THE LARVAL DEVELOPMENT OF *BATHYLAGUS GREYAE* (BATHYLAGIDAE)

by

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ABSTRACT. During the course of 25 years of ichthyoplankton investigations in the tropical and subtropical East Atlantic, 21 larval to juvenile specimens of deep-sea smelt *Bathylagus greyae* Cohen, 1958, were recorded from subtropical latitudes of both hemispheres. Morphology, development and pigmentation are described. Larger specimens had vertebrae counts of 44-46. *Bathylagus greyae* larvae have sessile, slightly oblong eyes of medium size, a relatively long head, high reaching gill slit, ventrally located pectoral fins, a straight gut with slightly trailing anus located at 72-83% of body length in early larvae and at 76-84% later. Diagnostic features are a paired series of numerous small, but conspicuous supraintestinal melanophores, early development of dorsolateral pigment above the anus, and a lateral series of melanophores developing from midbody. Yolk sac larvae of *B. greyae* were 2.1 to 4.3 mm long (at maximum). Notochord flexion and caudal fin skeleton development start at approximately 8 mm notochord length. Transformation to juvenile starts at approximately 20 mm length.

RÉSUMÉ. Le développement larvaire de *Bathylagus greyae* (Bathylagidae).

Pendant 25 ans de recherche sur l'ichthyoplancton de l'Atlantique Est tropical et subtropical, 21 exemplaires larvaires et juvéniles de l'éperlan de grands fonds *Bathylagus greyae* Cohen, 1958 ont été pêchés à des latitudes subtropicales des deux hémisphères. La morphologie, le développement et la pigmentation sont décrits. Les spécimens de plus grand taille possèdent 44 à 46 vertèbres. Les larves de *Bathylagus greyae* ont des yeux oblongs et sessiles de taille moyenne, une tête relativement longue, des ouvertures branchiales prolongées vers le haut, des nageoires pectorales en position ventrale, l'intestin droit avec l'anus situé à 72-83% de la longueur du corps chez les jeunes larves et à 76-84% chez des individus plus âgés. Les caractères diagnostiques sont une série de nombreuses paires de mélanophores supraintestinaux, petits mais distincts; le développement précoce d'une pigmentation dorsolatérale au-dessus de l'anus; et une série latérale de mélanophores commencant à mi-longueur du corps. Les larves à vésicule vitelline ont une longueur de 2,1 à 4,3 mm au maximum. La flexion de la notochorde et le développement du squelette caudal commencent à environ 8 mm de longueur notochordale. La transformation en juvénile commence à 20 mm de longueur environ.

Key words. Bathylagidae - *Bathylagus greyae* - ASE - Larval description.

The mesopelagic fish family Bathylagidae presently comprises 21 nominal species worldwide and probably several genera (Kobylyansky, 1986; Kobylyanskiy, 1990). According to Olivar *et al.* (1993), new bathylagid species are likely to be discovered; their larvae are morphologically far more diverse than adults; the systematics of the family or its relations within the suborder Argentinoidei are not yet understood, and larval taxonomy may contribute to phylogenetic analysis in the future.

Summarizing information from more comprehensive recent publications (Ahlstrom *et*

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al., 1984; Olivar *et al*., 1993; Moser and Ahlstrom, 1996; see literature therein for original descriptions), the larval development is presently known for a total of 14 identified species. Olivar *et al*. (1993) described the larval development of a further, still unidentified species, as well as a large larva plus a juvenile of *Bathylagus gracilis*. Olivar and Fortuño (1991) described and illustrated a juvenile *B. greyae*, which had been the least developed specimen known so far from that species. We can now add the descriptions of larvae and transforming specimens.

MATERIAL AND METHODS

From a larger number of fish larvae surveys in the tropical and subtropical Atlantic, five cruises yielded 21 specimens of *Bathylagus greyae*, 2.1 mm notochord length (NL) to 37.3 mm standard length (SL), see table 1. Nineteen specimens up to 22.7 mm retained larval characters. The material is deposited in the fish larvae collection of the Zoologisches Museum Hamburg (ZMH); the respective labels are a combination of the first three columns of table 1 (cruise, sample type, haul/net number, vial). Other abbreviations will be defined later at first use.

