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ORIGINAL ARTICLE

Larval stages of the deep-sea lobster *Polycheles typhlops* (Decapoda, Polychelida) identified by DNA analysis: morphology, systematic, distribution and ecology

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Abstract A total of 25 specimens of *Eryoneicus* larvae were collected near the Balearic Archipelago (Western Mediterranean Sea) in 2009 and 2010. Detailed morphological examination indicated that the smallest individual corresponded with the first zoea (ZI) stage of *Polycheles typhlops* hatched from a berried female by Guerao and Abelló (J Nat Hist 30(8):1179–1184, 1996). Only two species of deep-sea polychelid lobster, namely *P. typhlops* and *Stereomastis sculpta*, are known to occur in the Mediterranean. Genetic distance comparisons and phylogenetic analysis of the mitochondrial 16S rDNA and Cox I genes of this early larva together with adults from several *Polycheles* and *Stereomastis* species allowed us to assign it to *P. typhlops*. This is the first wild-caught larval stage of a polychelid lobster being identified using molecular techniques. The remaining specimens were attributed to zoeal stages II–III and decapodid stage based on morphological comparison. The arrangement of spines along the anterior part of the middorsal line (R, 1, 1, 1, 2, C_1), characteristic of the former species *E. puritanii*, discriminates these larvae from other *Eryoneicus* found in the Mediterranean. The clear presence of epipods on the third maxilliped and pereiopods of the decapodid stage gives further support to the identification of *E. puritanii* as the larval stages of *P. typhlops*. Additionally, information on the ecology of these larvae, their abundances during different seasons, as well as their bathymetric distribution is reported.

Keywords *Eryoneicus* · DNA barcoding · Crustacea · Western Mediterranean · Vertical distribution

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Introduction

Mediterranean deep-sea benthos is dominated by fishes and decapod crustaceans, but the biology of several key groups is still largely unknown (Cartes and Abelló 1992). Polychelid lobsters are often referred to as "deep-sea blind lobsters" because all extant forms live in deep water and have reduced eyes. These lobsters can be easily distinguished from other reptantia decapods by the presence of well-developed chelae on pereiopods 1–4 (Galil 2000; Ahyong 2009). The Polychelidae now includes over 40 extant and fossil species, but the systematics of the family is still under debate, especially at the genus level (Ahyong and Brown 2002; Ahyong and Chan 2004; Ahyong and

Galil 2006). Despite several taxonomic uncertainties have been clarified within this family in recent years (Ahyong 2009; Chan 2010), studies concerning the biology of polychelids are still lacking. There is some information available on the trophic role of these lobsters (Cartes 1993, 1998; Maynou and Cartes 1998; Cartes et al. 2007; Gastoni et al. 2010), but sampling difficulties have prevented scientists from understanding the ecology of polychelids in detail. Knowledge of the reproductive biology of deep-sea species is also scarce and mostly confined to a few species from deep continental slopes and hydrothermal vent habitats (Wenner 1979; Abelló and Cartes 1992; Mullineaux et al. 1995; Maiorano et al. 1998; Company and Sardà 1998; Company et al. 2003; Follesa et al. 2007; Cabiddu et al. 2008). Similarly, the links that have been established to date between deep-sea benthic adults and pelagic larval forms are uncertain.

Only two species of polychelid lobsters, namely *Polycheles typhlops* (Heller 1862) and *Stereomastis sculpta* (Smith 1880), are known to occur in deep-sea muddy sand bottoms of the Mediterranean Sea (Zariquiey-Alvarez 1968). Previous studies carried out in NW Mediterranean have reported *P. typhlops* at depths between 300 and 2,000 m and *S. sculpta* between 1,196 and 2,261 m (Abelló and Cartes 1992; Cartes et al. 1993; Company and Sardà 2000; Company et al. 2003, 2004; Follesa et al. 2007). Females of both species can be found in shallower depths than males, suggesting a relationship with reproductive behaviour (Abelló and Cartes 1992). In both *P. typhlops* and *S. sculpta*, females attain larger sizes than males, with the largest females being more likely to be found gravid than smaller females. Ovigerous females of *P. typhlops* have been captured throughout the year in the Western Mediterranean (Abelló and Valladares 1988; Maiorano et al. 1998; Company et al. 2003; Follesa et al. 2007). Gravid females of *Stereomastis nana* from the western north Atlantic were also caught throughout the year and presented a size-distribution pattern similar to local populations of *P. typhlops* (Wenner 1979). Spawning-related movements to locate the optimal depth range for hatching may explain the large proportion of ovigerous females at the shallowest depths of the species distribution, as found in other bathyal species (Wigley et al. 1975; Somerton 1981; Abelló and Macpherson 1991). Knowledge on larval morphology, vertical distribution and ecology of many decapod species is still scarce in the Western Mediterranean (Torres et al. 2013, 2014) and particularly for deep-sea species. This is largely due to the relative scarcity of plankton samples covering the entire water column and the lack of expertise for their correct identification. Moreover, the capture of living deep-sea lobsters and their larval-rearing under laboratory conditions presents serious difficulties.

Several planktonic specimens collected from Mediterranean or nearby Atlantic waters, and originally described under the generic name *Eryoneicus*, have been claimed to correspond to the larval stages of Polychelidae (Bernard 1953; Fredj and Laubier 1985). The first description for the genus *Eryoneicus,* a specimen "half an inch" long captured around 3,000 m depth in the Canary Islands, was reported as *Eryoneicus caecus* by Bate (1888) and later as *Eryoneicus faxoni* by Bouvier (1905). Several smaller specimens, ranging from 5 to 10 mm in total length, were caught in the Gulf of Napoli and described as *Eryoneicus puritanii* by Lo Bianco (1903). Another specimen captured around 3,000 m depth in Azores waters was named *Eryoneicus spinoculatus* by Bouvier (1905, 1917) and then Selbie (1914) described three new species, namely *E. hibernicus*, *E. scharffi* and *E. kempi*, based on late-stage larvae collected from north Atlantic waters. According to Fredj and Laubier (1985), out of the four different *Eryoneicus* species that can be found in deep Mediterranean Sea waters, one type (*E. puritanii*) could be assigned to *P. typhlops*, whereas the other three (*E. faxoni, E. kempi* and *E. spinoculatus*) could not be accepted as larval stages of *S. sculpta* and perhaps belong to adult species that still have to be discovered (Fredj and Laubier 1985). All of these late-stage *Eryoneicus* show a very inflated carapace with numerous spines and functional natatory pleopods (Bernard 1953).

Despite the *Eryoneicus* name was suppressed by the International Commission on Zoological Nomenclature (1965) (see also Holthuis 1962), the different larvae are still named referring to the old nomenclature given that no study has conclusively proved the assignment of any *Eryoneicus* to the corresponding adult species. Indeed, no information on polychelid larvae hatching in captivity was available until Guerao and Abelló (1996) described a first larval stage of *P. typhlops*. The larvae hatched by Guerao and Abelló (1996) had not yet extruded or only partially extruded the natatory setae of the cephalothoracic appendages, so the description may not reflect the actual morphology of the larvae when hatching under natural conditions. The smallest *Eryoneicus* sampled from the wild so far, with a carapace length (CL) of 2 mm, was attributed to the third larval stage of *E. connus* by Bernard (1953). Selbie (1914) also caught a "juvenile" stage of *Eryonicus* sp. which corresponds to an advanced zoeal stage (TL = 7 mm; Plate IV) with undeveloped pleopods. Later stages of *Eryoneicus* larvae have well-developed pleopods and fit the definition of megalopa in this respect (Williamson 1969). The concepts "post-larva", "decapodid" and "megalopa" have been interchangeably used in many decapod larval descriptions to refer to the transition phase between pelagic larvae and benthic phases (Gurney 1942; Kaestner 1970; Felder et al. 1985; Anger 2001). In the

present study, the general name "decapodid" is used to denote the final larval phase preceding the moult to the first juvenile stage and characterised by the existence of functional pleopods and uropods with long plumose natatory setae (Kaestner 1970).

The aim of this study is to provide new evidence on the occurrence, distribution and morphology of larval stages of *P. typhlops*. Complete morphological descriptions are provided for three zoeal and one decapodid stages, while identification of the first larval stage of *P. typhlops* is confirmed through DNA analyses. In addition, a comparison of our plankton-collected specimens with previous descriptions of the larval stages of other Polychelidae is included. Finally, information on the ecology of these larvae, their abundances during different seasons, as well as their bathymetric distribution in the aphotic layers of the water column is reported.

Materials and methods

Sampling

Two multidisciplinary research surveys were conducted off the Balearic Islands (Western Mediterranean) during late autumn (29 November to 18 December 2009) and summer (11–30 July 2010). The main objective of the surveys was to determine the taxonomic composition, abundance, structure and vertical distribution of the mero-planktonic community at two stations located off the north-west and south of Mallorca (Balearic and Algerian subbasin, respectively). The sampling sites were located over 200 and 900 m depth (shelf break and middle slope, respectively) and present different environmental conditions (Pinot et al. 2002; López-Jurado et al. 2008). At the southern station of Mallorca, the upper slope is irregular, with numerous small canyons, while it is smooth in the northern station (Acosta et al. 2002). Two additional polychelid zoeal stages were captured between 300 and 400 m depth over the slope of Blanes canyon (NW Mediterranean) during 2004 under the "Observation, analysis and modelling of the Mediterranenan Sea" (OAMMS-04) survey, and were also used for photographic record.

