Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*

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Abstract

In South Africa, modified flow regimes designed to maintain ecosystem functioning at some pre-determined level are recommended for all rivers involved in major water-resource developments. One component of such flow regimes of special interest in the winter-rainfall region of the country is the small pulses of higher flow that occur in the dry season (November-April), here called freshes. Research was carried out in the Olifants River, in the winter-rainfall region of South Africa, on the link between freshes and spawning of an endemic, vulnerable cyprinid, the Clanwilliam yellowfish Barbus capensis. Experimental releases from Clanwilliam Dam on the Olifants River in a previous year showed that a greater than usual spawning success, assessed by larval recruitment levels, was correlated with hypolimnetic freshes released during the species' breeding season (October-January). In the study reported on here, a hypolimnetic fresh of the same size, duration and timing as those linked with successful spawning failed to induce spawning. Differences in the thermal regime of water releases appeared to be responsible. Two warm (19–21 °C), epilimnetic freshes of 15 hours duration were then released, and correlated with fish moving onto the spawn beds and exhibiting pre-spawning behaviour. However, the fish moved downstream away from the spawn beds when cold $(16-18 \, ^{\circ}\text{C})$ hypolimnetic baseflows were released for 15 hours between the two epilimnetic freshes and continually after the second one. The presence of free embryos and larval B. capensis indicated, from their developmental stages, that spawning had probably occurred before the experimental releases began, when warm (21-23 °C) epilimnetic water was spilling over the dam, and had halted once spillage stopped and hypolimnetic releases began. Indeed, the presence of dead and deformed young suggested that the cold water may have had a detrimental affect on those spawned during the earlier warmer spell.

A summary table details the conditions, including the hydraulic characteristics of the spawn beds, believed to induce spawning and support early life stages of *B. capensis*. It is concluded that freshes released from Clanwilliam Dam at the appropriate time (October–January) should be able to increase spawning success of *B. capensis*, but only if the water temperature at the spawn site is at or above 19 °C and stable or rising. However, successful spawning will not necessarily lead to high recruitment if water temperatures are not then maintained at appropriate levels for some time for development of the embryos and larvae. This implies that additional epilimnetic releases will be required following critical trigger flows.

Introduction

The South African Department of Water Affairs and Forestry (DWAF) has adopted a policy of sustainable development of the nation's water resources (DWAF, 1997) and is in the process of writing this into a new Water Law. In essence, this policy requires that future water-resource developments will be undertaken with due regard to the present and desired future state of the aquatic systems concerned. As rivers are the major source of water for the nation, a routine part of any planned water-resource development now is an assessment of the flow required for maintenance of the targetted riverine ecosystem. The Building Block Methodology (BBM) has been developed within South Africa for making such assessments (King & Louw, in press).

In the BBM, components of the flow regime deemed to be of significant ecological and/or geomorphological importance are combined, in a specialised workshop, to describe a series of modified flow regimes. Each flow regime will, to the best available knowledge, maintain the river ecosystem at a different, specified level of ecosystem functioning. In parallel, a desired state for the river is ascertained through a participatory process involving the stakeholders. The public process incorporates economic, social and ecological issues. Information on the various scenarios for river condition, together with the outcome of the public participation process, is used by DWAF both in decisions regarding the proposed development, and throughout any ensuing planning, construction and operation phases.

The BBM recognises four main flow components: dry-season and wet-season low flows, small pulses of higher flow (freshes) and wet-season floods (King & Louw, in press). Research began recently to increase understanding of the important characteristics of some of these flow components, in order to ensure that they achieve the desired result when included in a modified flow regime.

One of the components being studied is the freshes. Cambray et al. (1997) arranged for experimental freshes to be released from Clanwilliam Dam, on the Olifants River (Western Cape, South Africa), at the beginning of the dry season in 1992, 1993 and 1994. This correlated with the suspected spawning season of a threatened large cyprinid endemic to the system, the Clanwilliam yellowfish *Barbus capensis* (Cambray, 1998). During the experiment, two spawn beds used by *B. capensis* were located downstream of the dam and spawning of the species was witnessed. Eggs, free embryos and larvae were collected and the stages of development described.

A picture began to emerge of multiple and possibly repeat spawning in late spring and early summer (November to January). This seemed to be linked to rising water temperatures in the river downstream of the dam, which brought the fish into breeding condition. In captive breeding experiments, temperatures at or above 20-22 °C were linked to achieving this condition (Bok, Cape Nature Conservation, pers. com.). Once in breeding condition, fluctuating releases of water from the dam appeared to trigger spawning. In recent years, appropriate fluctuations might fortuitously have occurred due to changes in releases for downstream irrigators. In 1994, however, extensive spawning followed the release of two experimental freshes, with subsequent recruitment levels that were considered unusually high (Impson, pers. com.). No

obvious changes in water quality and temperature occurred during these freshes, which merely increased the magnitude of hypolimnetic releases.

A link between freshes and spawning seemed to be emerging, but could the results of the previous experiment be repeated? To answer this, a further experiment was planned for the spring of 1995. This paper reports on the 1995 study of experimental releases and the responses to these of B. capensis. The aim was to further study the interactions of temperature and discharge, and their relative importance in triggering successful spawning of *B. capensis* downstream of Clanwilliam Dam. The following questions were addressed: what were the water temperatures in the reach downstream of Clanwilliam Dam in the weeks leading up to the experimental period; did these temperatures correlate with the distribution and movement of B. capensis in the river downstream of the dam; could the spawning success correlated with the 1994 experimental freshes be repeated, using the same pattern and magnitude of releases at the same time of year?

Study site

The study site was that described by Cambray et al. (1997). Essentially, it was in the sandy middle reaches of the Olifants River, 125 km from its source (Latitude $32^{\circ}10'26''$ S, Longitude $18^{\circ}52'16''$ E). The width of the complete macrochannel at that point was 70-100 m. Two spawn beds (A and B) had been found by Cambray et al. (1997) 1.5 km downstream of Clanwilliam Dam (Figure 1), in a braided reach of multiple channels and small sandy islands supporting palmiet (Prionium serratum; Juncaceae). Extensive surveying of the middle reaches of the river by divers during this study led to the conclusion that the two beds appeared to be the prime spawning areas, and possibly the only ones, available to the B. capensis population between the dam and Bulshoek Weir some 23 km downstream. This population is now stopped by the dam from migrating upstream to the river's cobble-bed headwaters. A road bridge arching over the site allows good observation of fish behaviour on the beds.

A larval site, about 2 km downstream of the spawn site, is more typical of the river's middle reaches. The single, sandy-bed channel has a wetted width of 50 m during low summer flow, and little instream vegetation. Extensive shallows over sand provide warm, nursery areas to which free embryos of *B. capensis* drift from the spawn beds and develop into larval fish.



Figure 1. Sketch map of spawn site for Barbus capensis in the middle reaches of the Olifants River, South Africa.

Five pools were also involved in the study. Numbered in sequence from upstream to downstream, their locations were as follows:

Pool 1: about 100 m downstream of the dam wall and upstream of the spawn site;

Pool 2: upstream of Spawn Bed A (Figure 1);

Pool 3: immediately downstream of the spawn site (Figure 1);

Pool 4: in the open channel, immediately upstream of the larval site;

Pool 5: in the open channel, about 0.5 km upstream of the full supply level of Bulshoek reservoir.

Activities involving the pools are explained in the Methods, and their character is detailed in the Results.

