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THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(*continued inside back cover*)

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LARVAL DEVELOPMENT OF *SARDINOPS OCELLATA* (PISCES : CLUPEIDAE)

By

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&

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Cape Town Kaapstad

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By

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M. J. O'TOOLE

*Sea Fisheries Branch, Walvis Bay**

(With 11 figures and 3 tables)

[*MS. accepted 23 August 1976*]

ABSTRACT

The development of yolk-sac, larval and metamorphic stages of *Sardinops ocellata* (Pappe) are described, together with notes on the transition to juveniles. Emphasis is placed on changes in body proportions, pigmentation, fin development and fin position relative to myotomes during development.

CONTENTS

INTRODUCTION

The pilchard or sardine, *Sardinops ocellata* (Pappe), has for about 30 years been of considerable importance to the commercial fisheries off the western Cape and South West African coasts. Research on the biology of this species has continued since its initiation by D. H. Davies in the 1950s. This research has been intensified since September 1970 with the commencement of the Cape

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Cross Programme (Cram & Visser 1972) which was instigated by the decline of the South West African pelagic fishing industry in 1968. The South West African Pelagic Egg and Larval Survey (SWAPELS), forming part of the Cape Cross Programme, was started in September 1972. The purpose of this SWAPELS programme was that of stock assessment of the pilchard and anchovy by means of an intensive quantitative egg and larva survey off the South West African coast. A prerequisite of this type of work is accurate identification of the larvae concerned, based on adequate descriptions of the larvae at all stages of their development so that pilchard and anchovy larvae can be readily distinguished from one another, and also from any other clupeid-type larvae which may occur in the area. It has thus been decided to present detailed descriptions of the development of the pilchard, *Sardinops ocellata*, and the anchovy, *Engraulis capensis*, as and when sufficient larval material of the two species becomes available. In addition, in western Cape waters, the larvae of the red-eye sardine, *Etrumeus teres*, are found in considerable numbers, and their similarity to the larvae of *Sardinops ocellata* and *Engraulis capensis* necessitates a detailed description of the larvae of *Etrumeus teres*. At present, however, the available material lacks certain stages of *Engraulis capensis* and *Etrumeus teres*. Consequently the present paper deals only with the development of *Sardinops ocellata*.

Some confusion exists in the taxonomy of *Sardinops* Hubbs, which is generally accepted as comprising five species, viz. *S. caerulea* (California), *S. sagax* (South America), *S. neopilchardus* (New Zealand and Australia), *S. melanosticta* (Japan) and *S. ocellata* (southern Africa). This distinction is followed for the purposes of this paper, although the authors are aware of Svetovidov's (1952: 193) classification which places all these as sub-species of *Sardinops sagax*.

Because of their importance in the commercial fisheries of the world, considerable interest has been shown in the biology of these species, including studies of their egg and larval development. Scofield (1934), Ahlstrom (1943) and Miller (1952) have considered the development of *S. caerulea*; Uchida (1958) described the eggs, larvae and juvenile stages of *S. melanosticta*; Baker (1972) included the eggs and larval stages in his study of the biology of *S. neopilchardus*; Hart & Marshall (1951) recorded larvae of *S. ocellata* off the South West African coast and Davies (1954) described the eggs and larvae of this species from Cape waters.

Davies (1954) obtained the early larval stages of *S. ocellata* by hatching fertilized eggs collected in plankton nets, and later stages directly from plankton samples. He pointed out that the most important diagnostic feature of the larvae is the characteristic pigmentation and described briefly the yolk-sac, larval and juvenile stages mainly in respect of their pigment pattern and the development of the fins. As has already been pointed out, it was found necessary to describe the development in greater detail to ensure reliable identification and separation from the larvae of *Engraulis capensis* and *Etrumeus teres*.

MATERIAL AND METHODS

Figure 1 shows the area off the South West African coast where pilchard larvae were collected between August and December 1972, at the start of the SWAPELS programme. Material was obtained by the R.S. *Sardinops* of the Sea Fisheries Branch, in monthly plankton samples at fixed stations between Cape Frio and Hollam's Bird Island. A detailed description of SWAPELS methods is given by King & Robertson (1973). Bongo nets of 57 cm and 18 cm diameters, with mesh sizes of 0,940 mm and 0,300 mm respectively, were fished in oblique tows from the surface to a depth of 50 metres at each station. Pilchard larvae sorted from the plankton were preserved in 5 per cent formalin. Yolk-sac larvae were not obtained in the plankton hauls, but information regarding these early stages was obtained by hatching, in the laboratory, fertilized pilchard eggs taken at sea and identified from the descriptions of *Sardinops* eggs (Davies 1954; Baker 1972). The larvae reared in the laboratory did not survive beyond the yolk-sac stage.

A total of 164 larval and juvenile specimens from the study area were examined in detail for pigmentation, fin development, fin position relative to myotomes (and relative to vertebrae in metamorphosing and early juvenile specimens) and changes in body proportions during development. Juvenile material was supplemented by specimens from Cape waters in order to document the development of scale cover.

In each specimen fin rays were counted and, in addition, the total number of myotomes, the number of myotomes from cleithrum to pelvic fin, cleithrum to dorsal fin, cleithrum to anal fin and end of dorsal fin to the origin of the anal fin were determined. Myotome counts were made from the first complete myotome behind the cleithrum to the myotome immediately preceding the fin concerned, this being taken at the extreme dorsal portion of the myotome in the case of the dorsal fin and the extreme ventral portion in the case of the anal and pelvic fins. However, since most earlier studies on clupeid larvae (e.g. Ford 1930) cleared larval specimens and stained bones using alizarin in order to relate fin position to vertebrae, 24 specimens between 18,8 mm s.l. and 38,58 mm s.l. were cleared and stained (Hollister 1934) so that fin movements at metamorphosis in *S. ocellata* could be compared with the changes described for other species during this stage of development.

Measurements of head length, eye diameter, snout length, body depth (at the base of the pectoral fin) and lengths to dorsal, anal and pelvic fins were related to standard length. In considering metamorphosis of the larvae it was found that measurements from snout to dorsal and anal fins (as used by Lebour 1921 and Baker 1972) did not reflect clearly the changes in fin position evident in myotome (and vertebral) counts. This was found to be attributable to the increased rate of head growth and therefore measurements between the cleithrum and dorsal fin and cleithrum and anal fin were used instead. The measurements in the figures refer to standard length.

