

Larval development of *Gilchristella aestuaria* (Gilchrist, 1914) (Pisces: Clupeidae) from southern Africa

E.H. Haigh and A.K. Whitfield *

J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown, 6140 Republic of South Africa

Received 4 June 1992; accepted 8 March 1993

The larval development of the southern African endemic clupeid *Gilchristella aestuaria* is described and illustrated from specimens collected in the Swartvlei and Sundays estuarine systems of the Cape Province. Free embryos have no visible gut, unpigmented eyes and bodies, and are dependent on the yolk sac contents for nutrition. This stage lasts until about 4 mm body length (BL) when the eyes become pigmented and a gut becomes visible. Between 4 mm and 7 mm BL melanophores on the ventral aspect of the body form, and the dorsal and caudal fin anlagen develop. Between 7 mm and 8 mm BL the swimbladder forms, flexion occurs and the anal fin anlage develops. By the 10 mm BL stage most of the skeletal elements have begun to differentiate, with the vertebral centra already showing signs of ossification. General ossification commences between 12 mm and 13 mm BL. All unpaired fins have the adult complement of rays by 15 mm BL. Scapulation starts between 16 mm and 17 mm BL and is complete by 20 mm BL. Body depth increases gradually, from about 5% of BL in the early larval stages to >14% of BL in the juveniles. The pre-anal length decreases from about 87% of BL in the larvae to approximately 69% of BL in the juveniles. Head length increases from approximately 11% of BL in the larvae to 24–29% of BL in the juveniles. The larval snout is initially 2% of BL, increasing to 7% of BL in the juvenile stages owing to the development of jaw elements.

Die larwale ontwikkeling van die endemiese clupeid *Gilchristella aestuaria* van suider Afrika word hier beskryf van monsters wat in Swartvlei en die Sondagsgetyrvier in die Kaapprovinsie versamel is. Vrye embryo's het geen sigbare spysverteringskanaal, die oë en liggame is sonder enige pigmentasie, en die embryo's is van die eiersakinhoud vir voeding afhanklik. Hierdie stadium duur totdat die vissies 4 mm liggaamslengte (LL) bereik, wanneer die oë verdonker en die spysverteringskanaal sigbaar word. Tussen 4 mm en 7 mm LL vorm melanofore op die ventrale deel van die liggaam, en die dorsaal- en stertvinne ontwikkel. Tussen 7 mm en 8 mm LL begin die swemblaas en die anaalvin ontwikkel en fleksie vind plaas. Teen 10 mm LL begin die skelet ontwikkel en die vertebrale elemente begin verbeeen. Algemene beenverplasing van die kraakbeen begin tussen 12 mm en 13 mm LL. Teen 15 mm het alle vinne die volwasse hoeveelheid strale. Skubontwikkeling begin tussen 16 mm en 17 mm LL en is voltooi teen 20 mm LL. Liggaamsdiepte vergroot geleidelik, van ongeveer 5% van LL in die larwes tot >14% van LL by jongvisse. Die vooranale lengte verminder vanaf ongeveer 87% van LL by die larwe tot 69% van LL by die jongvisse. Koplengte vergroot van ongeveer 11% van LL by larwes tot ongeveer 24–29% van LL in die jongvisse. Die larwale snoet is 2% van LL in die begin en verleng tot 7% van LL in die jongvisstadium as gevolg van die ontwikkeling van die kakebene.

* To whom correspondence should be addressed

The estuarine roundherring *Gilchristella aestuaria* is a small (maximum total length ± 75 mm) schooling clupeid, abundant in most estuaries along the southern African coast (Day, Blaber & Wallace 1981). This euryhaline species is also common in coastal lakes of the region, including freshwater Lake Sibaya (Natal) and Groenvlei (Cape Province), both of which were estuarine systems which have become isolated from the marine environment (Hill 1975). Although Ratte (1989) has reported *G. aestuaria* from rivers in the Cape Province, this is not a typical habitat occupied by the species on the sub-continent.

