LARVAL DEVELOPMENT OF THE CRAB XANTHO PORESSA (DECAPODA: XANTHIDAE) REARED IN THE LABORATORY

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ABSTRACT

Larvae of Xantho poressa were reared in the laboratory from an ovigerous female collected in the Gulf of Cádiz, Spain. The larval series included 4 zoeal and 1 megalopal stage, typical of the vast majority of xanthid species in the subfamily Xanthinae. Duration of each zoeal stage ranged from 2–4 days, that of the megalopa averaged 10 days, and the first crab stage was reached after 23 days. Zoeae are extremely similar to those of X. incisus, whereas the megalopa displays more noticeable differences. Zoeal characteristics conform to the Group I xanthid larvae as designated by Rice (1980) and Martin (1984); megalopal characteristics also are consistent with this grouping. Brief comparisons are made between our findings and those few reports of larvae of Xantho (notably that of Ingle, 1983, on X. incisus) from this and other regions.

The brachyuran genus Xantho Leach, as currently accepted, contains three or four species (Guinot, 1967, 1970) of small to medium-sized crabs in the eastern North Atlantic and South Atlantic oceans, from Norway and the North Sea south to Morocco, including the Shetland Isles, England, the Azores, Madeira, Ilhas Desertas, Canary Islands, Cape Verde Islands, and the Mediterranean Sea (Drach and Forest, 1953; Monod, 1956; Zariquiey Alvarez, 1968; Ingle, 1980; Manning and Holthuis, 1981). Several more species have been reported from the Indian Ocean and Indo-Pacific, as well as from the eastern Atlantic (see Monod, 1956; Guinot, 1966; Serène, 1984), but were removed from the genus by Guinot (1967). The group has proved to be taxonomically difficult, and unanswered questions remain concerning the extent of the ranges of species, and whether some of the recognized forms are deserving of subspecies or species status (see Drach and Forest, 1953; Holthuis, 1954; Almaça, 1972; García-Raso et al., 1987). Therefore, detailed descriptions of larval stages may help to resolve some of these uncertainties.

Although several early workers described larval stages of species of *Xantho* (reviewed by Martin, 1984, 1988), mostly from plankton collections, often there was uncertainty as to which species was in hand, and only rarely was any stage beyond the first zoea described. In this paper, we describe the zoeal stages, megalopa, and first crab of *Xantho poressa* (Olivi, 1792) (=*Xantho ri*- vulosus (Risso, 1816); see Holthuis, 1954), compare our findings to previous descriptions (primarily that of Ingle, 1983, on Xantho incisus Leach), and comment on the significance of the larval characters in X. poressa and in the genus Xantho as compared to those of other xanthids.

MATERIALS AND METHODS

An ovigerous female of Xantho poressa was collected on 14 June 1995 from El Chato Beach, Cádiz, Gulf of Cádiz, Spain. The female was transferred to the laboratory and maintained in an aquarium with filtered sea water until the eggs hatched. Larvae were then cultured in triplicate, at a density of 100 larvae per liter in each of three 2-1 bottles. Average salinity of the water was $35\%c \pm 1$ at a temperature of 26° C. Larvae were subjected to a continual artificial light regime of 12 h light/12 h dark, and fed on rotifers (Brachionus plicatilis (O.F. Müller)) from zoea I to zoea III. Beginning at zoea III, nauplii of Artemia sp. were fed to larval stages up to and including the first crab. Water was changed and new rotifers and nauplii of Artemia were supplied daily. Larvae of each developmental stage were fixed and preserved in buffered formaldehyde and transfered to 70% ethanol. Zoeal, megalopal, and first crab stages, as well as the parental female, have been deposited in the Museo Nacional de Ciencias Naturales de Madrid, reference number MNCN 20.04/3627. Another series of larvae was deposited in the Natural History Museum of Los Angeles County (LACM 95-125.1). All measurements were made with an ocular micrometer and were based on 20 individuals per stage. Measurements were as follows: for the zoeal stages, TT = rostrodorsal length, the distance between the tips of the dorsal and rostral spines, CW = carapace width, measured between the tips of the lateral spines, and CL = carapace length, measured from the base of the rostral spine to the posterior margin of the carapace; for the megalopa, CW is the maximum distance across the carapace, and CL is as above. Dissected appendages were mounted in CMC 10 (Turtox

