Description and ontogeny of young *Stolephorus baganensis* and *Thryssa kammalensis*, two Engraulididae from Peninsular Malaysia

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The morphology of the digestive system was useful to distinguish the larvae of *Stolephorus baganensis* and *Thryssa kammalensis* before the full development of their dorsal and anal fins. The relative positions of these fins, the length of the anal fin, and body depth, were good criteria for identifying individuals >10·0 mm L_S. For both species, the relative growth of the ten morphometric characters studied was best explained by linear piecewise regressions indicating inflection in allometry at specific standard lengths. Most of these sudden changes in growth rate occurred between 6·9 and 10·0 mm L_S for *S. baganensis* and between 5·8 and 8·9 mm L_S for *T. kammalensis*. Double-centred principal component analysis (PCA) confirmed important changes in the external morphology of both species during this transition period. Prior to this period, the main parameters characterizing the global morphological changes of both species were the length and position of dorsal and anal fins whereas they were body depth and eye diameter (only in *S. baganensis*) for larger specimens. Complete development of scales did not appear as a suitable criterion to define the end of the larval period, which, instead, was set at the size at which larvae presented an adult-like pigmentation (respectively 35·0 mm L_S and 55·0 mm L_S in *S. baganensis* and *T. kammalensis*).   © 2000 The Fisheries Society of the British Isles

Key words: *Stolephorus baganensis*; *Thryssa kammalensis*; ontogeny; description; tropics.

INTRODUCTION

Temporal occurrence, spatial distribution, and diet are commonly associated in studies on the ecology of fish larvae and juveniles while taxonomic identifications are generally treated as a separate subject. However, new approaches (Sagnes *et al.*, 1997; Gisbert, 1999) use the morphological characteristics of young fish not only for taxonomic purposes, but also as a tool for a better understanding of the relationships between ontogeny and ecology.

The allometric growth of the features and organs of young fish corresponds to specific functions at given periods of their life (Osse *et al.*, 1997). This succession of events during development does not occur randomly but corresponds to biological requirements for survival in specific environments (Simonovic *et al.*, 1999). A better knowledge of the development of fins may explain some habitat shifts during ontogeny (Simonovic *et al.*, 1999), and studies of sensory system development often help to understand young fish spatial distribution (Higgs & Fuiman, 1998).

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The Engraulididae includes 16 genera and 139 species (Nelson, 1984) mostly found in tropical and temperate shallow coastal waters and estuaries. Although much attention has been given to certain species such as *Engraulis mordax* Girard or *Anchoa mitchilli* (Valenciennes), little is known about the larval and juvenile stages of most tropical species. *Stolephorus baganensis* Hardenberg and *Thryssa kammalensis* (Bleeker) are the most abundant species among the five engraulid species recorded in the coastal waters of the Klang Strait (S. W. Zgozi, unpubl. data). A research project on the taxonomy, distribution and ecology of these two species in Sungai Selangor estuary (Klang Strait, Malaysia) was initiated in 1997. One of its first aims, the results of which are presented here, was to describe their ontogeny (1) to help identify the young stages, and (2) to detect if any thresholds occurred during ontogeny which could be related to the distribution of young anchovies in Sungai Selangor estuary.

MATERIALS AND METHODS

FIELD COLLECTION AND LABORATORY WORK

From January 1997 to April 1998, young fishes in Sungai Selangor estuary (3°19′ N; 101°13′ E, Malaysia) were regularly collected with a bongo net of 363 μm-mesh size. In order to minimize and make uniform the body shrinkage caused by net capture and preservation (Ferron & Leggett, 1994) towing time averaged only 4 min and the fishes were fixed in 5% formalin/sea water solution buffered with calcium carbonate immediately after retrieval of the net. In the laboratory, young engraulids were sorted out from the plankton collection and kept in a fresh 5% buffered formalin. For both species, specimens >50·0 mm L_S were identified following Whitehead *et al.* (1988), and younger ones (<50·0 mm L_S) by tracing back morphological and morphometric characters from the largest to the smallest fish. From randomly selected, non-distorted or non-damaged individuals, 11 external morphometric characters potentially associated with swimming abilities (body shape, fin development and positions), and vision (eye diameter) were measured to the nearest 0·1 mm using a calibrated ocular micrometer fitted on a binocular microscope. These characters were: (1) the standard length (L_S); (2) the distance from the anus to the tip of the notochord (tail length); (3) the distance between the tip of the head and the anterior margin of the anal fin (head to anal fin); (4) the distance between the anterior margin of the anal fin and the notochord tip (anal fin to tail fin); (5) the anal fin length; (6) the distance between the tip of the head and the anterior margin of the dorsal fin (head to dorsal fin); (7) the distance between the anterior margin of the dorsal fin and the notochord tip (dorsal fin to tail fin); (8) the dorsal fin length; (9) the horizontal eye diameter; (10) the vertical distance from the dorsal margin to the ventral margin of the body measured at the base of the pectoral fins (body depth); and (11) the distance between the base of the pelvic fin and the anus (pelvic fin to anus). For each individual the following were recorded also: (1) the external pigmentation, (2) the number of fin rays in the dorsal and anal fins; (3) the aspect of the notochord (straight or flexed); (4) the presence of pre- and postpelvic scutes (*sensu* Whitehead *et al.* 1988); (5) the presence of a spine before the dorsal fin; (6) the position of the mouth; and (7) the presence of scales, by using either a phase contrast microscope or by staining the specimens with methylene blue. General body shape was defined following Leis & Trnski (1989) as very elongate when body depth (D) <10% of L_S, elongate when $D=10$ to 20% of L_S and moderate when $D=20$ to 40% of L_S.

