Early development and larval behaviour of a minnow, *Barbus anoplus* (Pisces: Cyprinidae)

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The chubbyhead barb, *Barbus anoplus*, underwent a population explosion in the early phases of filling of Lake Le Roux on the Orange River. This successful colonization was possibly related to the survival strategy of the young stages of this minnow. It is suggested that some of the development traits of *B. anoplus* enabled it to become the most widespread freshwater fish species south of the Limpopo River. The development and behaviour of embryos and larvae of *B. anoplus* are described and discussed with reference to their survival strategy and potential colonizing ability. Some of the protolarvae were pelagic and the relevance of this behaviour is noted.

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Die dikkop-ghieliemientjie, *Barbus anoplus*, het 'n bevolkingsontploffing ondergaan tydens die vroeë volloopstadium van die Le Rouxmeer, wat aan die Oranjerivier geleë is. Hierdie suksesvolle kolonisasie was gedeeltelik moontlik weens oorlewingstrategieë gedurende die vroeë fase van ontwikkeling van hierdie klein vissoort. Dit word voorgestel dat sommige van die larwale ontwikkelingseienskappe van *B. anoplus* verantwoordelik is vir die feit dat hierdie klein vissoort vandag een van die mees wydverspreide varswatervisspesies suid van die Limpoporivier is. Die ontwikkeling en gedragspatrone van die embrio en larwe van *B. anoplus* met verwysing tot hul oorlewingstrategieë en potensiële kolonisasievermoë word beskryf en bespreek. 'n Aantal van hierdie protolarwes is pelagies en aantekeninge oor die toepaslikheid van hierdie optrede is gemaak.

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In Africa the dominance by *Barbus* species of the ichthyofauna is most evident south of 15 °S (Bowmaker, Jackson & Jubb 1978). Of the 52 *Barbus* species in southern Africa, 82% have a fork length (FL) of less than 150 mm (Cambray 1982) and are commonly known as minnows. Despite their importance, there have been no published accounts of the ontogenetic development of these minnows. In fact, there are very few published papers on the early development of African cyprinids. The notable exceptions are *Labeo victorianus* of Lake Victoria (Fryer & Whitehead 1959), *L. mesops* from Lake Malawi (Malawi Fisheries Research Report 1965), *L. umbratus* of the eastern Cape (Gaigher, Ntloko & Visser 1975), *Barbus holubi* from the Vaal River (Groenewald 1961) and *B. natalensis* of Natal (Wright & Coke 1975). Balon, Duyvené De Wit & Holčik (1962) used *B. anoplus 'Puntius anoplus'* males in a hybridization experiment with *Rhodeus ocellatus* females and include one drawing of a seven-day-old larva of *B. anoplus* and a description of this stage. Overall, Fryer & Whitehead (1959) have provided the most detailed published account of African cyprinid development supplemented with drawings.

B. anoplus is the most widespread freshwater fish species south of the Limpopo River (Skelton 1980) and it is suggested here that some of the developmental traits of this minnow have partially facilitated this success.

The present study on development was part of a wider investigation of the life history strategy of *B. anoplus* (Cambray 1982). The objective of this paper is to describe the gross embryogeny of *B. anoplus* and in particular to record the behaviour and potential colonizing ability of eggs, embryos and larvae.

Methods

After a rainy period during early November 1980 five golden males (breeding colouration) and five ripe females (distended abdomens) were collected on a daily basis from a small stream flowing into Lake Le Roux (29°59'S/24°43'E). The fish were taken live to the laboratory where eggs were stripped from the five females into a petri dish containing neutralized tap water. The males were then stripped, or in some cases the testes were dissected out and placed in the petri dish. The eggs and milt were stirred with a glass rod for 2 min and then transferred to a shallow plastic container which had a small-meshed plastic screen glued to the base. This container floated in a small aerated aquarium. In January 1981, six males and six females were injected with Pregnyl using the method suggested by Bok & Heard (1982).

Two of the fertilized eggs or larvae were removed periodically from the container and examined for development under

a 8-80× binocular dissecting microscope. When the larvae had hatched they were released into the aquarium and the plastic container was removed. After the larvae had switched from endogenous to exogenous nutrition, they were fed daily on cooked egg yolk and a commercial fish food (Liquifry, 4,6% protein) at 08h00 and 16h00.