Spawning is reported to take place mainly during the summer months in the upper reaches of estuaries, and the entire larval development apparently takes place within an estuary or coastal lake (Whitfield 1990). Earliest sexual maturity of *G. aestuaria* occurs at 26 mm total length (TL), with 50% of the population mature by 34 mm TL (Ratte 1989). Although some *G. aestuaria* are reputed to attain 7–8 years of age in southern Cape systems (Ratte 1989), high mortalities caused by fish and bird predation result in <1% of the population reaching more than 2 years of age in eastern Cape estuaries (Talbot 1982).

G. aestuaria was the single most abundant component of

ichthyoplankton catches in several estuaries which have been investigated, e.g. Kromme (Melville-Smith 1981), Swartvlei (Whitfield 1989) and Sundays (Harrison & Whitfield 1990) systems. This filter feeder preys predominantly on zooplankton and phytoplankton (Blaber 1979, Talbot & Baird 1985, White & Bruton 1983), but has also been recorded foraging selectively on larger benthic invertebrates (Coetzee 1982).

Despite the numerous biological and ecological studies on this clupeid in southern African coastal systems (e.g. Talbot 1982, Ratte 1989), no published description of the development of *G. aestuaria* larvae exists (McGowan & Berry 1984), although Melville-Smith (1978) does provide illustrations of a 4.9 mm and 10.6 mm BL larval *G. aestuaria*. Using pre- and postflexion larvae collected from Swartvlei (34°00'S/22°45'E) and the Sundays estuary (33°43'S/25°51'E), a size series has been assembled and the larval development of *G. aestuaria* is described and illustrated in this paper.

Materials and Methods

The development of fishes can be divided into the following stages; embryo (including cleavage egg, embryo and free

embryo stages), larva, juvenile and adult (Balon 1975). Only the stages between free embryo and juvenile are dealt with in this paper.

A total of 300 free embryos, larvae and juveniles from plankton net catches in both the Swartvlei and Sundays estuarine systems were used in this study. Swartvlei is an estuarine coastal lake in the southern Cape, and the Sundays River estuary is a permanently open system on the eastern Cape coast.

Embryos and larvae were fixed in 10% buffered formalin solution and then stored in 60% isopropyl alcohol. Each specimen was measured to within 0,02 mm using an ocular micrometer fitted to a stereoscopic dissecting microscope. Body length (BL) refers to notochord length in preflexion and flexion larvae, and standard length in postflexion larvae. Drawings were done with the aid of a camera lucida.

Myomere counts were made on the left-hand side of the body. To determine the number of fin rays, vertebral counts and the sequence of bone ossification, a total of 78 larvae and early juveniles from both estuaries were cleared and stained following the techniques of Taylor (1967), Dingerkus & Uhler (1977) and Balon & Noakes (1980). Larvae of the same size were stained for either bone only or both cartilage and bone. A further 44 larvae and juveniles from the Sundays estuary were cleared and stained within 30 days of capture in February 1992, and specimens from this sample were also used to obtain details of body pigmentation.

Skeletal formation takes place either by a process in which cartilage forms and is subsequently invaded by osteoblasts, or by direct ossification of epidermal or membranous tissues (de Beer 1971). The uptake of stain by structures is not necessarily a definitive indication of skeletal development. Alcian blue is absorbed by mucopolysaccharides, and in the transition stage between the chondrified and ossified states, neither alcian blue nor alizarin red S will be absorbed satisfactorily and the structures will remain unstained. These transparent structures can be regarded as bone in formation. In the following analysis it is not the nature (chondral or dermal) but rather the presence of the skeletal structure which is of interest.

All *G. aestuaria* examined in this study were deposited at the J.L.B. Smith Institute of Ichthyology in Grahamstown, South Africa (RUSI numbers 35209 and 35210).

Identification

According to Whitehead & Wongratana (1991) *G. aestuaria* is a member of the family Clupeidae, subfamily Pellonulinae. *G. aestuaria* is the only species of this subfamily to occur in southern Africa and is endemic to the region (Whitehead & Wongratana 1991).