Samples were always kept at a constant temperature of $24 \pm 1°$ C and measurements were taken within 4 weeks after field sampling. After examination, specimens were transferred into 70% ethanol and deposited at the University of Malaya, Kuala Lumpur, Malaysia.

DATA ANALYSIS

Piecewise regressions, i.e. linear relation in pieces where slope and intercept are different for each piece (Sokal & Rohlf, 1998), were fitted to log transformed values of the ten morphometric characters against log transformed L_S in order to examine their relative growth (Fuiman, 1983). Briefly, for each character, the NONLIN module of Systat 8.0 was used to compute estimates of the four parameters b_0, b_1, b_2 and B of the model:

$$y = b_0 + b_1 x + b_2 (x - B)$$

where y = log transformed value of the morphometric character and x = log transformed value of the standard length.

This single model represents two regressions depending on the value of the standard length relative to the breakpoint B:

when $x < B$ the model becomes $y = b_0 + b_1 x$ and
when $x > B$ the model becomes $y = (b_0 - b_2 B) + (b_1 + b_2) x$.

For each of the 10 morphometric characters the adjustment to the model, based on the minimization of the residual sum of squares along successive iterations, allowed the growth coefficient b to be obtained before $(b = b_1)$ and after $(b = b_1 + b_2)$ a given size equal to 10^B (in mm). A b value equal to 1 indicated that the morphometric character grew isometrically, i.e. proportionally to the body length, whereas its allometric growth was negative, i.e. slower than the body growth, or positive, i.e. faster than the body growth, when b was < or >> respectively (Gisbert, 1999).

The numbers of anal and dorsal fin rays v. L_S of both species were adjusted with the same NONLIN module of Systat 8.0 to linear in piece models where the second phase was a plateau. For all models the Pearson correlation between the observed and predicted values (R^2) was used to measure how closely the fitted values approximated the actual values (Wilkinson *et al.*, 1996)

Global morphological transformations of the two species during ontogeny were assessed by using nine morphometric characters: tail length, head to anal fin, anal fin to tail fin, anal fin length, head to dorsal fin, dorsal fin to tail fin, dorsal fin length, horizontal eye diameter and body depth. The distance between pelvic and anal fins was not used because too few big individuals with pelvic fins were available. Only the data for specimens for which all nine characters were available were retained (141 specimens for *S. baganensis* and 71 for *T. kammalensis*) and were log-transformed to account for size-related effects. Each resulting data set was treated with double-centred principal components analysis (PCA) following Sagnes *et al.* (1997) and using the ADE software package (Thioulouse *et al.*, 1996). The first component loadings of this method provide an accurate depiction of the pattern of relative growth when ontogenetic data are used (Shea, 1985).

RESULTS

ONTOGENY OF *STOLEPHORUS BAGANENSIS*

A total of 191 specimens ranging from 2·9–47·0 mm L_S were examined. The growth of all measured characters was described well by piece models (Table I). The ontogeny was divided arbitrarily into five groups by considering both the size at which the breakpoints occurred in the piece models and the development and position of the fins (Fig. 1).

Group 0: 2·9–4·2 mm L_S [Fig. 2(a)]

This group comprised individuals without anal and dorsal fins, and whose body was surrounded by a finfold. None of the specimens had a yolk sac. The

TABLE I. Parameters of the piecewise regression models (exponential: $y=ax^b$ or linear: $y=a+bx$) depicting the growth of 10 morphometric characters and the number of rays on anal and dorsal fins $v.$ L_S for *Stolephorus baganensis*

Regression model	Mensural character	n	Regression 1		Breakpoint	Range	Regression 2		R^2
			a	b			a	b	
Exponential	Tail length	191	0·39	0·81	7·3	6·6–8·0	0·16	1·27	0·995
	Head to anal fin	167	0·73	1·01	7·3	6·1–8·7	0·96	0·86	0·998
	Anal fin to tail fin	167	0·26	1·00	7·3	6·1–8·7	0·15	1·28	0·994
	Anal fin length	167	0·01	2·78	8·9	7·7–10·2	0·08	1·31	0·972
	Head to dorsal fin	171	0·81	0·86	27·3	22·6–32·9	0·50	1·01	0·997
	Dorsal fin to tail fin	171	0·25	1·20	24·1	19·8–29·3	0·48	1·00	0·997
	Dorsal fin length	171	0·01	2·94	7·1	6·7–7·5	0·10	1·13	0·985
	Eye diameter	170	0·07	0·70	10·0	9·4–10·7	0·01	1·58	0·995
	Body depth	170	0·13	0·85	10·0	9·3–10·7	0·02	1·72	0·995
	Pelvic fin to anus	43	2·75	0·12	23·3	21·8–25·0	0·09	1·19	0·984
Linear	Number of anal fin rays	173	− 11·83	4·25	7·5	7·3–7·6	20·01	0·00	0·951
	Number of dorsal fin rays	172	− 5·08	2·77	6·9	6·7–7·1	13·98	0·00	0·883

