



Description of a first-settled stage of *Aristeus antennatus* (Risso, 1816) and new insights into distribution and life history of early juveniles in the NW Mediterranean sea

Sara Dallarés^{a,*}, Aina Carbonell^b, Joan E. Cartes^c

^a Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193, Barcelona, Spain

^b Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Baleares, Muelle de Poniente s/n, 07015, Palma de Mallorca, Spain

^c Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003, Barcelona, Spain

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ABSTRACT

Knowledge on settlement stages of marine fauna is scarce, especially for mobile organisms such as crustaceans. This is most probably explained by the difficulty of capturing them at great depths in addition to their short lifespan and preference for special habitats. In the case of the red shrimp *Aristeus antennatus* (Risso, 1816), a species of outstanding importance in many Mediterranean fisheries, there is an important lack of knowledge regarding development between pelagic larval to benthic juvenile-adult phases. As a contribution to fill this gap, in the present study a first-settled stage of the red shrimp is described based on a specimen collected off Formentera (Algerian Basin, western Mediterranean) during October of 1996 at 1594 m depth with a Macer-GIROQ suprabenthic sledge. As a complement to this description, the seasonal distribution and density of small juveniles of *A. antennatus* (carapace length <16 mm) captured in the Balearic Basin during OTSB-14 bottom trawls performed between the years 2007–2020 at more than 1000 m depth is mapped and discussed. From these distribution maps, an increase in captures of juveniles from autumn to summer can be appreciated, as well as a phenomenon of migration of these small individuals from inner to outer regions of the Balearic Basin. Finally, a theoretical reconstruction of the early life history of these small juveniles, starting at hatching in July, which consistently fits with the size of the first-settled stage described here, is provided.

1. Introduction

Settlement, the time at which a given organism switches from a swimming planktonic to a benthic lifestyle, is a crucial step in the life history of many marine organisms. Indeed, recruitment occurs after successful settlement on or immediately above the seafloor (Mullineaux, 1988; Anger, 2001). Some experiments carried out with sessile epifauna settled on hard substrata proved that settlement patterns depend on the feeding modality of the organism under study and on the supply intensity of particulate organic matter (POM) (Mullineaux, 1988). POM arrival to the seafloor experiences seasonal peaks that condition its availability for deep-sea species and can thus determine intra-annual changes in its abundance (Durdan et al., 2020). Due to their feeding habits, predators like fish and shrimps may face additional uncertainty in finding food (i.e. prey) hotspots that foster settlement.

In general, knowledge on settlement life phases is scarce, especially

for mobile animals such as fish or crustaceans, being difficult to find detailed morphological descriptions of specimens at this stage. This lack of information may be related to: i) a short lifespan coupled to a fast development of these phases, and ii) the difficulty to capture them at great depths in the water-sediment interphase (the Benthic Boundary Layer, BBL), largely derived from the impossibility to perform specifically-designed surveys for their capture due to the generalized lack of knowledge on their ecology. We could add a third reason related to a certain preference by these first-settled stages for inaccessible and/or special habitats where they could find refuge, as has been reported for fish recruits in coral reefs (Montgomery et al., 2001). Hence the gaps of knowledge on these phases, since settlement must be done in a specific and short period of time and potentially in suitable areas out of reach of the conventional sampling methods designed for studies on adults and larvae. Understandably, most existing studies on settlement of mobile animals, such as fish and crustaceans, have focused on shallow depths (e.

* Corresponding author.

E-mail address: Sara.Dallares@uab.cat (S. Dallarés).

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g. Bastrikin et al., 2014; Faillettaz et al., 2020; Éélix-Hackradt et al., 2013; Vinuesa et al., 2010; Tamaki et al., 2020) while the deep-sea remains almost unexplored for these kind of studies. This lack of information on basic features of early stages is generalized in the marine environment and extends far beyond free-living organisms to, for example, many parasites with indirect development and more or less complex life cycles that belong to a diversity of taxonomic groups (Rohde, 2005).

The red shrimp *Aristeus antennatus* (Risso, 1816) is an important target species for fisheries of the Mediterranean Sea, where it is captured by bottom trawlers at the upper and middle slopes down to ca. 800 m depth. In the Mediterranean Spanish coast, this crustacean is among the ten most important species captured in terms of biomass, and is the first in terms of economic value (DGPAM, 2022). Furthermore, this species also bears a high ecological importance in benthic deep-sea ecosystems, being a dominant species in the crustacean community of the lower slope in the north-western Mediterranean area (Abelló et al., 1988; Cartes et al., 1994a). The species distribution extends to 2300 m depth and recruitment (and thus probably settlement) occurs beyond the depths where it is usually exploited (Sardà and Cartes, 1997; Cartes et al., 2017). Therefore, there is an important part of its population, represented by 1st year cohort, living at depths free of fisheries impact.

An adequate and sustainable management of commercially exploited natural stocks requires a deep knowledge and understanding of the development, spatial and temporal distribution and basic biology and ecology of target species. While this is obvious for juveniles and adults, it is equally valid for the small larval stages. Indeed, crustacean larvae, as those of many other animal groups, play an essential role in recruitment, population trends at different scales, populations connectivity and biogeography, among many others (Anger, 2001). This is the reason why stock management and conservation efforts for decapod crustaceans with commercial interest would benefit of a better knowledge of the dispersion patterns, settlement and ecology of their larval and juvenile stages.

In the specific case of the red shrimp, there are still tremendous gaps of knowledge regarding life phases that are switching from a pelagic to a demersal lifestyle (larvae vs. juveniles, respectively). These stages are sometimes defined as “post larvae” or “first-settlement stages”. While some aspects of the biology and ecology of this species being well-known (Carbonell et al., 2006; 2008; Cartes, 1994; Cartes et al., 2017), a special interest exists in completing the lack of information regarding its life cycle and basic biology, justified by the species’ enormous commercial and ecological significance. This would allow a better evaluation of the state of its commercial populations, which face great pressure from the fishing industry, better fishery management and a more adequate protection of the species.

