Larval development of the Cape silverside, *Atherina breviceps* Cuv. & Val., 1835 (Teleostei, Atherinidae) from southern Africa

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The egg and larval development of the Cape silverside, *Atherina breviceps*, are described and illustrated from material collected in the Swartvlei estuary. The eggs are spherical, 1.40–1.65 mm in diameter, with 6–12 uniformly spaced chorionic filaments attached at both ends to the chorion. The latter condition and the small size of the eggs are unique among the *Atherina* species. The larvae examined (5.1–15.7 mm) are elongate, have a yolk sac at hatching and are characterized by distinct body pigmentation and a prominent gas bladder. Flexion occurs between 7.6–11.2 mm, all fin elements are formed by 15.7 mm and scales develop by 20.0 mm. We compare the larval development of *A. breviceps* with that of other atherinids and discuss the spawning of this species and the seasonal occurrence of larvae along the southern coast of Africa.

The Cape silverside, *Atherina breviceps* Cuv. & Val. 1835, is a small schooling teleost found along the southern African coast, between Luderitz and St Lucia (Smith 1965; Ivantsoff 1978, 1986; Day, Blaber & Wallace 1981). This species is particularly abundant along sandy beaches and in estuaries of the Cape Province, where it breeds throughout the spring and summer months (Melville-Smith & Baird 1980; Lasiak 1982; Beckley 1983, 1986; Bennett, Hamman, Branch & Thorne 1985; Kok & Whitfield 1986).

The genus *Atherina* Linnaeus comprises five species, namely the European species *A. presbyter*, *A. hoyeri* and *A. hepsetus* (Kiener & Spillmann 1969, 1972), the northern African *A. lopeziana* (Rossignol & Blache 1961) and the southern African *A. breviceps* (Ivantsoff 1978, 1986). While the larval stages have been described for European atherinids (Viali 1937; Sparta 1942; Russell 1976; Palmer & Culley 1984; White, Lavenberg & McGowan 1984), comparable data for *A. breviceps* is restricted to a brief description of its unfertilized eggs (Gilchrist & Hunter 1919).

We now describe and illustrate the egg and larval development of *A. breviceps* using material obtained from a southern African estuary. We also present some ecological notes on the location and time of spawning of *A. breviceps* along the southern African coast and compare its early life history with that published for other atherinids.

Materials and methods

Material examined

A total of 90 larvae and 4 juvenile *A. breviceps* used in this study were collected in plankton tows during September and October 1986 in the Swartvlei estuarine system, southern Africa (34°00'S / 22°46'E) (Figure 1). A further 17 larvae collected in January and December 1980 in Algoa Bay (33°00'S / 23°40'E) (Beckley 1986) were also examined, but since the pigment in these specimens had faded, they were used only for morphometrics and meristic counts. The 35 eggs used in this study were obtained from a group collected from a multifilament gill net placed in the Swartvlei littoral zone adjacent to Potamogeton pectinatus beds. Larvae and eggs were fixed in 5–10% formalin and then placed in 70% ethanol. All the material examined in this study was deposited at the J.L.B. Smith Institute of Ichthyology in Grahamstown, South Africa, under the catalogue numbers RUSI 27000 and 27001.

Measurements and counts

Eggs and larvae of *A. breviceps* were measured to the nearest 0.05 mm and 0.1 mm respectively, using a dissecting microscope fitted with an ocular micrometer. Terminology and body measurements of larvae follow Leis & Rennis (1983). In addition, measurement was also made of the snout-posterior edge of swim bladder length.
Figure 1 (A) Map of southern Africa with distribution of Atherina breviceps around the coast. (B) Location of the Swartvlei estuarine system.

(SPSB), which is the distance from the tip of the snout along the midline to a vertical line through the posterior edge of the swim bladder. Body length (BL, mm) always refers to the notochord length in preflexion and flexion larvae and the standard length in postflexion larvae. Each of the morphometric measurements is expressed as a percentage of the respective body lengths given above. The term pigment refers to melanin. Drawings were done with the aid of a camera lucida.

Counts of all fin rays were based on 25 specimens stained with alizarin red S and a further eight (out of 15) which were cleared and double-stained following the technique of Potthoff (1984) as modified from Dingerkus & Uhler (1977). The latter group were also used for vertebrae counts and for determining the sequence of bone ossification. The terms 'visible' and 'ossified' refer to structures stained positively for cartilage and bone respectively. Myomere counts and ray counts of paired fins were made on the left side of the body.