A total of 218 depth-stratified meso-zooplankton samples, which were integrated in 34 hauls, were used to analyse decapod larvae composition. From these, 18 samples were collected using a multi-net (HYDRO-BIOS) in 2009 and 16 samples using a multiple opening–closing net and environmental sensing system (MOCNESS) in 2010 (Olivar et al. 2012). In order to determine the vertical distribution of decapod larvae, a series of oblique hauls were performed at four stations for 36 h at each site during the surveys in 2009 and 2010. Each oblique haul was performed down to 200 m depth on the shelf break and 500 m (in summer) or 850 m (in late autumn) on the middle slope, and seven or five depth strata were sampled depending on the season (summer and late autumn, respectively). The thickness of these strata changed with bathymetry and season (sampling protocols as in Torres et al. 2014). Supra-benthos samples were collected with a rectangular net rigged in a beam-trawl and used to catch mega-benthic fauna within 0.6 m above the bottom, with a cod-end mesh size of 500 μm in late autumn and 1,000 μm during summer. The catch speed was three knots, and the effective tow duration was 30 min. Supra-benthic samples were preserved in ethanol 96 % immediately after collection (sampling protocols as in Herrera et al. 2014). Once in the laboratory, decapod crustacean larvae were sorted and identified to species level and developmental stage whenever possible, using available descriptions and keys (Dos Santos and González-Gordillo 2004). Information on the stations where polychelid larvae were found is presented in Table 1. The zoeal stages and decapodid have been deposited at the Biological Collections of Reference of the Institut de Ciències del Mar (CSIC) in Barcelona under accession numbers ICMD000049-56.

In order to obtain reference DNA sequences for larval identification, several adult specimens for both *P. typhlops* and *S. sculpta* were sampled from Mediterranean deep-sea waters. *P. typhlops* was sampled from the region under the MEDITS2011 research cruise, and *S. sculpta* was sampled in July 2010 from the Catalano-Balearic basin, between Barcelona and Mallorca. DNA sequences for specimens from Atlantic waters were obtained from GenBank (Table 2).

DNA analyses

Total genomic DNA extraction from the first zoea specimen captured during supra-benthos sampling south of the Balearic Sea (Station: 39.067N–2.675E; Table 1) and the adult specimens from Mediterranean waters was performed using the Chelex-resin method (Palero et al. 2010). The standard universal primers for DNA barcoding (Folmer et al. 1994) were used for PCR amplification, given that they had been previously tested in *Polycheles* with positive results (see Palero et al. 2009). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1× buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The PCR thermal profile used was 94 °C for 4 min for initial denaturation, followed by 30 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s and a final extension at 72 °C for 4 min. Amplified PCR products were purified with QIAGEN-QIAquick PCR Purification Kit (QIAGEN Inc) prior to direct sequencing of the product. The

Table 1 Information on the stage of development, number (N), densities, date of capture, geographical location, time of day, capture depth and bottom depth for larvae of *Polycheles typhlops* during late autumn (2009), summer (2010) surveys

Season (net)	Stage of development	*N*	Densities (*N*/1,000 m^3)	Date	Latitude (N)	Longitude (E)	Time GMT	Capture depth (m)	Bottom depth (m)
Late autumn (HYDRO-BIOS)	Zoea I	1	1.2	04/12/2009	39.003	2.419	23:54	350–600	907
	Zoea I	1	0.8	04/12/2009	39.003	2.419	23:54	200–350	907
Summer (Beam-trawl)	Zoea I	1	2.5	19/07/2010	39.067	2.675	17:40	358	359
Summer (MOCNESS)	Zoea I	5	6.1	15/07/2010	38.904	2.496	2:01	400–500	668
	Zoea I	1	1.1	15/07/2010	39.060	2.461	16:42	400–500	853
	Zoea I	6	2.8	15/07/2010	39.053	2.453	16:56	200–400	858
	Zoea I	1	0.5	23/07/2010	39.813	2.151	4:16	200–400	957
	Zoea I	3	2.1	24/07/2010	39.804	2.136	23:45	200–400	966
	Zoea II	1	0.5	14/07/2010	38.974	2.457	7:11	200–400	893
	Zoea II	2	0.9	15/07/2010	39.053	2.453	16:56	200–400	858
	Zoea II	1	0.5	23/07/2010	39.813	2.151	4:16	200–400	957
	Zoea III	1	0.4	15/07/2010	38.959	2.435	21:02	200–400	905
	Decapodid	1	0.6	24/07/2010	39.804	2.137	5:54	600–800	964

Table 2 Samples included for phylogenetic analyses in the present study

Species	Voucher	GenBank acc	Locality
Polycheles typhlops	JSDUKdeep 58	JQ305984.1	57.30°N 9.00°W (Scotland, SW St Kilda)
Polycheles typhlops	JSDPX15-15	JQ306172.1	37.36°N 9.17°W (Portugal)
Polycheles typhlops	M11L031-1	KJ825708	Western Mediterranean
Polycheles typhlops	M11L031-2	KJ825709	Western Mediterranean
Polycheles typhlops	Eryoneicus_Majorca	KJ825710	Western Mediterranean
Polycheles enthrix	MNHN:IU200814828	HQ241553.1	France, Nouvelle-Calédonie (South)
Stereomastis nana	JSDUKdeep 41	JQ305991.1	58.29°N 9.00°W (Scotland, SW St Kilda)
Stereomastis nana	JSDUKdeep 43	JQ305992.1	58.29°N 9.00°W (Scotland, SW St Kilda)
Stereomastis sculpta	AI-101	KJ825706	Western Mediterranean
Stereomastis sculpta	AI-102	KJ825707	Western Mediterranean
Stereomastis sculpta	PSCU-2	EU377741.1	Sardinia, Italy
Sagmariasus verreauxii	KC3212	FJ174952.1	Australia

sequences were obtained using the Big-Dye Ready-Reaction kit v3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer from the Scientific and Technical Services of the Centre for Public Health Research (Valencia, Spain).

The DNA sequence alignment was conducted using the program MUSCLE v3.6 (Edgar 2004) with default parameters and then checked by eye. Before carrying out the likelihood-based analysis, model selection of nucleotide substitution was performed with MEGA5 (Tamura et al. 2011) according to BIC scores (Bayesian Information Criterion) and AICc value (Akaike Information Criterion, corrected). The aligned dataset was then used to estimate maximum likelihood (ML) phylogenies under the selected DNA substitution model using MEGA5 (Tamura et al. 2011). Bootstrap branch support values were calculated with 500 ML replicates. The aligned dataset was also used in MEGA5 (Tamura et al. 2011) to estimate Kimura 2-Parameter (K2P) distances among DNA sequences of the larval specimen and adults from different polychelid species.

Morphological descriptions

Dissection and measurements were taken with a Nikon SMZ800 stereo microscope equipped with an image analysing system (AnalySIS, SIS, Münster, Germany). An Olympus BH-2 microscope was used in the observation of

the features of the appendages. The following measurements were taken: CL was measured as the distance from the frontal margin to the posterior margin of the carapace; carapace width (CW) as the greatest distance across the carapace; total length (TL) was measured as the distance from the frontal margin of the carapace to the posterior tip of the telson. The number of individuals examined per stage varied between 1 and 4.

For scanning electron microscopy (SEM), two first zoeal stages were sonicated for 2–3 min for removal of surface debris and dehydrated in a graded ethanol series (70, 90 and 100 %). After critical point drying, individuals were mounted on SEM stubs with self-adhesive carbon stickers and were coated in gold. Dried specimens were observed with a Hitachi H-4100 FE SEM.

The long plumose setae on the distal exopod of the maxillipeds and pereiopods are drawn truncated for clarity. Larval descriptions follow the basic malacostracan body pattern from anterior to posterior, and setal armature on appendages is described from proximal to distal subdivisions and from endopod to exopod (Clark et al. 1998; Haug et al. 2013). The setal terminology used was established by Ingle (1993).

Results

Phylogenetic analyses

The new sequences for the *Eryoneicus* larva (Station: 39.067°N–2.675E; Table 1) and the adult samples used for molecular analyses have been deposited in GenBank with Accession numbers as shown in Table 2. The length of the aligned dataset for the COI gene was 679 bp and showed an excess for AT content (~60 %), as commonly found in mtDNA gene sequences. The TN93 + I DNA substitution model gave the lowest score under both the AICc (3,602.16) and the BIC (3,800.37), and therefore, it was used for subsequent ML searches. The phylogenetic tree obtained clearly showed the species-level assignment of the larvae, with the clade formed by the *Eryoneicus* specimen and the available *P. typhlops* adult specimens providing a 100 bootstrap support (Fig. 1). The K2P distance values observed when comparing the zoea collected from the plankton with either *S. nana* (21.7 %) or *S. sculpta* (24.8 %) fall within divergence levels observed among different genera, whereas the comparison with *P. typhlops* (0.17 %) is within the standard intra-specific distances observed in decapod crustaceans (see "Discussion").

Morphological descriptions

The first zoeal stage and the decapodid stage are described in detail. For the zoeal stages II and III, only the main differences from the first zoea are presented.

Zoea I

Size: TL = 1.8–2.0 mm; CL = 1.4–1.6 mm; CW = 1.3–1.5 mm.

Carapace (Figs. 2a, b, 3a, b). Globose, almost spherical, much wider than the pleon, with numerous (55–60) ramified spines and long plumose setae. Two robust processes (column) are placed along the middorsal line, one is at middorsal carapace (C_1, Fig. 2b, c) and the other is at the posterior part (C_2, Fig. 2b, d, e). The arrangement of spines on middorsal line is R, 1, 1, 1, 2, C_1, 2 C_2 (see Fig. 3b). Frontal margin with a rostral spine (Fig. 3c, f), long and ramified (Fig. 2e). Vestigial eyes-stalk present. Details of the first spine of dorsal carina and antennal spine are shown in Fig. 2g, h.

Antennule (Fig. 3d). Not subdivided and conical, with two aesthetascs and three setae distally. Inner flagellum bud present.

Antenna (Fig. 3e). Biramous, not subdivided and without setae.