The larval development of *A. antennatus* starts with the *nauplius* larval type, common to most crustaceans. In the case of the Dendrobranchiata, it is a nonfeeding free-living pelagic phase that undergoes from five to eight moults before the next stage (Anger, 2001). The next stage is the *zoea*, which comprises a variable number of the so called *protozoea* (early *zoea*) and *mysis* (late *zoea*) stages. Heldt (1955) described the development of *A. antennatus* from the second *protozoea* to the first *mysis* stage based on alive specimens collected in surface waters from the Balearic Sea. More recently, a complete description of the second *mysis* stage was provided by Torres et al. (2013) based on a single specimen found in plankton samples obtained at ca. 1000 m depth off the Balearic Islands (NW Mediterranean). Beyond this *mysis* stage, more advanced phases of development for the family Aristeidae are unknown. The last larval type preceding the first juvenile instar is the *decapodid*, which acquires juvenile characteristics gradually through a variable number of moults (Anger, 2001) before its bottom settlement. *A. antennatus* larvae have been recently documented and characterized molecularly off the Catalan coast (Carreton et al., 2019), confirming the adequacy of Heldt (1955) description for larval stages of this species.

As mentioned, the decapodid and early juvenile stages are yet to be

described for this species, as also are depths where first-settlement takes place. It is well known, however, that the ca. 1st year-old specimens (the smallest juveniles known, with a carapace length of 6–7 mm) have only been collected from very deep areas, at > 1000 m depth (Sardà and Cartes 1997; Cartes et al., 2017). The main difficulty for gaining an adequate knowledge of early stages of this species lies in the fact that, contrary to adults and large juveniles, and as explained above, captures of larval stages and small juveniles are extremely rare. The high similarity of the larval series of *A. antennatus* to that of other shrimps, such as *Aristaeomorpha foliacea* or *Gennadas elegans* (Carreton et al., 2019) is an added difficulty. Furthermore, and contrary to other shrimps (e.g. *Periclimenes aegylos*, see Di Muzio et al., 2018), larval rearing in laboratory conditions, which allows the observation and description of the complete life cycle of the species under study, is not possible in the case of *A. antennatus* and other Dendrobranchiata since eggs are released to the water column instead of being carried by females.

The present study describes, for the first time, a first-settled stage of the red shrimp. Due to its rarity, this stage has not been previously reported and the present description is based on a single specimen. Furthermore, spatial and temporal distribution of small specimens of *A. antennatus* (carapace length <16 mm) collected in deep waters of the Balearic Basin from 2007 to 2020 and their theoretical growth, starting from the theoretical hatching time and setting settlement at the size of the described individual, are explored. Therefore, this is an important contribution to the body of knowledge of this species, shedding light into the development and ecology of its early stages.

2. Materials and methods

2.1. Data sampling and specimen collection

A considerable number of research campaigns have been conducted off the continental margin of the Balearic basin since 1985. During these surveys, a semi-balloon otter trawl (OTSB-14; Merrett and Marshall, 1981) was used for capturing benthopelagic megafauna and a Macer-GIROQ suprabenthic sledge to collect suprabenthic macrofauna at the sediment-water interphase (0–1 m above the seafloor) (see detailed information below). Overall, surveys performed with both sampling gears covered all seasons and all slope depth ranges between the shelf-slope break at ca. 200 m to the maximum depths of the Balearic Basin (i.e. 2300 m). Details for OTSB-14 samplings can be found in Cartes et al. (2017) and as supplementary material in Table S1 of the present study, while the Macer-GIROQ suprabenthic hauls were mapped in Cartes and Figueroa (2020, Fig. 1). Immediately after collection, all samples were preserved in ~4% borax-buffered formaldehyde. Once in the laboratory, samples were sorted and decapod crustacean larvae were classified according to species and developmental stage, when possible, using identification keys (dos Santos and Lindley, 2001; dos Santos and González-Gordillo, 2004) and species descriptions monographs (Heldt, 1955; Torres et al., 2013 for *A. antennatus*).

During Macer-GIROQ suprabenthic hauls only two juvenile specimens of *A. antennatus* (the two smallest juveniles collected to date in the Balearic Basin) were collected, one of them being the first-settled stage described herein. This specimen was collected south off Formentera (Balearic Islands, NW Mediterranean) during the QUIMERA1 cruise (October of 1996 at 1594 m depth, coordinates: 38° 12.63' N – 1° 47.74' E). The second specimen was collected off Barcelona during the ReTro2 survey (December of 1991 at 1258 m depth). Model characteristics for this sampling gear can be found in Cartes et al. (1994b). Briefly, this sledge is armed with 0.5 mm mesh size nets attached to three rectangular mouths of 40 × 80 cm arranged one above the other and equipped with an opening-close mechanism. Hence, thanks to a system of spring and levers the mouths openings of the gear are open only when the sledge is in contact with the seafloor, while when the sledge leaves the bottom they are closed. This diminishes the probability of sample contamination in midwater, especially with quick swimming organisms