Morphometric measurements were made before preservation with an ocular micrometer accurate to 0,1 mm. Total length (TL) is defined here as the distance from the tip of the snout to the posterior end of the caudal fin or fin-fold.

In addition to behavioural notes, preliminary freehand drawings were made of each stage viewed. These sketches aided in drawing the final illustrations from preserved specimens, especially in the early stages of egg development. Final drawings were made with the aid of a camera lucida. Each drawing was based on a single specimen of the size indicated. The specimens were fixed in 10% formalin and then preserved in 5% buffered formalin.

The parents and preserved specimens of each developmental stage (n = 80) were deposited in the Albany Museum, Grahamstown (AMSA 8801 – 8881). A second batch of 40 developmental stages was deposited in the J.L.B. Smith Institute of Ichthyology, Grahamstown (RUSI 15691 – 15731).

The terminology of the larval phases used here follows Snyder (1976), who reviewed the application of a number of other terminologies including those of Hubbs (1943), Ahlstrom (1968) and Balon (1975). Snyder (1976) modified selected portions of these and other existing terminologies in an attempt at universal standardization. This terminology has recently been successfully applied to the larval development of several North American minnows (Snyder, Snyder & Douglas 1977; Fuiman & Loos 1978) and to other families (Cooper 1979, 1980; Rasmussen 1980).

Results

B. anoplus eggs were fertilized from fish collected on 7 November 1980 and were followed through the embryonic, larval and juvenile periods of development (Figure 1, Table 1). On 28 January 1981 another batch of eggs was fertilized and the embryonic to protolarval phases were observed.

The egg

The pale yellow, unfertilized ripe eggs of *B. anoplus* varied between 0,8 to 1,0 mm in diameter. When the eggs were placed in water, slight swelling occurred in the chorionic membrane of both fertilized and unfertilized eggs. The chorion of fertilized and unfertilized eggs adhered firmly to the substrate and the eggs were demersal. According to Breder & Rosen (1966), more than 75% of the families in the Cypriniformes produce demersal and adhesive eggs. When removing the *B. anoplus* eggs from the container the chorionic adhesive membrane could be stretched to over 10 mm before breaking. After a few hours the eggs could no longer re-adhere if the original adhesive contact was broken. The strength of adhesion appeared to increase with time and the eggs remained attached to the substrate until there were violent contractions of the embryo prior to hatching. Some of the eggs remained firmly attached until hatching occurred.

Early development

Development was followed from the first cleavage (Figure 1A). At the one-cell stage the width of the yolk was 0,8 mm and the width of the entire egg was 1,1 mm (n = 2). At the eight-cell stage the blastomeres were of various shapes, opaque and the yolk was pale yellow and granular (Figure 1C). The yolk-sac remained spherical until the embryo almost completely surrounded the yolk. At this stage the yolk-sac was pear-shaped (Figure 1I). Fryer & Whitehead (1959) noted that the shape of the yolk-sac in *L. victorianus* is distinctive with a posterior extension. The possible functional significance of the differentiation of the yolk-sac into these two regions could be to permit the flexing movement of the body (Fryer & Whitehead 1959). After 33 h of development the *B. anoplus* embryo was very active and the yolk-sac was indented where the embryonic head was positioned over the yolk. This may facilitate movement of the embryo within the egg. As in *L. victorianus* (Fryer & Whitehead 1959), curvature of the developing *B. anoplus* embryo was necessary (Figure 1I), as the egg width was only 0,8 to 1,0 mm, whereas the hatched larvae were over 3,0 mm in length. Development was more rapid in the eggs fertilized in January 1981 (24 – 25 °C) than in November 1980 (19 – 21 °C). In January the first larvae hatched in 28 h whereas in November they hatched at 53 h.

Newly hatched larvae

The heartbeat of the embryo was 90 (84 – 94) min^{-1} immediately prior to hatching. The newly hatched protolarvae had heartbeats of 108 (102 – 112) min^{-1} and were 3,3 mm long (TL) (n = 3) with heads flexed sharply over the yolk-sac, eyes pigmented, urostyles straight, mouths incomplete and the gut posterior to the yolk well developed (Figure 1J).

The yolk-sac was still globular and began to elongate several hours after hatching. The fin-fold extended posteriorly from the yolk around the caudal tip and anteriorly in the dorsal region of the trunk to a point opposite the ventral origin, interrupted only by the posteriorly located anus. Pectoral fins had not yet developed. All body surfaces were devoid of melanophores.

