# SPAWNING BEHAVIOUR AND EARLY DEVELOPMENT OF THE CLANWILLIAM YELLOWFISH (BARBUS CAPENSIS; CYPRINIDAE), LINKED TO EXPERIMENTAL DAM RELEASES IN THE OLIFANTS RIVER, SOUTH AFRICA

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### ABSTRACT

This paper describes an investigation of how experimental releases of pulses of high flow from Clanwilliam Dam (Olifants River, South Africa) affect spawning of the Clanwilliam yellowfish, *Barbus capensis*. This species is endemic to the Olifants River system and is listed as rare in the Red Data Book of fishes for South Africa. Spawning sites are described, as is the spawning behaviour of *B. capensis* after specific experimental pulses released during the suspected spawning season of the species. Spawning and the developmental stages of embryos, free embryos, and larval *B. capensis* were studied using direct observations, video recordings, and microscopic examination of live embryos. *B. capensis* was found to be a repeat-spawner over several days as well as a multiple-spawner throughout the 4 month reproductive season. At present, spawning of *B. capensis* occurs down-stream of the dam sporadically (and possibly with limited recruitment), concurrent with releases of water for irrigation purposes. Experimental pulses appeared to trigger an increase in spawning activity, as an abundance of larvae was found down-stream 2 months later. It is suggested that a water-release strategy from Clanwilliam Dam could be designed to increase the number of *B. capensis* in the Olifants River. @ 1997 John Wiley & Sons, Ltd.

KEY WORDS: African freshwater fish; building block methodology; conservation; controlled releases; endangered fish; multiple spawning; potamodromous; regulated river; reproduction; reproductive style

## INTRODUCTION

South Africa's human population is projected to increase from about 40 to 80 million over the next 60 years (Department of Water Affairs and Forestry, 1986). It is a semiarid country. Rainfall and runoff varies markedly between seasons, even in the higher rainfall areas. The mean annual rainfall is less than 500 mm and less than one third of its surface area is drained by perennial rivers. Because rivers remain the most important source of potable water, a programme of dam construction has taken place over the last few decades.

Until recently, as with most countries, consideration of water releases for maintenance of the down-stream riverine ecosystem formed no part of the decision process prior to dam construction. Nationwide, the country's rivers have deteriorated in condition at least partly due to the manipulation of their flow regimes. New policies on environmental protection create the opportunity to contain, and possibly to some extent reverse, this degradation. For each major new water-resource development involving a river, the national Department of Water Affairs and Forestry (DWAF) now requires an assessment of the flow requirements for maintenance of the targeted river down-stream of the development (Department of Water Affairs and Forestry, 1992a). The water requirements for the river and for all potential offstream users are then considered, and allocation decisions made.

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The building block methodology (BBM) is being developed in South Africa for making rapid instream flow assessments (King and Louw, in press). In the BBM, a description of a modified flow regime is produced for a targeted river by adding together (on paper) 'blocks' of flow deemed to have specific geomorphological or ecological significance. The 'blocks' are the dry season and wet season low flows, the dry season pulses of slightly higher flow and the wet season floods. The minimum amount for each 'block' is added (month by month) that is considered essential for maintenance of the river ecosystem to some predetermined desired state. In total, the blocks describe a recommended modified flow regime for the river.

Because of the poor knowledge of the specific flow requirements of South African riverine species, research has been initiated in parallel with application of the BBM to clarify the characteristics of the various flows that appear to be of ecological or geomorphological importance. This paper deals with initial research on the importance of one of these flow components—the dry-season pulses. The objective of the research was to release dry season pulses of high flow from a dam on a local river in order to study the effect on the spawning behaviour of a native fish species. The dam chosen for the research was Clanwilliam Dam on the Olifants River. Instream flow studies were already underway on this river. The fish species chosen was *Barbus capensis* which is endemic to the Olifants River system and is listed in the Red Data Book (Fish) (Skelton, 1987). Past records of releases from Clanwilliam Dam were analysed, experimental releases were devised and carried out and the results recorded in terms of water quality, fish behaviour, egg production and development.

# DESCRIPTION OF STUDY SITE

The Olifants River in the Western Cape of South Africa (Figure 1) has the highest conservation priority of any river in the region, ranking in the top few nationally. It rises in a high rainfall (1400 mm year<sup>-1</sup>) mountain range, and its mainstem is a powerful, perennial river 260 km long (King and Tharme, 1993). The river flows through a winter rainfall region, with about 85% of mean annual rainfall occurring between the months of May and September (King and Tharme, 1993). Before agricultural development of the catchment and construction of two large instream dams, showers in spring and early summer (October–December) brought small pulses of flow down-stream, with these gradually decreasing in number and size to be followed by about four dry months of low flows.

The two impoundments are in the middle reaches of the river. Bulshoek Weir, 23 km down-stream of the town of Clanwilliam, was built in 1919, and for ecological purposes effectively acts as an instream dam wall. Up-stream at Clanwilliam, the Clanwilliam Dam wall was constructed in 1932 and raised in 1966. The reservoir has a storage capacity of  $127 \times 10^6$  m<sup>3</sup> (Pitman *et al.*, 1981). Water is stored there for down-stream release, on demand, to Bulshoek Weir from where much is diverted into irrigation canals. The two dams have fragmented *B. capensis* into three semiisolated populations along the main channel only the most up-stream of which still occupies a cobble-bed river. The two down-stream populations exist in the sandy bed middle and lower reaches. Fish mass below these dam walls (Harrison, 1939; Scott, 1982), but cannot move further up-stream. Down-stream movement may still occur through fish being swept over the dam walls.

The study site, which is 1.5 km down-stream of the Clanwilliam Dam, was chosen because in a fish survey between 20 and 31 January 1992 (King and Tharme, 1993), eggs of *B. capensis* were found there by one of us (JAC) (Figure 1). The site is 125 km from the source of the river and is the only known area of cobble bed in the stretch of river between the two dams. A road bridge arching over it allows excellent viewing of fish behaviour on the cobble bed.

The river at this spawning site is about 30 m wide, with multiple channels separated by dense belts of the palmiet *Prionium serratum* (Juncaceae). The eggs were found in a shallow, minor channel characterised by a lack of instream or overhead vegetal cover and a substratum of 50% small boulder, 30% small cobble and 20% large gravel (Figure 1: Spawn Bed B). The eggs and free embryos were lodged under a large boulder between the cobbles and gravel, in a current speed of 20 cm s<sup>-1</sup> and water depth of 22 cm.



Figure 1. Olifants River system (western Cape) showing the *Barbus capensis* Spawn Beds A and B, the road bridge and the larval fish site below the Clanwilliam Dam wall

Up-stream toward the dam wall, the anastomosing channels are more pool-like with finer substrata, and down-stream the river becomes a wide, shallow, single channel with a sandy bed and little vegetation.

Measurements taken at the spawning site at intervals throughout 1992 (King and Tharme, 1993) revealed that the water was of high quality, clear, and with low conductivity  $(8.5-2.4 \text{ mS m}^{-1})$ . Depending on the time of the year water temperatures were somewhat lower or higher than neighbouring up-stream and down-stream reaches, due to hypolimnetic dam releases. Neighbouring irrigated fruit farms, plus the nearby town of Clanwilliam, must have an impact on the site.