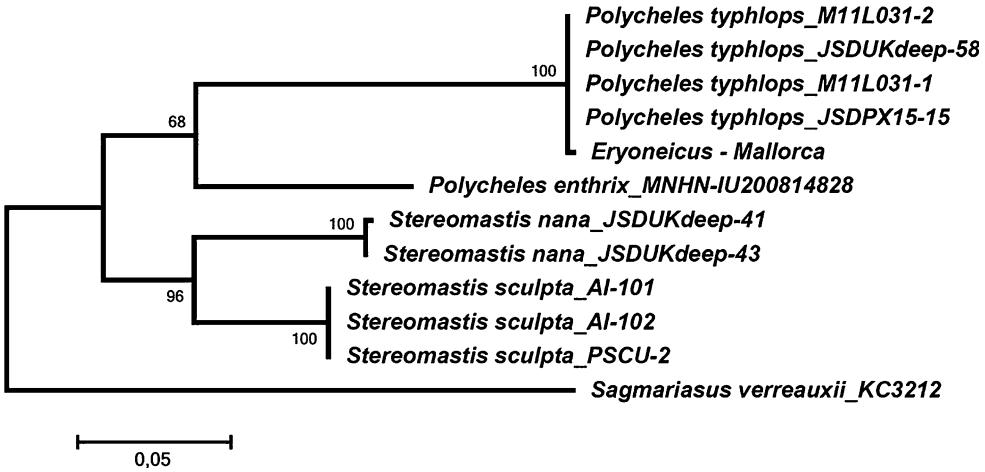

Fig. 1 Maximum-likelihood phylogenetic tree estimated from the COI sequence data, showing the position of the *Eryoneicus* specimen genetically analysed in the present study

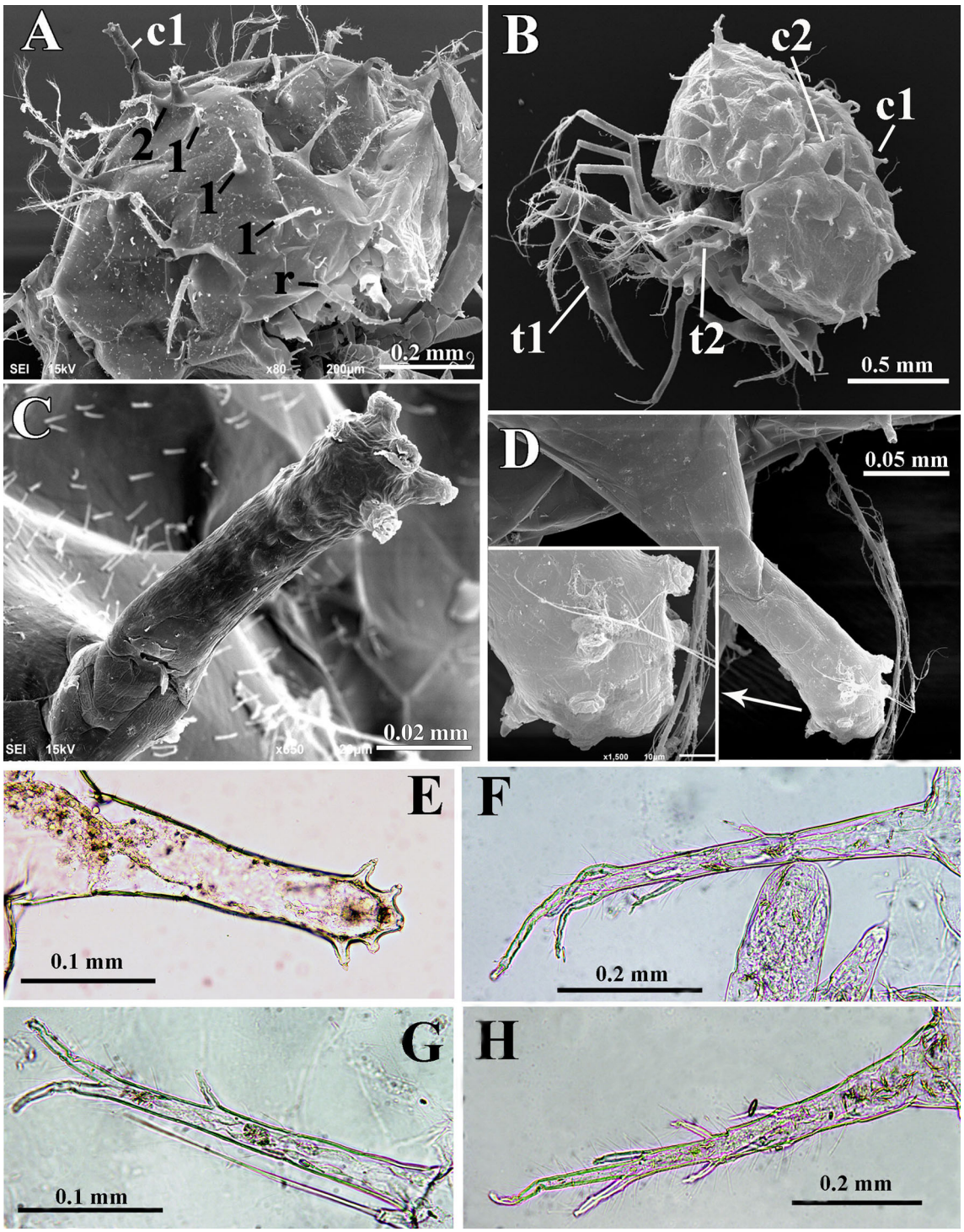

Fig. 2 *Polycheles typhlops*. First larval stage (ZI). **a** carapace, frontal view, indicating spines on middorsal line; **b** total animal, posterior view; **c** anterior column; **d**, **e** posterior column; **f** rostral spine; **g** first spine of dorsal carina; **h** antennal spine. *r* Rostral spine; *c1* anterior column; *c2* posterior column; *t1* first pereiopod; *t2* second pereiopod

Mandible (Fig. 3f). Well-developed, showing no distinction between molar and incisor portions, with eight teeth. Not subdivided palp bud present.

Maxillule (Fig. 3g). Coxal endite with five plumo-denticulate setae (four terminal + one long setae in the inner margin). Basipodal endite with eight setae (three cuspidate + five plumo-denticulate).

Maxilla (Fig. 3h). A single lobe present with two simple setae. Exopod (scaphognathite) with 26–28 marginal plumose setae.

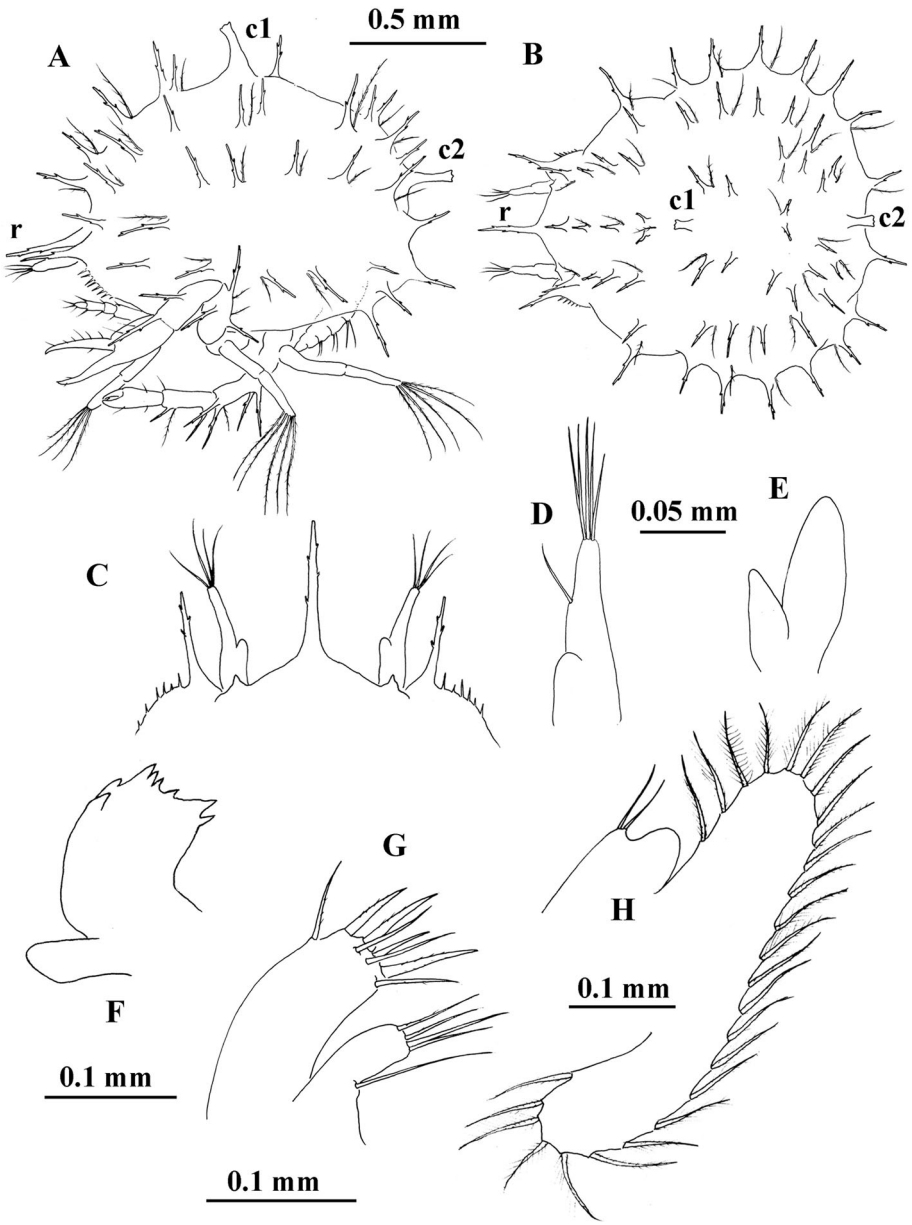

Fig. 3 *Polycheles typhlops*. First larval stage (ZI). **a** Total animal, lateral view; **b** total animal, dorsal view; **c** frontal margin, dorsal view; **d** antennule; **e** antenna; **f** mandible; **g** maxillule; **h** maxilla. *c1* Column anterior; *c2* column posterior; *r* rostral spine

First maxilliped (Fig. 4a). Biramous. Protopod with 4 setae on the inner margin. Endopod not subdivided with four terminal plumose setae and one subterminal simple setae. Exopod not subdivided with four lateral and four long terminal plumose setae.