Methods

Water temperature and associated physical variables

A maximum-minimum thermometer was placed in the river at the farm Hoopvol, 7 km downstream from Clanwilliam dam wall. From 3 September 1995, daily readings were taken by the farmer and faxed through to the University of Cape Town weekly. Temperature readings were also taken occasionally at the spawn site by the DWAF dam operator, when flows were sufficiently low to allow the thermometer to be in the river. These records indicated when the river's temperature was reaching the assumed critical level of 20–22 °C.

Once the experimental releases began, temperature readings at one or both spawn beds were taken at approximately hourly intervals during daylight hours, along with readings of air temperature, water level and dissolved oxygen (DO).

Fish surveys

Divers using snorkel or scuba gear completed fish counts at Pools 1, 3, 4 and 5 on three occasions before the experimental freshes and one occasion afterwards. The counts were designed to inform on whether or not *B. capensis* were distributed throughout the reach in early spring and moved upstream as water temperatures increased. Counts were limited in terms of visits and sites due to unfavourable spring weather, a shortage of experienced divers and inaccessibility of the area. It was intended to establish at least one site between pools 4 and 5. However, no fish refugia in the form of deep pools could be found in this reach, at least partly because extensive stretches had been bulldozed to raise the banks and decrease flooding of adjacent cropland.

During the fish surveys, the divers identified fish species and estimated their numbers as they moved downstream through a pool in line abreast. They then repeated the count in an upstream direction. Each diver was allocated a segment of water to his front and toward the nearest bank, and encompassing the whole water column. Effort was recorded to the nearest minute.

Larval counts and bridge watch

The authors could not maintain a constant presence at the spawn site. However, the decision to begin experimental releases could not be made without some knowledge of how fish behaviour was changing as temperatures increased. Thus, two activities were initiated, both carried out by local inhabitants of Clanwilliam. As sporadic spawning does occur at the site (Cambray et al., 1997), an employee of Cape Nature Conservation (CNC) visited the larval site daily from mid November to watch for the first appearance of fish larvae.

Additionally, a local volunteer carried out bridge watches as time allowed, to record signs of fish activity on or near the spawn beds.

Water release strategy

The same strategy for experimental releases as in 1994 was planned. Once temperatures were at the critical level and some larval fish had been found, releases from the dam were to be reduced to store water for the experimental freshes. This operation was managed by DWAF with the knowledge and co-operation of downstream irrigation farmers. The planned schedule of storage and releases was the same as in 1994; from a normal irrigation release of $7.5-8.0 \text{ m}^3 \text{ s}^{-1}$, discharge was to be dropped to about 3.5 $m^3 s^{-1}$ for four days to store water. Two experimental freshes were then planned, one of 17.0 m³ s⁻¹ for 12 hours overnight, and one of 9.0 m³ s⁻¹ for 12 hours the following night. Releases would drop to $3.5 \text{ m}^3 \text{ s}^{-1}$ between freshes, and return to the background level of about $7.0 \text{ m}^3 \text{ s}^{-1}$ a few hours after the second fresh because of irrigation demands. Developments during the experimental period led to changes in this release pattern, as described below.

Temporary gauge plates were erected at the edge of the spawn beds to record the water surface elevation (WSE) with fluctuating discharge. The plates were not surveyed in to a common datum, and so the same reading on both did not necessarily reflect the same WSE. The gauge plates showed that freshes lagged about two hours behind the time of release at the dam, as they flowed through the upstream braided channel and dense palmiet beds (also see Cambray et al., 1997).

Spawn bed hydraulics

Before the experimental freshes were initiated, hydraulic measurements were taken at Bed A (Figure 1), where spawning exclusively occurred during the 1994 observation period. No attempt had been made to measure hydraulic conditions at the bed in 1994, so as not to disturb the spawning fish. However, during water storage in the 1995 experiment, releases were at almost the same level as during spawning in 1994 ($3.4 \text{ m}^3 \text{ s}^{-1}$ in 1995 as opposed to $3.2 \text{ m}^3 \text{ s}^{-1}$ in 1994). The opportunity was thus taken to obtain data on the approximate hydraulic conditions prevailing at Bed A during the 1994 spawning. Immediately after the 1995 experimental freshes, hydraulic measurements were also taken at the other bed (Bed B) at a higher discharge, for reasons explained in the Results.

For each bed, a grid was delineated using tapes. This covered the whole wetted area around and including the spawn bed. For the large Bed A, measurements were taken every metre from bank to bank, at crosssections laid out every two metres along the river length. For the smaller Bed B, cross-sections were one metre apart. At every measurement point the following were recorded: distance from wetted edge, dominant and sub-dominant substrata, presence and nature of aquatic vegetation, overhead cover, water depth, visual appearance of flow (flow type) and velocity at sixtenths depth. Velocities were recorded with a Scientific Instruments AA flow meter. Particle sizes of substrata (after King & Tharme, 1994) were sand: < 2 mm; gravel 2–32 mm; small cobble 32–128 mm; medium cobble 128–256 mm; large cobble 256–512 mm; and boulder > 512 mm.

Since the functioning and interaction of stream hydrology and morphology directly influence the habitat and its quality for fish, Froude numbers were calculated for each measurement point. Froude number is defined as $v/(gd)^{0.5}$, where v = mean water velocity (m s⁻¹); d = water depth (m); and g = the acceleration due to gravity (m s⁻²). Gordon et al. (1992) state that it reflects the interaction between flow depth and velocity at a given point. Wadeson (1995) found that it distinguished well between different kinds of hydraulic habitats in rivers. Heede & Rinne (1990) also recommended the use of Froude numbers in microhabitat evaluation for stream fishes.

Fish response to experimental freshes

Before, during and after the experimental freshes, observations of fish activity at and near the spawn beds were recorded from the bridge. Four locations were observed (Figure 1): Spawn Beds A and B, and Pools 2 and 3. For Bed A, observations were sometimes continuous and sometimes for ten minutes in each daylight hour, whilst observations at the other locations were sporadic depending on time availability. An observation record consisted of a count of any fish seen in the area within the observation time. Movement could be upstream or downstream, and the count could be of one fish several times or of many different ones, as it was impossible to distinguish between the two. For Spawn Beds A and B, results were standardised to fish counts per ten minutes in each hour. Due to overhanging vegetation, fish movement was less visible in the two pools, and calculations of fish numbers seemed inappropriate. Instead, a simple record of fish movement was used (see Results).

Eggs, free embryos and larval fish were collected if present, before and after the experimental freshes,



Figure 2. Maximum and minimum water temperatures at the farm Hoopvol, 7 km downstream of Clanwilliam Dam on the Olifants River, from 4 September to 10 November 1995. Gaps in data are due to removal of thermometers during high flows.

as described in Cambray et al. (1997). They were also measured and photographed as described in that paper.

Results

Water temperature

Water temperature records for Hoopvol revealed daily maxima of 16–21 °C and minima of 12–19 °C in September and October (Figure 2). At this time the dam was spilling, and some fluctuations may have been due to a mixture of hypolimnetic releases and surface spillage. Two large floods in October increased discharges downstream of the dam to 80 m³ s⁻¹ at times, with the second one also noticeably reducing temperatures for two to three days.

