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Morphological variability of the megalopa of *Liocarcinus depurator* (Brachyura: Portunidae) in Mediterranean and Atlantic populations

Guillermo Guerao ^a, Pere Abelló ^b & Antonina Dos Santos ^c

^a Dept. Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain

^b Institut de Ciències del Mar (CSIC), Barcelona, Spain

^c Instituto Nacional de Investigação Agrária e das Pescas—IPIMAR, Lisboa, Portugal

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Morphological variability of the megalopa of *Liocarcinus depurator* (Brachyura: Portunidae) in Mediterranean and Atlantic populations

GUILLERMO GUERAO¹, PERE ABELLÓ² & ANTONINA DOS SANTOS³

¹Dept. Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain, ²Institut de Ciències del Mar (CSIC), Barcelona, Spain, and ³Instituto Nacional de Investigação Agrária e das Pescas—IPIMAR, Lisboa, Portugal

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Abstract

Megalopae of the portunid crab *Liocarcinus depurator* were captured from the plankton in the western Mediterranean and northeastern Atlantic. The megalopa stage is morphologically described and illustrated and compared with other previous descriptions of this stage in the species. The Mediterranean megalopae showed intrapopulational variability in setation, and meristic and morphometric characteristics showed important differences when compared to previous descriptions from the Atlantic populations. The Atlantic plankton specimens described herein are more similar to Mediterranean megalopae than previous descriptions of the megalopa stage of the species obtained from laboratory-reared material from North Atlantic populations. This study shows that, even in morphological characters considered conservative, meristic variation may be found.

Keywords: *Brachyura*, *Liocarcinus depurator*, *megalopa*, *morphological variability*, *Portunidae*

Introduction

Larval morphology from laboratory-reared specimens has been well documented in many species of crabs but little is known about natural morphological variability from specimens obtained directly from the plankton (DeBrosse et al. 1990; Anger 2001; Armendariz 2005). Additionally, most of the megalopal descriptions are based on a relatively low number of individuals and their morphological variability is not usually studied (Ingle 1992). Furthermore, for many species of crabs with a wide geographical distribution, the morphology of their larval stages is only known for one population and therefore, their geographical variability is unknown. Latitudinal and seasonal variation in larval morphology both from laboratory-reared larvae and larvae collected from the plankton have only occasionally been reported in decapods (Costlow 1965; Lang and Young 1977; Shirley et al. 1987; Montú et al. 1990; González-Gordillo and Rodríguez 2000; Anger 2001; Wehrtmann and Albornoz 2003). However, this information is important for

Correspondence: Guillermo Guerao, Dept. Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal 645, 08028 Barcelona, Spain. Email: gguerao@xtec.cat

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population studies (Ingle 1992). Additionally, the practical usefulness of identification keys for brachyuran larvae (mostly based on laboratory-reared individuals) becomes limited if they cannot be validated with studies on the actual morphology of plankton-captured individuals.

The larvae of polybiinid portunid crabs have been studied in many species from laboratory-reared material (see Ingle 1992; González-Gordillo et al. 2001), but insufficient information is available on plankton-caught specimens of this subfamily to evaluate comparative morphological features and their population variability. *Liocarcinus depurator* (Linnaeus, 1758) is a portunid crab occurring on the continental shelf and upper slope in the northeast Atlantic from the coasts of the western Sahara to Norway, encompassing also the whole Mediterranean Sea (Zariquiey-Álvarez 1968; d'Udekem d'Acoz 1999) where it is one of the commonest species of continental shelf and upper slope communities (Mori and Zunino 1987; Abelló et al. 1988, 2002; Ungaro et al. 1999; Rufino et al. 2005). It can be found on several types of sediment, but preferentially on muddy and sandy-muddy bottoms (Minervini et al. 1982; Rufino et al. 2004b). Information on the vertical and horizontal distribution of *L. depurator* megalopae was studied in the northwest Mediterranean by Abelló and Guerao (1999), showing that their distribution was restricted to neritic waters inshore of a shelf-slope jet current.

