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# THE EFFECTS ON FISH SPAWNING AND MANAGEMENT IMPLICATIONS OF IMPOUNDMENT WATER RELEASES IN AN INTERMITTENT SOUTH AFRICAN RIVER

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## ABSTRACT

The potamodromous smallscale redfin minnow (*Pseudobarbus asper*) spawned in the riffle areas of the regulated Groot River, the major tributary of the Gamtoos River system, during controlled releases of water from Beervlei Dam. Water had been released at irregular intervals from this flood control dam solely for irrigating agricultural lands. Flushing flows removed accumulated salts from riverine pools and were followed by reduced flows which initiated spawning of the minnow species. Developing embryos of *P. asper* were found in the riffle zone of the main river channel during the water releases. Ripe-running males were located under the boulders in the riffles. Several developing embryos of *Labeo umbratus* were found with the *P. asper* eggs. Very little is known about the effects of man-made alterations to the river flow regime on the reproductive activity of fishes in the majority of South African river systems. The agriculturally based flooding regime at Beervlei may have increased the recruitment of the redfin minnow species. Water management must give cognizance to the biological and environmental requirements within the regulated river systems. Water release strategies from Beervlei Dam should include instream flow decisions based on the requirements of the aquatic environment as well as for agriculture.

KEY WORDS African freshwater fish Beervlei Dam Conservation Controlled releases/flooding Groot-Gamtoos River Integrated river basin management *Labeo* Minnows Potamodromous *Pseudobarbus* Reproduction

## INTRODUCTION

There is very little known about the biology of the African redfin minnows of the genus *Pseudobarbus*. Several redfin minnow species are in the Red Data Book (Fishes) (Skelton, 1987) and one of the causal factors endangering the survival of these species is river regulation (Gaigher *et al.*, 1980). A better knowledge of the spawning ecology and suitable river regulation regimes will help to conserve riverine habitats for these species.

The native fish fauna of the Groot River is adapted to an environment of cyclical patterns with the amplitude of flow varying considerably from year to year. This pattern of hydrology is often found in semiarid areas. In southern Africa the average coefficient of variation for river flows is 0·7 which is comparable to Australia, but is three and half times greater than for European Rivers (Braune, 1985; O'Keeffe, 1989).

The Beervlei Dam, a flood control dam, has reduced the severity of floods in the Groot River since it was constructed in 1957. After heavy rains in March 1988 the impoundment filled in a matter of days. The stored water was subsequently released at regular intervals to flush out brackish water in the Groot River to improve the quality of irrigation water. Initially the river flowed at a high flushing velocity for 15 hours. Flow decreased over the following days and then completely stopped. These releases of water at regular intervals for agricultural purposes have altered the natural temporal pattern of flow fluctuations in the river below the dam. The present study was undertaken to establish what impact this flooding regime had on the breeding of the fish fauna.

There is a need to coordinate the instream flow requirements of the aquatic fauna with those of agriculture and other user agencies. At present there are ever increasing stresses on South African stream ecosystems

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which are a result of overutilization of water in a relatively dry country (Alexander, 1985). Recent studies by Bryen and Davies, 1989; Palmer and O'Keeffe, 1989; O'Keeffe *et al.*, 1990, and other ongoing studies in South Africa are providing some useful practical frameworks for the management of releases from impoundments.

## METHODS

The Groot River is the major tributary of the Gamtoos River system and flows predominately through semiarid ranch-farming land (Figure 1). This system is one of the major rivers in the southern Cape and has a gross catchment area of 34 450 km$^2$ and a virgin MAR of 501 × 10$^6$ m$^3$ a$^{-1}$ (Anon, 1986) and is approximately 600 km in length. The Gamtoos River has been grouped in with the southern Karoo rivers because it is usually very turbid with medium to very high dissolved salts (Noble and Hemens, 1978). The river is intermittent as the rainfall in the area is both low and sporadic. The average yearly precipitation for the period 1959–1980 at Beervlei Dam was 195 mm with a range of 68–351 mm. Rain can occur during any month. The peak rainfall months (averages) were February (31 mm), March (33 mm), and April (23 mm) for the 21 year period.

Beervlei Dam wall is a multiarch buttress design which was built in 1957 on the Groot River (Figure 1). The dam was built to control, or at least minimize, the impact of flash-flooding to farm lands below the dam wall. Originally the government was reluctant to build this dam because of the extremely irregular flow, high mineral content, and silt loads of the inflowing rivers. The Beervlei Dam wall is 20·7 m high from river bed level with a crest of 348 m and had a storage capacity at full supply level of 92.580 × 10$^6$ m$^3$ after the dam wall was raised in 1967 (Department of Water Affairs, Pretoria, personal communication). The last survey, which was conducted in October 1985, showed that the full supply capacity had been reduced, due to silt retention, to 90·828 × 10$^6$ m$^3$ (Department of Water Affairs, Pretoria, personal communication). The area under irrigation from the reservoir is 2660 ha. The yearly inflow pattern into the reservoir over the period 1958–1989 has been very irregular (Figure 2), varying from no inflow (1983–1985) to 524·2 × 10$^6$ m$^3$ (1960/61). The inflow pattern on a monthly basis for the period 1980–1989 also highlights the sporadic nature of the riverine flow varying from no inflow for long periods to 205 × 10$^6$ m$^3$ in March 1988 (Figure 3).

Prior to March 1988 Beervlei Dam last spilled in 1981. During the floods of February/March 1988 (Figure 3) Beervlei Dam rapidly went from 0 per cent to overflowing in less than 12 days. The dam reached

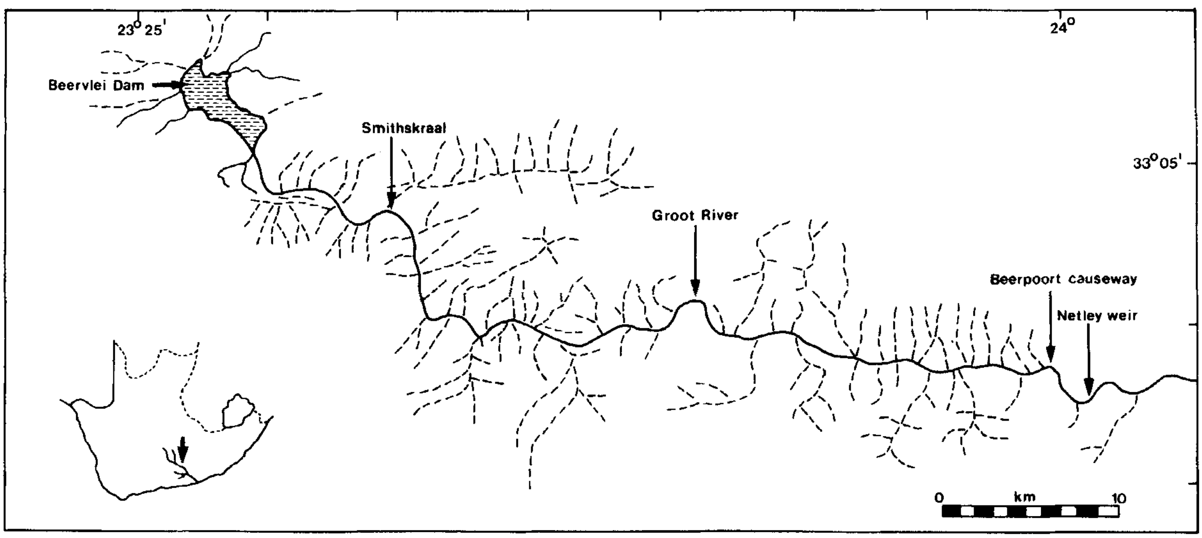


Figure 1. Location of the Beervlei Dam on the Groot River a tributary of the Gamtoos River system. Spawning sites are between the Beerpoort causeway and the Netley weir

