

**Early ontogeny of an endangered, relict,  
cold-water cyprinid from Lesotho,  
*Oreodaimon quathlambae*\* (Barnard, 1938)**

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ABSTRACT

The early ontogeny of the endangered relict minnow, *Oreodaimon quathlambae* is described. Developing embryos were collected from crevices in mid-channel of the Tsoelikana River in the Sehlabathebe National Park, Lesotho. Egg envelopes were slightly to non-adhesive and upon hatching the free embryos were poorly developed and 5.7 mm TL (5.6 mm NL). A swim-up phase carried the free embryos to backwaters where they became larval fish and fed on aquatic invertebrates, mainly chironomid larvae, ephemeropteran nymphs and copepods. Developmental osteogenesis was followed and revealed that several pharyngeal teeth were ossified at the beginning of exogenous feeding at 7.95 mm TL (7.5 mm NL). Pigmentation pattern of larval *O. quathlambae* was distinct and separated it from another co-habiting cyprinid species, *Barbus aeneus*. The effects of habitat degradation, including the effect of introduced trout, on the early life stages are discussed.

KEY WORDS : Freshwater fish — Ontogeny — Cyprinidae — Africa — *Pseudobarbus quathlambae*.

RÉSUMÉ

ONTOGÉNÈSE DE PREMIER ÂGE D'UN CYPRINIDÉ D'EAU FROIDE DU LESOTHO,  
SURVIVANT ET EN VOIE DE DISPARITION, *OREODAIMON QUATHLAMBAE* (BARNARD, 1938)

Description de l'ontogénèse de premier âge du vairon en voie de disparition *Oreodaimon quathlambae*. Des embryons en cours de développement furent pêchés dans une crevasse du mi-lit fleuve Tsoelikana dans le Parc National de Sehlabathebe, Lesotho. Les tuniques des œufs étaient légèrement non-adhésives et au moment de l'éclosion des embryons libres, ces derniers étaient mal développés, avec une LT de 5.7 mm (LN 5.6 mm). Une phase de nage transporta les embryons libres dans un bras de décharge où ils se transformèrent en poissons larvaires se nourrissant d'invertébrés aquatiques : principalement de larves chironomides, de nymphes éphéméroptères, ainsi que de copépodes. Le développement de l'ostéogénèse fut suivi et révéla que plusieurs dents pharyngiennes étaient ossifiées au commencement de l'alimentation exogène, à 7.95 mm LT (LN 7.5 mm). Le modèle de pigmentation du *O. quathlambae* larvaire était distinct et le séparait d'une autre larve de l'espèce des cyprinidés avec laquelle elle cohabitait, *Barbus aeneus*. Seront enfin discutés les effets de la dégradation de l'environnement (y compris l'effet de l'introduction de truites) sur les stades de vie du premier âge.

MOTS-CLÉS : Eaux douces — Poisson — Cyprinidae — Ontogénie — Afrique — *Pseudobarbus quathlambae*.

\* Since submission and acceptance of this paper the generic name of this species has been changed from *Oreodaimon* to *Pseudobarbus* (Skelton 1988).

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## INTRODUCTION

### Rationale of study

Studies to date have concentrated mainly on the taxonomy, habitat and ecology of the adults. Because this species is noted to have a highly specialised adult phenotype, we decided to investigate the early life history stages. In this paper we describe the eggs, developing embryos, and larvae of the Maloti minnow, so that when these stages are collected by ecologists they will be able to identify them. Some habitat and other ecological notes are included on these early life history stages. Comparison is made with several early stages of *Barbus aeneus*, an indigenous species, which can spawn in the same area and at the same time as the Maloti minnow. Early behaviour of *O. quathlambae* is discussed with relation to *Parasalmo mykiss* (exotic trout) predation. An understanding of the effect of siltation caused by habitat degradation on the early life stages, may offer important clues to the continued existence of this species. What happened to *O. quathlambae* in its type locality, the upper Umkomazana River in Natal, South Africa? Possibly they disappeared from this system because of the effects of habitat degradation including exotic fish predation on the critical early life history stages of the endangered minnow and not directly because of adult mortality.

### Taxonomy

After examining 58 specimens of between 30 to 90 mm TL BARNARD (1938) described the Maloti minnow as *Labeo quathlambae*. *Quathlambae* is derived from the local Sesotho name of the Drakensberg mountains, *Inthaba Zokhahlamba*. JUBB (1966) queried the generic status. GREENWOOD and JUBB (1967) redescribed the species and suggested that it was a unique African cyprinid, evolved from a *Barbus* or *Barbus*-like ancestor. They erected the genus *Oreodaimon* (mountain spirit — because the species was thought to be extinct in 1967) of which *quathlambae* is the sole species.

SKELTON (1974) described the life colours of *O. quathlambae* and compared the colouration on the bases of its fins with those of the redfin minnows of the southern Cape coastal drainage. Subsequently, SKELTON (1976, 1980) has shown the close phylogenetic relationships between *Oreodaimon* and the redfin minnows of the Cape Province. Gephard (1978) proposed that three varieties of *O. quathlambae* be recognized: Tsoelikana, Moremoholo and Senqu. If this was accepted, the recently discovered

Jordane and Bokong River specimens would also have to be considered (CAMBRAY and MEYER 1987).

There has been some confusion with the common name for this species. GEPHARD (1978) reports that the common name Maluti (= Maloti) (see SKELTON 1979) minnow was officially given to the species on September 25, 1975 by the Protection and Preservation Commission of the Lesotho government (Anon. 1975). In a publication on the common names of the fishes of southern Africa, JACKSON (1975) used Drakensberg minnow. The common name in Sesotho is *Thoboshana* (Rondorf 1976a), which conveys the meaning of speckled grey. One of us (K. Meyer) has established that the fish are normally referred to as *lithhapi tse nyane*, meaning small fishes. The name 'Maloti' refers to a mountain range where the fish was only recently discovered. We have chosen to use Maloti minnow because this species only exists in Lesotho.

### Distribution

*O. quathlambae* was originally collected from the Umkomazana River in Natal (BARNARD 1938). It subsequently became extinct in this system (GREENWOOD and JUBB 1967). However, CRASS (1977) believed that the species probably never occurred in Natal and that the original type locality was misidentified. The species was not rediscovered until 1970 when PIKE and TEDDER (1973) collected specimens from the Tsoelikana River in the Sehlaba-thebe area, south-eastern highlands of Lesotho.

*O. quathlambae* are known presently to occur in only six mountain streams of the Orange River drainage (fig. 1). These are the Tsoelikana River, the upper reaches of the Moremoholo River (SE Lesotho, 2590 masl), the upper Senqu River (NE Lesotho, 2740 masl) (RONDORF 1976). Three recent range extensions are the Jordane (1950-2100 masl) and Bokong (1990-2305 masl) Rivers in central Lesotho which are tributaries of the Senquyane River (CAMBRAY and MEYER 1987). One pool in the Senquyane River immediately below the Jordane River inflow contained 20-40 *O. quathlambae*. The river above this pool did not have any *O. quathlambae*.

*O. quathlambae* is the only regular indigenous resident fish species in these high elevation streams of the Orange River and has a relict distribution isolated from other redfin minnow species which occur in the Cape Province, South Africa. SKELTON (1980) suggested that this isolation and resulting restricted distribution of *O. quathlambae* in the Drakensberg occurred in conjunction with the evolution of the Orange River system. All the rivers with *O. quathlambae* are upper catchment streams, and

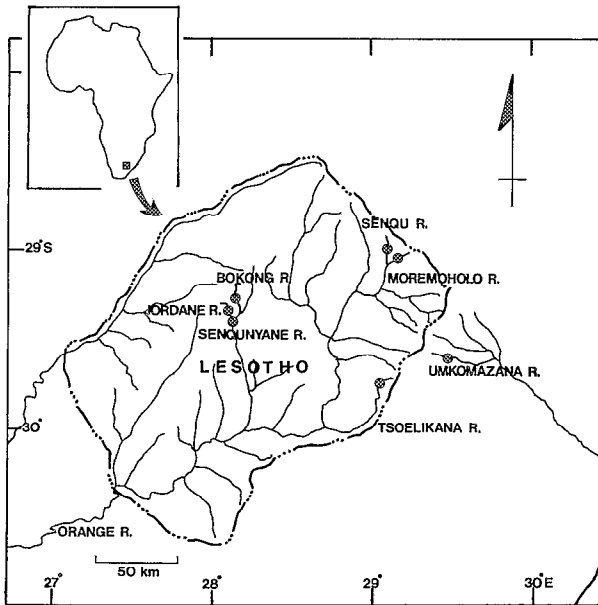


FIG. 1. — Upper catchment of the Orange River system in Lesotho, where populations of *Oreodaimon quathlambae* occur. Study area is indicated by a closed circle in the Tsoelikana River. *Le haul du bassin versant du fleuve Orange, au Lesotho, peuplé par Oreodaimon quathlambae. La zone étudiée est indiquée par un cercle sur le fleuve Tsoelikana*

are derived from seepage bogs which provide clear acidic water (GROBBELAAR and STEGMANN 1976). These high elevation streams form an ecological island with regard to the ichthyofauna (GEPHARD 1978).

GEPHARD (1978) speculated that the specialised habitat of *O. quathlambae* is eroding away from the east at 2-3 m per 1000 years. Three of the known populations of this minnow are only found on the highest ridge of the eroding escarpment. Man is also speeding up this natural erosional process to the detriment of *O. quathlambae* habitat.

Endangered status has been given to *O. quathlambae* because of its limited distribution and specialisations (IUCN 1977, SKELTON 1977, 1987). The endangered category, indicates that the species is in danger of extinction and that its survival is unlikely if the causal factors continue operating.

#### Adaptations to high altitude mountain streams

*O. quathlambae* is well adapted to its high altitude mountain stream environment (GREENWOOD and Jubb 1967, GEPHARD 1978, SKELTON 1980). GREENWOOD and JUBB (1967) list some of the distinctive adult phenotypic characters of *O. quathlambae* which are probably the result of adaptations to mountain stream habitats, such as small scales, naked chest, flattened ventral profile and horizontally inserted pectoral fins (fig. 2). The high vertebral count (38-40) and the relatively small scales are characters associated with adaptations to cool temperatures, swift currents and may also be associated with the possible crevice spawning habits of *Oreodaimon*. SKELTON (1980) gave the number of vertebrae in *O. quathlambae* compared to other redfin minnows an autapomorphic character rating.

SKELTON (1980) suggests that it is reasonable to consider that *O. quathlambae* has become highly

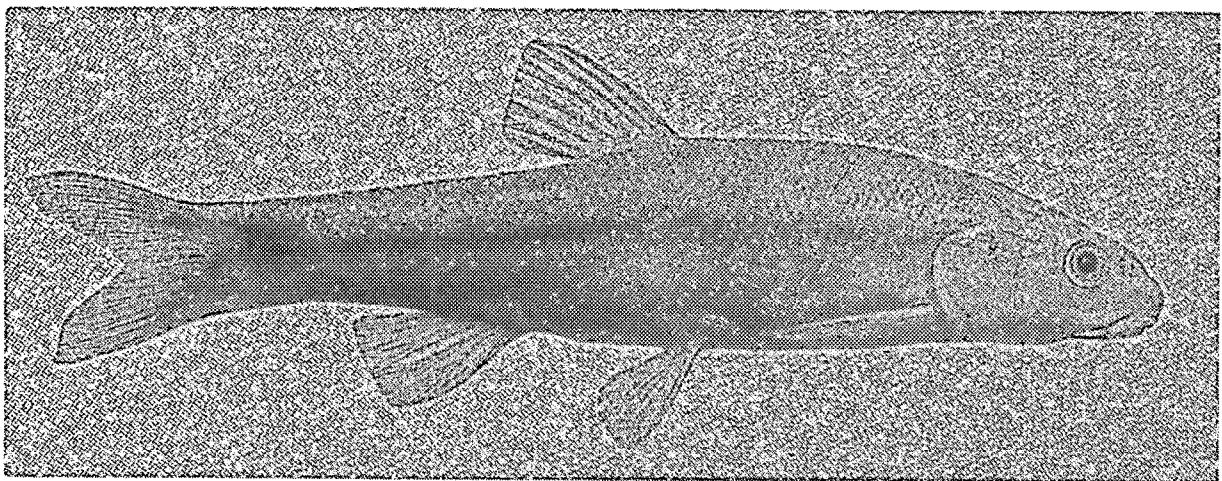


FIG. 2. — Adult *Oreodaimon quathlambae* (Photograph by R. and H. JUBB). *Oreodaimon quathlambae* adulte (Photographie par R. et H. JUBB)

adapted in response to higher altitude and probably more extreme environments in the past than occur at present. Physical environmental parameters such as temperature, current and substratum appear to dominate the evolutionary directions taken by the Maloti minnow.

In the present study we recorded a river temperature of 15 °C (16h00) the day after a hail storm. The fish had bred during this period. The low temperatures were therefore experienced by the developing embryos when the determination of the ultimate vertebral number was being set. Harsher climates in the past during early ontogeny of *O. quathlambae* are possibly the cause of the relatively high vertebral number (38-40) and small scales compared with other small *Barbus* species with radiately striated scales. A slow growth rate in the early ontogeny of fish associated with low temperatures can result in the formation of more serial elements such as vertebrae (FOWLER 1970). This premise would indeed be applicable to *O. quathlambae* compared to other redfin minnows. If the higher vertebral number is an adaptation to have a greater body flexibility for crevice spawning (GEPHARD 1978) then the historical temperature regime during development would not be as important. However, we noted that *O. quathlambae* adults utilised crevices throughout the year, not only during the breeding season.

GEPHARD (1978) foresaw extinction as the inevitable fate of this highly specialised species which occurs in a habitat that is diminishing due to man's impact and the natural erosional cycle. GREENWOOD and JUBB (1967) suggested that the greater specialisation (physiologically and anatomically) of *O. quathlambae*, compared to other *Barbus* species, contributed to its extinction in Natal. A thorough study of the entire life history of this species would possibly reveal more developmental, behavioural and physiological adaptations than we know at present. The early life history stages are highly susceptible to man's impact, changes in flow regime and siltation. Exotic fish predation may be the added factor that pushes this highly adapted species into extinction.