n, Number of observations; a, b parameters of the models; breakpoint, value of L_S for which the regression models switch from regression no. 1 to regression no. 2; range, Wald 95% CI of the breakpoint; R^2, square of the Pearson's correlation between the observed and the predicted values.
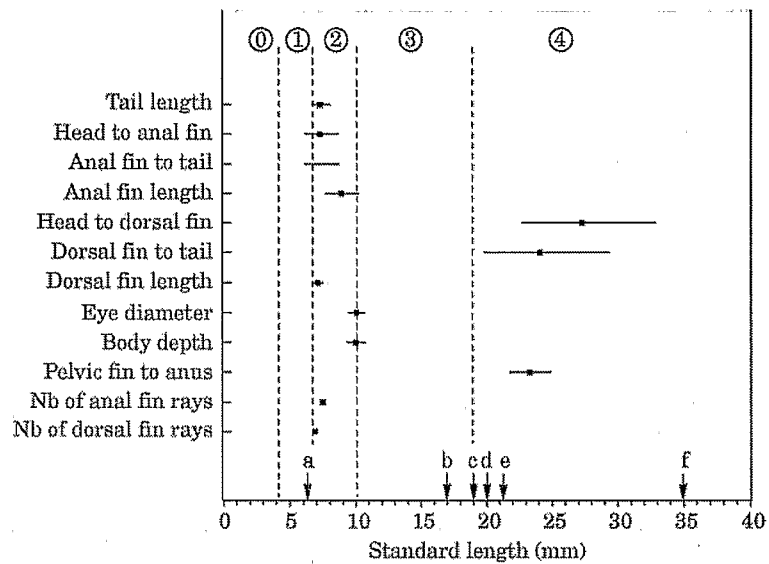
FIG. 1. Major events during the ontogeny of *Stolephorus baganensis*. (■), standard length (range limited from 0–40·0 mm L_S for clarity) at which the breakpoints in the growth of the 10 mensural characters and the number of rays on anal and dorsal fins occur, with horizontal bar=95% CI. Vertical arrows correspond to first observation of (a) flexion of the notochord, (b) scales, (c) spine before dorsal fin, (d) mouth in inferior position, (e) scutes, (f) adult pigmentation. Vertical dotted lines separate the five groups: (0) 2·9–4·2 mm L_S; (1) 4·2–6·9 mm L_S; (2) 6·9–10·1 mm L_S; (3) 10·1–19·0 mm L_S; (4) 19·0–47·0 mm L_S.

mouth was open but the eyes were pigmented only from 3·0 mm L_S onwards. The body was unpigmented. The thin and elongated liver reached the anterior margin of the air bladder and the gut appeared as a straight anterior portion followed by a striated-like posterior part that started at the anterior margin of the air bladder and ended at the anus. The height of this posterior striated part was never >25% of the body depth. A good criterion for identifying the early stages of this species is a conspicuous orange band of tissue, of unknown function, near the terminal section of the gut. The digestive system remained morphologically identical until it was hidden by the body muscles organized in myomeres, and therefore was not described further for older individuals.

Group 1: 4·2–6·9 mm L_S [Fig. 2(b)]

The lower size of this group was set at the onset of dorsal and anal fin development, and its upper limit at the size at which the first breakpoint occurred (Fig. 1). Larvae at this stage had a very elongate body and a concave snout. Flexion of the notochord occurred at c. 6·3 mm L_S. Two pigment spots were present below the air bladder and one near the anus. The dorsal fin position overlapped that of the anus. Growth in length of the anal and dorsal fins was strongly positively allometric whereas the other segments grew either isometrically or negatively allometrically (Table I).

Group 2: 6·9–10·1 mm L_S [Fig. 2(c)]

This range of sizes included nine of the 12 breakpoints obtained with the piecewise regressions (Fig. 1, Table I). The body shape changed from very
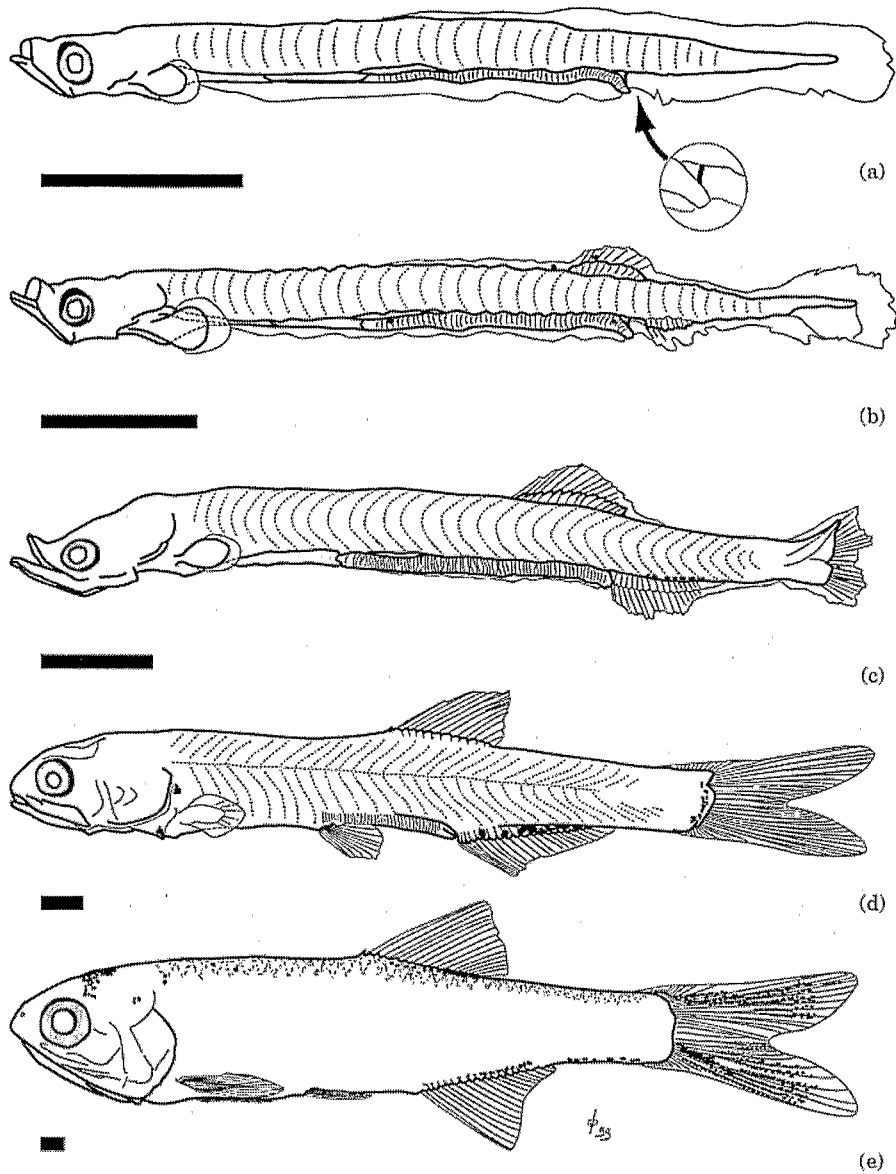
FIG. 2. Ontogeny of *Stolephorus baganensis*: (a) individual of size group 0 with an enlargement of the conspicuous orange (on freshly preserved specimens) band of tissue (see explanations in text); (b) individual of size group 1; (c) individual of size group 2; (d) individual of size group 3; (e) individual of size group 4. Scale bars represent 1·0 mm. Note that the scales are not drawn.

