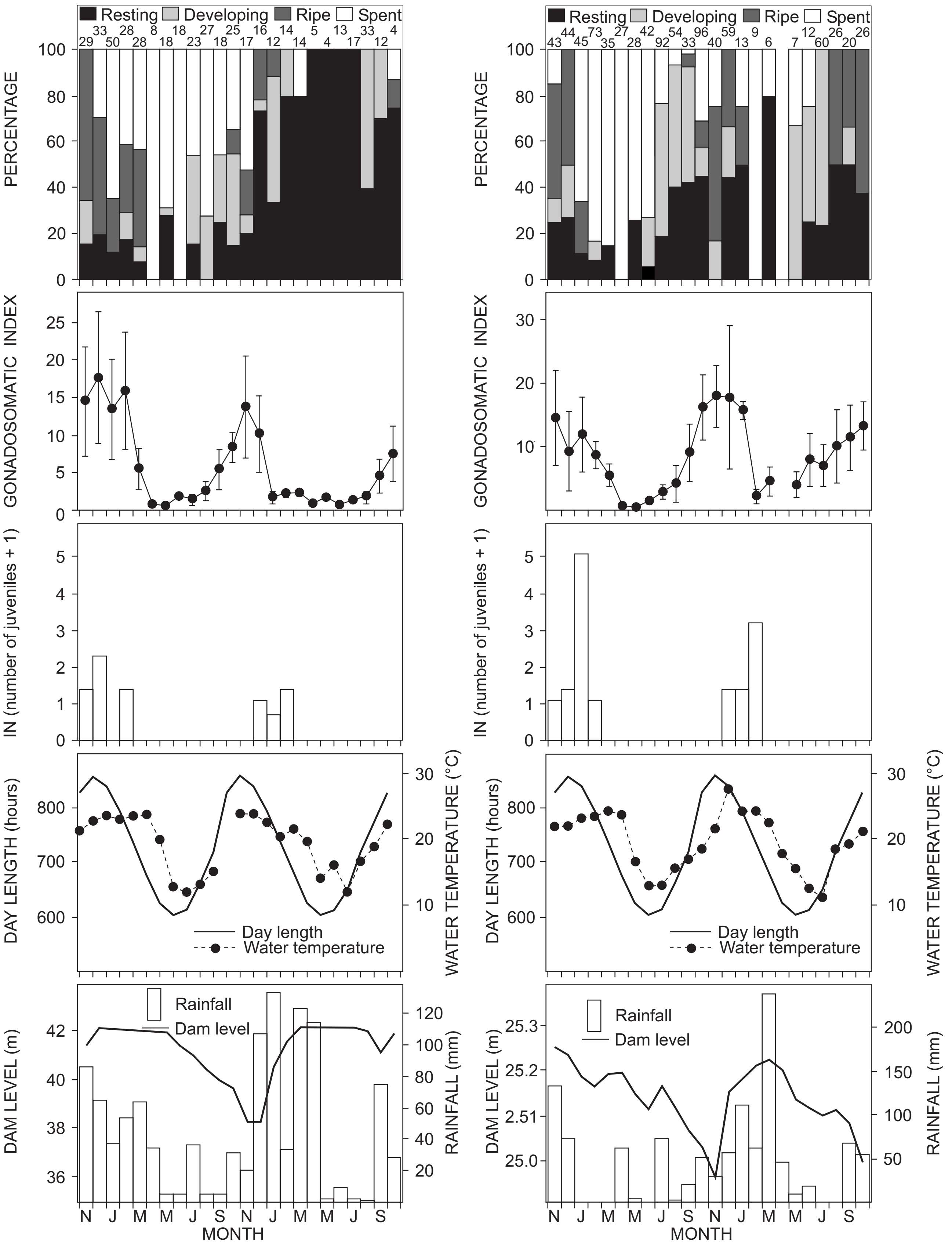

Figure 2: Female monthly maturity stages, gonado-somatic indices (GSI) and CPUE of juvenile *Labeo umbratus*, and monthly water temperature, rainfall (bars) and reservoir water level (line) in the Katriver and Laing reservoirs between August 1998 and October 2000