## COLLECTION SITE

Tedder (*in Anon.* 1971) has described the Tsoelikana River as a slow, peaceful little river, meandering along the bottom of a big flat valley which is quite unlike most other Lesotho rivers where *O. quathlambae* occur. All the *O. quathlambae* stages for the present study were collected below the waterfall (approx. 20 m in height) on the Tsoelikana River

within the Sehlabathebe National Park, Lesotho (fig. 1). The river was approximately 6 to 7 m wide and flowed in a gorge incised through Cave sandstone. The river bed was scattered with basaltic rocks, and there was very little silt in this area under natural conditions. Several of the pools above the site were large, with silt deposits up to 30 cm deep. Other than these pools there was very little silt in this section of the river. PIKE and TEDDER (1973) presented a good photograph (their figure 2) of typical *O. quathlambae* habitat along the upper Tsoelikana River. The river flow is usually low for eight months of the year. Over the rest of the year there are high flows periodically.

Free embryos and larval fish were collected mainly in backwaters along the vegetated banks of the Tsoelikana River. The most common plants, which were partially submerged after the rainfall on the 17-1-86, were the reed *Juncus effusus*, a grass *Eragrostis plana* and the lily *Kniphofia* sp. Other submerged plants were *Crassula natalensis*, *Diascia capsularis* and *Senecio polyodon*.

By scoop netting amongst this vegetation we were able to collect a wide range (7.38 to 25.0 mm TL) of larval fish from the 19-1-86 to the 21-1-86. During these three days one 6.45 mm TL (6.15 mm SL) free embryo was collected in a drift net. Several days after hatching the free embryos probably undertook a swim-up period in which they were carried from the main channel (spawning site) to quiet backwaters, where they could begin exogenous feeding in a less turbulent and comparatively food-rich area. The gauge readings (fig. 3) indicate that if rainfall is the trigger for *O. quathlambae* breeding, then in December 1985 they had a number of opportunities to spawn. The peak periods of rainfall were well spaced throughout the month. Also in January it was likely that the fish could have bred on the 4 or 5, 11 or 12 and did spawn between the 17 to 19. It is possible that this rainfall pattern permits the *O. quathlambae* to serial spawn throughout December (or earlier) to March.

## METHODS

The developing embryos and larval fishes were collected with set drift nets, or by standing in the fast flowing water and lifting rocks and at the same time holding a net or Surber sampler downstream. Netting was also carried out along the marginal vegetation. Specimens were collected over the period December 1985 to August 1986. Drift nets were made of "nytal" nylon cloth no 4466n with an aperture of 410 $\mu$ , sewn in a cone shape with nylon

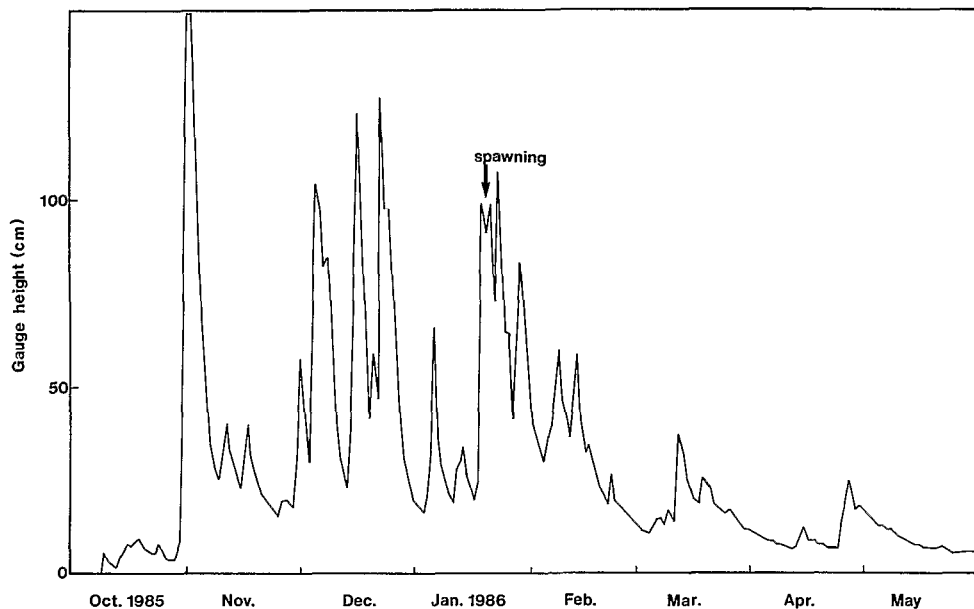


FIG. 3. — River height readings in the Tsoelikana River, 12 km downstream of drift net site. *Niveau d'eau du fleuve Tsoelikana, à 12 km en aval de l'emplacement du filet flottant*

reinforced seams. Each net measured 30 cm in diameter at the face and tapered to a tail equipped with a collection cup of PVC, 5 cm in diameter and 15 cm in length, with a brass mesh "window" to allow the current to pass through the cup. Collections from these nets were made daily. The hand net had an opening of 20 cm by 20 cm covered with netting of 400 $\mu$  apertures. The Surber sampler was constructed similarly to the drift net with a 30 cm by 30 cm opening.

Photomicrographs were taken of live material, and these colour slides are housed in the Albany Museum. Because so few ova were collected the photomicrographs do not always have a voucher specimen. Several embryos were allowed to develop under laboratory conditions. The developing embryos were placed in small plastic containers with meshed bottoms, which were put into an aerated aquarium. Water temperature was recorded when the photomicrographs were taken. All material was preserved in 5% phosphate buffered formalin.

Meristic counts and morphometric measurements follow those of CAMBRAY (1985a, c). Clearing and staining of specimens followed the method outlined by POTHOFF (1983) for early life history stages. Using a camera lucida attached to a stereoscopic microscope drawings were made of both live and preserved material.

Thirty of the cleared and stained specimens were examined for gut contents. The contents were

viewed while still inside the cleared fish, and numerical counts and percentage frequency values were recorded. Osteological development of the pharyngeal teeth and suspensorium was also observed in these specimens.

Specimens from this study are now housed in the Albany Museum, AMG/P 11224. Comparisons were made with specimens collected by RONDORF (1975, 1976b) which were made available from the collection at the Sehlabathebe National Park.

## RESULTS AND DISCUSSION

### Review of the reproductive biology of *Oreodaimon quathlambae*

Very little is known about the reproductive biology of *O. quathlambae*. RONDORF (1975, 1976b) and GEPHARD (1978) have put forward a number of speculations but more work is needed. The gonadal development of both sexes indicated that spawning occurred between January and April 1975 (RONDORF 1975). Spawning could have occurred intermittently from 13-1-76 to 28-2-76 (RONDORF 1976b). RONDORF (1976b) also found that the frequency of drift ova was most common during late February and early March, which correlated well with his data on gonadal development. RONDORF (1976b) collected

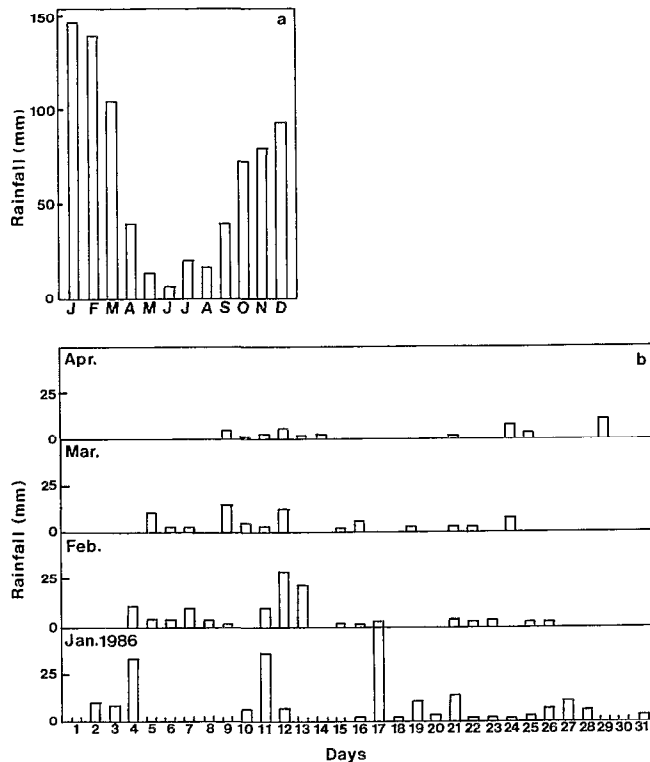


FIG. 4. — Rainfall data collected within the Sehlabathebe National Park, Lesotho, 4 km NW of drift net collection sites in the Tsoelikana River. *Quantités de précipitations recueillies dans le Parc National de Sehlabathebe au Lesotho, à 4 km au nord-ouest de l'emplacement du filet flottant placé dans le fleuve Tsoelikana*

a : Monthly average rainfall (1975-1986); b : Rainfall records for January to April 1986. a : *Moyenne mensuelle des précipitations (1975-1986)*; b : *Précipitations enregistrées de janvier à avril 1986*

very few young-of-the-year. One 24 mm TL specimen was collected on 2-2-86, which he said indicated an early January spawning. In our work we collected ova as well as O<sup>+</sup> group fish in mid-December 1985. This would indicate a much earlier spawning, possibly late November 1985. Ripe-running males have been collected as early as 22-11-84 by one of us (K. Meyer), which helps substantiate the early spawning of this species.

The rainfall data for ten years (fig. 4a) indicates that the rainy season in the area is between October and March, with peak rainfall usually in January and February. By scoop netting amongst the marginal vegetation we collected a wide range (7.38 to 25.0 mm TL) of larval fish from the 19-1-86 to the 21-2-86 (fig. 5) which indicated a number of spawnings. There was one major peak between 9 and 10 mm TL. In addition we collected one or more fish in each millimetre length group from 6 to 25 mm FL

(fig. 5). It is unfortunate that the November and December rainfall figures are unavailable. However, from the river flow gauge readings (fig. 3) it was evident that if spawning was triggered by rainfall and/or subsequently river flow, then in December 1985 *O. quathlambae* had a number of opportunities to spawn. The peak flow periods were well spaced throughout the month. In January it was likely that the fish could have bred on the 4 or 5, 11 or 12 and did spawn between the 17 and 19. It was possible that this rainfall pattern permitted *O. quathlambae* to serial spawn throughout December (or earlier) to March. This again adds weight to the proposal that *O. quathlambae* are serial spawners and spawn throughout their breeding season when conditions are favourable. The hail storm on the 17-1-86 during this study lowered the river temperature to below 15 °C and this in turn could also have been a trigger to initiate spawning.

Selection pressures operating through the high and variable mortality rate of newly-hatched 'larval' fish may result in the evolution of an iteroparous species (MANN and MILLS 1986) such as *O. quathlambae*. The staggering of hatching times of free embryos from a single spawning, or from separate spawnings, is a strategy which increases the probability that at least some young will hatch into suitable

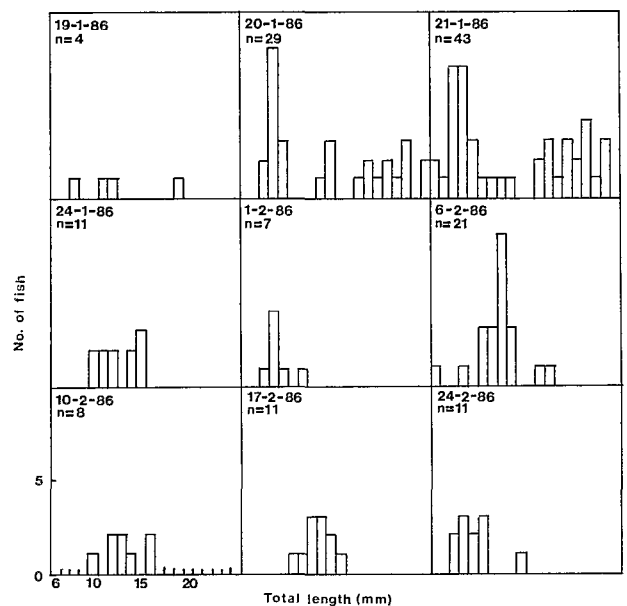


FIG. 5. — Length frequency plots of free embryos and larval *Oreodaimon quathlambae* collected in the Tsoelikana River, 19-1-86 to 24-2-86. *Relevés des fréquences de longueurs des Oreodaimon quathlambae aux stades d'embryon libre et larvaire, recueillis dans le fleuve Tsoelikana, du 19/1/86 au 24/2/86*

conditions and maintain the population. It can also be viewed as a means of dispersing the swim-up stages along the marginal river bank. Serial spawning also enables the species to utilise larval food and space (backwaters) throughout the summer. Possibly both or one of these may be limiting, and therefore serial spawning would increase the carrying capacity. It also permits the female to produce more eggs in one season. It appears that the probability of survival of a given genome is enhanced by dispersal through time, that is an extended spawning season. This spreads recruitment of larvae over a range of conditions, some favourable and some not.

RONDORF (1976b) described one spawning site, which occurred in the middle of the river on a short run below a pool tail but above a riffle. The water depth was between 20 to 40 cm, current speed of approximately  $0.52 \text{ m sec}^{-1}$  with water temperatures ranging from 14 to 22 °C over a 24 h period, with a reading of 20 °C at 12 h 00. GEPHARD (1978) raised a number of interesting speculations in his paper, one of which hypothesized that the enlarged pectoral fins of *O. quathlambae* indicated that they might spawn in crevices, on the side, or underneath rocks. One field observation by RONDORF (1976b) was used to substantiate GEPHARD's (1978) suggestion. On 3-2-76, RONDORF observed *O. quathlambae* exhibiting courtship-like behaviour in and around crevices between boulders at a 40-60 cm depth. All six rivers in which the minnow has been collected have abundant boulders, angular rocks, and crevices suitable for this type of spawning (JUBB 1966, PIKE and TEDDER 1973, RONDORF 1976b, K. MEYER pers. obs). Heavy siltation would fill these crevices, and therefore the minnow would not be able to crevice spawn. A crevice spawning habit would limit the species distribution in the mainly silt-laden Orange River system (CAMBRAY *et al.* 1986). We collected fertilized ova from a riffle area and it is highly likely that in our search for ova we 'released' them from crevices by lifting rocks, and collected them in our nets held downstream. The section of stream we searched was very similar to the one described by Rondorf above. However, we were not able to observe any fish behaviour in the fast flowing waters. In fact we could not see any adult fish at all between the 19 to 21-2-86.