Mouth and feeding

Initially the mouth formed in a ventral position and then migrated to a terminal position as the yolk supply diminished. After 6 days the larvae had good control of their jaw movements and appeared to search for food. After 7 days they took food actively from the water column, orientating visually to small food particles and had a fully functional gut.

Growth rates

The growth rates obtained in this study were determined under laboratory conditions (Table 1) and therefore can be used only as a rough indication of the rates of incubation and development under variable natural conditions.

Five of the fish spawned in November reached 30 mm FL after 13 months. Their comparable year class in the impoundment would have reached 45 to 50 mm FL (Cambray 1982). The fish were therefore stunted under laboratory conditions.

Development of pigmentation

The first pigmentation occurred on the eyes before the larvae hatched. After hatching, pigmentation developed immediately dorsal to the yolk-sac and appeared to camouflage the rudimentary vascular system. Dorsal pigment developed next under the caudal fin-fold. Melanophores appeared on the dorsal region of the head which gradually became heavily pigmented. The head region became pale yellow at this stage (93 h old). Pigmentation of the trunk continued in two longitudinal rows. The third row of pigment occurred mid-laterally after 28 days. At 68 days the juvenile fish had fine dot-like pigments on the

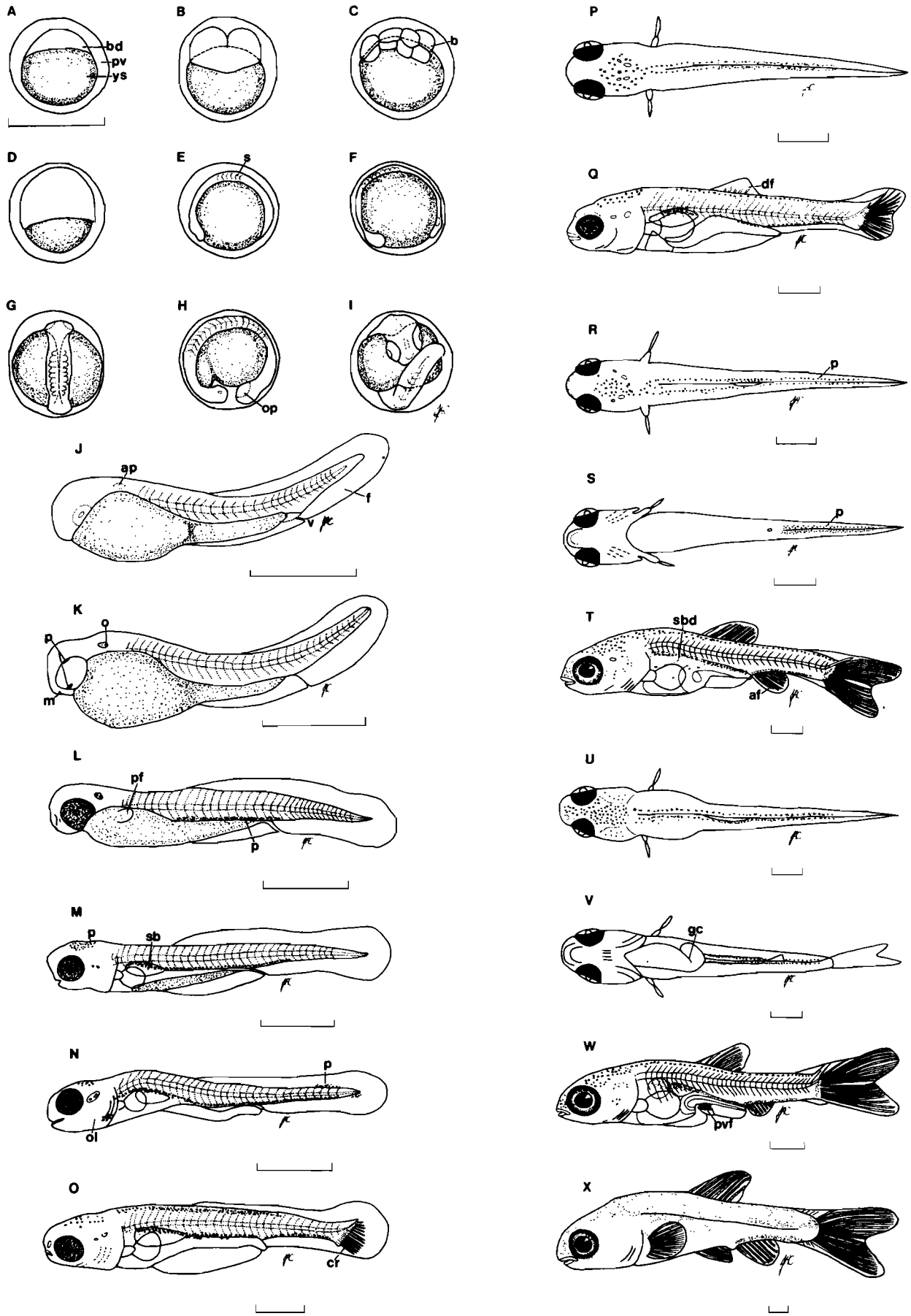

Figure 1 The early developmental stages of *B. anoplus* at 20 – 25 °C. A. One-cell stage. B. Two-cell stage. C. Eight-cell stage. D. Blastoderm. E. Five-somite stage. F. & G. 14 h, embryo. H. 30 h, embryo, I. 51 h, embryo, J. Early protolarva. K. 55 h, protolarva. L. 89 h, protolarva. M. 5,7 days, protolarva. N. 10 days, protolarva. O. 28 days, mesolarva. P. 28 days, mesolarva, dorsal view. Q. 33 days, mesolarva. R. 33 days, mesolarva, dorsal view. S. 33 days, mesolarva, ventral view. T. 51 days, metalarva, U. 51 days, metalarva, dorsal view. V. 51 days, metalarva, ventral view. W. 60 days, metalarva. X. 68 days, juvenile. Scale bar = 1 mm. af: anal fin. ap: auditory placode. b: blastomere. bd: blastodisc. cr: caudal fin-ray. df: dorsal fin. f: fin-fold. gc. convoluted gut. m: mouth. o: otolith. ol: operculum. op: optic placode. p: pigment. pf: pectoral fin. pv: perivitelline space. pvf: pelvic fin. s: somite. sb: swimbladder. sbd: swimbladder dividing. v: vent.

Table 1 Sequence and rate of development of the early developmental stages of *Barbus anoplus* at 20 to 25 °C in an aerated aquarium from 7.11.80 to 3.2.81 at the Douglas Hey Limnological Research Station