At a second site (about 2 km down-stream (Figure 1), larval *B. capensis* were present in January 1992. Flow at the 'larval' site was placid, with extensive shallow edge areas over sand. It appears likely that, in common with some other *Barbus* species, larval *B. capensis* disperse from the spawning site in the late free-embryonic stage, through a swim-up period during which they are swept down-stream.

## DESCRIPTION OF STUDY SPECIES

All eight endemic Olifants River fish species (Table I) are listed in the South Africa's Red Data Book (Fish) (Skelton, 1987). Several are close to extinction because of habitat destruction, fragmentation of the river continuum by dams, extensive water abstraction, and predation by the alien smallmouth bass, *Micropterus dolomieui* (Gaigher, 1973; Gaigher *et al.*, 1980; Scott, 1982; Skelton, 1987; King and Tharme, 1993).

*B. capensis* is the largest of these endemic fish species, attaining a length of almost 1 m and taking 5-7 years to mature (Scott, 1982). The following is what was known of its natural spawning habitats or the triggers required for spawning.

Before the two dams were built, *B. capensis* congregated below natural rapids and then undertook mass up-stream migrations between September and December (Harrison, 1950; Jubb, 1974). "In spring the yellowfish ascend the rivers in large numbers in search of suitable spawning beds, (which) would appear

Table I. Fish species occurring in the Olifants River system, their distributions and Red Data Book status as of 1987. Endemic species are confined to the Olifants River system, indigenous species are native to southern Africa, and alien species are introduced. Information from Skelton (1987) and de Moor and Bruton (1988)

Species	Distribution	Red Data Book
Family Bagridae Austroglanis banardi	Endemic	Endangered
Austroglanis gilli	Endemic	Rare
Family Cyprinidae Barbus capensis Barbus serra Barbus calidus Barbus erubescens Barbus anoplus Basuda parbus phlogether	Endemic Endemic Endemic Indigenous Endemic	Rare Vulnerable Rare Vulnerable
Labeo seeberi	Endemic	Rare
Family Galaxiidae Galaxias zebratus	Indigenous	
Family Anabantidae Sandelia capensis	Translocated indigenous	
Family Centrarchidae Lepomis macrochirus Micropterus dolomieui Micropterus salmoides	Alien Alien Alien	

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to be clean gravel beds in the shallow portion of the river. The fish mass in countless numbers on the spawning beds and the eggs and milt appear to be shed indiscriminately . . . After spawning, the adults drift back to the deeper waters and the eggs are left to their own devices" (Hey, 1947). Bok (Department of Eastern Cape Nature Conservation, personal communication) observed an accumulation of large adults at the spawning site down-stream of Clanwilliam Dam in January 1990.

*B. capensis* gonad mass increases in August and September, peaks in October to December, and declines in January (Van Rensburg, 1966). Van Rensburg (1966) collected larvae (10–20 mm) a few kilometres up-stream of the Clanwilliam reservoir in November and December, and Barnard (1943) found small juveniles in February.

The adults are most often found in clear, rocky pools, or deeper reaches, often with strong flow (personal observation by JAC). Juveniles mostly inhabit pools, sheltered backwaters and shallow, marginal areas of the mainstream (Skelton, 1987), but can also be active in the main channel, where they maintain position in the gentler summer flows (personal observation by JAC).

Under hatchery conditions *B. capensis* eggs were negatively buoyant and slightly adhesive, until water-hardened after 45 min of immersion (Bok, personal communication). The eggs were not adhesive once water-hardened, unlike those of some *Barbus* species which have strongly adhesive egg envelopes (Cambray, 1983).

From captive breeding experiments, Bok (personal communication) reported water-hardened eggs of *B. capensis* with diameters of 2.60 mm (n = 20; S.D. = 0.09 mm) in December 1987; 2.61 mm (n = 11; S.D. = 0.05 mm) in December 1989; and 2.67 mm (n = 51; S.D. = 0.2 mm) in November 1991. In the 1987 investigation, yolk diameter was recorded as 1.98 mm (n = 20; S.D. = 0.04 mm). Van Rensburg (1966) reported that in gonad stage four (active to ripe), the largest group of eggs had attained a diameter of 2.0 mm in the ovary, so the eggs appear to enlarge approximately 0.6 mm in diameter with water-hardening to 2.6 mm. Eggs kept at 22–23°C took 63 h before free embryos hatched which were 7.38 mm TL (total length) (n = 5; S.D. = 0.23) and 7.2 mm NL (notochord length) (S.D. = 0.27) (Cambray and Bok, personal communication). These free embryos were photophobic. After 10–12 days the larval fish began to feed. Thus, at water temperatures of 22–23°C the embryos were predicted to spend at least 9–10 days on the spawning beds before the 'swim-up' occurred. They would then be carried down-stream by currents to shallow, quieter waters where they would commence feeding and develop to larval fish (Figure 1).

## METHODS

#### Water release strategy

Experimental releases of pulses from Clanwilliam Dam were planned for 1993 and 1994 to induce an up-stream migration and spawning. The strategy was devised bearing in mind the observations of earlier years. The *B. capensis* eggs located down-stream of the dam in January 1992 indicated that spawning had occurred when water releases from the dam had been held relatively steady over the preceding weeks, with all fluctuations being less than 24 h long (DWAF personal communication). The collected eggs were viable. The developmental stage (embryo with tail free and moving) indicated that they had probably been spawned several days prior to collection. Eggs were not abundant, possibly due to the lack of flow pulses.

DWAF staff agreed to vary, within certain limits, the timing and magnitudes of water releases from the dam. Over the experimental periods, the same amount of water as usual had to be delivered to Bulshoek Weir for irrigators and so some water was held back prior to the release of the experimental high flows. The pattern of releases changed from one of constant flow to a combination of a low flow followed by a pulse of high flow.

Different release strategies were followed in the two spring seasons (Table II). To investigate if dusk or dawn spawning could be induced in December 1993, three pulses of higher flow were released at different times and for different durations. In the 6 weeks preceding the exercise, releases were held within the range  $7.6-8.1 \text{ m}^3 \text{ s}^{-1}$ , to supply irrigators and then reduced to  $4.6 \text{ m}^3 \text{ s}^{-1}$  on 10 December in order to

Date	Time	Discharge (m <sup>3</sup> s <sup>-1</sup> )	Flow description
1993			
Mid November to 9 December		7.6-8.1	Normal irrigation release
10 December		4.6	Storage
14 December	11:20 h	8.0	Release P1/93
	15:20 h	4.6	Low flow for study
15 December	11:00 h	12.0	Release P2/193
	15:00 h	4.6	Low flow for study
16 December	16:00 h	12.0	Release P3/93
17 December	04:30 h	4.6	Low flow for study
18 December		8.0	Normal irrigation release
1994			
Mid November to 25 November		7.5 - 8.0	Normal irrigation release
25–29 November		5.0	Storage
29 November	17:00 h	2.0 - 3.0	Low flow for egg search
1 December	17:45 h	17.0	Release P1/94
2 December	06:00 h	3.0	Low flow for study
	18:00 h	9.0	Release P2/94
3 December	06:00 h	3.0	Low flow for study
4 December		7.5 - 8.0	Normal irrigation release

Table II. Release pattern of experimental high flow pulses from Clanwilliam Dam. P, experimental pulse

store water for the experimental pulses. After initial inspection of the spawning site for eggs on 13 December, three experimental pulses were released over the next 4 days. The first two were designed to attempt trigger dusk spawnings and the third to trigger a dawn spawning. The first two releases were of 4 h duration, and magnitude 8.0 and 12.0 m<sup>3</sup> s<sup>-1</sup> respectively, both decreasing to the background level of 4.6 m<sup>3</sup> s<sup>-1</sup> about 3 h before dusk. The third release, also of magnitude 12 m<sup>3</sup> s<sup>-1</sup>, but of 12 h duration finished at dawn, when discharge was reduced to 4.6 m<sup>3</sup> s<sup>-1</sup>. The usual release of 8.0 m<sup>3</sup> s<sup>-1</sup> was resumed on 18 December. The magnitude of the artificial pulses was restricted by the size of the dam release structures. These releases were deemed acceptable, however, as they were within the magnitude expected of high flow pulses at that dry time of the year.