Table 1. Mean size and standard deviation in mm of rostrodorsal length (TT), carapace width (CW), carapace length (CL), and days to appearance and duration of the larval stages of *Xantho poressa* (Olivi, 1792) reared in the laboratory at 26° C.

Stage	TT	CW	CL	Mean days to first appearance/duration
Zoea I	1.44 ± 0.19	0.58 ± 0.18	0.50 ± 0.18	0/2.5
Zoea II	1.79 ± 0.37	0.74 ± 0.18	0.58 ± 0.17	2.5/3
Zoea III	2.67 ± 0.50	0.88 ± 0.22	0.85 ± 0.23	5.5/3
Zoea IV	3.27 ± 0.50	1.19 ± 0.30	1.10 ± 0.30	8.5/4
Megalopa		1.04 ± 0.18	1.45 ± 0.25	12.5/10
				Appearance of first crab, 23 days

Ltd.) and stained with lignin pink. At least 10 specimens were mounted for each larval stage. Drawings and measurements were made using a Wild M5 dissecting microscope and a Zeiss compound microscope with Nomarski interference, both equipped with a camera lucida. All setal counts are proximal to distal.

RESULTS

The ovigerous female, weight = 4.75 g, CL = 17.2 mm, CW = 25.7 mm, released about 5,100 zoeae (all zoea I) on 16 June 1995. In the triplicate rearing experiment, four zoeal stages and a single megalopa were obtained. No intermediate stages and no "prezoeae" were observed. The mean duration of each stage at 26° C is shown in Table 1, together with measurements of TT, CL, and CW. Metamorphosis to the first juvenile crab stage occurred 23 days after hatching from eggs. All zoeal stages were translucent with orange and black chromatophores on the carapace and abdominal somites.

Descriptions

Zoea I

Carapace (Fig. 1A).—Wider than long. Dorsal spine curved distally and approximately equal in length to rostral spine, both well developed. Lateral spines prominent. One pair of minute setae at base of dorsal spine. Posterolateral margins lacking setae. Eyes elliptical and sessile.

Antennule (Fig. 2A).—Unsegmented, with 4 terminal aesthetascs and 1 seta. Endopod absent.

Antenna (Fig. 2F).—Spinous process equal to rostral spine in length, with strong spines along distal half. Endopod absent. Exopod small, with 2 very small distal setae.

Mandible.—Incisor and molar processes differentiated. Endopod (palp) absent.

Maxillule (Fig. 3A).—Coxal and basial endites with 7 and 5 marginal spines and setae, respectively. Endopod 2-segmented, with 1, 2 + 4 setae. Exopod without seta at basis.

Maxilla (Fig. 4A).—Coxal and basial endites 2-lobed with 4 + 4 and 5 + 4 marginal spines and setae, respectively. Endopod 2-lobed with 8 setae, arranged 3, 2 + 3. Scaphognathite (exopod) with 4 marginal plumose setae and elongate posterior process.

Maxilliped 1 (Fig. 5A).—Basis with 10 medial setae, arranged 2, 2, 3, 3. Endopod 5-segmented, with 3, 2, 1, 2, 5 setae. Exopod 2-segmented with 4 natatory plumose setae.

Maxilliped 2 (Fig. 5E).—Basis with 4 medial setae. Endopod 3-segmented with 1, 1, 5 setae. Exopod as in maxilliped 1.

Maxilliped 3.—Absent.

Abdomen (Fig. 6A).—Five somites. Acute dorsolateral knobs on somites 2 and 3. Single pair of posterior setules on dorsal surface of somites 2–5. Pleopods absent.