Water temperatures at Hoopvol began to climb in early November until surface spillage stopped on 15 November (Figure 3). At this time, water temperatures at the spawn site were 22–23 °C, and at Hoopvol 22– 28 °C. Hypolimnetic releases then became the only source of downstream water, causing temperatures to drop to 15–16 °C at the spawn site. Daily maxima at Hoopvol fell by about 8 °C and minima by about 5 °C. Although daily maxima rose again at Hoopvol within about two weeks, to close to the temperatures occurring before surface spillage stopped, daily minima did not approach a sustained recovery until toward



Figure 3. Water temperatures at the spawn site and at Hoopvol, and water release and spillage patterns at Clanwilliam Dam, both in the middle reaches of the Olifants River, from 10 November to 28 December 1995. Temperatures shown for Hoopvol are daily maxima and minima. The sequence of days with similar values shown for the spawn site are the result of occasional spot readings, which indicated the temperature range recorded by maximum-minimum thermometers during the preceding few days. Releases from the dam fell to zero on two occasions in late December, for operational reasons.

the end of December. Thus, the cold water released during the day was being warmed by high air temperatures, but water temperatures at Hoopvol at night were little above those of the hypolimnetic release. Occasional temperature readings at the spawn site until 17 December reflected this sluggish recovery (Figure 3).

Fish surveys

Late rains and flooding in the river up to the end of October delayed diving trips, whilst the irregular releases of hypolimnetic water from the dam produced cold turbid waters that made counts difficult. Surveys were completed on 20 September and 15 November, and then on the days before and after the first experimental fresh (28 and 29 November).

The pools used for the fish surveys reflect the general character of that stretch of river (Table 1). They were not identical in size, but by repeating the sampling effort at each pool on each visit, results over time for any one pool could be compared. Average depth of pools was similar, varying between

1.5–3.0 m. Substrata consisted primarily of cobbles, boulders and bedrock in current, with sandy vegetated beds common out of current. Pools 3 and 4 had abundant submerged and emergent macrophytes, with extensive stands of marginal vegetation. Pool 3 was part of a vegetated, braided reach and was substantially smaller than the other three pools. The pools were similar in terms of water chemistry, and reflected the pure, slightly acidic water characteristic of the region (Table 1). Further details of the water chemistry of this stretch were given by King & Tharme (1994) and Cambray et al. (1997).

A single upstream or downstream count took from 2–5 minutes in Pools 1 and 3, and 5–9 minutes in Pool 4. Effort was related to current speed, with faster currents resulting in quicker completion of the counts. *B. capensis* dominated the fish communities in Pools 1, 3 and 4 (Table 2). It was, however, progressively replaced in the slower-flowing, downstream Pools 4 and 5 by alien species such as smallmouth bass *Micropterus dolomieu*, bluegill sunfish *Lepomis macrochirus* and banded tilapia *Tilapia sparrmanii*.

Table 1. Characteristics of fish survey pools

	Pool 1				Pool 3				
Latitude/Longitude	32°11′00′	″S, 18°52′.	30″E		32°10′20″S, 18°52′18″E				
Location	100 m dov	wnstream c	of dam		30 m downstream of spawn site				
Approximate Length (m)	30				15				
Approximate Width (m)	10				6				
Average Depth (m)	1.5 - 2.0				1.0–2.0				
General Appearance	Cobble, b	edrock and	some boul	ders in	Bedrock and some boulders in current				
	current wi	th sandy b	eds in back	waters.	with vegetated sandy beds in backwaters.				
	Moderate presence of palmiet and Salix			Profuse marginal plant cover.					
Date of visit	20 Sep	15 Nov	28 Nov	29 Nov	20 Sep	15 Nov	28 Nov	29 Nov	
Visibility (m)	2.0-3.0	2.0-3.0	1.5 - 2.0	1.0 - 1.5	2.0-3.0	3.0-4.0	3.0-4.0	3.0	
рН	6.4	6.3	6.2	6.4	6.4	6.3	5.9	6.3	
Water Temperature (°C)	16.7	23.0	17.5	18.0	16.6	23.2	18.5	17.2	
Conductivity (mS m ⁻¹)	22.0	15.5	7.1	8.1	13.9	15.5	6.5	7.1	

	Pool 4				Pool 5				
Latitude/Longitude	32°10′04	″/18°52′3	0''		32°03′50″/18°49′30″				
Location	1 km dow	nstream of	spawn site	e	0.5 km upstream of Bulshoek reservoir				
Approximate Length (m)	100 (60 n	n surveyed))		150 (60 m surveyed)				
Approximate Width (m)	10				30				
Average Depth (m)	2.0-3.0				2.5–3.5				
General Appearance	Bedrock	and some b	oulders in	current	Bedrock and some boulders in current				
	with vege	tated sandy	y beds in ba	ackwaters.	with vegetated sandy beds in backwaters.				
	Profuse marginal plant cover.			Moderate presence of palmiet at margins					
Date of visit	20 Sep	15 Nov	28 Nov	29 Nov	20 Sep	15 Nov	28 Nov	29 Nov	
Visibility (m)	3.0	1.5	4.0	3.0	3.0	-	4.0	1.0-1.5	
pН	6.6	6.1	6.7	_	6.6	_	6.3	6.1	
Water Temperature (°C)	17.3	20.6	19.4	_	19.0	_	24.4	17.4	
Conductivity (mS m^{-1})	8.8	6.6	8.0	-	13.6	-	10.9	9.8	

Only one adult *B. capensis* was observed in Pool 5 during the four surveys, and this pool is not considered further here.

Although Pools 1, 3 and 4 contained *B. capensis* on all visits, the numbers varied. The counts are inadequate for statistical analysis, but some general comments on fish movements can be made, albeit at low confidence level. Pools 1 and 3, closest to the dam, showed similar trends, with the number of *B. capensis* counted generally being higher on 15 November than on 20 September. This possibly reflected the upstream movement of fish, encouraged by spillage of warm surface waters from the dam. The counts at these pools were considerably lower again on 28 November, although they increased at Pool 4, perhaps reflecting a downstream movement of fish to warmer water (Ta-

ble 1) in response to the cold, hypolimnetic releases that started on 15 November. Numbers in Pools 1 and 3 were generally higher again after the first (hypolimnetic) experimental fresh, possibly reflecting upstream movement in response to the higher flows. This was most noticeable at Pool 3, immediately downstream of the spawning site, where the average number of fish counted per diver before and after the first experimental fresh increased from 2.8–9.5 (downstream survey) and 0.8–7.5 (upstream survey) (Table 2). The diving team could not monitor *B. capensis* movements in response to later experimental freshes, due to other commitments.