### Reproductive guild of *O. quathlambae*

KRYZHANOVSKY (1949) suggested that adaptations of fishes for spawning and early development reflect not only the essential ecological factors of the embryonic period, but also the essential factors of all

the other intervals of the fish. These adaptations mark the biology of adults, and define the type of migrations, invasion abilities and limits of distribution. BALON (1985) has been a strong supporter of the above premise and notes that if we understand the principles of early ontogeny, we may understand the reasons behind the life styles of adults. The theory of reproductive guilds as put forward by BALON (1975) has as its basic premise that predators and availability of oxygen play a leading role in the development of reproductive strategies.

*O. quathlambae* spawn in mid-channel amongst boulders. The photokinetic response of the free embryos and larval stages are not known. From our limited work the early free embryo stage probably exhibits a photoneutral to photonegative response which would keep it in the crevice. At a later stage the free embryo, although still negatively buoyant, probably uses its wide finfold to drift with the current from the oxygen-rich lotic habitats to the food-rich lentic environment (backwaters). When the fish are in their transitional endogenous feeding stage they would exhibit a positive photokinetic response. This would alter their behaviour and increase their availability to the drift, as occurs in other fish species (MUTH and SCHMULBACH 1984). If the transitional fish drift mainly at night, then a positive photokinetic response would not be required.

The drift period may also conserve energy (PAINE 1984). As the early larval *O. quathlambae* were poorly developed skeletally, as shown by the cleared and stained material examined during the present study, they would probably not be able to maintain position in flowing waters. In a study on several species of darters (Etheostomatini) PAINE (1984) suggested that the presence of a drift interval should correlate with habitation of large streams, rivers and lakes, where plankton is more abundant than in low order streams. A long drift interval would therefore be associated with larvae incapable of feeding on aquatic insects as first prey and therefore requiring plankton. A reduced drift interval, such as probably occurs in *O. quathlambae* larval fish, is an adaptation for small stream habitation (Drakensberg and Maloti streams), where drift to plankton food sources is not required. However, in this case it would also be equally adapted for large streams (see PAINE 1984).

We have placed *O. quathlambae*, for the present, in the lithopelagophils (A.1.2) reproductive guild (BALON 1975). The eggs are placed in crevices in mid-stream, with egg envelopes that are not adhesive to slightly adhesive for a short while. Subsequently, the free embryo or early larval fish is then carried by the current to a food-rich environment and out of the strong flow of the main current.

This raises the question of why the eggs were not deposited in the food-rich environment in the first place? There are various possible reasons, such as high oxygen requirements of the developing embryo or fluctuating river levels which would leave the eggs marooned. With the cold water temperatures experienced even in January, in the Drakensberg streams, development will be slowed down, unlike more lowland species of *Barbus*, which develop quickly at high temperatures (CAMBRAY 1983a). Fluctuating water levels will therefore have less impact on fish developing quickly, than for *O. quathlambae* developing in colder waters.

In the backwater nursery areas the early life history stages may be subjected to heavy losses. Insect predators were located here such as Odonata, Anisoptera (dragonflies), and many Zygoptera (damselflies). The platanna (*Xenopus laevis*) were common in these areas. Should food in the backwater areas be patchy further losses may be incurred. Siltation in this area would also reduce feeding efficiency of the larval fishes.

#### *Oreodaimon quathlambae* eggs

After the heavy rains on the 17-1-86 (fig. 4b) the river rose by 72 cm between the 17 and 18 of January (fig. 3). Eggs were collected in the main current, at a depth of between 50 and 80 cm. Large boulders were lifted and a collecting net held downstream. In addition boulders were inspected in case the egg envelopes were adhering to the rocks. No adhesive eggs were found, and only a few live embryos were collected. We can only assume that by disturbing the boulders we released the eggs from crevices. Possibly, the eggs were being dispersed in the system anyway. Sometimes egg adhesiveness only persists at the point of attachment (PAINE and BALON 1985) and once broken would be difficult to assess at a later date.

The drift nets would only collect eggs which had been naturally disturbed in the system, except for the days when we worked in the river. The collecting cups of the drift nets were often full of organic debris after the heavy rains which made it difficult to locate the small clear eggs.

The eggs we collected were round to slightly ellipsoidal. In the latter case both the long axis and short axis (greatest distance perpendicular to long axis) were recorded, pooled and divided by two for a comparative diameter. The eggs were clear to a pale yellow colour making them difficult to detect. A total of only four live eggs were measured  $\bar{x} = 1.8 \pm \text{SD } 0.09$  mm envelope diameter, and only one of these was of an early enough stage to measure the yolk diameter, which was 1.35 mm.

Five more eggs were collected, preserved and later found in the laboratory when sorting through drift net samples. These preserved eggs had a mean diameter of  $1.82 \pm \text{SD } 0.08$  mm. Of these, the yolk diameter could be measured on four specimens ( $1.43 \pm \text{SD } 0.02$  mm). RONDORF (1976b) described the size of seven *O. quathlambae* eggs which measured  $1.92 \pm \text{SD } 0.07$  mm outer envelope diameter, and the yolk was  $1.31 \pm \text{SD } 0.14$  mm ( $n = 4$ ). Taking into consideration both live, preserved and RONDORF's (1976b) results the outer envelope diameter varied between 1.7 to 2.0 mm and the yolk diameter from 1.15 to 1.45 mm. We can therefore assume that mature eggs in the adult fish would be those above 1.0 mm in diameter.

#### Adhesiveness of eggs

RONDORF (1976b) was the first to report that *O. quathlambae* ova appeared to be non-adhesive when found in riffle areas or collected in drift nets and from observations on a few eggs he had in aquaria. As in the present study no attached eggs were found when RONDORF (1976b) examined gravel and rubble from the spawning area. However, RONDORF does state that some eggs were 'slightly' adhesive. RONDORF (1976b) concluded that the ova can be considered non-adhesive to only very slightly adhesive at certain times.

GEPHARD (1978), trying to fit all available data into his crevice spawning hypothesis, suggested that RONDORF (1976b) collected so few eggs in the drift nets, most of which were dead, because the healthy eggs were adhesive, and thus well anchored further upstream of the nets. Once again GEPHARD (1978) relied on *O. quathlambae* adult morphology, which is well adapted to swift flowing stream habitats. Fish which spawn in swift flowing water characteristically have adhesive eggs (LAGLER *et al.* 1962). Work on another cyprinid, *Labeo capensis*, in the lower Orange River has shown that non-adhesive eggs can be spawned in swift-flowing water (CAMBRAY 1985a). Work done on a species related to *O. quathlambae*, the redfin minnow *Barbus* [Now *Pseudobarbus* (Skellon 1988)]  *afer*, indicated that this riverine species had non-adhesive eggs which were placed in crevices (J. A. CAMBRAY pers. obs). However, some small African *Barbus* species, such as *B. anoplus* and *B. trevelyani*, do have adhesive eggs (CAMBRAY 1983a, 1985c).

The fact that RONDORF and ourselves collected so few eggs was more likely due to placement of drift nets, quantity of sampling gear, the small size of the eggs to be found amongst all the debris, the relatively small quantity of eggs laid during any one spawning session, and a crevice spawning habit. In



January 1986 we recovered healthy, developing embryos in the drift nets. The egg membranes were reasonably clear of debris even though the nets contained a lot of material which could have adhered to the eggs. Even small amounts of organic debris, which flowed through the rearing troughs, became attached to the highly adhesive egg envelopes of *B. trevelyani* to such an extent that it obscured observation of the developing embryo (CAMBRAY 1985c). On re-examination of the ova RONDORF collected, plus the eggs collected in January 1986, it appears that the eggs were non-adhesive to slightly adhesive as some debris occurred on several healthy egg envelopes.

RONDORF (1976b) speculated that eggs washed out of the riffle areas could be entrapped on a lower riffle, settle into pools or be exported far downstream. It seems reasonable to state that depending on flow velocities and original placement in the river, the ova which do not settle into a crevice immediately after spawning could be transported a long way from the actual spawning ground. This in turn poses problems for workers trying to pinpoint spawning sites in the Tsoelikana River. RONDORF (1976b) determined that in still water ova fell at a rate of 2.1 — 2.4 cm sec<sup>-1</sup>, and that at this rate the transported ova would settle out in pools where silt and fine shifting sands could bury them. Possibly eggs would end up in the backwaters along the river banks where we found free embryos, larval and juvenile fish, but they would also be subjected to siltation at this locality.

If we assume that *O. quathlambae* are crevice spawners, the advantage of having non-adhesive eggs would be that they could fall into crevices and any organic debris would not adhere to them. The disadvantages would be wash-outs into less hospitable habitats like pools and lower elevations. Excessive siltation would smother the eggs in either case.

The size of the perivitelline space can sometimes be used as an indication of egg habitat. Indian cyprinids which spawn in mountain streams have a large perivitelline space (MOOKERJEE 1945). *O. quathlambae* has a relatively small perivitelline space (yolk diameter is 68.2-78.6% of total water-hardened egg diameter), which would indicate that these eggs are not supposed to be bounced along a rocky river bed, but remain in a crevice. In *L. capensis* eggs taken from the rocky mid-channel of the Orange River the swelling of the egg envelope accounted for 48% of the diameter of the shed, water-hardened egg (CAMBRAY 1985a). This large space could offer protection to the developing embryo in turbulent waters. *O. quathlambae* have a relatively small perivitelline space. Possibly this is because they do not normally need protection from turbulent water.

A smaller space would increase their negative buoyancy and enhance their ability to sink into crevices.

When we were collecting the early life history stages of *O. quathlambae* we noted a number of crabs in the area. Possibly the eggs fall into crevices too small for crabs to get into. One of us (K. Meyer) has noted the presence of crabs and platannas (*X. laevis*) in all localities where *O. quathlambae* are found especially in the Tsoelikana River. In future it would be worth-while to study the predation on *O. quathlambae* developing eggs by crabs and other predators.

### Developing embryos

The earliest stage of development was collected on 19-1-86, which would have been spawned after or during the rainfall on the 17-1-86 (fig. 4). In this egg the blastodermal cap covered ca 75% of the surface of the yolk and the outer envelope was not adhesive. The germ ring and embryonic shield were visible as thickened areas of the blastodisc. This egg was collected in mid-channel after moving boulders. The water temperature was 15 °C at 16 h 00. This egg was kept in the laboratory aquarium, and at 09 h 00 on 20-1-86, water temperature 15 °C, the embryo was in a late gastrulation stage (fig. 6A) prior to closure of the germ ring. During the embryonic phase several stages of organogenesis were viewed. Figure 6B shows the embryo at the beginning of segmentation of trunk mesoderm, somite and fore-brain differentiation where optic vesicles had evaginated from the forebrain. The embryo is ca. two-thirds of the circumference of the yolk, and the head of the embryo was elevated 0.16 mm.

An embryo collected on 18-1-86 at 14 h 00 and photographed at 17 h 30 is shown in fig. 6C. The tail tip had separated from the yolk sac, the optic vesicle had become much larger than the previous stage and segmentation of the body had continued, consisting now of 20 pairs of somites. No muscular contractions were observed. The yolk sac at this stage was pear-shaped with the embryonic head over the wider section of yolk. Figure 6D depicts a specimen collected from the river on 21-1-86 at 13 h 00 and photographed at 18 h 00, note the pear-shaped yolk. Therefore, on the 18 and 21-1-86 there were eggs at approximately the same stage of development which indicated that there was more than one spawning during this survey period.

A later embryonic stage (fig. 6E) was collected on 21-1-86 from the main channel and photographed in the laboratory on 22-1-86 at 08 h 00, WT 18 °C. There were active trunk movements at irregular intervals, the post bulbous yolk section of the

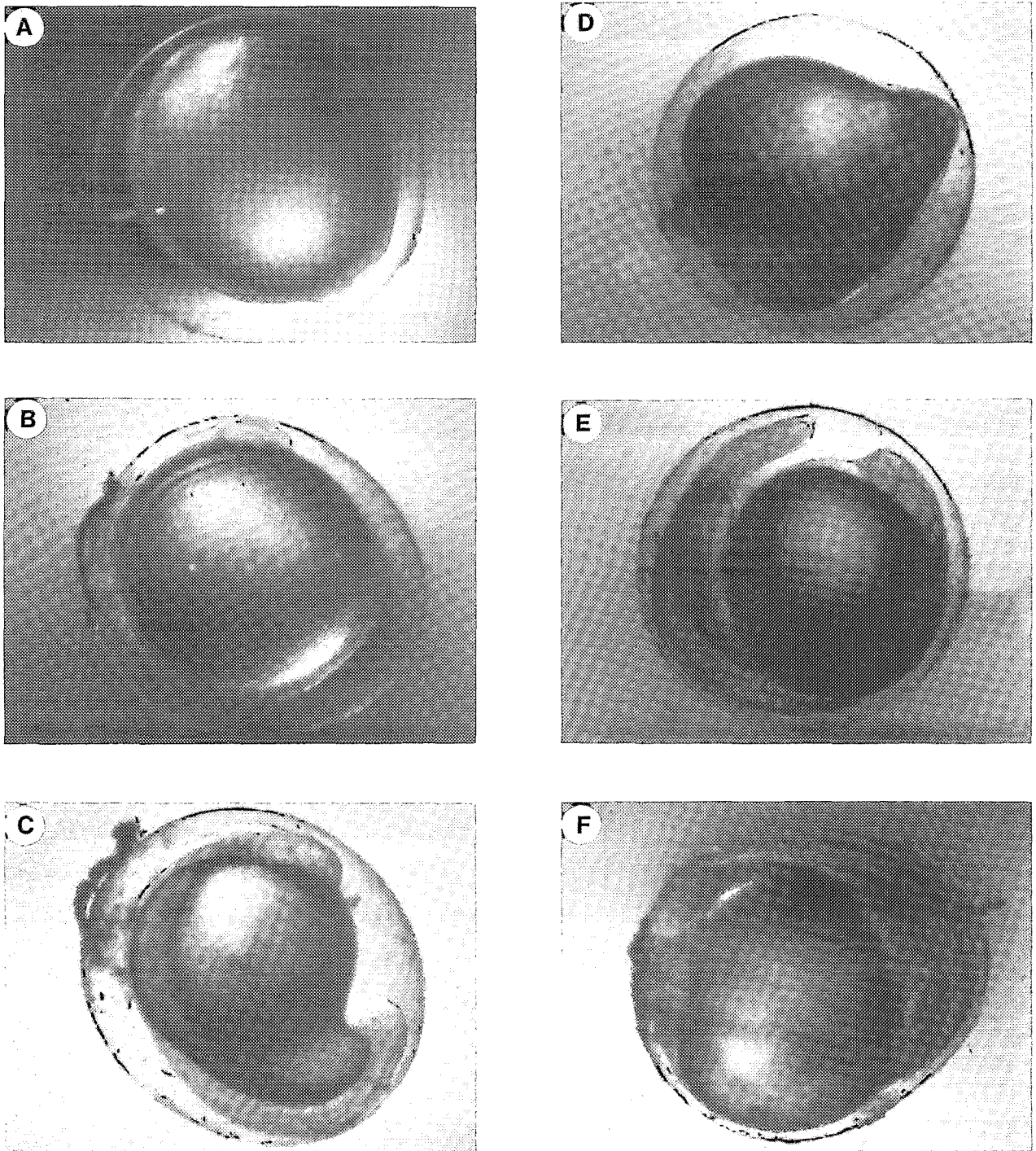


FIG. 6. — Photomicrographs of several early embryonic stages of *Oreodaimon quathlambae* collected in the Tsoelikana River. *Microphotographies de plusieurs stades embryonnaires du premier âge de Oreodaimon quathlambae recueillis dans le fleuve Tsoelikana.*

