Larval stages of *Brachynotus atlanticus* Forest, 1957 (Crustacea: Decapoda: Grapsidae) reared under laboratory conditions

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Abstract. The complete larval development of the Eastern Atlantic grapsid crab, *Brachynotus atlanticus*, was obtained in the laboratory. Five zoeal stages, the megalopa and the first crab stage are described and illustrated. Under laboratory conditions at 23°C the first crab appeared on the 25th day. This is the first species of the genus for which the complete larval development is known. Larval features are compared with those of other members of the subfamily Varuninae.

Introduction

The four species of *Brachynotus* (De Haan) (subfamily Varuninae) are recorded from the atlantic–mediterranean region: *B. gemellari* (Rizza), *B. foresti* (Zariquiey), *B. sexdentatus* (Risso) and *B. atlanticus* (Forest). Only two forms are localized in Mediterranean waters (Zariquiey, 1968; Frogliola and Manning, 1978). *Brachynotus sexdentatus*, is a typically Mediterranean species, reported in the Atlantic only in Swansea (UK), where it was introduced (Naylor, 1957a,b). No specimens were found in Swansea by Bullimore *et al.*, (1978) between October 1976 and February 1977 and the existence of an established population must be in doubt. The remaining Atlantic records of *B. sexdentatus* (Monod, 1933, 1956; Bouvier, 1940) were referred to *B. atlanticus* by Manning and Holthuis (1981), this species being distributed along the north-western coast of Africa (Manning and Holthuis, 1981) and the southern coast of the Iberian Peninsula, on both the Mediterranean (García Raso, 1985) and Atlantic sides. Two important populations, El Portil (Huelva) (González-Gordillo *et al.*, 1990) and El Chato (Cádiz) are present in south Iberian Atlantic waters.

There are a number of descriptions of larval development in the Grapsidae, but these are incomplete, being based on planktonic material or confined to the first zoeal stage hatched in the laboratory. The information on larvae of the subfamily Varuninae is sparse; however, the complete larval development is known for *Acmaeopleura parvula* (Kurata, 1968), *Euchirograpsus americanus* (Wilson, 1980), *Eriocheir japonicus*, *Gaetice depressus*, *Hemigrapsus sanguineus*, *H. penicillatus* and *H. longitarsis* (Terada, 1981), *H. nudus* and *H. oregonensis* (Hart, 1935), and the first zoea of *H. crenulatus* and *H. edwardsii* (Wear, 1970). Larvae of members of the genus *Brachynotus* are poorly known. Only the incomplete larval development of *B. sexdentatus* (Bourdillon-Casanova, 1960) has been described, and the second zoea and a possible fifth zoea (Paula, 1987).

This study describes the first complete larval life history for the genus

Brachynotus and larval features are compared with those known in *B. sexdentatus* and other members of Varuninae.

Method

Ovigerous females of *B. atlanticus* were collected from El Chato beach (Cádiz) in May–June 1990. They were maintained in aquaria with filtered sea water until hatching. The larvae were then cultured in 2 l plastic bottles at a density of 1000 larvae l⁻¹. The culture method was similar to that used by Ingle and Clark (1977). Single larvae were also reared in compartmented boxes to characterize developmental stages. Natural sea water was used at a temperature of $23 \pm 1^\circ\text{C}$ and salinity of $33 \pm 1\%$, under a 16 light/8 dark lighting regime. The larvae were fed on rotifers *B. plicatilis* from Z-I to Z-III and nauplii of *Artemia* from local sources (Román and Rodríguez, 1989) from Z-III to first crab. Larvae were preserved in buffered 4% formaldehyde or in 70% ethanol.

All measurements were made using an ocular micrometer on a binocular microscope, and are based upon measurement of 20 specimens at each stage. Total length (TL) for zoeal stages was measured from the tip of the rostral spine to the tip of the dorsal spine; carapace length (CL), from the base of the rostrum to the posterior margin; carapace width (CW), as the distance between the tips of lateral spines. For the megalopa, CW was measured as the greatest distance across the carapace, and CL was measured as above. Drawings of the entire larvae and dissected appendages were made using a Wild M-5 stereomicroscope and a Wild compound M-20 microscope, both with a camera lucida. Mandibles of zoea larvae were photographed using a scanning electron microscope. Semipermanent mounts were made of whole larvae and dissected appendages using CMC 10 and lignin pink.