elongate to elongate at *c.* 8·0 mm L_S and the snout started to become pointed at *c.* 8·3 mm L_S. A few pigment spots were present on the anal fin while those on the peritoneum disappeared. The number of rays in the anal and dorsal fins stabilized at 7·5 and 6·9 mm L_S, respectively, the fin lengths shifting from a strong positive allometric to an almost isometric growth at 8·9 and 7·1 mm L_S, respectively. Once fully developed, the dorsal fin comprised between 13 and 15 rays and averaged 13% of L_S whereas the anal fin comprised 19 to 20 rays and
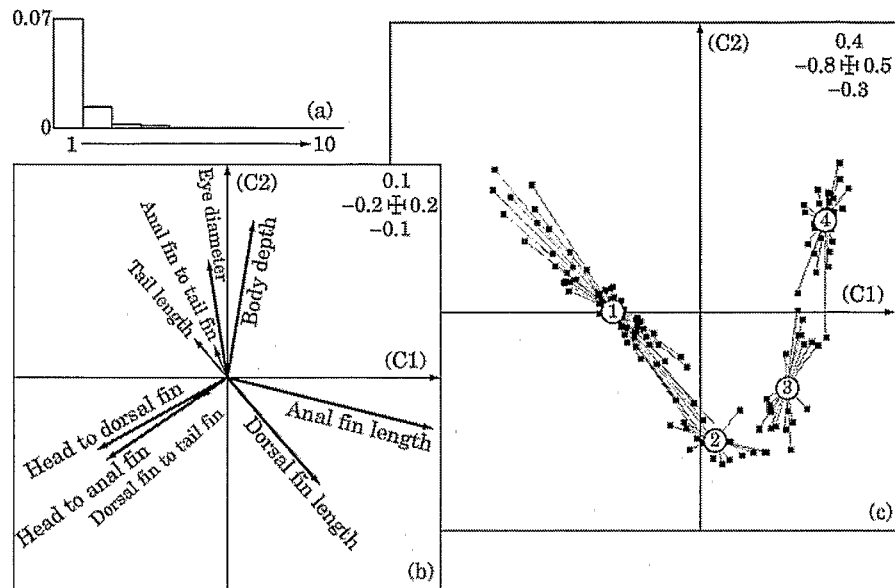
FIG. 3. Ordination of the 141 *Stolephorus baganensis* individuals based on nine morphological variables (i.e. all except L_S and distance between pelvic fins and anus) using doubled-centred principal component analysis. The first two components explain 85·5% of the total variation of the data. (a) Eigenvalues of components; (b) position of the ten morphological variables on the ordination plane; (c) the centre of each star corresponds to the centre of gravity (average of the factorial co-ordinates on the first and second axes) of the size groups defined in Fig. 1 (1, 4·2–6·9 mm; 2, 6·9–10·1 mm; 3, 10·1–19·0 mm; 4, 19·0–47·0 mm).

reached 20 to 22% of L_S. Double-centred PCA revealed that anal and dorsal fin lengths were the characters contributing the most to the morphological changes of individuals <10·1 mm L_S (Fig. 3). The position of dorsal and anal fins relative to the head and body depth contributed to a much lesser extent.

Group 3: 10·1–19·0 mm L_S [Fig. 2(d)]

Individuals of this group were characterized by differential growth of their body segments that induced changes in the relative position of the anus and the anal and dorsal fins. These processes, referred as forward migrations by Leis & Trnski (1989), started at 10·0 mm L_S for the anus and dorsal fin and 13·0 mm L_S for the dorsal fin, and ended all at 19·0 mm L_S. At that size c. 49% and 33% of the body were situated before and after the dorsal fin respectively. From 10·1 mm L_S onwards, two pigment spots were observed on the isthmus and two others on the posterior margin of the cleithrum. Pelvic fin rays appeared first at 11·3 mm L_S. At 16·0 mm L_S the number of pigment spots above the anal fin increased rapidly, reaching an average number of 15 at 19·0 mm L_S. A row of pigment spots also formed at the peduncle margin. Scales were observed first on the posterior part of the body at 17·0 mm L_S. The small spine at the anterior margin of the dorsal fin was observed at 19·0 mm L_S. From c. 10·1 mm L_S onwards, body depth and eye diameter were the characters contributing the most to morphological changes (Fig. 3).

