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Larval development of *Philocheras fasciatus* (Risso, 1816) (Decapoda, Caridea) reared in the laboratory, comparison with plankton larvae and occurrence of accelerated development

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Abstract. The complete larval development of *Philocheras fasciatus*, consisting of four zoeae stages, was obtained in the laboratory at 23 ± 1ºC and 33‰ of salinity. The present study provides a description of larval stages that developed in rapid succession. In the genus *Philocheras*, the normal developmental sequence includes five or more discrete zoeae stages before metamorphosis into a juvenile. In this study, four zoeae stages of *P.fasciatus* appeared before the juvenile stage. It is possible that complete food requirements, together with a high temperature (8ºC above the natural temperature) and low culture density, had induced an irregular accelerated development. In addition, plankton surveys were carried out from January to April 1996 in the coastal waters of Cádiz Bay. A total of 105 specimens were examined and a morphometric comparison was made between the laboratory-reared and planktonic zoeae. The first zoeae obtained in the laboratory did not differ morphologically from those obtained from plankton samples, but they were significantly smaller. Size variations in stages of *P.fasciatus* seem to be due to culture conditions, and are considered 'laboratory artefacts' rather than natural variation in this species.

Introduction

Six species of *Philocheras* are known in European waters: *P.bispinosus bispinosus* (Hailstone, 1835), *P.bispinosus neglectus* (Sars, 1883), *P.echinulatus* (Sars, 1861), *P.fasciatus* (Risso, 1816), *P.monacanthus* (Holthuis, 1961), *P.sculptus* (Bell, 1847) and *P.trispinosus* (Hailstone, 1835). Larvae of these species have been described, although in the majority of cases, the descriptions have been based on planktonic material or confined to the first zoeae stage hatched in the laboratory. So far, the laboratory rearing of *Philocheras* larvae has been carried out on only two species: *P.bispinosus neglectus* and *P.trispinosus* [(Pike and Williamson, 1961; Pessani and Godino, 1992), respectively].

In *P.fasciatus*, some larval stages have been described from material reared in the laboratory and samples collected from plankton. Gurney (Gurney, 1903a) reared the first larval stage of, then, *Aegeon fasciatus*, and presented a key for its identification. In the same year, Gurney (Gurney, 1903b), described the first and last larval stages of, now, *Crangon fasciatus*, from hatched specimens and plankton samples. Later papers by Williamson (Williamson, 1915), Webb (Webb, 1921), Lebour (Lebour, 1931), Bourdillon Casanova (Bourdillon Casanova, 1960), Williamson (Williamson, 1960), Pessani and Godino (Pessani and Godino, 1991) and Barnich (Barnich, 1996) only commented on some characteristic features based on Gurney's work. Nevertheless, the complete larval development of *P.fasciatus* is still unknown. Complete descriptions of larval stages are essential for studies on phylogenetic relationships (Clark and Webber, 1991), interspecific and subspecific differentiation of specimens from different geographic areas (Pohle, 1991), ecological studies (Pereyra, 1993), and other biological aspects.

Differences in size are known in caridean, and particularly in crangonid shrimps (Pike and Williamson, 1961), between specimens reared in the laboratory and those collected from the plankton. We have noted, during the course of extensive plankton sampling for *P.fasciatus* larvae in Cádiz Bay (Spain), considerable variability in size compared with hatched specimens.

The purpose of the present study is to complement Gurney's work, describing the complete larval development of *P.fasciatus* from hatched specimens and comparing them with larvae obtained from plankton samples.

Method

Rearing of larvae

An ovigerous shrimp of *P.fasciatus*, carrying eggs in an advanced state of development, was collected from San Pedro River inlet (Cádiz Bay, southwest Spain) in May 1998 and brought to the laboratory in a 3 l container with filtered natural sea water. Larvae hatched within 48 h. and zoea I larvae were collected. The larvae were reared in a 3 l glass bucket, with sea water gently aerated at a temperature of 23 ± 1ºC (8ºC above the natural temperature) and an average salinity of 33‰. Larvae were subjected to a natural light–dark regime. First and second zoeae were fed on a mixture of algae, *Nannochloropsis gaditana*, rotifers, *Brachionus plicatilis*, and *Artemia* nauplii from the third zoeae stage. The container was checked daily to remove exuviae and dead larvae; the water was changed every 48 h and food supplied.

Specimens at all stages were fixed in 4% buffered formaldehyde during 48 h and preserved in 70% ethanol. Measurements of entire specimens were made with an ocular micrometer on a microscope, and 10 specimens were recorded for each stage. Microdissections were made under a Wild MZ8 stereomicroscope. Drawings and measurements of dissected larvae were made with the aid of a camera lucida attached to a Zeiss Axioskop compound microscope with Nomarski interference. Setal counts and other morphological features are described according to Clark *et al.* (Clark *et al.*, 1998).

Plankton samples

Philocheras fasciatus zoeae were collected from Cádiz Bay (southwest Spain) from January to April 1996, using a 40 cm diameter WP-2 net with a mesh of 250 µm. Samples were preserved in 4% buffered formaldehyde in sea water. For each specimen, three measurements were taken: carapace length (from the tip of the rostrum to the posterior dorsal margin of the carapace); length of fifth abdominal somite lateral spine; and protopod antennule length. Specimens with damaged rostral or abdominal spines were excluded.