Results

Identification

Eggs were identified as those of atherinids by the presence of adhesive chorionic filaments and the numerous oil globules at the vegetative pole (Schmitt 1983; White et al. 1984). Embryos and newly hatched larvae were linked together using the pattern of body pigmentation.

Larvae were identified as atherinids by their elongate and laterally compressed body, short and rounded gut, presence of two dorsal fins, the pattern of body pigment and the lack of head spination (Schmitt 1983; White et al. 1984). Larvae and juveniles were assembled together in a series using body pigmentation and degree of fin development. Larger specimens were identified as belonging to the genus Atherina by the number of vertebrae (42–44) and the presence of a maxillary shelf (Ivantsoff 1978) and specifically as A. breviceps Cuv. & Val., 1835 by their fin ray counts (D V–VIII + I, 11–15, A I, 15–18, P; 13–16) and number of midlateral scales (44–50), which are unique for atherinids in southern Africa (Smith 1965; Ivantsoff 1986). The identification was also supported by the fact that the Cape silverside is the only Atherina species found along the southern coast of Africa (Smith 1965; Ivantsoff 1978; 1986).

Eggs

Late stage eggs of A. breviceps are translucent and spherical, 1.40–1.65 mm in diameter (ś = 1.58; S.D. = 0.06; n = 35), with 6–12 (usually 8) uniformly spaced chorionic filaments and a small perivitelline space (Figure 2). The filaments are attached at both ends to the chorion, forming loops of about 4.15–4.55 mm in length. Embryos close to hatching have pigmented eyes, formed mouth, dorsal and anal finfolds and a yolk sac containing one to five oil globules. Pigment is present on top of the head, along the dorsal, ventral and lateral midlines of the tail, at the tip of the notochord, dorsally on the gut and sometimes on the yolk sac. The pigment on the head consists of three groups of dorsal melanophores on the
Figure 3 Development of preflexion *Atherina breviceps* from the Swartvlei estuary. (A) 5.1 mm BL larva. (B) Dorsal view of the head of specimen shown in A. (C) 6.9 mm BL larva. (D) Dorsal view of the head of specimen shown in C.

Table 1 Morphometric characters of larvae of *Atherina breviceps*. Size class ranges are in mm of body length and \( n = \) number of individuals. Mean values are percentage of body length, followed by the standard deviation in parentheses. Values without S.D. are based on only one specimen. Blanks indicate absence of character and values with additional \( n \) indicate number of specimens (when > 1) where character was observed and measured. Individuals between dashed lines were undergoing notochord flexion.

<table>
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<tr>
<th>Size class (mm)</th>
<th>( n )</th>
<th>Head length</th>
<th>Snout length</th>
<th>Eye diameter</th>
<th>Body depth at P(_1) base</th>
<th>Prenal length</th>
<th>SPSB length</th>
<th>Pre-second dorsal fin length</th>
<th>Pre-anal fin length</th>
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midbrain and one (occasionally two) expanded melanophore(s) on the hindbrain whose assemblage resembles a triangle with its apex pointing backwards.

Larval development

The smallest larva examined in our series (5.1 mm) had a distinct yolk sac, an elongated and compressed body, a short and coiled gut, pectoral buds and a continuous dorsal and anal fin fold (Figure 3A). The largest larva containing yolk sac remnants measured 7.5 mm. There were 42-46 myomeres (\(\bar{x} = 43.6; S.D. = 1.0; n = 65\)).

The gas bladder becomes apparent in some preflexion individuals over 6.0 mm and its posterior edge is located at about the same level as the anus. The gut is short and coiled in preflexion larvae and the preanal length constitutes 26-28%. As the intestine lengths, the preanal distance increases to 30-38% during the flexion stage and reaches 42% in late postflexion individuals (Table 1). Simultaneously, the gas bladder also increases in length and its posterior edge extends beyond the anus.