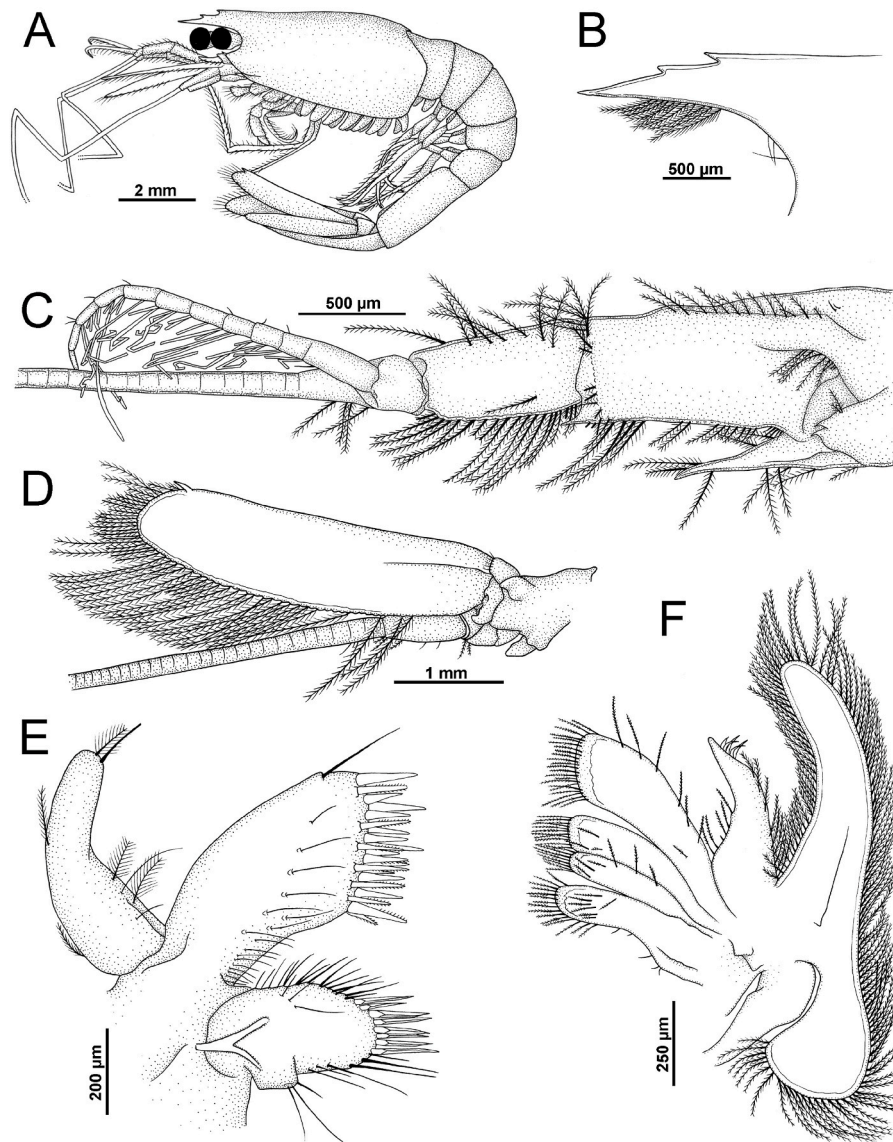


Fig. 1. First-settled stage of *Aristeus antennatus* (CL < 4.7 mm). A, whole specimen in lateral view. B, rostrum. C, antennule. D, antenna. E, maxillule. F, maxilla.

such as shrimp larvae. It was during a recent revision of these samples for the analyses of isopod communities, in 2020, when the *A. antennatus* specimen described herein was rediscovered and identified.

In order to complement the unique capture of this small specimen, the present study also includes the mapping by season of the distribution and abundance of 180 juvenile specimens (caparace length (CL, measured as the distance between the posterior margin of eye orbit to the posterior margin of pereion) < 16 mm) of *A. antennatus* captured in the Balearic Basin during several hauls performed between the years 2007 and 2020 (Table S1). Briefly, a total of 80 hauls (16 between October and December, 31 between March and May, and 34 between June and July) were performed at depths comprised between 423 and 2233 m in the context of different research projects. All these hauls were carried out using a OTSB-14 bottom trawl with an average horizontal width of 7 m, a vertical opening of 1.2 m and a codend of 6 mm mesh size, being captures of juvenile *A. antennatus* thus comparable across sampled seasons and depths. After capture, specimens were counted, measured (CL) and weighed to the nearest 0.01 g.

2.2. Morphological description of the first-settled stage of *A. antennatus*

For the morphological description of the first-settled stage of *A. antennatus*, appendices of the single specimen available for examination were carefully dissected and examined as temporary mounts in distilled water. Drawings were made with the aid of a *camera lucida* attached to an Olympus BH light microscope with Nomarski interference contrast. Measurements were obtained with a stage micrometer. The following measurements were taken: total length (TL, measured as the distance between the anterior tip of the rostrum to the posterior margin of pleon) and CL (defined above). Nomenclature used for integumental elements follows Garm and Watling (2013). The specimen is deposited at the Institut de Ciències del Mar (ICM-CSIC) biological collection (*Col·leccions Biològiques Marines de Referència*, Ref.: ICMD002714).

2.3. Data analysis

The abundance and density (n° individuals/ha) of small specimens of *A. antennatus* (CL < 16 mm) collected during OTSB-14 samplings in the Balearic Basin between the years 2007 and 2020 was calculated and mapped seasonally according to haul locations using the mapping

software SURFER. The locality of the second small juvenile specimen captured during Macer-GIROQ suprabenthic hauls, apart from the specimen described herein, was also mapped.

Using the same individuals, a theoretical life history for juveniles of *A. antennatus* was reconstructed, starting from the base of theoretical hatching and setting settlement at a size of 4.74 mm CL, using as reference the individual described herein.

3. Results

3.1. Morphological description of the first settled-stage of *A. antennatus*

Description (Figs. 1–4).

[Based on a single specimen fixed in buffered formaldehyde and further preserved in ethanol].

Size: 17.59 mm TL and 4.74 mm CL.

Rostrum (Fig. 1A and B) short, pointing anteriorly, about one fourth of CL, with two dorsal spines projected anteriorly and located in the first two thirds of its length and a group of ventral pappose setae on the middle region. Orbit bearing a few simple setae at the level of eyes

(Fig. 1B); eyes well developed. Antennal and pterygostomian spines observed (Fig. 1A); no carinae appreciated.

Antennule (Fig. 1A, C): first segment bearing numerous plumose setae along ventral, dorsal and anterior margins, small ventral spine on anterior margin; stylocerite sharp, length about two thirds of first segment, with a row of sparse plumose setae on ventral margin; second segment length about one half of first one in length, bearing a row of ca. 20 and plumose setae on ventral margin and some sparse plumose setae on dorsal side; third segment naked and short, length about one third of second one. Outer flagellum segmented, bearing a few short simple setae and ca. 30 aesthetascs (between two and four per segment except in the first and last segments that don't have these structures). Aesthetascs single or in pairs, originating in joints between segments or at mid-level of segments, ranging from ca. 100–800 μ m in length, irregularly distributed regarding size, although longest ones located in the middle or distal region of the outer flagellum. Inner flagellum with four plumose setae on its base, full length not observed.