A : Late epiboly, 20.1.86; B : Embryo, commencement of trunk mesoderm segmentation; C : Embryo, tail tip free, 18.1.86; D : Embryo, showing pear-shaped yolk, 21.1.86; E : Embryo, active trunk movements, 21.1.86; F : Prehatching embryonic stage. *A : Épibolie avancée, 20/1/86; B : Embryon, commencement de la segmentation mésodermique du tronc; C : Embryon, bout de la queue libre, 18/1/86; D : Embryon, montrant un vitellus piriforme, 21/1/86; E : Embryon, mouvements actifs du tronc, 21/1/86; F : Période embryonnaire précédant l'éclosion.*

embryo was free from that part of the yolk sac, the pericardial cavity was inflated and the posterior extension of the yolk sac was very clear. The heart tube was as yet not visible.

A later, prehatching embryonic stage is shown in fig. 6F. The heart tube was visible with heart beats of  $38 \text{ min}^{-1}$  ( $n = 3$ ), the caudal area overlapped the head, no pigment was apparent (WT  $15^\circ\text{C}$ ). The embryo revolved up to  $180^\circ$  by lateral flexions inside the egg envelope at irregular intervals, and the caudal area stretched the outer egg envelope. The lens placodes had invaded the optic vesicles and the swollen brain lobes were obvious. The auditory vesicles were quite distinct.

In addition to the above mentioned embryonic stages a preserved embryo was studied. The specimen was at a similar developmental stage to fig. 6F. As this specimen had been collected in a drift net on the 16-12-85, it is likely that this egg was spawned on the 14-12-85 when the river rose 60 cm (fig. 3). No river temperatures are available for this period. It is evident, even from this limited data set, that *O. quathlambae* spawned several times during this breeding season.

#### Description of free embryo and larval *Oreodaimon quathlambae*

Recently hatched *O. quathlambae* (fig. 7A) were 5.8 mm TL live (preserved 5.7 mm TL); 39 myomeres; yolk sac bulbous anteriorly, tubular posteriorly; yolk grainy, lacked large oil globules; had pectoral fin buds; blood elements were visible and flowed from dorsal aorta to lower caudal vein and back to the heart via Cuvier's duct over the yolk sac; head deflected ventrally over anterior margin of yolk sac until ca. 7.3 mm TL; posterior gas bladder chamber inflated ca. 7.3 mm TL; yolk absorbed at ca. 7.95 mm TL, with a very short transitional period between 7.3 and 7.95 mm TL when the minnows changed from endogenous to completely exogenous feeding, one 8.4 mm TL specimen contained a small amount of yolk; functional mouthparts formed ca. 7.95 mm TL; the dorsal aorta which formed posterior to the yolk became the caudal artery which proceeded to within 0.53 mm of the tip of the notochord, then turned ventrally to form the caudal vein which returned to the heart directly under the caudal artery and passed over the yolk sac (CUVIER's duct) and then ventrally under the bulbous yolk section to the heart; anterior gas bladder chamber forming ca. 12.82 mm TL; caudal finfold paddle-shaped 7.15 mm TL started to fork at 12.5 mm TL; first caudal fin rays 9.2 mm TL; notochord flexion commenced at 8.02 mm TL; first dorsal rays formed 10.1 mm TL; incipient dorsal fin

margin partially differentiated 8.02 mm TL and completely differentiated 17.46 mm TL; dorsal fin origin over myomeres 16-17, incipient anal fin margin partially differentiated at 9.32 mm TL and completely differentiated at 16.9 mm TL; pelvic buds formed anterior to dorsal fin origin at 15.66 mm TL; first pelvic rays at ca. 19.46 mm TL; gut commenced to loop at 17.7 mm TL; entire finfold absorbed at ca. 25.36 mm TL; smallest individual with some scales 36.1 mm TL (29.21 mm SL); paired posterior maxillary barbs were forming at between 24.8 mm TL (20.67 mm SL) when they were buds and 25.2 mm TL (19.88 mm SL) when they were 0.2 mm long.

The meristics and morphometry of the early life history stages collected during this study are given in Tables I and II. This study is based on developmental stages of *O. quathlambae* collected only in the Tsoelikana River and may not cover the entire phenotypic variation that may occur among larval populations (see BOSLEY and CONNOR 1984) of this species.

#### Pigmentation

FABER and GADD (1983) and FUIMAN *et al.* (1983) amongst others have noted the importance of pigmentation patterns for identification of the early developmental stages of fish. Figures 7A to 7V are dorsal, lateral and ventral views of *O. quathlambae* free embryos and larval fish. The main purpose of these drawings is to record pigmentation pattern. All stippling indicates pigment and is not included solely for artistic improvement (FABER and GADD 1983). The only exception is the granular pattern used for depicting yolk in the early stages. Other features are included, such as fin rays where they do not obscure pigmentation pattern. Mainly external pigmentation is given in the figures. However, some internal pigmentation patterns are included with the external pigmentation on the dorsum of the neurocranium.

SKELTON (1980 : 154) described the adult pigmentation as follows: «*Pigmentation variable, usually dark lateral band from ventral head to posterior end of caudal peduncle; dorsal surface plain or more frequently with a series of prominent bilateral spots or vermiculations. Body greyish brown to deep bluish black in breeding males, ventral region creamy white; iris golden, operculum metallic golden; adults proximal portion of fins and adjacent body regions scarlet.*» GEPHARD (1978) described the adult pigment pattern of three populations of this species. In specimens examined for the present study the dorsal spots only became prominent in specimens over 57 mm TL and began in the area between dorsal and caudal fins.

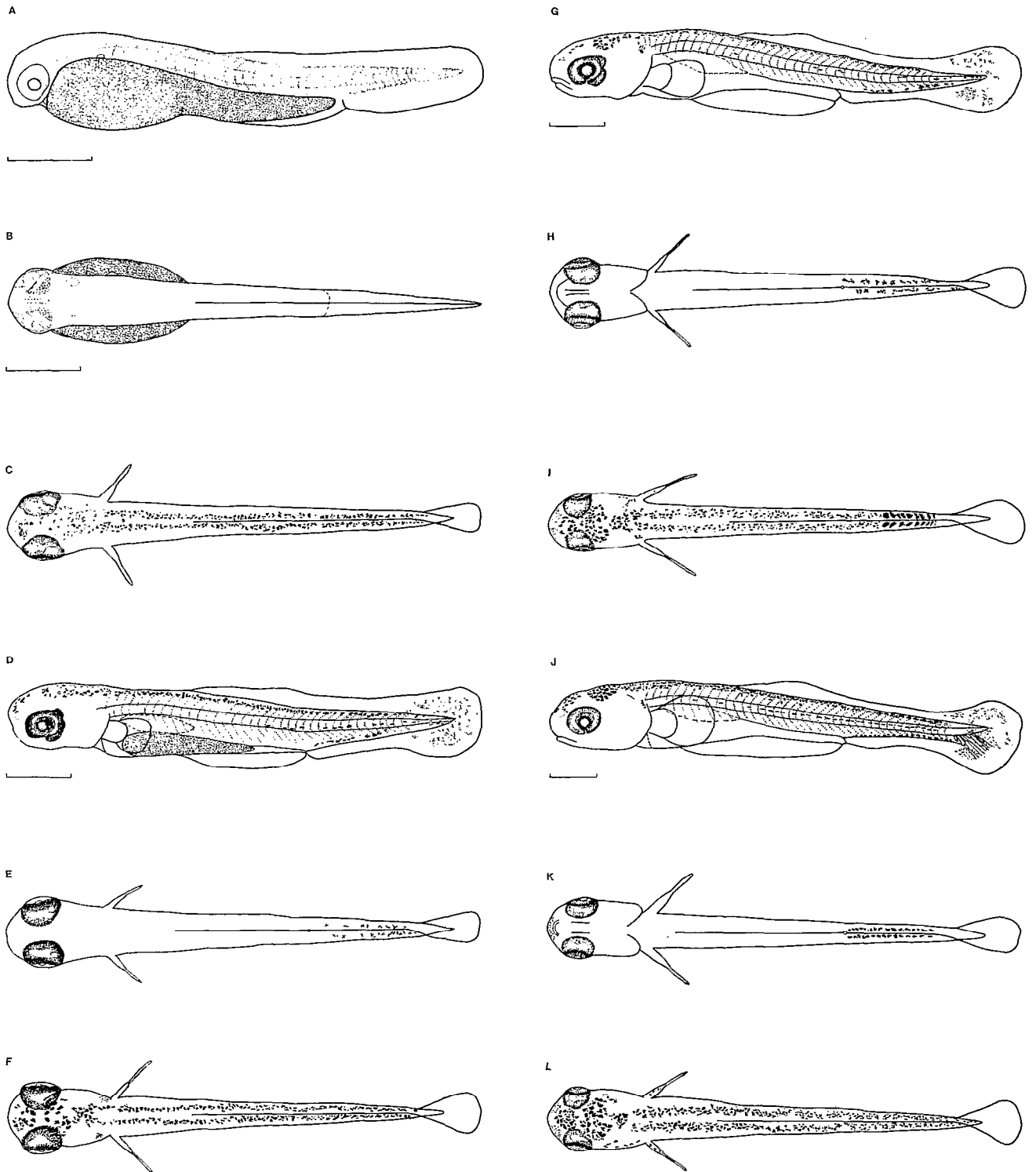
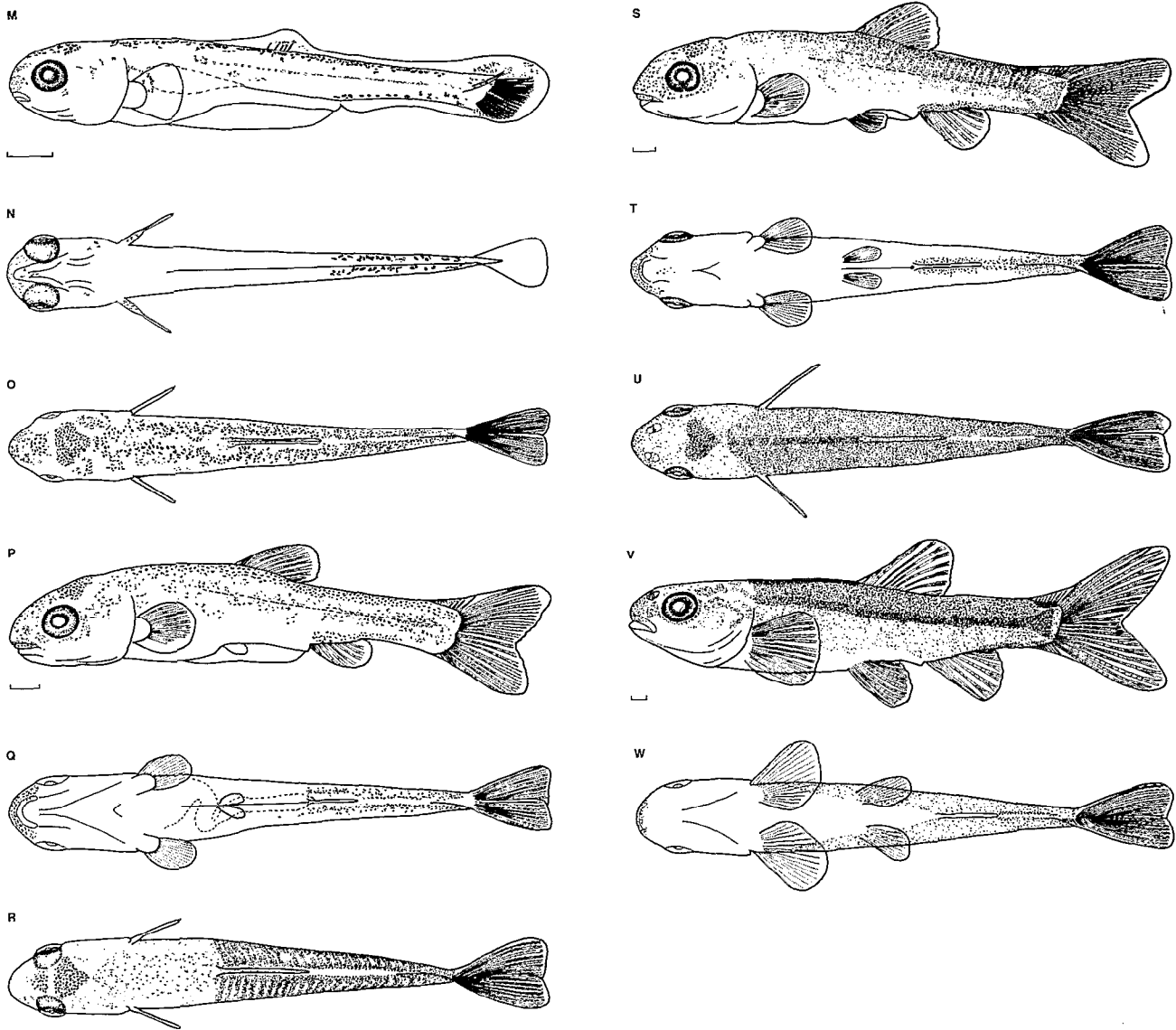


