

Larval development of *Dagetichthys marginatus* (Soleidae) obtained from hormone-induced spawning under artificial rearing conditions

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SUMMARY: *Dagetichthys marginatus* (formerly *Synaptura marginata*) larvae were laboratory-reared from wild caught adult broodstock as part of an aquaculture research project in temperate South Africa. A larval description for the species is provided in this paper. This work also represents the first larval description for the genus *Dagetichthys*, which is represented by five species, three of which occur in the western Indian Ocean. Larval development in *D. marginatus* is typical of Soleidae. *Dagetichthys marginatus* larvae are heavily pigmented, with four characteristic melanophore "blotches" on the fin-fold. These larvae are easily distinguished from other soleid larvae commonly encountered in temperate South Africa based on the large size at flexion (5-7.06 mm BL) and the heavily pigmented body. Laboratory-reared postflexion larvae in this study showed similar meristic counts to those of wild caught adult fish. Despite the common occurrence of mature adults of this species in shallow marine waters off temperate South Africa, larvae are absent from nearshore ichthyoplankton catches. As yet, the spawning strategy of the species is unknown.

Keywords: *Synaptura*, fish larvae, description, temperate ichthyoplankton, soleids, aquaculture.

RESUMEN: DESARROLLO LARVARIO DE *DAGETICHTHYS MARGINATUS* (FAMILIA: SOLEIDAE) A PARTIR DE PUESTA INDUCIDA POR HORMONAS EN CONDICIONES DE CULTIVO ARTIFICIALES. – Las larvas de *Dagetichthys marginatus* (anteriormente *Synaptura marginata*) se cultivaron en el laboratorio a partir de adultos capturados en el medio natural como parte de un proyecto de investigación en la zona templada de Sudáfrica. En este trabajo se presenta la descripción de las larvas de esta especie. Este trabajo también representa la primera descripción del *Dagetichthys*, representado por cinco especies, tres de las cuales se encuentran en el Oeste del Océano Índico. El desarrollo larvario de *D. marginatus* es el típico de la familia Soleidae. Las larvas de *Dagetichthys marginatus* están fuertemente pigmentadas con cuatro característicos bloques de melanóforos en la aleta primordial. Estas larvas se distinguen fácilmente de otras larvas de soleidos comúnmente encontradas en la zona templada de Sudáfrica en base a su gran longitud en el estadio de flexión (5-7.06 mm BL) y a su cuerpo fuertemente pigmentado. Las larvas en estado de postflexión obtenidas en el presente cultivo mostraron similares contajes que los adultos capturados en el medio natural. A pesar de la común aparición, en aguas someras, de adultos maduros de esta especie frente a la zona templada de Sudáfrica, las larvas estuvieron ausentes en las muestras de ictioplankton recolectadas en dicha zona. Hasta el momento, la estrategia de puesta de esta especie es desconocida.

Palabras clave: *Synaptura*, larvas de peces, descripción, ictioplankton de zonas templadas, soleidos, acuicultura.

INTRODUCTION

The white-margined sole, *Dagetichthys marginatus*, was identified as a suitable candidate species for aquaculture in South Africa, based on

life history strategy (fecundity, maturity, egg size, *inter alia*), good natural growth rates and an established, lucrative market for flatfish (Thompson, 2004). Wild broodstock were successfully induced to spawn and the larvae were

reared through to metamorphosis under controlled laboratory conditions.

Dagetichthys marginatus (Boulenger, 1900), formerly *Synaptura marginata* (Vachon *et al.*, in press), is one of 56 flatfish species that occur in southern African waters, 16 of which are soleids (Smith and Heemstra, 1986). The new soleid genus *Dagetichthys* consists of five species, three occurring in the western Indian Ocean (Vachon *et al.*, in press), namely *D. marginatus*, *D. albomaculatus* (Kaup, 1858) and *D. commersonnii* (Lacepède, 1802). The distribution of *Dagetichthys marginatus* is listed by Heemstra and Gon (1986) as extending from the Mozambique Channel southwards to Durban on the east coast of South Africa. However, Thompson (2004) recorded the distribution of *D. marginatus* to extend into temperate waters as far south as Gansbaai (34°35'S, 19°20'E), where it is the most abundant shallow water sole species on intertidal and sub-tidal sandbanks.