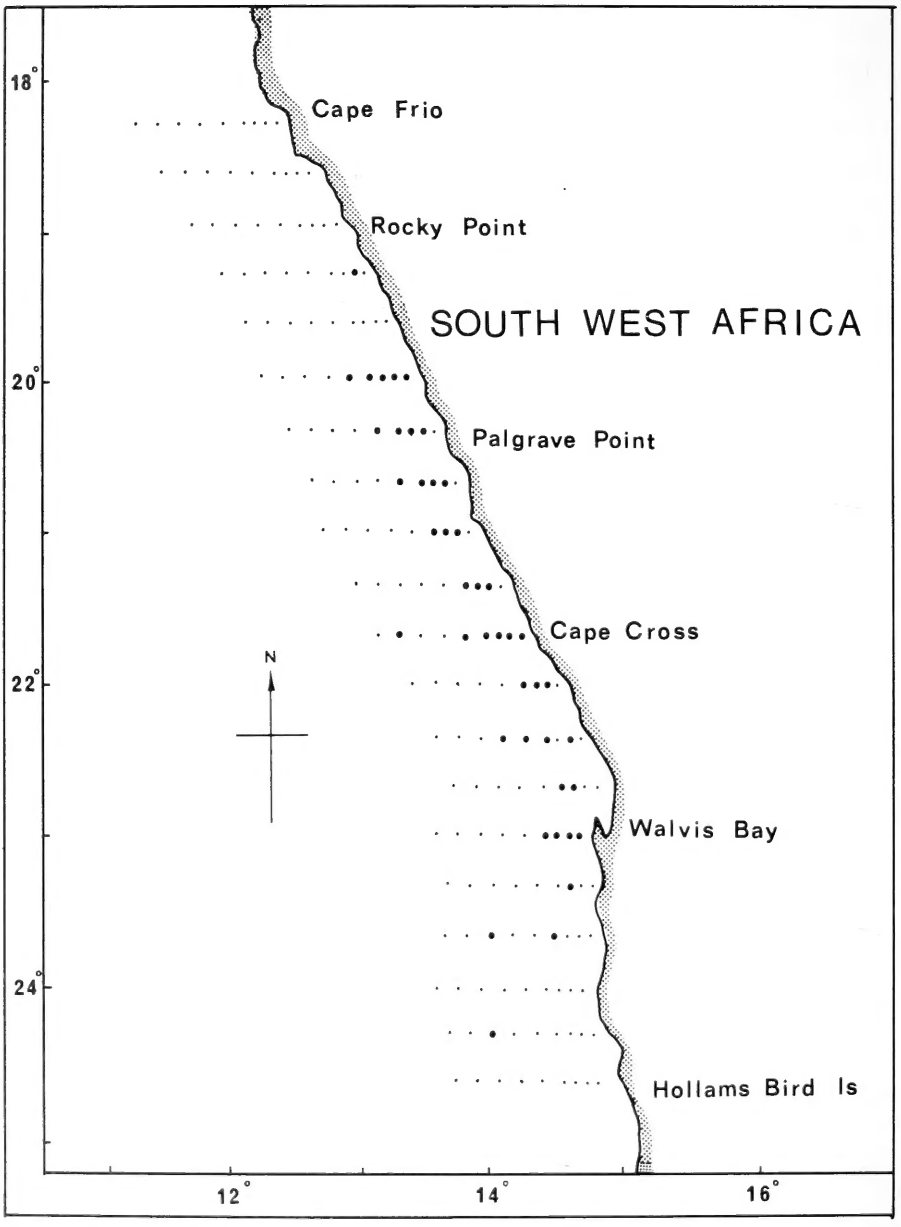

Fig. 1. Map of South West African coast, showing the grid (small dots) of the SWAPELS programme. Large dots indicate stations at which *Sardinops ocellata* larvae were obtained.

GENERAL DESCRIPTION

Sardinops ocellata larvae pass through three stages of development after hatching and before attaining the juvenile stage. These stages are the yolk-sac stage which may be regarded as a continuation of embryonic development subsequent to hatching; the larval stage; and the metamorphic stage when the larvae undergo changes and begin to acquire characteristics of the adult. The juvenile stage is that in which the fish possess all the basic adult characteristics.

YOLK-SAC STAGE LARVAE (Figs 2–3)

The newly hatched larvae of *S. ocellata* are 2,75–2,95 mm in length. The head, with unpigmented eyes and undeveloped mouth, is flexed downward over the prominent yolk-sac. This yolk-sac is segmented and has a single spherical oil globule which is posterior in position. Both yolk-sac and oil globule are devoid of pigmentation. The yolk-sac measures 0,8 × 0,6 mm in the newly hatched stages but diminishes in size with utilization of the yolk material. The dorsal, caudal and anal fin folds are broad and continuous at this stage, and the anus is situated closer to the posterior end of the body than to the head. The distance from snout to anus is 82–87 per cent of notochordal length in newly hatched larvae.

Even in newly hatched larvae most myotomes (44–47) are clearly defined and only the most posterior ones are not very distinct. The end of the vertebral column is straight. Pigmentation in newly hatched *S. ocellata* is typical of *Sardinops*, and indeed of most clupeid larvae (Lebour 1921; Miller 1952; Orton 1953; Baker 1972) in that it consists of a few scattered melanophores on the dorsal surface of the head and a row of expanded, finely branched melanophores on either side of the dorsal fin fold (Fig. 2A). During the period of utilization of the yolk-sac this dorsal pigmentation migrates ventrally as illustrated in Figure 2B. The melanophores in the posterior part of the body are the first to complete the ventral migration (Fig. 3A), and this trend continues anteriorly until all the melanophores, except those on the head, have attained the ventral position (Fig. 3B).

Soon after the end of pigment migration the arrangement of the melanophores is as follows:

(i) a few scattered melanophores on the dorsal surface of the head;
(ii) a single large melanophore at the base of the pectoral fin;
(iii) two (or occasionally three) elongated melanophores mid-ventrally, anterior to the pectoral fin;
(iv) six to seven pairs of slightly elongated melanophores along the dorsal edge of the anterior half of the gut, i.e. along the ventral edges of the myotomes, on either side of the body;
(v) a double row of four to five alternating pairs of elongate melanophores along the ventral surface of the gut, extending from the position of the swim-bladder posteriorly, to the anus.

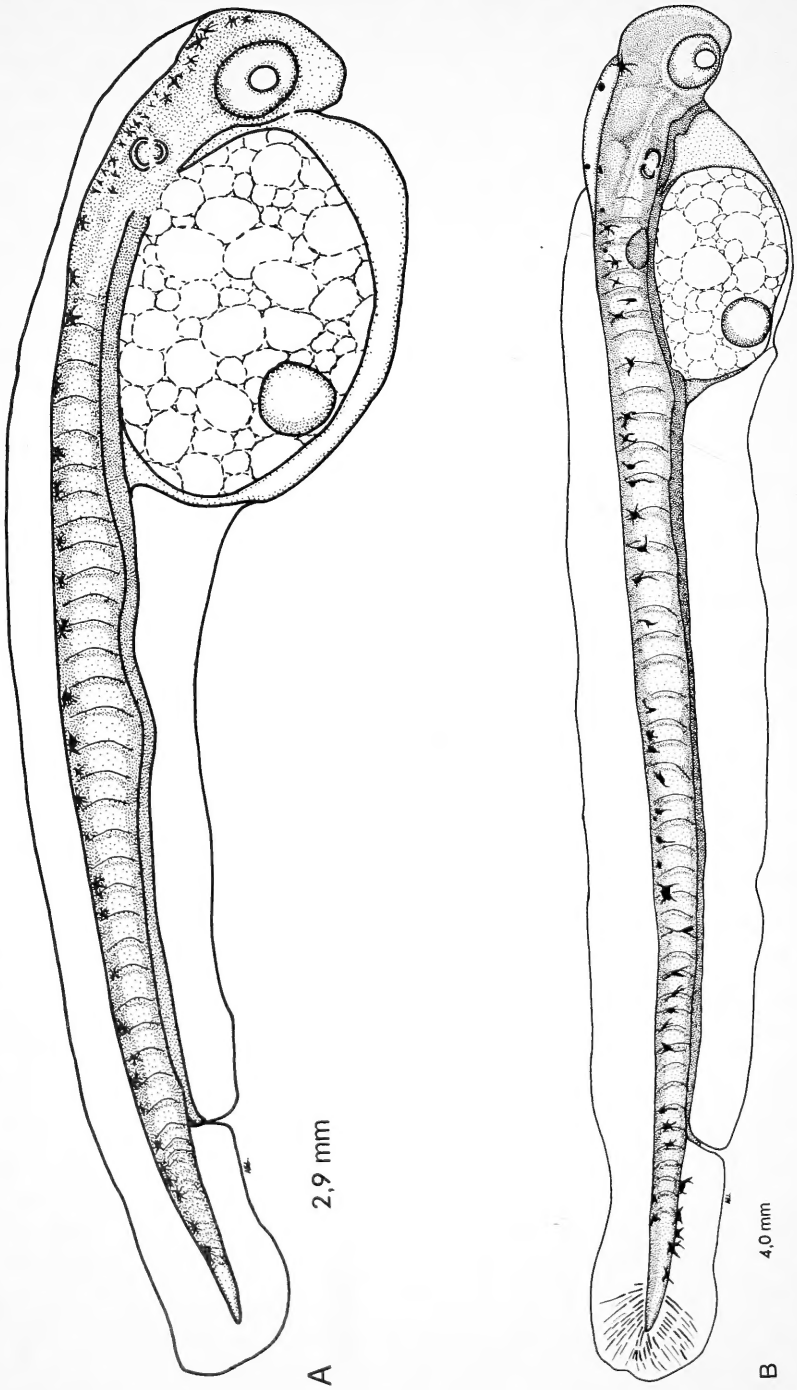

Fig. 2. Yolk-sac stage larvae. A. Newly hatched yolk-sac stage showing dorsal pigmentation. B. More advanced yolk-sac stage (2–3 days old) with pigment migrating ventrally.