			20 Sept		15 No	v	28 No	ov –	29 Nov	
Diver	Equipment	Direction	YF	Alien	YF	Alien	YF	Alien	YF	Alien
Pool 1										
1	Snorkel	downstream	6	0	2	1	4	0	13	0
		upstream	3	0	1	0	3	0	7	0
2	Scuba	downstream	1	0	_	-	3	0	-	_
		upstream	0	0	_	_	1	0	-	_
3	Scuba	downstream	14	1	13*	2	2	0	4	0
		upstream	8	0	6	1	0	0	3	1
4	Snorkel	downstream	4	0	_	-	5	1	-	_
		upstream	10	1	_	-	6	0		-
		Total downstream	25		15		14		17	
		Average per diver	6.3		7.5		3.5		8.5	
		Total upstream	21		7		10		10	
		Average per diver	5.3		3.5		2.5		5.0	
Pool 3										
1	Snorkel	downstream	7	0	16	0	0	0	6	0
	Shorner	upstream	3	0	15	0	0	4	2	0
2	Snorkel	downstream	0	ů 0	_	_	0	0	_	_
-	Shorner	upstream	11	ů 0	_	_	0	0	_	_
3	Scuba	downstream	6	0	17	0	0	0	13	0
5	Seudu	upstream	7	0 0	6**	0 0	0	0 0	13	0 0
4	Scuba	downstream	2	0	_	_	11	0	_	_
-		upstream	0	0	_	_	3	0	_	_
		Total downstream	15	0	33		11	0	19	
		Average per diver	3.8		16.5		2.8		9.5	
		Total upstream	21		21		3		15	
		Average per diver	5.3		10.5		0.8		7.5	
Deel 4										
1	Sauha	downatesam	14	0	2	1	11	0		
1	Scuba	uowiistream	14	0	5	1	21	0	-	-
2	Smonleal	downatroom	10	0	2	5	12	0	-	_
2	SHOIKEI	uowiistream	0 20	5	4	1	2	0	5	0
2	Sauba	downstroom	20 14	1	4	2	5 7	0	ע ד	2
3	Scuba	uowiistream	14	1	-	-	/	0	15	2
4	Sportel	downstream	14	0	- 5	-	ע 24	0	15	2
4	SHOLKEL	uowiisuealli	14 25	0	20	2	24 0	0	-	_
		Total downstream	23 50	0	20	Z	55	0	12	_
		Average per diver	12.5		22		13.8		60	
		Total unstream	12.3		2.2 20		15.0		24	
		Average per diver	175		29 07		42 10 5		24 12.0	
		Average per diver	17.5		9.7		10.5		12.0	

Table 2. Fish counts at Pools 1, 3, and 4 on three occasions before and one occasion after the first experimental fresh. YF = Clanwilliam yellowfish, Alien = alien fish species

* May be overcount. ** Probably undercount.

Larval counts and bridge watch

The larval counts and bridge watch were designed to aid the authors to decide, from a distance, when the fish were ready to spawn, and thus when water storage for the experimental freshes should begin.

Quantitative counts of the larvae in the sheltered edge areas of the larval site were attempted, with the hope of ascertaining from these the approximate dates and degree of success of earlier upstream spawning events. These proved unsuccessful, as fluctuating releases from the dam and the vagaries of weather meant that larval numbers differed widely between days and areas. When unquantified larval counts began on 13 November, however, six larval *B. capensis* were found, followed by approximately 40, 50, 20, 60 and 100–120 larvae on 17–21 November. The presence of the larvae indicated that it was time to begin storage for the experiment.

Bridge watches did not develop into a structured programme. Anecdotal information for the two weeks up to the experiment revealed that there had been many fish around the two spawn beds up to about 18 November, but none after that. Their disappearance correlated well with the switch to hypolimnetic releases.

Water-release strategy and related fish activity

The fish survey on 15 November and the presence of larval fish on 13 November showed that B. capensis was in spawning condition. Males exhibited nuptial gold colouration and females had extended abdomens. Thus, water for the experiment was stored from 25-28 November (Figure 2) through reducing the releases to meet downstream agricultural demand. At the same time, and coincidentally, wet-season spillage over Clanwilliam Dam became insufficient for downstream needs and epilimnetic releases were halted. Thus, as the experiment began, the switch was made from warm surface spillage to cold hypolimnetic releases. As a result, water temperatures at the spawn site at the beginning of the experiment were 3-4 °C cooler than during the observed spawning in 1994. This situation may well have accounted for the disappearance of the fish from the immediate vicinity of the spawn beds. However, it was decided to proceed with the experimental freshes in the hope that these would trigger an upstream spawning run. The first fresh was released on 28 November, three days earlier than in 1994.

Records of fish activity, linked to discharge, air and water temperatures and DO concentrations, were maintained throughout the daylight hours of the day before the first release and for the next four days (Figure 4). By that time three releases had been completed. The values of physical and chemical variables mentioned refer to Bed B unless otherwise stated. The pattern of percent saturation of DO shadowed that for its concentration, ranging between 73–99% saturation, and is not shown in Figure 4. The weather was sunny and hot apart from a short period of rain (Figure 4).

The first experimental fresh

The first experimental fresh, of magnitude 14.0 m³ s⁻¹, was released hypolimnetically for 13 hours overnight on 28–29 November, commencing at 17h00. It was reduced to a hypolimnetic release of 4.2 m³ s⁻¹ at 06h00.

Water temperatures showed a modest increase during the day before the first release, but only within the range 16.9–17.5 °C (Figure 4). Judging by those pertaining at daybreak next day, they did not increase with the first fresh. DO levels rose by up to 2 mg l^{-1} during the fresh, presumably mainly due to aeration from the highly-pressured bottom release. As the fresh declined at dawn to a lower flow, DO levels fell again, while water temperatures held steady.

No fish were seen on Bed A before the release (Table 3), although there were many present immediately downstream in Pool 3 (Table 2). Nor did the fish arrive on Bed A after the experimental fresh (Figure 4). By mid afternoon it was clear that the fresh had not triggered the same spawning response from the fish as in the previous year. Low water temperatures were the suspected cause, although light rain during the afternoon introduced a confounding factor. The planned release pattern was then changed, to allow a release of warm epilimnetic water. Its magnitude and duration were dictated by dam design and water-resource considerations, but it did run for sufficiently long to change the temperature conditions at the spawn site.

The second experimental fresh

The second experimental fresh, of magnitude $11.0 \text{ m}^3 \text{ s}^{-1}$, was released from the top of the dam wall for 15 hours overnight on 29–30 November, commencing at 15h15. It was reduced to a hypolimnetic release of 2.3 m³ s⁻¹ at 06h08.

The water temperature rose slightly during the day after the first fresh, then fell slightly with the rain (Figure 4). It then began to increase noticeably in mid-afternoon, two hours after the top release began, and by daybreak the next morning was 4 $^{\circ}$ C higher

Table 3. Average numbers of fish on Spawn Beds A and B per ten minutes in each listed time span, and observed movement in two pools from observations of approximately ten minutes duration in each listed time span. * denotes a spot record, \checkmark denotes fish movement, and $\checkmark \checkmark$ more than 10 movements observed. Note that periods with no difference in results have been condensed into one line. Gaps indicate times when no observations were made