Age	Part of Figure 1	Stage of development	Behaviour
0	A	Fertilized egg 1,0 mm in diameter. Perivitelline space about 20% of egg diameter.	Adheres to substrate.
1 h 35 min	B	Two and four-celled phases. Second division perpendicular to the first.	Adheres.
1 h 50 min	C	Eight-celled phase. The eight large blastomeres are irregularly shaped and occupy the upper third of the yolk.	Adheres.
3 h 45 min	D	Many-celled phase. Blastodermal cap in equatorial position giving characteristic acorn shape.	Adheres.
12 h	E	Embryo surrounds about 2/3 of yolk surface. Five-somite stage.	Stronger adhesion of eggs to substrate.
14 h	F & G	Optic placode and notochord forming, nine-somite stage.	Adheres.
28 h		About 14 pairs of somites present. Enlarged caudal region; fin membrane apparent posteriorly. Yolk pear-shaped, granular and pale yellow in colour.	Adheres.
30 h	H	Embryo completely surrounds the yolk. About 18 somites. Caudal fin-fold well developed and spoon-shaped. Embryo clear.	Adheres. First muscular flexures noted.
33 h		Coiling stage. Caudal region of embryo twists around yolk, and yolk indented. Frequent flexures. Lens placodes present.	Loss of adhesion in some eggs.
34 h		Similar to 33 h.	Violent contractions; embryo rotates 180° every 10 to 20 s.
41 h		Heartbeat stage. Heart distinct and pulsating. Auditory placode apparent. Jaws started to form.	Violent 180° twisting of embryo continues.
43 h		Auditory vesicle migrates forward. Both lapillus and astericus visible. Embryo clear; yolk granular, pale yellow, considerably reduced in size.	Embryo very active. Heart contracts at 69 pulses min^{-1}.
47 h		Pigmentation first appears in eyes. Caudal region overlapped head.	Embryo active. Heart pulses 78 min^{-1}.
51 h	I	Pre-hatching stage. Eye more pigmented. Yolk more vacuolated. Remnant of adhesive membrane still visible.	Frequent twirling within egg. Heartbeat 90 min^{-1}.
53 h	J	*Protolarval phase.* Late embryo prior to hatching. Tip of tail loose. While observing, larva hatched with one quick lash of tail. Larva, 3,1 mm TL and dorso-ventrally 0,6 mm. Larvae were melanophore-free except for the eyes. Yolk-sac bulbous anteriorly and tubular posteriorly.	Heartbeat 108 min^{-1}. Larva rests on lateral surface. Moved with quick whip-like action, then rested on substrate.
55 h	K	About 32 myomeres. Eye more pigmented.	Protolarvae move tail region up to eye and then rapidly flick their tails, propelling themselves in a haphazard way on the substrate. Other larvae swim to surface (10 cm) and then spiral down. Some larvae float 1 cm above substrate.
57 h		Pectoral fin primordia present. Neurocranium area yellowing.	Some larvae cluster and float in aeration bubbles. Long periods without movement. Yolk upwards with the angle of body to substrate approximately 30°. Most of larvae positioned on side of container or free-floating.
67 h		Uninflated single-chambered swimbladder observed. Body pigmentation appears dorsally to yolk-sac over the developing vascular system. Dot-like isolated melanophores. Circulation observed on dorsal surface of yolk. Larvae 3,4 mm TL.	Larvae more active, swimming, more dispersed, and move away from water movement. Float at about 20° to substrate. Some larvae on substrate.