The log-sheet for sample M30, Bo 50 does not record any position, but date and time of sampling. The position has been interpolated from the data for the adjacent stations, which were spaced along 30°00'N. The material was initially preserved in a buffered solution of approximately 4% formaldehyde in seawater. Material from M30 and M64 remained after

Table 1. Station data of the material available (grouped by ontogenetic sequence). The first column abbreviates those cruises where specimens were caught as follows: Meteor 30 (M30), Meteor 64 (M64), Heincke 20 (H20), Meteor 37 (M37), and Poseidon 250 (Po250).

Ship and sampler cruise		Haul/net and (vial)	Length (mm)	Latitude	Longitude	Date	Depth (m)
Po250	MCN	39/3 (e1)	2.1	19°01'S	08°00'E	21 Apr 99	50 - 100
Po250	MCN	39/3 (e2)	3.6	19°01'S	08°00'E	21 Apr 99	50 - 100
Po250	MCN	40/2 (d)	3.9	19°44'S	08°00'E	22 Apr 99	100 - 150
H20	MUV	32/3 (b2)	4.3	32°00'N	10°36'W	17 Jan 92	400 - 600
Po250	MCN	45/3 (f2)	3.9	19°45'S	09°49'E	23 Apr 99	50 - 100
Po250	MCN	45/3 (f1)	4.1	19°45'S	09°49'E	23 Apr 99	50 - 100
M37	MUV	5/5 (f)	4.2	28°40'N	13°06'W	8 Jan 97	0 - 100
M37	MUV	7/3 (c)	4.2	28°44'N	13°22'W	8 Jan 97	400 - 600
Po250	MCN	41/3 (b1)	4.4	20°21'S	07°59'E	22 Apr 99	50 - 100
Po250	MCN	41/3 (b2)	4.8	20°21'S	07°59'E	22 Apr 99	50 - 100
M37	MUV	3/3 (a)	4.8	28°38'N	12°54'W	8 Jan 97	100 - 200
M64	MCN	283/3 (a)	5.0	19°46'N	17°19'W	16 Feb 83	60 - 90
M64	MCN	311/2 (a1)	5.2	20°41'N	17°43'W	18 Feb 83	90 - 120
M64	MCN	311/2 (a2)	5.2	20°41'N	17°43'W	18 Feb 83	90 - 120
M64	MCN	299/4 (a)	7.7	20°21'N	18°04'W	18 Feb 83	30 - 60
M37	MUV	20/2 (a)	22.7	32°15'N	13°10'W	17 Jan 97	600 - 800
M37	MUV	22/2 (a)	22.2	32°15'N	12°10'W	18 Jan 97	600 - 800
M30	Bo	50/300(a)	21.8	ca. 30°N	ca. 14°W	20 Feb 73	0 - 80
M30	Bo	50/300(b)	22.2	ca. 30°N	ca. 14°W	20 Feb 73	0 - 80
M30	Bo	27/300	ca. 35	34°01'N	08°53'W	9 Feb 73	0 - 80
M30	Bo	31/300	37.3	33°58'N	11°18'W	10 Feb 73	0 - 80

sorting in a 4% freshwater/formaldehyde solution and deteriorated somewhat. Ten to 16 years later these larvae were transferred into a Steedman solution (Steedman, 1976). H20-, M37-, and Poseidon material was stored in Steedman solution immediately after sorting. For the transforming larva MUV 22/2(a) the living coloration was recorded immediately after catch; one larva 4.8 mm (MUV 3/3(a)) was investigated the second day after catch. Counts or observations were made by transmitted light only, to avoid damage of the scarce material by clearing and staining.