Date	Time	Spawn Bed A	Spawn Bed B	Pool 2	Pool 3	Comments
27 Nov	12:00 20:00	0				Bottom release continuous at 4.2 m ³ s ⁻¹
27 NOV 28 Nov	12:00-20:00	0	0			Bottom release continuous at 4.2 m s
20100	08:00-15:00	0	0			
	15:00-17:00	0				Fish_count survey
	17:00-18:00					Bottom release increased to $14.0 \text{ m}^3 \text{ s}^{-1}$ at 17:00
	18:00-19:00	0	1*			Bottom recease increased to 14.0 m s at 17.00
29 Nov	06:00-10:00	0	1			Bottom release reduced to $4.2 \text{ m}^3 \text{ s}^{-1}$ at 6:00
291101	10:00-12:00	0				Scattered rain
	12:00-14:00	0				
	14:00-15:00	0				Light rain
	15:00-17:00	0				Bottom release stopeed. Changed to
	10100 17100					top release of 11.0 m ³ s ⁻¹ at 15:15
	17:00-18:00	0				Heavy rain
30 Nov	05:00-06:00	2.0				
201101	06:00-07:00	1.3				Top release stopped. Changed to
	00100 07100	110				bottom release of 2.3 m ³ s ⁻¹ at 06:08
	07:00-08:00	0				
	08:00-09:00	6.2		1		
	09:00-10:00	1.3				
	10:00-11:00	0.3		1		
	11:00-12:00	0			1	
	12:00-13:00	1.0				
	13:00-14:00				1	Sporadic viewing only, as searching for
	14:00-15:00	0		1	•	eggs and photographing larvae
	15:00-16:00	, in the second se				-998 L9L9
	16:00-17:00			0		Bottom release stopped. Changed to
						top release of 11.0 m ³ s ⁻¹ at 16:20
	17:00-18:00	0		\checkmark		t the second
	18:00-19:00	0.2				
	19:00-20:00	0.1				
1 Dec	06:00-07:00	0.2		\checkmark		
	07:00-08:00	0	1*	1	\checkmark	Top release stopped. Changed to
						bottom release of 3.0 m ³ s ⁻¹ at 07:00
	08:00-09:00	1.7				
	09:00-10:00	2.0		\checkmark	\checkmark	
	10:00-11:00	0.7		$\checkmark\checkmark$	\checkmark	
	11:00-12:00	0		$\checkmark\checkmark$	$\checkmark\checkmark$	
	12:00-13:00	0			$\checkmark\checkmark$	Bottom release increased to 8.0 $\text{m}^3 \text{ s}^{-1}$ at
						12:00 to meet irrigation demand
	13:00-14:00					Searched for eggs and embryos
	14:00-15:00	0	0	0	$\checkmark\checkmark$	
	15:00-16:00	0.7	0	0	$\checkmark\checkmark$	
	16:00-17:00	0	0	\checkmark	$\checkmark\checkmark$	
	17:00-18:00	0.8	0	\checkmark	\checkmark	
2 Dec	08:00-09:00	0	0	\checkmark	\checkmark	
	09:00-10:00			0		
	10:00-11:00	0		0	\checkmark	
	11:00-12:00			\checkmark		
	12:00-13:00	0	0	\checkmark	\checkmark	



Figure 4. Water level, water temperature, air temperature and dissolved oxygen levels at the spawn site downstream of Clanwilliam Dam on the Olifants River during the experimental hypolimnetic (bottom) and epilimnetic (top) releases from the dam, related to the presence of *Barbus capensis* on Spawn Bed A. Sunrise was at approximately 06h15 and darkness fell at 20h00. White circles represent Spawn Bed A and black circles Spawn Bed B. Solid horizontal lines show times of observation at Bed A, and dashed lines, the presence of the fish on Bed A. A final spot reading of water height and temperature was made before departure on 2 December.

(21 °C) than before the release. It did not decline as the fresh gave way to a low hypolimnetic release, but rather showed a further modest increase during the hot, sunny morning. It eventually began to decrease in late afternoon, some ten hours after the top release had ceased.

By this time it had been realised that Bed A was responding differently to B in terms of WSE and water temperature. Readings of both were thus initiated at Bed A during the day of 30 November. These showed that changes in discharge were being reflected in terms of water levels and water temperatures sooner at Bed A than at Bed B, where it had to filter through the dense palmiet beds (Figure 1). Whereas Bed B took ten hours for water temperatures to decrease after the top release stopped, those at Bed A took less than five hours. Both had reached the same low of 17.7–18.0 °C by 12 hours after the top release ceased.

In contrast to conditions with the first fresh, DO concentrations at Bed B did not increase with the second fresh. Instead they showed a decline at dusk, as the water temperatures rose (Figure 4). The DO levels were still lower at daybreak and did not increase until late in the afternoon, coinciding with the decline in water temperature. Thus, the highly-pressured bottom releases appeared to oxygenate the downstream water more than did top spillage.

Fish were on Bed A at daybreak on 30 November (Table 3 and Figure 4), sometimes in groups of up to 15 individuals, presumably in response to the presence of warm top-release water. There was continuous activity at Bed A until about 11h00, five hours after the top release stopped. Fish biologists felt the fish were 'preparing to spawn' (K. Hamman, CNC, pers. com.). All activity then ceased and the fish disappeared. Shortly after that the water temperature at Bed A was measured for the first time, at 18.8 °C and falling. In addition to those fish present at Bed A, there was a moderate amount of activity upstream and downstream of Bed A, at Pools 2 and 3 respectively (Table 3).

As a result of these observations, another fresh of epilimnetic water was arranged. As before, there were restrictions to its duration and magnitude.

The third experimental fresh

The third experimental fresh, of magnitude $11.0 \text{ m}^3 \text{ s}^{-1}$, was released from the top of the dam wall for almost 15 hours overnight on 30 November-1 December, commencing at 16h20. It was reduced to a hypolimnetic release of $3.0 \text{ m}^3 \text{ s}^{-1}$ at 07h00 (Figure 4).

Water temperatures began to rise at the spawn site two hours after the top release began, with the rise beginning earlier and more sharply at Bed A. By next morning both beds were at 21.6–21.7 °C. The temperature began to fall at Bed A about three hours, and at Bed B five hours, after the top release stopped.

The DO level began to increase in late afternoon of 30 November, mirroring the falling water temperature at the end of the second fresh (Figure 4). It then showed a slight decline till dusk, as the effect of the third fresh manifested as increasing water temperatures. By the following morning DO was still considerably higher than at the same time after the second fresh, for reasons not understood. The level began to rise again in the afternoon, again mirroring the falling water temperature at the end of the third fresh.

Fish were again moving around Bed A at daybreak of 1 December, though in smaller numbers than the previous day and mostly as single individuals or pairs. Again, the fish disappeared at about 11h00, some four hours after the top release stopped. Water temperature at Bed A at that time was 19.3–19.9 °C and falling. More activity than on the previous day was noticed at Pools 2 and 3, with both pools showing much movement as the fish left Bed A. Within an hour of leaving Bed A, however, most seemed to have moved downstream to Pool 3.

After the freshes

The hypolimnetic release was increased to $8.0 \text{ m}^3 \text{ s}^{-1}$ at 12h00 on 1 December, in order to meet irrigation demand. Water temperatures remained low and, apart from two brief sightings, no more fish were seen at Bed A that day or until observations ceased the following midday.

Daily observations at the bridge by a volunteer observer continued during December, with 15-minute counts of fish movement made at each of the two spawn beds and each of the two pools. Although the high irrigation releases reduced visibility through the water, fish appeared to be absent from these areas until 17 December. At that time, in a complex sequence of events, light rain occurred, fish were seen at the study site and the dam release was stopped completely overnight for operational reasons (Figure 3). When the release began again next day, spawning occurred prolifically throughout the day, with up to 15 fish on Spawn Bed A at any one time (D. du Toit, volunteer observer, pers. com.). The discharge at the time of spawning is not known as releases and thus hydraulic conditions fluctuated for some time after the shut-down. Up to 14 December, water temperature immediately downstream of the two spawn beds had ranged 17–19 °C. At the time of spawning, it was between 18 °C and 20 °C.

Presence of eggs and larvae

Small samples of larval fish were collected from the larval fish site in the two weeks before the experimental flows. These were more than likely all from the same spawning. Those collected on 15 November 1995 were approximately 17 days old (Table 4), based on a developmental temperature of 22 °C (Cambray et al., 1997).