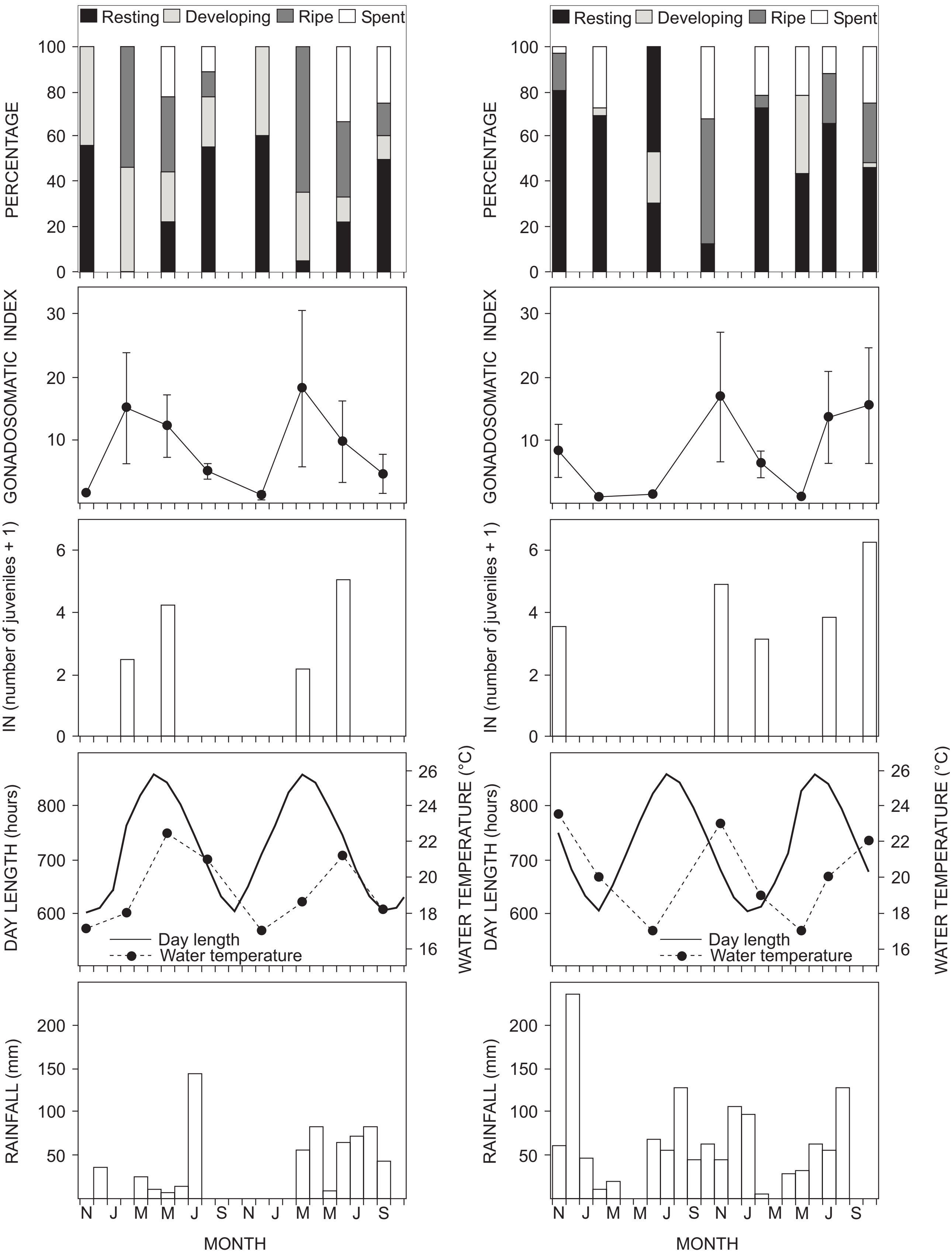

Figure 3: Female monthly maturity stages, gonado-somatic indices (GSI) and CPUE of juvenile *Labeo umbratus*, and monthly air temperature and rainfall (bars) in the Ndlambe and Dimbaza reservoirs between June 1999 and January 2002