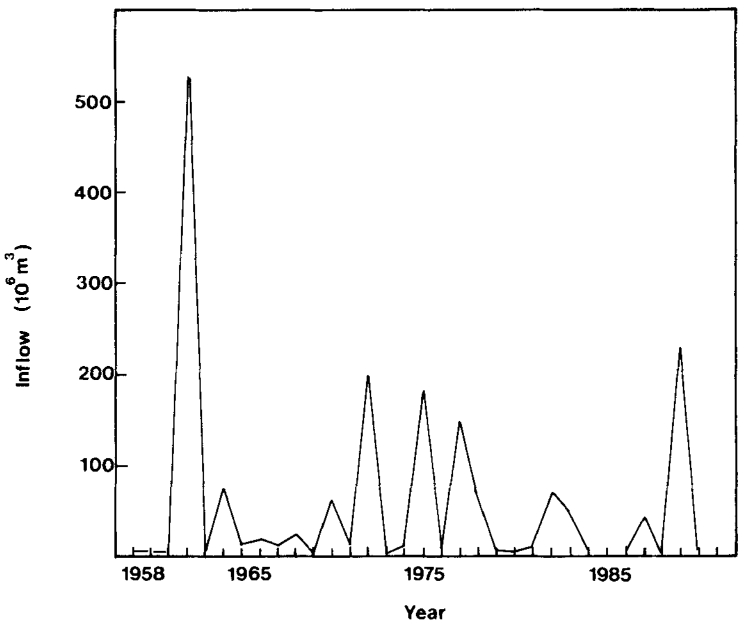


Figure 2. The yearly inflow into Beervlei Dam over the period 1958–1989

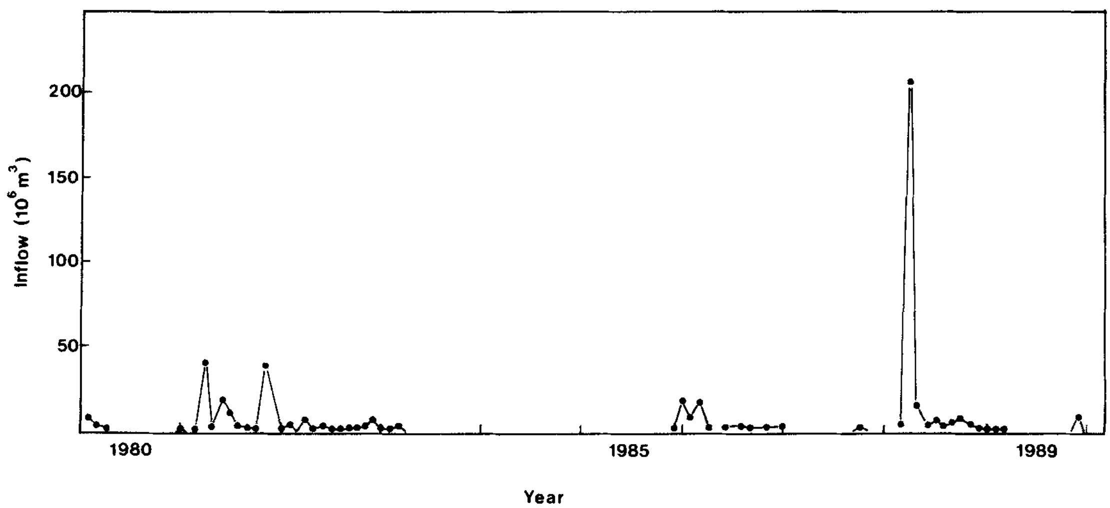


Figure 3. The monthly inflow pattern into Beervlei Dam over the period 1980–1989

145 per cent on 10 March, 1988 and continued to spill until May 1988. Subsequently, the Department of Water Affairs, together with the local farming community, planned a series of eight water releases during the summers of 1988/89 and 1989/90 (Figure 4) to flush out the pools of brack water between the Beervlei Dam wall and Steytlerville in order to improve the water quality in the river for irrigation. The releases were in decreasing volumes of water over a 4–5 day period commencing with a strong flushing flow of between 56·64 and 65·35 $m^3 s^{-1}$ (Figure 4). The varying release flows were a result of experimentation by the Advisory Committee of the water scheme in order to reach an acceptable release pattern to satisfy the needs of all irrigators along the system.

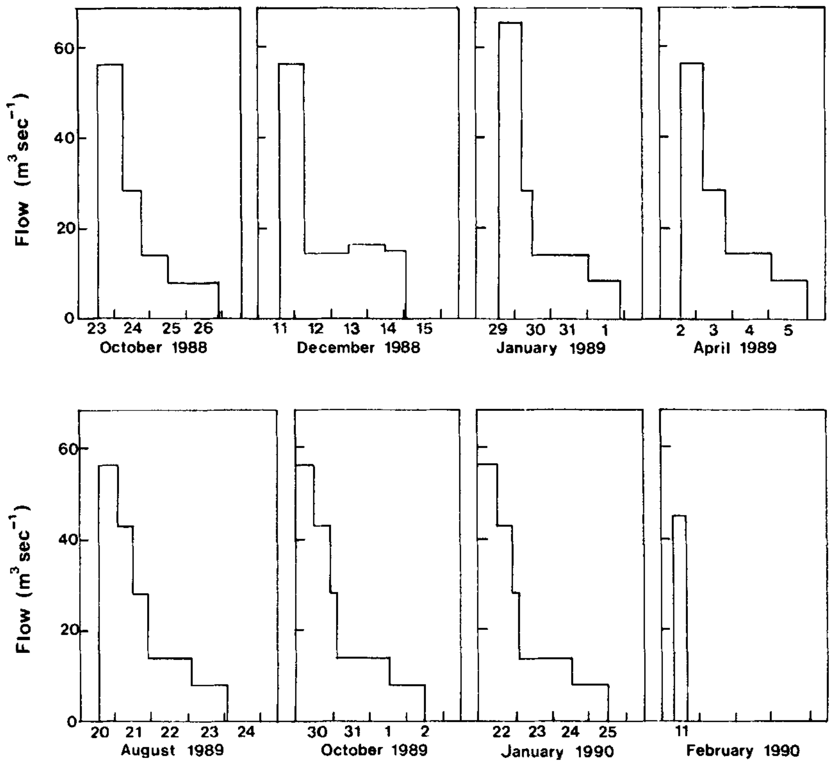


Figure 4. The release pattern of water for the eight releases from Beervlei Dam as noted in the text

The study sites were on the farms Smithskraal owned by Mr D. Hume and Beerpoort (Figure 1) owned by Mr J. Erasmus where a broader study on the life history of the smallscale redfin minnow (*Pseudobarbus asper*) was being studied (Cambray, unpublished data).

Field trips were undertaken to study the effect of several of these water releases on the fish community of the Groot River on 23-25 October 1988, 2-4 February 1989 and 2-5 April 1989. On 24 January 1990, during a water release, ripe-running *P. asper* breeding stock were collected for a developmental series of this species and several hours were spent searching for *P. asper* eggs in the rapids.