Second maxilliped (Fig. 4b). Biramous. Protopod with 6 setae in the inner margin. Endopod 3-subdivided with 2, 6, 5 setae. Exopod long (around three times longer than the endopod) with four long terminal plumose setae.

Third maxilliped (Fig. 4c). Biramous. Protopod with two setae. Endopod 5-subdivided with 1, 4, 4, 7, 5 setae. Exopod with six long terminal plumose setae.

First pereiopod (Fig. 4d). Biramous. Coxa with three setae. Basis with five setae. Endopod 4-subdivided and cheliform; ischio-merus (ischium and merus not separated) with four strong ramified spines and with a long plumose seta adjacent to each spine; carpus with two strong ramified spines and two distal simple small spines, and with a long plumose seta adjacent to each spine; propodus longer than the ischio-merus and with about 14 setae, including small setae on fixed finger; dactylus half the length of the propodus, apically curved with about ten setae randomly distributed on both margins. Exopod with six long plumose setae.

Second pereiopod (Fig. 4e). Biramous. The coxa was lost. Basis with four setae. Endopod four-subdivided and cheliform, shorter than the first pereiopod; ischio-merus with five strong ramified spines and with a long plumose seta adjacent to each spine; carpus half the length of the ischio-merus with two strong ramified spines and five

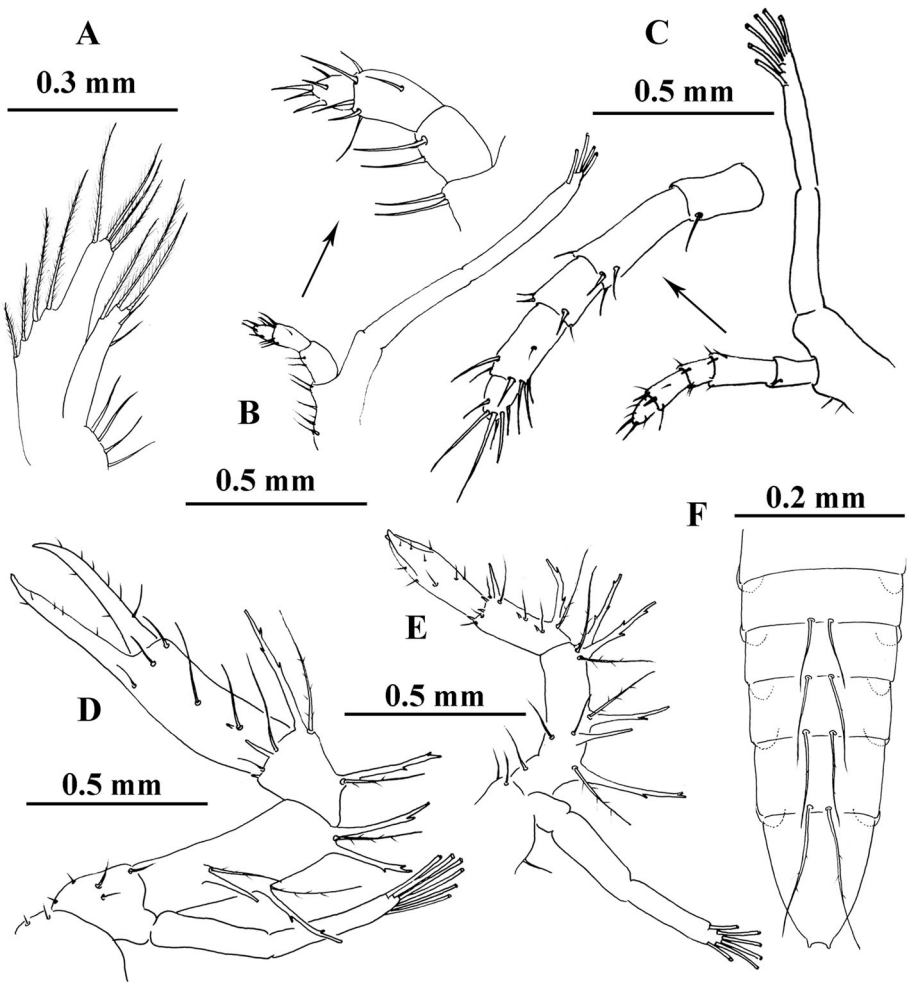

Fig. 4 *Polycheles typhlops*. First larval stage (ZI). **a** First maxilliped; **b** second maxilliped; **c** third maxilliped; **d** first pereiopod; **e** second pereiopod; **f** pleon, dorsal view

simple minute spines, with a long plumose seta adjacent to each spine; propodus longer than carpus with several minute setae randomly distributed; dactylus 2/5 times the length of the propodus with several minute setae distributed as figured. Exopod with six long plumose setae.

Third pereiopod. Present as bud (not figured).

Fourth and fifth pereiopods: absent.

Pleon (Fig. 4f). Small and six-segmented. With a pair of postero-dorsal long sparsely setose setae on pleonites 3–6.

Minute pleopod buds are present on pleonites 2–6.

Telson: triangular, with two posterior minute processes on each side of the small concave posterior margin.

Zoea II

Size: TL = 3.3 mm; CL = 2.3 mm; CW = 2.2 mm.

Carapace (Figs. 5a, 6a, b). Frontal region with rostrum and a pairs of long (shorter than rostrum) ramified spines. The arrangement of spines on middorsal line is R, 1, 1, 1, 2, C_1, 2, 2, C_2, 2.

Antennule (Fig. 6c). Outer flagellum two-subdivided, with two subterminal aesthetascs and three terminal setae on distal subdivision. Inner flagellum longer than previous stage.

Antenna (Fig. 6d). Incipiently subdivided. Renal bud process present.

Mandible (Fig. 6e). Now with ten teeth.

Maxilla. Exopod (scaphognathite) with 33 marginal plumose setae.

Second maxilliped. Protopod with seven setae in the inner margin. Endopod three-subdivided with 3, 6, 5 setae.

Third maxilliped. Endopod five-subdivided with 2, 6, 4, 7, 5 setae.

Second pereiopod. Ischio-merus with one additional simple spine in the inner margin. Carpus with one additional minute distal spine.

Third pereiopod. Biramous, not subdivided and unarmed.

Pereiopods 4 and 5. Uniramous, present as a bud.

Pleon (Fig. 6f–h). Pleonites completely differentiated.

Pleopods (Fig. 6g) Biramous buds on pleonites 2–5. Pleonite six with biramous uropod buds.

Telson (Fig. 6h). Unarmed, two times longer than wide, posterior end 1/3 length of anterior part.

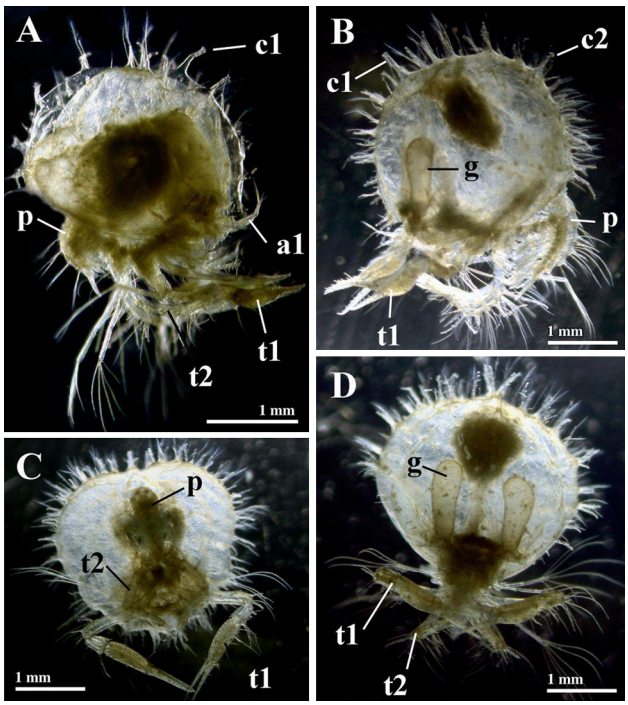

Fig. 5 *Polycheles typhlops*. Second zoeal stage (ZII). **a** Lateral view. Third zoeal stage **b** lateral view; **c** ventral view; **d** frontal view. *a1* Antennule; *c1* anterior column; *c2* posterior column; *g* antennal gland; *p*, pleon; *t1* first pereiopod; *t2* second pereiopod. (material from OAMMS-04 surveys)

Zoea III

Size: TL = 4.7 mm; CL = 3.3 mm; CW = 3.4 mm.

Carapace (Figs. 5b–d, 7a, b). Cervical groove and branchial carinae incipiently developed. The number of the spines increases, many scattered between carinae.

Antennule (Fig. 7c). Biramous. Statolith present in the peduncle, with two short spines. Inner flagellum incipiently three-subdivided with 0, 2, 2 aesthetascs and 0, 0, 3 setae. Outer flagellum not subdivided with 3 terminal setae.

Antenna (Fig. 7d). Biramous. Exopod incipiently subdivided, without setae; endopod not subdivided, shorter than renal process and with one terminal setae.

Mandible (Fig. 7e). Now with ten teeth. Palp two-subdivided with a simple seta on distal subdivision.

Maxilla (Fig. 7f). Two endites with three and two setae, respectively. Scaphognathite with 50–54 plumose marginal setae (not figured).

First maxilliped. Protopod with five setae on the inner side. Exopod not subdivided with eight plumose setae.

Second maxilliped. Protopod with nine setae. Endopod three-subdivided with 6, 8, 5 setae.

Third maxilliped. Protopod with six setae. Endopod five-subdivided with 4, 12, 6, 10, 5 setae.