Biometric differences in zoea I of larvae from plankton and laboratory samples were tested statistically by means of Student's *t*-test. They were considered statistically significant at $P < 0.01$.

Results

General morphology of zoeae stages of P. fasciatus (Risso, 1816)

Carapace (Figure 1). In all stages, rostrum sharp extending beyond eyes. Without pterygostomian and ventral spines.

Antennule (Figure 2A–D). Peduncle unsegmented with long conical process bearing setae in the first stage. Exopod unsegmented in all stages not reaching middle of peduncle. Setation and other features are shown in Table I.

Antenna (Figure 2F–H). Endopod armed with diminutive spines, mainly in the two first stages. Scaphocerite (exopod) unsegmented and elongated. Setation and other features are shown in Table I.

Mandible (not figured). Without palp, and incisor and molar processes present.

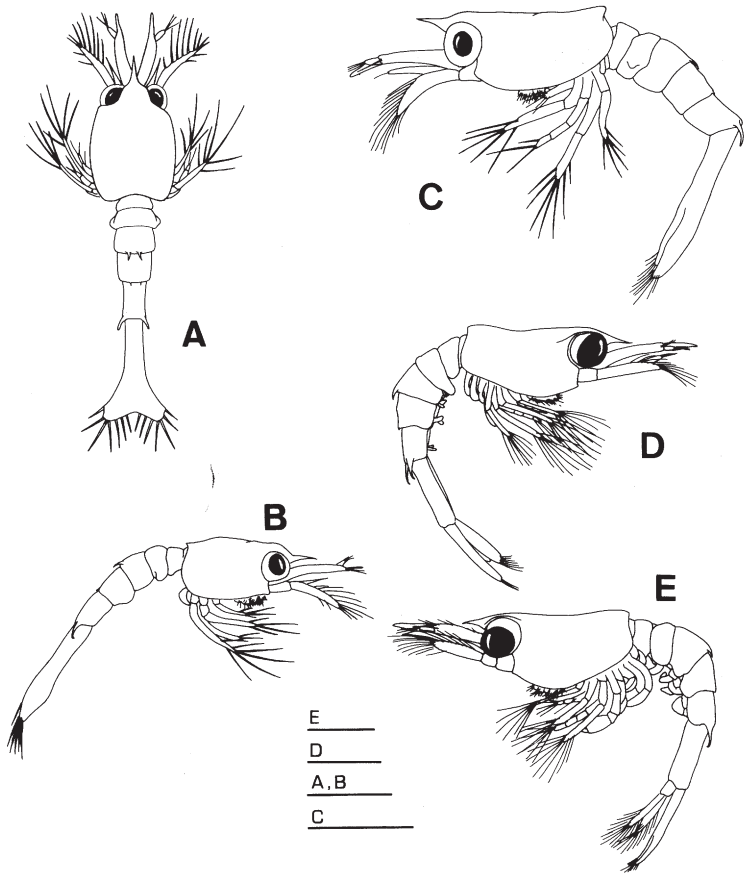

Fig. 1. *Philocheras fasciatus.* (**A**) Zoea I, dorsal view; (**B**) zoea I, lateral view; (**C**) zoea II; (**D**) zoea III; (**E**) zoea IV. Scale bars: 500 μm.

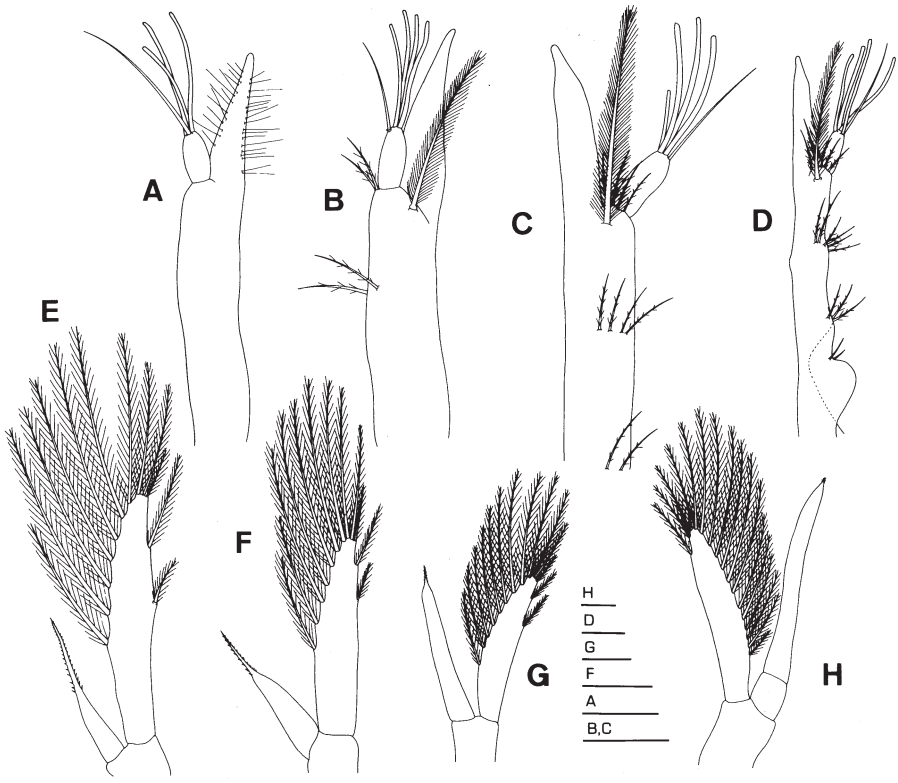

Fig. 2. *Philocheras fasciatus* antennule: (**A**) zoea I; (**B**) zoea II; (**C**) zoea III; (**D**) zoea IV. Antenna. (**E**) zoea I; (**F**) zoea II; (**G**) zoea III; (**H**) zoea IV. Scale bars: 100 μm.