In *G. aestuaria* preflexion larvae the melanophores are confined to the ventral area of the body. The most anterior melanophores are between the myomeres and the dorsal aspect of the intestine and extend from the pectoral fin to the pylorus. A further 12 melanophores are visible along the ventral surface of the hindgut from the pylorus to the anus (Melville-Smith 1978). There are usually a few melanophores at the base of the developing caudal fin. Late post-flexion larvae with fins are distinguishable from other southern African clupeoid larvae by the fact that the anal fin

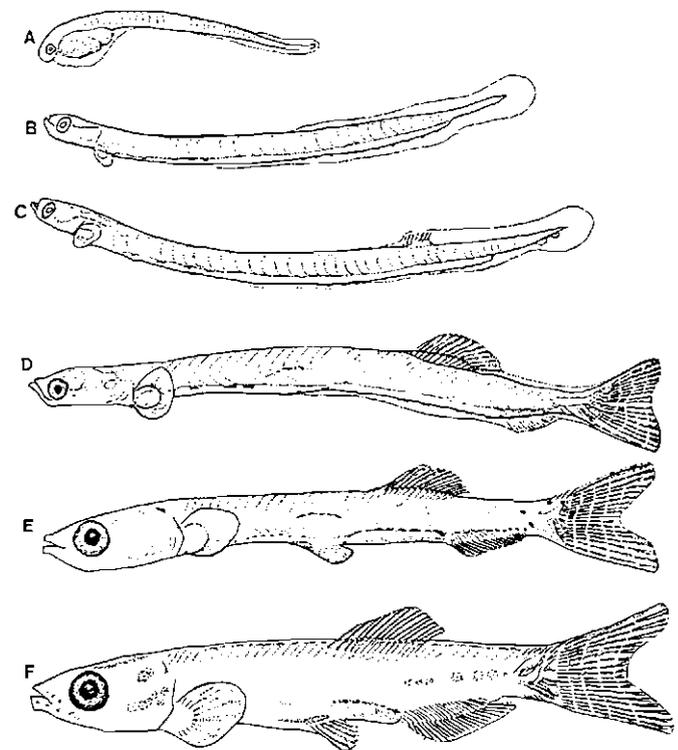


Figure 1 Larval development (not drawn to scale) of *Gilchristella aestuaria* (A = 2,1 mm BL; B = 4,9 mm BL; C = 7,0 mm BL; D = 10,0 mm BL; E = 14,5 mm BL; F = 17,5 mm BL).

origin is just before the end of the dorsal fin and that the paired ventral fins are anterior to the dorsal fin origin. Meristic characteristics of adult *G. aestuaria* are as follows: D iii, 11–12; A iii, 17; P I, 10–11; V I, 7 (Whitehead & Wongratana 1991).

Results

Embryonic development is characterized by an independence from external food sources and the head flexed over the yolk sac. Free embryos have no visible gut, unpigmented eyes and bodies (Figure 1A). This stage lasts until about 4 mm BL when the eyes become pigmented and a gut develops. The yolk reserves are depleted towards the end of this size range.

Between 4 mm and 7 mm BL melanophores on the ventral aspect of the body become visible, and the cartilaginous dorsal and caudal fin anlagen develop (Figure 1B, 1C). At approximately 7,5 mm BL the swimbladder forms, flexion occurs and melanophores becomes established in the characteristic pattern seen in Figure 1D. Between 8,5 and 10 mm BL the specimens exhibit a wide range of development, particularly in the differentiation of various skeletal elements. The skeletal development is cartilaginous until 9 mm, when the first signs of ossification can be seen. Sclerotization starts between 16 mm and 17 mm BL and is complete by 20 mm BL.

Tables 1 and 2 detail some morphometric changes which take place during the course of *G. aestuaria* development. The major proportional changes which occur are as follows: body depth increases gradually from about 5% of body length in the early larval stages (Figure 1B) to >14% of BL

Table 1 Morphometrics of *Gilchristella aestuaria* from Swartvlei (Length = Mean body length in mm, Range range in body length, n = number of fish measured, S/L = snout length/body length, E = diameter of eye in mm, E/L = eye diameter/body length, H/L = head length/body length, DF/L = distance from snout to dorsal fin origin/body length, AF/L = distance from snout to anal fin origin/body length, BD = body depth in mm, BD/L = body depth/body length)