Group 4: 19·0–47·0 mm L_S [Fig. 2(e)]

The upper limit of this group corresponded with the largest individual caught. At 20·0 mm L_S the mouth took its final inferior position and the spine before the pelvic fin developed. At *c.* 21·0 mm L_S the body was fully covered by scales and the abdominal cavity entirely covered by body muscles. Ventral scutes appeared first at 21·3 mm L_S. At 23·0 mm L_S the general body shape became moderate although the distance between the pelvic fins and the anus switched from a strong negatively allometric growth ($b=0·12$) to an almost isometric growth ($b=1·19$) at 23·3 mm L_S. At 22·0 mm L_S pigment spots on the isthmus and the cleithrum disappeared but others developed on the inner side of the operculum and increased in number with fish size. Pigments on the back started forming at 22·0 mm L_S and spread towards the posterior margin of the dorsal fin to form the double line characteristic of the adults of this species (Whitehead *et al.*, 1988) when those on the head appeared at 25·0 mm L_S. The adult pigmentation was completed at *c.* 35·0 mm L_S. Maturing gonads for males and females were observed first at *c.* 40·0 mm L_S. From *c.* 19·0 mm L_S onwards, PCA analyses (Fig. 3) revealed a stronger contribution of the eye diameter in the ontogeny.

ONTOGENY OF *THRYSSA KAMMALENSIS*

A total of 119 specimens ranging from 3·9–67·5 mm L_S were examined. The relative growth of all morphometric characters was also described best by piecewise regressions (Table II) and specimens were separated into different size groups (Fig. 4). One small individual ($L_S=3·9$ mm), not included in these groups, had the remains of its yolk sac, pectoral buds and a dorsal fin with four rays.

Group 1: 4·0–5·7 mm L_S [Fig. 5(a)]

This group included individuals before inflexion points of the piecewise regressions occurred (Fig. 4). At 4·0 mm L_S, specimens had a dorsal fin with seven rays and an anal fin with 10 rays. Two pigment spots were present on the tip of the finfold and at 4·7 mm L_S two others, sometimes joined in a line, appeared on the middle line of the isthmus. At 4·9 mm L_S, pigment spots were observed on the posterior part of the gut. The body shape changed from very elongate to elongate at 5·3 mm L_S. The liver was short and bulbous and the gut had a striated aspect all along its length, with striation height reaching up to 32% of body depth at the mid-portion of the intestine. Most morphometric characters grew isometrically (Table II), except the tail length which grew negatively allometrically ($b=0·73$).

Group 2: 5·7–10·0 mm L_S [Fig. 5(b)]

This range of sizes included 10 of the 12 breakpoints obtained with bivariate analyses (Fig. 4, Table II) and its upper limit was set at the start of the forward migrations (*sensu* Leis & Trnski, 1989) of the anus, dorsal and anal fins. The notochord flexed at 6·3 mm L_S. The pigment spots on the peritoneum developed rapidly until 6·3 mm L_S, then decreased and disappeared at 7·2 mm L_S while those on the caudal peduncle increased in number. At 8·2 mm L_S, two pigment spots were observed also at the base of the pectoral fins. The snout, initially

TABLE II. Parameters of the piecewise regression models (exponential: $y=ax^b$ or linear: $y=a+bx$) adjusted to the growth of 10 morphometric characters and the number of rays on anal and dorsal fins $v.$ L_S for *Thryssa kammalensis*

Regression model	Mensural character	n	Regression 1 a	b	Breakpoint	Range	Regression 2 a	b	R^2
Exponential	Tail length	96	0·46	0·73	6·2	5·2–7·4	0·21	1·15	0·992
	Head to anal fin	88	0·65	1·06	6·9	5·5–8·6	0·91	0·89	0·996
	Anal fin to tail fin	88	0·33	0·88	6·8	5·3–8·6	0·17	1·23	0·988
	Anal fin length	89	0·01	2·94	7·5	6·7–8·4	0·09	1·33	0·978
	Head to dorsal fin	88	0·61	0·98	6·2	3·9–9·8	0·73	0·88	0·994
	Dorsal fin to tail fin	88	0·36	1·08	5·8	1·9–17·3	0·32	1·13	0·994
	Dorsal fin length	88	0·01	2·63	7·4	6·7–8·1	0·20	0·83	0·964
	Eye diameter	119	0·06	0·92	16·0	13·7–18·8	0·02	1·28	0·988
	Body depth	119	0·01	2·70	6·4	6·0–6·8	0·04	1·47	0·992
	Pelvic fin to anus	38	2·14	0·16	22·0	20·1–24·1	0·08	1·23	0·978
Linear	Number of anal fin rays	89	−6·10	4·49	8·9	8·3–9·4	33·87	0·00	0·926
	Number of dorsal fin rays	88	−1·05	2·00	7·3	6·9–7·7	13·54	0·00	0·839

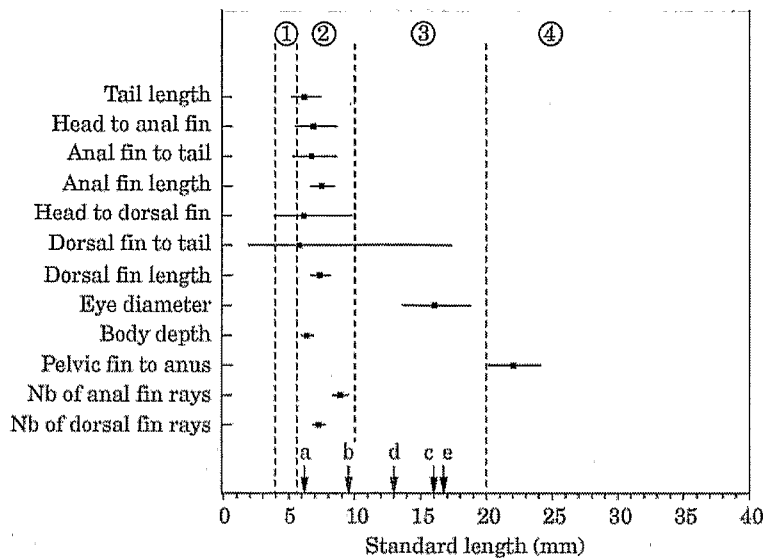n, a, b, Breakpoint, range, R^2 as Table I.