First pereiopod (Fig. 7g). Ischio-merus with four strong ramified spines; carpus with five spines (two strong ramified + three simple); propodus with seven simple spines. Setation as shown.

Second pereiopod (Fig. 7h). Ischio-merus with nine spines (five strong ramified + four simple); carpus with eight spines (two strong ramified + six simple). Setation as shown.

Pereiopods 3–5. Short and not subdivided.

Pleon (Fig. 7i–k). Small. First pleonite with one dorsal simple setae; second pleonite with a small postero-dorsal process and two long plumose setae; pleonites 3–5 each with one long postero-dorsal process, two long plumose setae and two simple setae; pleonite six with one long postero-dorsal process, two long and two small setae; all pleonites with rounded pleura, except the sixth that ends with a small process.

Pleopods (Fig. 7i, k). Without setae, propodus incipiently separated from the ramus; endopod presenting a small *appendix interna*.

Telson (Fig. 7i, j). Triangular shape in dorsal view, ending in a sharp median point, with one long antero-dorsal spine and two small simple setae on dorsal margin, lateral margins with 7–8 spines on each side.

Decapodid

Size: TL = 16.3 mm; CL = 8.5 mm; CW = 7.7 mm.

Carapace (Fig. 8a–c). Longer than wider, pear-shaped in dorsal view. Frontal margin with rostral spine simple, shorter than antennular peduncle. Orbital sinus well defined, internal angle of orbital sinus sparsely setose ending in a pointed process. Surface with more than 180 spines and long plumose setae, some in rows and carinae but many scattered between them. The arrangement of spines on median carina, between the rostral spine and the posterior margin is R, 1, 1, 1, 2, C_1, 2, 2, C_2, 2 (see Fig. 8a, b). Brachial region with 4 carinae; branchial upper carina with 11–13 spines; lateral carina with about 25 spines, including the antennal spine; longitudinal brachial carina with 6 spines in the posterior half of the carapace and about 24 minute spines in the anterior half of the carapace. Branchial lower carina with 17 small spines in the posterior half of the carapace; this carina does not reach the anterior part of the carapace. Eyestalks with a spine.

Antennule (Fig. 8d). Peduncle three-subdivided, basal subdivision flattened and enlarged with two distal long simple setae, the inner margin extends in the form of a long ridge triangular whose outer margin has about six long spines; posterior subdivisions unarmed. Outer flagellum approximately three times shorter than inner flagellum with 9–10 subdivisions, inner flagellum with 27 subdivisions.

Antenna (Fig. 8e). Renal process long, oblique, distally dilated. Scaphocerite short, lingulate, with 23–25 plumose setae. Flagellum of the endopod with 30 subdivisions.

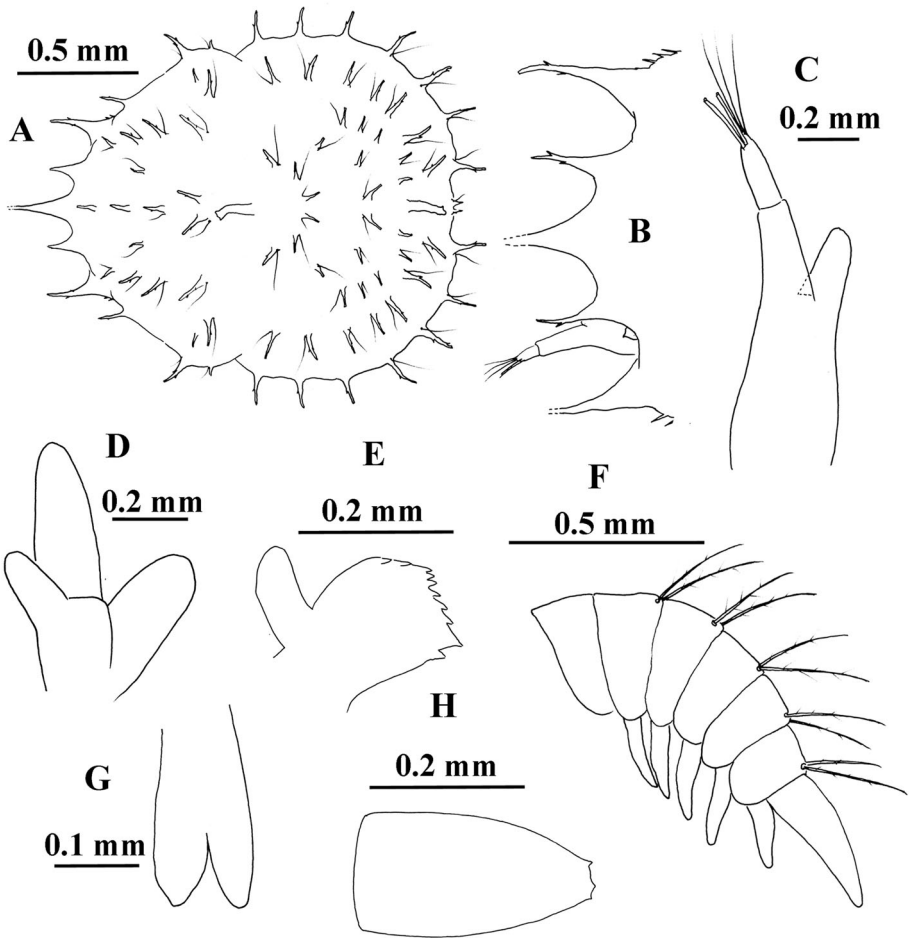

Fig. 6 *Polycheles typhlops*. Second zoeal stage (ZII). **a** Cefalothorax, dorsal view; **b** frontal margin, dorsal view; **c** antennule; **d** antenna; **e** mandible; **f** pleon; **g** first pleopod; **h** telson

Mandible (Fig. 8f). Similar to the zoeae with 14–15 triangular teeth, no show distinction between molar and incisor portions. Palp two-subdivided with 20–24 and more than 30 setae, respectively.

Maxillule (Fig. 8g). Coxal and basipodal endite with about 15 and 23 setae, respectively; without endopod.

Maxilla (Fig. 8h). Biramous, two maxillar lobes present, the smaller one with three distal simple setae and the longer one with 13 marginal simple setae. Scaphognathite large, with numerous marginal plumose setae.

First maxilliped (Fig. 9a). Endopod slender; exopodal lobe membraneous, reniform, extending further back than scaphognathite, exopod anteriorly divided into two lobes enclosing efferent passage.

Second maxilliped (Fig. 9b). Endopod four-subdivided densely setose.

Third maxilliped (Fig. 9c). Endopod five-subdivided densely setose, with vestigial epipod.

First pereiopod (Fig. 9d). First pereiopod very long, more robust than P2–5, ischium and merus now separated; spination as shown. Podobranch, epipod and two arthrobranch present.

Pereiopods 2–5 (Fig. 9e–h). Successively shorter posteriorly. Pereiopods 2–4 cheliform. Long spines present in ischio-merus and carpus of the second pereiopod (Fig. 9e). Third pereiopod with a distal long spine on carpus. Pereiopods 2–4 with podobranch, epipod, two arthrobranch and one pleurobranch present. Pereiopod five with one pleurobranch.

Pleon (Fig. 8a, b). Well-developed, spinulation indicated in Table 3; pleura of pleonites 1–2 rounded; pleura of pleonites 3–6 ending in a short sharp spine on the third and fourth but long and pointed on the fifth and sixth.

Pleopods (Fig. 9i). Biramous and functional; endopod with 30–32 plumose setae and bears an *appendix interna* with 10 coupling hooks; exopod with 34–36 plumose setae. Uropods functional, with numerous long plumose setae (endopod and exopod with more than 50 and 65, respectively).

Telson (Fig. 8a, b). Lanceolate in dorsal view, dorsal surface with one small and one strong spine placed anteriorly and several short simple setae randomly distributed. Each lateral margin with 6–9 spines.