RESULTS

Identification

The critical specimen for species identification was the transforming larva from M37, MUV 22/2(a). The combination of a low position of the pectoral fin, straight gut, 2 branchiostegal rays, and midbody location of the dorsal fin (D 13, commencing at 50.9% of SL) conformed with family Bathylagidae, but not with families Argentinidae and Microstomatidae. The transforming larva showed a blunt, relatively long head (23.9% of SL), high gill opening, pelvic position below the rear margin of the dorsal fin, and the short anal fin with a low finray count of A 12, specific for *B. greyae* (at least when compared with other North Atlantic bathylagids, see Ahlstrom *et al.*, 1984: table 41). This transforming specimen retained (easily visible when fresh, less so after a year of preservation) such larval pigment as the supraintestinal and lateral series of melanophores and anal pigment traced back to preflexion

Table 1. Selected meristic and morphometric data, arranged by ontogenetic sequence as in table 1. Measurements are expressed in percent of NL or SL. HL: Head length; ED1: Larger eye diameter; Eds: Smaller eye diameter; PDL: Predorsal length; PAL: Preanal length; PoA: Position of anus; VS: Vertebrae number; D, A, V, P: Dorsal, anal, ventral and pectoral fin rays number. See text for explanation.

Specimen label	NL/SL (mm)	HL	EDl	EDs	PDL	PAL	PoA	VS	D	A	V	P
39/3(e1)	2.1	23	14	10		>66	?	?				
39/3(e2)	3.6	23	?	?		77		>38				
40/2(d)	3.9	23	?	?		77	33	>36				
32/3(b2)	4.3	21	9	7		72	29	>33				
45/3(f2)	3.9	26	?	?		80	34	>34				
45/3(f1)	4.1	24	?	?		?	?	>34				
5/5(f)	4.2	24	9	7		74	33	>37				
7/3(c)	4.2	21	8	6		74	33	>37				
41/3(b1)	4.4	21	?	?		77	33	>40				
41/3(b2)	4.8	23	8	6		73	31	>38				
3/3(a)	4.8	25	10	7		77	31	>38				
283/3(a)	5.0	22	10	5		80	30	>35				
311/2(a1)	5.2	25	10	6		83	30	>35				
311/2(a2)	5.2	25	10	6		81	31	>35				
299/4(a)	7.7	29	10	6	54	84	33	44	bud	bud		3
20/2(a)	22.7	24	6	6	49	83	34	46	13	11	7	8
22/2(a)	22.2	24	7	6	51	78	31	44	13	12	8	4
50/300(a)	21.8	26	9	7	51	80	32	45	13	11	8	12
50/300(b)	22.2	26	9	8	51	78	32	44	13	11	7	8
27/300	35.0	?	?	?	?	?	?	46	13	11	?	8
31/300	37.3	26	10	9	?	76	30	46	13	12	11	?