Telson (Fig. 6A).—Branches of furca curved dorsally, with 2 lateral spines, anterior of which being by far larger, and 1 dorsal spine. Posterior median indentation with 3 pairs of serrate setae.

Zoea II

Carapace (Fig. 1B, C).—With 2 pairs of minute anterodorsal setae and 2 pairs of setae on posterolateral margin. Eyes stalked. Otherwise unchanged.

Antennule (Fig. 2B).—Five terminal aesthetascs and 1 seta. Endopod bud present, minute.

Antenna (Fig. 2G).—Spinous process



Fig. 1. Xantho poressa (Olivi, 1792), zoeae. A, first zoea, lateral view; B, second zoea, lateral view; C, second zoea, frontal view; D, third zoea, lateral view; E, fourth zoea, lateral view.



Fig. 2. Xantho poressa (Olivi, 1792), larval antennule (A–E) and antenna (F–J). A, F, first zoea; B, G, second zoea; C, H, third zoea; D, I, fourth zoea; E, J, megalopa.

slightly less spinose. Endopod bud present. Exopod unchanged.

Mandible.—Incisor process with several small teeth.

Maxillule (Fig. 3B).-Coxal and basial en-

dites with 7 and 8 marginal spines and setae, respectively. Basis with 1 plumose seta. Endopod unchanged.

Maxilla (Fig. 4B).—Coxal and basial endites 2-lobed with 4 + 4 and 5 + 4 mar-



Fig. 3. Xantho poressa (Olivi, 1792), larval maxillule. A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, megalopa.



Fig. 4. Xantho poressa (Olivi, 1792), larval maxilla. A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, megalopa.

ginal setae and spines, respectively. Endopod unchanged. Scaphognathite (exopod) with 10 or 11 marginal plumose setae.

Maxilliped 1 (Fig. 5B).—Basis and endopod unchanged. Exopod with 6 natatory plumose setae.

Maxilliped 2 (Fig. 5F).—Basis and endopod unchanged. Exopod with 7 natatory setae.

Maxilliped 3.—Absent.

Abdomen (Fig. 6B).—With dorsal seta on somite 1. Posterolateral spines (acute exten-

sions) on somites 3–5 longer, not quite reaching midlength of succeeding somites. Pleopods absent.

Telson (Fig. 6B).—Second lateral spine on branches of furca reduced. Otherwise unchanged.

Zoea III

Carapace (Fig. 1D).—Seven pairs of setae along posterolateral margin, and additional pair of minute setae on anterodorsal region. Otherwise unchanged.



Fig. 5. Xantho poressa (Olivi, 1792), larval first and second maxillipeds. A-D, first maxilliped, first through fourth zoea; I, megalopa. E-H, second maxilliped, first through fourth zoea; J, megalopa.



Fig. 6. Xantho poressa (Olivi, 1792), larval abdomen and telson. A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, megalopa; F, telson and uropods of megalopa; G, pleopod 1 of megalopa.

Antennule (Fig. 2C).—Four terminal plus 1 subterminal aesthetascs and 1 seta. Endopod bud present.

Antenna (Fig. 2H).—Endopod bud longer than in Zoea II. Otherwise unchanged.

Mandible .--- Endopod bud present.

Maxillule (Fig. 3C).—Coxal and basial endites with 8 and 10 marginal spines and setae, respectively. Outer margin of basis and endopod unchanged.

Maxilla (Fig. 4C).—Coxal and basial endites with 5 + 4 and 5 + 5 marginal spines and setae, respectively. Endopod unchanged. Scaphognathite (exopod) with 19 (18–20) marginal plumose setae.

Maxilliped 1 (Fig. 5C).—Basis unchanged. Distal segment of endopod with 6 setae. Exopod with 8 natatory plumose setae.

Maxilliped 2 (Fig. 5G).—Exopod with 9 natatory plumose setae. Otherwise unchanged.

Maxilliped 3.-Present, reduced.