Results

Full-term eggs were slightly oval and measured 0.49×0.42 mm (mean of 10 measurements). Development through five zoeal stages to megalopa was completed in a minimum of 17 days from hatching, and the first crab appeared at 25 days. Size, morphometrics, survival and duration data of the zoea and the megalopa stages are shown in Table I and Figure 1.

The major features of each larval stage and changes of the setation appendages which do not appear in the Tables II and III are described below.

Features of zoeal stages

Carapace (Figure 2). In all stages, carapace globose and smooth, broader than longer and bearing a lateral spine; rostral and dorsal spines well-developed. Setation and other features shown in Table II.

Abdomen and telson (Figure 3A–E). Six subequal somites and telson, last somite appearing in third zoeal stage; second somite bears two dorsolateral knobs directed anteriorly. Telson bifid with a deep median cleft in inner margin and

Fig. 1. Percentage survival and duration of larval stages of *B. atlanticus* reared under laboratory conditions.

Table I. Mean size and standard deviation in μm of total length (TL), carapace width (CW), carapace length (CL), and days to appearance and duration of the larval stages of *B. atlanticus* reared in the laboratory at 23°C

Stage	TL	CW	CL	Mean days of first appearance (duration mean 50%)
Zoea I	1484.7 $\pm$ 29.3	720.1 $\pm$ 11.1	473.2 $\pm$ 12.7	0-3
Zoea II	1828.7 $\pm$ 20.5	760.2 $\pm$ 15.3	571.2 $\pm$ 14.4	3-3
Zoea III	2408.5 $\pm$ 38.7	828.2 $\pm$ 12.5	731.2 $\pm$ 15.1	6-3.5
Zoea IV	2792.4 $\pm$ 44.2	1025.6 $\pm$ 19.5	820.5 $\pm$ 18.5	9-4
Zoea V	3416.1 $\pm$ 54.3	1258.3 $\pm$ 18.2	1173.7 $\pm$ 19.8	13-4.5
Megalopa	-	1112.6 $\pm$ 11.1	1488.6 $\pm$ 11.2	17-7
First crab	-	-	-	25

plumodenticulate setae on both sides; furcae with rows of tiny teeth; pleopod buds appearing in fourth zoeal stage. Setation and other features shown in Table II.

Antennule (Figure 4A-E). Unsegmented and conical, with a group of terminal aesthetes and spines. Numbers of aesthetes and spines shown in Table II.

Antenna (Figure 5A-E). Elongated protopod with two rows of a variable number of denticles; unsegmented endopod appears in third zoeal stage; exopod also elongated and acute in distal half. Setation and other features shown in Table II.

Table II. Setation and other characteristics of the carapace, abdomen, antennule and antenna of zoeal stages of *B. atlanticus*

Features	Stages				
	Zoea-I	Zoea-II	Zoea-III	Zoea-IV	Zoea-V
Carapace (Figure 2)					
Ratio width/length	1.5	1.31	1.13	1.23	1.07
Ratio dorsal/rostral spines	longer	equal	equal	equal	equal
Ratio dorsal/lateral spines	5:1	5:1	4:1	4:1	4:1
No. pairs of setae					
Dorsal-anterior	0	1s	2s	2s	3s
Dorsal-posterior	1s	1s	1s	1s	1s
Lateral-posterior	0	1sp	2sp	3p	5p
Ventral-posterior	0	1sp	5sp	13p	17p
Dorsal-spine	0	0	2s	5s	6s
Eyes	round sessile	round stalked	round stalked	round stalked	round stalked
Abdomen (Figure 3A-E)					
Som. prox.	0	1sp	3sp	5sp	8sp
Som. 2	2 knob, 2s	2 knob, 2s	2 knob, 2s	2 knob, 2s	2 knob, 2s
Som. 3	2s	2s	2s	2s	2s
Som. 4	2s	2s	2s	2s	2s
Som. 5	2s	2s	2s	2s	2s
Som. 6	absent	absent	absent	2s	2s
Telson	(3,3)pd	(3,3)pd	(4,4)pd	(4,4)pd	(4,4)pd
Pleopod buds	absent	absent	absent	rudimentary	present
Antennule (Figure 4A-E)					
Terminal	2a, 1s	4a, 1s	4a, 1s	5a, 1s	8a, 1s
Antenna (Figure 5A-E)					
Protopod	7-9e	8-10e	13-14e	15-17e	15-16e
Endopod	absent	absent	bud present	present	present
Exopod	2e	2e	2e	2e	2e