FIG. 4. Major events during the ontogeny of *Thryssa kammalensis* (range limited from 0–40·0 mm L_S for clarity). Symbols as for Fig. 1. Note that adult pigmentation is acquired only at 55·0 mm L_S. Vertical dotted lines separate the four groups: (1) 4·0–5·7 mm L_S; (2) 5·7–10·0 mm L_S; (3) 10·0–20·0 mm L_S; (4) 20·0–67·5 mm L_S.

concave, started to become pointed at 8·8 mm L_S. After its completion at 8·9 mm L_S the anal fin had 34 rays. It reached about 30% of L_S and extended along most of the caudal peduncle. The dorsal fin had 14 rays and corresponded to *c.* 8% of L_S. The first rays on the pelvic fins were observed at 9·0 mm L_S. Scales were observed first at 9·4 mm L_S on the caudal peduncle and then spread towards the head, and from the belly to the back.

Breakpoints in the relative growth of the tail length and the body depth occurred at 6·2 mm L_S and 6·4 mm L_S respectively. The first one reflected a shift from negative to positive allometry while the latter marked a decrease in its positive allometric growth. The growth of anal and dorsal fins shifted to a slower rate close to isometry at *c.* 7·4 mm L_S (Table II). PCA showed that dorsal and anal fin lengths contributed the most in the morphological changes of *T. kammalensis* $L_S<10·0$ mm along with, to a lesser extent, the position of dorsal and anal fins relative to the head (Fig. 6).

Group 3: 10·0–20·0 mm L_S [Fig. 5(c)]

The upper limit of this group corresponded with the size at which the relative positions of dorsal fin, anal fin and anus stabilized. At 15·0 mm L_S, pigment spots on the isthmus disappeared, while others formed on the dorsal part of the fish. The body shape switched from elongate to moderate at 18·0 mm L_S. The mouth became inferior at 13·0 mm L_S and the snout acquired its characteristic bulbous shape at 14·7 mm L_S. The spine at the anterior margin of the dorsal fin formed at 16·0 mm L_S. At *c.* 16·5 mm L_S the abdominal cavity was hidden by the body muscles and at 16·7 mm L_S the pre- and postpelvic scutes appeared. The dorsal fin was always located anteriorly to the anus and when its position stabilized 52% and 40% of the body were before and after the fin, respectively.
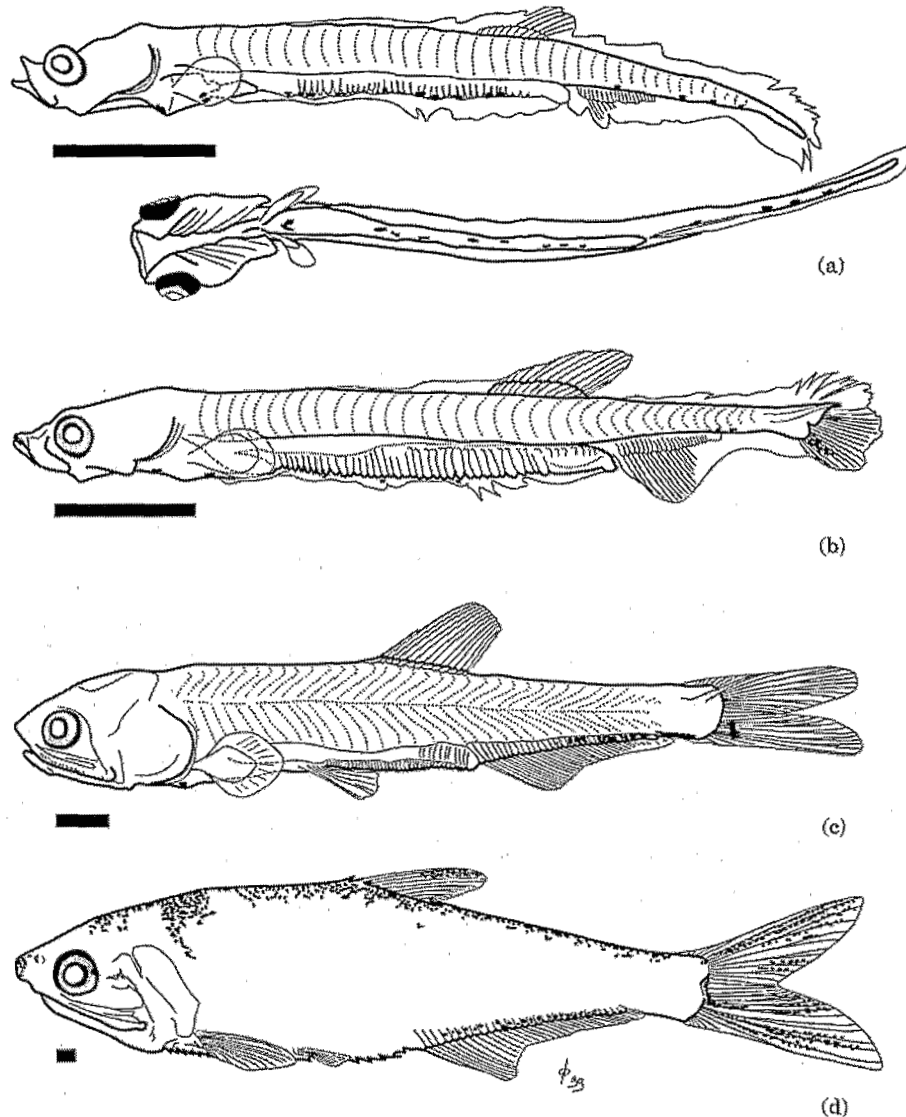
FIG. 5. Ontogeny of *Thryssa kammalensis*: (a) individual of size group 1; (b) individual of size group 2; (c) individual of size group 3; (d) individual of size group 4. Scale bars represent 1·0 mm. Note that the scales are not drawn.