Abdomen (Fig. 6C).—With 6 somites, and with 3 dorsal setae on somite 1. Posterolateral spines (acute extensions) on somites 3– 5 reaching midlength of succeding somites. Pleopod buds present.

Telson (Fig. 6C).—Additional (fourth) pair of serrate setae at posterior indentation, smaller than and located between innermost of existing pairs.

Zoea IV

Carapace (Fig. 1E).—With 9 or more pairs of setae along posterolateral margin. Otherwise unchanged.

Antennule (Fig. 2D).—Four terminal and 8 subterminal aesthetascs, 1 terminal and 1 subterminal seta. Endopod bud present, with proximal part bearing 2 small setae.

Antenna (Fig. 2I).—Spinous process with no more than 4 or 5 subterminal spines. Exopod with 2 terminal short setae. Endopod reaching approximately to midlength of spinous process and articulating with (distinct from) protopod.

Mandible.—Palp more developed, but unsegmented and unarmed.

Maxillule (Fig. 3D).—Coxal and basial endites with 12 and 13 marginal spines and

setae, respectively. Endopod and outer margin of basis unchanged.

Maxilla (Fig. 4D).—Coxal and basial endites with 5 + 4 and 6 + 7 marginal spines and setae, respectively. Endopod unchanged. Scaphognathite (exopod) with 28 or 29 marginal plumose setae.

Maxilliped 1 (Fig. 5D).—Endopod and basis unchanged. Exopod with 10 natatory plumose setae.

Maxilliped 2 (Fig. 5H).—Endopod and basis unchanged. Exopod with 11 natatory plumose setae.

Maxilliped 3.-Present.

Abdomen (Fig. 6D).—Posterolateral spines (acute extensions) on somites 3–5 longer, extending well beyond midlength of following somite. Pleopods larger than in previous stage; endopod buds present on each.

Telson (Fig. 6D).—Sometimes with additional unpaired medial serrate seta at posterior indentation. Otherwise unchanged.

Megalopa

Carapace (Fig. 7A).—Rostrum directed obliquely downward, with pair of acute anterolateral spines flanking it. Posterior region of carapace broader than anterior. Surface and margins sparsely setose.

Antennule (Fig. 2E).—Peduncle 3-segmented, with 2, 2, 3 setae. Endopod 2-segmented, with 3 terminal plus 2 subterminal setae on distal segment and no setae on proximal segment. Exopod 5-segmented, with 0, 10, 6, 4, 0 aesthetascs and 0, 0, 3, 0, 2 setae, respectively.

Antenna (Fig. 2J).—Peduncle 3-segmented, with 4, 2, and 2 setae. Flagellum 8-segmented, with setation 0, 0, 3, 0, 5, 0, 4, 5.

Mandible (Fig. 7F).—Palp 2-segmented, with 10–12 setae on distal segment.

Maxillule (Fig. 3E).—Coxal endite with 16 setae. Basial endite with 20 spines/setae on lateral margin and 3 setae on inner margin. Basis with 2 long setae. Endopod 2-segmented, with 2 setae on proximal segment and 1 subterminal plus 2 small terminal setae on distal segment.

Maxilla (Fig. 4E).—Coxal and basial endites 2-lobed, with 10 + 8 and 6 + 12 setae, respectively. Endopod with 7 dorsal plu-



Fig. 7. Xantho poressa (Olivi, 1792), characters of megalopa. A, megalopa, dorsal view; B, cheliped; C, second pereiopod; D, third pereiopod; E, fifth pereiopod; F, mandible; G, third maxilliped.

mose setae. Scaphognathite with 55–57 marginal plumose setae and 2 short setae on each surface.

Maxilliped 1 (Fig. 5I).-Coxal endite with

14 setae. Basial endite with 27 setae. Endopod 2-segmented, with 4 short terminal setae on distal segment. Exopod 2-segmented, with 2 terminal setae on proximal segment and 5 plumose setae on distal segment. Epipod well developed with 2 long setae and 8–10 gill-grooming setae.