(S = simple; p = plumose; a = sparsely setose; pd = plumodenticulate; e = spine; som. = somite.

Mandible (Figure 6A-E). Asymmetrical, scoop-shaped process; incisor and molar processes irregularly dentated; palp appears as rudimentary bud in fourth stage.

Maxillule (Figure 7A-E). A developed, plumose setae appearing on opposite side of basal endite in second and subsequent zoeal stages; 2-segmented endopod with setation remaining unchanged throughout all zoeal stages. Setation and other features shown in Table III.

Maxilla (Figure 8A-E). Maxilla consisting of bilobated coxal and basal endites; unsegmented endopod and scaphognathite; slightly bifurcated endopod. Setation and other features shown in Table III.

First maxilliped (Figure 9A-E). First maxilliped with basis, 5-segmented endopod and exopod; 2-segmented exopod appears in fourth and fifth zoeal

Table III. Setations of maxillule, maxilla and the first and second maxillipeds of zoeal stages of *B. atlanticus* (for coding see Table II)

Features	Stages				
	Zoea-I	Zoea-II	Zoea-III	Zoea-IV	Zoea-V
Maxillule (Figure 7A-E)					
Coxa	0	1	1	1p	1p
Coxal endite	4pd,1sp	4pd,1sp	4pd,1sp	6pd,2sp	6pd,1sp
Basal endite	4pd,1sp	4pd,2sp	6pd,(1,1)sp	10pd,(1,1)sp	10pd,(3,3)sp
Endopod					
seg. distal	(2,2,1)sp	(2,2,1)sp	(2,2,1)sp	(2,2,1)sp	(2,2,1)sp
seg. proximal	1sp	1sp	1sp	1sp	1sp
Maxilla (Figure 8A-E)					
Coxal endite	6sp	6sp	6sp,1pd	7sp,1pd	12sp,1pd
Basal endite					
prox.	2sp,2pd	2sp,2pd	2sp,2pd	4sp,2pd	6sp,3pd
dist.	4sp,1pd	4sp,1pd	4sp,1pd	4sp,2pd	4sp,2pd
Endopod	(2,2)sp	(2,2)sp	(2,2)sp	(2,2)sp	(2,2)sp
Scaphognathite	5p	(5,3)p	(9,5)p	25p	29p
First maxilliped (Figure 9A-E)					
Basis	(2,2,3,3)sp	(2,2,3,3)sp	(2,2,3,3)sp	(2,2,3,3)sp	(2,2,3,3)sp
Endopod					
seg. prox.	2sp	2sp	2sp	2sp	2sp
seg. 2	2sp	2sp	2sp	2sp	2sp
seg. 3	1sp	1sp	2sp	2sp	2sp
seg. 4	2sp	2sp	2sp	2sp	2sp
seg. 5	4p,1sp	4p,1sp	4p,1sp	4p,2sp	4p,2sp
Exopod	4p	6p	8p	10p	12p
Second maxilliped (Figure 10)					
Basis	4sp	4sp	4ssp	4sp	4sp
Endopod					
seg. prox.	0	0	0	0	0
seg. 2	1s	1s	1s	1s	1s
seg. 3	(2,3,1)sp	(2,3,1)sp	(2,3,1)sp	(2,3,1)sp	(2,3,1)sp
Exopod	4p	6p	8p	10p	12p

stages. At first stage, endopodial segment bears a group of hairs. Setation and other features shown in Table III.