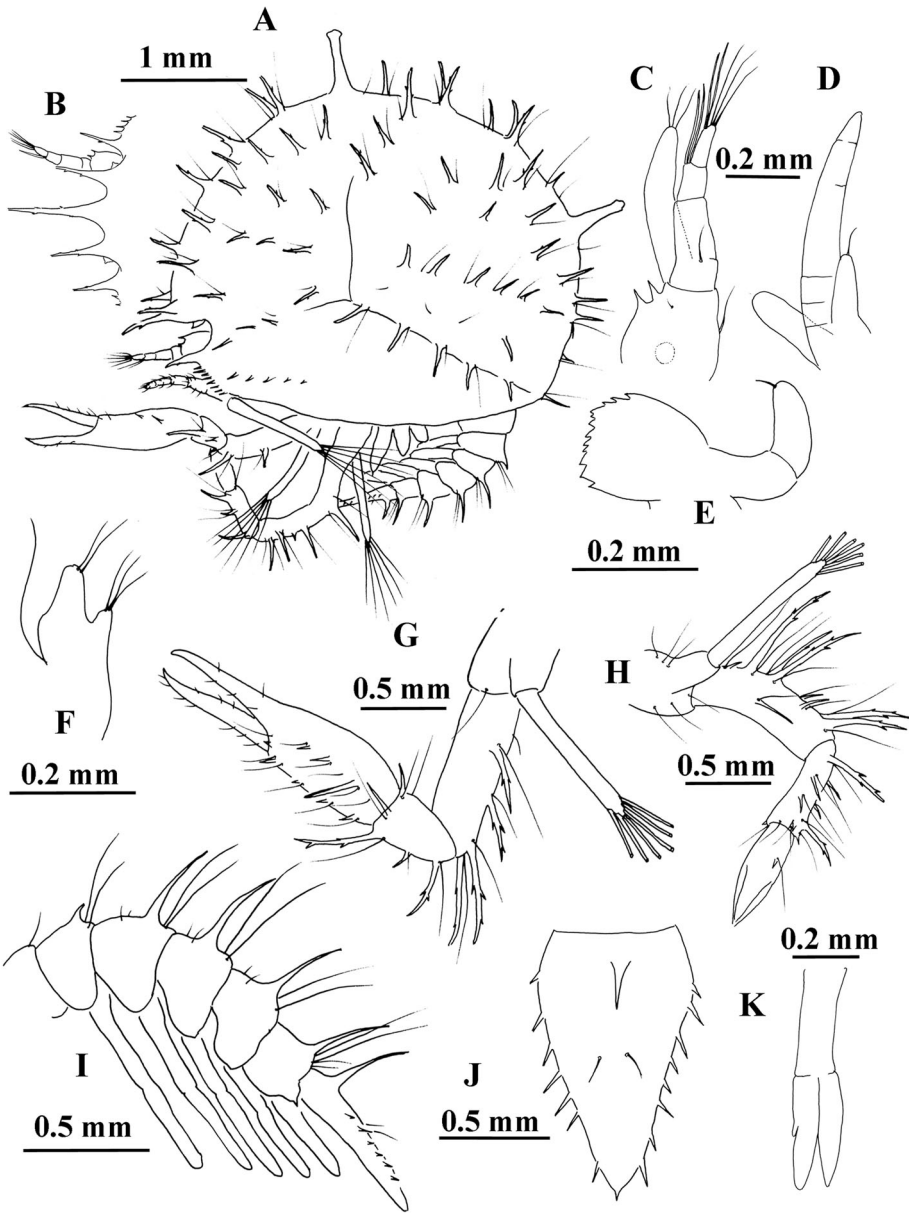

Fig. 7 *Polycheles typhlops*. Third zoeal stage (ZIII). **a** Total animal, lateral view; **b** frontal margin, dorsal view; **c** antennule; **d** antenna; **e** mandible; **f** maxilla, endites; **g** first pereiopod; **h** second pereiopod; **i** pleon; **j** telson; **k** first pleopod

Spatial and vertical distribution of *Polycheles typhlops* larvae

Twenty-five specimens of *P. typhlops* larvae were identified from samples taken in the Balearic Sea (Fig. 10). The larvae were captured mainly during the summer season (2010) but also in late autumn (2009). Relevant information about sampling details, such as location of sampling sites, density of larvae, date, time of sampling, water depth stratum and bottom depth is shown in Table 1. All zoea larvae and decapodid stages were found below the 200 m depth (Table 1; Fig. 11). Additionally, one first zoea stage was captured in the upper slope, near the bottom in the supra-benthos compartment (Table 1). Regarding their vertical distribution, the first zoeal stage could be found from 200 to 600 m depth, but mean abundances were higher in the layer between 300 and 500 m depth (Fig. 11) and in the southern study area. The last two zoeal stages were captured in a shallower layer (200–450 m depth), while the decapodid stage was collected near the bottom, between 600 and 800 m depth, in the north-west area. The vertical profiles of fluorescence during the late autumn survey were homogeneously distributed in the south and the north-west, ranging between 0.1 and 0.3 mg/m^3 (Fig. 11a). Higher values were observed during the summer, with values ranging between 0.05 and 1.03 mg/m^3 (Fig. 11b) and the presence of clines.

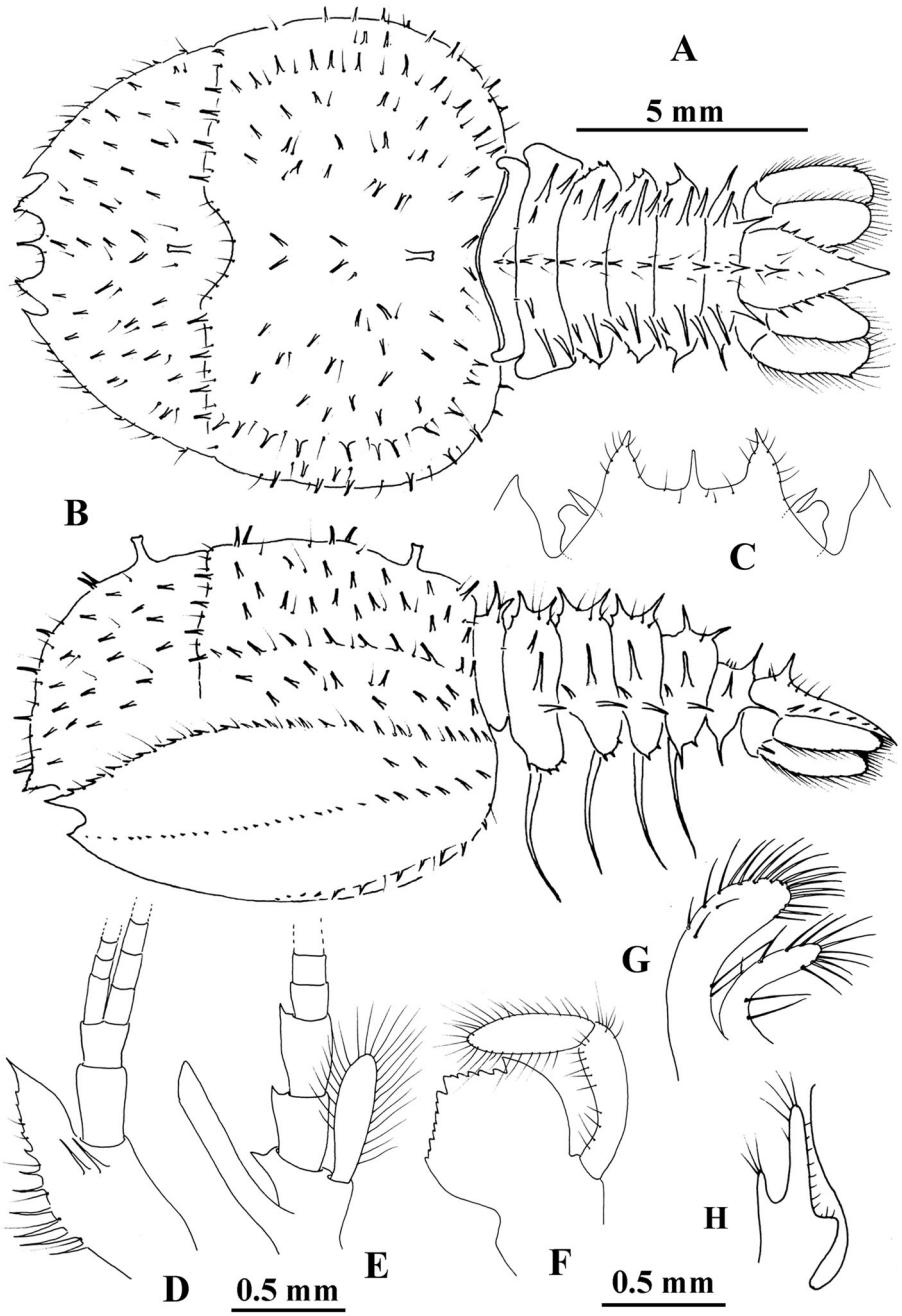

Fig. 8 *Polycheles typhlops*. Decapodid stage. **a** Total animal, dorsal view; **b** total animal, lateral view; **c** frontal region, dorsal view; **d** antennule; **e** antenna; **f** mandible; **g** maxillule; **h** maxilla, endopod and endites

Discussion

Morphology of *Polycheles typhlops* larvae

Accurate identification of marine larvae has traditionally required the rearing of larval stages in aquaria, but the development of species-specific markers (DNA barcoding) facilitates now the assignment of wild-caught planktonic larvae (Palero et al. 2008; Marco-Herrero et al. 2013). Matzen da Silva et al. (2011) have recently shown that the standard DNA barcoding COI gene region resolves relationships among decapod crustaceans. In their study, the observed mean K2P distance values did range from 0.29 to 1.38 % within species, 6.38–20.92 % within genus and 11.39–25.62 % within family. The K2P distance values found here when comparing our smallest zoea specimen (Station: 39.067 N–2.675E; Table 1) with either *S. nana* (21.7 %) or *S. sculpta* (24.8 %) fall within divergence levels observed among different genera, whereas the comparison with *P. typhlops* (0.17 %) is well within the K2P distance observed inside species. The molecular phylogeny also showed significant statistical support for the clustering of the larval sequence with DNA sequences obtained from adult specimens of *P. typhlops*. Therefore,