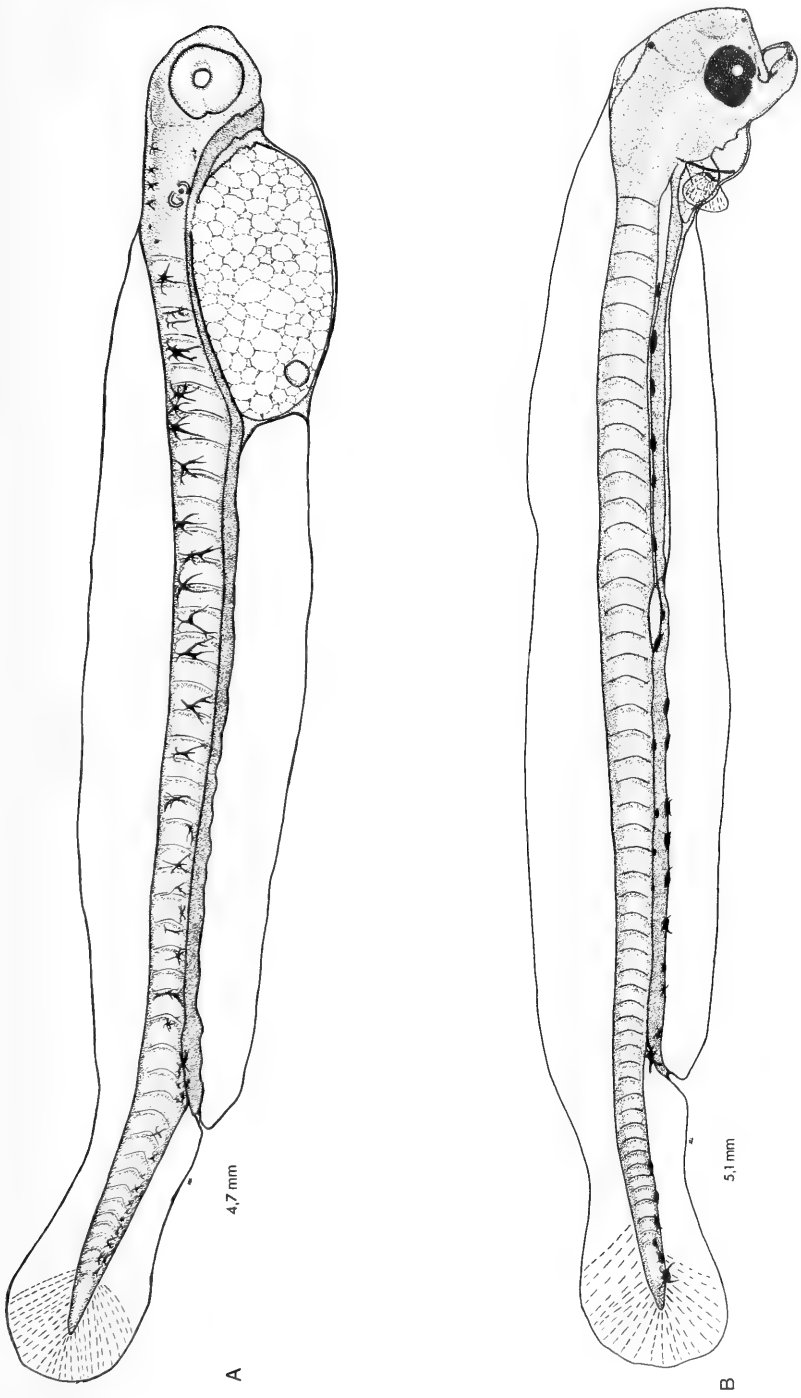

Fig. 3. Yolk-sac stage larvae. A. Stage with pigment migration well advanced (3–4 days). B. End of yolk-sac stage (5–6 days) with pigment migration complete and eye pigmented.

(vi) a few (4–5) small melanophores along the ventral edge of the myotomes, above the posterior part of the gut (these melanophores are not superficial, but visible through the muscle tissue of the myotomes);
(vii) a single very prominent melanophore on the dorsal part of the gut, in the position where the gut curves ventrally to the anus; and
(viii) two groups of melanophores situated mid-ventrally along the tail region of the body, 4–5 lying just dorsal to the base of the anal fin (once this is developed) and 5–7 close to the tip of the tail and associated with the caudal lepidotrichia once these are formed.

A small pectoral bud develops in larvae of about three days and length 4,0 mm and the first pigmentation of the eye commences a little later, at 5,0 mm notochordal length (n.l.). By the time of completion of pigment migration (6-day-old larvae, 5,1 mm n.l.) the yolk-sac is almost entirely used up and the head is no longer flexed. Up to this stage the gut is simple, comprising a long narrow tube which, towards the end of the yolk-sac stage, becomes slightly wider over its posterior half. Mid-way along the gut and in the position of the 17th–18th myotomes a small inconspicuous swim-bladder is formed.

The pectoral fins also show a slight further development by the end of the yolk-sac stage in that they are no longer only minute buds but have well-formed blades. The dorsal, caudal and ventral fin folds are still fairly broad and continuous at this stage, with a slight constriction just before the caudal region, especially in the dorsal fin fold. The caudal fin fold is the only region to have developed lepidotrichia at this stage. At the end of the yolk-sac stage all myotomes are visible and number between 48 and 50, with 38 to 40 myotomes preceding the anus.

LARVAE (Fig. 4)

The end of yolk-sac utilization marks the beginning of a period of larval development (5,5 mm n.l.–22 mm s.l.) during which the major changes taking place are in body shape and gradual fin formation. The body becomes elongated, the larvae having a characteristic very slender appearance. The continuous fin fold which was broad during the yolk-sac stage diminishes progressively and has marked constrictions before the caudal region. The ventral fin fold, anterior to the anus, becomes obliterated with the increased development of the gut, presumably coincidental with the commencement of feeding in the larvae.