Second maxilliped (Figure 10A-E). Second maxilliped comprising basis, 3-segmented endopod and exopod; 2-segmented exopod appears in fourth and fifth zoeal stages. Setation and other features shown in Table III.

Third maxilliped. Third maxilliped a rudimentary bud in fourth and fifth zoeal stages; unsegmented naked process.

General morphology of the megalopa

Carapace (Figure 11A). Longer than broad; subquadrate and laterally inflated; orbital margin proximally right-angled, showing 2 simple setae on external

Fig. 2. *Brachynotus atlanticus*: (A) first zoea lateral view; (B) second zoea; (C) third zoea frontal view; (D) third zoea; (E) fourth zoea; (F) fifth zoea. Scale bar in mm.

Fig. 3. *Brachynotus atlanticus*: abdomen. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

angle; frontal margin with small central tooth; posterior margin rounded and fringed with short setae.

Abdomen and telson (Figure 3F; 11F). The abdomen comprising 6 somites (broader than longer) and a semicircular telson, all with setae as illustrated; 3-segmented uropods with 9 plumose setae on distal segment; second segment with a single proximal plumose seta.

Antennule (Figure 4F). Antennule biramous with a bulbous basal segment well-developed with 2 simple setae; 2-segmented peduncle with 4, 1 simple setae;

Fig. 4. *Brachynotus atlanticus*: antennule. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

endopod with 3 apical setae; 3-segmented exopod with 16 aesthetes and 2 plumose setae.

Antenna (Figure 5F). Ten-segmented, setation: 2 simple, 2 simple, 0, 0, 0, 4 simple, 2 plumose, 2 simple and 2 plumose, 2 simple and 2 plumose, 2 plumose and 1 sparsely setose setae.

Mandible (Figure 11G). Smooth incisor process, spatulated, well-developed; molar process rounded and fringed with short setae; 3-segmented palp bearing 8 sparsely setose setae on distal segment.

Fig. 5. *Brachynotus atlanticus*: antenna. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

Maxillule (Figure 7F). Coxa with 3 simple setae; coxal endite with 17 sparse and 5 plumodenticulate setae; basal endite with 11 sparsely setose and 12 plumodenticulate setae; 2-segmented endopod with 4, 2 simple setae; fine epipodite with 2 apical simple setae.

Maxilla (Figure 8F). Coxal endite bilobated with 13 sparsely setose and 3 simple setae on the outer lobe and 5 sparsely setae on the inner lobe; basal endite also bilobated with 5 sparsely setose and 3 plumodenticulate setae on the inner lobe and 9 sparsely setose and 3 plumodenticulate setae on the outer lobe; endopod reduced to sub-acute lobe with 2 sparsely setose setae; scaphognathite with 42 plumose setae.

Fig. 6. *Brachynotus atlanticus*: mandible. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea.

First maxilliped (Figure 9F). Coxal endite with 19 sparsely setose setae; basal endite with 8 sparsely setose setae; unsegmented endopod with 2 simple setae; 2-segmented exopod 3, 4 plumose setae; epipodite with sub-acute lobe and 7 long setae.

Fig. 7. *Brachynotus atlanticus*: maxillule. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

Second maxilliped (Figure 10F). Undifferentiated coxal and basal endites; 4-segmented endopod with 1 simple, 1 simple, 9 sparsely setose, 9 sparsely setose setae; 2-segmented exopod with 1 spine, 5 plumose setae; epipodite unarmed and reduced.

Third maxilliped (Figure 11B). Undifferentiated coxal and basal endites; 5-segmented endopod with 14, 9, 7, 10, 8 simple setae; 2-segmented exopod with 0, 5 plumose setae; epipodite with 5 simple, 15 sparsely setose and 19 long naked setae.

Fig. 8. *Brachynotus atlanticus*: maxilla. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

Pereiopods (Figure 11C–E). Stout and equal chelipeds; coxa with 7 plumose setae on the outer and 2 on the inner side, respectively; propodal inner margin denticulate; dactylar inner margin toothless. Pereiopods 2–4 similar; propodal distal inner margin armed with 1 serrate setae; dactylus armed with 3 short teeth. Basis pereiopod 5 with a plumose setae; dactylus with 3 long hook-shaped and highly denticulate setae on apex. Setation as illustrated.