Prior to the first experimental fresh, on 27 November, free embryos were found at Spawn Beds A and B which were approximately 10–17 days old (Table 4). No eggs were found. On the 28 November, immediately before the first fresh, more free embryos of about the same age were found at the two spawn beds, the largest of which had just inflated its swimbladder and actively attempted to avoid capture. After the second and third experimental freshes, that is, on 30 November and 1 December, Spawn Beds A and B were again searched for eggs. None were found at either bed (Table 4).

The presence of free embryos and larvae indicated that some spawning had occurred at least three to four weeks prior to the experimental releases, when water temperatures had been above 20 °C. Several of the free embryos were deformed, which may have been due to water temperature or chemical changes during their development. The collections also suggested that no spawning had occurred from when the cold, hypolimnetic releases began on 15 November, to the end of the experimental period.

Hydraulics of the spawn beds

Hydraulic conditions in the channel encompassing Bed A were investigated using data collected from 97 points along six cross-sections. The readings were taken when water was being stored for the first experimental fresh and thus discharge was similar to

Date and time of collection	Locality (see Figure 1)	Early life history stage	n	mm TL (SL or NL)	Approximate age in days (see text)
15 November 1995	LFS	Larva	11	11.1 (10.5) - 12.0 (11.2)	17
17 November 1995	LFS	Larva	9	11.1 (10.2) – 12.3 (11.3)	
21 November 1995	LFS	Larva	11	11.4 (10.3) – 12.8 (11.7)	
24 November 1995	LFS	Larva	12	12.0 (11.0) - 14.0 (12.5)	
27 November 1995 (16h30)	Spawn bed B	Free embryo	5	11.0 (10.4) - 12.0 (11.4)	10–17
27 November 1995 (18h00)	Spawn bed A	Free embryo	1	11.2 (10.7)	
28 November 1995 (11h20)	LFS	Larva (swim bladder	5	12.3 (11.5) – 15.5 (13.4)	17–21
		starting to divide)			
28 November 1995 (13h00)	Spawn bed B	Free embryo	6	11.2 (10.6) – 12.4 (11.5)	10–17
30 November 1995 (14h00)	LFS	Larva	28	13.6 (12.0) - 17.0 (14.4)	21->21
1 December 1995	Spawn beds A	No recently spawned			
	and B	developing embryos			

Table 4. Summary of the early life history stages of *Barbus capensis* collected before and after the experimental freshes. Approximate age is from Cambray et al. (1997). LFS = larval fish site

that occurring when spawning was observed in 1994. From the results, vegetation and substrata maps were drawn of the whole channel at that point (Figure 5), as well as contour maps of water depth and average water-column velocity (Figure 6) and Froude numbers (Figure 5). The actual spawning area within Bed A used in 1994 (Figure 5) was located on the maps from study of the video footage taken by Cambray et al. (1997).

Beds of submerged aquatic vegetation, Aponogeton, occurred along the edges of the wetted channel, extending well into the channel along the left bank. Dense stands of Typha flanked the outside edge of the Aponogeton on the left bank, whilst overhead cover on the right bank was provided by trees such as the native willow Salix mucronata. Fine sediments, up to the size of gravel, were confined to the vegetated edge areas, with larger particles in the open channel. Boulders and large cobble dominated Bed A, giving way downstream to medium and small cobble. Away from the vegetation, the substrata were clean and not embedded in fines. Water depths at Bed A were mostly in the range 0.3-0.5 m, and mean column velocities 0.8-1.3 m s⁻¹. Froude numbers were in the range 0.4-0.6.

The hydraulic conditions in the channel encompassing Bed B were also investigated. The first eggs of *B. capensis* found in this study were at this bed (Cambray et al., 1997), and fish visited it during the successful spawning period at Bed A in 1994. However, individuals never held position there for long, and always left without spawning. Possibly, when the release was then at a low $3.0 \text{ m}^3 \text{ s}^{-1}$, water depths were too shallow at Bed B. In 1993, when the dam release was $4.6 \text{ m}^3 \text{ s}^{-1}$, 11 spot measurements of hydraulic conditions at Bed B had shown water depths of no more than 0.26 m and velocities of $0.2-1.0 \text{ m s}^{-1}$ (King, pers. com.). Thus, at a higher discharge than was present during spawning in 1994, the velocities at Bed B encompassed the range present during spawning at Bed A, but the depths were lower.

Fish do spawn at Bed B, however, as eggs have been found there on several occasions (Cambray et al., 1997). It might be that the bed becomes more suitable for spawning when the higher irrigation releases are occurring. Thus, at the end of the 1995 experimental freshes, when the release was increased to 8.0 m³ s⁻¹ for irrigation purposes, the hydraulics of Bed B were further investigated. Addressing the same variables as for Bed A, 48 readings were taken from eight crosssections (Figures 7 and 8).

Dense beds of palmiet lined the left bank, with the right bank being low and grassy. An upstream deep pool (Figure 1) gave way to a confined fastflowing reach encompassing Bed B. The bed consisted of mixed large, medium and small cobbles with areas of submerged boulders. Most had a slippery epilithic coating, but those in the area of 'Spawn Rock' (Figure 7), where eggs and free embryos were found, were clean. Water depths at Bed B were in the range 0.3– 0.6 m and, excluding the areas in hydraulic cover,



Figure 5. Vegetation and substrata maps (A), and contour maps of Froude numbers (B), at a dam-release volume of $3.4 \text{ m}^3 \text{ s}^{-1}$, for the channel area encompassing the designated Spawn Bed A in the Olifants River. Solid lines demarcate categories of substrata; dotted lines the limit of the macrophyte *Aponogeton*; and dashed lines the limit of the *Typha* stand. All observed spawning of *Barbus capensis* in 1994 (Cambray et al., 1997) occurred in the shaded area. Flow direction is from the top of the map.

mean column velocities were $0.6-1.2 \text{ m s}^{-1}$. Froude numbers were in the range 0.4-0.8.

Thus, it seems possible that the hydraulic characteristics at Bed B at high irrigation releases are more similar to those pertaining at Bed A during the 1994 spawning than to those at Bed B when discharges are lower. This suggests that, despite its small size, the smaller channel might be an important spawning area for much of the summer when releases are driven by irrigation demands.



Figure 6. Contour maps of water depths (A) and average column velocities (B) at a dam-release volume of $3.4 \text{ m}^3 \text{ s}^{-1}$, for the channel area encompassing the designated Spawn Bed A in the Olifants River.

Discussion

Upstream migrations

A complex interplay of environmental factors appears to be involved in fish migration in rivers (Northcote, 1984). Many studies have noted that increasing discharges initiate spawning migrations (e.g. Libosvarsky, 1976; Welcomme, 1985; Cambray, 1991; Masse et al., 1991). Jonsson (1991) stated that in some cases initiation of migrations appears to be associated with temperature or discharge or, for some species, with an increase in discharge within a certain temperature range. Tyus & Karp (1990) also identified discharge levels and temperature as associated with spawning migrations. In further work using telemetry, discharge appeared as the most consistent cue for movement to the primary spawning location (Modde





Figure 7. Vegetation and substrata maps (A), and contour maps of Froude numbers (B) at a dam-release volume of $8.0 \text{ m}^3 \text{ s}^{-1}$, for the channel area encompassing the designated Spawn Bed B in the Olifants River. No spawning was observed at Bed B on any of the research trips, but live eggs and free embryos of *Barbus capensis* were found downstream of 'Spawn Rock', each summer from 1992–95. Flow direction is from the top of the map.