Antenna (Fig. 1D): protopod naked; scaphocerite width:length ratio 1:3.9, bearing approximately 75 plumose setae along inner and distal margins and a small spine on distal outer margin. Flagellum apparently

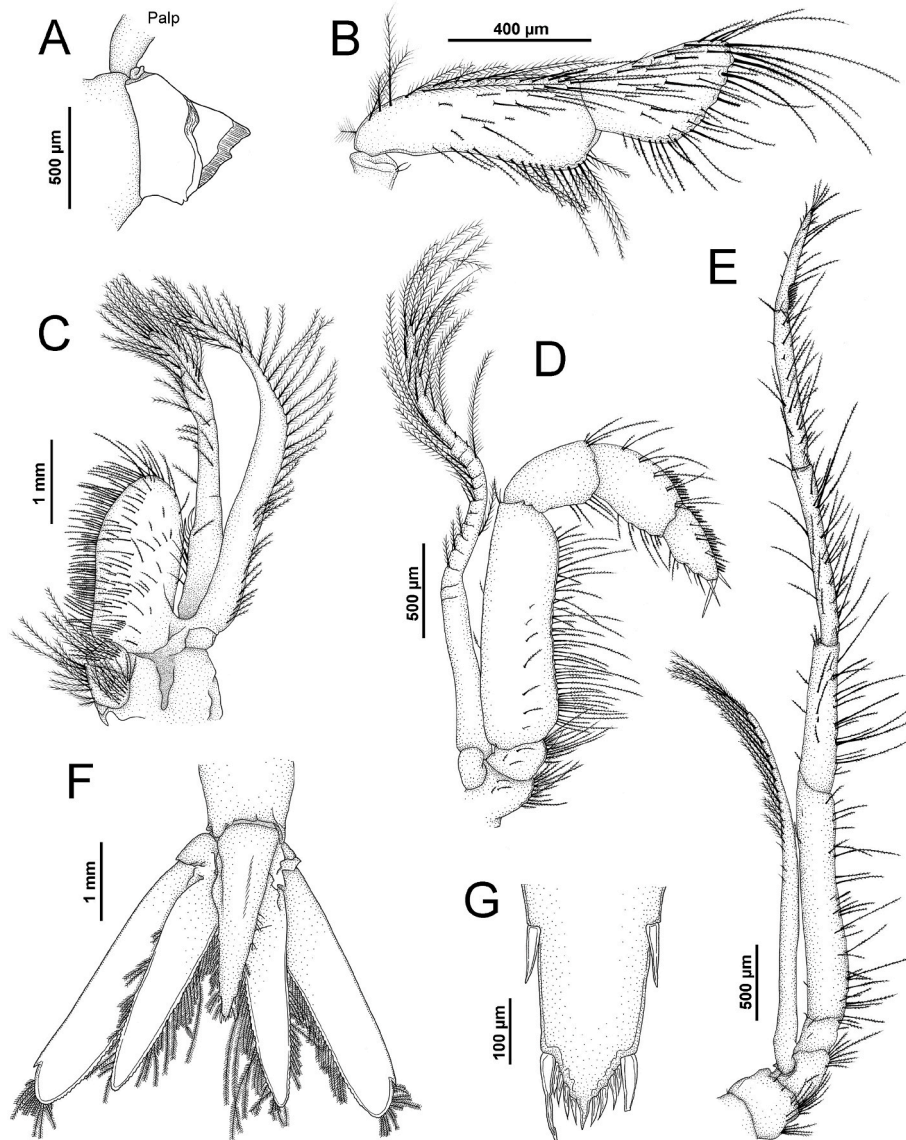


Fig. 2. First-settled stage of *Aristeus antennatus* (CL < 4.7 mm). A, mandible. B, mandible palp. C, first maxilliped. D, second maxilliped. E, third maxilliped. F, telson and uropods. G, telson tip.

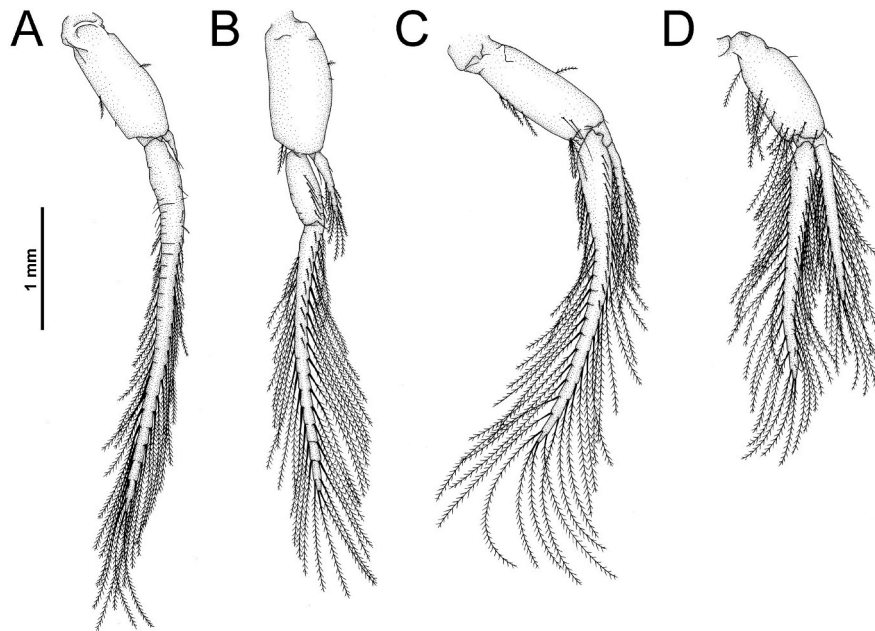


Fig. 3. First-settled stage of *Aristeus antennatus* (CL < 4.7 mm). A, second pleopod. B, third pleopod. C, fourth pleopod. D, fifth pleopod.