Nothing is known about the early life history of this species prior to the allocation of this species to the genus *Dagetichthys*. An isolated report on egg size (2.08 mm) (Ochiai, 1966) was shown to be inaccurate due to the misidentification of adult fish (Vachon *et al.*, in press), while a record of three *D. marginatus* larvae (2.8-3.2 mm) (Beckley, 1986) in temperate South Africa remains unconfirmed. The only information for larvae of the 14 species in the genus *Synaptura* (Eschmeyer, 1998) was an isolated description for *Synaptura kleinii* (Brownell, 1979), which was subsequently moved to the genus *Synapturichthys* (Heemstra and Gon, 1986). Hence there are no published larval descriptions for the new genus *Dagetichthys*.

Laboratory rearing of *D. marginatus* for aquaculture provided an ideal opportunity to study and describe larval development. Understanding the critical changes in morphology and behaviour of this species, as well as the timing and duration of

TABLE 1. – Meristic, morphological and pigmentation (melanophore) information on soleid species occurring in South African waters for which larval descriptions are available (* denotes size at completion of flexion, while the others are size at commencement of flexion). Information provided is taken directly from literature cited (adapted from Wood, 2000).

Species	Myomeres (range for preflexion and flexion)	Vertebrae	Size at flexion (mm)	Pigment	Reference
<i>Austroglossus microlepis</i>	56-58	55-57	5.2-5.5	Dorsal and ventral midline; gut; lower jaw; behind eyes; pectoral fins	O'Toole, 1977; Brownell, 1979
<i>Austroglossus pectoralis</i>	50-58 (8-10 + 40-49)	58	3.5-3.8	Dorsal and ventral midline; fore- and hind-brain; snout; lower jaw; ventral and lateral gut; small spots on finfold	Wood, 2000
<i>Dicologossa cuneata</i>	44-47 (9 + 35-38)	43-45	6.3-6.5	Dorsal and ventral midline; midbrain; hindbrain; finfold; swim bladder, gut; head	Lagardère and Aboussouan, 1981
<i>Heteromycteris capensis</i>	39-41 (10 + 29-31)	40-43	6.2*	Midline body contour; Three spots on ventral finfold; ventral gut wall; lower pectoral fin margin	Brownell, 1979
<i>Monochirus lutens</i>	36-38	36-40	5	Dorsal and ventral midline; midbrain; posterior tail (early); finfold; ventral abdominal wall	Nichols, 1976 in Olivar and Fortuño, 1991
<i>Monochirus ocellatus</i>	34-37 (8-9 + 26-28)	37-38	4	Three dorsal and two ventral concentrations of small spots on finfold; caudal tip; dorsal and ventral body contour	Palomera and Rubies, 1971 in Olivar and Fortuño, 1991
<i>Pegusa lascaris</i>	47 (9 + 38)	42-47	5.3	Many small melanophores scattered over head, body and fins. Heaviest concentrations over lateral and ventral gut surface and laterally on tail	Clarke, 1914 in Ahlstrom <i>et al.</i> , 1984; Russell, 1976
<i>Synapturichthys kleinii</i>	42-45 (9-10 + 33-35)	46-47	6.5*	Densely packed stellate melanophores scattered over all body surfaces and finfold	Brownell, 1979
<i>Dagetichthys marginatus</i>	40 (preflexion)	42	5-7.6	Three distinct clusters on the dorsal and one on the ventral finfold and later on fins, when the last dorsal and ventral cluster fuses to form a band over the body	This study

each of these events, will facilitate larval rearing protocols.

Larval descriptions for coastal fishes are generally lacking in South Africa (Strydom and Neira, in press). Descriptions are, however, available for eight of the 16 soleid species occurring on the South African coast (Table 1). This paper presents the first description of the early larval development of the white-margined sole, *D. marginatus* (Boulenger, 1900). This information will assist in the identification of this species in ichthyoplankton samples and in so doing provide much-needed information on its spawning and its larval and juvenile distribution in coastal waters off South Africa.