Maxillule (Figure 3E–H). Coxal endite bilobed with setation remaining unchanged throughout all zoeae stages. Endopod two-segmented with setation unchanged. Setation and other features are shown in Table I.

Maxilla (Figure 3A–D). Maxilla consisting of bilobed coxal and basial endites. Unsegmented endopod tetralobed and with setation unchanged throughout all zoeae stages. Setation and other features are shown in Table I.

First maxilliped (Figure 4). Endopod three-segmented not reaching middle of exopod. Exopod unsegmented. In this appendage, from second stage to last zoeae stage, setation variation is not present. Setation and other features are shown in Table I.

Second maxilliped (Figure 5). Coxa and basis with constant setation in zoeae stages. Endopod four-segmented in first stage and five-segmented in the remaining zoeae stages. Endopod extending beyond middle of exopod. Exopod not segmented. Setation and other features are shown in Table I.

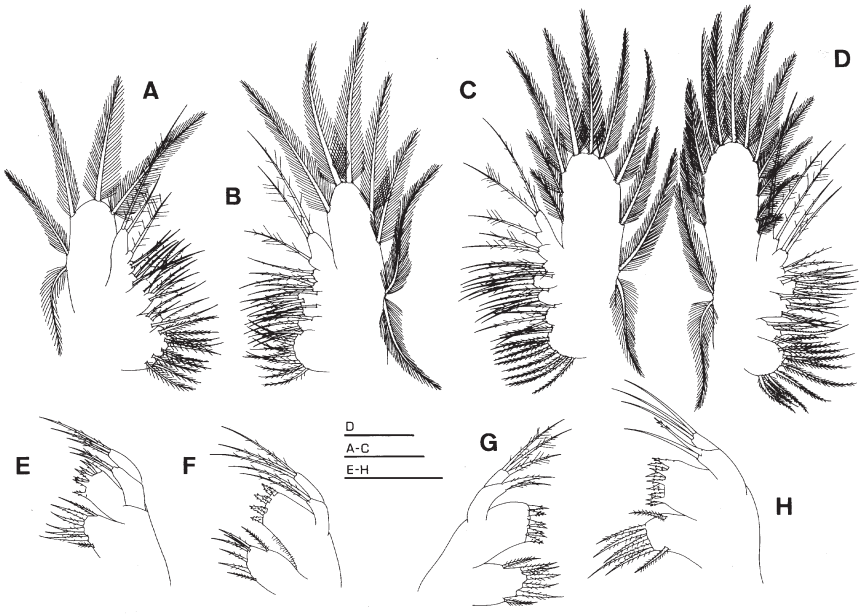

Fig. 3. *Philocheras fasciatus*. Maxilla: (**A**) zoea I; (**B**) zoea II; (**C**) zoea III; **(D**) zoea IV. Maxillule: (**E**) zoea I; (**F**) zoea II; (**G**) zoea III; (**H**) zoea IV. Scale bars: 100 μm.

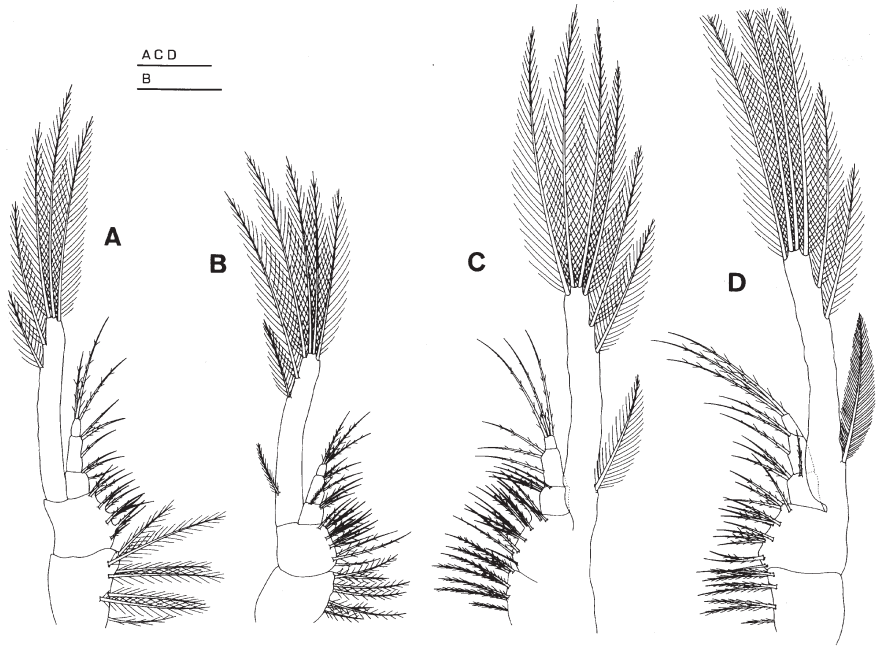

Fig. 4. *Philocheras fasciatus*. First maxilliped: (**A**) Zoea I; (**B**) zoea II; (**C**) zoea III; (**D**) zoea IV. Scale bars: 100 μm.