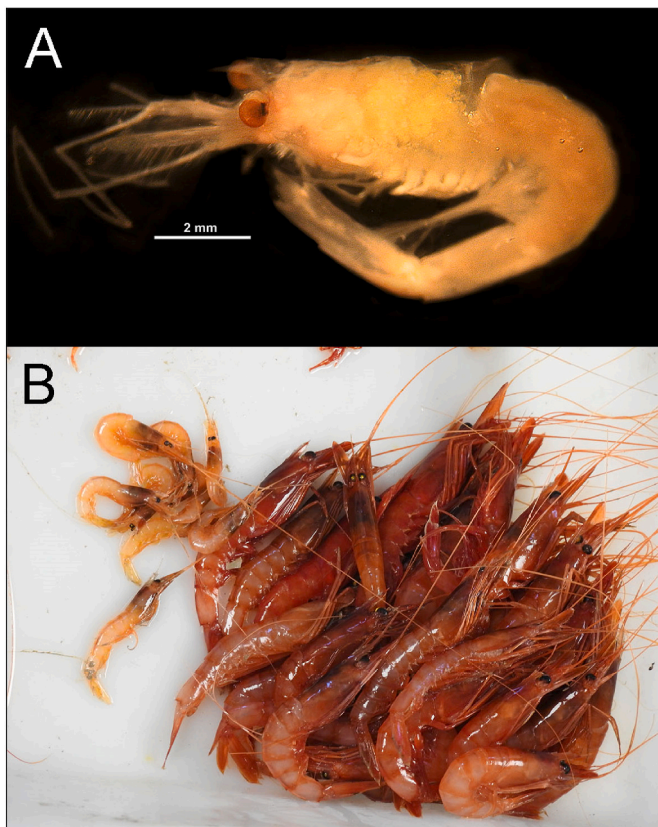


Fig. 4. Image of the first-settled stage of *Aristeus antennatus* (CL < 4.7 mm) described herein (A) before its dissection. Colour can be compared to that of small juveniles (CL ≥ 6.4 mm) and adults collected in recent cruises (B).

naked, full length not observed.

Mandibles (Fig. 2A): symmetrical, incisor part of mandible covering all the outer part, with a single, intermediate, rather dull tooth; molar process long, not very protruding, as illustrated. Mandible palp (Fig. 2B) two-segmented, with two small naked setae on its basis; first segment

bearing ca. 30 plumose and composite setae along margins and with ca. 30 composite setae on inner and outer surfaces; second segment length about two thirds of second one; with ca. 22 composite setae along margins and ca. 30 composite setae on inner and outer surfaces.

Maxillule (Fig. 1E): coxal endite oval-shaped, with a proximal protuberance, bearing ca. 22 simple setae along lateral margins and eight faceted cuspidate setae along distal margin. Basal endite broadening towards distal part, with ca. 17 simple setae on inner surface and several (more than 20) cuspidate setae (either with or without small setules on distal region) along distal margin. Endopod unsegmented, bearing a few simple, pappose or plumose setae.

Maxilla (Fig. 1F): coxal and basal endites bilobed and elongated, bearing a row of composite setae along distal margins (ca. 25 and 35 setae on coxal and basal endites, respectively) and some sparse composite setae on inner surface; proximal lobe of coxal endite with a few simple setae on posterior margin; distal lobe of basal endite with a few composite setae along anterior margin. Endopod unsegmented, with a few composite and pappose setae along its inner and outer margins, respectively, and five stout, curved and naked cuspidate setae on its distal margin. Scaphognathite bearing ca. 120 plumose setae along its margin.

First maxilliped (Fig. 2C): protopod irregular, with two compact protuberances bearing ca. 20 plumose setae on outer margin and several plumose and pappose setae on inner and outer surfaces, and an enlarged and flattened oval-shaped extension with ca. 73 composite setae along outer margin and several composite setae scattered on inner and outer surfaces. Endopod unsegmented, with ca. 30 plumose setae increasing in density towards distal region, bearing a row of five simple setae followed by two cuspidate curved setae on inner margin of proximal region. Exopod unsegmented, approximately equal in length as endopod, slightly curved and flattened, bearing a row of ca. 35 plumose setae along its outer margin, four plumose setae along its inner margin and two terminal plumose setae.

Second maxilliped (Fig. 2D): basis with ca. 11 pappose-composite setae along inner margin and a few composite setae on inner surface and on outer margin. Endopod flattened, with five segments; first segment with ca. 10 pappose-composite setae along inner margin and a few composite setae on inner surface; second segment with ca. 48 composite setae along inner margin and a row of few composite and simple setae on inner surface; third segment with five and four

composite setae along inner and on outer distal margins, respectively; fourth segment with eight composite setae along inner margin, ca. 12 composite setae on inner surface, generally grouped by pairs, and with a row of at least nine serrate setae along second half of outer margin; fifth segment with seven composite and simple setae along inner margin, five composite setae on inner surface, generally grouped by pairs, at least 16 serrate setae along outer margin and three large cuspidate setae on its distal region. Exopod unsegmented, slightly shorter than endopod, bearing ca. 17 and nine plumose setae along outer and inner margins, respectively, and two terminal plumose setae.

Third maxilliped (Fig. 2E): coxa with ca. 20 composite and simple setae along inner and distal margins. Basis with ca. eight composite setae on inner distal region. Endopod with six segments; first and second segments with ca. four and 30, respectively, composite setae along inner margin and a few simple setae along outer margin; third to sixth segments with composite setae mostly along inner (ca. 20, 25, 17 and ten setae, respectively) and outer (ca. three, eight, five and three setae, respectively) margins and a few sparse simple setae; fourth and fifth segments with a patch of small spiniform projections on proximal inner region; sixth segment with a row of ca. ten serrate setae on proximal inner region and with four terminal composite setae. Exopod unsegmented, reaching to mid-length of third endopodal segment, bearing ca. 16, plumose setae along second half of outer margin and two terminal plumose setae.