The gut is narrow and straight in the anterior region, curving slightly ventrally for a short distance in the mid-body region, below the swim-bladder. Posterior to the swim-bladder the gut is wider in diameter and the wall is thicker than in the anterior part. Some authors (e.g. Baker 1972) have described this posterior region of the gut as a convoluted tube. Examination and dissection of the gut in this region have shown, however, that in *S. ocellata* the gut is in fact a straight tube with the wall slightly constricted at close and regular intervals. Corresponding to these constrictions are thickened areas of the wall which protrude into the lumen of the gut. These projections presumably form what

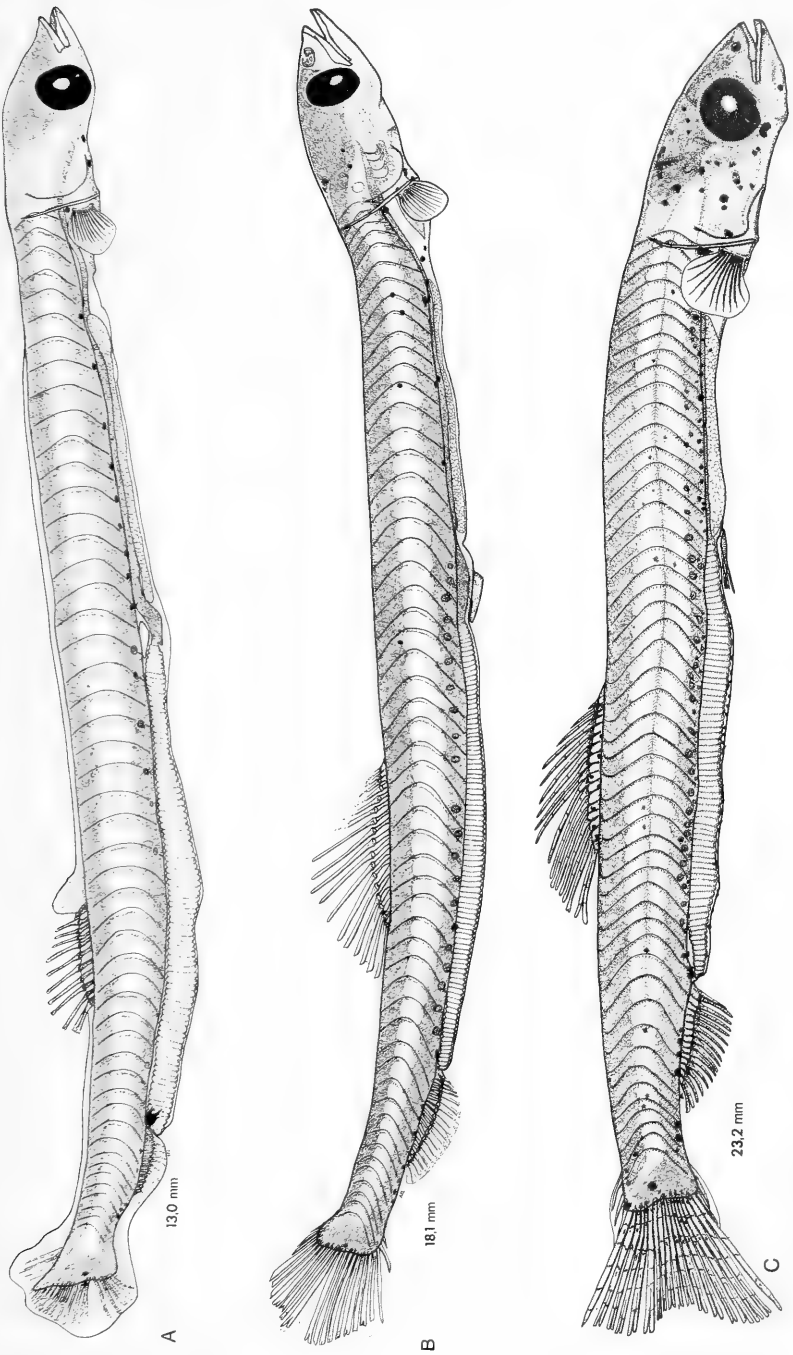

Fig. 4. Larval stages. A. Early phases of fin development. B. Fin development well advanced and bud of pelvic fin present. C. Fin development almost complete (except for pectoral fin rays); also increased amount of pigment present on head and body and myotomes extending slightly ventrally over the gut.

D'Ancona (1931) referred to as the spiral valve of the posterior intestine of larval clupeids. These thickened areas give the gut a striated appearance which we believe has led some authors to regard the gut as convoluted.

In larvae of *S. ocellata* the head is slightly elongated and the snout pointed. This snout is 3,5–4,6 per cent standard length (s.l.) and slightly longer than the diameter of the eye. The post-orbital distance (posterior edge of the eye to the cleithrum) is greater than the snout length. The bones of the head (not described here in any detail) are thin and the lobes of the brain are clearly visible through them. The jaws are well formed from an early stage (5–6 mm n.l.) and in larvae from about 15 mm s.l. the maxilla reaches to the anterior third of the eye. A pair of nostrils, with a complex internal structure, is clearly visible in larval stages and becomes increasingly developed through to the juvenile stage.

Flexion of the notochord occurs between 7,4 mm n.l. and 11,3 mm s.l. Fin development progresses fairly rapidly in the larvae from about 9,0 mm s.l., when the first rays appear in the dorsal fin fold followed by the first caudal rays at 10,5 mm s.l. and the first anal rays at 11,5 mm s.l. Prior to this only lepidotrichia were present in the unpaired fins and in the pectorals. The latter, however, do not advance beyond this condition, apart from an increase in size, until late in larval life. Subsequent development of the dorsal and anal fins proceeds apace until 16–17 rays are present in each fin prior to the commencement of metamorphosis of the larvae at 22 mm s.l. Additional rays ossify in the anterior regions of these fins during metamorphosis so that the full complement of dorsal rays (18–20) is reached by 26 mm s.l. and the anal is complete with 18–20 rays by 29 mm s.l. The last dorsal and anal rays are double from about 19 mm s.l., and, in addition, the second last anal ray is very deeply branched (almost from its base). The last two anal rays are slightly elongated and form a 'finlet' which is characteristic of *Sardinops* (Svetovidov 1952: 189). Ossification of the caudal rays which commenced at 10,5 mm s.l. progresses rapidly so that by 13,0 mm s.l. 13–15 rays are visible, although not completely developed. At this stage the ventral part of the caudal fin is more advanced than the dorsal part. By 18,1 mm s.l. (Fig. 4B) all 19 primary caudal rays are formed, and some of them are slightly branched. Some secondary rays are also present. By 20,0 mm s.l. the branching of the 17 inner primary caudal rays is appreciable and from 23,0 mm s.l. the caudal fin rapidly assumes its deeply forked shape (Fig. 5A). The pelvic fin appears as a small bud at 18,0 mm s.l. and its first rays start to develop at 22–23 mm s.l. The pelvic fin with its full complement of 8 rays, of which all except the anterior ones are branched, is fully formed by 26,0 mm s.l. The pectoral fin, in which lepidotrichia formed at a very early stage, is the last of the fins to complete development. The fin rays form only from 23,0 mm s.l., although these are then laid down rapidly so that 15–16 are present by 29 mm s.l. and the full complement of 18 rays is reached by 33 mm s.l. Details of fin ray development in the paired and unpaired fins are given in Table 1.