MATERIALS AND METHODS

All broodstock fish were identified as *Dagetichthys marginatus* based on meristic counts given in Heemstra and Gon (1986) and Vachon *et al.* (in press). Male and female fish were collected with a hand-held, multiprong spear between Port Elizabeth (33°57'S; 25°38'E) and Great Fish River Point (33°31'S; 27°06'E) during the spawning season (October to March) (Thompson, 2004) and transported to the marine hatchery at Rhodes University, Grahamstown. Females were induced to ovulate using Aquaspawn®, a GnRH analogue (Millar's Clinical Laboratories, Touws River, South Africa) at a dosage of 0.5 ml per kg of body weight. Eggs were obtained by strip-spawning the females approximately 38 h after the single hormone injection. Males were sacrificed and the testes were homogenized in a small volume (1 ml) of saline solution (0.9 ppt). Eggs were fertilized with the testicular homogenate. After fertilisation and hardening, eggs were thoroughly washed with seawater and divided among six 60 L black upwelling incubators at a density of 20 eggs/L for egg incubation and larval rearing. Hatching occurred between 42 and 49 h after fertilisation and exogenous feeding began three days after hatching (dah). Larvae were fed twice daily on newly hatched brine shrimp, *Artemia salina* nauplii, from first feeding to 16 dah. After this, larvae were fed two-day old, Super Selco (INVE) enriched *A. salina*. A new batch of enriched nauplii was provided every 24 h at a density of five individuals/ml. Temperature and salinity were kept constant at $19 \pm 0.8^\circ\text{C}$ and 35 ppt, respectively, for the duration of egg incubation and larval rearing.

Although three successful larval batches were reared, larvae from only one spawning were used to avoid differences in broodstock condition and thus egg quality, which affect larval development (Bromage, 1995). Ten larvae were collected at specific intervals representing developmental endpoints after hatching. All samples were fixed in 5% buffered formaldehyde for 24 h and then transferred into 70% ethanol. Representatives of the larvae examined and described in this paper were lodged in the national fish collection at the South African Institute of Aquatic Biodiversity (SAIAB 77531).

All terminology pertaining to larval fishes follows that of Neira *et al.* (1998). The term "larva" was used to designate all stages in the early life history from hatching to the attainment of a full fin ray complement, squamation and the subsequent loss of all larval characters, at which stage the "larva" becomes a "juvenile". Settlement stages still in possession of isolated larval characters and in a planktonic state were considered as larvae. Newly settled individuals were called "early juveniles" and were included in the study. The term "larva" was further subdivided into yolk-sac, preflexion, flexion and postflexion stages. The following body measurements were made for all developmental stages: body depth (BD), body length (BL), eye diameter (ED), head length (HL) and pre-anal length (PAL). All measurements were made according to Neira *et al.* (1998) to the nearest 0.01 mm using a Leica dissecting microscope fitted with an eyepiece micrometer for larvae <10 mm and Vernier calipers for larger specimens. Body length (BL) represents notochord length in preflexion and flexion stage larvae, and standard length in postflexion larvae and early juveniles. All proportional values are a proportion of BL unless otherwise noted.

RESULTS

Age and size range of developmental stages

A total of 104 laboratory-reared larvae (2.09–14.75 mm BL) were examined to describe morphometrics, meristics and pigmentation. Newly hatched larvae (0 h) ranged in size between 2.09 and 2.19 mm BL. The yolk-sac was completely absorbed after 4 days, while the oil globules persisted for approximately 12 hours. Yolk-sac larvae ranged from 2.09 to 3.41 mm BL (Table 2). The preflexion

TABLE 2. – Body length and body proportions of the larval and settlement stages of *Dagetichthys marginatus* reared under laboratory conditions (n, number of larvae; BL, body length; HL, head length; BD, body depth; PAL, preanal length; SD, standard deviation).

n		Yolk-sac 40	Preflexion 30	Flexion 20	Postflexion 10	Settlement 4
BL	Range	2.09 – 3.41	3.44-5.15	5.00-7.06	9.50-11.60	13.50-14.75
	Average	2.79	4.04	5.96	10.59	14.03
	SD	0.50	0.48	0.70	0.57	0.58
HL (%BL)	Range	12.35-17.14	17.86-25.23	22.02-28.04	25.47-30.77	26.32-31.19
	Average	14.63	21.17	24.50	27.95	28.99
	SD	1.12	2.04	1.45	1.80	2.04
ED (%HL)	Range	35.29-70.00	28.57-45.00	21.67-30.43	15.63-23.21	14.71-16.67
	Average	52.74	35.91	25.92	19.34	15.43
	SD	9.95	3.66	2.25	1.94	0.93
BD (%BL)	Range	10.09-19.12	22.22-34.23	28.44-36.28	39.62-50.00	30.70-33.05
	Average	13.61	26.59	31.65	44.99	32.30
	SD	3.02	3.28	1.96	3.73	1.10
PAL (%BL)	Range	42.20-62.69	40.00-48.65	42.59-49.56	32.76-46.32	22.88-25.93
	Average	51.54	43.52	46.60	39.65	24.53
	SD	6.84	2.55	1.89	4.03	1.26

stage lasted for 6 days after yolk-sac absorption. During the preflexion stage the larvae ranged from 3.44 to 5.15 mm BL. Flexion of the notochord tip started 11 dah and was completed between 20 and 30 dah. Flexion stage larvae ranged from 5.00 mm (11 dah) to 7.06 mm BL (15 dah). The smallest post-flexion larva measured 9.50 mm BL at 30 dah.