Pereiopods: not available for examination.

Pleon (Fig. 1A): unarmed, with similar length than the cephalotorax. First pleopod: not available for examination. Second to fifth pleopods (Fig. 3A–D) progressively decreasing in length posteriorly, biramous, with endopods increasingly developed posteriorly; endopods and exopods unsegmented.

Second pleopod (Fig. 3A): about 18% of specimen TL. Protopod with a few sparse plumose and simple setae. Endopod ca. 8% of exopod length, bearing two terminal small plumose setae. Exopod with ca. 24 and 25 plumose setae along inner and outer margins, respectively, and two terminal plumose setae.

Third pleopod (Fig. 3B): protopod with a few sparse plumose and simple setae. Endopod ca. 20% of exopod length, bearing ca. four and five plumose setae along inner and outer margins, respectively, and two terminal plumose setae. Exopod with ca. 21 and 17 plumose setae along inner and outer margins, respectively, two terminal plumose setae and a row of ca. 15 short composite setae along anterior margin.

Fourth pleopod (Fig. 3C): protopod with some sparse plumose and simple setae and a row of ca. four plumose setae along the outer margin. Endopod ca. 41% of exopod length, bearing ca. nine plumose setae along inner and outer margins and two terminal plumose setae. Exopod with ca. 20 and 22 plumose setae along inner and outer margins, respectively, two terminal plumose setae and a row of ca. 13 short composite setae along anterior margin.

Fifth pleopod (Fig. 3D): protopod with some sparse plumose setae and a row of ca. 12 plumose setae along the outer and inferior margins. Endopod ca. 65% of exopod length, bearing ca. 15 plumose setae along inner and outer margins and two terminal plumose setae. Exopod with ca. 18 and 20 plumose setae along inner and outer margins, respectively, two terminal plumose setae and a row of ca. 16 short composite and simple setae along anterior margin.

Uropods (Fig. 2F): protopod naked. Endopod with long plumose setae along whole margin. Exopod about 1.2 times longer than endopod, with long plumose setae along inner and outer margins and a spine on distal outer region.

Telson (Fig. 2F): shorter than uropods, reaching half the length of the endopods of the uropods, bearing plumose setae along margins of distal half and a few simple setae along margins of middle region, with six cuspidate setae along distal lateral margins, three on either side. Telson tip (Fig. 2G) bearing two large (ca. 150 μ m long) cuspidate setae on either side, one conical central spine and eight cuspidate setae with sharp tips arranged in two groups of four setae, each group on either side

of the central spine.

The specimen was pale orange-apricot in colour (Fig. 4A), as the first fully developed juvenile stages (Fig. 4B) for which CL was >4.7 mm.

3.2. Other observations on the first-settled stage of *A. antennatus* described herein

The content of the stomach, which was almost empty, only consisted of a few isolated fragments of copepods.

3.3. Temporal and spatial distribution of small specimens of *A. antennatus* (CL < 16 mm)

Some temporal and spatial patterns in the distribution of the smallest (CL < 16 mm) specimens of *A. antennatus* collected with OTSB-14 in the Balearic Basin during cruises performed between 2007 and 2020 were identified. In first place, the seasonal distribution of the abundance of these specimens evidenced a significant increase in captures and associated estimated densities from autumn to spring and summer (Fig. 5). Additionally, a certain migration of these small individuals from the inner to the outer regions of the Balearic Basin from autumn to the next spring and summer was observed.

3.4. Theoretical growth from hatching of small specimens of *A. antennatus* (CL < 16 mm)

The size and season of capture of the first-settled stage individual described in the present study fits in the plot displaying the theoretical growth trend of the smallest specimens of *A. antennatus* (Fig. 6), taking hatching (which occurs from mid-spring to the end of summer) as origin. This reconstruction further suggests that within the 1st year of life *A. antennatus* specimens would reach an approximate size of 11–12 mm CL.

4. Discussion

4.1. Identity and developmental stage of the first-settled stage described herein

There are few descriptions of pre-settlement stages for deep-sea shrimps, and the knowledge on the developmental cycle for these species is, hence, still very fractioned. Both the lack of surveys performed during the specific time and in the habitat in which settlement occurs and, likely, an ephemeral existence prevent the study of these stages, occurring between larval and adult phases. Captures like the present one mostly occur by chance.

The specimen described herein was categorized as a juvenile stage in a previous work based on the observation of its rostrum and telson morphology (Carbonell et al., 2020). However, after the dissection labour and thorough examination carried out in the present study, it can be now more precisely identified as a transition phase between the decapodid (the most advanced larva stage preceding metamorphosis to the first juvenile, formerly known as “post-larvae”) and an early juvenile stage of Aristeidae. Actually, a clear distinction between these two developmental stages cannot be made since, for the Dendrobranchiata, the transition between the two mentioned developmental phases is gradual (Anger, 2001). Given the absence of descriptions for Aristeidae decapodids, the characteristics of some specific anatomical elements such as the rostrum and telson are important diagnostic features to be taken into account when performing comparisons to early stages of other shrimp species. In the case of the specimen described in the present study, the mentioned structures are very different to those shown by decapodids of Penaeidae distributed in deep and shallow waters of the same area (e.g. genera *Parapenaeus*, *Penaeus*, *Solenocera* or *Sergestes*, see Calazans, 1993).