Within this size group, bivariate analyses indicated a marked change in the relative growth of the eye diameter which switched from negative to positive allometric growth at 16·0 mm L_S (Table II). PCA revealed important morphological differences between individuals of size groups 2 and 3 (Fig. 6). From 10·0 mm L_S onwards, the character contributing the most to the morphological changes of *T. kammalensis* was body depth (Fig. 6).

Group 4: 20·0–67·5 mm L_S [Fig. 5(d)]
The upper limit of this group corresponded with the largest individual caught. From 20·0 mm L_S onwards, the number of pigment spots on the anal fin
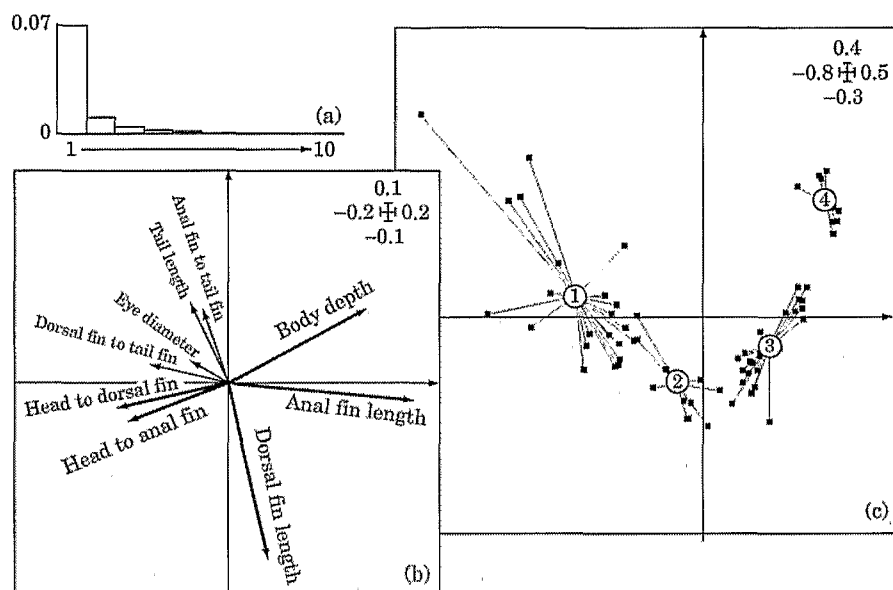
FIG. 6. Ordination of the 71 *Thryssa kammalensis* individuals based on nine morphological variables (i.e. all except L_S and distance between pelvic fins and anus) in a doubled-centred principal component analysis. The first two components explain 80·7% of the total variation of the data. (a) Eigenvalues of components; (b) position of the ten morphological variables on the ordination plane; (c) the centre of each star corresponds to the centre of gravity (average of the factorial co-ordinates on the first and second axes) of the size groups defined in Fig. 4 (1, 4·0–5·7 mm; 2, 5·7–10·0 mm; 3, 10·0–20·0 mm; 4, 20·0–67·0 mm).

increased rapidly until 50·0 mm L_S and then decreased in number, with only few pigment spots remaining at 54·5 mm L_S and none at 67·5 mm L_S. At 28·0–30·0 mm L_S, pigment spots on the tail fin grew in size and formed lines at its lower, middle and upper parts. Simultaneously, pigment spots appeared along the tail fin-caudal peduncle margin and those on the back spread slowly towards the midline. Another patch of pigment spots formed at the back of the head, spreading slowly ahead and downwards to the posterior margin of the operculum. At 35·0 mm L_S they covered the top of the head. Scale development was completed at c. 25·0 mm L_S. At 22·0 mm L_S, the growth of the region between the pelvic fins and the anus switched from a strong negative allometry ($b=0·16$) to a positive one ($b=1·23$). Beyond this standard length, and until 67·5 mm L_S, all morphometric parameters exhibited constant relative growth coefficients (Table II). Maturing gonads were observed first in males and females at c. 62·0 mm L_S.