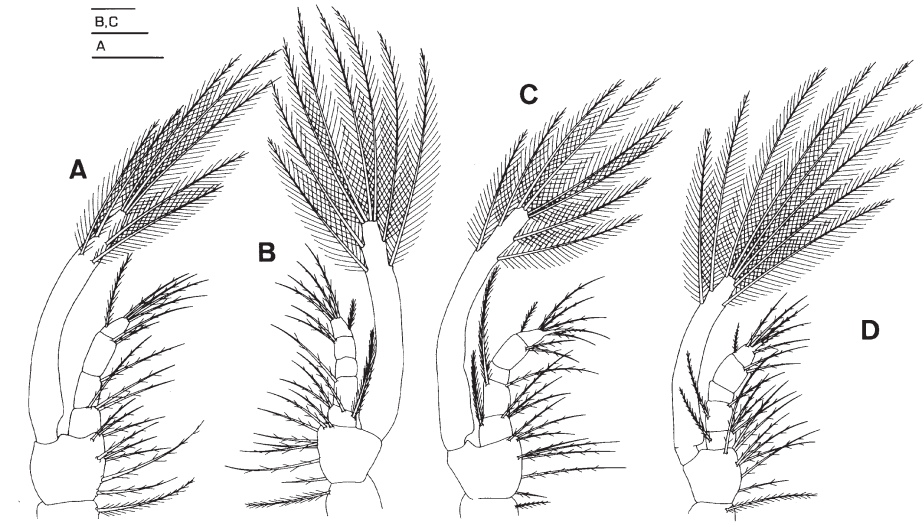

Fig. 5. *Philocheras fasciatus*. Second maxilliped: (**A**) Zoea I; (**B**) zoea II; (**C**) zoea III; **(D**) zoea IV. Scale bars: 100 µm.

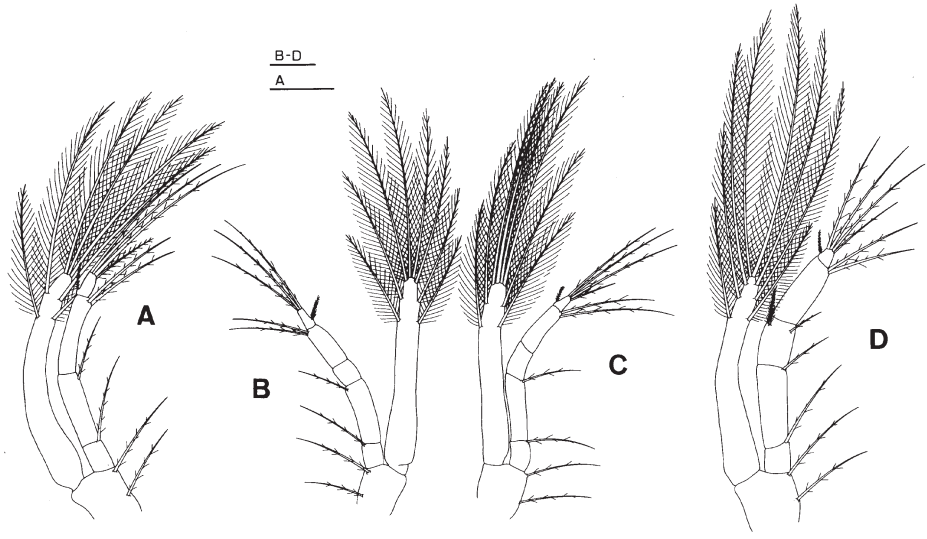

Fig. 6. *Philocheras fasciatus*. Third maxilliped: (**A**) Zoea I; (**B**) zoea II; (**C**) zoea III; (**D**) zoea IV. Scale bars: 100 µm.

Third maxilliped (Figure 6). Coxa naked and basis with constant setation in all zoeae stages. Endopod four-segmented in first stage and five-segmented in subsequent stages. Exopod not segmented. Setation and other features are shown in Table I.

Pereiopods (Figure 7). Progressive development throughout zoeae stages. First pereiopod biramous in all stages. Setation and other features are shown in Table I.

Abdomen and telson (Figure 8). Five somites and telson in the two first stages and six somites in subsequent stages. Second somite bears lateral expansions dorsally visible. Spines of fifth somite are very typical, being curved in distal end. Distal margin of telson slightly concave and armed with small spines with a deep cleft, mainly in two first stages. Setation and other features are shown in Table I.