A one metre wide and 50 cm deep D-net with a 3 mm mesh and a minnow seine net were used to sample fish in the river. A 50 cm wide small meshed (0·5 mm) net was used to sample for newly spawned eggs or fish that were in the rapids. The eggs were collected by lifting rocks in the river and holding the net downstream, as was done in the Upper Orange River to collect *P. quathlambae* eggs (Cambray and Meyer, 1988).

The eggs of *P. asper* can be positively identified by using Scanning Electron microscopy to study the ultrastructure of the egg envelope. *P. asper* have distinctive egg envelopes which separates them from co-occurring species such as *B. anoplus* (Cambray, 1991). Several of the eggs collected were studied using the SEM techniques (Cambray, 1991).

Water samples were collected before, during and after releases from Beervlei Dam. Secchi disk, water temperature (thermometer accuracy 0·1°C) and pH readings (Lovibond Comparator) were done on site. Conductivity readings were made with a Zeiss CON 602 conductivity meter. Additional water samples were frozen and later analysed for anions and cations at the Department of Geography at Rhodes University.

The findings for *P. asper* are compared to similar studies of the Maloti redfin, *P. quathlambae* which only occurs in the upper catchment of the Orange River (Cambray and Meyer, 1988).

## RESULTS

The overall pattern of the seven major water releases from Beervlei Dam was from a high flushing flow of between 56·64 to 65·35 $m^3 s^{-1}$ over a 12 to 15 h period followed by gradually reduced flows over the next 64 to 72 h (Figure 4). For the last 20 to 36 h of the water release period the flow was usually 8·5 $m^3 s^{-1}$. The total volume released over the 78 to 84 h periods was between 6·2 and 7·1 × $10^6$ $m^3$. The dam was emptied on 11 February 1990 with a release of 1·4 × $10^6$ $m^3$ at 45·82 $m^3 s^{-1}$ for 8·5 h (Figure 4). There was no regular pattern between the major releases, which varied between 44 to 135 days (Table I). The water releases during the breeding season (October to April) varied between 44 to 79 days. The 135 day period occurred during the winter months.

*First survey (23–25 October 1988)*

The netting site was below a weir on the farm Smithskraal (Figure 1). The water rose a total of 60 cm during the 56 $m^3 s^{-1}$ release which took two hours to reach the weir from Beervlei Dam. The water was very turbid with a Secchi disk reading of 2 cm. The weir was continuously observed for the movement of fish. At 06h05 on the 24 October 1988 the first movement of fish was observed when a 40 cm TL *L. umbratus* tried to jump the weir. At 15h30 another large *L. umbratus* was observed jumping followed by five *L. umbratus* between 25–40 cm TL. None of these fish were successful. On the 25 October 1988 the river channel below the weir was searched for fish eggs by lifting rocks and holding a net downstream but none were found. Scoop netting only collected one ripe-running male *P. asper* and two ripe-running male *B. anoplus.* No fish were observed jumping on the 25 October.

It was noted that there was an abundance of *Daphnia* being washed down the system. Whether these came from Beervlei Dam or from the pools higher up is not known.

During this survey the spawning site of *P. asper* was not located. The collection of one ripe-running male redfin minnow indicated that the fish were ready to spawn.

*Second survey (2–4 February 1989)*

The area between the Beerpoort causeway and Netley weir was examined for evidence of spawning activity (Figure 1). The survey commenced after the main flushing flow on the 29 January and subsequent lower flows (Figure 4). The high flows during the first few days of water release made it impossible to sample in the main river channel. The first *P. asper* egg was found in the riffles immediately above a pool on 3 February 1989 at 11h00 and was at the yolk plug stage. Fish reared in the laboratory reached this stage of development after 15h at 22–24°C. The diel temperature range, as recorded with a minimum-maximum

Table I. Dates, length, spacing and amount of water releases from Beervlei Dam between October 1988 and February 1990

| No. Dates of releases | Total hours of release | Total water released × $10^6$ $m^3$ | Days between releases |
|---|---|---|---|
| 1988 | | | |
| 1. October 23–26 | 79 | 6·2 | — |
| 2. December 11–15 | 82 | 6·6 | 45 |
| 1989 | | | |
| 3. January 29–February 1 | 78 | 6·3 | 44 |
| 4. April 2–6 | 84 | 6·9 | 59 |
| 5. August 20–24 | 84 | 7·1 | 135 |
| 6. October 30–November 2 | 84 | 6·9 | 66 |
| 1990 | | | |
| 7. January 22–25 | 84 | 6·9 | 79 |
| 8. February 11 (dam was emptied with this release) | 8·5 | 1·4 | 16 |

thermometer at the spawning site was 18–24°C. The boulders at the spawning site varied in size from 10 × 10 × 10 cm to 50 × 60 × 20 cm.

Approximately 1 km upstream from the previous site another spawning area was located where a number of eggs were collected. In addition two ripe-running males were located under the boulders. There were also many small $0^+$ *P. asper* in the riffle zone. Eggs were found in the main channel of the river 2–3 m upstream of a pool. An area up to 10 m from the pool was examined for eggs and none were found higher up in the river channel. All the eggs were identified as *P. asper*. The eggs were negatively buoyant and non-adhesive. Another sample of eggs was collected at 13h00 on 3 February 1990, water temperature 22°C. These embryos were in several stages of development. These stages ranged from 8 blastomeres (n = 1), multicelled blastula (n = 5), neural keel (n = 2) to the oldest where the tail-tip of the developing embryo touches the optic placode (n = 6). This range in developmental stages suggests that the fish spawned over a time period. Under laboratory conditions these stages are reached after 2h, 5-6h, 14h and 43-44h respectively at 22–24°C.

No eggs were collected drifting in the main channel except when boulders were lifted and the area underneath the boulders was stirred.

Spent females were collected at the Beerpoort causeway (Figure 1) at 16h30 on the 3 February 1989 and redfin minnows were migrating upstream at this point.

More *P. asper* eggs were collected on the 4 February 1989. Some of these eggs were returned to the laboratory alive and their development was followed. The larval fish could be positively identified as *P. asper* by the caudal fin pigmentation (Cambray, unpublished data). Eggs were also positively identified by examining the ultrastructure of their egg envelopes using a Scanning Electron microscope (Cambray, 1991). The subsample collected between 09h00–10h00 on the 4 February 1989 were in several different developmental stages. Five were at a neural keel stage (laboratory 14 h), one was at the tail bud stage (laboratory 26 h), and five were ready to hatch (laboratory 60 h).

Over the period of this survey a total of 31 eggs were preserved in the field for later laboratory analysis. Five of these eggs were not viable (diameters 1·5–1·6) and are not included in the following calculations. The mean diameter for 26 eggs was 1·56 mm (SD = 0·09, range 1·3–1·75 (mm)). For 15 of the eggs the yolks could be measured and had a mean diameter of 1·29 mm (SD = 0·07, range 1·15–1·4).

*Third survey (2–5 April 1989)*

As with the previous survey the water releases were enough to initiate spawning of *P. asper*. Ripe-running males were collected from the riffle area and also from the irrigation canal samples (Cambray, 1990a). The only ripe-running female was collected from the irrigation canal sample (Cambray, 1990a). Twenty-four female *P. asper* ranging in size from 48·8 (41·1) to 93·2 (79·8) mm TL (SL), had mature eggs (even though it was late in the breeding season) and could have participated in the spawning in early April (Cambray, 1990a).