The present specimen can be allocated within the superfamily

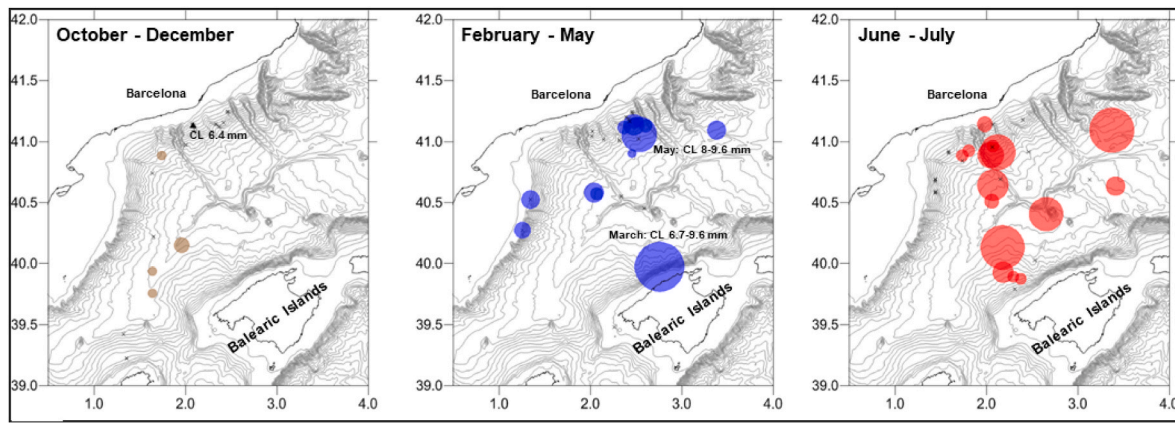


Fig. 5. Distribution of juveniles of *Aristeus antennatus* (CL < 16 mm) captured in the Balearic basin between the years 2007–2020 during OTSB-14 hauls. A buffer area proportional to estimated density is displayed for each sampling point. Largest buffer corresponds to a maximum density of 4.9 individuals/ha. Crosses indicate hauls without captures. ▲: Location of capture of the small juvenile collected in December of 1991 at 1258 m with a Macer-GIROQ suprabenthic sledge. CL: caparace length.

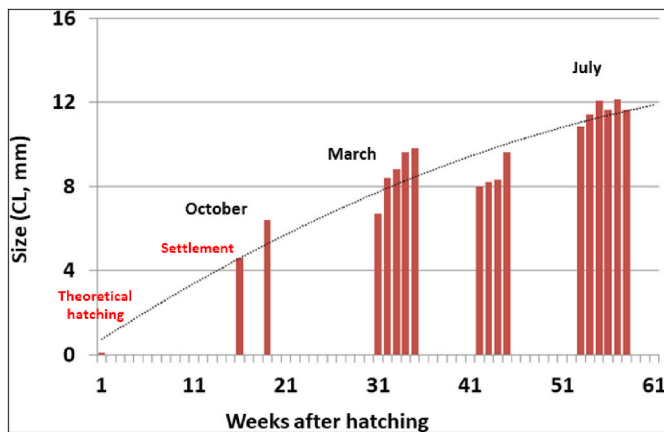


Fig. 6. Theoretical reconstruction of the early life history of juvenile *Aristeus antennatus* (CL < 16 mm), starting from the base of theoretical hatching and setting settlement at the size (CL of 4.74 mm) of the individual here described. Bars represent the smallest sizes found in each of the seasons sampled at depths >1000 m. Curve fitted to bars represents the theoretical growth that these small specimens might follow.

Penaeidea based on rostrum surpassing the orbital ring and on the absence of stiliform projections in the middle part of orbital ring. Within the Penaeidea, it can be further assigned to the family Aristeidae, discarding the possibility of belonging to Penaeidae, based, for example, in the lack of an inner antennular scale and in the presence of well-developed exopods on the maxillipeds. Within the Aristeidae, an evident diagnostic feature for *A. antennatus* is the conspicuous spine present in the outer part of the scaphocerite, as observed in the specimen described in the present work, which is less marked in other members of the family present in the Mediterranean deep-sea such as *Aristaeomorpha foliacea* (Zariquiey, 1968). Both *A. antennatus* and *A. foliacea* show antennal and branchiostegal spines, but only *A. foliacea* bears a hepatic spine, which is effectively absent in the specimen described in the present work. Moreover, and still regarding morphological features, the rostrum of *A. foliacea* bears five basal teeth and three distal teeth, the latter sparsely distributed, while the rostrum of *A. antennatus* only displays three basal teeth. Over its still-developing rostrum the present specimen shows two teeth. In addition to the described morphological aspects, the extreme depths (1700 m) inhabited by the specimen described herein are in accordance with the known characteristics and ecology of *A. antennatus*, whereas *A. foliacea* bathymetric distribution

barely reaches 700 m in the Mediterranean deep-sea, even considering the smallest juveniles (14 mm CL) collected (Belcari et al., 2003).

Regarding the developmental stages of decapods, the decapodid phase is characterized by the existence of functional pleopods and by cephalic and anterior thoracic appendages assuming new functions as mouthparts (Anger, 2001). The presence of functional larval organs, which are also characteristic of decapodids, such as natatory exopods on the pereopods, were unfortunately not verified in the present specimen due to the absence of these appendages. As already explained above, in the Dendrobranchiata the transition between the decapodid and first juvenile phase is gradual (a true metamorphosis does not occur) since juvenile characteristics are attained progressively over a variable number of moults (Anger, 2001). However, the general shape of the specimen described here seems to be closer to an early juvenile than to a decapodid stage. A more specific indication of this is that pleopods, for example, were well developed and setose. Furthermore, and in relation to this, the morphology of the pleopodal endopods is of particular interest since it provides evidence of this specimen being a transitional form. Indeed, the increasing development of such structures, which display the same morphology on adult stages (Zariquiey, 1968), observed from the second to the fifth pleopod evidences the gradual acquisition of juvenile morphology described for this group (Anger, 2001).