FIG. 7. — Several early developmental stages of *Oreodaimon quathlambae* to depict changing pigment patterns. *Plusieurs stades de développement de premier âge de Oreodaimon quathlambae illustrant les changements de la pigmentation*



A : Recently hatched free embryo 5.64 mm TL (5.45 mm NL); B : A 6.4 mm TL (6.15 mm NL) free embryo, dorsal view; C : Free embryo, 7.3 mm TL (6.9 mm NL) dorsal view. D : Free embryo, 7.3 mm TL (6.9 mm NL) lateral view; E : Free embryo, 7.3 mm TL (6.9 mm NL), ventral view; F : Larva, 8.4 mm TL (8.0 mm NL), dorsal view; G : Larva, 8.4 mm TL (8.0 mm NL), lateral view; H : Larva, 8.4 mm TL (8.0 mm NL), ventral view; I : Larva, 10.1 mm TL (9.4 mm NL), dorsal view; J : Larva, 10.1 mm TL (9.4 mm NL), lateral view; K : Larva 10.1 mm TL (9.4 mm NL), ventral view; L : Larva, 11.84 mm TL (10.77 mm SL), dorsal view; M : Larva, 11.84 mm TL (10.77 mm SL), lateral view; N : Larva, 11.84 mm TL (10.77 mm SL), ventral view; O : Larva, 18.2 mm TL (15.2 mm SL), dorsal view; P : Larva, 18.2 mm TL (15.2 mm SL), lateral view; Q : Larva, 18.2 mm TL (15.2 mm SL), ventral view, note loop in gut; R : Larva, 24.33 mm TL (19.82 mm SL), dorsal view; S : Larva, 24.33 mm TL (19.82 mm SL), lateral view; T : Larva, 24.33 mm TL (19.82 mm SL), ventral view; U : Juvenile, 34.52 mm TL (27.5 mm SL), dorsal view; V : Juvenile, 34.52 mm TL (27.5 mm SL), lateral view; W : Juvenile, 34.52 mm TL (27.5 mm SL), ventral view. A : Embryon libre récemment éclos, 5,64 mm LT (5,45 mm LN); B : Un embryon libre de 6,4 mm LT (6,15 mm LN), vue dorsale; C : Embryon libre de 7,3 mm LT (6,9 mm LN), vue dorsale; D : Embryon libre de 7,3 mm LT (6,9 mm LN), vue latérale; E : Embryon libre de 7,3 mm LT (6,9 mm LN), vue ventrale; F : Larve de 8,4 mm LT (8,0 mm LN), vue dorsale; G : Larve de 8,4 mm de LT (8,0 mm LN), vue latérale; H : Larve de 8,4 mm LT (8,0 mm LN), vue ventrale; I : Larve de 10,1 mm LT (9,4 mm LN), vue dorsale; J : Larve de 10,1 mm LT (9,4 mm LN), vue latérale; K : Larve de 10,1 mm LT (9,4 mm LN), vue ventrale; L : Larve de 11,84 mm LT (10,77 mm SL), vue dorsale; M : Larve de 11,84 mm LT (10,77 mm SL), vue latérale; N : Larve de 11,84 mm LT (10,77 mm SL), vue ventrale; O : Larve de 18,2 mm LT (15,2 mm SL), vue dorsale; P : Larve de 18,2 mm LT (15,2 mm SL), vue latérale; Q : Larve de 18,2 mm LT (15,2 mm SL), vue ventrale, notez la boucle dans le ventre; R : Larve de 24,33 mm LT (19,82 mm SL), vue dorsale; S : Larve de 24,33 mm LT (19,82 mm SL), vue latérale; T : Larve de 24,33 mm LT (19,82 mm SL), vue ventrale; U : Juvénile de 34,52 mm LT (27,5 mm SL), vue dorsale; V : Juvénile de 34,52 mm LT (27,5 mm SL), vue latérale; W : Juvénile de 34,52 mm LT (27,5 mm SL), vue ventrale.

TABLE I

Some meristic characters of free embryos, larval and juvenile *Oreodaimon quathlambae* used in this developmental description  
*Caractéristiques méristiques d'Oreodaimon quathlambae aux stades d'embryon libre, larvaire et juvénile, utilisées dans cette description de leur développement*

| Length interval<br>TL(mm) | n  | Myomeres |          |       | Dorsal         |                | Caudal fin |                | Dorsal fin | Anal fin | Pelvic fin | Pectoral fin |
|---------------------------|----|----------|----------|-------|----------------|----------------|------------|----------------|------------|----------|------------|--------------|
|                           |    | Preanal  | Postanal | Total | Secondary rays | Principal rays | Ventral    | Secondary rays |            |          |            |              |
| 5                         | 1  | 28       | 11       | 39    | 0              | 0              | 0          | 0              | 0          | 0        | 0          | 0            |
| 6                         | 1  | 27       | 8        | 35    | 0              | 0              | 0          | 0              | 0          | 0        | 0          | 0            |
| 7                         | 3  | 24-26    | 12-13    | 37-39 | 0              | 0              | 0          | 0              | 0          | 0        | 0          | 0            |
| 8                         | 16 | 24-26    | 11-13    | 37-39 | 0              | 0              | 0          | 0              | 0          | 0        | 0          | 0            |
| 9                         | 12 | 24-27    | 11-13    | 37-40 | 0              | 0-5            | 0          | 0-6            | 0          | 0        | 0          | 0            |
| 10                        | 7  | 24-26    | 13-14    | 37-40 | 0              | 4-8            | 0          | 4-8            | 0-1        | 0        | 0          | 0            |
| 11                        | 5  | 25-26    | 13       | 38-39 | 0              | 10             | 0          | 7-9            | 0-5        | 0        | 0          | 0            |
| 12                        | 3  | 25       | 13       | 38    | 0              | 10             | 0          | 9              | 5-6        | 0        | 0          | 0            |
| 13                        | 7  | 25-26    | 12-14    | 37-40 | 0              | 10             | 0          | 9              | 5-8        | 0        | 0          | 0            |
| 14                        | 5  | 25-26    | 13-14    | 38-39 | 0              | 10             | 0-1        | 9              | 5-7        | 0-3      | 0          | 0            |
| 15                        | 4  | 25-26    | 13       | 38-39 | 0-1            | 10             | 0-1        | 9              | 7-9        | 3-8      | 0          | 2            |
| 16                        | 4  | 25-26    | 12-13    | 38    | 0-2            | 10             | 1-2        | 9              | 9-11       | 5-7      | 0          | 5            |
| 17                        | 2  | opaque   | 13       | -     | 3              | 10             | 2-3        | 9              | 9-10       | 7-8      | 0          | n.s.         |
| 18                        | 4  | opaque   | 13       | -     | 3-4            | 10             | 2-4        | 9              | 9-10       | 6-8      | 0          | 7            |
| 19                        | 7  | opaque   | 13       | -     | 4-5            | 10             | 3-5        | 9              | 9-11       | 7-8      | 0-6        | 7            |
| 20                        | 3  | opaque   | opaque   | -     | 5              | 10             | 5          | 9              | 9-11       | 8        | 4-5        | n.s.         |
| 21                        | 5  | -        | -        | -     | 5-7            | 10             | 4-6        | 9              | 10-11      | 8-9      | 3-7        | 8            |
| 22                        | 6  | -        | -        | -     | 5-7            | 10             | 5-6        | 9              | 10-11      | 8-9      | 6-8        | n.s.         |
| 23                        | 2  | -        | -        | -     | 7-9            | 10             | 6-7        | 9              | 11         | 8-9      | 7          | 12           |
| 24                        | 3  | -        | -        | -     | 7-8            | 10             | 7          | 9              | 10         | 8-9      | 6-8        | n.s.         |
| 25                        | 2  | -        | -        | -     | 8              | 10             | 8          | 9              | 10         | 8        | 8          | 13           |
| 26                        | 3  | -        | -        | -     | 8-9            | 10             | 7-8        | 9              | 10         | 8        | 8          | 13           |
| 27                        | 4  | -        | -        | -     | 7-10           | 10             | 7          | 9              | 9-10       | 8        | 8          | 14           |
| 28                        | 5  | -        | -        | -     | 8-9            | 10             | 7-8        | 9              | 10         | 8        | 8          | 15           |
| 29                        | 2  | -        | -        | -     | 9-10           | 10             | 7-8        | 9              | 10         | 9        | 8          | 14           |
| 30                        | 2  | -        | -        | -     | 8-9            | 10             | 7-8        | 9              | 10         | 8        | 8          | 17           |
| 31                        | 1  | -        | -        | -     | 7              | 10             | 5          | 9              | 9          | 8        | 8          | n.s.         |
| 32                        | 5  | -        | -        | -     | 10-11          | 10             | 7-9        | 9              | 10         | 8-9      | 8          | 16           |
| 33                        | 2  | -        | -        | -     | 9-10           | 10             | 8-9        | 9              | 10         | 8-9      | 8          | n.s.         |
| 34                        | 2  | -        | -        | -     | 10             | 10             | 7-8        | 9              | 9-10       | 8-9      | 8          | n.s.         |
| 35                        | 4  | -        | -        | -     | 9-10           | 10             | 7-9        | 9              | 9-10       | 8-9      | 8          | 16           |
| 36                        | 4  | -        | -        | -     | 9-11           | 10             | 8          | 9              | 9-10       | 8        | 8          | 16           |
| 37                        | 4  | -        | -        | -     | 10-13          | 10             | 8-10       | 9              | 10         | 8        | 8          | 16           |
| 38                        | 6  | -        | -        | -     | 9-12           | 10             | 7-9        | 9              | 10         | 8        | 8          | 17           |
| 39                        | 1  | -        | -        | -     | 11             | 10             | 10         | 9              | 10         | 8        | 8          | 17           |
| 40                        | 1  | -        | -        | -     | 11             | 10             | 10         | 9              | 10         | 8        | 8          | 17           |

TABLE II

Proportional measurements relative to notochord length or standard length for some *Oreodaimon quathlambae* free embryos, larvae and juveniles, collected from the Tsoelikana River, Lesotho, between 16-8-85 and 7-8-86. Fish were grouped by 1 mm intervals of total length ( $n$  = sample size). Standard length and total length are means  $\pm$  SD for the 1 mm length group

Mesures relatives à la longueur notochorde ou à la longueur standard, pour des *Oreodaimon quathlambae* aux stades d'embryon libre, larvaire et juvénile, pêchés dans le fleuve Tsoelikana au Lesotho, entre le 16/8/85 et le 7/8/86. Les poissons sont groupés selon des classes de 1 mm de longueur totale ( $n$  = taille échantillon). Les longueurs standard et les longueurs totales sont des moyennes  $\pm$  DS pour le groupe de longueur 1 mm