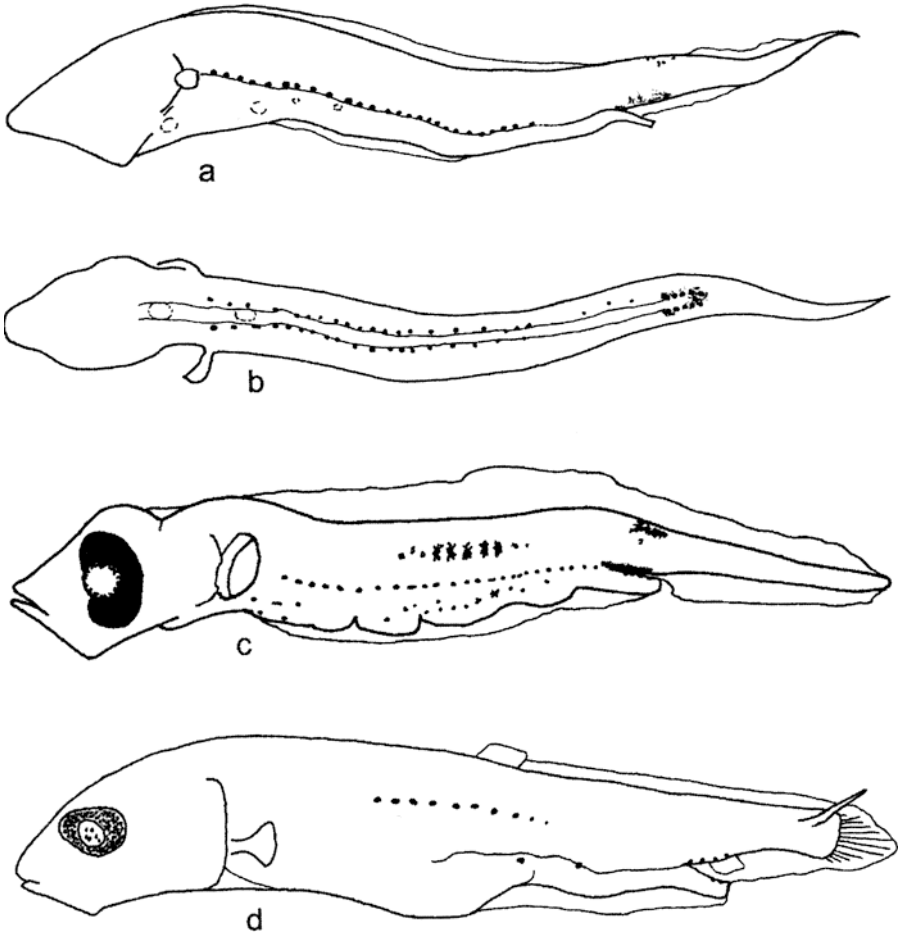

Fig. 1. Larvae of *Bathylagus greyae*. **a**: A yolk sac larva 3.6 mm seen from the side, partly reconstructed. The interrupted circles indicate oil-globules. The specimen was damaged, with eyes lost, and contorted. Specimen Po250, MCN 39/3(e2). **b**: The same specimen, ventral view. **c**: A preflexion larva 4.2 mm. Specimen M37, MUV 5/5(f). **d**: A flexion larva 7.7 mm SL (8.0 mm NL). The specimen (M64, MCN 299/4(a)) was largely discoloured due to storage in formaldehyde.

larvae. Also it is similar in morphology and pigmentation to the smallest *B. greyae* previously described (Olivar and Fortuño, 1991: juvenile 28.0 mm). Our transforming specimen had 44 vertebrae. The total range was 44-46 vertebrae, as quoted in literature (Kobylyanskiy, 1985, 1990; Olivar and Fortuño, 1991).

Description and development (Table II)

The position of the anus PoA is referred to as the myomere number above the rear margin of the anus. The vertebrae number could only be counted with reasonable accuracy from flexion onwards, because in earlier stages the hind part of the body was undifferentiated.

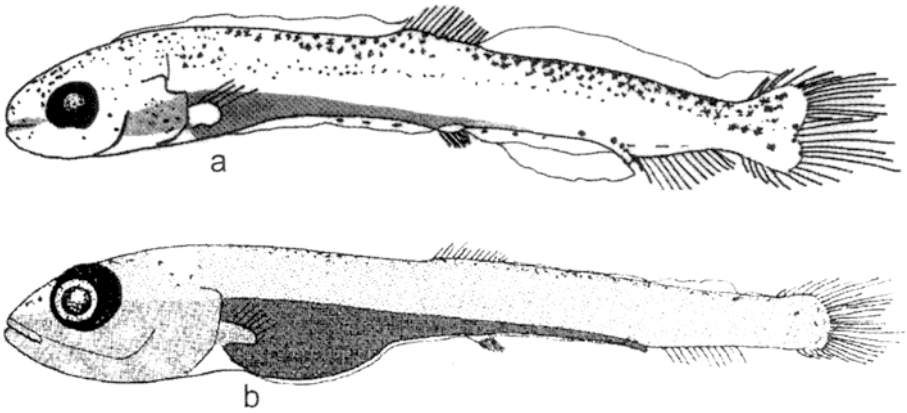

Fig. 2. Transforming larvae of *Bathylagus greyae*. **a**: An early transforming larva 22.2 mm. Specimen M37, MUV 22/2(a). Opercle reconstructed from another specimen of similar size. **b**: A late transforming larva 22.2 mm, showing juvenile pigmentation, but retaining some larval characters. Specimen M30, Bo 50/300(b).