General morphology of the first crab (Figure 12)

Carapace quadrate-shaped, with 3 acutely denticulate protrusions on antero-lateral margin, with 5, 4, 2 teeth in each respectively; frontal margin rounded, denticulated, with a medial dip; posterior-lateral and posterior margins rounded

Fig. 9. *Brachynotus atlanticus*: first maxilliped. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

and fringed with short setae. Abdomen permanently flexed under sternum. Chelipeds stout and equal in size; pereiopods subequal, 3–5 with dorsal acute seta on distal margin of merus and pereiopod 2 with dorsal acute seta on distal margin of propodus. Third maxilliped with endopod 5-segmented with 18, 15, 7, 3, 9 setae respectively; 2-segmented exopod with 6 terminal plumose setae on distal segment; epipodite prolonged with 17 pairs of sparsely setose setae and 22 long non-plumose setae.

Discussion

Based mainly on the features of the adult crab, four subfamilies within the family Grapsidae were proposed by Balss (1957): Grapsinae, Plagusinae, Sesarminae and Varuninae. Wear (1970) reviewed the morphological characters of grapsid larvae and confirmed this division. But Franzoso and Hebling (1986) reported that there are no characters distinguishing larval groups corresponding to these subfamilies. Schlotterbeck (1976) reported that *Pachygrapsus crassipes* zoea acquire lateral carapace spines from the second stage, and proposed that the presence or absence of lateral carapace spines should not be tenable as a taxonomic feature in a primary division among grapsid zoea. The same should

Fig. 10. *Brachynotus atlanticus*: second maxilliped. (A) first zoea; (B) second zoea; (C) third zoea; (D) fourth zoea; (E) fifth zoea; (F) megalopa. Scale bar in mm.

also apply to *P.marmoratus* and *P.transversus* in which the lateral carapace spines also appear from the second stage (A.Rodríguez, unpublished data). However, Rice (1980), using different larval features, recognized the subfamilies Grapsinae and Plagusiinae as valid.

Wear (1970) and Rice (1980) were unable to distinguish larval groups corresponding to the subfamilies Varuninae and Sesarminae, though they could separate them from the Grapsinae and Plagusiinae by the presence of a well-developed antennal exopod, at least half as long as the spiny process, and by the presence of at least 10 medial setae on the basis of the first maxilliped. Later, Wilson (1980), for *E.americanus* (Varuninae) and Fielder and Greenwood (1983) for *Bresedium brevipes* (Sesarminae), reported a rudimentary and short

Fig. 11. *Brachynotus atlanticus*: megalopa. (A) dorsal view; (B) third maxilliped; (C) cheliped; (D) pereopod; (E) fifth pereopod; (F) pleopod; Scale bar in mm.

antennal exopod in all zoeal stages. Additionally, Wilson (1980), when comparing larval development of numerous grapsid species, emphasized that the number of setae on the basis of the first maxilliped was an unequivocal taxonomic character.

In *B. atlanticus* the basal segment of the endopod of the second maxilliped is unarmed and could not, therefore, be classified in the Varuninae according to Rice (1980). This feature, together with a carapace bearing lateral spines and telson forks, lacking lateral spines, suggest an affinity between *B. atlanticus*, and the subfamily Sesarminae (part: Genera *Cyclograpsus*, *Chasmagnathus* and *Helice*).

Fig. 12. *Brachynotus atlanticus*: first crab. (A) dorsal view; (B) third maxilliped; (C) cheliped. Scale bar in mm.

Bourdillon-Casanova (1960) briefly described the larval development of *B.sexdentatus* and reported that the zoeae bear dorsolateral knobs on the second and third abdominal somites, of the second zoeal stage, as also described by Paula (1987). However, *B.atlanticus* lacks such knobs on the 3rd abdominal somite. Considering that these earlier works are based on larvae from the plankton, it is uncertain whether the larvae are correctly identified. Detailed comparisons of the larvae of *Brachynotus* will be possible only when the complete larval development of *B.sexdentatus*, *B.foresti* or *B.gemmelari* has been adequately described.

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