| n  | NL or SL(mm) | TL(mm) | SL:TL | Preanal: SL | Snout:SL | Head:SL | ED:SL | HD:SL | BDp:SL | BDa:SL | HW:SL | BWp:SL |
|----|--------------|--------|-------|-------------|----------|---------|-------|-------|--------|--------|-------|--------|
| 1  | 5.6          | 5.7    | 0.982 | 0.804       | 0.039    | -       | 0.071 | 0.089 | 0.214  | 0.071  | 0.089 | 0.161  |
| 1  | 6.15         | 6.4    | 0.961 | 0.732       | 0.036    | 0.132   | 0.081 | 0.098 | 0.172  | -      | 0.114 | 0.114  |
| 3  | 7.07(0.38)   | 7.47   | 0.946 | 0.682       | 0.037    | 0.212   | 0.082 | 0.141 | 0.150  | 0.093  | 0.127 | 0.099  |
| 16 | 7.99(0.21)   | 8.46   | 0.944 | 0.667       | 0.040    | 0.233   | 0.081 | 0.141 | 0.140  | 0.083  | 0.126 | 0.090  |
| 12 | 8.86(0.23)   | 9.37   | 0.946 | 0.672       | 0.042    | 0.236   | 0.079 | 0.143 | 0.143  | 0.086  | 0.129 | 0.094  |
| 7  | 9.86(0.20)   | 10.48  | 0.941 | 0.694       | 0.041    | 0.243   | 0.075 | 0.145 | 0.147  | 0.092  | 0.126 | 0.093  |
| 5  | 10.67(0.23)  | 11.6   | 0.920 | 0.685       | 0.052    | 0.240   | 0.073 | 0.154 | 0.155  | 0.093  | 0.133 | 0.107  |
| 3  | 11.56(0.47)  | 12.59  | 0.918 | 0.692       | 0.048    | 0.244   | 0.084 | 0.149 | 0.149  | 0.088  | 0.134 | 0.106  |
| 7  | 12.2(0.26)   | 13.66  | 0.893 | 0.693       | 0.058    | 0.258   | 0.078 | 0.162 | 0.168  | 0.104  | 0.143 | 0.125  |
| 5  | 13.04(0.44)  | 14.56  | 0.896 | 0.670       | 0.055    | 0.263   | 0.081 | 0.161 | 0.163  | 0.106  | 0.150 | 0.116  |
| 4  | 13.33(0.27)  | 15.37  | 0.897 | 0.707       | 0.061    | 0.266   | 0.081 | 0.170 | 0.176  | 0.112  | 0.155 | 0.128  |
| 4  | 14.37(0.43)  | 16.6   | 0.866 | 0.696       | 0.065    | 0.263   | 0.077 | 0.175 | 0.185  | 0.118  | 0.155 | 0.129  |
| 2  | 14.94(0.29)  | 17.6   | 0.849 | 0.693       | 0.066    | 0.274   | 0.076 | 0.179 | 0.194  | 0.122  | 0.173 | 0.144  |
| 4  | 15.32(0.45)  | 18.23  | 0.840 | 0.674       | 0.071    | 0.276   | 0.078 | 0.181 | 0.195  | 0.127  | 0.160 | 0.137  |
| 7  | 16.41(0.37)  | 19.49  | 0.842 | 0.662       | 0.071    | 0.290   | 0.079 | 0.189 | 0.204  | 0.135  | 0.175 | 0.155  |
| 3  | 17.01(0.23)  | 20.57  | 0.827 | 0.664       | 0.072    | 0.294   | 0.082 | 0.198 | 0.210  | 0.139  | 0.180 | 0.154  |
| 5  | 17.98(0.26)  | 21.67  | 0.830 | 0.663       | 0.069    | 0.282   | 0.079 | 0.186 | 0.210  | 0.144  | 0.176 | 0.162  |
| 6  | 18.68(0.59)  | 22.58  | 0.827 | 0.660       | 0.074    | 0.294   | 0.077 | 0.197 | 0.208  | 0.145  | 0.182 | 0.156  |
| 2  | 19.51(0.07)  | 23.74  | 0.822 | 0.656       | 0.077    | 0.302   | 0.077 | 0.200 | 0.223  | 0.177  | 0.183 | 0.172  |
| 3  | 20.35(0.46)  | 24.6   | 0.827 | 0.661       | 0.069    | 0.279   | 0.075 | 0.187 | 0.207  | 0.144  | 0.178 | 0.156  |
| 2  | 20.37(0.06)  | 25.27  | 0.807 | 0.657       | 0.079    | 0.297   | 0.082 | 0.201 | 0.237  | 0.151  | 0.182 | 0.173  |
| 3  | 20.72(0.47)  | 26.19  | 0.791 | 0.653       | 0.074    | 0.303   | 0.085 | 0.204 | 0.233  | 0.158  | 0.190 | 0.181  |
| 4  | 21.99(0.33)  | 27.43  | 0.802 | 0.646       | 0.077    | 0.295   | 0.081 | 0.207 | 0.239  | 0.159  | 0.194 | 0.187  |
| 5  | 22.76(0.43)  | 28.47  | 0.799 | 0.637       | 0.076    | 0.283   | 0.082 | 0.191 | 0.221  | 0.152  | 0.181 | 0.173  |
| 2  | 23.2(0.26)   | 29.05  | 0.799 | 0.644       | 0.079    | 0.300   | 0.086 | 0.196 | 0.231  | 0.161  | 0.185 | 0.180  |
| 2  | 23.96(0.45)  | 30.26  | 0.792 | 0.654       | 0.081    | 0.303   | 0.081 | 0.207 | 0.227  | 0.154  | 0.179 | 0.173  |
| 1  | 25.57        | 31.9   | 0.802 | 0.628       | 0.082    | 0.309   | 0.086 | 0.203 | 0.223  | 0.160  | 0.192 | 0.180  |
| 5  | 25.65(0.44)  | 32.5   | 0.789 | 0.642       | 0.085    | 0.300   | 0.081 | 0.194 | 0.223  | 0.165  | 0.185 | 0.181  |
| 2  | 26.68(0.25)  | 33.49  | 0.797 | 0.666       | 0.078    | 0.292   | 0.082 | 0.195 | 0.225  | 0.160  | 0.176 | 0.178  |
| 2  | 27.7(0.28)   | 34.67  | 0.799 | 0.657       | 0.081    | 0.285   | 0.078 | 0.186 | 0.213  | 0.155  | 0.164 | 0.180  |
| 4  | 28.05(0.82)  | 35.55  | 0.789 | 0.640       | 0.090    | 0.304   | 0.083 | 0.199 | 0.223  | 0.169  | 0.191 | 0.188  |
| 4  | 28.95(0.73)  | 36.4   | 0.795 | 0.657       | 0.083    | 0.299   | 0.079 | 0.195 | 0.233  | 0.171  | 0.189 | 0.190  |
| 4  | 30.5(0.32)   | 37.7   | 0.809 | 0.636       | 0.082    | 0.290   | 0.080 | 0.192 | 0.223  | 0.164  | 0.185 | 0.183  |
| 6  | 30.75(0.54)  | 38.42  | 0.800 | 0.647       | 0.080    | 0.295   | 0.076 | 0.194 | 0.222  | 0.160  | 0.183 | 0.182  |
| 1  | 30.78        | 39.36  | 0.782 | 0.661       | 0.088    | 0.305   | 0.078 | 0.198 | 0.227  | 0.179  | 0.195 | 0.195  |
| 1  | 31.92        | 40.0   | 0.798 | 0.654       | 0.069    | 0.282   | 0.078 | 0.188 | 0.226  | 0.163  | 0.183 | 0.188  |

BDa = Body Depth at anus, BDp = Body Depth at pectoral fin, BWp = Body Width at pectorals, ED = Eye Diameter, HD = Head Depth, HW = Head Width.

BDa : hauteur du corps à l'anus; BDp : hauteur du corps à la nageoire pectorale; BWp : largeur du corps aux pectorales; ED : diamètre de l'œil; HD : hauteur de la tête; HW : largeur de la tête.

### Developmental osteology of *Oreodaimon quathlambae*

Thirty developmental stages ranging in size from 7.15 mm TL (6.8 mm NL) to 44.13 mm TL (35.27 mm SL) in approximately 1 mm steps were cleared and double stained for cartilage and osteological examination. This was sufficient to provide a general understanding of the sequence of cartilage formation and ossification in the species.

#### NEUROCRANIUM AND BRANCHIOCRANIUM DEVELOPMENT

In the smallest specimen 7.15 mm TL (6.8 mm NL) there was no ossification and the branchials, dentary and otic capsules were weakly stained for cartilage. At 8.25 mm TL (7.8 mm SL), three pharyngeal teeth on the fifth ceratobranchial were partly ossified and the fifth ceratobranchial was stained dark blue. There was more cartilagenous formation in the skull, most notably in the maxilla and the anterior edge of the opercle was just starting to ossify. At 9.2 mm TL (8.7 mm SL) there were four pharyngeal teeth and the dentary and maxilla were partly ossified. The premaxilla and two branchiostegal rays were slightly ossified at 10.53 mm TL (10.01 mm SL), and five ossified pharyngeal teeth were present. The basioccipital process had started to form and was lightly ossified in the 12.54 mm TL (11.28 mm SL) specimen. The exoccipital and parasphenoid were partially ossified. The third branchiostegal ray was slightly ossified and the otoliths were stained red in the 13.98 mm TL (12.32 mm SL) specimen. At 15.0 mm TL (12.9 mm SL) there were seven pharyngeal teeth and the developing basioccipital process was well ossified. The premaxilla, maxilla and dentary were well ossified by 16.95 mm TL (14.81 mm SL) and the entopterygoid, preopercle, parasphenoid and exoccipital were all slightly ossified. The opercle series (opercle, preopercle, subopercle and interopercle) were all ossified at 18.11 mm TL (15.04 mm SL). The quadrate was now ossified as were most of the mandibular arch bones and the angulo-articular had started to ossify. In the hyoid arch the three branchiostegal rays were well ossified and the posterohyal and anterohyal were about 50% ossified. The first four ceratobranchials were ossified and the fifth, the pharyngeal bone, was heavily ossified. Most of the neurocranium was still cartilagenous except for the parasphenoid, exoccipital and basioccipital which almost touched the anterior of the swimbladder.

At 19.86 mm TL (16.88 mm SL) the neurocranium was about 20 to 30% ossified, and the frontal, orbitosphenoid, pterosphenoid, protic and supraethmoid had begun to ossify. In the neurocranium of

the 23.86 mm TL (19.56 mm SL) specimen the posttemporal was now ossified. The major change in the 25.12 mm TL (20.4 mm SL) specimen was more ossification of the bones in the dorsal area of the neurocranium and the rest of the skull was well ossified. At 27.28 mm TL (21.66 mm SL) the nasal, orbital areas and parietal remained unossified. Only the edges of the quadrate were ossified. The parietal was partly ossified in the 32.85 mm TL (26.34 mm SL) specimen. Mainly the nasal area remained cartilagenous as well as the dorsal edge of the orbitosphenoid in the 41.12 mm TL (33.0 mm SL) specimen.

SKELTON (1980) has detailed the striking reduction of ossification of bone at the anterior end of the neurocranium of large adults of *O. quathlambae*. This is a synapomorphic feature shared with *Barbus tenuis* when compared to the other redfin minnows.

#### VERTEBRAL DEVELOPMENT

In the smallest specimen examined, 7.15 mm TL (6.8 mm NL), there was no ossification of the undifferentiated notochord which had a diffuse retention of alcian blue stain suggesting initial chondrification. At 8.25 mm TL (7.8 mm SL) nine darker blue areas (centra) indicated that the notochord had started to differentiate anteriorly. In a 9.2 mm TL (8.7 mm SL) specimen 23 centra were observable starting at myomere one. At 10.53 mm TL (10.00 mm SL) there were 34 centra and the first 14 had neural spines. The 12.54 mm TL (11.28 mm SL) specimen had 39 centra (full complement), 35 with neural spines. The first three centra and first two pairs of neural spines were partly ossified. At 14.56 mm TL (13.1 mm SL) there was a slight ossification of the fourth and fifth centra and modification of the first four vertebrae as discussed below. All 39 centra were showing signs of ossification at 16.95 mm TL (14.81 mm SL), with the precaudal vertebrae the most developed. At 18.11 mm TL (15.04 mm SL) there were 40 well ossified centra. On vertebrae 21 the haemal spines had fused to form a haemal arch and the second and third centra were now fused. At 19.86 mm TL (16.88 mm SL) there were 40 centra, the pleural ribs, haemal and neural arches were ossified and the first haemal arch was on centra 22. In the 22.14 mm TL (18.46 mm SL) specimen the preneurapophyses, postneurapophyses and parapophyses were beginning to ossify.

#### WEBERIAN APPARATUS FORMATION

There was only undifferentiated notochord, where the Weberian apparatus would form, in the 7.15 mm TL (6.8 mm SL) specimen. At 8.25 mm TL (7.8 mm SL) the notochord had started to differentiate under



the 4th myomere. At 10.55 mm TL (9.9 mm SL) the first four vertebrae were marked by dark blue blocks in the notochord and all four had pairs of neural spines with basal swellings. In addition the fifth set of neural spines had basal swellings. At 11.24 mm TL (10.3 mm SL) the first seven pairs of neural spines had basal swellings. In the 12.54 mm TL (11.28 mm SL) specimen, the scaphium was forming and the first three centra were starting to ossify. The intercalarium on centra two as well as a lateral process and the tripus from the third centra, with the os suspensorium from the fourth centra were forming.

At 13.98 mm TL (12.32 mm SL) the scaphium was more enlarged on centra one. In the 15.0 mm TL (12.96 mm SL) specimen the scaphium was larger, claustrum forming and the lateral process was ossified. On the third centra the neural spine was larger with the base enlarged. The tripus was starting to ossify and made contact with the anterior of the swim bladder. On the third centra the neural arch was greatly enlarged and a large block of cartilage had formed above the anterior section of the second centra to posterior of the fourth centra. On the fourth centra the neural arch had greatly enlarged, and the pleural rib was reduced compared to the one on the fifth centra. The os suspensorium was well developed, partially ossified and touched the swim bladder. The fifth centra also showed signs of modification, the base of the neural spines were enlarged and the pleural ribs were arched anteriorly, not posteriorly as were the others. At 16.95 mm TL (14.81 mm SL) the scaphium and intercalarium were ossified. At 18.11 mm TL (15.09 mm SL) the second and the third centra were fused. At 19.86 mm TL (16.58 mm SL) there were two ossified crests on the dorsum of the cartilage block over vertebrae 1-4, the scaphium had a posterior process and the claustrum was ossified. At 22.14 mm TL (18.46 mm SL) only the anterior tips of os suspensorium were not ossified. The cartilage block extended and touched the anterior of the exoccipital of the neurocranium, the dorsal part of the claustrum, scaphium complex and neural arches 2, 3 and 4.

At 26.0 mm TL (20.18 mm SL) the cartilagenous block extended from the exoccipital to neural arch of the fifth vertebrae. At 27.28 mm TL (21.66 mm SL) the cartilagenous block had retracted from the 5th neural arch. The dorsal crest was still the only ossified section of this complex, but at 28.28 mm TL (22.45 mm SL) this neural complex was approximately 40% ossified. At 32.8 mm TL (26.34 mm SL) an anterior neural complex was visible which was ossifying and a posterior neural complex which was well ossified. There was still cartilage connecting the anterior neural complex to the exoccipital and the

posterior neural complex to the fourth neural arch and spine. In the 41.12 mm TL (33.0 mm SL) specimen both the anterior and posterior neural complexes were ossified.

#### CARTILAGE FORMATION OF THE CAUDAL FIN

At 8.5 mm TL (8.0 mm NL) there were three hypurals with the fourth hypural just forming. At 9.2 mm TL (8.7 mm SL) the two most dorsal hypurals had two rays each. At 10.55 mm TL (9.9 mm SL) a parhypural and four hypurals had formed. A broad haemal spine was forming ventral to the parhypural. At 12.54 mm TL (11.28 mm SL) flexion was well advanced, and each hypural and the parhypural had at least one ray. At 13.98 mm TL (12.32 mm SL) the fifth hypural was distinct, PU1 and U1 had fused. Uroneural 1 and 2 had fused (= urostyle). At 14.56 mm TL (13.1 mm SL) the sixth hypural was forming. At 15.0 mm TL (12.9 mm SL) an epural was now present. The broad haemal spine on PU2 had fin rays. At 18.11 mm TL (15.04 mm SL) the hypurals and parhypural as well as the 19 principal rays were about 50% ossified, and there were four procurrent dorsal and three procurrent ventral rays. At 25.12 mm TL (20.41 mm SL) the only cartilagenous parts of the caudal skeleton were the posterior edges of the hypurals.