Preflexion larvae

Preflexion larvae ranged from approximately 2.1 mm (specimen contorted and slightly damaged) to 5.2 mm NL. The notochord tip was not surrounded by the primordial finfold, but projected freely until flexion (Fig. 1). The head length and intestine were rather long (Table II). The intestine was straight and without transverse rugae. The anus was slightly trailing. The finfold commenced at about the shoulder girdle. It was low ventrally along the intestine, but elsewhere it reached a height of almost half the body depth. The smallest specimens 3.6 to 4.3 mm NL showed yolk and 4 (Fig. 1a) to 1 oil globules. Yolk sac larvae had medium sized, sessile, weakly pigmented, and ovoid eyes. In all other preflexion larvae eyes were sessile, slightly ovoid, pigmented, and directed slightly forward (Fig. 1c, Table II). Preflexion larvae had a pectoral fin base without rays, located deep ventrally, and flexed forwards. Buds of other fins were not present. The anus was located below body segments 29 to 34; 33 to 40 segments could be counted in total. The undifferentiated hind parts of the notochord were estimated to bring the definite count to 44.

Flexion larvae

A larva of 7.7 mm SL was in flexion, with developing caudal skeleton (Fig. 1d). The urostyle was slightly angulated upwards in its front part, but the notochord tip did not yet show the curvature of postflexion larvae. It projected beyond the hind margin of the developing hypural elements to 8.0 mm NL. The larva had a preanal length of 84% of SL and a definite count of 44 vertebrae, the trailing gut becoming detached from the body at myomere 29, and the anus located below myomere 33. Head length was 29% of SL, two branchiostegal rays were discernible, the eye diameters were 10 and 6%. Twelve central caudal rays were differentiating. Buds of the dorsal and anal fin bases were visible, but devoid of rays. The pectoral fin had initially three differentiating rays. The primordial finfold persisted, being highest at the caudal peduncle.

Transforming larvae

It is debatable whether the specimen of 22.2 mm or that of 22.7 mm was morphologi-

cally less developed, whilst all other specimens ≥ 11.8 mm already showed some juvenile features. The specimen of 22.7 mm differed from the smaller one by a still rudimentary pectoral fin, as well as hyaline strands in the dorsal fin base in contrast to the seemingly full complements of dorsal and anal fin ray bases. However, compared with the both smaller and larger larvae available, this specimen seems somewhat untypical in showing little overall pigmentation, with the lateral series being scant. Therefore, the specimen 22.2 mm long described above in chapter "Identification" was illustrated (Fig. 2a). The data in table I and figure 2 suggest that, besides variability, retarded growth or even some reduction in length may occur during transformation.

Transforming larvae (and juveniles) had 44-46 vertebrae, 2 branchiostegal rays, and transverse rugae in the hindgut. The anus was located below myomeres 30 to 34, with preanal lengths 76-83% of SL. Head lengths were 24 to 26% and larger eye diameters 6-10%. Procurrent caudal rays had developed, and the larva had definite counts in the unpaired fins (13 dorsal and 11-12 anal rays, the last ray split). The primordial fin fold persisted all along the dorsal contour, and ventrally along the intestine. In the illustrated larva the finfold was higher than noted in the smaller specimens. The notochord tip still projected beyond the hypural plate by 0.2 mm, it was closely attached to the rear procurrent caudal ray. The pectoral and pelvic fins showed in only two juveniles definite counts of P = 12, respectively V = 11 rays.