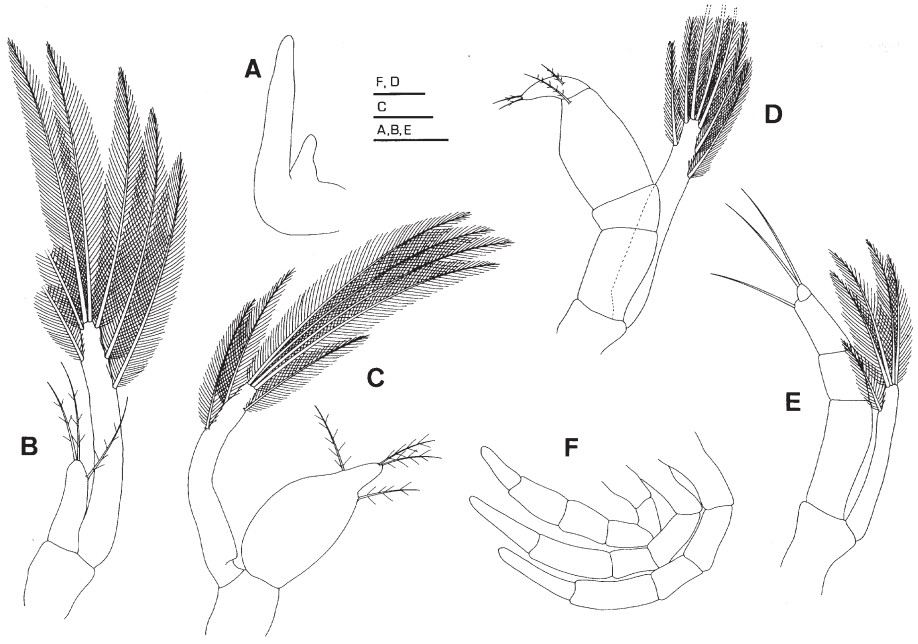

Fig. 7. *Philocheras fasciatus*. First pereiopod: (**A**) Zoea I; (**B**) zoea II; (**C**) zoea III; (**D**) zoea IV. Second pereiopod: (**E**) zoea IV. Third, fourth and fifth pereiopod: (**F**) zoea IV. Scale bars: 100 μm.

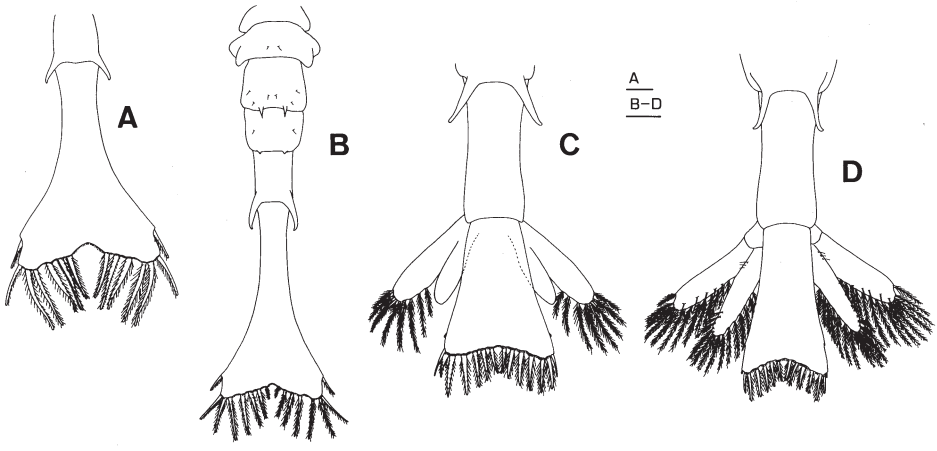

Fig. 8. *Philocheras fasciatus*. Telson: (**A**) Zoea I; (**B**) zoea II; (**C**) zoea III; (**D**) zoea IV. Scale bars: 100 μm.

Table I. Setation and others characteristics of zoeal stages I, II, III and IV of *P.fasciatus*

Features	Stages			
	Zoea I	Zoea II	Zoea III	Zoea IV
Eyes	Sessile	Stalked	Stalked	Stalked
Abdomen				
Somites	0,0,2b,2b,2b	0,0,2b,2b,2b	0,0,2b,2b,2b,0	0,0,2b,2b,2b,0
Pleopods	Absent	Absent	Small buds	Biramous
Telson	7p+7p	8p+8p	1r+7p+7p+1r	2r+6p+6p+2r
Uropods				
Endopod	Absent	Absent	Naked	8e+12p
Exopod	Absent	Absent	8p	5e+14p
Antennule				
Peduncle	Naked	2e+2e+1p	2e+4e+4e+1p	2e+3e+6e+5e+1p
Exopod	3a+1s	4a+1s	4a+1s	4a+1s
Antenna				
Endopod	Unsegmented	Unsegmented	Unsegmented	Two-segmented
Scaphocerite	9p+1j+2p	9p+1j+2p	11p+1j+2p	17p
Maxillule				
Coxal endite	7e	7e	7e	7e
Basal endite	5t	7t	7t	9t
Endopod	2e,3e	2e,3e	2e,3e	2e,3e
Maxilla				
Coxal endite	10p+4e	10p+4e	10p+4e	10p+4e
Basal endite	4e+4e	5e+5e	5e+5e	6e+6e
Endopod	3e+2e+1e+2e	3e+2e+1e+2e	3e+2e+1e+2e	3e+2e+1e+2e
Scaphognathite	3p+2p	5p+2p	8p+2p	12p+2p