General morphology

Larvae are elongate (Fig. 1A) in body shape during the yolk sac stage (mean BD = 13.61%), becoming more moderate (Fig. 1B) at the preflexion stage (mean BD = 26.59%). Body depth increases from the onset of flexion as the gut enlarges and coils prior to the settlement stage. Larvae remain moderately deep-bodied until metamorphosis into juveniles (BD 28.44-50.00%). The head is compressed and small during the yolk-sac stage (HL 14.63%), becoming moderate in size during later developmental stages (HL 21.17-28.99%). The snout is short, giving the head a rounded, convex dorsal profile during preflexion and flexion (Fig. 1). A dorsal hump forms during the postflexion stage. This very distinct fleshy extension protrudes over the anterior, dorsal surface of the head and joins with the dorsal fin (Fig. 1D). The head and snout profile becomes convex after eye migration is complete. Both body depth and head length increase proportional to BD during development. Pre-anal length gradually decreases throughout development, from long to moderate (PAL 62.69-32.76%) during early stages

to short (mean PAL 24.53%) at the settlement stage (Table 2).

Newly hatched larvae have a moderate to large, unsegmented yolk-sac (0.50-0.59 mm diameter). In excess of 50 oil globules are distributed in the yolk-sac and are clustered together in groups of eight or less situated at the posterior end of the yolk-sac. An additional dense cluster of about 30 oil globules is also situated at the posterior end of the yolk-sac. Prior to first feeding, the oil globules fuse to form one large globule situated in a posterior-dorsal position in the reduced yolk-sac. The eyes are unpigmented in yolk-sac larvae and become fully pigmented and functional in early preflexion larvae by 3.44 mm. The mouth becomes functional at the same time as the gut is fully formed in preflexion larvae at 3 dah (3.44 mm BL) and larvae start feeding on *Artemia salina* 4 dah. Two to five small villiform teeth were first observed at 16 dah (6.60 ± 0.27 mm BL) on the blind and ocular side of the dentary. Villiform teeth are present on the premaxilla at 31 dah, while the number of teeth on the blind side dentary increases. At this stage, the teeth on the ocular side dentary disappear. No further teeth develop on the ocular side premaxilla at any stage during development (Ende, *in prep.*). Preflexion larvae have a myomere count of 40, while the vertebral count is 42 after ossification. Myomeres could not be counted during any other larval stage due to heavy pigmentation. The air bladder is visible in isolated larvae 7 dah and not in older larvae due to heavy pigmentation. Larvae are, however, positively buoyant until