As is evident from Figure 4A–C little change occurs in the general appearance of the larvae after the end of the yolk-sac stage until 20–22 mm s.l., apart

TABLE 1

Development of fin rays in *S. ocellata* larvae between 8 mm and 33 mm standard length

Size range (mm)	*Mean* (mm)	*No.*	*Dorsal rays*	*Anal rays*	*Caudal rays*	*Pectoral rays*	*Pelvic rays*
8,0– 8,9	8,90	1	5–6	†	†	†	—
9,0– 9,9	9,55	2	9	†	†	†	—
10,0–10,9	10,40	4	9–12	0– 4	†	†	—
11,0–11,9	11,65	6	10–14	5– 8	5– 9	†	—
12,0–12,9	12,53	7	10–14	7– 9	12–15	†	—
13,0–13,9	13,45	22	11–16	8–10	13–15	†	—
14,0–14,9	14,41	12	12–16	10–13	15–17	†	—
15,0–15,9	15,61	9	13–16	13–15	16–18	†	—
16,0–16,9	16,18	1	15	13	18	†	—
17,0–17,9	17,50	2	15	14–16	18–19	†	—
18,0–18,9	18,51	9	15–16	15–17	½+ 19 +½	†	bud
19,0–19,9	19,53	15	15–17	15–17	1+ 19 +½	†	bud
20,0–20,9	20,27	8	16–17	15–17	2+ 19 +1	†	bud
21,0–21,9	21,60	3	16–17	15–17	2+ 19 +1	†	bud
22,0–22,9	—	0	—	—	—	—	—
23,0–23,9	23,41	3	17–18	17	3+ 19 +2	3–5	4–5
24,0–24,9	24,70	3	18	17	5+ 19 +4	6–8	6–7
25,0–25,9	25,06	1	18	17	5+ 19 +4	7	7
26,0–26,9	26,29	2	18–20	17–18	6+ 19 +5	10–12	8
27,0–27,9	27,27	1	19	17	6+ 19 +5	11	8
28,0–28,9	28,58	1	20	17	7+ 19 +5	15	8
29,0–29,9	29,59	3	19–20	18–20	8+ 19 +7	15–16	8
30,0–30,9	30,97	1	20	18	8+ 19 +7	17	8
31,0–31,9	31,33	2	19–20	19–20	8+ 19 +7	17	8
32,0–32,9	—	0	—	—	—	—	—
33,0–33,9	33,67	2	18–19	19–20	8+ 19 +7	18	8

† indicates lepidotrichia present, but no rays.

Caudal fin counts, from 18 mm s.l. are preceded and followed by additional counts; these indicate the number of secondary caudal rays on the dorsal and ventral parts of the caudal fin respectively.

from the fin development described above. The dorsal and anal fins are situated far posteriorly on the long slender larvae. The origin of the dorsal fin occurs above the 29th myotome when thickening first appears in the dorsal fin fold, but lies over myotomes 23–26 once the dorsal fin nears completion, since the anterior rays are the last to develop. The anal fin origin lies below 39–41 in very young larvae and below myotomes 36–38 in older larvae. The end of the dorsal fin and origin of the anal fin are separated by 6–8 myotomes. At the time when the pelvic fin first forms it occupies a position corresponding to the 15th, 16th or 17th myotome, and is situated well in front of the origin of the dorsal fin. The pelvic fin and the origin of the dorsal fin are separated by 8–10 myotomes prior to metamorphosis.

The pattern of pigmentation of the larvae shows little change during larval development and remains basically that attained at the end of the yolk-sac stage. However, there is an increase in the number of melanophores contributing to this pattern. The 6–7 pairs of elongate melanophores along the ventral edge of the myotomes, adjacent to the anterior half of the gut increase

to 9–11 pairs at 11 mm s.l. and become even more numerous, but less elongate, at the end of the larval stage (Fig. 4C). There is a similar increase in the number of mid-ventral melanophores on the posterior half of the gut and the number of embedded melanophores above the posterior half of the gut increases to 10 pairs at 11 mm s.l. and there are as many as 17 pairs of these melanophores at 23 mm s.l. with additional smaller melanophores scattered in between them. Moreover, at the end of the larval stage, there is some pigmentation of the caudal fin. This comprises melanophores formed along the edges of the rays and arranged to form transverse rows, parallel to the outline of the caudal fin (Fig. 4C). A few melanophores also develop on the proximal radials of the dorsal fin base. From 17–18 mm s.l. a few isolated melanophores appear mid-laterally along the body and these gradually become more numerous. From the time the pelvic rays commence development there is usually a single large melanophore just anterior to the base of the pelvic fin.

METAMORPHIC STAGE LARVAE (Fig. 5A)

From 22 mm s.l. the larvae of *S. ocellata* undergo marked changes in body proportions and pigmentation, which result in larvae of 22–32 mm s.l. being termed metamorphic stage larvae. The various body proportions which were studied for the complete developmental series are illustrated in Figures 6–10. These graphs show that the body proportions all remain constant relative to standard length until the larvae attain the size of 22 mm s.l., at which stage changes in body depth, head length and in the position of the dorsal, anal and pelvic fins commence. Some of these characters show further changes at 33–36 mm s.l., thus indicating the final transition to the juvenile condition.

The onset of metamorphosis is indicated by changes in head growth and body depth and in the commencement of the ventral growth of the myotomes. During the larval stage the head length increases constantly in relation to the standard length. At the start of metamorphosis, however, the rate of increase of the head length accelerates (Fig. 6). The increase in body depth (measured as depth at the pectoral base) follows the pattern of change in head growth but to a more marked degree (Fig. 7). In addition to this overall increase in body depth in larvae of more than 22 mm s.l., it may be seen from Figure 4C that the myotomes at this stage start to grow ventrally so that they begin to cover the gut. At 23 mm s.l. the myotomes merely obscure the dorsal edge of the gut, but their expansion becomes more marked, first over the anterior half of the gut and later extending also over the posterior half of the gut, so that by 29,5 mm s.l. the gut is almost entirely covered by myotome tissue, except for a small area close to the anus. At this stage, however, they have not yet fused ventrally. In larvae of 30–31 mm s.l. most myotomes anterior to the pelvic fins are fused mid-ventrally and the first two or three scutes have developed in the most anterior mid-ventral region.

In common with the development of other clupeids, one of the most marked features of metamorphosis in *S. ocellata* is the alteration in the position