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**Figure 4** Development of postflexion *Atherina breviceps* from the Swartvlei estuary. (A) 10.5 mm BL larva. Dashed lines indicate damaged caudal fin. (B) Dorsal view of the head of specimen shown in A. (C) 12.5 mm BL larva. Myomeres have been omitted. (D) Dorsal view of the head of specimen shown in (C). (E) 24.0 mm juvenile. Scales have been omitted and arrow shows position of anus. (F) Dorsal view of the head of specimen shown in (E). Pectoral fins are indicated with dashed lines.
reaching ca 51% in late postflexion individuals (Table 1; Figures 3C, 4A). The anus is finally located at the level of the tips of the pelvic fins in postflexion individuals, well in front of the posterior edge of the swim bladder (Figure 4E). Throughout the development, a distinctive gap remains between the anus and the origin of the anal fin.

The head of *A. breviceps* remains relatively small throughout the development (15–25%). The dacyryosphenoid, hypobranchials and other portions of the cranium stained positively for cartilage in larvae over 5.4 mm. The premaxilla and maxilla are visible by 7.6 mm and ossified by 12.5 mm. The operculum is visible by 10.4 mm and starts to ossify at 12.5 mm. Five branchiostegal rays are visible by 10 mm and all six are ossified by 12.5 mm. The dentary ossifies shortly thereafter and all the remaining bony structures in the head are ossified by 14 mm. Small teeth are present along the edges of the premaxilla and dentary from 11.5 mm, while the maxillary shelf, although somewhat reduced, is noticeable in specimens over 20 mm (Figure 5).

The first vertebral elements start to differentiate at 7.6 mm, sequentially from anterior to posterior. Notochord flexion also begins by 7.6 mm and is completed by 12 mm. All vertebral elements (i.e. vertebrae, neural and haemal spines and hypurals) are visible by 10.5 mm. The ossification of the vertebral column commences shortly thereafter and proceeds from the trunk to the caudal region by 14 mm. There are 42–44 (usually 43) vertebrae.

Five pleural ribs are visible by 10.4 mm, increasing to ten at 12.5 mm and to fourteen by 13.5 mm. All these are ossified by 14 mm and the number finally reaches 19 in specimens over 20 mm.

The sequence of fin development is shown in Table 2. Pectoral buds are present in yolk sac specimens. The co- racoids become visible at about 6 mm and the first incipient pectoral fin rays start to form sequentially from the posterior end of the developing body (Table 1). The first somites become visible by 8.3 mm and are completed by 10 mm. The first somites then proceed to differentiate sequentially from anterior to posterior.

Table 2: Fin development in larvae and juvenile *Atherina breviceps*. Blanks indicate absence of character.

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<th>Body length (mm)</th>
<th>n</th>
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<th>Second dorsal fin</th>
<th>Anal fin</th>
<th>Pectoral fin*</th>
<th>Pelvic fin*</th>
<th>Principal caudal fin rays</th>
<th>Procurent rays**</th>
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<td>9 + 8</td>
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<td>9 + 8</td>
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<td>9 + 8</td>
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* Counts made on the left side. ** Dorsal elements / ventral elements.

![Figure 5](image-url) Mouth bones of a 24 mm juvenile *Atherina breviceps* from the Swartvlei estuary. (A) Maxilla, arrow indicates maxillary shelf. (B) Premaxilla. (C) Dentary.
dorsal to ventral by 10 mm. Pelvic fins appear shortly after and are formed by 11.8 mm. The soft rays of the pectoral fins are all ossified by 13.5 mm.

The caudal fin rays begin to appear just prior to flexion and the full complement (9 + 8) is visible by 9.6 mm and ossified by 12 mm. The procurent elements start to form at 10.6 mm and all are present after the completion of notochord flexion (Table 2). The soft rays of both the anal and second dorsal fins appear simultaneously at about 8.5 mm, shortly after flexion has commenced. The full complement of rays in the anal and the second dorsal fins is present by 12 mm and completely ossified by 13.5 mm. The spines of the first dorsal fin begin to appear at about 11.2 mm and all six are present and ossified by 13.5 mm. Scales appear by 20 mm and specimens are fully scaled by 24 mm.

The order of fin appearance is P1–C–A–D2–P2–D1 and the sequence of fin ray full ossification is C–P2–A–D2–D2–P1. Throughout the whole development and also in the adults, the anal fin is located slightly in front of the origin of the second dorsal fin, both separated by a distance no greater than 4% (Table 1; Figure 4A, C, E).