*P. asper* eggs were found in the riffle area on the 4 April 1989 between 12h00 and 17h00 when the water temperature ranged from 19·6–20·5°C. The eggs were amber in colour, with non-adhesive egg envelopes and ranged in size from 1·35 to 1·55 mm in diameter. The diameter of the yolk ranged in size from 1·05 to 1·2 mm. In the ripe-running female collected it was determined that unshed, ripe ovarian eggs of *P. asper* are between 1·1 and 1·3 mm in diameter. Various developmental stages were collected with the earliest being a multicelled blastula stage and the furthest developed having a neural keel. Under laboratory conditions the multicelled blastula stage was reached after 5–6 h and the neural keel formed after 14 h at 22–24°C (Cambray, unpubl. data). This range in developmental stages would indicate that the population was spawning over an extended time interval. Other areas in the riffle zone were searched to no avail. *P. asper* eggs were only collected from the area at the lowest point of the main channel and only several metres upstream of the pool.

*Breeding stock survey (24 January 1990)*

Using the knowledge gained from previous survey work a trip was undertaken after the main flow had been released from Beervlei Dam on 22 January (Figure 4) which would have induced the fish to migrate to the riffle area at Beerpoort. In addition to collecting ripe-running *P. asper* the riffle area was sampled for both fish and eggs. Two *P. asper* eggs were collected, with 1·4 (1·1) mm and 1·5 (1·1) mm egg envelope (yolk) diameters. They were both in an early stage of development (multicelled blastula). Under laboratory collections this stage was reached after 5-6 h at water temperatures of between 22–24°C. The fish had probably started spawning during the morning of the 24 January. The eggs were collected in the same area as the previous two surveys. In the laboratory the fish which were collected in the area were successfully stripped and the development of this species was followed.

At the same site five *Labeo umbratus* eggs were collected. The *Labeo* had probably spawned earlier than the minnows as the developing embryos were quite advanced and approximately 5 mm TL. *L. umbratus* egg envelope diameters were 2·7; 2·9; 3·0; 3·1; 3·15 mm. As the egg envelopes were very clear and had no debris adhering to them they were probably non-adhesive.

*Water chemistry data*

There were a number of physical and chemical changes in the Groot River at the spawning site before, during, and after water releases in April 1989 from Beervlei Dam (Table II). The main objective of the flushing flow was to displace the accumulated salts. Conductivity went up to 1001 mS $m^{-1}$ during the flushing stage (56 cumecs) of the water release and was 258 mS $m^{-1}$ after the water release (Table II). High turbidity readings also occurred during this period with subsequent low Secchi disk readings (Table II). There were also large fluctuations in the anion and cation levels before, during, and after flushing (Table II).

*Water flow*

The flow in the Groot River for the 32 year period, 1958–1990 indicates a widely fluctuating flow regime (Figure 2). There is a seasonal summer rainfall pattern in the area but there is also a longer term rhythm of rainfall in this region which can be cyclic with a mean wavelength of 10 years (Dyer, 1976). The extended droughts experienced in the main channel catchment area of the Groot River are part of this longer cycle.

*Interstitial travel of juvenile redfins*

At Beerpoort causeway on the 19 November 1988 it was observed that during recent repairs an area of up to 3 m wide had been bulldozed below the causeway. The boulders below the causeway were arranged so that there was no definite river channel and no surface water flow. Migrating juvenile *P. asper* managed to overcome this potential barrier by swimming under the rocks and reemerging at the culvert where there was a surface flow of water. Possibly this would indicate that this fish species can move between riverine pools even though there is no surface water flow. This would be a distinct advantage in the fluctuating environment

Table II. Physical and chemical changes in the Groot River, at point of water extraction on 2 April 1989 (before), 3 April 1989 (during 56 cumec flow), and on 5 April 1989 (after the Beervlei Dam water releases flushed the riverine pools)

| | Before | During | After |
|---|---|---|---|
| pH | 8·2 | 8·1 | 8·4 |
| Conductivity (mS $m^{-1}$) | 44 | 1001 | 258 |
| Turbidity (ntu) | 42 | 74 | 26 |
| Secchi disk (cm) | 30 | 2 | 25 |
| Anions | | | |
| Chlorides (mg $l^{-1}$) | 1176·0 | 2420·1 | 477·2 |
| $CaCO_3$ (mg $l^{-1}$) | 20·0 | 25·0 | 20·0 |
| Cations | | | |
| Calcium (mg $l^{-1}$) | 90·0 | 218·0 | 45·0 |
| Magnesium (mg $l^{-1}$) | 154·0 | 307·0 | 64·0 |
| Sodium (mg $l^{-1}$) | 788·0 | 1600·0 | 410·0 |
| Potassium (mg $l^{-1}$) | 15·0 | 20·0 | 9·5 |

of the Groot River. This movement between and under boulders could also indicate that the redfin minnows might breed in this zone.

## DISCUSSION

Controlled water releases offer field experimental information on how certain fish species react to specified flow regimes at different times of the year. The timing of annual spawning(s) has evolved to ensure that optimal environmental conditions are present and that the young hatch and commence feeding at the optimum season for survival (Nikolsky, 1963; Bye, 1984; Nesler *et al.*, 1988).

The internal reproductive cycle of individuals in a population is synchronized by certain environmental factors, such as water temperature and photoperiod (De Vlaming, 1972; Lam, 1983). To initiate the final phase of gonad maturation (ovulation and spermiation) and the release of gametes, specific stimuli are required (Lam, 1983). These stimuli may include current velocity, water quality, substrate, barometric pressure, or pheromone releases due to aggregation of potential mates (Lam, 1983; Stacey, 1984; Nesler *et al.*, 1988). There is a subtle relationship between the internal and external rhythms so that the timing of a species' reproductive cycle is a compromise which involves many environmental considerations (Bye, 1984).

There is very little comparative material about the breeding biology of the African redfin minnows of the genus *Pseudobarbus* (Cambray and Meyer, 1988). The reproductive guild of two of the redfin minnows, *P. asper* and *P. quathlambae*, appears to be very similar. In these two species the eggs are placed in crevices in mid-channel and the egg envelopes are slighly to non-adhesive. Later in development the free embryos or early larval fish are carried by the current to pools or backwaters which are food-rich environments and out of the main flow. Cambray and Meyer (1988) put *P. quathlambae* in the lithopelagophil (A.1.2) reproductive guild (Balon, 1985). *P. asper* could also be placed into this reproductive guild.

*P. asper*, in the Groot River, usually spawns within the months of October to February. A spawning as late as April would indicate an element of risk taking which has probably ensured this species' survival in a highly unpredictable environment. The young are hatched at a time of year when the water temperatures are beginning to cool. In cyprinids ovulation and spawning are known to occur rapidly in response to specific external factors which are relevant to reproductive success (Stacey, 1984). The experiments conducted by Stacey *et al.* (1979) on *Carassius auratus* are relevant here. Even at suboptimal temperatures *C. auratus* spawned when aquatic vegetation was present, whereas in the absence of vegetation the goldfish only spawned when their preferred temperature threshold was reached. In the Groot River *P. asper* spawned in the presence of a water release at a time of the year which would expose the spawn to suboptimal temperatures. The increased flow and the associated water chemistry changes were probably sufficient to induce the redfin minnows to spawn this late in the season.

*P. asper* and the other native fishes of the Groot River have evolved in a highly unpredictable environment. The Groot River is characterized by extended droughts, which can last for several years, followed by devastating flash floods (Figure 2). In this kind of river system where the natural flow is governed by a long-term irregular rainfall pattern, one would expect large natural variations in population size. The plasticity of life history characteristics of *P. asper*, such as an extended breeding season, would increase their probability of survival. That the fish bred as late as April indicated that the *P. asper* population took advantage of river flows to initiate spawning. The adaptive significance of a long reproductive season, from October to April, has survival value in the fluctuating environment of the Groot River and now allows this minnow species to survive and take advantage of the man-made perturbations to the system for breeding. The last release during February 1990 (Table I) was only 16 days after the January release. This release may have been detrimental to the early life history stages of the fish which spawned during the January water release. The other releases were well spaced (Table I).