DISCUSSION

Although the external morphology of engraulid early life stages usually appears very similar (Leis & Trnski, 1989; Young *et al.*, 1995), young *S. baganensis* and *T. kammalensis* differed in several aspects and their identification was easy (Table III). For <10·0 mm L_S larvae, with incompletely developed fins, the shape of the liver, the height of the intestine, and the pattern of the striations on the gut, were useful features to identify them. The relative positions of the

TABLE III. Simple criteria for identifying *Stolephorus baganensis* Hardenberg and *Thryssa kammalensis* (Bleeker) larvae and juveniles

	S. baganensis	*T. kammalensis*
Larvae with incompletely developed anal and dorsal fins	Thin and elongated liver reaching the anterior margin of the air bladder	Short and bulbous liver
	Striations on the gut starting at the anterior margin of the air bladder	Gut with a striated aspect all along its length
	Height of the intestine never >25% of body depth	Height of the intestine >30% of body depth
Older individuals with completely developed anal and dorsal fins	Position of dorsal fin overlapping the position of the anus	Position of dorsal fin not overlapping the position of the anus
	Anal fin with 19–20 rays representing 20–22% of L_S	Anal fin with 33–34 rays representing $c.$ 30% of L_S and extending along most of the caudal peduncle
	Slender body	Relatively deep body
	Pre-pelvic scutes only	Pre- and postpelvic scutes

unpaired fins, the length of the anal fin, and the body depth were good criteria for identifying larger individuals. Leis & Trnski (1989) stated that striations on the gut of engraulid larvae start at the posterior margin of their gas bladder and later extend to its anterior margin during ontogeny, but this generalization does not apply to the two present species. Larvae of *S. baganensis* possess striations starting at the anterior margin of the gas bladder regardless of their development stage, whereas the entire gut of *T. kammalensis* larvae as small as 4·0 mm L_S is already covered by striations. These differences in the morphology of the gut and liver of these two species are not only useful landmarks for identifying their larval stages but also suggest differences in their diet.

The ontogeny of both species is characterized by a first period prior to 6·9 mm L_S for *S. baganensis* and prior to 5·7 mm L_S for *T. kammalensis* when the length of dorsal and anal fins exhibit a strongly positive allometric growth (Tables I and II) and contribute the most to the global morphological changes of the larvae (Figs 3 and 6). This priority towards fin development is a common feature among teleosts (Faustino & Power, 1999). The primordial finfold, that increases drag and may contribute to the high cost of fish larval locomotion (Osse & van den Boogaart, 1995), is replaced by dorsal and anal fins. This corresponds usually to an improvement of fish larval escapement capabilities and feeding success (Webb & Corolla, 1981) upon which their survival depends strongly (O'Connell, 1981; Fuiman, 1993; Kesel *et al.*, 1993). Some differences were detected also in the ontogeny of these species during this period: (1) the onset of dorsal fin development occurred at a larger size for *S. baganensis* larvae (L_S >4·2 mm) than for *T. kammalensis* (L_S <3·9 mm), and (2) the growth of the body depth was negatively allometric ($b=0·85$) for *S. baganensis* and positively allometric ($b=2·7$) for *T. kammalensis*. The latter may reflect discrepancies in the swimming ability of these two species at the onset of exogenous feeding because body depth is one of the factors that may influence the swimming efficiency of small larvae (Osse & van den Boogaart, 1999).

Both bivariate and multivariate analyses revealed a transition period in the ontogeny of *S. baganensis* from 6·9–10·0 mm L_S and from 5·7–8·9 mm L_S for *T. kammalensis*. For both species, the relative growth of most morphometric characters changed and the number of rays on anal and dorsal fins stabilized (Table I and II). The main factors describing the morphological changes of both species (Figs 3 and 6) changed from the development of dorsal and anal fins to the increase in body depth, the relative decrease in head to dorsal and anal fin distances, and the relative increase in eye diameter (especially in *S. baganensis*). This sudden transformation when compared with the whole ontogeny is not uncommon and has been reported for example for the minnow *Phoxinus phoxinus* (L.) (Simonovic *et al.*, 1999). If this transition period is a significant threshold (*sensu* Balon, 1979) in the early life of *S. baganensis* and *T. kammalensis*, it can be hypothesized that it will correspond with shifts in habitat (Poling & Fuiman, 1999). For instance, in fresh water, Copp & Kováč (1996) reported that the offshore migration of *Rutilus rutilus* (L.) coincided with a full development of their swimming ability and Kováč *et al.* (1999) showed that breakpoints related to fin growth coincided with movement of *Barbatula barbatula* (L.) larvae towards deeper water. For marine species, Higgs & Fuiman (1998) linked the shifts in the

habitat of young Atlantic menhaden to the increase of retinal sensitivity and bulla inflation.

After this transition period, the highest coefficients of positive allometry for both species were displayed by body depth, eye diameter and anal fin length. Since the body depth of *T. kammalensis* presented positive allometric growth already in its earlier stages, individuals of this species rapidly acquire a less slender body than *S. baganensis* (Figs 2 and 5). Differences in body shape may correspond to different capabilities for escaping predation (Webb & Weihs, 1986) or exploiting habitats (Hurlbut & Clay, 1998). The positive allometric growth of eye diameter may correspond to an increase in number and size of visual cells (McCormick & Shand, 1992) and thus to an improvement of prey detection (Blaxter, 1986) as well as evasive behaviour (Higgs & Fuiman, 1998).

The beginning of the juvenile period was not detected clearly with the morphometric measurements used in this study. Indeed, between the end of the transition period and the onset of gonad maturation, PCA analyses did not reveal major changes in the global morphological transformations of both species. Some authors have proposed the completion of scale development as a limit between larval and juvenile periods (e.g. Fuiman, 1994). However, this definition can hardly be applied for *S. baganensis* because some breakpoints (Table I) and meristic changes (Fig. 1) occurred after the body was fully covered by scales at *c.* 21 mm L_S. Therefore, it is proposed that the onset of the juvenile period should be set at the point at which the specimens show adult pigmentation, i.e. at 35·0 mm L_S for *S. baganensis* and 55·0 mm L_S for *T. kammalensis*.

Further studies in Sungai Selangor estuary will test whether the temporal and spatial distributions of the different size groups match the ontogenetic development of these two species.

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