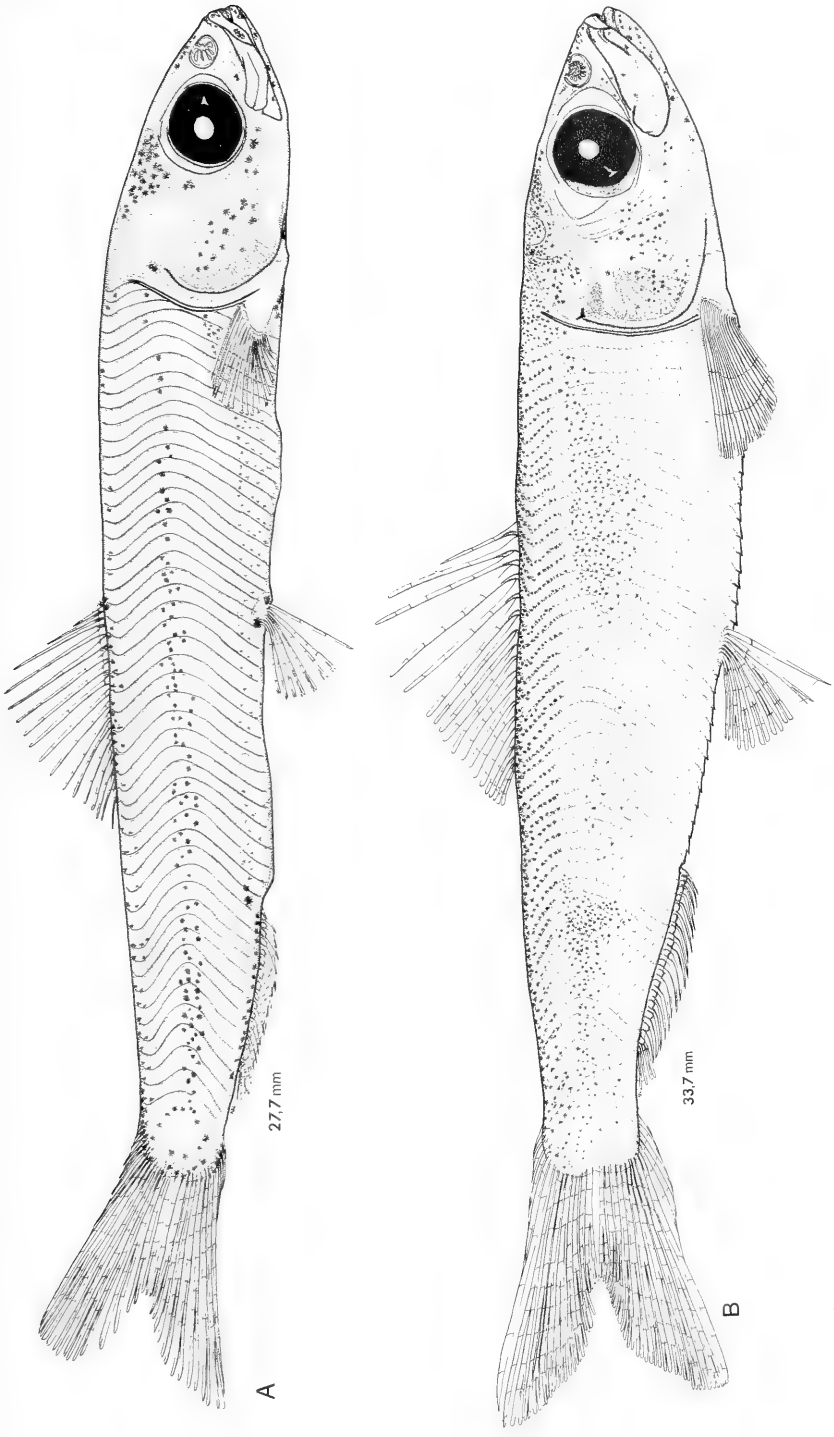

Fig. 5. A. Metamorphic stage larva showing alteration in fin positions. B. Early juvenile stage with fin migration complete and a considerable amount of dorsal pigmentation.

of the dorsal and anal fins which occurs during this stage. Instead of the steady rate of increase shown in the distances from cleithrum to dorsal fin and cleithrum to anal fin (Figs 8–9) during the larval stage, metamorphic stage larvae show a slight decrease in cleithrum to dorsal fin distance and only a very slight continued increase in cleithrum to anal fin distance. These changes in the pattern of growth occur in larvae of 24–33 mm s.l. They can be attributed to the anterior migration of the dorsal and anal fins, relative to myotomes and vertebrae. Most authors (Lebour 1921; Ford 1930; Ahlstrom 1943, 1968) documented fin migration relative to vertebrae, but others (Schnakenbeck 1929; Baker 1972) used myotomes. Attempts to stain vertebrae in specimens 18–20 mm s.l. were not satisfactory as the most anterior vertebrae did not take up the alizarin dye, although older stages stained satisfactorily. This precluded the determination of fin position relative to vertebrae in pre-metamorphic larvae. For this reason fin position relative to myotomes was used as this could be determined through-

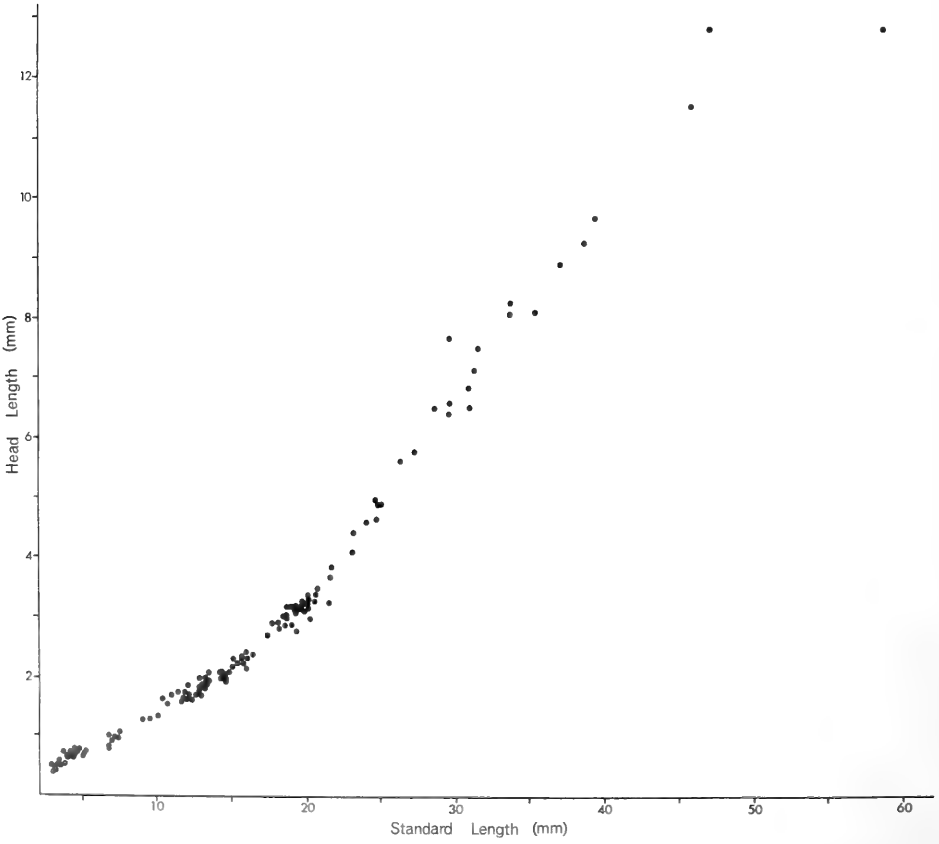

Fig. 6. Graph of increase in head length with increase in standard length. Note acceleration of head growth from 22 mm s.l.

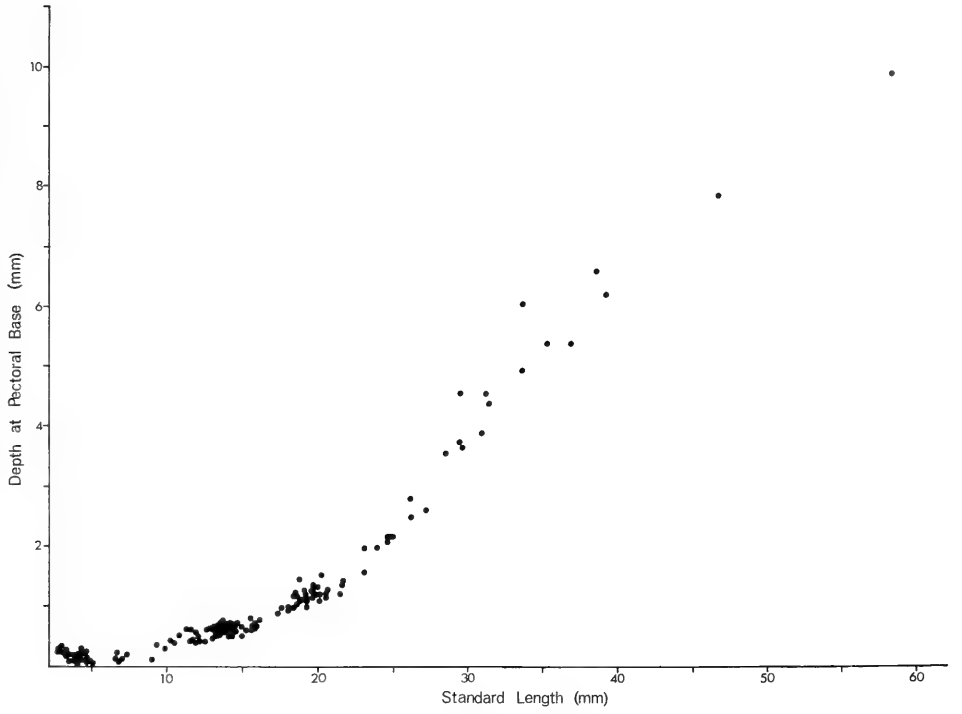

Fig. 7. Graph of body depth (as depth at pectoral base) versus standard length. Initial decrease (2–5 mm s.l.) is due to yolk-sac utilization. Note increased rate of deepening of body from 23 mm s.l.