The status of all the species in the Groot River is not known as there is a lack of information on their past distribution and relative abundance. It is not known what the species composition was during prolonged droughts compared to periods of flow prior to river regulation. In some of the better studied areas in South-central Africa Jackson (1989) has reviewed the species diversity changes during the long-term dry–wet cycles. However, the three main phenotypically plastic species which he describes as being able to thrive in harsh environments do not occur naturally in the Gamtoos River.

In the upper catchment area of the Orange River in Lesotho the Maloti redfin, *P. quathlambae*, which is an endangered species (Skelton, 1987), spawned after rains in the main river channel of the Tsoelikana River in the Sehlabathebe National Park (Rondorf, 1975, 1976; Cambray and Meyer, 1988). The eggs of this species were found in a riffle area above a pool. Free embryos and early larval developmental stages of *P. quathlambae* were located in the pool backwaters immediately below this spawning site (Cambray and Meyer, 1988).

The gonadal development of *P. quathlambae* indicated that this species could have spawned between January and April 1975 (Rondorf, 1975) and that spawning could have occurred intermittently from 13 January 1976 to 28 February 1976 (Rondorf, 1976). Cambray and Meyer (1988) also established by sampling for eggs, free embryos, and larval fish that *P. quathlambae* have an extended breeding season. They suggested that spawning could have occurred from late November to March. *P. quathlambae* may be serial spawners and may spawn throughout their breeding season when conditions (rainfall = river flow) are favourable. Presumably the manipulated water flow regime studied in the Groot River would also induce spawning in *P. quathlambae.* There are vast ecological differences (e.g. in rainfall and flow regime) between the Drakensberg streams and the Groot River, however, it has been shown that both *P. quathlambae* and *P. asper* can react quickly to an increase in river flow and spawn (Cambray and Meyer, 1988; this study). That segments of the *P. asper* population or individuals were ready to spawn during a number of water releases indicated a prolonged state of readiness in this fluctuating environment and that the main stimuli were an increase in water velocity and probably the resulting change in water quality.

Cambray and Stuart (1985) studied several aspects of the biology of Burchell's redfin (*P. burchelli*). *P. burchelli* is a threatened species and its Red Data Book status is rare (Skelton, 1987). This species has an extended breeding season, from September to February, with a peak in December. Spawning and hatching of *P. burchelli* free embryos was found to coincide with the drawing-off of the greatest quantities of water for irrigation in the Breede River system which would have an adverse impact on the population. There is no published information on the flow requirements for this species during spawning.

*L. umbratus spawning*

*L. umbratus* and the introduced *Cyprinus carpio* are the only large cyprinids in the Gamtoos River system. The diameter of the five large eggs collected in January 1990 ranged from 2·7–3·15 mm. This is similar to the egg diameters of *L. capensis* collected in the Orange River (2·7–3·4 mm) (Cambray, 1985 a). The developing embryos and their yolk sacs were of cyprinid form and the egg envelopes were non-adhesive unlike the highly adhesive egg envelopes of *C. carpio* (Breder and Rosen, 1966). Mitchell (1984) recorded that the egg envelopes of *L. umbratus* were non-adhesive. However, Jackson and Coetzee (1982) observed that *L. umbratus* had adhesive egg envelopes. Both Jackson and Coetzee (1982) and Mitchell (1984) have observed the spawning behaviour of *L. umbratus.* Jackson and Coetzee (1982) found eggs in a floodplain on vegetation whereas Mitchell (1984) collected eggs in the main rocky channel of the Modder River, a similar spawning habitat to that found in the Groot River. Mitchell (1984) speculated that the eggs of *L. umbratus* would settle in the irregularities of the stream bottom. Gaigher *et al.* (1975) also found *L. umbratus* spawning in the main river channel. This would indicate that this species is not an obligatory floodplain spawner. Jackson and Coetzee (1982) suggested that this species was mainly a floodplain spawner, if a floodplain was available. In the P. K. le Roux impoundment on the Orange River *L. umbratus* were found to migrate upstream into tributaries to spawn. Spawning was triggered by local rainfall events (Tómasson *et al.*, 1984).

In the Groot River *L. umbratus* spawned earlier than *P. asper* and therefore this larger species was spawning during a faster flow and was able to initiate spawning quicker in response to the water release than the minnow species.

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

The pattern of river discharge can have a direct bearing on the upstream migration of certain fish species (Mann, 1989) as well as on the spawning success of potamodromous species. One of the best studied areas in southern Africa with regard to inducing fish to spawn using a specified flooding regime is the Pongolo floodplain in Zululand (e.g. Pott, 1969; Coke, 1973; Kok, 1980; Heeg and Breen, 1982; Merron and la Hausse de Lalouviere, 1987; Drewes and Slinger, 1987; Merron *et al.*, in press). Water releases from the Pongolapoort Dam are now partly used to fill the floodplain spawning grounds below the dam wall (Heeg and Breen, 1982). Whereas the water releases from Beervlei Dam were solely for agricultural purposes as were the earlier releases from the Pongolapoort Dam (Jackson, 1989). River regulation in the Pongolo River is very important to the continued productivity and functioning of the Pongolo floodplain. The majority of fishes of the Pongolo floodplain are potamodromous although potamodromesis need not be obligatory (Kok, 1980). Manipulation of the hydrology of the floodplain which is important to both the fish and the fishery on the floodplain is now recommended (Merron and la Hausse de Lalouviere, 1987). Adequate summer flooding is needed to maintain the system. Salinification of the pans is one of the major impacts to the floodplain as a result of the Pongolapoort Dam (Kok, 1980). Following the cessation of a released flood from the Pongolapoort Dam there were considerable aggregations of adult fish of all species in the stilling pool below the dam wall (Heeg and Breen, 1982). Many of these species, which are flood dependent spawners, can be stimulated to spawn in the newly flooded pans by the artificial flooding of this system. The preimpoundment summer floods in the Pongolo River were mainly of short duration and occurred repeatedly throughout the rainy season with the greatest frequency in February. In the early post-impoundment flooding regime there were continuous flood conditions which extended over much of the breeding season and some of the adult fish were able to spawn resulting in increased recruitment (Kok, 1980). It has been recommended that in order to maintain a natural, self-sustaining population of fishes in the floodplain it is necessary to release, from the Pongolapoort Dam, a series of small floods and one large flood between November and March (Merron and la Hausse de Lalouviere, 1987).

In the highly regulated Orange River Cambray (1985a) observed and collected eggs from a spawning of *Labeo capensis* and *Clarias gariepinus* which probably bred due to hydroelectric water releases from the upstream P. K. le Roux Dam power station. Large numbers of migrating smallmouth yellowfish (*Barbus aeneus*) have been observed below the P. K. le Roux Dam trying to negotiate the barrier by jumping into the 200 cumec hydroelectric turbine discharge (Cambray, personal observations; Cambray, 1985b). These fish were on a spawning migration run, probably triggered by water releases, and were prevented from reaching suitable upstream spawning grounds above the barrier.