The passage of released water through the down-stream river was recorded in two ways. At the spawning site (Figure 1), changes in water surface elevations were recorded at irregular intervals from a temporary gauge plate erected in the small channel where eggs were first found in 1992 (Spawn Bed B). There was no attempt to measure discharge at this site because of the complex, anastomosing nature of the river. Down-stream, at the larval site, depth and velocity distributions were recorded on five occasions along a bank-to-bank cross-section, and discharges calculated. Spot readings of velocity and depth were also taken where larval *B. capensis* were found.

Based on the results of this experiment, an experimental pulse of 17 m<sup>3</sup> s<sup>-1</sup> was released for 12 h overnight on 1–2 December 1994. Prior to this, the release had been at 5.0 m<sup>3</sup> s<sup>-1</sup> until 29 November when it had been reduced to 2.0 m<sup>3</sup> s<sup>-1</sup> in order to store water for the pulses (Table II). A further smaller pulse of 9.0 m<sup>3</sup> s<sup>-1</sup> was released overnight on 2–3 December to meet demands at Bulshoek Weir. No hydraulic measurements of the passage of water through the study site were taken during the 1994 visit. Instead, activities focused on recording and filming fish behaviour from the vantage point of the bridge.

## Water chemistry

During the 1993 experimental releases, conductivity and water temperature of the Olifants River were recorded at intervals at Spawn Bed B. Water samples were also collected at intervals throughout that study for analysis of Kjeldahl nitrogen, pH, ammonium ( $NH_4$ -N), nitrate and nitrite ( $NO_3 + NO_2$ -N), fluoride (F), total alkalinity, total dissolved solids (TDS), dissolved organic carbon (DOC), sodium (Na),

magnesium (Mg), silicon (Si), chloride (Cl), potassium (K), and calcium (Ca). Water samples were stored in bottles specially prepared and provided by the Institute for Water Quality Studies (DWAF), preserved in the field with mercuric chloride and analysed by the Institute (Department of Water Affairs and Forestry, 1992b). During the 1994 experimental release, no water samples were collected, but spot readings of water temperature, pH, and conductivity were taken at Spawn Bed B and at the larval site.

### Biological data collection

The objective during the December 1993 sampling period was to assess the importance of the site as a spawning ground for *B. capensis* and establish what environmental variable(s) might trigger spawning. Water samples were collected and hydraulic measurements taken as described above. Searches for and collections of eggs, free embryos, larval, and juvenile *B. capensis* were made before, during, and after each artificial pulse. Eggs and free embryos were examined immediately after collection and photographed microscopically to record their developmental stage. From these records it was possible to establish the approximate time of spawning of the eggs. Limited qualitative sampling of larval fish was carried out at the down-stream larval site, as intense quantitative sampling is not ethical for a Red Data Book species. Small samples of eggs, free embryos, and larval fish were preserved in 4% buffered formalin for later examination and measurement using an ocular micrometer in a dissecting microscope. These specimens are now housed at the Albany Museum.

In the 1994 study, fish behaviour on and around the spawning site was recorded from the bridge using a video camera, notes, and tape recorder. No measurements of water depths and velocities were taken at the spawning site in order to reduce any possible disturbance to the fish.

In summary, the 1993 study concentrated primarily on: an assessment of the records of dam releases preceding the experimental pulses; gaining an understanding of the general pattern of attenuation of the experimental pulses as they flowed through the study site; the water quality conditions linked to the experimental pulses; and an investigation of whether or not a pattern of *B. capensis* embryonic development could be linked to any of these. The 1994 study concentrated on activities that did not require moving in the water or on the banks; activities were mainly limited to recording of fish behaviour from the bridge following two artificial pulses.

### Age determination of B. capensis embryos and larvae

*B. capensis* developmental times in the wild are based on an unpublished study by Cambray and Bok in which development of hatchery bred *B. capensis* was followed under aquarium conditions at controlled temperatures of  $22-23^{\circ}$ C. As is well documented, water temperature, oxygen conditions, and biochemical resources supplied by the female parent can influence the rate of fish development (Mills, 1991). The laboratory rates are therefore used with caution in the interpretation of developmental rates of embryonic *B. capensis* on the spawning beds but are considered useful for determining spawning frequency and estimating their timing.

## Definitions of terms used

Due to the confusion in the literature the following terms have been defined for use in this paper. *Multiple spawning:* capacity to ripen successive batches of eggs within a season (Bagenal, 1978). *Repeat spawning* within days: spawning may be spread over several days but draws on a single batch of matured eggs (Horvath, 1986). This is distinct from multiple spawning as there must be a longer time period between two ovulations for multiple spawning. A repeat-spawner can also be a multiple-spawner. Reproductive style terminology follows that of Balon (1975).

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### RESULTS

## Local hydraulics

The local hydraulics of the river reach down-stream of the dam are largely dictated by the anastomosing nature of the channel and the dense growth of *P. serratum* on the mid-channel islands. In 1993, there was about a 2 h time lag before volume changes in the release pattern at the dam were recorded as changes in water surface elevations at Spawn Bed B (Figure 2). At the larval fish site, further down-stream, the discharge measurements showed that the increased volume of water reached there with little additional time lag. This was probably because the character of the river changed down-stream of the spawn site, from vegetated multiple channels to a single channel with no instream vegetation. Attenuation of the flood peaks, as shown by gauge heights, could not be well assessed from the measurements, but the hydrograph of the third release fell quite sharply from its peak and had roughly the same duration as its corresponding release (Figure 2). This suggests that attenuation was not great. Outside of the peaks the base flow gradually increased; however, indicating that some storage and slow release of water was occurring from the vegetated up-stream areas.

## Water quality

Sixty-two sets of water samples were collected during the 1993 study, together with accompanying readings of on-site instruments and the gauge plate (Table III). Samples were taken at half-hour intervals during the releases, and less frequently at other times due to the demands of other tasks. Plots of water level versus any single water chemistry variable (Figure 2) revealed no obvious trends of variation linked to the three artificial pulses. Linear regression analysis was used to further assess if the experimental pulses were affecting water chemistry. Because of the possibility of the concentration of chemical variables differing during a pulse (Britton, 1990), the data were split into a group collected on the rising limb of the releases (n = 40), and a group collected on the falling limb of the releases (n = 17). There were no significant relationships between water level and individual water chemistry variables in either of the groups, with the exception of water temperature (y = 22.1 + 1.76x;  $r^2 = 0.129$ ; p = 0.0231) on the rising limb of the release from the dam.