The remaining, partly bleached and damaged specimens ≥ 11.8 mm SL are exemplified by figure 2b. The primordial fin fold was ventrally reduced from a narrow fringe to absent, and dorsally to a rudiment above the caudal peduncle. The adipose fin was developed in the largest juvenile 37.3 mm long, but with a rudiment of the primordial finfold still visible in front of it.

Pigmentation

Oil globules of yolk sac larvae were greenish-yellow, but their colour faded during storage. Dorsally of the intestine, a paired series of lateral, embedded melanophores extended from the shoulder girdle backwards. Its length increased during ontogeny. Except for the smallest specimen, all preflexion larvae showed ventral "blotch-like" pigment above the trailing part of the gut. In fact, this blotch was composed of 5-7 pairs of melanophores (e.g., Fig. 1b), spaced and located as the above mentioned supraintestinal series, but larger, less accentuated and merging with each other to a pigment blotch. In larger specimens this pigment blotch appeared to be homogeneous and confluent with the supraintestinal series. Most larvae larger than 4.2 mm had minute dorsal melanophores on the anus.

Another ontogenetically rather consistent feature was dorsolateral pigment located on the body above the anus. It was traceable from the smallest specimen (weak and scattered, located along myosepta) onwards, and extended anteriad and ventrad to form one or two patches in larger preflexion larvae (Fig. 1). Somewhat later a lateral row of diffuse melanophores developed in about the middle of the body. It appeared first (and weakly) in the specimen of 3.9 mm NL; larger preflexion larvae showed 5 to 10 stellate lateral melanophores. Later during preflexion, pigment ventrally at the cleithral symphysis developed from 4.2 mm onwards (partly diffuse, partly showing up to 7 minute, but accentuated melanophores), and laterally on the intestine there appeared series of small melanophores, developing first along the hindgut. However, there is no strict relation between the latter described two pigmentation features and length.

From long storage in formaldehyde the flexion larva was soft, transparent and almost discoloured. Pigment remained at the eyes, midlaterally (10 melanophores), supraanally to middle of the anal fin bud (four spots) and at the anus. From the supraintestinal series only

two melanophores remained. The specimen was damaged where the dorsolateral patch might have been.

The pigmentation of the preserved transforming specimen is illustrated in figure 2a. The dorsal part of the body became pigmented (including minute melanophores on the central dorsal fin ray bases), making the dorsolateral series inconspicuous among the general colour. The foregut became almost black. The lateral series remained visible, as did the formerly supraintestinal paired series. It remained in a supraintestinal position, however, only near the anus (both transforming specimens). More anteriorly it continued ventrally of the intestine, as a paired series up to the pelvic fin, but interspersed along the foregut. The anus showed pigment dorsally, but the earlier pigment at the anal fin base had disappeared and all unpaired fins were unpigmented. There were prominent melanophores on the caudal fin base.

For this specimen the living colour had been noted immediately after catch. Dorsally an almost continuous pattern of black, stellate melanophores from the snout to the caudal fin was noted, extending down to below the lateral line, at the caudal base down to almost the ventral body contour. The lateral series, however, was more conspicuous than in the preserved specimen, and the other dorsolateral line (above the anal fin) was traceable, too. The opercle and snout was black, but the area above the otocyst, the unpaired fins, pectoral and pelvic fins were colourless. The minute melanophores at the dorsal base were also visible. The peritoneum was bluish-black, extending (when fresh) until the hindgut became free-trailing. The "supraintestinal" series was overshaded along the foregut by the peritoneal pigment, but clearly visible from just in front of the pelvic fins to the anus.

The juvenile pigmentation was generally uniform, dark ventrally from snout to anus, and lighter brown dorsally, and at the caudal peduncle. Of the larval pigmentation some melanophores persisted above the hindbrain, along the dorsal body contour, at the caudal base and at the anus, and traces of the lateral series were visible up to lengths of 22.2 mm in our specimens, but also in the juvenile 28.0 mm illustrated by Olivar and Fortuño (1991).

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