#### CARTILAGE FORMATION OF DORSAL FIN

Six pterygiophores with five rays first started to form in the 12.54 mm TL (11.28 mm SL) specimen. At 14.56 mm TL (13.1 mm SL) there were six pterygiophores and six rays. The pterygiophores were not as yet divided into radials. The 15.0 mm TL (12.96 mm SL) specimen had a full complement of eight pterygiophores. At 19.86 mm TL (16.58 mm SL) the eight pterygiophores were divided into two radials, and there were 10 rays with the last one double. At 23.86 mm TL (19.56 mm SL) there were 10 rays with the second to eighth starting to ossify. Not until 41.12 mm TL (33.0 mm SL) did the third radial form in pterygiophores five to eight, with three unbranched and seven branched rays.

#### CARTILAGE FORMATION OF ANAL FIN

At 14.56 mm TL (13.1 mm SL) there were no pterygiophores. By 15.0 mm TL (12.96 mm SL) the full complement of six pterygiophores were not as yet divided into radials and there were eight rays. At 19.86 mm TL (16.88 mm SL) there were two radials in each pterygiophore and eight rays with the last one double. At 23.86 mm TL (19.56 mm SL) the rays had started to ossify and by 30.0 mm TL (23.64 mm SL) the pterygiophores had commenced ossification. As in the dorsal fin, the pterygiophores (fourth to

sixth) started to divide into three radials only at the 41.12 mm TL (33.00 mm SL) stage.

#### CARTILAGE FORMATION OF PECTORAL GIRDLE

The cleithrum was visible at 7.15 mm TL (6.8 mm) as weakly stained cartilage. At 8.25 mm TL (7.8 mm SL) the cleithrum had started to ossify. The supracleithrum and the scapula were first observed in the 11.24 mm TL (10.3 mm SL) specimen. The coracoscapular cartilage was weakly stained in the 14.56 mm TL (13.1 mm SL) specimen, and the supracleithrum was slightly ossified. At 19.86 mm TL (16.58 mm SL) the post-temporal was visible and partly ossified and the proximal radials were forming. The postcleithrum was first visible at 23.86 mm TL (19.56 mm SL). Three distal radials were forming in the 25.12 mm TL (20.41 mm SL) specimen and the coracoid and scapular cartilagenous plates were distinct and well-stained as were the four proximal radials. There were now 13 rays, with the first four slightly ossified. The scapula was ca. 50% ossified at 32.85 mm TL (26.34 mm SL), the coracoid, postcleithrum as well as 12 of the 16 rays were ossified, and the proximal radials were starting to ossify. In the largest specimen examined (44.13 mm TL [35.27 mm SL]), the pectoral girdle was well ossified except for the distal radials and the extremities of the scapular bones and the proximal radials.

#### CARTILAGE FORMATION OF PELVIC GIRDLE

The pelvic bones were very weakly stained for cartilage in the 19.86 mm TL (16.88 mm SL) specimen and there were six rays in each fin. At 23.86 mm TL (19.56 mm SL) the pelvic bones were well-stained for cartilage and there were eight rays and one stay per fin. At 25.12 mm TL (20.41 mm SL) there were three radials in each girdle. In the largest specimen examined (44.13 mm TL [35.27 mm SL]) the pelvic bone and radials were still cartilagenous and the eight rays were ossified.

#### SUPRANEURALS

In the cleared and stained material, vestigial supraneurals were present as two small blocks of cartilage above vertebrae five and six in the 26.0 mm TL (20.18 mm SL) specimen only. No other fish had supraneurals.

#### SQUAMATION

On the cleared and stained material, scales were first observed as small platelets on a 36.1 mm TL (29.21 mm SL) specimen. In the 41.12 mm TL (33.0 mm SL) specimen the mid-body scales had two to three radii.

#### Larval fish habitat

One of us (K. MEYER) was able to continue sampling the area after the main study period. Each collection period lasted between 10 to 15 minutes along the backwaters amongst vegetation, using a Surber sampler as a scoop net. The length frequency plot of the free embryo and larval fish (fig. 5) indicates that the length group of 8 to 10 mm TL of the 20/21-1-86 grew to 11 to 14 mm TL by the 6-2-86. Unfortunately we do not have a good water temperature data set for this period. Air temperatures recorded near our collection site are given in fig. 8. Maximum daily temperatures were over 20 °C as early as October, however, there were 10 days when 0 °C was recorded. The monthly mean maximum temperature range showed little variation between October and April and ranged from 20.4 °C in January to 18.9 °C in April. January also had the highest mean minimum (7.0 °C) and April the lowest (0.5 °C). Since speed of development is temperature related, one would expect more rapid development in January spawned fish compared to fish spawned earlier or later in the reproductive season. The length frequency data also indicated a movement of the larger fish (16 mm TL) out of the backwaters by the 24-1-86 when the flow started to decrease (fig. 3). Sixteen millimetre larval fish were quite advanced (fig. 7), however, they still had their ventral finfold, but all fins were well-developed and rayed except the pelvic fins. The serial spawning habit of *O. quathlambae* makes it difficult to interpret fig. 5. It is clear that there was another spawning in mid-February, which might be correlated to the rainfall of the 12-13 of that month (fig. 4).

When the flow rate subsided on 10-2-86, larval fish could be observed in numerous backwaters. The smaller fish (10 mm) were in the mid-water column while a school of between 150 to 200 fish ca. 20 to 30 mm TL were observed in the shallows of a rocky, 25 cm deep pool. On the 17-2-86, ca. 25 YOY (20-30 mm TL) were seen in 10 cm of water over a gravel substratum. On the 19-2-86, a school of ca. 100 fish of ca. 20 mm TL were observed in a small, shallow (10 cm deep) inlet, with no cover, and a silt-covered substratum. Another school of 20 fish (ca. 15 mm TL) were observed on a silt and sand point that led into a deeper pool, again with no cover. Between the 20/22-2-86 about 40 YOY were seen over a sand/silt substratum with occasional boulders, at a depth of 20-40 cm. On the 5-5-86, 59 YOY (22-44 mm) were collected from a similar habitat as the adults, i.e. rubble/boulder substratum, at a depth of 20-100 cm and in groups of 2-3. On the 6-5-86 in a similar habitat (rubble/boulder) a large school (ca. 150 YOY), swam around after they were

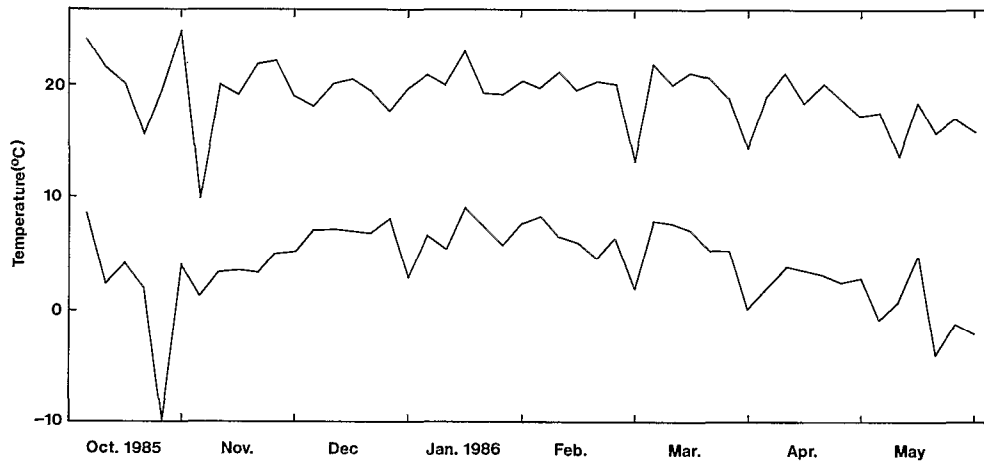


FIG. 8. — Maximum-minimum air temperature records, for the period October 1985 to May 1986, collected within the Sehlabathebe National Park, Lesotho, 4 km NW of drift net collection sites in the Tsoelikana River. *Relevés maxima-minima de la température de l'air, pendant la période d'octobre 1985 à mai 1986, recueillis à l'intérieur du Parc National de Sehlabathebe au Lesotho, à 4 km au N.-O. des emplacements des filets flottants placés dans le fleuve Tsoelikana*

disturbed by the collecting team instead of hiding under rocks as the adults do. YOY could be collected in the same area between February and May, therefore there was probably little seasonal migration during this period. From the observation of YOY and juvenile behaviour between February and May it appeared that *O. quathlambae* school until they reached a length of 60 mm TL. Then they became more solitary and secretive, although adults could occasionally be seen in large groups.

In general, the smaller YOY fish were found higher in the water column with the larger fish hugging the bottom. This spatial separation between the year classes has also been observed in another redfin minnow, *B. afer* (J. A. Cambray pers. obs.). The distributional separation of young and adult *O. quathlambae* may be due to habitat preference or it could indicate that cannibalism occurs in this species. It was observed that the YOY 'scared' more easily than adults and quickly moved to deeper, open water, unlike adults which hid under rocks. This evasive behaviour of the YOY might have evolved from avoiding insect predators but the YOY and juveniles would therefore be easier prey to exotic fish predators. In August YOY were in a similar habitat as the adults (rubble/boulder), at a depth of 30-40 cm, with the YOY in small groups (4-8). Adults were also present but there appeared to be no interaction between the two groups.

### Feeding

Larval fish commenced feeding at a length of ca. 7.95 mm TL. Table III shows the feeding habits of several 0<sup>+</sup> length groups. The youngest fish with food in the gut was 7.8 mm NL (8.25 mm TL). This specimen contained a nematode, a calanoid copepod and an ephemeropteran nymph. In an 8.7 mm SL (9.2 mm TL) specimen an Oligochaeta occupied 50% of the gut. The fish between 10 and 15 mm SL started to feed on dipteran larvae, pupae and adults, consisting of members of the families Simuliidae, Chironomidae sub-families Orthocladinae, Tanytarsini and Tanypodinae. Ephemeropteran nymphs were still quite common. In fish between 15 and 20 mm SL, the dominant food items were ephemeropteran nymphs and Orthocladinae larvae. In the larger specimens, greater than 20 mm SL, which were collected in May or August, there were mainly Cladocera numerically. Large ephemeropteran nymphs and Orthocladinae larvae were present and important in the diet.

### EXOGENOUS FEEDING

After the Tsoelikana River had come down in flood during mid-January 1986, the larval fish collected from backwaters were possibly feeding mainly on organisms which had been displaced. These included calanoid copepods, ephemeropteran

TABLE III

The feeding habits of five different length groups of *Oreodaimon quathlambae* collected from the Tsoelikana River. Specimens  $\leq 20$  mm SL collected in January 1986, specimens  $> 20$  mm SL collected in May or August 1986

*L'alimentation de 5 groupes de longueurs d'Oreodaimon quathlambae pêchés dans le fleuve Tsoelikana. Spécimens  $\leq 20$  mm LS pêchés en janvier 1986, spécimens  $> 20$  mm LS pêchés en mai ou août 1986*

| FOOD ITEM                     | Fish Length Group (mm SL) |     |       |    |       |    |       |    |       |    |
|-------------------------------|---------------------------|-----|-------|----|-------|----|-------|----|-------|----|
|                               | <10                       |     | 10<15 |    | 15<20 |    | 20<25 |    | 25-35 |    |
|                               | n=4                       |     | n=6   |    | n=6   |    | n=5   |    | n=7   |    |
|                               | N*                        | F** | N     | F  | N     | F  | N     | F  | N     | F  |
| Nematoda                      | 1                         | 25  | -     | -  | -     | -  | -     | -  | -     | -  |
| Annelida                      |                           |     |       |    |       |    |       |    |       |    |
| Oligochaeta                   | 1                         | 25  | -     | -  | 2     | 33 | -     | -  | -     | -  |
| Crustacea                     |                           |     |       |    |       |    |       |    |       |    |
| Cladocera-Chydoridae          | -                         | -   | 3     | 50 | -     | -  | 76    | 80 | 189   | 71 |
| Copepoda-Cyclopoid            |                           |     |       |    |       |    |       |    |       |    |
| <i>Alona</i> sp               | 4                         | 50  | 2     | 33 | 5     | 50 | 1     | 20 | -     | -  |
| -other                        | -                         | -   | -     | -  | 3     | 17 | -     | -  | -     | -  |
| Hydracarina                   | -                         | -   | 1     | 17 | -     | -  | -     | -  | -     | -  |
| Ephemeroptera                 | 1                         | 25  | 8     | 33 | 10    | 67 | 5     | 40 | 18    | 57 |
| Coleoptera                    | -                         | -   | 1     | 17 | -     | -  | -     | -  | -     | -  |
| Diptera                       |                           |     |       |    |       |    |       |    |       |    |
| Tipulidae                     | -                         | -   | -     | -  | 1     | 17 | -     | -  | -     | -  |
| Simuliidae                    | -                         | -   | 9     | 67 | 1     | 17 | 1     | 20 | 1     | 14 |
| Chironomidae adult            | -                         | -   | 1     | 17 | 1     | 17 | -     | -  | -     | -  |
| Chironomidae pupae            | -                         | -   | 2     | 33 | 1     | 17 | -     | -  | 1     | 14 |
| Orthocladiniinae              | -                         | -   | 15    | 67 | 20    | 83 | 6     | 50 | 13    | 86 |
| Tanytarsini                   | -                         | -   | 2     | 33 | -     | -  | 1     | 20 | -     | -  |
| Tanypodinae                   | -                         | -   | 6     | 33 | -     | -  | -     | -  | -     | -  |
| Unidentified insect fragments | -                         | -   | 2     | 33 | 1     | 17 | -     | -  | -     | -  |

\*N = Numerical abundance

\*\*F = Percentage frequency

nymphs and chironomid larvae. The switch in feeding from mainly ephemeropteran nymphs and chironomid larvae in January to up to 100% Cladocera in fish collected in May/August, possibly does not only reflect a change in diet with growth (see PIKE and TEDDER 1973, RONDORF 1975), but an unspecialised, facultative feeding habit similar to many minnows of the genus *Barbus* in Africa (CAMBRAY 1983b). RONDORF (1975) examined the gut contents of 11 *O. quathlambae* adults ranging in size from 79 to 116 mm FL. Using numerical, volumetric and gravimetric methods he determined that the nymphal stages of Ephemeroptera are the most important food item through the year with Diptera larvae of secondary importance. PIKE and TEDDER (1973) examined the gut contents of two specimens, 7.5 cm and 6.4 cm. These fish contained, once again, ephemeropteran nymphs, chironomid larvae, Plecoptera and planktonic crustaceans. It has been pointed out by PIKE and TEDDER (1973) and

RONDORF (1975) that the diets of *O. quathlambae* and *P. mykiss* overlap.