The few spot measurements of water quality taken at Spawn Bed B during the 1994 releases (Table IV) suggested that water temperature and conductivity dropped slightly during the two experimental pulses and then recovered. The temperature changes may have been due to overnight changes in air temperature. Water temperature and conductivity were slightly lower than during the 1993 experiment, but were in the same general range. pH was also lower than in 1993, but this may have been a reflection of different analytical methods in the 2 years, as pH values are known to be affected by storage.

### General overview of biological results

Spawning appears to have occurred over an extended 4 month period from October to January. Four ripe-running males (34:39, 58:68, 44:54, 59:69 cm standard length (SL):total length (TL)) and one spent female (47:54 cm SL:TL) were recorded down-stream of the spawning site in December 1993. All fish were measured live and released. In 1993, two possible spawning beds were identified by the presence of eggs. One (Figure 1: Bed A) was in the fast-flowing water of the main channel and the other one (B) was in the quieter side channel where the eggs were found in 1992. Both had cobble beds, with no overhead vegetal cover and ample marginal vegetation nearby. Bed A was larger than B and had noticeably faster and deeper flow.

No spawning was observed at these beds in 1993 possibly due to the activities of the survey team beside and in the river, and also because a limited time was available for observations from the bridge. Much of the evidence of what happened that year was pieced together from analysis of the collected eggs, free embryos and larval *B. capensis*. The general evidence pointed to sporadic spawning, some of which had happened before, and some during, the experimental period.

	Before P1/93	During P1/93	Between P1/93 and P2/93	During P2/93	Between P2/93 and P3/93	During P3/93	After P3/93
Water level (cm)	13.5	14.0-26.0	26.5-19.0	24.0-32.2	32.8-15.0	15.0-32.5	32.0-13.0
Conductivity (mS $m^{-1}$ )	11.0 - 11.2	9.7 - 11.4	9.9-11.3	10.2 - 11.6	10.2 - 11.4	9.8-11.3	9.7 - 11.0
Temperature (°C)	21.8 - 22.9	22.0 - 22.3	22.3 - 22.5	22.7 - 23.0	22.1-22.9	22.5 - 23.1	22.1 - 22.2
Total alkalinity (mg $l^{-1}$ )	7 - 9	7 - 9	7 - 10	7 - 11	7 - 10	7-12	7-12
Calcium (mg $l^{-1}$ )	3	2 - 4	2-4	2-3	2-3	2-4	3-4
Fluoride (mg $1^{-1}$ )	0.2	0.1 - 0.5	0.2 - 0.6	0.1 - 0.3	0.1 - 0.5	0.2 - 0.6	0.2 - 0.5
Nitrogen (mg $1^{-1}$ )	0.26 - 0.43	0.24 - 0.46	0.21 - 0.30	0.22 - 0.40	0.25 - 0.37	0.23 - 0.34	0.21 - 0.29
Potassium (mg $1^{-1}$ )	0.4 - 1.4	0.4 - 1.9	0.4 - 0.5	0.4 - 1.2	0.4 - 0.7	0.4 - 0.8	0.3 - 2.0
Magnesium (mg $1^{-1}$ )	2-3	2 - 4	3-4	2-3	3-4	3-4	3-4
Sodium (mg $1^{-1}$ )	11-12	11-16	11-12	11-13	11-13	11-12	11-12
Ammonium (mg $1^{-1}$ )	0.04 - 0.07	0.04 - 0.07	0.04 - 0.10	0.04 - 0.05	0.04 - 0.06	0.04 - 0.06	0.04 - 0.07
Nitrate and Nitrite $(mg 1^{-1})$	0.14-0.18	0.14 - 0.20	0.15-0.27	0.16-0.19	0.14-0.21	0.15-0.21	0.14-0.19
Phosphate (mg $1^{-1}$ )	0.009 - 0.120	0.010 - 0.015	0.009 - 0.017	0.008 - 0.026	0.006 - 0.017	0.011 - 0.019	0.007 - 0.023
Silicon (mg $1^{-1}$ )	1.9 - 2.3	1.8 - 2.2	1.9 - 2.3	2.1 - 2.3	2.1 - 2.4	2.0 - 2.5	1.9 - 2.5
Sulphate(mg $1^{-1}$ )	12-15	6-12	6-10	6-18	6-14	6-13	6-12
Total dissolved solids $(mg l^{-1})$	62–64	53-69	56-63	58-61	53-69	55-68	57-64
Total phosphorus $(mg 1^{-1})$	0.014-0.016	0.015-0.020	0.014-0.020	0.012-0.029	0.012-0.034	0.013-0.033	0.016-0.024
$DOC (mg^{-1})$	2.4 - 2.9	2.0 - 4.3	2.4 - 3.4	1.8 - 3.2	$2.0-5\ 3$	2.2 - 4.0	2.1 - 2.9
Chloride (mg $1^{-1}$ )	20 - 21	20 - 25	20 - 22	19-24	20-23	20-24	20 - 22
pН	7.3-7.4	6.4-7.4	6.9-7.2	6.8 - 7.2	6.4-7.2	6.8-7.3	6.8 - 7.5

Table III. The ranges in values of physical and chemical water quality variables measured at Spawn Bed B before, during, and after experimental pulses P1, P2 and P3 in December 1993

During the visit in December 1994 viewing and filming fish activity from the bridge was made difficult by the turbulent flow and submerged vegetation. However, 100 or more fish were observed moving up-stream over the 2 days after the first experimental pulse. Frequent spawning behaviour was observed and filmed. Two months later, "far more larvae and young juveniles than usual" (D. Impson, Western Cape Nature Conservation, personal communication) were found at the down-stream larval fish site. The evidence suggested a far more successful season of recruitment. Records of these observations of



Figure 2. (a) Movement of water through the study area below the dam in December 1993 is illustrated by the dam release pattern (-) and measured discharge levels at the larval site (▲); discharge (m<sup>3</sup> s<sup>-1</sup>) readings at the larval site were taken as follows: (1) 14 December 13:00 h (5.1); (2) 14 December 17:00 (8.7); (3) 15 December 11:15 h (4.8); (4) 15 December 13:45 h (9.1); and (5) 15 December 15:45 (10.5). (b) Water level at Spawn Bed B. (c) Conductivity at Spawn Bed B

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Date	Time	Comment	pН	Temperature (°C)	Conductivity (mS $m^{-1}$ )
Spawn Bed B—	1994				
1 December	17:40 h	Just before P1/94 P1/94 released overnight		22.3	
2 December	05:00 h	Just before end of P1/94		18.3	8.4
	12:15 h		5.94	20.7	9.3
	17:15 h		5.83	20.4	8.5
	18:10 h		6.73	20.2	8.4
	18:45 h		6.71	20.1	8.4
		P2/94 released overnight			
3 December	05:00 h	Just before end of P2/94	5.55	19.1	7.4
	09:00 h	,	5.92		7.7
	11:10 h		5.99	19.7	7.9
Larval site— 1994					
1 December	18:00 h			27.7	9.0

Table IV. Spot readings of water conditions at Spawn Bed B and at the larval site, linked to the 1994 experimental pulses P1/94 and P2/94

behaviour, together with measurements of the collected eggs, free embryos, and larvae from both trips are summarised below.