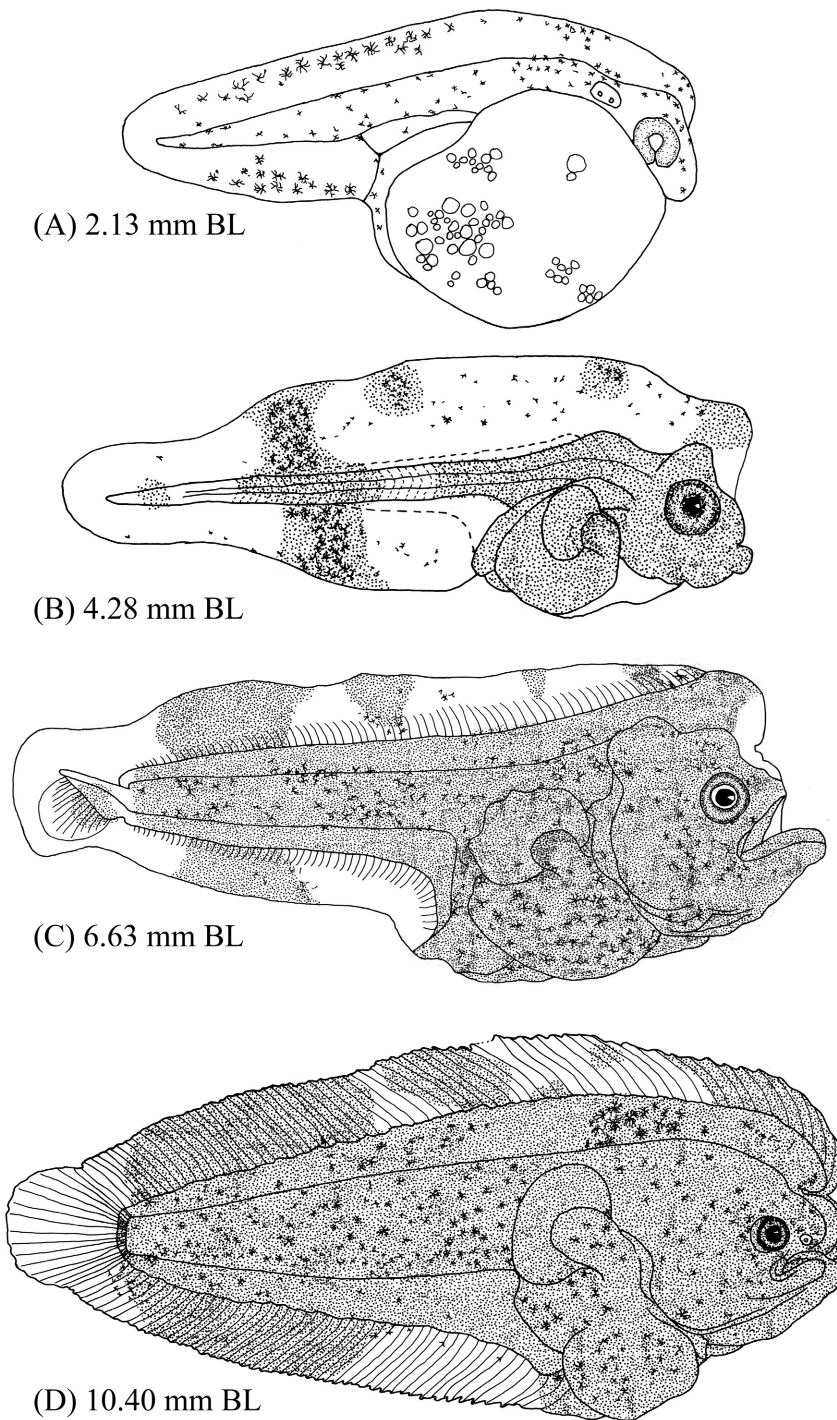


FIG. 1. – Larvae of laboratory-reared *Dagetichthys marginatus*. (A) newly hatched yolk-sac stage (myomeres, although present, were too indistinct to draw accurately). (B) preflexion. (C) flexion. (D) postflexion.

flexion, after which they become substratum-associated. This indicates the presence and use of an air bladder during the early stages of larval development. The gill membrane is also free from the isthmus at this stage. No head spination is present at any stage of development.

Development of fins

Pectoral fin buds appear in late yolk-sac or early preflexion larvae from 3.03 mm BL. These increase in size throughout development up to settlement (13.52 mm BL), when the fins decrease in size and

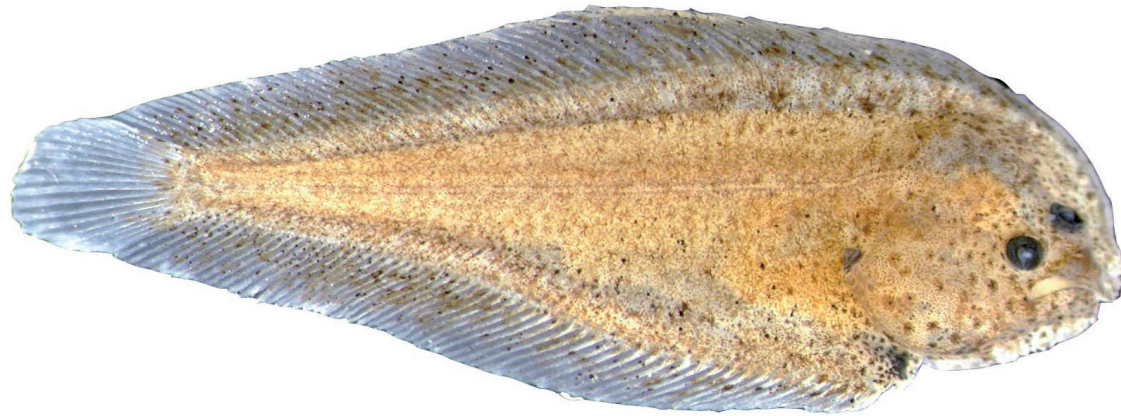


FIG. 2. – Settlement stage larva of *Dagetichthys marginatus* (10.53 mm BL) reared under laboratory conditions.