Length	Range	n	S/L	E	E/L	H/L	DF/L	AF/L	BD	BD/L
4,0	3,5-4,0	4	0,02	0,10	0,03	0,11	-	0,87	0,17	0,04
4,6	4,1-5,0	7	0,02	0,11	0,02	0,13	-	0,86	0,21	0,05
5,2	5,1-5,4	11	0,02	0,14	0,03	0,11	0,75	0,88	0,24	0,05
5,5	5,5-6,0	5	0,02	0,12	0,02	0,10	0,77	0,89	0,28	0,05
6,1	6,1-6,5	11	0,02	0,16	0,03	0,11	0,75	0,88	0,34	0,06
6,8	6,6-7,4	15	0,02	0,18	0,03	0,13	0,73	0,88	0,40	0,06
7,7	7,5-8,0	15	0,02	0,22	0,03	0,13	0,71	0,88	0,44	0,06
8,7	8,1-9,0	16	0,03	0,24	0,03	0,13	0,68	0,87	0,51	0,06
9,5	9,1-10,0	8	0,03	0,28	0,03	0,13	0,67	0,87	0,55	0,06
10,2	10,1-11,0	7	0,03	0,30	0,03	0,14	0,67	0,85	0,66	0,06
11,5	11,1-12,0	16	0,04	0,42	0,03	0,16	0,66	0,82	0,76	0,06
12,6	12,1-13,0	12	0,04	0,42	0,03	0,16	0,65	0,78	0,86	0,07
13,8	13,1-14,0	4	0,06	0,83	0,06	0,22	0,66	0,77	1,24	0,09
14,9	14,1-15,0	2	0,06	1,15	0,08	0,25	0,64	0,75	1,50	0,10
15,8	15,1-16,0	7	0,07	1,29	0,08	0,26	0,64	0,74	1,57	0,10
16,4	16,1-17,0	7	0,07	1,38	0,08	0,28	0,63	0,73	1,97	0,12
17,7	17,1-18,0	7	0,07	1,48	0,08	0,28	0,59	0,70	2,33	0,13
18,4	18,1-18,5	11	0,07	1,55	0,08	0,29	0,59	0,70	2,45	0,13
18,8	18,6-19,0	8	0,07	1,60	0,08	0,29	0,59	0,69	2,64	0,14

in the juveniles (Figure 1F). The pre-anal length decreases from about 87% of BL in the larvae to approximately 69% of BL in the juveniles. Head length increases from approximately 11% of BL in the larvae to 24-29% of BL in the juveniles. The larval snout is initially 2% of BL, increasing to 7% of BL in the juvenile stages owing to the development of jaw elements.

A detailed description of the development of *G. aestuaria*, excluding morphometric characteristics given in Tables 1 and 2, follows.

Head development

The smallest hatchlings found in the samples ranged from 2-4 mm BL, had yolk sacs 0,4 mm \times 0,2 mm and pectoral lobes. Some specimens in this size interval showed some pigmentation of the eyes and an open mouth. Between 5 and 6 mm BL the eyes enlarge and there are signs of four gill arches and the lower jaw differentiating. By 7-8 mm BL the cartilaginous lower jaw, the cleithrum and branchial basket differentiate further. Gillraker Anlagen develop on the gill arches between 8 and 9 mm, and between 9 and 11 mm BL the upper jaw develops. Meckel's cartilage, the presumptive dentary and the quadrate also form. The ear-capsules and cleithra ossify. The eyes are ovoid and the olfactory bulbs are visible. Otoliths can be seen in some specimens by 11-12 mm BL, and small operculae which do not cover the gill chamber openings are also discernible.