Table 3: Summary of Pearson product-moment correlation coefficients describing the relationship between gonado-somatic index, juvenile CPUE of *Labeo umbratus* and environmental variables in the Katriver and Laing reservoirs

	Gonadosomatic index	Ln (juvenile density + 1)	Water temperature
		Katriver reservoir	
Day length	0.61*	–0.05	0.81*
Rainfall	0.08	–0.24	
Water level	–0.34	0.36	
Water temperature	0.34	–0.04	
		Laing reservoir	
Day length	0.77*	–0.06	0.81*
Rainfall	0.20	0.21	
Water level	–0.33	–0.03	
Water temperature	0.56*	0.26	

* indicates significant relationship

Table 4: Estimates of the number of eggs per 1 000 fish, total population fecundity and total fecundity as a ratio of surface area of the *Labeo umbratus* populations in the four reservoirs

	Katriver	Laing	Ndlambe	Dimbaza
Million eggs (.1 000 fish^{-1})	30	25	32	17
Population estimate (Potts 2003)	1 348	4 928	4 594	7 784
Total population fecundity (million)	40.2	121.7	145.9	133.5
Fecundity by surface area (million.ha^{-1})	0.19	0.58	9.00	2.89

Table 5: Mean seine net CPUE of juvenile (3–4cm FL) *Labeo umbratus* in the four reservoirs

Reservoir	Juvenile CPUE (fish.haul^{-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

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 and streams of all of the reservoirs studied is unlikely, as the substratum is dominated by silt. 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 that of large reservoirs, and after heavy rains their conditions become more riverine than lacusterine. Thus, in small water bodies, the flooded terrestrial vegetation provides a typical floodplain environment, which is required by moggel to spawn.

The water-hardened eggs of *L. umbratus* are non-adhesive and slightly negatively buoyant (Bok 1987). This allows them to be transported into the reservoir with receding water levels. An abbreviated embryogenesis (1–3 days), which is normal for labeines (Tømmason *et al*. 1984, Bok 1987), and rapid larval development (Gaigher *et al*. 1975, Bok 1987) allows moggel larvae to move away from areas with unfavourable conditions such as receding water, decreasing oxygen concentrations and rapidly fluctuating temperatures, soon after spawning. Similar larval development is seen in other floodplain spawners such as *L. victorianus* (Fryer and Whitehead 1959) and *L. capensis* (Mulder 1971).

Although small reservoirs may provide suitable habitat for moggel to spawn, successful reproduction of fishes is dependent on the recognition of environmental cues which allow them to spawn in conditions that will ensure maximum reproductive success (Hontela and Stacey 1990). In the 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 factor regulating spawning in almost all moggel populations that have been studied (Jackson and Coetzee 1982, Gaigher 1984, Mitchell 1984, Tómasson *et al*. 1984). Heavy rain causes flooding of terrestrial vegetation, together with a change in water chemistry, and has been identified as the ultimate cue for spawning in 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 anoplus*, another riverine South African cyprinid.

The poor recruitment of moggel in all study reservoirs in 1999 may be explained by the timing of rainfall. Generally, the highest CPUE of 3–4cm fish was recorded between October and January, suggesting that reproduction is most successful after rainfall between July and October. In 1999, the poor rainfall between August and October and falling water levels in the reservoirs corresponded with poor recruitment. Gaigher (1984) and Tómasson *et al*. (1984) showed that when the spawning requirements of moggel in the Wuras reservoir and Lake Le Roux were not satisfied, the fish failed to spawn, and re-absorbed their gonads. This may have occurred in the four reservoirs in 1999, which is supported by the large number of spent/regressed females observed. Unfortunately, histological validation was not conducted, and further investigation into the mode of gonadal regression in moggel is required. In addition, falling water levels in 1999 probably resulted in an absence of suitable spawning sites in all the reservoirs, which may have contributed to lower recruitment.