Table I. continued

First maxilliped				
Coxa	7e	7e	7e	7e
Basis	12e	15e	15e	15e
Endopod	3e,1e+2e,3e	3e+1p,1e+2e,3e	3e+1p,1e+2e,3e	3e+1p,1e+2e,3e
Exopod	1n+1n+3n	1n+1n+4n	1p+1n+1n+4n	1p+1n+1n+4n
Second maxilliped				
Coxa	1e	1e	1e	1e
Basis	8e	8e	8e	8e
Endopod	3e,1e,2e,1p+4e	3e+1p,1e,0,2e,1p+4e	3e+1p,1e+1p,0,2e,1p+5e	3e+1p,1e+1p,0,2e,1p+5e
Exopod	2n+2n+3n	2n+2n+4n	2n+2n+4n	2n+2n+4n
Third maxilliped				
Basis	2e	2e	2e	2e
Endopod	1e,1e,2e,1p+3e	1e,1e,0,2e,1p+3e	1e,1e,0,2e,1p+4e	1e,1e,1e+1p,2e,1p+4e
Exopod	2n+2n+3n	2n+2n+4n	2n+2n+4n	2n+2n+4n
First pereiopod	Small buds			
Endopod		3e	4e	0,0,1e,1e+2e
Exopod		1n+2n+4n	1n+2n+4n	1n+2n+4n
Second pereiopod	Absent	Absent	Rudimentary	
Endopod				0,0,1e,2e
Exopod				1e+4e

a: aesthetasc; b: abdominal spine; c: spine; e: sparsely plumose seta; j: spiny projection; n: plumose natatory seta; p: plumose seta; r: degenerate plumose seta; s: simple seta; t: plumodenticulate teeth.

General morphology of first juvenile stage

Caparace (Figure 9A). Rostrum short with rounded apex. Eyes stalked.

Antennule (Figure 10C). Smaller than antenna. Peduncle three-segmented with two long sparsely plumose setae on proximal segment. Endopod three-segmented with four aesthetascs on distal segment. Placement and number of setae as shown.

Antenna (Figure 9D). Basis with one short simple seta on outer margin. Endopod 20-segmented with three or four short simple setae in each segment. Scaphocerite with 20 plumose setae plus one simple seta and three short setae on outer margin.

Maxillule (Figure 10A). Coxa with four sparsely plumose setae. Basis with six strong teeth and six sparsely plumose setae. Endopod bears a sparsely plumose seta distally.

Maxilla (Figure 10B). Endite coxal indistinguishable and basal very reduced bearing one sparsely plumose seta. Endopod not segmented, with one plumose seta on outer margin and one sparsely plumose seta distally. Scaphognathite with 29 plumose setae.

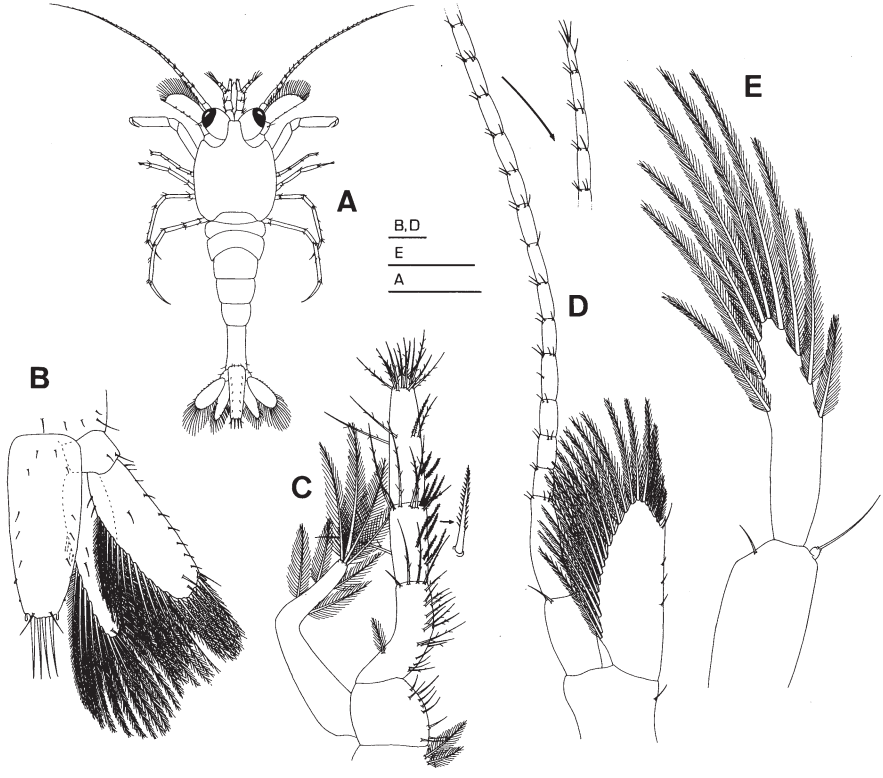

Fig. 9. *Philocheras fasciatus.* First juvenile: (**A**) dorsal view; (**B**) telson and uropods; (**C**) third maxilliped; (**D**) antenna; (**E**) first pleopod. Scale bars: A: 1000 µm; B–E: 100 µm.

First maxilliped (Figure 10D). Basis naked. Endopod not segmented with four plumose setae. Exopod as in previous stage.

Second maxilliped (Figure 10E). Basis bearing two sparsely plumose setae. Endopod five-segmented with the three first segments naked. Fourth segment with three sparsely plumose setae and four serrate setae. Fifth segment with nine sparsely plumose setae and two serrate setae. Exopod as in previous stage.

Third maxilliped (Figure 9C). Coxa with two plumose setae. Basis with nine simple setae on inner margin. Endopod three-segmented with 20, 16 and 20 setae, respectively; placement as shown. Exopod as in previous stage.

Pereiopods (Figure 11). All uniramous except second pereiopod. Number of setae and placement as shown.