In comparison with the previous developmental stage for which a description is available (i.e. mysis II, described by Torres et al., 2013), the first-settled stage of *A. antennatus* described herein displays a number of differential features. Most obvious differences consist in larger overall body size, an abdomen as large as or a little larger than the cephalothorax, more developed and complex general structures and appendages and more numerous and diverse integumental structures (i.e. setae or spines). Other, more specific features that distinguish first-settled from mysis II stage are: proportionally shorter rostrum, directed frontally, with two dorsal spines and a group of ventral pappose setae (vs. longer rostrum, upward-pointing, with no dorsal spines or ventral setae), presence of antennal spine (vs. absence of such structure), absence of supraorbital spine (vs. presence of such structure), proportionally longer stylocerite, mandible with different morphology (see Torres et al., 2013), developed pleopods (vs. only existing as small uniramous buds) and telson uniramous and almost equal in length than uropods (vs. telson biramous posteriorly and markedly shorter than uropods).

In comparison with the adult stage, the first-settled stage of *A. antennatus* shows, as described above for the mysis II stage, less complex general structures and appendages and fewer integumental elements. In particular, some important differences between adult and

first-settled stages that can be remarked are: rostrum with three dorsal spines (vs. with two spines), proportionally shorter uropods and telson and proportionally longer scaphocerite. The mentioned differences were also observed in early juveniles with respect to the adult stage by [Sardà and Cartes \(1997\)](#), except for the three dorsal spines on the rostrum, already present in early juvenile stages of 6–7 cm TL ([Sardà and Cartes, 1997](#)). Furthermore, in comparison with the smallest juveniles described, the abdomen of the first-settled stage is similar in length to the cephalothorax (vs. clearly longer than the cephalothorax).

Despite the described specimen could suffer from a certain decoloration by formaldehyde preservation, it still showed a pale orange-apricot colour, especially in the abdomen and in the anterior part of cephalothorax ([Fig. 4A](#)), similar to the colour of the smallest fully-developed juvenile stages (CL > 6.4–6.7 mm) regularly caught at > 1000 m in the Balearic Basin ([Fig. 4B](#)).

4.2. What does occur beyond the first-settlement stage?

Assuming a theoretical average time for hatching in July ([Carbonell et al., 2008](#); [Cartes et al., 2017](#)), the life history and distribution of smallest individuals of *A. antennatus* captured in the Balearic Basin can be reconstructed during the first year of life. The age of the current specimen, representing the first-settlement stage, can vary, since this species displays a relatively long reproductive period which extends from April–May to September–October ([Carbonell et al., 1999](#)), and larvae of quite different stages can be found in the water column at the same time (Mysis II and Protozoa II in July for example, see [Torres et al., 2013](#)). After settlement, the geographical occurrence of *A. antennatus* smallest individuals (CL < 16 mm), compiled on the basis of a number of oceanographic cruises performed in the Balearic Basin between 2007 and 2020, evidenced temporal and spatial patterns in the distribution of these small shrimps (see [Fig. 5](#)). In October–December (minimum CL of 6.4 mm) these small specimens were not abundant, which points to an initial phase of settlement. These specimens were mainly distributed on the head of the large Valencia Trough, the southern part of the Balearic Basin, relatively close to the location where the first-settled specimen described in the present work was found. The distribution and density of these smallest *A. antennatus* at the end of winter and spring (minimum CL of 6.7–8.2 mm) and in summer (minimum CL of 10.9–11.5 mm) suggests a progressive displacement from the south-west to the north-east of the Balearic Basin along the Valencia Trough, with higher densities at deeper and insular areas, mostly on the eastern side of the Valencia Channel. The growth of the smallest individuals of *A. antennatus* was established by [Cartes and Demestre \(2003\)](#), and it is well-known that the distribution of juveniles of the 1st year cohort is almost completely restricted to depths >1000 m, and thus within the western Mediterranean deep-water mass ([Cartes et al., 2017](#)). These juveniles live in benthic habitats and feed on the benthos-suprabenthos ([Sardà and Cartes, 1997](#)). In the present case we can glimpse a temporal distribution pattern of “bigger-offshore” that could be linked to seasonal changes in the water column conditions in the study area, since the water mass (the Western Mediterranean Deep Water current, WMDW) is the same. During winter-spring the water column is homogeneous, but downwelling phenomena of winter waters in the north, from the Gulf of Lyons ([Millot, 1999](#)), could act as a barrier for juvenile dispersion to deeper grounds, somehow limiting the distribution of juveniles in the central region of the Balearic Basin. By contrast, the flow of winter waters in the N is interrupted by the water column stratification occurring by late spring-early summer, which would allow the displacement of small specimens of *A. antennatus* to higher depths of the Balearic Basin valley.

5. Conclusions

The generalized scarcity of known first-settled stages for all deep-sea fauna (including the red shrimp) is, in all likelihood, related to the lack

of knowledge about their ecology and the subsequent scarcity and difficulty of specially designed surveys to capture these stages. Probably, a preference by these organisms to find refuge in inaccessible or special habitats ([Montgomery et al., 2001](#)) also contributes to this pattern. For instance, small specimens of *A. antennatus* were sometimes found associated to mature fields of *Isidella elongata* ([Maynou and Cartes, 2012](#)). However, these first-year specimens can also be captured out of bamboo coral fields, in flat muddy bottoms without generating-habitat at > 1000 m. Therefore, and in our opinion, the lack of specifically-designed samplings performed in particular areas and periods is the main obstacle to fill the gap of first-settled phases. Remarkably, the two smallest individuals collected up to date in the Balearic Basin (including the *post-larvae* described in the present study) were captured with suprabenthic sledges equipped with 0.5 mm plankton nets.

In light of these difficulties, the present description of a first-settled stage of *A. antennatus* represents an important and valuable contribution to the knowledge on the life cycle of this species. In conjunction with the development and spatio-temporal distribution of first-year specimens, a clearer vision on the life history of the red shrimp juveniles is presented.

It is out of doubt that additional and more frequent surveys are needed in deep waters to unravel life history traits and morphological features of a wide array of marine species. Early stages of many commercial species are yet to be discovered and characterized, an important task to be done in order to achieve the understanding required for the correct and sustainable management of commercially exploited natural stocks, as is the case of *A. antennatus*.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2023.104020>.

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