Table 2 Morphometrics of *Gilchristella aestuaria* from the Sundays River estuary (Length = Mean body length in mm, Range = range in body length, n = number of fish measured, S/L = snout length/body length, E = diameter of eye in mm, E/L = eye diameter/body length, H/L = head length/body length, DF/L = distance from snout to dorsal fin origin/body length, AF/L = distance from snout to anal fin origin/body length, BD = body depth in mm, BD/L = body depth/body length)

Length	Range	n	S/L	E	E/L	H/L	DF/L	AF/L	BD	BD/L
6,5	6,0-6,5	3	0,02	0,15	0,02	0,12	0,69	0,88	0,40	0,06
7,1	7,0-7,5	4	0,02	0,17	0,02	0,12	0,69	0,86	0,40	0,06
7,8	7,5-8,0	4	0,02	0,17	0,02	0,13	0,69	0,86	0,48	0,06
8,3	8,1-8,5	8	0,02	0,22	0,03	0,13	0,68	0,86	0,53	0,06
8,9	8,5-9,0	5	0,03	0,24	0,03	0,14	0,69	0,88	0,58	0,07
9,5	9,1-9,5	4	0,03	0,28	0,03	0,15	0,65	0,84	0,66	0,07
10,0	9,6-10,5	7	0,03	0,29	0,03	0,16	0,67	0,85	0,69	0,07
10,7	10,6-11,0	6	0,03	0,33	0,03	0,16	0,66	0,84	0,76	0,07
11,9	11,1-12,0	2	0,04	0,45	0,04	0,17	0,64	0,80	0,90	0,08
12,6	12,1-13,0	6	0,04	0,45	0,04	0,17	0,65	0,81	0,93	0,07
13,2	13,1-13,5	5	0,04	0,55	0,04	0,18	0,64	0,78	1,27	0,10
13,9	13,6-14,0	3	0,04	0,62	0,04	0,18	0,64	0,77	1,23	0,09
14,6	14,1-15,0	4	0,06	0,75	0,05	0,22	0,61	0,74	1,58	0,11
16,7	15,1-17,4	7	0,06	1,10	0,07	0,24	0,57	0,67	2,40	0,14
18,1	17,5-18,5	4	0,07	1,23	0,07	0,25	0,57	0,67	2,75	0,15
19,7	18,6-20,0	3	0,07	1,43	0,07	0,25	0,55	0,66	3,23	0,16
20,7	20,1-21,0	2	0,07	1,50	0,07	0,26	0,55	0,69	3,60	0,17

At a size range of 12-13 mm BL the following skull bones show ossification; maxilla with small teeth, dentary, quadrate, pre-operculum, operculum, cleithrum, supracleithrum and post-temporal. The other skull structures and branchial basket are cartilaginous. Between 13 and 16 mm BL the gill-rakers start to ossify. Ossification of the skull bones increases rapidly above 16 mm BL. The premaxilla and the small teeth on the central area of the dentary also ossify. The articular areas of the following bones are now ossified; angulo-articular, quadrate, hyomandibular, pre- and suboperculum. The central areas of the symplectic and palatine are ossifying, as are those of the parasphenoid, ethmoid, pterotic, otic capsules, frontal trabeculae and the supra-occipitals. The pharyngeal elements are still largely cartilaginous but the basihyal, ceratohyals, basi- and ceratobranchials show signs of ossification. The gill-rakers are ossified and there are six branchiostegals. At 15 mm the dorsum of the head becomes pigmented, gradually extending onto the operculae as the fish assume the juvenile form (Figure 1F).

Myomere and swimbladder development

Because of the transparency of the fish, the newly forming myomeres are difficult to count accurately. Twenty-nine myomeres were counted in the free embryos and there are up to 31 myomeres present in specimens between 4 and 6 mm BL. By 8 mm BL up to 36 myomeres were present and by 11 mm BL 37 myomeres were counted. The ultimate myomeres form slowly during the final stages of larval development, so that only by 16 mm BL could the full

number of 40 myomeres be clearly seen.

The swimbladder begins to form between 7 and 8 mm BL, and by 9 mm BL the swimbladder pushes the gut away from the lateral muscles.

Fin development

The dorsal fin anlage is visible in a few specimens between 4 and 5 mm BL (25 myomeres from the head). By 6 mm BL a higher proportion of specimens show the dorsal fin anlage. By 7 mm BL the anlage is above myomeres 25–28 and the first 4–6 dorsal finrays form (Figure 1C). By 8–9 mm BL the dorsal fin has between five and six rays, and the anal fin anlage is also visible.