seven pectoral-fin rays develop on both the ocular and blind sides. Paired pelvic-fin buds start developing during the late flexion stage from 6.50 mm BL (15 dah) and are fully developed in early settlement stage larvae from 13.52 mm BL, with 3 rays present. The dorsal, caudal and anal-fin anlagen appear simultaneously in late preflexion larvae by 4.72 mm BL. Incipient rays form during early flexion and a full adult ray complement (D 70, A 55, C18) is present by late flexion stages from 6.13 mm BL (15 dah). The dorsal, caudal and anal fin membranes remain fused throughout development and in adults. No fin spines or extraordinary rays are present in *Dagetichthys marginatus* larvae during any stage of development.

General pigmentation pattern during development

Pigmentation increases from sparsely pigmented yolk-sac larvae to heavily pigmented settlement stage larvae. The general pattern of occurrence of melanophores on the head and trunk remains similar from first feeding (3 dah) to postflexion larvae, although intensity and melanophore type (e.g. punctate and/or stellate) increase with development (Fig. 1). Distinctive melanophores are described in the text but the body of the larva is also covered with very small punctate melanophores that are randomly distributed in the areas as shown in Figure 1. Xanthophores (not indicated in Fig. 1 as these disappear in preserved specimens) dominate the pigmentation of live yolk-sac larvae, mirroring the melanophore pattern observed in four-day-old larvae. Xanthophores, however, decrease in number and intensity until they disappear completely around

4 dah and are replaced by branched, stellate melanophores.

Head pigmentation

Head pigmentation is characterised by melanophores on the lower lip (extending along the lower jaw line in later stages), preopercle, behind the eye and the isthmus in preflexion larvae, increasing in number and intensity in flexion larvae. In some flexion specimens, a melanophore ring appears around the eye. Postflexion larvae lose this general pattern of pigmentation, as the whole head region becomes covered with many random melanophores. An isolated group of internal melanophores is visible at the join of the lower and upper jaw, as well as on the dorsal hump of the head in preflexion larvae.

Trunk and tail pigmentation

Trunk pigmentation in early preflexion larvae consists of three large clusters of melanophores or “blotches” on the dorsal finfold and one on the ventral finfold (Fig. 1B). The first of the dorsal blotches is situated anterior to the nape, the second occurs opposite the anal opening (midway down the trunk) and the third occurs two thirds along the length of the trunk. The ventral blotch is in line with the third dorsal blotch. This third dorsal and the ventral blotch expand laterally over the trunk, across the myomeres, until the two fuse and become an “hour-glass shaped” band across the larva during late preflexion. This band widens during flexion to form one solid band and continues to be visible as a “dusky bar” in postflexion larvae. The first two dorsal blotches remain visible during and after fin ray

development. In live larvae, iridiophores overlay the melanophore pattern of the three dorsal blotches at the start of flexion and continue to exist until the end of flexion. The notochord, during preflexion, is sparsely pigmented with punctuate melanophores that become heavily stellate during flexion, covering almost the entire thickening of the myomeres. With this thickening during flexion, internal pigmentation appears on the ventral side along the notochord and above the gut, and become increasingly difficult to see as the external pigmentation develops. The gut is even, but lightly pigmented in preflexion larvae. This pigmentation pattern remains the same although individual melanophores expand and the pigmentation becomes heavy, concealing any internal pigmentation that might be present in and around the gut during flexion and later stages of the development. Pelvic fins become pigmented with melanophores during the postflexion stage and remain so through to the juvenile stage. The base of the pectoral fin becomes pigmented during preflexion stages.

A cluster of melanophores appears on and around the notochord, anterior to the tip, during the preflexion stage and disappears at the end of flexion. Other than this cluster, the caudal peduncle and caudal fin remains free of melanophores.