Two large *Barbus* species, the smallmouth yellowfish (*B. aeneus*) and the largemouth yellowfish (*Barbus kimberleyensis*), spawn on gravel beds within the main river channel below the Hendrik Verwoerd Dam on the Orange River. The hydroelectric releases from the power station at the dam have created a continuously flowing regulated river. Tómasson *et al.* (1984) found that the time of spawning of these two *Barbus* was governed by water temperatures. Unseasonal releases of cold water from the upstream impoundment resulted in poor reproductive success. 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 two species (Tómasson *et al.*, 1984).

### *Conservation*

For conservation, the consequences of river regulation are mainly detrimental (Hellawell, 1988). Stanford and Ward (1979) stated that 'stream regulation has exerted more profound and irrevocable effects on the character of the world's rivers than pollutants. Altered ecosystems below dams and diversions are now the most prevalent lotic environments on the earth.' This statement holds true for a water-stressed region such as South Africa (Davies, 1979). The present short-term economic policies have left some river ecologists with a pessimistic view of the long-term conservation of rivers in this region (O'Keeffe, 1989). In the U.K. recent legislation and general public awareness of the importance of conservation had created a more 'sympathetic' atmosphere, however, the negative effects of man's activities within river catchments remain intractable (Hellawell, 1988). In the U.S.A. there have been a number of studies on the impact of river flows below dams on spawning grounds (e.g. Chapman *et al.*, 1986). For example, the Colorado squawfish, *Ptychocheilus lucius*, is an endangered species in the Colorado River basin. Studies have been initiated to provide an understanding of the spawning ecology of this species which will provide river managers with data on the required instream flows for the recovery of this species (Nesler *et al.*, 1988). This approach should be used in South Africa where fish species and their habitats are threatened by river regulation.

In South Africa there are ever increasing barriers to the movement of migrating fish species in the river systems caused by dams, weirs, causeways, and culverts, (Cambray, 1990b). The river morphology of the Groot River has been altered by all of the above mentioned barriers. As in many countries there is an increasing demand on freshwater resources and in future more barriers will be built. In the Groot River the upstream movement of *P. asper* is now completely prevented by the 20·7 m high Beervlei Dam wall. This barrier to fish movement has probably caused a loss in spawning grounds and fragmentation of the population, resulting in a loss of continuity and preventing recolonization of the area following severe drought periods. Downstream refuge-seeking movements are now limited because of predation by introduced species such as largemouth bass, *Micropterus salmoides* (Cambray, 1990b; Cambray and Cambray, 1988). Water abstraction for agriculture reduces available fish habitat and in addition inadequately screened intakes can result in large numbers of fish being entrained (Cambray, in press a). Without even basic information with regard to fish population structure it will be difficult to assess the impact of river regulation on many of the rivers of southern Africa.

In Australia bank erosion resulting from poor farming practices, such as allowing livestock direct access to the river, has changed many streams from narrow, clear waters with deep holes to wide, shallow muddy tracts (Wharton, 1969). Stock are allowed direct access to the Groot River on many of the farms and this negative impact to the river is difficult to assess. The Groot River is highly turbid especially during periods of high flow (Table II; Cambray, 1990b). How much of this turbidity and the resulting changes in river morphology is the result of poor farming practices is not known. The resulting silt fills holes between boulders and prevents the possible interstitial travel of fish between disconnected pools as well as destroying the spawning habitat for the species with demersal, non-adhesive eggs. The infilling of interstices can also reduce the amount of cover available for the young of some species (Crisp, 1989). Previously flash-flooding would have scoured some of the river reaches but with the building of the Beervlei Dam wall the extent of scouring has been reduced and silt deposits may accumulate which could asphyxiate the eggs and early free embryos. However, reservoirs also trap silt and less scouring may be required to keep the spawning areas suitable for breeding. Flood velocity flows in many rivers are necessary to cleanse the substrate and maintain the physical integrity of the river channel (Stalnaker, 1980). In the Groot River the 56 cumec flow for 15 h was sufficient to clean the spawning substrate in the study area.

Dams commonly alter the natural flow pattern below dam walls and there is usually a reduction in the incidence and the extent of floods (Cambray *et al.*, 1986). In Australia, as in other countries, water-control schemes in rivers impose more stable conditions, which can be more favourable to introduced fish such as carp (*Cyprinus carpio*) and disadvantageous for the native ichthyofauna (Glover and Inglis, 1971). In contrast the Groot River water releases for agriculture increased the 'flashyness' (*sensu* Crisp, 1989) of the river. In the Groot River the water releases for agriculture to remove accumulated salts have probably been favourable to some of the native fishes. The interval between releases was long enough so that eggs and young fish were probably not subjected to unfavourable conditions. The impact of the frequency of the water releases on the early life history stages of fish should be investigated in the Groot River. In some systems large and sudden releases can cause high mortalities to the young stages of fish (Elliot, 1976; 1987).

It has been suggested that regulated instream flows should mimic nature (Tessman, 1980 in Stalnaker, 1980). This rule-of-thumb management strategy may be sound for some river systems. The Groot River can have flash floods followed by years of no surface flow. A water release strategy during drought years would not be able to mimic nature if water has to be supplied to downstream agriculture. In the Groot River agricultural water releases from Beervlei Dam mimicked the natural flow pattern of a flash flood to which the fish species are adapted, however there was no natural flow in the river at this time. In rivers subject to short duration floods, such as many rivers in South Africa, it would be a distinct advantage for fish species to spawn in the main channel of the river to prevent stranding of the developing embryos. *P. asper* are adapted to the type of flow regime imposed on the river by water releases and only spawned in the middle of the river channel.

O'Keeffe (1989) has stressed that in southern Africa conservation aims must be viewed within the context of different priority uses for rivers. The reservoir release strategy for the Beervlei Dam should not only consider the agricultural requirements of the farmers downstream of the dam wall but also the instream flow requirements of the aquatic environment. The present release strategy is based solely on agricultural needs. Agricultural as well as conservation management of the water releases from the Beervlei Dam could prove a useful tool in ameliorating some of the negative environmental impacts to the dynamics of fish populations in the Groot River caused by river regulation. It is difficult to compare the impact of these water releases with those of a natural flow pattern on the fish population as there were no preregulation studies. Releases from dams sometimes produce a community which is atypical of the river (Hellawell, 1988).

Opportunistic as well as multiple spawning species which can spawn during every water release will be favoured in the present river management programme below the Beervlei Dam wall. The water release must not only stimulate spawning but also ensure the survival of eggs and young. The large quantity of zooplankton observed in the flowing water would also increase the food availability for the fish species. Flow spikes were probably the environmental cue to adult Colorado squawfish to initiate spawning (Nesler *et al.*, 1988) and similarly the flow spike of 56 cumecs was enough to initiate the spawning of both *P. asper* and *L. umbratus* in the Groot River. As with Nesler *et al.* (1988) there is the need to consider that one or more variables coincidental to the flow spike cue may be serving as the actual cue perceived by the adult fish.

As with any scarce resource there must be an attempt to reconcile the water resource requirements of agriculture and the aquatic environment. The Pongolapoort Dam on the Pongolo River, KwaZulu closed in March 1970 and the cost was justified solely on irrigation possibilities (Jackson, 1989). There were no allowances made for the downstream fish populations. As Mann (1988) has suggested for the U.K., there is a distinct and urgent need for more research on the long-term problems as well as benefits (e.g. in this paper the induced spawning of two fish species) of river regulation schemes on resident fish populations in South African rivers. In Britain some of the water resource developments have also been beneficial to the fish (Mann, 1988).