# Fish movements observed (December 1994)

After the two experimental pulses (Table II) observations were carried out from the bridge from dawn onwards. Flow reduction at the spawning site, combined with improving light conditions, facilitated observations through the water from about 08:00 h onwards, although on both days movement of *B. capensis* could be detected earlier. Throughout the day, and almost without exception, fish movement was up-stream singly, or in small groups, using cover from partially-submerged bank-side vegetation. Many larger individuals moved out of cover to hold position at Spawn Bed A, and a few at Spawn Bed B, in the fast-flowing current.

Once in position on the spawn beds, neither full sunlight onto the bed nor movements on the bridge appeared to affect the fish, although movement along the bank drove them from the site. It was difficult to keep track of individual fish, but some held station on the spawn beds for up to 1 h. All eventually moved on up-stream, many at Spawn Bed A having spawned first. All observed individuals that held station at Spawn bed B eventually moved on without spawning. There smaller individuals did not attempt to hold position on the spawn beds but tended to stay hidden under the nearby vegetation.

## Spawning activity (December 1994)

Spawning acts were observed at Bed A as early as 06:28 h and as late as 18:00 h. There were about 20 separate incidents recorded over the 2 days (Table V). Large individuals maintaining position on the bed were joined by smaller fishes darting out of the vegetal cover. Two, sometimes three, fish quickly lined up facing up-stream and close together. Rapid vibrations of the fish for 2-10 s released a cloud of milt across the bed. On no occasion did any of the fish break the surface of the water during spawning. After the spawning act, the smaller fish moved away, usually up-stream or to the edge cover. The larger fish either moved on up-stream, fell away in a tumbling manner down-stream or maintained position on the bed, suggestive of a repeat-spawner. At intervals over the 2 days, eggs were collected from Spawn Bed A for examination. A few were also found and collected at Bed B.

Date	Time	No. fish	Behaviour	Comment
2 December	07:30 h	Several groups of three to eight fish	Moved up-stream, crowding under overhang- ing vegetation	Most were small $30-40$ cm. Occasional large ones $50 +$ cm. Between $50-100$ in total. Some moved up-stream. Some moved out of cover onto gravel bed in current, then back under cover
	08:30 h	3	Large fish holding position on bed	May have been there earlier, light and visibil- ity poor, Bed in shade from bridge, but with no hydraulic or overhead cover
	09:00 h	2	Large fish holding position on bed	Sun shining on bed. Several small fish under marginal vegetation
	09:40 h	4	1st spawn	Two fish spawning, others nearby
	10:00 h	5-6	2nd spawn	
	10:15 h	10-12	3rd spawn	
	10:25 h	3	4th spawn	
	10:40 h	2	5th spawn	
	10:50 h	1	Large fish moving down-stream	
	11:15 h	3	6th spawn	Large fish involved may have been the same ones there since 09:00 h and involved in more than one spawn
	11:45 h	4	7th spawn	
	11:50 h		8th spawn	
	11:55 h 12:00 16:00 h		· · · · ·	Eggs collected from bed
	13.00 - 10.00 II 17.00 18.00 h		Fish still holding position. Five more snowing	Water depth 40, 50 cm
	17.00-18.00 II		seen	Water temperature 20°C, conductivity 8.4 mS
				m <sup>-1</sup>
3 December	05:00-05:30 h		No fish seen	Light poor, water temperature 19.1°C
	06:25 h	1	Small fish moving up-stream	
	06:28 h	?	1st spawn	
	07:30 h	3	Medium-size fish moving up-stream	40-45  cm
	07:35-08:00	2	Large fish holding position on bed	50–60 cm
	08:00 h	5	Moved in, milled around, moved up-stream	Original large fish still there
	08:04 h	6	Large fish moved through site up-stream	
	09:20 h	2	2nd spawn	
	09:50-10:00 h	3	Holding position. Then all three involved in 3rd spawn. (Eggs collected)	Recorded on video. Temperature 19.7°C

Table V. Movement of *Barbus capensis* at Spawn Bed A in December 1994. Data from video recordings and on-site tape recordings. (All fish measurements in table are estimated TL)

## Egg development (1993 and 1994)

Eggs were collected before, during, and after the experimental releases in both 1993 and 1994. Most were collected at Spawn Bed B in 1993 and at Spawn Bed A in 1994. All the wild spawned eggs were clear to pale yellow, non-adhesive, and located in interstitial areas in cobble beds. None were attached to the cobbles. In 1993 the eggs had a mean total diameter of 3.55 mm (S.D. = 0.21, n = 209) with a yolk diameter of 2.93 mm (S.D. = 0.15, n = 75) (Table VI). In 1994, the eggs had a mean total diameter of 3.6 mm (S.D. = 0.16, n = 127) with a yolk diameter of 3.00 mm (S.D. = 0.15, n = 118). In 1992 at Spawn Bed B one of us (JAC) collected eggs which were considerably smaller than these (3.01 ± 0.12 mm, yolk 2.4 ± 0.36 mm, n = 7).

Developmental stages of the embryos indicated that in both 1993 and 1994 *B. capensis* had spawned prior to the releases of the experimental pulses (Table VI). However, some embryos collected were clearly from spawnings during the experimental periods. For instance, on 16 December 1993 at 08:00 h, embryos were collected that were 1-2 days old, and on 17 December 1993 at 08:00 h eight- to 32-celled embryos were collected that were less than 12 h old.

In 1994 the embryonic stages collected prior to the experimental pulse indicated that there had already been at least three spawnings. However, the four-celled embryos collected on 2 December 1994 at 18:00 h were spawned during the experimental period.

#### Larval and juvenile habitat (1993 and 1994)

Larval and juvenile *B. capensis* (but no eggs or free embryos) were found at the larval site (Figure 1) during December 1993 and December 1994. Several hundred larvae and about 50 juveniles were observed on 13 December 1993, prior to the first set of experimental releases. Numbers remained at this general level throughout the visit (Table VII). Viewing conditions at the larval site were poor in December 1994, owing to high winds. There seemed to be far fewer larvae and juveniles present before and immediately after the two experimental releases than in 1993. As stated above, however, larvae and young juveniles were unusually abundant some months later.

The wetted channel at the larval site was about 60 m wide, with a coarse sandy substratum, extensive shallows along the right bank, and no overhead or structural cover. All larvae found were in very shallow, edge areas on the right bank, where there was little or no flow. As discharges changed, the larvae moved backwards and forwards across the sandy expanse near the fluctuating water edge. Random hydraulic measurements taken along the edge in December 1993 suggested that larval distributions were dictated both by current speed and by water depth (Figure 3). All larvae found were in water less than 28 cm deep. With two exceptions the larvae were also present in areas with a velocity of less than 18 cm s<sup>-1</sup>. Froude numbers (the ratios of inertial to gravity forces which have been described as universal indicators of free surface flow (Henderson, 1966 in Wadeson, 1995)), revealed a similar picture. Larval *B. capensis* were not present in any measured areas with Froude numbers greater than 0.172. Thus, the trend was that larvae tended to congregate in shallow water with low current speeds. Deeper areas with low current speeds were not selected.

The larval fish did not school, but moved independently, often feeding from the substratum. During the visits in both 1993 and 1994, spot daytime water temperatures recorded in the vicinity of the larvae were between 25.5 and 27.7°C, and conductivities were in the range recorded for the spawn site (Tables III and IV).