77 h		Auditory capsule migrates more anteriorly. Cranium more developed.	Larvae floating at surface or in water column. When larvae are disturbed they wriggle away to surface and then float downwards to rest.
89 h	L	Pigmentation begins on dorsal surface under fin-fold. Eye pale golden colour. 4,0 mm TL.	Larvae still floating or on substrate.
93 h		Melanophores present on covering over brain. Head yellowish. Blood in heart obvious. General pigmentation make larvae easy to locate in aquarium.	Larvae difficult to collect. Floating about 80° to the substrate.

Table 1 (Continued)

Age	Part of Figure 1	Stage of development	Behaviour
97 h		Rudimentary opercles and gill arches developing. Mouth more developed, antero-ventral in position. Yolk-sac not visible from dorsal view. Larvae 4,1 mm TL. Dorso-ventral width of yolk-sac 0,4 mm, of body plus yolk-sac 0,7 mm.	Swallowing action noted.
105 h		Pectoral fins loose, used in swimming.	Mouth opens and closes in gasps. Larvae more active, swim then float or lie on substrate.
4,5 days		One otolith larger. Gill slits more developed.	Mainly active swimmers now, only short rest periods.
4,7 days		Heart well developed, two distinct chambers. Eye movement noted for first time. Swimbladder increased in size and bulges into yolk. Larva length 4,5 mm TL, dorso-ventral width of yolk 0,3 mm, of body 0,6 mm. About 32 myomeres.	Mouth remains open after gulps. Larvae very active and swim in a more horizontal position, in quick dashes.
5,2 days		Mouth in terminal position.	Use pectoral fins in swimming, flipper-like. Also use pectoral fins to remain upright on substrate. Some larvae still floating. Rapid eye movements.
5,7 days	M	Indentation of caudal fin-fold, becoming a more paddle-shaped structure.	
6 days		Swimbladder very enlarged, almost full lateral width of body. Very little yolk remains.	Opercular movement obvious. Larvae very active, appeared to be visually searching for food.
6,7 days		Yolk absorption completed. Barbel rudiment present. Larvae 4,5 mm TL, dorso-ventral width 0,6 mm.	Free-swimming larvae, wriggle and glide, behave as juvenile fish.
7 days		Gut continuous from mouth to anus and functional. Vertebrae clearly observed.	Larvae feed actively. Food particles present in gut.
10 days	N	Eye movements more pronounced. Pigment in dorsal caudal region.	Do not swim against current but float with it.
11 days		Some caudal fin-ray anlages present.	
28 days	O & P	*Mesolarval phase.* Caudal fin-rays present.	Very active.
33 days	Q, R & S	Dorsal fin with ray development. Caudal fin with segmented rays. Larvae 8,4 mm TL and 1,5 mm dorso-ventral width.	
43 days		Pigment along lateral line, blood in gills. Dorsal fin-rays branching. Swimbladder dividing. About 32 vertebrae visible.	Active in midwater, feed at all levels in aquarium.
51 days	T, U & V	*Metalarval phase.* Anal fin rayed. Swimbladder separated into two chambers. Caudal fin homocercal.	
60 days	W	Gut convoluted. Pelvic fins forming with ray anlages.	
68 days	X	*Juvenile period.* Pelvic fins rayed. Silvery peritoneum. Body opaque. Pigmented dorsal surface with fine pigment spots. Length 15,9 mm TL.	
88 days		Scales well developed. Most adult characteristics present. Pigmentation similar to adult.	