Maxilliped 2 (Fig. 5J).—Coxa/basis with 1 short seta. Endopod 5-segmented, with 1, 3, 1, 6, 9 spines/setae. Exopod 2-segmented, with 2 short spines and 1 seta on proximal segment and 5 terminal plumose setae on distal segment. Epipod bilobed, with 5 setae on longest lobe.

Maxilliped 3 (Fig. 7G).—Coxa/basis with row of 25 or 26 plumose setae. Endopod 5-segmented, with approximately 22, 15, 9, 10, and 9 spines/setae, respectively. Exopod 2-segmented, with 3 setae on proximal segment and 5 terminal plumose setae plus 1 or 2 short setae on distal segment. Epipod long, with 19 or 20 gill-grooming setae.

Pereiopods (Fig. 7B–E).—All with spine on coxal endite. Cheliped with prominent curved spine on basi-ischium and with setae as shown. Pereiopods 2–5 thin and setose. Pereiopod 2 with small spine on basiischium. Ventral margin of dactylus of periopods 2–4 with 3 spines and 2 shorter subterminal spines. Dactylus of pereiopod 5 with no spines and with 3 long, distally curved, subterminal setae.

Abdomen (Fig. 6E, G).—With 6 segments, sparsely setose, with setation as shown. Exopods of pleopods (Fig. 6G) 1–4 with 17–20, 16–19, 16 or 17, and 14 or 15 natatory plumose setae, respectively, and with 3 coupling hooks on inner margin.

Telson (Fig. 6E, F).—Posteriorly somewhat truncate, broader than long, with 3 long plumose setae on posterior margin, and with 3 pairs of dorsal and 2 pairs of ventral small setae. Uropods (Fig. 6F) without endopod, and bearing 9 natatory plumose setae on distal segment and 1 such seta on proximal segment.

First Crab

Carapace (Fig. 8) length and width approximately equal, with sparse setation and minute granules and protuberances as shown. Lateral margin with 3 denticulate teeth, decreasing in size posteriorly; last of these teeth with fewer or no denticulations. Pereiopods (not illustrated) shorter and broader than in megalopal stage.



Fig. 8. Xantho poressa (Olivi, 1792). First crab, dorsal view of carapace and eyes.

DISCUSSION

Although most previous accounts of the larvae of species of Xantho (see Martin, 1984: table 1) are somewhat suspect, in part because of the reliance on planktonic material of unknown parentage and in part because so many species in the past were treated as being in this genus (e.g., see index in Serène, 1984), several authors have described all four zoeal stages and the megalopal stage. Cano (1892) was apparently the first to do so, although it is difficult to say with certainty what species he was working with, and Hyman (1925) repeated Cano's figures. It is slightly troubling to note that Cano (and consequently Hyman) included 2 megalopal stages, an almost certain indication that they were dealing with larvae of more than one species. Thus, these descriptions and figures, as well as the first zoea drawn by Gourett (1884), are of little help in resolving questions of systematics. Furthermore, it is clear from the current study that the first zoea described by Bourdillon-Casanova (1960: fig. 53) could not belong to Xantho poressa. The specimen described by Bourdillon-Casanova has a rostral spine that is spinose and clearly shorter than the antennal protopod; the rostrum of X. poressa described by us is lacking spinules and is approximately equal in length to the antenna (Fig. 1). The dorsal spine of the zoea described by Bourdillon-Casanova is also unusual, in that it is curved posteriorly along its entire length and bears serrations along the anterior margin and at the base of the posterior margin; the rostral spine in our specimens curves posteriorly only at its distal extremity and is completely smooth throughout its length. It is curious that Bourdillon-Casanova equated her descriptions with those of Gourett (1884) (as X. rivulosus Osorio) and Lebour (1928) (as X. hydrophilus Balss) (see Holthuis, 1954; Martin, 1984), because the description by Lebour (1928: plate II, fig. 4) (based on only the first zoea, which did not survive further) did not include these morphological features. In fact, Lebour noted that, other than being slightly more curved distally, the dorsal spine was "otherwise very like X. incisus."