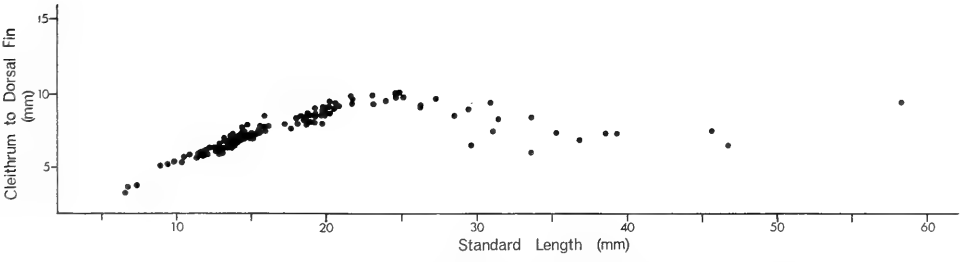

Fig. 8. Graph of distance from cleithrum to dorsal fin versus standard length, showing a decrease during the phase of anterior migration of the dorsal fin.

out development. However, to permit comparison of fin migration in *S. ocellata* with that which occurs in other species of *Sardinops*, fin positions relative to vertebrae in late larval and metamorphic stages are given in Table 2. Some differences in counts (usually of 1–3) are evident between the two methods and these differences can be attributed to two factors. Firstly, only complete myotomes posterior to the cleithrum were counted and this omits 1–2 incomplete myotomes at the anterior region of the body. Secondly, vertebral counts were taken at positions vertically below or above the fins concerned, but myotome counts at dorsal and ventral edges adjacent to the fin origins. The <-shape of the myotomes makes a further difference of 1–2 in the counts as the anterior region of the myotome corresponds to a vertebral centrum 1–2 centra anterior to the one below the posterior part of the myotome. (This difference is slightly greater in older specimens, e.g. 38,58 mm juvenile.) However, as the two methods reflect similar changes during metamorphosis, myotome counts can be accepted as a reliable method of documenting fin migration.

TABLE 2

Fin position relative to myotome (M) and vertebral (V) counts in late larval and metamorphic stages of *S. ocellata*.

Standard Length (mm)	*Dorsal Fin*		*Anal Fin*		*Pelvic Fin*	
	M	V	M	V	M	V
18,80	25	—	38	—	—	—
19,00	24	—	37	—	—	—
19,22	25	—	38	—	17	—
19,63	24	26	37	39	16	18
19,71	24	—	37	—	15	—
19,87	25	26	37	39	15	17
19,96	24	—	36	—	15	—
20,54	24	—	38	—	16	—
20,70	23	—	38	—	15	—
21,68	22	24	36	38	15	17
23,16	23	25	36	38	16	18
24,64	22	24	36	38	16	17
24,64	22	24	36	38	15	17
24,81	23	26	36	39	16	18
25,06	21	25	35	38	15	17
26,29	21	24	35	37	16	17
26,29	21	23	35	37	16	17
28,58	19	22	34	36	16	18
29,56	19	22	33	36	17	18
29,56	13	15	33	36	16	18
29,64	19	22	33	36	17	18
30,97	17	19	33	36	15	17
31,20	14	17	31	34	16	19
38,58	13	17	31	36	16	20

As is evident from Figure 11 the number of myotomes preceding the dorsal fin (open triangles) is 22–25 in larvae of 20–23 mm s.l., but from 24 mm s.l. the number decreases sharply due to the forward migration of the fin. This continues until the fin reaches the position of myotomes 10–13 at 33–35 mm s.l. Migration of the dorsal fin ceases at this size, having covered the extent of 10–12 myotomes. Migration of the anal fin (Fig. 11—closed triangles) is not as extensive as that of the dorsal fin, but nevertheless is quite considerable. The origin of the anal fin shifts from the position of myotomes 36–38 at 20–25 mm s.l., to reach myotome 31 at 31–33 mm s.l.—thus involving a shift over 5–7 myotomes. At the end of migration the end of the dorsal fin and the origin of the anal fin are separated by five myotomes. Once the larvae attain the size of 33–35 mm s.l. the increases in the distances from cleithrum to dorsal fin and cleithrum to anal fin resume their pre-metamorphic rates (Figs 8–9). This can be regarded as an indication of the end of the metamorphic stage and the attainment of the juvenile stage.

During metamorphosis the rate of increase in distance from cleithrum to pelvic fin diminishes for a short growth interval (23–26 mm s.l.) (Fig. 10). This cannot be explained by any forward shift in pelvic fin position relative to myotomes as the fin retains its position at myotomes 15–17 (or vertebrae 17–18) as in the late larval stages when the pelvic bud first appeared. However, later in development the pelvic fin shifts posteriorly relative to vertebrae (but not relative to myotomes) and comes to lie vertically below vertebrae 19–20. With the migrations of the dorsal and pelvic fins, their positions relative to one

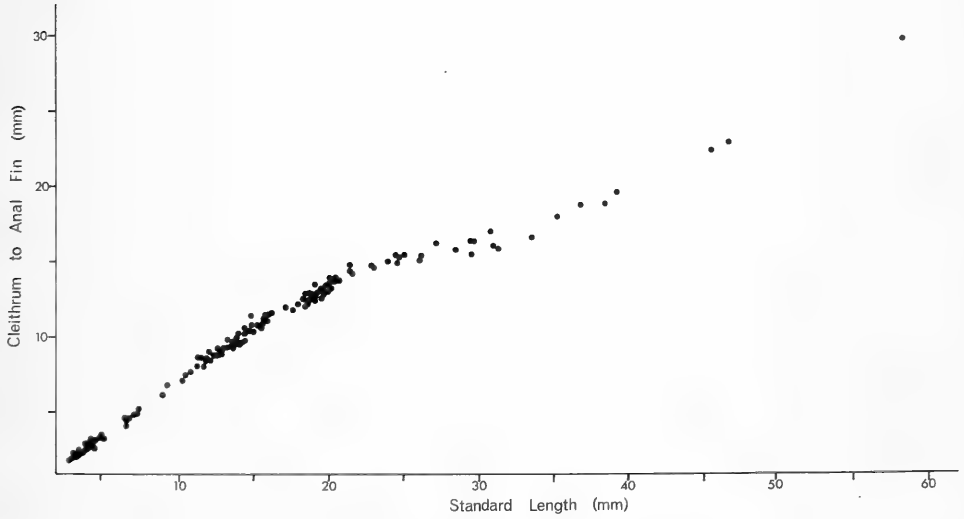

Fig. 9. Graph of distance from cleithrum to anal fin versus standard length, showing reduction in rate of increase whilst anal fin undergoes anterior migration between 23 mm and 33 mm s.l.

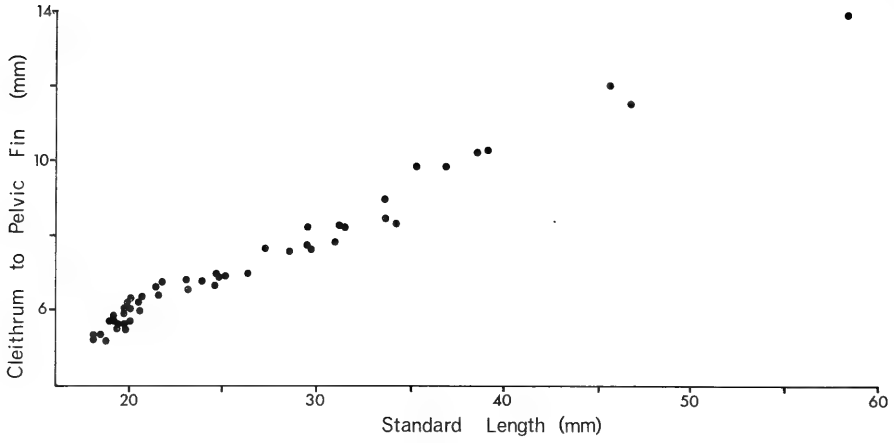

Fig. 10. Graph of distance from cleithrum to pelvic fin versus standard length.