### Larval development (1993 and 1994)

The larval fish collected on the 13 December 1993 were c 17 days old (Table VII). Assuming that all the larval fish collected in 1993 were from the same spawning, over the period from 13 December at 16:00 h until the 17 December at 13:00 h the fish grew from a mean length of  $13.12 \pm S.D.$  0.55 mm TL ( $11.6 \pm S.D.$  0.41 mm SL) to  $14.38 \pm S.D.$  0.54 mm TL ( $12.5 \pm S.D.$  0.43 mm SL, n = 47). The main developmental changes were increases in ray numbers especially in the anal fin, and the formation of a distinguishing black vertical stripe on the caudal peduncle.

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Date	Spawn bed	Egg sizes		Embryos ( $\pm$ age in days <sup>a</sup> or hours)	Free embryos	Temperature (°C)	Comments
		Diameter (mm ± S.D.)	Yolk diameter $(mm \pm S.D.)$	-	TL and NL (mm $\pm$ S.D.) ( $\pm$ age in days <sup>a</sup> )		
1992 29 January (12:00 h)	В	$3.01 \pm 0.12$ ( <i>n</i> = 7)	$2.4 \pm 0.36$ ( <i>n</i> = 3)	Near hatching, no eye pigment (2.4 days)	9.8 $\pm$ 0.62 TL (n = 32) 9.32 $\pm$ 0.56 NL (n = 32) (6 days) eye pigment (preserved specimen measurements)	25.0	Fish had spawned at least twice in past week. Larval fish stages down-stream indicated two more spawnings.
1993 13 December (16:00 h)	В	$3.68 \pm 0.2$ ( <i>n</i> = 29)	$3.00 \pm 0.2$ ( <i>n</i> = 26)	Head to tail of embryos cover $2/3$ circumference of yolk ( $n = 28$ ) one embryo was ready to hatch, tail loose, revolved inside egg envelope ( $2.4$ days)	9.43 $\pm$ 0.38TL (n = 16); 9.14 $\pm$ 0.33NL (n = 16) (5.3 days) light eye pigmenta- tion, dorsum of head in line with body	_	Fish had spawned at least twice in past week
					12.4 TL (11.0 NL) ( $n = 1$ ) (13.8 days) more advanced: cau- dal rays, four dorsal ray anlages, heavily pigmented eyes and body pigmentation	_	
14 December (11:00 h)	В	$3.44 \pm 0.14$ ( <i>n</i> = 25)	$2.79 \pm 0.15$ ( <i>n</i> = 17)	Earlier stage than for 13/12/93 (head not enlarged); seven embryos ready to hatch (caudal area free from anterior yolk) (2.4 days)	9.0 TL (8.7 NL), 9.4 TL (9.1 NL), (5.3 days) anterior yolk bulges, slight eye pigmentation, head partly free from anterior yolk sac, posterior yolk tube still distinct	22.1	Free embryos collected with eggs after several cobbles lifted

Date	Spawn bed	Egg sizes		Embryos ( $\pm$ age in days <sup>a</sup> or hours)	Free embryos	Temperature (°C)	Comments
		Diameter $(mm \pm S.D.)$	Yolk diameter $(mm \pm S.D.)$	_	TL and NL (mm $\pm$ S.D.) ( $\pm$ age in days <sup>a</sup> )		
1993 15 December (09:00 h)	В	$3.80 \pm 0.13$ (n = 39) (similar development stage)		Well developed, ready to hatch revolving inside egg envelope	8.2 TL (8.0 NL) (3.3 days) no eye pig- ment, anterior of yolk sac bulbous, head curved over yolk	22.3	Free embryos probably same spawn as embryos
15 December (10:00 h)	Α	$3.48 \pm 0.09$ ( <i>n</i> = 78)	_	Well developed, ready to hatch, revolving revolving inside egg envelope (2.4 days)	_	22.3	At A and B, eggs were at same development stage
16 December (08:00)	В	$3.52 \pm 0.06$ ( <i>n</i> = 20)	$2.91 \pm 0.17$ ( <i>n</i> = 20)	Embryo near mid-epiboly (<1.4 days)	$10.4 \pm 0.95$ TL (9.93 ± 0.9 NL) (7.8 days). Heavily pigmented eye, mouth developed, anterior yolk bulge not pronounced	22.1	Mid-epiboly embryos possibly from dusk spawn on 15/12/93. First eggs spawned since manipulated flows. Three separate spawnings on bed now
		$3.4 \pm 0.08$ ( <i>n</i> = 4)	_	Well developed, tail loose, no eye pigment (2.3 days)			
16 December (11:45 h)	В	3.6 ( <i>n</i> = 1)	3.4 ( <i>n</i> = 1)	Embryo in mid- epiboly (<1.4 days)	(1) 9.0 TL (8.7 NL) slight eye pigmenta- tion, anterior yolk sac bulge (2) $11.16 \pm 0.32$ TL $(10.54 \pm 0.4$ NL) (n = 5). Heavy eye pigmentation, no anterior yolk sac bulge		
16 December (14:00 h)	В	3.6 ( <i>n</i> = 1)	2.8 ( <i>n</i> = 1)	Mid epiboly (<1.4 days)	9.5 TL (9.0 NL) (5.3 days) Slightly pigmented eyes anterior yolk bulbous		

Table VI. (Continued)

16 December B

17 December B

17 December B

(16:00 h)

(08:00 h)

(10:00 h)

Spawn

bed

Egg sizes

Diameter

 $3.4 \pm 0.06$ 

 $3.45 + 8 \ 3.5$ 

(n = 2)

 $3.13 \pm 0.1$ 

(n = 4)

3.0

(n = 3)

 $(mm \pm S.D.)$ 

Yolk diameter

 $(mm \pm S.D.)$ 

3.3 + 3.2

 $2.63 \pm 0.1$ 

(n = 4)

2.4

(n = 2)

Date

1993

 $(\pm age in days^a)$ 10.9 TL (10.4 NL) Eggs at similar stage to \_\_\_\_ (8.8 days) Eye well those collected earlier pigmented, head same dav straight with body. mouth open and closes 22.1 Recently spawned (1)  $10.08 \pm 0.21$  TL \_\_\_\_ (9.7 + 0.18 NL)(n = 4) (8.8 days). Eye well pigmented, head straight, pectoral fin buds, anterior volk sac still bulbous, mouth forming, three gill arches formed (2) 11.13 + 0.78 TL  $(10.53 \pm 0.81 \text{ NL})$ (n = 3) (9.8 days) three to four caudal

fin ray anlages, eye well pigmented, mouth well developed, yolk tubuler, pigment on dorsum of head, body and

laterally

Embryos ( $\pm$  age in

days<sup>a</sup> or hours)

Well developed

Mid epiboly

(<1.4 days)

Eight to 32 cells

64 cells (< 6 h)

(2-4 h)

embryos and tails loose and revolving actively in egg envelope (<2.3 days) Free embryos

TL and NL

(mm + S.D.)