Although heavy rain only occurred in October 2000 in the Ndlambe catchment, 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 sustained rainfall may have increased juvenile survival in the Ndlambe reservoir by providing food and refuge in the submerged terrestrial vegetation. In 2000, the early and consistent rainfall in the Dimbaza reservoir correlated with high levels of recruitment. This study, therefore, provides some evidence to suggest that early summer rainfall may increase the reproductive success of this species and that substantial post-spawning rainfall may increase juvenile survival.

The number of adult fish and the potential number of eggs that could be produced by the population may have influenced the density of juveniles. The CPUE of adult moggel was considerably higher and juvenile CPUE was approximately 20 times higher in the Dimbaza than in the Katriver reservoir. Both fecundity by surface area and juvenile CPUE were highest in those resevoirs with the highest adult densities. It may be assumed that a high abundance of adults would result in an increase in the fecundity of the population, the number of eggs deposited, and the number of juvenile fish. However, since there was a low number of larger, highly fecund females in the Dimbaza reservoir, the total population fecundity there was just over three times higher than that in the Katriver reservoir. The higher juvenile density in the Dimbaza reservoir is therefore not only a result of higher egg production by the population. Other factors, such as differences in juvenile mortality, number of predators and availability of spawning habitat, may strongly influence juvenile density. Quantifying the influence of these factors on recruitment is important for the management of moggel fisheries in small reservoirs and is an area worthy of further research attention.

Acknowledgements — We thank Greg Williams, Lucy Scott, Cally Fawcett and Garth Webb for assistance in the field, and Terry Longman for much technical support. This study was funded by a grant from the Eastern Cape government.

References

Andrew TG, Rouhani QA and Seti SJ (2000) Can small-scale fisheries contribute to poverty alleviation in traditionally non-fishing communities in South Africa? *African Journal of Aquatic Science* **25:** 49–55.

Bagenal TB (1978) *Methods for Assessment of Fish Production in Freshwaters.* Blackwell Scientific Publications, Oxford.

Balon EK (1975) *Reproductive guilds of fishes: a proposal and definition*. Journal of the Fisheries Research Board of Canada **32:** 821–864.

Batchelet E (1981) *Circular Statistics in Biology.* Academic Press, London.

Bok AH (1987) Induced spawning of moggel, *Labeo umbratus* (Smith) (Pisces: Cyprinidae). *Journal of the Limnological Society of Southern Africa* **13:** 23–24.

Booth AJ and Weyl OLF (2000) Histological validation of gonadal macroscopic staging criteria for *Labeo cylindricus* (Pisces: Cyprinidae). *African Zoology* **32:** 223–231.

Cambray JA (1982) *The Life History Strategy of a Minnow, Barbus anoplus, in a Man-made Lake.* MSc Thesis, Rhodes University, South Africa.

Davies B and Day J (1998) *Vanishing Waters.* University of Cape Town Press, University of Cape Town, South Africa, 186pp.

De Vlaming VL (1972) Environmental control of teleost reproductive cycles: a brief review. *Journal of Fish Biology* **4:** 131–140.

Draper NR and Guttman I (1995) Confidence intervals *versus* regions. *The Statistician* **44**(3): 399–403.

Fryer G and Whitehead PJP (1959) The breeding habits, embryology and larval development of *Labeo victorianus* Boulenger. *Revue de Zoologie et de Botanique Africanes* **59:** 33–49.

Gaigher IG (1984) Reproduction of *Labeo umbratus* (Pisces, Cyprinidae) in Wuras Dam, a shallow, turbid impoundment. *South African Journal of Zoology* **19:** 105–108.