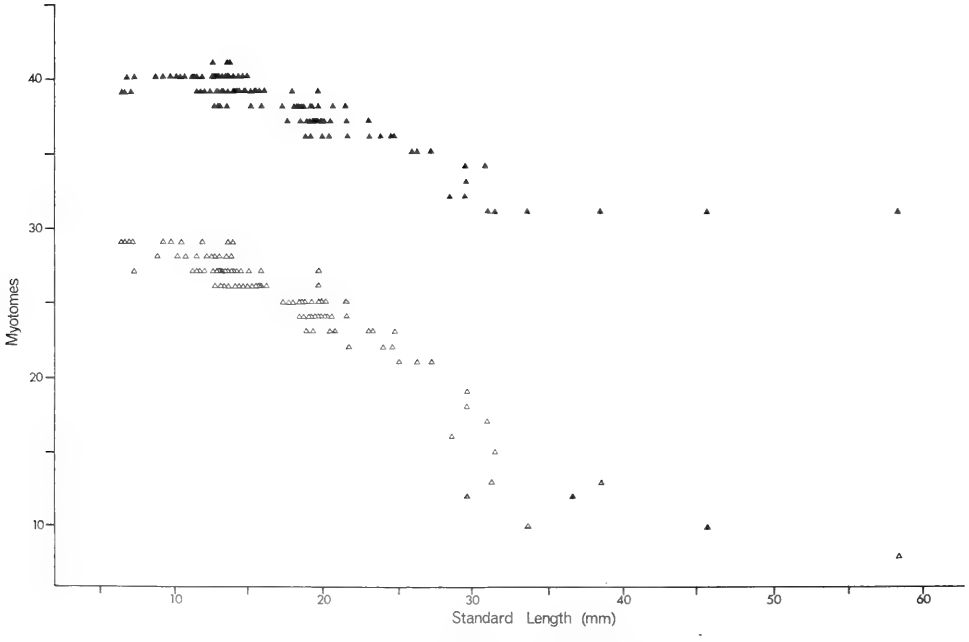

Fig. 11. Graph of the number of myotomes from cleithrum to anal fin (closed triangles) and cleithrum to dorsal fin (open triangles) indicating the anterior migration of the fins from 23 mm s.l. The gradual decrease in number of myotomes to 23 mm s.l. is due to development of additional fin rays.

another alter and instead of the pelvic fin lying anterior to the dorsal origin, it lies vertically below the dorsal origin at 27–29 mm s.l. and by 32–33 mm s.l. the pelvic origin corresponds to a position below the middle of the base of the dorsal fin as is the case in adults of the species.

Throughout the larval stage both pectoral and pelvic fins lack ossified rays. Ossification of rays in the paired fins commences in larvae over 22 mm s.l., i.e. at the onset of the metamorphic stage. By the time the juvenile stage is reached fin ray development is complete in paired and unpaired fins (Table 1).

Pigmentation also changes quite markedly during the metamorphic stage. With the ventral growth of the myotomes, much of the larval pigment pattern near the gut is obliterated or lost. It is replaced by pigment spots which form beneath the myotomes, along the dorsal surface of the gut (? on the peritoneum) and which are partially visible through the myotomes. The melanophores which first appeared in larvae of 17–18 mm s.l. along the mid-lateral sides of the body, become far more numerous, especially from 25–26 mm s.l., so that the larvae develop a fairly dark mid-lateral band of pigment (Fig. 5A). Furthermore, a large number of melanophores appears along the dorsal surface of the body. These are stellate melanophores and are arranged in lines which follow closely the edges of the myotomes, with a few melanophores scattered in between. In spite of the appearance of this quite considerable amount of pigment on the dorsal surface of the body, which might be considered an approach towards the adult coloration, larvae of 30–32 mm s.l. are still predominantly pale, as were the earlier larvae. Pigmentation on the head also increases, particularly on the dorsal surface of the head, in the region of the parietals, and there are scattered melanophores on the opercular and circumorbital bones.

Scale development commences towards the end of the metamorphic stage. Since few specimens of 30–45 mm s.l. were available from the main study area, the material was supplemented with specimens of that size range used in the study by Davies (1954) and the 1950–67 egg and larval survey in Cape waters (Haigh 1972: 49, 66, fig. 9). Scales are first formed at 30 mm s.l. These develop on the caudal peduncle and are arranged in an anteriorly pointing 'V' pattern. The scale-covered area enlarges rapidly so that it reaches the area above the anal fin by 31,5 mm s.l. and by 33 mm s.l. all of the body posterior to the mid-region of the dorsal fin base is covered. By 36 mm s.l. scale cover reaches anteriorly to the cleithrum, but anterior to the dorsal fin the scales do not overlap. Scale development is completed early in the juvenile stage.

JUVENILE STAGE (Fig. 5B)

The juvenile stage is that in which the metamorphic changes are complete and the young fish resembles the adult. As can be seen from Figure 5B the juvenile fish resembles the adult in shape; in addition to the pigment which appeared during metamorphosis, the dorsal part of the body is covered with small closely arranged melanophores, which give the fish the dark dorsal and light ventral appearance of the adult; the head is extensively pigmented, and

on the opercular bones the radial ridges are clearly visible; the entire body is covered with scales and ventral scutes are present anterior to and behind the pelvic fins; the last two anal rays are distinctly longer than the more anterior rays, and the pelvic and pectoral fins are well developed.

As juvenile development proceeds pigmentation on the dorsal area of the body increases further, and silvery pigment develops on the lateral and ventral parts of the body from about 37 mm s.l. and the row of dark pigment spots which is characteristic of adult pigmentation forms from 45 mm s.l.

DISCUSSION

In yolk-sac and larval stages of development *Sardinops ocellata* follows closely the pattern of development described for *S. caerulea* (Miller 1952), *S. neopilchardus* (Baker 1972) and *S. melanosticta* (Uchida 1958). However, it is evident that some differences do occur in the development of these species, during the later phases of larval life. These differences are in the number of myotomes or vertebrae over which the fins migrate and also the relative sizes at which the changes occur. These differences are summarized in Table 3.

TABLE 3

Comparison of late stages of development in species of *Sardinops*

	ocellata	*caerulea* (Ahlstrom 1968)	*neopilchardus* (Baker 1972)	*melanosticta* (Uchida 1958*)
Posterior migration of pelvic fins	2 vertebrae	3 vertebrae	5 myotomes	?
Final position of pelvic fins	18–20th vertebrae	22nd vertebra	22nd myotome	?
Anterior migration of dorsal fin	10–12 myotomes	10 vertebrae	10–12 myotomes	?
Final position of dorsal fin	10–13th myotomes	18th vertebra	14–16th myotomes	?
Metamorphic stage	22–32 mm s.l.	25–40 mm s.l.	25–35 mm s.l.	? 30–40 mm s.l.
Juvenile	33 mm s.l.	40 mm s.l.	35 mm s.l.	? 42 mm s.l.

* Text in Japanese, information from figures and legends only.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype
SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

ELIZABETH LOUW & M. J. O'TOOLE

LARVAL DEVELOPMENT OF *SARDINOPS OCELLATA* (PISCES : CLUPEIDAE)