Comments

Temperature

(°C)

Date	Spawn bed	Egg sizes		Embryos ( $\pm$ age in days <sup>a</sup> or hours)	Free embryos	Temperature (°C)	Comments
		Diameter (mm ± S.D.)	Yolk diameter $(mm \pm S.D.)$	-	TL and NL (mm $\pm$ S.D.) ( $\pm$ age in days <sup>a</sup> )		
1993 17 December (11:45 h)	В	3.1	2.6	Cytoplasmic streaming, late cleavage of blastodisc (<1 day)	<ul> <li>(1) 9.8 TL (9.5 NL)</li> <li>(6 days) eyes well pigmented head straight with body, anterior yolk sac bulged, pectoral fins paddle-shaped</li> <li>(2) 10.7 TL (10.2 NL (8.8 days) three ray anlages, pigment on dorsum of head and body and lateral</li> </ul>	22.3	
17 December (11:45 h)		3.25	2.9	Epiboly of above embryos had com- menced (<1 day)	_	22.5	
1994 1 December (11:00 h)	В	_	_	Neural ridge, optic cup, tail tip 3/4 way loose (1 4 days)	None	20.4	Three different embryonic stages indicate three spawnings
1 December (12:00 h)	А	—	_	Four-celled embryo (<6 h)	None	22.3	Possibly spawned early on 1/12/94
2 December (12:00 h)	Α	_		Late high blastula, late gastrula, optic cup and nine somites, 20–21 somites (all <1.4 days)	None	18.7	Three to four separate spawnings
2 December (18:00 h)	А	_	_	4-, 8-, 16-, 32- and 64 celled (<12 h) embryos; late gastrula	4-None	22.1	Earlier stages spawned after the water release and correlate to observed spawnings on morning of 2/12/94

<sup>a</sup> Age estimated from laboratory raised embryos at 22-23°C

Date	Time	No. individuals	Developmental stage	$\begin{array}{l} TL \pm S.D. \\ (mm) \end{array}$	SL ± S.D. (mm)	Description	Approximate age (days) from experimental work at 22–23°C
1993 13 December	16:00 h	14	Larvae	$13.12 \pm 0.55$	11.60 ± 0.41	In smallest fish: dorsal ray an- lages just forming. In most de- veloped fish up to nine dorsal rays but no anal rays and pelvic buds just forming	17
14 December	10:30 h	15	Larvae	13.16 $\pm$ 0.35 11.60 $\pm$ 0.38 Six to 11 dorsal rays, no anal rays		17	
15 December		1	Larvae	14.16 (12.90 NL)		Full caudal rays, nine dorsal rays anal fin with five ray an- lages, caudal peduncle pigment spot	21
		1	Larvae	16.40 (14.40 NL)		As above, but pelvic fin buds also just formed	>21
		1	Juvenile	24.90	21.00	All fins fully formed, caudal peduncle vertical pigment stripe present	53
		1	Juvenile	27.70	22.70	As above	>53
17 December	13:00 h	47 Largest of these	Larvae Larvae	$\frac{14.38 \pm 0.54}{15.33}$	$\frac{12.50 \pm 0.43}{12.90}$	Six anal fins, pelvic fin buds, vertical pigment stripe on cau- dal peduncle just forming	21
		Smallest	Larvae	13.50	12.00	No anal rays	19
1994 1 December		12	Larvae	$14.10 \pm 0.50$		Range 13.2–15.00 mm TL. Swimbladder commencing divi- sion into anterior and posterior chambers, and distinctive black caudal peduncle marking just forming	17–21

Table VII. Larval and early juvenile Barbus capensis developmental records, from fish collected 2 km down-stream of Spawn Beds A and B in December 1993 and 1994

In December 1993 juveniles were about the same size (24 mm TL) as reached by those in the laboratory study after approximately 50 days at 22-23°C. If the same growth rate held true in the wild, the juveniles found in December would have been spawned in late October. However, temperatures at the larval site were around 27.7°C, so the wild juveniles may have been developing faster than those in the laboratory study. In 1994 the larval *B. capensis* collected prior to the experimental pulse were calculated to be between 17 and 21 days old, which would indicate a spawning in early- to mid-November.

## Summary of developmental stages linked to dam releases

On-site microscopic examination of live eggs and free embryos proved invaluable for allocation of the various developing embryonic stages into the periods, before, during and after experimental pulses. This information guided determination of the facts that the fish had spawned, in both 1993 and 1994, several times prior to the experimental releases and had also spawned throughout the experimental periods. Observations from the bridge in 1994, linked with the knowledge 2 months later of high larval numbers, indicated that 1994 had been an unusually successful year for recruitment. Although the evidence gathered so far is fragmented and many gaps in understanding and proof exist, it was tentatively concluded that the two experimental pulses in 1994 appeared to enhance thee spawning success of *B. capensis*. Spawning appeared to be triggered by pulses of high flow but not necessarily by changes in water chemistry.

## DISCUSSION

### Spawning season of the genus Barbus

Annual spawning(s) that are successful occur when optimal conditions are present and the young hatch



Figure 3. Plot of hydraulic conditions at *Barbus capensis* larval fish site below Clanwilliam Dam. Froude numbers are given for each point measured. Larval fish present ( $\bigcirc$ ); and larval fish absent ( $\bullet$ ). Dotted line denotes tentative boundary between presence and absence

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and commence feeding at the optimum season for survival (Nikolsky, 1963; Bye, 1984; Nesler *et al.*, 1988). Wherever conditions permit, *Barbus* species spread their reproductive effort in order to minimise egg predation (Kortmulder, 1982). This translates into different spawning months depending on whether the species occurs in a tropical or temperate area; when the dry- and wet-seasons occur and whether they are in the Northern or Southern hemisphere. Spawing seasons of *Barbus* species in general are very variable, from those that spawn in wet-season high flows to dry-season, low flow spawners and those that spawn throughout the year. Flow is a very important spawning trigger in tropical areas as most freshwater fish, which includes many *Barbus* species, spawn seasonally during the rainy periods (Lowe-McConnell, 1975; Payne, 1986).

In summer rainfall, temperate areas many African Barbus species spawn after an increase in flow (Cambray and Bruton, 1984; Tómasson et al., 1984; Cambray and Meyer, 1988; Cambray, 1991, 1994), but some do not. Barbus guildi (West Africa) spawn only in the second rainy peak (Loiselle, 1973) and B. nigrofasciatus, B. titteva and B. dorsalis in Sri Lanka (Silva et al., 1985), and B. lorenzi from southeastern Dahomey spawn throughout the year (Loiselle and Welcomme, 1971). Some Barbus species have been recorded spawning in the dry-season, similar to B. capensis in the Olifants River. Two such species are an unspecified Barbus species from Togo (Loiselle and Welcomme, 1971) and B. melanampyx from southern India (Harikumar et al., 1994). In the B. melanampyx population it was argued that the dry-season spawning was probably related to the more constant conditions prevailing compared to the monsoon season. Dry-season spawners, such as B. melanampyx, spread their reproductive effort over a number of days, whereas, wet-season spawners "... make the most of each opportunity" (Harikumar et al., 1994 p. 134). These authors also suggest that the timing of the reproductive season of B. melanampyx is not proximately influenced by flow rates but the fish are 'programmed' not to start breeding before November. In temperate conditions, such as in the Western Cape of South Africa, both winter photoperiod and low water temperatures would ensure that the Olifants River cyprinids would not spawn during the wet, winter season. Instead minor increases in flow during the dry-season may be the spawning trigger for B. capensis.

## Spawning and reproductive style of Barbus capensis

The reproductive style of *B. capensis* belongs in the: ethological section of nonguarders (A.); the ecological group of open substratum spawners (A.1.); and the guild lithophils (A.1.3.) which are rock and gravel spawners with benthic free embryos. When hatched, the free embryos are photophobic, and hide between and under cobbles. *B. capensis* eggs are nonadhesive whereas many other lithophilic cyprinids have adhesive eggs (Mills, 1991).