Tissue development commences in the hypural region at approximately 5 mm BL (Figure 1B), and gradually becomes more dense in comparison with that above the notochord. The hypural elements enlarge and flexion commences at approximately 7 mm BL. From 8 mm BL onwards, fin and notochordal differentiation takes place. In specimens of between 9 and 11 mm BL the larvae have up to 13 anal rays, 7–12 dorsal rays with nine pterygiophores, and 6–10 dorsal and 8–9 ventral caudal rays. Ossification of the rays commences, with the hypurals differentiating and in some specimens the urostyle appears ossified.

At 11–13 mm BL the dorsal fin has 12–14 rays and 12 pterygiophores, and the anal fin has 11–15 rays with 14–16 pterygiophores. At 13 mm BL the ventral finfold is reduced and the pelvic fins and girdle differentiate, followed by rapid ossification. In the caudal peduncle there are three elements in the urostyle; two large dorsal, one small median and two larger ventral hypurals, all of which ossify from 13 mm BL onwards. Attached to these are 10 dorsal and nine ventral rays, outside of which are four short dorsal and ventral rays.

By 12–13 mm BL the ventral finfold is still present but the pelvic anlage is now visible. The relative positions of the fins change, with the dorsal fin (14 rays) moving from an insertion above vertebra 23 at 12 mm to vertebra 21 at 17 mm, and the anal fin (19 rays) moving from below vertebra 30 to vertebra 25. By this stage seven dorsal and 18 anal rays are ossified. The pre-anal distance shortens (relative to body length) and the anal fin moves anteriorly so that the insertion is below that of the posterior end of the dorsal. By 17–19 mm BL the dorsal has moved to above vertebra 18 and the anal below vertebra 22. All the median fin rays are ossified along their entire length, as are the epurals and hypurals.

Pectoral lobes are present in the smallest free embryos and increase in size during larval development. By 16 mm BL the pectoral fin is beginning to differentiate with the cartilagenous rays, coracoid and scapula forming. By 17–19 mm BL, 12 pectoral rays are present and ossified at the bases.

Axial skeleton development

Between 8 and 9 mm BL the differentiation of the notochord commences and in some specimens the first indication of the centra can be distinguished by 8–9 mm BL. In well-cleared specimens up to 33 faintly ossified centra can be distinguished by 11 mm BL. Between 11 and 12 mm BL the neural (28) and haemal (16) spines form from the posterior

end anteriorly, except for three neural spines behind the cranium which form before those in the middle area of the vertebral column. By 12–13 mm BL ossification has taken place in 40 centra and in four urostylar elements. Between 16 and 17 mm BL, 17 haemal and 20 neural processes ossify from the posterior anteriorly, except for the most anterior neural processes which begin to ossify at the tips.

Between 13 and 15 mm BL the cartilaginous ribs are laid down and by 17 mm they start to ossify so that by 19 mm there are 17 pleural ribs and all the haemal and neural spines are ossified.

Melanophore development

At 5 mm BL, four melanophores are visible above the gut and 10 ventrally (Figure 1B). These increase gradually and by 10 mm there are two melanophores on the isthmus, four at the base of anterior myomeres, two below the airbladder, nine ventral to the gut, one above the anus and one on the caudal fin. Between 11 and 12 mm BL post-anal melanophores appear, and by 13 mm melanophores are coalescing into lines as shown in Figure 1E. In juvenile specimens, pigment appears on the dorsal surface of the airbladder and body. A few small melanophores appear on the lateral surface of the hypurals from 14 mm BL, and from 16 mm BL on the lateral surface in front of the caudal fin.

Discussion

The larvae of *G. aestuaria* are typically clupeid in appearance, being long and threadlike. When compared to the descriptions and illustrations in McGowan & Berry (1984) and Leis & Trnski (1989), they exhibit typical clupeid features, i.e. free embryos are characterized by a moderate to large yolk sac, unpigmented eyes and unformed mouth. Later development of ventral pigmentation comprising a row of melanophores superior to the anterior area of the gut and a further row ventral to the gut, posterior to the airbladder, is also typical. The two melanophores in the gular region are also characteristic of clupeid larvae.