In the U.S.A. there have been a number of publications on the habitat suitability index models and instream flow suitability curves for specific fish (e.g. McMahon *et al.*, 1984). There is a need in South Africa to develop suitability index graphs (Milhous *et al.*, 1984) for each of the major life stages of some of the fish species. As more rivers are modified by man, river managers require information on what allowances should be made for the maintenance of the aquatic environment. The U.S. Fish and Wildlife Service use the Instream Flow Incremental Methodology (IFIM) (Bovee, 1982) to assess instream flow problems. Within this methodology the Physical Habitat Simulation System (PHABSIM) (Milhous *et al.*, 1984) can be used to determine the amount of available instream habitat (water depth, water velocity, and substrate size) for a fish species as a function of streamflow. These methodologies are being considered for use in the aquatic environments in South Africa (Cambray *et al.*, 1989). Given the nature of many of the rivers in South Africa PHABSIM should be used with extreme caution until we understand the life histories of the native fish species more fully. Even in North America PHABSIM does not always provide sound flow regimes on which to base water management decisions (Shirvell, 1989).

## CONCLUSIONS

Any manipulation that dampens the environmental flux may be less favourable for the native biota. In the Groot River regular releases from the Beervlei Dam reduced the environmental flux during the period of study. The fact that the fish were able to spawn during these water releases indicates that the natural flow pattern was being mimicked. It is suggested here from the data available that the natural flow pattern of the Groot River is so stochastic that the spawning of *P. asper* can be induced under a wide variety of water release patterns. How successful these releases would be so that fish are recruited requires further study. This data set supports O'Keeffe (1989: 259) who noted that 'The stochastic hydrology, lack of well-defined seasonality, and variability of the environment (in southern Africa) might be expected to select for an opportunistic generalist biota, environmentally rather than biologically regulated.'

There is a distinct need in the integrated river basin management of the Gamtoos River system to take into consideration the habitat and spawning requirements of the native ichthyofauna. Water abstraction, barriers to fish movement, and artificial flow regimes have resulted in a number of negative impacts. The results in this paper offer some criteria for the protection and management of redfin minnow species in regulated river environments. It is only by chance that *P. asper* and *L. umbratus* spawned under the water discharge strategy below the Beervlei Dam which was solely designed for agricultural purposes. The success of integrated river basin management in the United Kingdom is based on cooperation between the various user groups. A similar approach is now developing in South Africa which is most evident in the Pongolo River studies (Merron *et al.*, in press). In southern Africa O'Keeffe (1989) has quite clearly demonstrated that due to the longitudinal nature of rivers conservation management of them can only be planned within the context of multiple uses.

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## REFERENCES

Alexander, W. J. R. 1985. 'Hydrology of low latitude Southern Hemisphere landmasses', in Davies, B. R. and Walmsley, R. D. (Eds), *Perspectives in Southern Hemisphere Limnology*, Junk, Dordrecht, 75-84.

Anon. 1986. *Management of the Water Resources of the Republic of South Africa*, The Dept of Water Affairs, Pretoria.

Balon, E. K. 1985. *Early Life Histories of Fishes. New Developmental, Ecological and Evolutionary Perspectives*, Junk, Dordrecht, 280 pp.

Bovee, K. D. 1982. 'A guide to stream habitat analysis using the Instream Flow Incremental Methodology', *Instream flow information paper 12*, U.S. Fish Wildl. Serv. FWS/OBS/-82/26, 248 pp.

Braune, E. 1985. 'Aridity and hydrological characteristics: Chairman's summary', in Davies, B. R. and Walmsley, R. D. (Eds), *Perspectives in Southern Hemisphere Limnology. Developments in Hydrobiology*, **28**, 131-136.

Breder, C. M. and Rosen, D. E. 1966. *Modes of Reproduction in Fishes.* T.F.H. Publications, N.J., 941 pp.

Bryen, B. A. and Davies, B. R. 1989. 'The effect of stream regulation on the physicochemical properties of the Palmiet River, South Africa', *Reg. Rivers; Res. & Mngmnt*, **3**, 107-121.

Bye, V. J. 1984. 'The role of environmental factors in the timing of reproductive cycles', in Potts, G. W. and Wootton, R. J. (Eds), *Fish Reproduction: Strategies and Tactics*, Academic, London, 187-205.

Cambray, J. A. 1985a 'Early ontogeny of *Labeo capensis* (Pisces: Cyprinidae)', *S. Afr. J. Zool.*, **20**, 190-196.

Cambray, J. A. 1985b. 'Observations on the number of piscivorous birds below the P. K. le Roux Dam wall, Orange River', *Ostrich*, **56**, 202-204.

Cambray, J. A. 1990a. 'Fish collections taken from a small agricultural water withdrawal site on the Groot River, Gamtoos River Systems', *Sth. Afr. J. aquat. Sci.* **16**, (1), 78-89.

Cambray, J. A. 1991. 'Comparative scanning electron microscopy of the egg envelopes of several African *Barbus* and *Pseudobarbus* species', *NOAA Technical Report NMFS*, **95**, 109-119.

Cambray, J. A. 1990b. 'Adaptive significance of a longitudinal migration of juvenile freshwater fish in the Gamtoos River System', South Africa, *S. Afr. J. Wildl. Res.*, **20**, (4), 148-156.

Cambray, J. A. and Cambray, E. S. 1988. 'The Eastern Cape Redfin (*Barbus afer*) and the Loerie Dam Nature Reserve', *The Naturalist*, **32**, (1), 4-7.

Cambray, J. A., Davies, B. R., and Ashton, P. J. 1986. 'The Orange-Vaal system', in Davies, B. R. and Walker, K. F. (Eds), *The Ecology of River Systems. Monographiae Biologicae*, **30**, 89-122.

Cambray, J. A. and Meyer, K. 1988. 'Early ontogeny of an endangered, relict, cold-water cyprinid from Lesotho, *Oreodaimon quathlambae* (Barnard, 1938)', *Rev. Hydrobiol. trop.*, **21**, (4), 309-333.

Cambray, J. A. and Stuart, C. T. 1985. 'Aspects of the biology of a rare redfin minnow, *Barbus burchelli* (Pisces, Cyprinidae), from South Africa', *S. Afr. J. Zool.*, **20**, 155-165.

Cambray, J. A., Alletson, D. J., Kleynhans, C. J., Petitjean, M. O. G., and Skelton, P. H. 1989. 'Flow requirements of fish', in Ferrar, A. J. (Ed.), *Ecological Flow Requirements for South African Rivers, S. Afr. Nat. Scient. Progm. Rep.*, **162**, 71-93.

Chapman, D. W., Weitkamp, D. E., Welsh, T. L., Dell, M. B., and Schadt, T. H. 1986. 'Effects of river flow on the distribution of chinook salmon redds', *Trans. Am. Fish. Soc.*, **115**, 537-547.

Coke, M. M. 1973. 'The fish ecology of the Pongolo floodplain pans', *Natal Parks Board, Research Communication No. 8*, Pietermaritzburg, 6 pp.

Crisp, D. T. 1989. 'Some impacts of human activities on trout, *Salmo trutta*, populations', *Freshwater Biology*, **21**, 21-33.

Davies, B. R. 1979. 'Stream regulation in Africa: a review', in Ward, J. F. and Stanford, J. A. (Eds), *The Ecology of Regulated Streams*, Plenum Press, New York, 113-142.

De Vlaming, V. L. 1972. 'Environmental control of teleost reproductive cycles; a brief review', *J. Fish Biol.*, **4**, 131-140.