B. capensis occurs in a temperate area with a dry summer season. The species appears to spread its reproductive effort over the first half of the dry-season and 'makes the most of each opportunity' of increased flow, even minor ones, during this period. The number of developmental stages noted on the spawning beds at any one time, linked with the observations from the bridge in 1994, suggest that B. capensis is a repeat-spawner over several days (Table VI). Although final proof must wait until individual fish are tagged and observed. B. capensis is also a multiple-spawner during a breeding season (Table VII; Van Rensburg, 1966). This provides the capacity to have successive batches of eggs ripen within a season, together with a fairly long spawning season (3-4 months), are reproductive traits which B. capensis has in common with many other temperate African cyprinids (Cambray and Bruton, 1984; Tómasson et al., 1984; Cambray, 1991, 1994). Additional reproductive traits of B. capensis include relatively late maturity, increasing reproductive effort with age, and the potential to spawn in successive years (Van Rensburg, 1966). This suite of reproductive traits is well suited to a large species which inhabits the main channel of the Olifants River. The high probability of the fish being repeat- as well as multiple-spawners, is important when recommending suitable floods to trigger spawning below Clanwilliam Dam wall, because one flood would probably not be sufficient. Several well spaced floods to trigger spawning during a season would result in higher recruitment.

### Linking dam releases with spawning of B. capensis

The eggs found in 1992 were about 2 days old. Records of releases from Clanwilliam Dam for the relevant period showed that only a modest change from 7.06 to 7.38 m<sup>3</sup> s<sup>-1</sup> had occurred. However, records are only kept for flow changes of greater than 24 h duration. Shorter fluctuations in flow, which have been shown here to trigger abundant spawning activity, may have occurred and not been recorded. Similarly, spawning had occurred before the experimental releases in both 1993 and 1994, but again the record of dam releases makes correlation with spawning impossible. Thus, spawning that occurred before the experimental pulses may have been triggered by small sustained increases in flow, or by unrecorded larger releases of less than 24 h duration, or by conditions unrelated to flow changes.

The difficulty of interpreting results was compounded by the fact that the extent of any earlier spawning activities could not be gauged simply by the number of eggs on the spawn beds. Observations had indicated that most eggs seemed to be washed from the very spawn beds into deep, sandy pools down-stream. In any case, no attempt was made to systematically search and collect eggs from spawn beds because of the threatened status of the species. Thus, the best available indicator of the success and magnitude of spawning was the survival of larvae and juveniles. Using this as a guide spawning success did appear to be enhanced by the 1994 experimental pulses, as reflected in the unusually high abundance of larvae found 2 months later. The poorer success rate of the 1993 experimental pulses may have been due to the presence of researchers working in and along the river or by other factors not yet understood.

Water quality did not differ significantly in any way measured during the experimental releases. This is not surprising considering the experimental pulses were simply increases in the hypolimnetic releases already occurring. It was concluded that water quality during the experimental pulses did not appear to change significantly from that during lower flows and had thus probably not played a major role in influencing any flow-related fish behaviour.

It was concluded that although much remains unclear and unproven regarding spawning triggers, spawning of *B. capensis* in the Olifants River is occurring through the fortuitous occasional chance occurrence of favourable conditions. Spawning appeared to be enhanced by specifically designed and timed experimental pulses. It is suggested that such releases aid the synchronised arrival of individuals at the spawning bed, and in this way probably increase the overall success of the spawning period.

#### River regulation and spawning in other southern African river systems

Cambray (1991) reviewed some of the studies that have included work on river regulation and spawning in southern Africa. In the flood plains below the Pongolapoort Dam, it was recommended that a series of small floods and one large flood between November and March would maintain a natural, self sustaining population of fishes (Merron and la Hausse de Lalouviere, 1987). Many of these species are flood-dependent spawners, which could be stimulated to spawn in the newly flooded pans by the flooding of this system. They are not main-channel spawners as is the case with *B. capensis* in the Olifants River.

Two large *Barbus* species in the Orange River, *B. aeneus* and *B. kimberleyensis*, spawn on gravel/cobble beds within the main channel below Gariep Dam. It was recommended that hydrological manipulations such as releasing epilimnetic water in spring and early summer would lead to earlier breeding and higher recruitment for these species (Tómasson *et al.*, 1984).

## Management of flows in the Olifants River

For riverine fish the final phase of gonad maturation and the release of the gametes at a specific spawning site may require one or all of the following stimuli: increased current speed; water quality changes; barometric pressure changes; or pheromone releases (Lam, 1983; Stacey, 1984; Nesler *et al.*, 1988).

This study has shown that small increases in discharge and thus current speed appear to trigger spawning of *B. capensis*. However, the construction of Clanwilliam and Bulshoek Dams now store such small pulses of high flow, making the species extremely vulnerable at spawning time. A formal

water-release strategy during the critical breeding season should thus be considered. Such a strategy would have to include attention being paid to the water temperature of the released water as well as its quantity. At present, hypolimnetic releases result in released water being up to 10°C cooler than that flowing into the impoundment (JMK, unpublished data). The effects of these temperature differences and the hydraulics of the spawn beds are presently being studied. Meanwhile, a fairly simple strategy of changing release patterns during the critical spawning period, as in this study, would seem a first useful step forward in enhancing recruitment of this magnificent native fish species. At the same time, careful monitoring of such releases in terms of their effect on spawning will continue to enhance our ability to justify why dry-season pulses of high flow are needed. Improving our understanding in this respect in order to more effectively apply the building block methodology, was the main goal of this study.

### CONCLUSIONS

Experimental releases of high flow pulses from Clanwilliam Dam on the Olifants River appeared to trigger spawning of the Red Data Book cyprinid, Barbus capensis. Collections and immediate microscopic examination of live eggs, free embryos, larval, and juvenile fish, combined with direct observations and video recordings of spawning behaviour helped to interpret the reproductive biology of B. capensis and its response to the experimental flows. B. capensis is a mid-channel spawner, and probably a repeat-spawner over several days. It is also a multiple-spawner over the 4 months October-January. Its spawning beds were a mixture of gravel, cobble, and boulders with fast flow and no overhead cover. Large individuals (greater than 60 cm) maintained position for up to an hour on the spawning bed and were occasionally joined by smaller individuals which aligned beside the larger one, all vibrated, with a resultant release of milt and eggs, and then the smaller ones returned to edge cover or moved up-stream. The large individuals remained in position on the spawning beds, moved up-stream or fell away down-stream. Spawning episodes occurred throughout the day and often in full sun. The eggs and the photophobic free embryos appear to remain in the spawn bed for 10-12 days, followed by a swim-up stage when the fish are carried by currents to a larval fish site several kilometres down-stream. The larval B. capensis favour areas characterised by shallow (less than 30 cm), warm water (more than  $25^{\circ}$ C) of low velocities (less than 20 cm s<sup>-1</sup>) with a sand substratum.

It is suggested that water releases from Clanwilliam Dam can be used as a management tool to help conserve and possibly enhance the population of *B. capensis* down-stream of the dams on the Olifants River. Such releases should be guided by the understanding already gained, and further monitored in terms of this effect on recruitment of *B. capensis*. This in turn will enhance understanding of the role that small dry-season pulses of high flow play in African river ecosystems and strengthen motivations for them to be included in the modified flow regime of regulated rivers.

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