Figure 8. Contour maps of water depths (A) and average column velocities (B) at a dam-release volume of $8.0 \text{ m}^3 \text{ s}^{-1}$, for the channel area encompassing the designated Spawn Bed B in the Olifants River.

& Irving, 1998). Spawning migrations of the quillback *Carpiodes cyprinus* were initiated after an increase in discharge, as long as temperatures exceeded 5 °C (Parker & Franzin, 1991). For the migration of white suckers, *Catostomus commersoni*, discharge explained a greater variation in the number of fish migrating than temperature, but the greatest variation was explained by the product of the two variables (Barton, 1980).

Northcote (1984) felt that increasing and decreasing photoperiod was the predictive, proximate factor in temperate areas, enabling the fish to sense spawning and non-spawning seasons. In most parts of the world, there are obvious links between photoperiod, temperature and river flow, with the natural variability in the two latter factors at least partly accounting for the annual variation in spawning migrations (Jonsson, 1991).

In the Olifants River, *B. capensis* gonad mass begins to increase as early as August (Van Rensburg, 1966), whilst water temperatures are still low and discharges high. Photoperiod may well be implicated in these early signs of reproductive activity, but there is still much to be learnt about the causal mechanisms that eventually lead to spawning migrations. As with a North American cyprinid, the Colorado squawfish *Ptychocheilius lucius* (Tyus, 1990), the influence of environmental cues in initiating spawning migrations of *B. capensis* is not yet clear. Such understanding is a vital component of the efforts to conserve species such as *B. capensis*.

Whatever triggers migration, when it does occur in the Olifants River in spring, the population of *B. capensis* inhabiting the stretch of river between Clanwilliam Dam and Bulshoek Weir appears to show some co-ordinated movement upstream in an attempted migration run to headwater spawning grounds. The dam prevents accessibility to these spawning grounds, however, and potential spawning grounds are further limited by the virtual nonexistence of cobble beds in the middle reaches of the river. Nevertheless, some spawning does occur at the two areas downstream of the dam wall as identified by the presence of young life-history stages in this study and spawning in the previous study (Cambray et al., 1997).

Water temperature and flow as triggers for spawning

At the spawning grounds, water temperature is clearly one of the major factors influencing fish spawning (Wootton, 1990). Most authors report temperature in terms of the general condition of the river at the spawning season. It is less common for temperature to be reported in relation to the effects of dams on spawning. Such effects are important, because for some distance downstream of dams, normal river temperatures may no longer pertain. Indeed, water temperatures may be providing environmental cues at variance with other possible ones such as photoperiod. Both discharge and temperature can be greatly altered below dams and impact on the annular timing and frequency of spawning migrations. Two large Barbus species, the smallmouth vellowfish (B. aeneus) and the largemouth yellowfish (B. kimberleyensis), whose spawning is governed by water temperatures (Tómasson et al., 1984), spawn on gravel beds within the main river channel below the Gariep Dam on the Orange River, South Africa. In this reach, hydroelectric releases from the power station at the dam have altered both discharges and temperatures in the downstream river. It appears that the unseasonal releases of cold water from the upstream impoundment have resulted in poor reproductive success. These authors recommended that hydrological manipulations, such as releasing epilimnetic water in spring and early summer, would lead to earlier spawning and higher recruitment for these two Barbus species.

For B. capensis, Cambray et al. (1997) found that dam releases of high-flow freshes in spring did correlate with successful spawning in 1994. It seemed probable that *B. capensis* had been brought into spawning condition by the general spring increase in river temperatures (Figure 2), possibly linked to factors such as photoperiod. Port Elizabeth, at almost the same latitude, records photoperiod increasing from a July mid-winter low of 9.9h (day):14.1h (night), through August (10.5h:13.5h) and October (12.4h:11.6h) to a mid-summer value in January of 14.4h:9.6h (Weather Office, Department of Transport, Port Elizabeth Airport). Once in condition, spawning then appeared to be triggered by a small increase in discharge. The 1995 experiment, designed to repeat the previous year's spawning success, did not however result in any acts of spawning. The extension of winter conditions into spring, characterised by snow on the mountains of the headwaters and floods, resulted in heavy flows of cold water arriving in Clanwilliam reservoir later than usual. This was reflected in spillage from the dam, which continued until 15 November 1995, compared to 1994, when it stopped in August. When spillage stopped in November 1995, coincidentally just before the experimental period, relatively warm epilimnetic releases were replaced by cold, hypolimnetic releases. As a result, daytime water temperatures during the experimental period in 1995 (outside of the period linked to the top experimental releases) were 16.6-17.5 °C at both Beds A and B, compared to 19.1-20.0 °C at Bed A and 21.8-23.1 °C at Bed B in 1994. At the same time (3 December 1995) temperature of the river water flowing into the upstream end of Clanwilliam reservoir was 24.2 °C (King, pers. com.).

The fish had been in the spawning area in November 1995 prior to the switch to hypolimnetic releases, and divers completing fish counts immediately before the experimental releases reported that the fish downstream of the spawning area were in breeding condition. Fish were scarce in the spawning area after hypolimnetic releases began, but arrived on Bed A once warm top releases began. All arrived from a downstream direction, exhibiting what was interpreted as pre-spawning behaviour. The behaviour never culminated in spawning, and the fish left Bed A again, after the first top release but before the first temperature reading was taken there (18.8 °C). They appeared on Bed A again with the second top release, but left it again after the top release stopped and when the temperature was dropping 19.9-19.3 °C. In comparison, as noted above, the temperature at Bed A during spawning in 1994 was 19.1-20.0 °C. Thus, a hypothesis for future testing is that water temperature on the spawn beds for successful spawning of B. capensis has to be at least 19 °C and stable or rising. It may be further hypothesised that if the fish are in breeding condition and these temperature conditions are met, then experimental freshes of the size described in these studies will trigger spawning.

Thermal spawning thresholds have been identified for other species of cyprinids, below which spawning will not occur. For example, in a review of the minimum spawning temperature of ten populations of tench (*Tinca tinca*), it was established that the lower limits were between 18-20 °C (Horoszewicz et al., 1981). Lower temperatures resulted in interruption of spawning and reabsorption of maturing eggs. Baras et al. (1996) noted that in the River Ourthe in Belgium, the common barbel *Barbus barbus* started spawning when the daily minimum water temperature was 13.5 °C but suspended breeding whenever temperatures fell below this threshold.

Although no spawning was induced during the 1995 experiment, *B. capensis* free embryos approximately two to three weeks old (based on development at a constant 22 $^{\circ}$ C) were found on the spawn beds

during the study. Conditions prior to the experiments, that is, in mid-November or earlier, thus must have been suitable for spawning. In early November, water temperatures thought to be suitable for spawning (22-23 °C) were recorded downstream of the dam (Figure 3), with temperatures of about 20 °C recorded since early October (Figure 2). If these temperatures had brought the fish into breeding condition, then the floods in late October (Figure 2) would have been the most likely trigger for spawning. After the fish had spawned in late October or early November, the embryos would then have experienced temperatures below 18 °C after 15 November (Figure 3), which probably considerably slowed their development. It is thus possible that the free embryos collected during the experiment were over four weeks old. That some of the collected embryos were dead or deformed may have been due to these temperature fluctuations (Hempel, 1984).