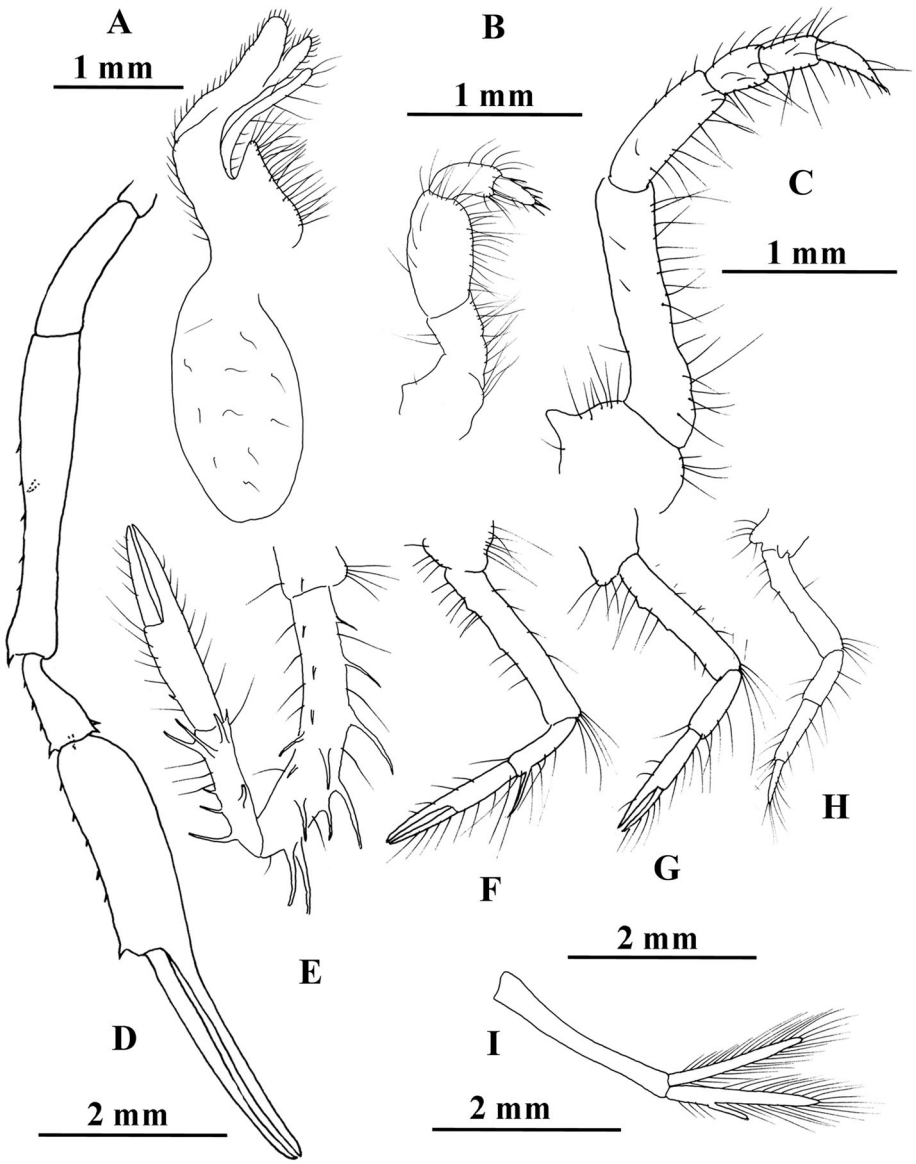

Fig. 9 *Polycheles typhlops.* Decapodid stage. **a** First maxilliped; **b** second maxilliped; **c** third maxilliped; **d–h** pereiopods 1–5; **i** first pleopod

the genetic results obtained in the present study, together with the fact that *Stereomastis* and *Polycheles* are the only polychelid genera known to occur in the Mediterranean, indicate that the first zoea larva collected from Western Mediterranean waters corresponds to *P. typhlops.* The larval development of *P. typhlops* is found to include at least three zoeal and one decapodid stages. Despite no molecular confirmation was made for the identity of ZII–ZIII and decapodid stages, species identification is inferred on morphological evidence (spination on the anterior part of middorsal line along the larval development and presence of epipodites on the decapodid stage). Following Ahyong (2009), the presence of epipodites on maxilliped three and pereiopods is used as one of the key features that allow for discrimination between the genera *Stereomastis* and *Polycheles*.

The smaller larvae of *P. typhlops* presented in this study were assigned to the first zoea (ZI) stage because they showed similar size (~1 mm CL) and the same degree of development as the first zoeal stage described from material reared in the laboratory (Guerao and Abelló 1996). The first zoea of *P. typhlops* had in both cases well-developed first and second pereiopods (biramous) and rudimentary pleopods. However, the description by Guerao and Abelló (1996) may not reflect the actual morphology of the larvae when hatching under natural conditions, given that many spines and setae on the carapace and appendages were not yet extruded. The degree of development indicates that the two later zoeae described here may correspond to the second (ZII) and third (ZIII) zoeal stages. These stages have well-developed interorbital spines, which are tiny in the first stage, pereiopods 4–5 present as buds and

biramous pleopods. In the third zoeal stage, the pleopods are much more developed, even though the number of functional pereiopods does not increase. The main features that separate stages ZII and ZIII are the presence of appendix interna on the pleopods (but ramus without setae) in the third zoea, antennal exopod incipiently subdivided, telson triangular and setal development. From our observations, the zoea of Polychelidae are characterized by the presence of natatory exopods on the appendages of the pereion (maxillipeds and pereiopods), rostrum projecting and the absence of functional pleopods (see also Bernard 1953; Williamson 1983). The morphology and size of the most advanced zoea and the decapodid indicate that intermediate larval stages should exist between these two. In fact, the carapace of the decapodid is ~150 % longer than the zoea III carapace, while the increasing progression in size of the carapace among the zoeal stages does not exceed 44 %. The morphology of *Eryoneicus* larvae appears to change gradually, and no true metamorphosis has been observed between different stages (Bernard 1953; Williamson 1983). The most dramatic change that occurs between ZIII and the decapodid, besides the change in relative size of the pleon, is the appearance of well-developed and uniramous pereiopods.

Early stages of *Eryoneicus* species are seldom captured, and the complete zoeal development of a polychelid lobster is still unknown (e.g. Balss 1925; Stephensen 1935; Bernard 1953). The first description of a zoeal stage was reported by Selbie (1914) as a "juvenile" *Eryonicus* sp. from NW Atlantic waters. According to Selbie (1914):

Table 3 *Polycheles typhlops*, decapodid

Spines	Pleonites											
	1		2		3		4		5		6	
Dorsal	A	B	A	B	A	B	A	B	A	B	A	B
Anterior small	0	0	1	1	1	1	1	1	0	0	0	0
Median small	0	0	0	0	0	0	0	0	0	0	3	0
Anterior strong	0	0	1	1	1	1	1	1	1	1	0	0
Posterior strong	1bi	1	1	1	1	1	1	1	1	1	1	1
Lateral												
Posterior small	1	0	0	0	0	0	0	0	0	0	0	0
Pleural strong (su)	0	0	1	1	0	0	0	0	0	0	0	0
Pleural strong (me)	0	0	1	1	2	1	2	1	2	1	1	1
Pleural strong (in)	0	0	1	1	1	1	1	1	1	1	1	1

Number of spines of the pleonites (1–6)

A, Present study; B, Bouvier (1917); bi, bifurcated; in, inferior; me, median; su, superior

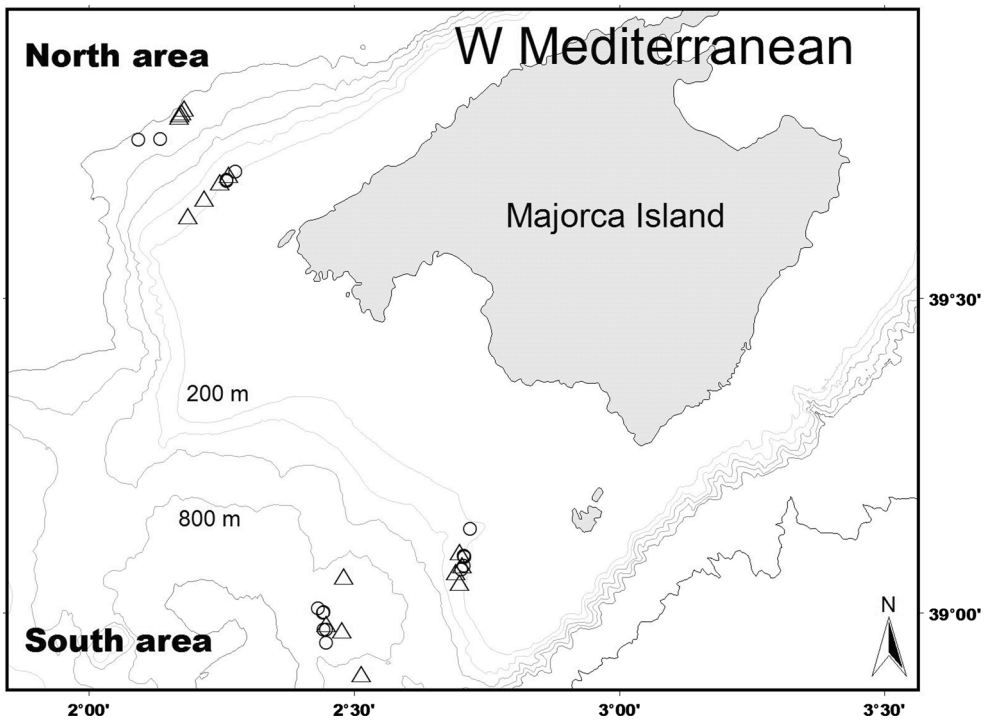

Fig. 10 Study area with haul's position during late autumn 2009 (*open circle*) and summer 2010 (*open triangle*), at four stations located over shelf break (250 isobath) and middle slope (900 isobath) off the north-west area and south of Mallorca Island. *Grey lines* indicate isobaths (200, 400, 600, 800 and 1,000 m)