Pigmentation

Pigment increases continuously in A. breviceps during development. The smallest yolk sac larvae have a pattern of pigmentation similar to that of late embryos (see above), except that they have more melanophores scattered on the midbrain (Figure 3B). Just prior to flexion, melanophores appear on the forebrain, tip of the snout, the angle of the jaws, the opercular area and on the otic capsule, increasing in number in these areas throughout flexion, particularly on the midbrain (Figure 4B, D, F).

As the intestine lengthens during flexion, pigment develops on the lateral surface of the gut and on the dorsal surface of the swim bladder (Figures 3C, 4A). By 12.0 mm, a V-shaped stripe of melanophores extends backwards on both sides of the gut, ending at the origin of the anal fin. Pigment on the ventral surface of the gut develops only by 15 mm and is no longer externally visible in scaled specimens (Figure 4E).

Pigment on the tail of young A. breviceps larvae consists of a single row of melanophores on the dorsal, lateral and ventral margins, being much more abundant on the latter (Figure 3A). During flexion, pigment intensifies on the tail and the dorsal and ventral rows become double at the bases of the second dorsal and anal fins. At the same time, pigment develops on the urostyle and along the base of the caudal fin. From 15 mm, pigment extends downward from the dorsal surface while melanophores on the midlateral line increase in number and form a very distinct pigmented band, which runs from above the pectoral fin base to the base of the caudal fin (Figure 4E). Juveniles attain the adult colouration soon thereafter.

In all preflexion specimens, a group of melanophores is present dorsally at the tip of the notochord (Figure 3A). This patch becomes very distinct in flexion and postflexion specimens (Figure 4A, C) and less intense in juveniles, owing to the constant increment in pigmentation (Figure 4E). Melanophores form internally on the dorsal surface of the notochord by 6.5 mm and persist thereon (Figures 3C, 4A, C).

Melanophores appear along the caudal fin rays by 9.5 mm and become fully pigmented by 13 mm (Figure 4C). Pigment appears shortly thereafter along the second dorsal and anal fin rays and all elements of both fins become pigmented by 20 mm. Melanophores form at the pectoral fin bases and along the rays by 14 mm and lastly on the pelvic fin rays, by 24 mm (Figure 4E).

Discussion

Similar taxa

Most Atherinidae produce eggs and larvae which resemble those of other atherinomorpha species e.g. belonids, hemiramphids and exocoetids (Schmitt 1983; Collete, McGowen, Parin & Mito 1984). However, unlike late stage eggs and early larvae of these families, atherinid embryos never develop fin elements either before or immediately after hatching (White et al. 1984). Two hemiramphid species, Hemiramphus far and Hyporhamphus capensis, have been recorded in the Swartvlei estuary and their eggs and larvae could be confused with those of A. breviceps (Melville-Smith & Baird 1980; Whitfield, Allanson & Heinecken 1983). However, H. far eggs (> 2.8 mm) are larger than those of A. breviceps while eggs of Hyporhamphus have chorionic filaments grouped in tufts (Breden & Rosen 1966; White et al. 1984). Larvae of hemiramphids, on the other hand, can be easily distinguished by the larger preanal length (to 50% BL), the distinct preanal finfold and the much earlier fin formation (Schmitt 1983; Collete et al. 1984).

Of the other atheriniform species recorded in southern Africa, only Iso natalensis (Notochereidae) is sympatric with A. breviceps in our study area (Ivantsoff 1986; Kok & Whitfield 1986). Although the larval stages of I. natalensis are still undescribed, they are very similar to those described for Iso hawaiiensis (Miller, Watson & Leis 1979; Neira unpublished data). Larvae of Iso natalensis, however, can be distinguished from those of A. breviceps by their markedly different pattern of head pigmentation (two large expanded melanophores overlying the midbrain) and the lack of pigment on both the dorsal and ventral margins of trunk and tail.

Spawning and seasonal occurrence of larvae

Available ecological information indicates that A. breviceps spawns in marine, estuarine and coastal lake environments. Ripe adults have been found along the sandy beach surf-zone of Algoa Bay in December (Lasiak 1982) and larvae have been recorded from the nearshore region of the same bay during December and January (Beckley 1986). Larval A. breviceps have also been collected in the inner surf zone of the bay adjacent to the Swartvlei estuary during October and November (Whitfield in prep.).