Hydraulic conditions related to spawning

Conditions other than those discussed above are also important for successful spawning. Variables such as availability of spawning grounds and the use of such features as flooded vegetation or clean cobbles are mentioned in the literature (Wootton, 1990). Hontela & Stacey (1990) give water level, water quality, nutrients, temperature, breeding substrate and vegetation as the factors which may determine spawning success of cyprinids. All of these factors may fluctuate on a seasonal basis. More recently, authors have reported in detail on the substrata and local hydraulics of spawning grounds. The main features usually mentioned are water depth and velocity, area, and particle size of the substratum. For instance, Baras et al. (1996) described spawning pits for Barbus barbus that had a gravel substratum (20-50 mm diameter), water depth of 0.10-0.26 m and water velocity of 0.26–0.67 m s⁻¹. The Colorado squawfish spawned at 22 °C over a rubble substratum at a water depth of 0.9-2.1 m and a velocity of 0–0.1 m s⁻¹ (Tyus & McAda, 1984). These are deeper water and lower velocities than recorded here for the Clanwilliam yellowfish (0.3-0.6 m; 0.6-1.3 m s^{-1} : Figures 5 & 6).

Heede & Rinne (1990) urged the use of Froude numbers to quantify objectively the type of flow, thereby allowing improved mathematical-statistical analysis of fish-flow relationships. Moir & Soulsby (1996) included Froude number in their report, describing spawning areas, or redds, for Atlantic salmon Salmo salar, with the following mean characteristics: utilised depth of 0.25 m, velocity of 0.54 m s⁻¹, mean Froude number of 0.34 (Froude numbers for *B. capensis*: 0.4–0.8) and substratum particle size of close to 15 mm (*B. capensis*: substrata > 256 mm). They, and Wadeson (1995), pointed out that the Froude number is useful because it is dimensionless and can therefore be applied to a range of sizes of river and fish. Wadeson (1995) also found that Froude number was a useful index distinguishing hydraulic biotopes such as riffle, rapids and cascades on the one hand, and pools and runs on the other. He identified areas with Froude numbers as high as those recorded for *B. capensis* spawning grounds as riffles.

Reproductive style

Many species with extended spawning seasons are multiple spawners with individual females producing several clutches of eggs, as does B. capensis. In many oviparous teleosts multiple clutches of eggs are spawned periodically in a reproductive season and ova undergo group synchronous development (Wallace & Selman, 1981; Heins & Robito, 1986). The ovaries of these species cycle through maturing, mature and ripe stages, as noted for Notropis leedsi (Heins & Robito, 1986), B. anoplus (Cambray & Bruton, 1994) and Pseudobarbus asper (Cambray, 1991). This implies for species such as B. capensis, which have the ability to spawn more than once per season, that it is important to provide spawning and recruitment flows more than once per spawning season in order to ensure survival of a year group.

Conservation considerations

Cueing to the natural hydrographic and thermal regimes in riverine environments may congregate fish at spawning sites and increase spawning success. Modde & Irving (1998) suggested, for the razorback sucker in North America, that increasing discharges initiate movement and aggregation of reproducing adults. This maximizes the reproductive success of small genetically isolated populations. Tyus & Karp (1990) suggested several other factors that would need to be considered in the recovery plans for this species. These included habitat alteration and loss in the form of curtailment of spring flooding, loss of historic hydrological and temperature regimens, and reduced flooding of floodplains. A further important factor requiring active management was predation by nonnative fishes. Tyus (1990) pointed out that migration and other reproductive behaviour traits of the Colorado squawfish are attuned to a variety of stimuli, including intrinsic mechanisms and dependable environmental clues. He suggested that a better understanding of these mechanisms and cues could assist management and recovery efforts for this endangered species.

Most of the above factors are relevant to the continued presence of *B. capensis* in the middle reaches of the Olifants River. The stretch of river downstream of Clanwilliam Dam is unusual and conservationworthy, as it is the only part of these middle reaches where *B. capensis* appears to be successfully resisting the predatory impacts of the alien *M. dolomieu*. At present, the area is conserved as a sanctuary for *B. capensis*.

Suitable discharges and temperatures for spawning of B. capensis have been discussed, and the need to synchronise aggregation in the spawning areas noted. There is also an obvious adaptive significance in synchronising the occurrence of eggs and larval stages with seasonal conditions which are most suitable for survival. Additionally, Spawn Bed A appears to be very sensitive to changes in dam releases. The water level there drops rapidly after the release is reduced (Figure 4). If the release were halted, this area, being a high point in the channel, would be particularly vulnerable to drying out. Until this vulnerability has been investigated, it is recommended that special caution be taken to avoid total shut down of releases during the summer breeding season. A summary of conditions now believed to induce spawning and support early life stages of *B. capensis* is provided (Table 5).

A further factor that may be affecting successful spawning and recruitment is the small size of the spawning area described in this study. It is considered to be the most important spawning area, and possibly the only such area, available to the *B. capensis* population between the two dams, and most eggs released there may be swept to downstream pools by the strong current. Thus, it is strongly recommended that both spawn beds be artificially extended to increase the available spawning area. A question that remains unanswered is the extent to which the delay in the onset of summer temperatures downstream of the dam allows sufficient time for the species to complete early life stages before winter.

Stage or condition	Requirement
Gonadal development	Increase in gonad mass in August to October
	(Van Rensburg, 1966) possibly linked to spring
	increase in photoperiod and water temperature
Spawning period	October to January
Spawning style	Repeat and multiple
Photoperiod during spawning period (day:night)	October (12.4h:11.6h) – January (14.4h:9.6h)
Synchronised arrival on spawn bed	When in breeding condition, triggered by a fresh of suitable magnitude, duration and water
	temperature
Spawning temperature threshold	19 °C
Preferred spawning temperature	Above 19 °C
Hydrograph of fresh;	
magnitude	$9-17 \text{ m}^3 \text{ s}^{-1}$
duration	12 hours
Spawning conditions at bed:	1
average column velocity	$0.6-1.3 \text{ m s}^{-1}$
water depth	0.3–0.6 m
Froude number	0.4–0.8
substratum	Cobbles and boulders; > 256 mm; free of silt and algae
Embryonic development	Probably temperatures of above 19 °C at spawn
	beds for at least 9-20 days after spawn
Larval habitat:	
average velocity	$< 0.18 \text{ m s}^{-1}$
water depth	< 0.28 m
Froude numbers	< 0.17
substratum	Coarse sand; sparse submerged vegetation
temperature	Known to occur at 25-27 °C
Juvenile survival	Not known

Table 5. Summary of conditions believed to induce spawning of *Barbus capensis* at the spawn site downstream of Clanwilliam Dam in the Olifants River, and to support early life history stages. Information, unless otherwise indicated, is from this study and from Cambray et al. (1997)

Conclusions

In all instream flow assessments made so far for rivers in the winter-rainfall area encompassing the Olifants River, dry-season freshes have been recommended (King, pers. com.). They are mostly included to promote fish spawning. Correlation has been reported between the release of such freshes from Clanwilliam Dam and spawning of the Clanwilliam yellowfish *B. capensis* (Cambray et al., 1997). This latest study has shown, however, that providing the right hydraulic conditions at the right time will not trigger spawning if the water temperatures are not suitable. The temperature of released waters can be manipulated from dams with multiple release structures. This strategy may have limited success, though, unless the temperatures are then maintained at levels that are suitable for the developing young.

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