McGowan & Berry (1984) emphasize that when a series of field-caught larvae is compared with a laboratory-reared series, there may be differences in size at a particular stage of development owing to the rearing environment. *G. aestuaria* larvae used in this study were derived from two contrasting water bodies. Swartvlei is an estuarine coastal lake which has an extremely low phytoplankton productivity (Robarts 1976) and poor zooplankton stocks (Coetzee 1981), whereas the Sundays River estuary is a permanently open system which has frequent phytoplankton blooms (Hilmer & Bate 1991) and a rich zooplanktonic fauna (Wooldridge & Bailey 1982). Evidence from Tables 1 and 2 indicate that larval *G. aestuaria* from the Swartvlei system are narrower bodied than those from the Sundays River estuary. Blaber, Cyrus & Whitfield (1981) suggested that zooplanktonic prey abundance may influence the morphometrics of *G. aestuaria*, with juveniles and adults from the zooplankton-rich Lake St Lucia having deeper bodies when compared to specimens from other zooplankton-poor estuarine systems. It is possible that differences in larval body depths, which increase with increasing size, between specimens from the Sundays and Swartvlei estuarine systems, may also be

linked to food availability.

Blaber *et al.* (1981) also noted that the eye diameter of juvenile and adult *G. aestuaria* from Lake St Lucia were smaller than those from other estuaries. Underwater observations (Whitfield, unpubl.) in the Swartvlei littoral zone revealed that *G. aestuaria* selects individual prey items in this habitat. It is possible that individual prey selection in the relatively clear Swartvlei system, as opposed to filter feeding in the turbid Sundays estuary, may have given rise to greater eye development (Tables 1 and 2) in the former system.

Spawning by adult *G. aestuaria* in the study systems is mainly during spring/summer (September–December) and occurs predominantly in the upper reaches of both estuaries (Melville-Smith, Baird & Wooldridge 1981; Ratte 1989). *G. aestuaria* larvae are most abundant during spring and summer (October–March), but have also been recorded in the Swartvlei and Sundays estuaries at other times of the year (Whitfield 1989; Harrison & Whitfield 1990). In Swartvlei, the smallest larvae (2–4 mm BL) occur predominantly in the littoral zone of the lake, whereas the larger larvae (6–8 mm) are found mainly in offshore waters (Whitfield 1989). The highest densities of *G. aestuaria* larvae (>14 mm BL) in the Sundays estuary were in the middle reaches (Harrison & Whitfield 1990), where densities of zooplanktonic prey organisms were also greatest (Wooldridge & Bailey 1982).

Acknowledgements

We thank Trevor Harrison, Hendrik Jerling, Koos Wagner and Elspeth Whitfield for their assistance in the collection and sorting of plankton samples. Financial assistance was provided by the Estuaries Joint Venture Programme of the Foundation for Research Development (FRD).