DISCUSSION

Dagetichthys marginatus larvae follow the typical pattern of soleid development (Leis and Trnski, 2000). Fin development as well as the lack of extraordinary long rays and spines is characteristic. The anterior dorsal fin supports (pterygiophores and the proximal portion of rays) form a deep notch with the top of the snout and head of postflexion larvae. The eye migrates through this notch and the notch closes following eye migration. This anterior extension of the dorsal hump on the head is, however, not common among soleids. The only other described larval soleid with a similar morphological feature is *Heteromycteris japonicus* (Ahlstrom *et al.*, 1984).

All the larvae used for this description were laboratory-reared from eggs, which according to Watson (1982) may result in heavier pigmentation. Laboratory reared larvae may also show slightly different meristic characteristics to those of wild-caught individuals. Variable laboratory rearing conditions can manifest in those characteristics that are

partially controlled by environmental conditions, such as vertebral and fin ray counts (Hunter 1984). In this study, however, fin ray and vertebral counts observed in laboratory-reared larvae fell within the range for wild-caught adult *Dagetichthys marginatus*; D 70-81, A 55-64, P 7, C 18, V 42-45 (Vachon *et al.*, in press).

Dagetichthys marginatus larvae are easily distinguished from other pleuronectiform larvae commonly found in temperate nearshore waters of South Africa. The larvae of the cynoglossid, *Cynoglossus capensis* (Brownell, 1979) are easily distinguishable from those of *D. marginatus* by four elongated anterior dorsal rays that only start disappearing in late postflexion stages. At this stage *C. capensis* is a left-eyed (sinistral) flatfish, while *D. marginatus* is right-eyed (dextral). Similarly, *Cynoglossus zanzibarensis* (Wood, 2003) can be distinguished from *D. marginatus* by two elongated anterior dorsal fin rays up to flexion, after which it becomes a sinistral flatfish. Other characteristics that could be used to make a distinction between Cynoglossidae and *D. marginatus* are the higher meristic counts, a coiled gut and a single pelvic fin (Leis and Carson-Ewart, 2000).

Except for *Arnoglossus capensis* and *Pseudorhombus arsius*, bothid larvae are not commonly found in ichthyoplankton samples in temperate coastal waters of South Africa (Strydom, unpublished data). The larvae of *A. capensis* have been partially described by Brownell (1979). Despite the paucity of descriptive information, *D. marginatus* can be distinguished from bothids by the presence of a continuous dorsal, caudal and anal fin membrane that remains fused until the fin rays ossify. Other notable bothid characteristics are the elongated dorsal fin rays during early larval stages and the fact that they are sinistral flatfish.

Soleids commonly encountered in temperate inshore waters of South Africa are *Heteromycteris capensis*, *Solea turbynei* (formerly *S. bleekeri*) and *Austroglossus pectoralis* (Table 1). The larvae of *A. pectoralis* and *S. turbynei* are notably smaller than those of *D. marginatus*, reaching flexion at a size of 3.5-3.8 mm (Wood, 2000) and ~3.5-3.9 mm (Strydom, unpublished data.), respectively, whereas *D. marginatus* range from 5 to 7.06 mm BL at flexion. *A. pectoralis* and *H. capensis* larvae are light to moderately pigmented, *S. turbynei* larvae are moderate to heavily pigmented and *D. marginatus* larvae are heavily pigmented. Postflexion larvae of all these species can also be separated by fin ray counts.

Dagetichthys marginatus can also be separated from *H. capensis* by the presence of the fused anal, caudal and dorsal fins. *Synapturichthys kleini* (Brownell, 1979) has a very different melanophore arrangement to *D. marginatus*, although fin ray counts and sizes at different developmental stages are similar. *Synapturichthys kleini* has densely packed stellate melanophores scattered randomly over the body and finfold, while *D. marginatus* has a distinctive melanophore pattern with four characteristic melanophore blotches on the finfold.

The actual spawning habitat of *D. marginatus* has not been identified, mainly due to the lack of eggs, larvae and juveniles in shallow surf or nearshore plankton catches (Lasiak, 1983, 1984; Strydom, 2003; Watt-Pringle and Strydom, 2003) and the lack of larval fish research in offshore waters of South Africa. Although there is no evidence to suggest a spawning migration given the prevalence of mature females intertidally, it is not unlikely among flatfish, as Dagang *et al.* (1992) and Shuozen (1995) showed this to be the case for most flatfish species in the Yellow Sea, China. Further research is required on soleid spawning strategies off temperate South Africa.

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