Gaigher IG, Ntloko MM and Visser JG (1975) Reproduction and larval development of *Labeo umbratus* (Pisces: Cyprinidae) in the Tyume River, Eastern Cape. *Journal of the Limnological Society of Southern Africa* **1:** 7–10.

Gayanilo FC and Pauly D (eds) (1997) *FAO-ICLARM Stock Assessment Tools (FiSAT) Reference Manual.* FAO Computerized Information Series (Fisheries). No. 8. FAO, Rome, 262pp.

Hilborn R and Walters CJ (1992) *Quantitative Fisheries Stock Assessment*. Choice, Dynamics and Uncertainty (1st edn). Chapman and Hall, London.

Hontela A and Stacey NE (1990) *Cyprinidae.* In: Munro AD, Scott AP and Lam TT (eds) Reproductive Seasonality in Teleosts: Environmental Influences. CRC Press, USA, pp 53–78.

Jackson PBN and Coetzee PW (1982) Spawning behaviour of *Labeo umbratus* (Smith) (Pisces: Cyprinidae). *South African Journal of Science* **78:** 293–295.

Kolding J (1993) Population dynamics and life history styles of Nile Tilapia, *Oreochromis niloticus,* in Ferguson's Gulf, Lake Turkana, Kenya. *Environmental Biology of Fishes* **37:** 25–46.

Mattson NS (1997) *Fish Production and Ecology in African Small Water Bodies with Emphasis on Tilapia.* PhD Thesis, Stockholm University, Sweden.

Merron GS and Tómasson T (1984) Age and growth of *Labeo umbratus* (Pisces: Cyprinidae) in Lake le Roux on the Orange River, South Africa. *Journal of the Limnological Society of Southern Africa* **10:** 5–10.

Merron GS, Bruton M and La Hausse de Lalouviere P (1993) *Changes in fish communities of the Pongolo floodplain, Zululand (South Africa) before, during and after a severe drought.* Regulated Rivers: Research and Management **8:** 335–344.

Midgley DC, Pitman WV and Middleton BJ (1994) *Surface water resources of South Africa, 1990.* Book of Maps, Vol. 5. Water Research Commission Report 298/5.2/94. WRC, Pretoria, South Africa.

Mitchell SA (1984) Further observation on the breeding behavior of *Labeo umbratus* (Smith) (Pisces: Cyprinidae). *Journal of the Limnological Society of Southern Africa* **10:** 28–30.

Mulder PFS (1971) *'n Ekologiese Studie van die Hengelvisfauna in die Vaalriviersisteem met Spesiale Verwysing na Barbus* *kimberleyensis* Gilchrist and Thompson. PhD Thesis, Rand Afrikaans University, South Africa.

Mulder PFS (1973) Aspects on the ecology of *Labeo capensis* and *Labeo umbratus* in the Vaal River. *Zoologia Africana* **8:** 15–24.

Noble RG and Hemens J (1978) *Inland water ecosystems in South Africa — a review of research needs.* South African National Scientific Programs Report 34, 150pp.

Pitcher TJ and Hart PJB (1982) *Fisheries Ecology* (1st edn). Chapman and Hall, London.

Potts WM (2003) *Towards the Development of Species-Specific Fish Production Models for Small Reservoirs in Southern Africa.* PhD Thesis, Rhodes University, Grahamstown, South Africa.

Skelton P (1993) *A Complete Guide to the Freshwater Fishes of Southern Africa.* Southern Book Publishers, Halfway House.

Tómmason T, Cambray JA and Jackson PBN (1984) Reproductive biology of four large riverine fishes (Cyprinidae) in a man-made lake, Orange River, South Africa. *Hydrobiologia* **112:** 179–195.

Welcomme RL (1985) *River fisheries.* FAO Fisheries Technical Paper 262. FAO, Rome.

Welcomme RL (2001) *Inland Fisheries. Ecology and Management.* Food and Agriculture Organization of the United Nations, Blackwell Science Press, Oxford.