Abdomen. Without spines on dorsal margins.

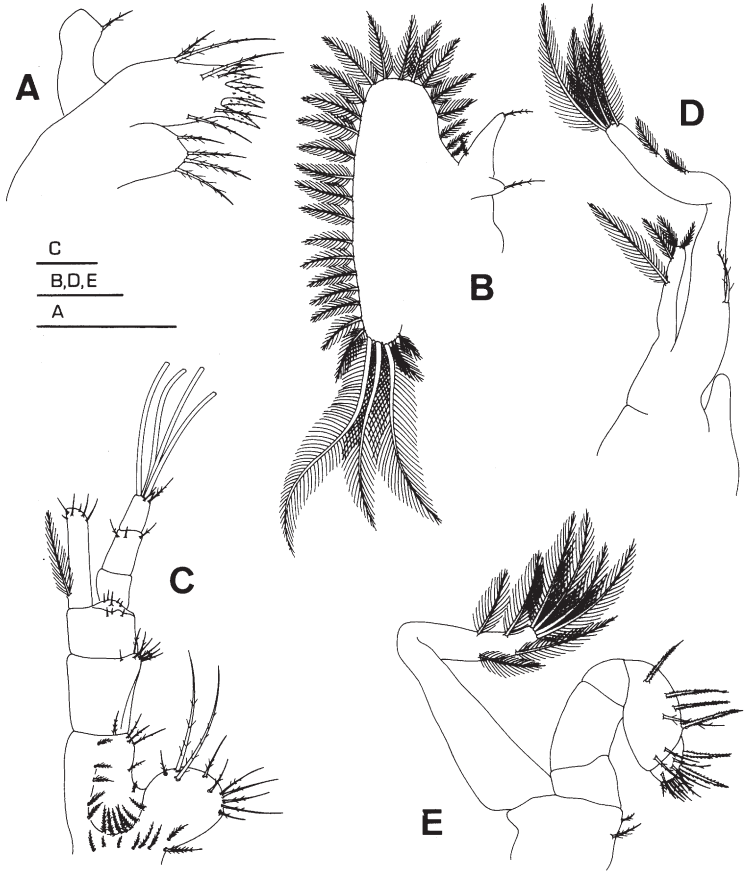

Fig. 10. *Philocheras fasciatus.* First juvenile: (**A**) Maxillule; (**B**) maxilla; (**C**) antennule; (**D**) first maxilliped; (**E**) second maxilliped. Scale bars: 100 μm.

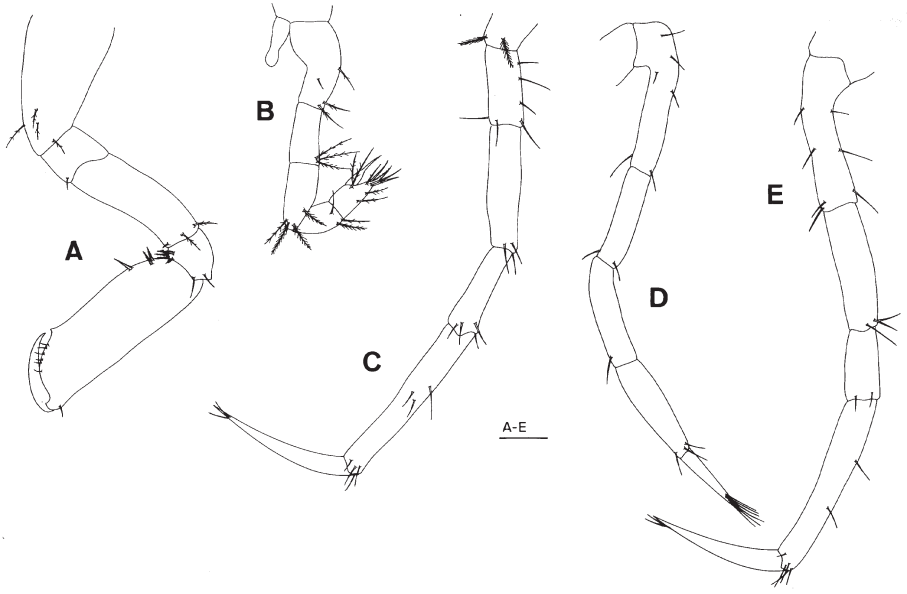

Fig. 11. *Philocheras fasciatus.* First juvenile: (**A**) First pereiopod; (**B**) second pereiopod; (**C**) third pereiopod; (**D**) fourth pereiopod; (**E**) fifth pereiopod. Scale bars: 100 μm.

Pleopods (Figure 9E). Functional and biramous. Basis with one simple seta. Small endopod bears a sparsely plumose seta. Exopod with nine plumose setae.

Telson (Figure 9B). Bearing three reduced setae on each lateral margin, two submarginal simple setae and four simple setae on posterior margin. Several diminutive setae on dorsal surface as illustrated.

Morphometric differences in plankton and laboratory larvae

In Cádiz Bay, *P.fasciatus* is a well established species but its populations are constituted by few individuals. During a plankton survey, 105 specimens of *P.fasciatus* were collected, 92% being in the first larval stage. This offered the possibility of determining whether morphometric differences exist between larvae found in nature and those obtained under artificial culture conditions. The results obtained are presented in Table II. The mean sizes of the carapace and antennule were significantly smaller in the reared specimens (t-test, $P < 0.01$), but no significant differences were observed in the abdominal spine length.