Drewes, A. K. and Slinger, J. H. 1987. 'Modelling of the Pongolo floodplain pans for management purposes', in Walmsley, R. D. and Botten, M. L. (Eds), *Ecology and Conservation of Wetlands in South Africa, CSIR, Pretoria, Occasional Rep.*, **28**, 261-268.

Dyer, T. G. J. 1976. 'Expected future rainfall over selected parts of South Africa', *S. Afr. J. Sci.*, **72**, 237-239.

Elliot, J. M. 1976. 'The downstream drifting of eggs of brown trout, *Salmo trutta* L.', *J. Fish Biol.*, **9**, 45-50.

Elliot, J. M. 1987. 'Population regulation in contrasting populations of trout *Salmo trutta* in two Lake District streams', *J. Anim. Ecol.* **56**, 83-98.

Gaigher, I. G., Hamman, K. C. D., and Thorne, S. C. 1980. 'The distribution, conservation status and factors affecting the survival of indigenous freshwater fishes in the Cape Province', *Koedoe*, **23**, 57-88.

Gaigher, I. G., Ntloko, M. M., and Visser, J. G. 1975. 'Reproduction and larval development of *Labeo umbratus* (Pisces: Cyprinidae) in the Tyume River, Eastern Cape', *J. Limnol. Soc. Sth. Afr.*, **1**, 7-10.

Glover, C. J. M. and Inglis, W. G. 1971. 'Freshwater fish of South Australia', South Australian Yearbook, 1971, 27-34.

Heeg, J. and Breen, C. M. 1982. 'Man and the Pongolo floodplain', *S. Afr. Scient. Progm. Rep.*, **56**, 117 pp.

Hellawell, J. M. 1988. 'River regulation and nature conservation', *Regul. Rivers*, **2**, (3), 425-443.

Jackson, P. B. N. 1989. 'Prediction of regulation effects on natural biological rhythms in South-Central African freshwater fish', *Regul. Rivers*, **3**, 205-220.

Jackson, P. B. N. and Coetzee, P. W. 1982. 'Spawning behaviour of *Labeo umbratus* (Pisces: Cyprinidae)', *S. Afr. J. Sci.*, **78**, 293-295.

Kok, H. M. 1980. *Ecological studies of some important fish species of the Pongolo floodplain, Kwazulu, South Africa*, PhD thesis, University of Natal, Pietermaritzburg, 341 pp.

Lam, T. J. 1983. 'Environmental influences on gonadal activity in fish', in Hoar, W. S., Randall, D. J., and Donaldson, E. M. (Eds), *Fish Physiology, Volume 3*, Academic, New York, 65-116.

Mann, R. H. K. 1988. 'Fish and fisheries of regulated rivers in the U.K.', *Regul. Rivers*, **2**, (3), 411-424.

Mann, R. H. K. 1989. 'Fish population dynamics in the River Frome, Dorset', *Regul. Rivers*, **4**, 165-177.

McMahon, T. E., Gebhart, G., and Nelson, P. C. 1984. 'Habitat suitability index models and instream flow suitability curves: warmouth', *U.S. Fish Wildl. Serv., Fws/OBS-82/10.67*, Washington, DC. 21 pp.

Merron, G. S. and la Hausse de Lalouviere, P. 1987. 'The response and recovery of fish stocks of the Pongolo Floodplain during and after a period of prolonged drought', in Walmsley, R. D. and Botten, M. L. (Eds), *Ecology and Conservation of Wetlands in South Africa, CSIR, Pretoria, Occasional Rep.*, **28**, 230-244.

Merron, G. S., la Hausse de Lalouviere, P., and Bruton, M. N. in press. 'Implications of water releases from the Pongolapoort dam to the fish and fisheries of the Pongolo floodplain', in Walmsley, R. D. (compiler), *CSIR, Pretoria, Occasional Rep.*, a.

Milhous, R. T., Wegener, D. L., and Waddle, T. 1984. 'User's guide to the Physical Habitat simulation System', *Instream flow information paper 11*, U.S. Fish Wildl. Serv., FWS/OBS-81/43.

Mitchell, S. A. 1984. 'Further observations on the breeding behaviour of *Labeo umbratus* (Smith) (Pisces: Cyprinidae)', *J. Limnol. Soc. Sth. Afr.*, **10**, (1), 28-30.

Nesler, T. P., Muth, R. T., and Wasowicz, A. F. 1988. 'Evidence of baseline flow spikes as spawning cues for Colorado squawfish in the Yampa river, Colorado', *Am. Fish. Soc. symposium*, **5**, 68-79.

Nikolsky, G. V. 1963. *The Ecology of Fishes*, Academic, London, 352 pp.

Noble, R. G. and Hemens, H. 1978. 'Inland water ecosystems in South Africa—a review of research needs', *S. Afr. Nat. Scient. Progm. Rep.*, **34**, CSIR, Pretoria.

O'Keeffe, J. H. 1989. 'Conserving rivers in southern Africa', *Biol. Conserv.*, **49**, 255-274.

O'Keeffe, J. H., Palmer, R. W., Byren, B. A., and Davies, B. R. 1990. 'The effects of impoundment on the physicochemistry of two contrasting southern African River systems', *Reg. Rivers Res. Mngmnt*, **5**, 97-110.

Palmer, R. W. and O'Keeffe, J. H. 1989. 'Temperature characteristics of an impounded river', *Arch. Hydrobiol.*, **116**, 471-485.

Pott, R. McC. 1969. *The fish life of the Pongolo River before the closure of the J. G. Strijdom Dam*, MSc thesis, Witwatersrand University, Johannesburg.

Rondorf, D. W. 1975. *Progress report, the rare and endangered* Oreodaimon quathlambae *(Barnard, 1938)*, Fisheries Section, Gov't of Lesotho, 23 pp.

Rondorf, D. W. 1976. *Progress report on the study of* Oreodaimon quathlambae *during the period October 1975 to April 1976*, Fisheries Section, Gov't of Lesotho, 41 pp.

Shirvell, C. S. 1989. 'Ability of PHABSIM to predict chinook salmon spawning habitat', *Regul. Rivers*, **3**, 277-289.

Skelton, P. H. 1987. 'South African Red Data Book—Fishes', *S. Afr. Scient. Progm. Rep.*, **137**, CSIR, Pretoria, 199 pp.

Stacey, N. E. 1984. 'Control of the timing of ovulation by exogenous and endogenous factors', in Potts, G. W. and Wootton, R. J. (Eds), *Fish reproduction: strategies and tactics*, Academic, London, 207-222.

Stacey, N. E., Cook, A. F., and Peter, R. E. 1979. 'Spontaneous and gonadotropin-induced ovulation in goldfish, *Carassius auratus* L.: effects of extreme external factors', *J. Fish Biol.*, **15**, 349-361.

Stalnaker, C. B. 1980. 'Effects on fisheries of abstractions and perturbations in streamflow', in Grover, J. H. (Ed.), *Allocation of Fishery Resources*, UNFAO.

Stanford, J. A. and Ward, J. V. 1979. 'Stream regulation in North America', in Ward, J. V. and Stanford, J. A. (Eds), *The Ecology of Regulated Streams*, Plenum Press, New York, 215-236.

Tómasson, T., Cambray, J. A., and Jackson, P. B. N. 1984. 'Reproductive biology of four large riverine fishes (Cyprinidae) in a man-made lake, Orange River, South Africa', *Hydrobiologia*, **112**, 179-195.

Wharton, J. C. F. 1969. 'Recreation and conservation in the aquatic environment', *Proc. R. Soc. Vict.*, **83**, 47-54.