References

- BALON, E.K. 1975. Terminology of intervals in fish development. *J. Fish. Res. Board Can.* 32: 1663–1670.
- BALON, E.K. & NOAKES, D.L.G. 1980. Principles of ichthyology: supplements to lectures and laboratory exercises. University of Guelph, Ontario, Canada. 285 pp.
- BLABER, S.J.M. 1979. The biology of filter feeding teleosts in Lake St Lucia, Zululand. *J. Fish Biol.* 15: 37–59.
- BLABER, S.J.M., CYRUS, D.P. & WHITFIELD, A.K. 1981. The influence of zooplankton food resources on the morphology of the estuarine clupeid *Gilchristella aestuarius* (Gilchrist, 1914). *Env. Biol. Fish.* 6: 351–355.
- COETZEE, D.J. 1981. Zooplankton distribution in relation to environmental conditions in the Swartvlei system, southern Cape. *J. Limnol. Soc. sth. Afr.* 7: 5–12.
- COETZEE, D.J. 1982. Stomach content analyses of *Gilchristella aestuarius* and *Hepsetia breviceps* from the Swartvlei system and Groenvlei, southern Cape. *S. Afr. J. Zool.* 17: 59–66.
- DAY, J.H., BLABER, S.J.M. & WALLACE, J.H. 1981. Estuarine fishes. In: Estuarine ecology with particular reference to southern Africa, (ed.) Day J.H. pp. 197–222. A.A. Balkema, Cape Town.
- DE BEER, G. 1971. The development of the vertebrate skull. Oxford University Press, England. 774 pp.
- DINGERKUS, G. & UHLER, L.D. 1977. Enzyme clearing of alcian blue stained whole small invertebrates for demonstration of cartilage. *Stain technol.* 52: 229–232.
- HARRISON, T.D. & WHITFIELD, A.K. 1990. Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *S. Afr. J. Zool.* 25: 161–168.
- HILL, B.J. 1975. The origin of southern African coastal lakes. *Trans. Roy. Soc. S. Afr.* 41: 225–239.
- HILMER, T. & BATE, G.C. 1991. Vertical migration of a flagellate-dominated bloom in a shallow South African estuary. *Bot. Mar.* 34: 113–121.
- LEIS, J.M. & TRNSKI, T. 1989. The larvae of Indo-Pacific shorefishes. New South Wales University Press, Australia. 371 pp.
- MCGOWAN, M.F. & BERRY, F.H. 1984. Clupeiformes: development and relationships. In: Ontogeny and systematics of fishes, (eds) Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Dendal, A.W. & Richardson, S.L. pp. 108–126. *Amer. Soc. Ichthyol. & Herpetol.*, Special Publ. No. 1: 760 pp.
- MELVILLE-SMITH, R. 1978. Aspects of the ecology of fish larvae in the Swartkops estuary, Port Elizabeth. M.Sc. thesis, University of Port Elizabeth, South Africa.
- MELVILLE-SMITH, R. 1981. The ichthyoplankton of the Kromme River estuary. *S. Afr. J. Zool.* 16: 71–72.
- MELVILLE-SMITH, R., BAIRD, D. & WOOLDRIDGE, T. 1981. The utilization of tidal currents by the larvae of an estuarine fish. *S. Afr. J. Zool.* 16: 10–13.
- RATTE, T.W. 1989. Population structure, production, growth, reproduction and the ecology of *Atherina breviceps* Valenciennes, 1935 (Pisces: Atherinidae) and *Gilchristella aestuaria* (Gilchrist, 1914) (Pisces: Clupeidae), from two southern Cape coastal lakes. Ph.D. thesis, University of Port Elizabeth, South Africa. 319 pp.
- ROBARTS, R.D. 1976. Primary productivity of the upper reaches of a South African estuary (Swartvlei). *J. Exp. Mar. Biol. Ecol.* 24: 93–102.
- TALBOT, M.M.J-F. 1982. Aspects of the ecology and biology of *Gilchristella aestuarius* (G & T) in the Swartkops estuary. M.Sc. thesis, University of Port Elizabeth, South Africa. 128 pp.
- TALBOT, M.M.J-F. & BAIRD, D. 1985. Feeding of the estuarine round herring *Gilchristella aestuarius* (G & T) (Stolephoridae). *J. Exp. Mar. Biol. Ecol.* 87: 199–214.
- TAYLOR, W.R. 1967. An enzyme method for clearing and staining small vertebrates. *Proc. U.N. natn. Mus.* 122: 1–17.
- WHITE, P.N. & BRUTON, M.N. 1983. Food and feeding mechanisms of *Gilchristella aestuarius* (Pisces: Clupeidae). *S. Afr. J. Zool.* 18: 31–36.
- WHITEHEAD, P.J.P & WONGRATANA, T. 1991. Family No. 54: Clupeidae. In: Smiths' Sea Fishes, (eds) Smith, M.M. & Heemstra, P.C. pp. 199–207. Southern Book Publishers, Johannesburg.
- WHITFIELD, A.K. 1989. Fish larval composition, abundance and seasonality in a southern African estuarine lake. *S. Afr. J. Zool.* 24: 217–224.
- WHITFIELD, A.K. 1990. Life-history styles of fishes in South African estuaries. *Env. Biol. Fish.* 28: 295–308.
- WOOLDRIDGE, T. & BAILEY, C. 1982. Euryhaline zooplankton of the Sundays estuary and notes on trophic relations. *S. Afr. J. Zool.* 17: 151–163.