In the permanently open Swartkops estuary (33°52'S / 25°38'E), larval A. breviceps have been collected from
September to March (Melville-Smith & Baird 1980; Beckley 1985) and the maximum number of juveniles recorded during the late summer months in the lower reaches (Beckley 1983). Breeding of A. breviceps has also been reported in both the Swartvlei estuary, which is seasonally open to the sea (Kok & Whitfield 1986; this study) and in the Bot estuary (34°20’S/19°06’E) which is closed from the sea for periods of usually 2 to 4 years (Bennett et al. 1985). Populations of A. breviceps are found in the coastal lakes of Groenvlei (34°01’S/22°51’E) and Lake Sibaya (27°20’S/32°41’E) (Ratte & Hanekom 1980; Bruton 1980), which have been isolated from the sea for more than 3000 years (Martin 1962; Bruton 1975).

Egg and larval development

The eggs of A. breviceps examined in this study are the smallest yet described for Atherina species. The eggs of A. hepetas, which are the largest among atheriniforms, are 2,0-2,5 mm in diameter compared to 1,40-1,65 mm of A. breviceps, while those of the other Atherina fall between both size categories (Marion 1894; Vialli 1937; Sparta 1942; Palmer & Culley 1984). The presence of filaments attached at both ends to the chorion was previously observed in unfertilized mature eggs of A. breviceps (Gilchrist & Hunter 1919) but has never been reported in eggs of other Atherina species. Eggs of A. breviceps also have few uniformly spaced chorionic filaments while they are numerous and randomly spaced in eggs of A. boyeri and A. presbyter (Vialli 1937; Palmer & Culley 1984).

White et al. (1984) regard Atherina as having eggs with chorionic filaments gathered in a tuft, a view probably based on the condition found in A. hepetas (Breder & Rosen 1966). As mentioned by these authors, however, not all atherinids assigned to the same genus produce eggs with chorionic filaments arranged in one specific way, variability which seems to apply not only for Menidia and Austroenidia, but also for Atherina.

The early life history of A. breviceps follows the normal mode of atheriniform development, and although it resembles that of A. boyeri, it does differ in some respects from that of the other Atherina species. Larvae of A. breviceps hatch between 5,1-7,5 mm, with a very distinct yolk sac, whereas larvae of A. presbyter and A. hepetas hatch between 6,5-7,2 and 7,0-8,0 mm respectively, with no traces of yolk sac (Palmer & Culley 1984). In addition, notochord flexion in larval A. breviceps commences by 7,6 mm and the second dorsal and anal fin rays are evident by 9,6 mm while both events occur by 10,7 and 13,4 mm in A. presbyter and 12,0-14,0 and 14,0-16,0 mm in A. hepetas (Marion 1894; Vialli 1937). There is also a noticeable difference in the overall external pigmentation (much darker in A. breviceps) and the size of the swim bladder at flexion (considerably larger in A. breviceps) (Vialli 1937; Russell 1976; Palmer & Culley 1984). Despite these differences, however, these species apparently attain the juvenile stage at more or less the same size, i.e. just over 20 mm.

The arrangement of three dorsal melanophores on the midbrain and one on the hindbrain of late embryos of A. breviceps is identical to that found in flexion larvae of A. boyeri, A. hepetas and A. presbyter (Vialli 1937; Palmer & Culley 1984). However, while the larvae of the European Atherina retain this arrangement throughout the development, it is lost in A. breviceps after hatching. A similar case has also been observed in the larvae of two south-western Australian populations of Atherinosoma, a genus closely related to Atherina (Ivantsoff 1978). In these species, the triangular pattern of melanophores remains in larvae of the marine Atherinosoma prebyteroides but it is lost in those of the estuarine Atherinosoma wallacei, which instead resemble A. breviceps in having scattered melanophores on the head (Neira unpublished data).

Our developmental study was based entirely on a series of larval A. breviceps collected within an estuary and it is possible that differences exist between these estuarine larvae and the larvae from marine populations. It is worth noting that current comparative studies on the osteological development of marine and estuarine atherinids from eastern Australia, indicate that the larvae of the estuarine species ossify at a smaller size than those of the marine species, are more heavily pigmented and possess a more conspicuous swim bladder (A. Steffe & B. Said pers. comm. 1987).

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