Plotted relationships between carapace length, antennule length and abdominal spine length of specimens from both populations fell into two distinct groups. A linear regression for each group showed a high variability, and good correlations between variables were not found ($R^2 < 0.04$ in all cases). The growth of the antennule and abdominal spine could not be considered to be proportional to the growth in carapace length. This feature was observed in both plankton and laboratory larvae. Comparisons between others larval stages were not statistically

Table II. Mean dimensions (μm; mean ± 95% confidence intervals) of some morphological features of the first zoeal stage of *P.fasciatus* reared in the laboratory and collected from plankton

	Laboratory		Plankton		*P*
	n	Mean	*n*	Mean	
Cephalothorax length	11	724.869 ± 14.50	36	800.218 ± 11.12	<0.01
Antennule length	11	396.205 ± 23.99	36	460.623 ± 9.77	<0.01
Abdominal spine length	10	112.837 ± 10.60	36	116 ± 6.06	>0.05

possible due to scarce numbers of specimens collected. However, we observed that planktonic larvae were larger in all cases.

Discussion

The complete larval development of *P.fasciatus* has not been previously described from laboratory-reared material. Gurney described some larval stages from laboratory and plankton, providing valuable information (Gurney, 1903a). Until now, numerous authors have commented on the features noted by Gurney without contributing new descriptions to complete the larval development.

The general characters of the larvae of the Crangonidae were given by Lebour (Lebour, 1931), and they could be summarized for zoeae stages in the presence of antennules not separated by an appreciable gap and with an elongated protopod in the form of a stout rod. *Philocheras* species are distinguished from other crangonid shrimps by the presence of a maxillule with a two-jointed palp, a fifth abdominal segment with lateral spines (except *P.trispinosus*), third and fourth abdominal segments usually with paired spines (but no median spine) and the flagellum of the antennule shorter than the carapace. Finally, *P.fasciatus* is easily identified by the presence of a protopod of the antennule elongated and a pair of lateral spines of the fifth segment which end in a sharply down-curved hook.

For *Philocheras* species whose complete development is known, the normal development consists of five larval stages (Pike and Williamson, 1961; Pessani and Godino, 1991; González-Gordillo *et al.*, 2000). In the present work, *P.fasciatus* passed through four subsequent zoeae stages to the juvenile under laboratory conditions. The fourth larval stage appeared to be an intermediate stage between the fourth and fifth typical stages described for other crangonids. The fourth larval stage was characterized by well developed uropods not reaching the posterior margin of the telson (Pike and Williamson, 1961). In contrast, the reduction of the outer setae of the telson to rudimentary setae [see (Gurney, 1903b)], or differences in meristic features of the maxilla and the development of pleopods, are characteristics of the fifth larval stage in other *Philocheras* species [e.g. (González-Gordillo *et al.*, 2000)]. Therefore, and according to Gore (Gore, 1985), it should be considered as the occurrence of irregular accelerated development in this study.

The intraspecific morphological variability in caridean shrimp larvae is very wide, even among sibling larvae reared under identical controlled conditions. Moreover, there is significant variability among different hatches (females), and

seasonal and regional differences in size and morphology [see e.g. (Criales and Anger, 1986)]. This variation has also been found in nature for other larvae of benthic marine invertebrates (Pechenik, 1999) and related to intrinsic and extrinsic factors, such as material source of larvae, food, heavy metals, etc. Broad (Broad, 1957) concluded that the number of stages varied according to the quantity of food available, and Criales and Anger (Criales and Anger, 1986) noted that high temperature caused increased moulting frequency and increasing morphological variation. In the present study, complete food requirements, together with a high temperature and low culture density, induced the occurrence of irregular development. This particular type of development is considered to be 'accelerated', as larvae are observed in a more developed state than that seen in their congeneric relatives, and development is condensed by the elimination of one terminal stage in ontogeny (Rabalais and Gore, 1985). In our case, the elimination of an intermediate zoeae stage should be considered to be occasional. The occurrence of zoeae IV and V in the plankton, at the same time and locality as when the ovigerous female was collected, would corroborate this hypothesis.

Variation in developmental time could have advantages, prolonging or reducing the planktonic larval phase. In the first case, this could provide a great potential for larvae to disperse and colonize new habitats. In contrast, a decrease in time of development with increasing temperature could be important because it could reduce horizontal larval dispersal. This would retain the larvae in the vicinity of the parental population, ensuring sufficient recruits to maintain the population, and also would avoid encounter with planktivorous predators, initiating major survival (McConaugha, 1992; Pinheiro *et al.*, 1994).

In addition to the differences in morphological features of the fourth zoea and the number of larval stages, we also noted that first zoea larvae reared under laboratory conditions were significantly smaller. Christiansen (Christiansen, 1973) noted that size in brachyuran larvae might vary with environmental conditions, and a similar phenomenon was reported by Knight (Knight, 1970) from planktonic/laboratory-reared albuneids. Our results may be a consequence of rearing, reflecting, in part, the effects of laboratory conditions. Size variation stage in *P.fasciatus* might be due to culture conditions, and be considered a 'laboratory artefact'. Other possible interpretations would be supported by a natural variation of this species. However, this hypothesis would be a minor probability, as larvae caught from the plankton came from the same locality as the ovigerous shrimps and statistical analysis revealed two different populations.

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