dorsal surface and medially on the lateral surfaces (Figure 1X). A few large melanophores were scattered on the head and along the dorsal surface. Ventrally, pigment extended from the anus to the caudal fin.

Larval behaviour

One of the most interesting aspects of larval behaviour was that some larvae floated in the water column while other larvae remained on the substrate, yolk upwards. The protolarvae on the substrate periodically underwent a rapid undulation of the caudal area which propelled them upwards. *L. victorianus* (Fryer & Whitehead 1959), *L. mesops* (Malawi Fisheries Research Report 1965) and *L. umbratus* (Gaigher *et al.* 1975) larvae have also been recorded as behaving in this manner.

The swimming behaviour of the protolarvae i.e. active upward swimming and passive sinking, is characteristic of many fish species (Shelton & Stephens 1980). This behaviour is possibly of adaptive significance in that it reduces the chances of suffocation in the bottom mud. Similarly the floating habit of some *B. anoplus* larvae would be a further adaptation to reduce suffocation. In contrast, *B. holubi* (Groenewald 1961) and *B. natalensis* (Wright & Coke 1975) larvae burrow into the gravel substrate, and *B. natalensis* larvae succumbed to heavy silt loads passing through a rearing trough. Differences in larval fish behaviour deserve wider attention with regard to survival value of the large and small *Barbus* species under silty conditions.

The angle of the floating larvae decreased with time as the

yolk-sac was absorbed. The difference between the substrate larvae and the floating larvae was probably due to the structure of their respective yolks. This aspect deserves further investigation.

In addition to floating, some larvae were capable of moving off the substrate and adhering to the side of the container with the dorsal area of their heads. This trait would be the third way to avoid suffocation in the early larval stages.

Discussion

Very little is known about the embryology of southern African cyprinids. The present paper is the first detailed description of the early development of a minnow species from this region. Although the study was done in an attempt to explain the successful colonization of *B. anoplus* both in a newly formed impoundment and on a wider basis within southern Africa, the results should have application in other fields such as taxonomy and ecological studies where the correct identification of eggs and larvae is important. The behaviour of larval *B. anoplus* provided some of the answers as to why this minnow has been successful.

B. anoplus adults migrate into shallow, temporary areas prior to breeding (Cambray 1982). Under the harsh conditions of receding water level or high silt loads, the rapid rate of embryo development and the ability of some of the protolarvae to float would increase their chances of survival compared to larvae restricted to the substrate, which are only capable of limited movement.

In Lake Le Roux, as well as in river systems, the floating larvae could be carried by water movements and dispersed throughout large areas. This adaptation might have aided the small founder stock of chubbyhead barbs to rapidly colonize the newly created shoreline of the reservoir. It may also have aided dispersal of the species between and in river systems in the past. The larvae which remained on the substrate would disperse at a more leisurely pace and would thus have more control over their dispersal. Another important larval characteristic is the ability of some larvae to adhere to surfaces. This trait would be advantageous in a situation in which heavy silt loads would cause suffocation of larvae on the substrate. In these cases the negatively buoyant larvae could swim upwards and adhere to plants or rocks.

Cambray (1982) speculated that *B. anoplus* has been a successful colonizer of the shallow unstable rivers of southern Africa due to the following factors: small size, rapid growth-rate in the first year, early age at sexual maturity, distributional migration, high fecundity and tolerance of low water temperatures. The fast embryonic development rate, and the ability of some larvae to float and others to adhere to surfaces are also traits which may have improved the potential of this small species to colonize both lotic and lentic habitats within southern Africa.

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