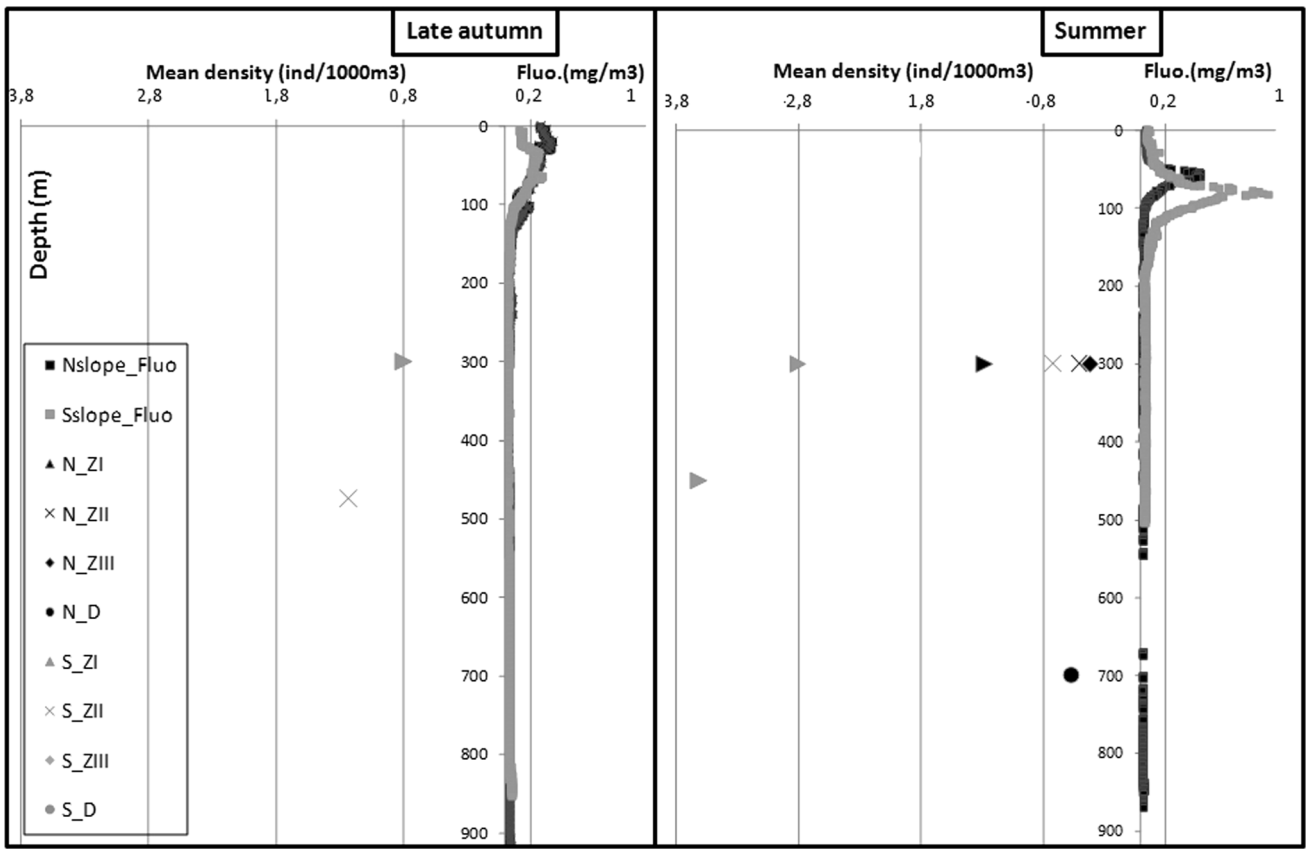

Fig. 11 Seasonal fluorescence (late autumn *left*; summer *right*) vertical profiles at north-west in black (Nslope_Fluo) and south middle slope in grey (Sslope_Fluo) from surface down to maximum sampled depth, adapted from Torres et al. (2014). Mean seasonal densities ontogenetic distributions of *Polycheles typhlops* larvae in the water column (depth mean) during the late autumn (*black*) and summer (*grey*) cruises, at north-west (N) and south (S) over middle slope (*ZI* first larval stage, *ZII* second larval stage, *ZIII* third larval stage, *D* decapodid)

"This very interesting specimen was taken by the midwater otter trawl off the south-west coast; at the same station a small *E. Faxoni* was taken, and it is possible that the present specimen belongs to the same species". Indeed, the zoea described by Selbie (1914) presented an arrangement of spines on the anterior part of the middorsal line (R, 1, 2, C_1) clearly different from that found in our zoeal and decapodid stages (R, 1, 1, 1, 2, C_1) and belongs probably to another species. Other early-stage *Eryoneicus* larvae described by Balss (1925) from Valdivia (SE Atlantic) and from the Arctic by Stephensen (1935) do not correspond to the zoeae of *P. typhlops*. Nevertheless, the decapodid described in the present study agrees very well with the description of *E. puritanii* given by Bouvier (1917). Only small differences were noted compared with Bouvier's account (Table 3), such as the branchial lower carina not ending at the longitudinal carina, no pre-cervical grooves present, and minor differences in the spinulation pattern (see Table 3; Fig. 8a, b). In our decapodid stage, the dorsal spine of the first pleonite is forked at the base, and there are two median pleural spines in pleonites 3–5 and pleonite six bears 3 minute spines dorsally. These small differences could be attributed to the fact that the decapodid phase may include various stages, of which the latter would be neotenic forms with secondary sexual characteristics (see Williamson 1983).

Descriptions of *E. puritanii* specimens by Lo Bianco (1903), Bouvier (1917) and Bernard (1953) have been previously attributed to *P. typhlops* (Bouvier 1940; Kotthaus 1966). Lo Bianco (1903) samples were captured in the Gulf of Napoli (Western Mediterranean Sea), but several specimens attributed to *E. puritanii* have also been captured along the eastern Atlantic Ocean (Bernard 1953; Kotthaus 1966; Hernández and Tiefenbacher 1999; Hernández et al. 2007). *E. puritanii* larvae described by Bernard (1953) were ascribed to *P. typhlops* by Bouvier (1940) and Kotthaus (1966). Despite Bernard's description (1953; Fig. 21) does not fit present standards, it seems to correspond to our second zoeal stage. Regarding the comparison of our decapodid with Lo Bianco's original description, a different telson was figured (with a terminal spine) and therefore his description may not correspond to a

decapodid stage of *P. typhlops* (Lo Bianco 1903, see Fig. 25 plate 8). Recall here that the decapodid (megalopa; see Anger 2001) denotes the final larval phase preceding moulting to the first juvenile stage and it is characterized by the existence of functional pleopods and uropods, subdivided and with long plumose natatory setae. Apart from *E. puritanii* catches by Lo Bianco (1903), other *Eryoneicus* forms were captured in the Mediterranean, namely the *E. faxoni* and *E. kempi* forms (Williamson 1983). The descriptions for *E. kempi* (Selbie 1914) and *E. puritanii* (Bouvier 1917) are similar, sharing the spine formula on the middorsal line (Bernard 1953). However, several differences can be observed between both species, such as the long spines and basal subdivision of the antennules or the cheliform 5th pereiopod.

Spatial and vertical distribution of *Polycheles typhlops* larvae

Although occurrences of adult polychelid lobsters on the epibenthos of the middle slope are common in the study area (Ramón et al. 2014), *P. typhlops* larvae were rare among all the collected material and were found exclusively in aphotic layers, corresponding to the lowest fluorescence values (Torres et al. 2014). The highest peak of *P. typhlops* larval abundances during the summer agrees with the highest frequency of ovigerous females in the Mediterranean (Follesa et al. 2007), and the bi-seasonal presence of larvae is in agreement with the fact that *P. typhlops* males are sexually active during the whole year (Cabiddu et al. 2008; Gastoni et al. 2010). The occurrence of *P. typhlops* larvae in deep plankton just above the adult populations is also in accordance with previous larval records. Bernard (1953) had already noted that all the *Eryoneicus* forms were captured below the euphotic zone and pointed towards the possibility of vertical ontogenetic migrations. The present study confirmed that *P. typhlops* larvae inhabit waters below the euphotic layer and that the decapodid stage is to be found in the deepest layers. This pattern further supports the idea that the larvae descend into deeper waters throughout their development, approaching the bottom at the end of the last larval stage in order to search for a suitable place to settle (Marta-Almeida et al. 2008; Shanks 2009). The lack of accounts for zoeal stages of *P. typhlops* in the previous literature is probably related to the low frequency of plankton sampling on deep waters, given that plankton studies usually focus on the photic layer. The larvae included in this study were captured at depths (between 200 and 800 m) where the photosynthetically active radiation (PAR) does not penetrate (e.g. Crise et al. 1998) and where local hydrographic currents are weaker than in shallower layers (Pinot et al. 1996; Amores et al. 2013). By staying within this depth range and through depth-keeping mechanisms (Shanks and Brink 2005), *P. typhlops* larvae might avoid the passive transportation suffered by other deep species spreading their larvae to the surface layers (Marta-Almeida et al. 2008).

The highest early-zoea larval densities were observed in the south slope during the summer season, coinciding with the maximum values of surface fluorescence and organic matter fluxes. Organic matter mean content of settling material, opal and $CaCO_3$ fluxes to the necto-benthic communities estimated during the same oceanographic surveys show that the major inputs of marine organic matter (phytoplankton blooms) took place during summer in the south, being lithogenic fraction higher in the north area (Pasqual et al. submitted). On the north-west study area, where the shelf is narrower and the slope is quite pronounced, the currents over the shelf create mixed conditions (Torres et al. 2014). Laboratory studies on captured bathyal echinoids indicate that an increase in gonad size in response to food enhancement could increase spawning production (Eckelbarger and Watling 1995), and a similar response could also explain the highest *P. typhlops* larval abundance in the southern slope. Stomach contents for *E. puritanii* taken between 500 and 2,500 metres deep showed that they are able to feed on cnidaria, cyanophyceae, diatoms or coccolithophores (Bernard 1953) and support the classical view of deep-sea organisms being nourished by a "rain" of organic detritus coming from surface waters (Agassiz 1888). The capacity of decapod larvae to feed on microorganisms (Anger 2001) would be crucial in aphotic layers, where most C and N is sequestered in prokaryotes and bacterial biomass is dominant over phytoplankton biomass (Cho and Azam 1990; Lasternas et al. 2010). These facts give light in understanding the presence of polychelid *Eryoneicus* in dark oligotrophic waters where the larvae could take advantages of faecal pellets of herbivorous organisms covered with bacteria (Marshall 1954).

Conclusions

Detailed morphological examination, analysis of DNA sequences and comparison with previous studies provide evidence to support the assignment of the ancient species *E. puritanii* to the larval stages of *P. typhlops*. The larvae of *P. typhlops* are found to possess functional cheliform pereiopods and undeveloped eyes from the early zoeal stages. Besides the arrangement of spines on the anterior part of the middorsal line and the results from the DNA analysis on the ZI stage, the clear presence of an epipodite on maxilliped three and the pereiopods provides further support to the connection between *E. puritanii*, our decapodid specimen and *P. typhlops*. The results obtained in this study provide new information on the distribution and

abundance of larval stages for one of the key groups of deep-sea fauna. The scarcity of conclusive data in the previous literature indicates the need for further descriptions in conjunction with the use of molecular techniques. An improvement of our knowledge about the larval ecology and recruitment of deep-sea species will be of utmost importance for the management of bathyal fauna.

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