The account of the larvae of Xantho incisus by Lebour (1928) is likely a more reliable description; it was based on larval stages reared from a berried female (as was the case with her X. hydrophilus, but with X. incisus all stages, including young crab, were reached). Ingle (1983), whose description of the larvae of X. incisus based on laboratory-reared specimens is by far the most detailed, noted few substantial differences between the description by Lebour and his own account. Differences between larvae of X. incisus as described by Ingle (1983) and larvae of X. poressa described here are very slight. In fact, other than a few setal counts on parts of appendages where setae are admittedly difficult to see, the only noticeable difference was that the antennal protopod of X. incisus bears few (2 or 3) distal spines at all zoeal stages, and thus by the fourth zoeal stage the reduction in spination is primarily one in size of spinules rather than number. In X. poressa, the antennal protopod is spinulose along almost the entire distal half in the first zoeal stage, and these spines are reduced in size as well as in number, until only 4 or 5 remain by the fourth zoea (where it is still more spinulose than that of X. incisus). An additional record of a zoea attributed to Xantho was given by Paula (1987) from off the southwest coast of Portugal, but could not at that time be attributed with certainty to species level.

As to the megalopa, in addition to the previously mentioned accounts of Cano (1892), Hyman (1925), and Lebour (1928), only Kurian (1956) and Ingle (1983) have described megalopae attributed to this genus. Kurian (1956) included no illustrations, and for description stated only that it "closely resembles the specimen described by Lebour." Martin (1988) used only the description by Ingle in his analysis of xanthid megalopal characters in phylogeny, and was of the opinion, as are we, that earlier descriptions either should be viewed with some skepticism or, in the case or the work of Lebour (1928), were exceeded in detail by Ingle's description. Only one slight difference was noted by Ingle (1983) between his description of the megalopa of X. incisus and that of Lebour: the specimen studied by Ingle had slightly more setae on the distal segment of the uropodal exopod (12 versus 10). Thus, it seems likely that the material of this species studied by Lebour was correctly identified.

Differences between the above two accounts of megalopae of X. incisus and our description of this stage in X. poressa are more significant, and include different setal formulas on the antennular exopod (0, 2 in X. incisus versus 0, 5 arranged 1 + 3 + 1in X. poressa), antennal peduncle (0, 2, 1 versus 4, 2, 2), antennal flagellum (0, 1, 1, 0, 4, 0, 3, 5 or 6 versus 0, 0, 3, 0, 5, 0, 4, 5), maxillule endopod (unsegmented with 3 or 4 setae versus 2-segmented with 2, 1 +2 setae), and uropods (1, 12 versus 1, 9), and the presence in X. poressa of minute coxal spines on the pereiopods (although this could have been overlooked in other descriptions), among other slight differences.

Concerning the first crab, Ingle (1983: 972, fig. 15e) described four denticulate teeth (counting the first postorbital tooth) on the carapace of X. *incisus*, whereas Lebour (1928) described only three. Our first crab stage of X. *poressa* also bore only three such teeth, and these are smaller and less denticulate than those described by Ingle for X. *incisus*. Thus, in this character at least, published descriptions of the first crab may differ more within a species (X. *inci*-

sus) than between accounts of different species in the genus.

The form of the antennal exopod, setation of the mouthparts, and morphology of the abdomen place the zoeae of X. poressa in the "Group I" xanthid larvae as described by Rice (1980) and Martin (1984). This is not surprising, since this grouping includes most known descriptions of xanthid larvae, including all previous descriptions of larvae attributed to Xantho, and more or less corresponds to the subfamily Xanthinae Alcock of Balss (see Martin, 1984, 1988). Morphological characters of our megalopa of X. poressa also are in agreement with those of megalopae from other xanthid species that display "Group I" larvae (Martin, 1984, 1988).

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