#### Effects of silt on early stages of *Oreodaimon quathlambae*

Within the Tsoelikana River *O. quathlambae* distribution indicated their low tolerance to silt, and their preference for boulders and rubble (PIKE and TEDDER 1973). RONDORF (1976b) and GEPHARD (1978) have noted that *O. quathlambae* appeared to be very susceptible to siltation. The deterioration of the Umkomazana catchment area could have been one of the reasons for the disappearance of this species in that system (Anon. 1971, JUBB 1966). In 1972 the wash-out of soil construction works in the upper catchment area of the Tsoelikana River might have been the cause of why very few 'small' *O. quathlambae* were collected during April 1972 (PIKE

and TEDDER 1973). They suggested that heavy sedimentation of the gravel beds between the 1970 and 1971 breeding seasons could be the cause of so few 'juveniles'. The trout dams at the headwaters were poorly built and began to fail in March 1976, which resulted in substantial quantities of silt being washed into the river (GEPHARD 1978). Stabilisation of these dams and veld restoration should be given top priority as a 'wash-out' would cause massive and continuous siltation.

RONDORF's (1976b) work on the early development of the species provided the first concrete proof that this species is susceptible to siltation. The river flow during the present study was comparatively silt-free, so we could not assess the impact of siltation on the embryos we collected. Since the eggs occurred in crevices they could easily be suffocated by silt. In addition, we recorded a very brief transitional period between endogenous feeding to a complete reliance on exogenous food sources. Fish larvae are very vulnerable to starvation when they have exhausted their yolk and HJORT (1926) called this the 'critical period' in which year-class strength is determined mostly by availability of food. The length of time involved between the complete reliance on internal food resources, through the transitional phase in *O. quathlambae*, requires more work, and is an area for future investigation.

*O. quathlambae* eggs are laid in mid-channel, possibly for oxygenation. A swim-up stage takes place and the fish are carried by the current to backwaters where they can feed, and move without being washed away. Reduced visibility, due to high silt loads, may lead to starvation during these early critical stages. The onset of exogenous feeding long before the yolk reserves are exhausted can be an adaptation for uncertain trophic conditions in an unpredictably perturbed environment (BALON 1985). Possibly selective pressures have led to serial spawning, instead of a long transitional period for *O. quathlambae*. There is also the detrimental effect of the silt on the food organisms on which young *O. quathlambae* feed. As the larval fish are carried from mid-channel to back-waters, so too would quantities of silt be carried to their nursery area. Possibly high silt loads in the lower reaches of the Orange River (CAMBRAY *et al.* 1986) limit this species distribution.

### Trout predation

As early as 1938 BARNARD (1938) had noted that because of the impact of trout on the indigenous fish fauna, every opportunity should be taken to obtain long series of fish, such as *O. quathlambae*. After 48 years, we have completed this series for the Maloti minnow. «*Barbus anoplus may possibly have*

*been exterminated by trout in certain places and the failure of recent collecting to bring to light any specimens of Labeo quathlambae (= Oreodaimon quathlambae) might be due to destruction of indigenous stocks by the introduced predator» (CRASS 1964 : 30). JUBB (1966) and PIKE and TEDDER (1973) express similar concerns about trout predation on *O. quathlambae*.*

*O. quathlambae* do coexist with trout in the Tsoelikana River, where rainbow trout were introduced over 40 years ago (HARRISON 1970, also see JUBB 1979). GEPHARD (1978) suggested that the difference between survival (Tsoelikana River) and extinction (Umkomazana River) is probably a reflection, of differences in an optimum environment for this specialised species. A combination of changing land-use and exotic predators eliminated the Maloti minnow in the lower altitude marginal environment of the Umkomazana River. Crass states that habitat deterioration not trout, is to blame for the disappearance of fish (Anon. 1971, also CRASS 1977) unlike his earlier statement (CRASS 1964).

In fact we have very little scientific evidence of trout predation on *O. quathlambae*, but then again no one has studied this aspect in any detail. PIKE and TEDDER (1973) found one 6 cm *O. quathlambae* in the stomach of a 1.8 kg trout. GEPHARD (1978) noted that Rondorf examined the stomach contents of 142 legalised trout (greater than 10 inches) from the Tsoelikana and did not find any *O. quathlambae*.

Whilst conducting distribution studies in the Tsoelikana River, one of us (K. MEYER) found that after heavy rains had washed some trout down from the waterfall area for about 500 m, the density of *O. quathlambae* dropped from 143 to 10 per 100 m. While in three lower sections the density dropped from 150 to 50 minnows on average. An aspect which is rarely considered is the predation by trout on the other life history stages of this minnow, not just adults. In May and August 1986 four, 100 m sites in the Tsoelikana River were electrofished. YOY fish were found at the lower three sites but none were found at the upper site which was the only one inhabited by trout. These early life stages should be examined in more detail in the field with regard to the impact of predators. Unless trout are caught in the act of predating upon the early stages, the young fish would quickly become indistinguishable in stomach contents, and therefore go unobserved and unrecorded. Trout are known to be egg-eaters and they normally eat aquatic invertebrates. The free embryo and early larval stages are very comparable in size to aquatic invertebrates, and these stages are very vulnerable to predation.

Our observations on the schooling behaviour of YOY in open areas would make *O. quathlambae* easy

prey for exotic predators. This may explain why there are no fry when trout are present. Adult *O. quathlambae* are more secretive and solitary, and use boulders for cover, they are also more mobile.

We recommend that future workers take a closer look at trout predation on early life history stages of the Maloti minnow.

### Fish community

PIKE and TEDDER (1973) found three species of fish in the Tsoelikana River, *Barbus aeneus*, *Parasalmomykiss* and *O. quathlambae*. *O. quathlambae* and *P. mykiss* are the only regular resident fish species in high elevation streams in Lesotho. RONDORF (1976b) tried to establish whether the smallmouth yellowfish (*B. aeneus*) was present during the breeding season of *O. quathlambae*. RONDORF (1976b) set gill nets in pools of the Tsoelikana River and did not collect any *B. aeneus* only trout (*P. mykiss*). GEPHARD (1978) noted that *B. aeneus* are usually only found in the stream during a spring spawning run. One of us (K. MEYER) established that young yellowfish (0+ to 2+) are present all year round in high altitude streams, up to 2150 masl. The range of *B. aeneus* is expanding since they tend to take over when an area gets too silted for trout (K. MEYER pers. obs.).

The eggs and free embryos of trout are considerably larger than either yellowfish or the minnow so there could be no confusion of the early life history stages, also trout spawn in the winter months.

It is worthwhile to make a comparison of early stages of *B. aeneus* and *O. quathlambae*. Since both are cyprinids, there may be some confusion between the two (table IV). GROENEWALD (1961) gave the dimensions of water-hardened eggs for *B. aeneus*, which are larger than those of *O. quathlambae* (table IV). Also the yolk diameter is larger for the yellowfish  $2.13 \pm \text{SD } 0.26$  mm as compared to 1.15 to 1.45 mm in diameter for the Maloti minnow. Egg size would also be helpful for ecologists when they want to determine the spawning periodicity and fecundity of this minnow species. The yolk colours appear to be different. GROENEWALD possibly viewed the eggs of *B. aeneus* against a red soil background. In the present study the *O. quathlambae* were viewed in the field, and also in the laboratory with substage lighting and/or overhead lighting. Size at hatching is also quite distinct, 8.5 mm TL for *B. aeneus* and 5.7 mm TL for *O. quathlambae*. *B. aeneus* commenced feeding at 11.0 mm TL compared to 7.95 mm TL for *O. quathlambae*. GROENEWALD (1961) provided drawings of various larval stages which can be compared to the figures in this paper.

If one compares GROENEWALD's (1961) figure of a newly hatched *B. aeneus* of 8.5 mm TL (his fig. 6b)

TABLE IV

Early life history comparisons between *Oreodaimon quathlambae* and *Barbus aeneus*  
*Comparaisons entre le développement de premier âge d'Oreodaimon quathlambae et de Barbus aeneus*

| Character                             | <i>Oreodaimon quathlambae</i><br>mean (range)   | <i>Barbus aeneus</i> <sup>4</sup><br>mean(range) |
|---------------------------------------|---|--|
| Egg envelope                          | non-adhesive  | ?  |
| Egg shape                             | round - ellipsoidal   | ellipsoidal                                      |
| Egg diameter (mm)                     | 1.92 (1.7-2.0) n=7 <sup>1</sup>   | 3.4 (3.0-3.9) by<br>3.1 (2.7-3.1)                |
| (water hardened)                      | 1.8 (1.7-1.85) n=4 <sup>2</sup><br>1.82 (1.72-1.89) n=4 <sup>3</sup>                              |  |
| Yolk diameter (mm)                    | 1.31 (1.15-1.45) n=4 <sup>1</sup><br>1.35 (n=1) <sup>2</sup><br>1.43 (1.41-1.45) n=4 <sup>3</sup> | 2.13 (1.75-2.43) n=6                             |
| Yolk diameter as %<br>of egg diameter | 68.2 <sup>1</sup> ; 75.0 <sup>2</sup> ; 78.6 <sup>3</sup>   | 65.5   |
| Colour                                | yolk clear to pale yellow   | pale pink  |
| Size at hatching<br>(mm TL)           | 5.7   | 8.5  |
| Larval pigment<br>patterns            | refer to text   |  |
| Commencement of<br>feeding (mm TL)    | 7.95  | 11.0   |
| First dorsal rays<br>(mm TL)          | 10.1  | 11.0   |
| First caudal rays<br>(mm TL)          | 9.2   | 11.0   |

1. Data from Rondorf (1976)
2. Live material (this study)
3. Preserved material (excluding 2 above): this study
4. Data from Groenewald (1961), (yolk diameters from his figs 1 & 2)  
- unfortunately we could not locate Groenewald's developmental series.

with our figure 7G of a 8.4 mm TL *O. quathlambae*, there is a distinct difference in finfold shape and heavier pigmentation on the *O. quathlambae* specimen. In addition, the *B. aeneus* is a free-embryo (yolk present) and *O. quathlambae* at this length are larval fish and feeding on exogenous food sources. BARNARD's (1943) drawing of a 'juvenile' (= larval) *B. aeneus* of 12 mm TL does not agree at all with GROENEWALD's (1961) figure of a 12.6 mm TL 'fry' (= larval fish). Barnard collected wild fish, whereas Groenewald used hatchery reared fish of known parentage.

Observations by one of us (J. A. CAMBRAY) on larval and juvenile *B. aeneus* as well as GROENEWALD's (1961) figures indicated that the later stages of *B. aeneus* are not as heavily pigmented as *O. quathlambae*. A good character to separate *B. aeneus* of around 18 mm TL and upwards is the distinct dark stripe on the caudal peduncle. The 'myomere

pattern' of the dorsal pigmentation of *O. quathlambae* of between 16 and 24 mm TL is quite distinctive when compared with *B. aeneus* juveniles of between 18 and 20 mm TL taken from the lower Orange River (AMG/P 10184). Dorsally, the 18.9 mm TL (14.8 mm SL) *B. aeneus* is relatively poorly pigmented. The distinctive pigment pattern around the nares of *O. quathlambae* is not present in *B. aeneus*. Ventrally, there is also considerably less pigment, and no pigmentation occurs on the dentary of *B. aeneus*. In addition the ventral finfold has been completely resorbed and the pelvic fins are fully rayed and large, compared to the 18.2 mm TL *O. quathlambae* (fig. 7P). In *B. aeneus* the posterior barbels started to form at 20-21 mm TL and the anterior at 26-27 mm TL (BARNARD 1943). In *O. quathlambae* the posterior barbels did not occur in the 20-21 mm TL specimens and there are no anterior barbels for this species. In a 34.52 mm TL (27.5 mm SL) specimen (fig. 7V), the heavy pigmentation on the dorsal and lateral views will easily separate a YOY *O. quathlambae* from a *B. aeneus* juvenile, which has comparatively little dorsal or lateral pigmentation (34.3 mm TL (26.5 mm SL) *B. aeneus* from Orange River (AMG/P 10184). These differences would be useful for field observations to separate young of the two co-occurring species. In the laboratory the long posterior barbels of *B. aeneus* and other characters can be used to separate the two species.

## CONCLUSION

The Lesotho government is proud of its natural heritage. It has set aside land in the Sehlabathebe National Park for the conservation of *O. quathlambae*. To show its strong identity with the species, the Government issued a 25 cent stamp depicting two *O. quathlambae* (PISTOR 1979). In the past decade the Lesotho government has initiated, with the help of the U.S. Peace Corps, a number of studies on the Maloti minnow. It is hoped that these studies will be continued. There is still much to be learnt on even the first step in conservation, the complete distribution of this species. While doing trout surveys in May 1986 one of us (K. MEYER) discovered three additional *O. quathlambae* localities. How many more sites are there? Only when all these sites are found will we be able to quantify the environmental barriers GEPHARD (1978) referred to in his paper.

Several projects within the Lesotho Highlands Water Scheme are new threats to this species. The planned Mohale Dam will flood 86% of the *O. quathlambae* habitat in the Jordane River and 29% of the Bokong River habitat. SKELTON (1987) speculated that the new Lesotho Highlands Water Scheme will increase human access to the rivers which will probably lead to increased pressure for stocking with trout.

We have demonstrated that the early life history stages do get carried along in the Tsoelikana River, in what habitats will they not be able to survive? Have these habitats changed due to man's impact or are there natural barriers? It is now important to establish the flexibility in life-history tactics of *O. quathlambae*. How adaptable is this species to the changes it faces through man's manipulation of the environment? A good start would be to quantify the abiotic factors which severely limits this species distribution to only the extreme upper area of the 2300 km long Orange River system.

It is hoped that through a sound research base, *O. quathlambae* will not only be known from Museum samples and a stamp, and 'live' up to its name and become 'the spirit of the Drakensberg'. If the extinction of this species will be determined by the natural erosional cycle of the Drakensberg, then some control should be placed on habitat degradation by man within *O. quathlambae*'s range, so that we do not speed-up the time to extinction of this endangered, relict, cold-water cyprinid.

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