Previous descriptions of larval stages of *L. depurator* have been based on Atlantic specimens only and no specific study on their complete larval development exists. Information on the morphology of the first three zoeal stages of this species has been documented by Lebour (1928). Clark (1984) described from the second to the last zoea, and Ingle (1985, 1992) presented some descriptions for all zoeal stages. Concerning the megalopal stage, Lebour (1928) figured the dorsal view of the carapace and Ingle (1985) compared some morphometric and meristic features with those of other polybiinids. In his monograph on the larval stages of northeastern Atlantic crabs, Ingle (1992) described the morphology of the megalopa of laboratory-reared larvae of *L. depurator*, widely scattered throughout the text, and did not describe several important features such as the maxillipeds and the sternum. The early juvenile development of the species was described by Lebour (1928) and Ingle and Rice (1984) based on specimens from Atlantic populations.

Concerning population variability in *L. depurator*, several authors have identified biological and genetic differential characteristics between Mediterranean and Atlantic populations. Thus, Mantovani et al. (1992) and Passamonti et al. (1997) showed genetic differentiation between several European populations of *L. depurator* based on gene-enzyme data sets. Additionally, Rufino et al. (2006) detected carapace shape differences between Mediterranean areas under the immediate influence of the incoming Atlantic waters and typical Mediterranean populations. In this context, the present paper describes and presents figures of the megalopa of *L. depurator* from plankton samples taken in the western Mediterranean Sea off Catalonia and in the eastern Atlantic Ocean off Portugal, and aims to compare its morphology with previous megalopal descriptions of this species. It further aims to provide additional evidence concerning the variability between Mediterranean and Atlantic populations, and laboratory-reared individuals of this species.

Material and methods

In the western Mediterranean, a large number of megalopae were collected from a neuston sample taken off the Ebre river delta (latitude 40°07.4'N, longitude 0°51.6'E; bottom depth 89 m) on 20 February 1997, just after the main *L. depurator* breeding season (Abelló 1989).

Surface water temperature was 13.5°C (Olivar et al. 2001; Sabatés 2004). Samples were preserved in 70% ethanol. They were firstly identified as belonging to the species *Liocarcinus depurator* based mainly on Ingle's (1992) descriptions. Additionally, some individuals were kept alive and reared up to the fifth juvenile crab, which confirmed identification.

Liocarcinus depurator megalopae from Atlantic waters were collected in plankton hauls taken off the Portuguese coast along a transect (latitude 40°54'N; longitude between 08°47'W and 09°09'W) in May 2002. The samples were taken using a Pro-LHPR system, fitted with a 280 µm mesh net and was towed at 3–4 knots on oblique hauls from 10 m above the bottom to the surface. All samples were preserved in 4% borax-buffered formaldehyde prepared using seawater.

To study meristic and morphometric variation, 30 megalopae from the Mediterranean and seven megalopae from the Atlantic were dissected on glass slides in polyvinyl alcohol using a Wild M8 binocular microscope and the appendages were allowed to clear for 24 h before examination. Coverslips were sealed with clear nail varnish. Appendages were drawn using an Olympus BH-2 microscope equipped with differential interference contrast (DIC) and a camera lucida. Carapace width (CW) was measured as the greatest distance across the carapace, and carapace length (CL) as the distance between the tip of the rostrum and the posterior margin of the carapace. The megalopa is described using the basic malacostracan somite plan from anterior to posterior and appendage segments are described from proximal to distal, endopod then exopod (Clark et al. 1998). The number of setae present in each segment of the appendages is that stated in the text; some setae present in the concealed face of the appendages are not shown in the drawings. The long aesthetascs on the antennules and the long plumose setae on distal exopod segments are drawn truncated.

A selection of 30 Mediterranean megalopae of *L. depurator* have been deposited in the Reference Biological Collections of the Institut de Ciències del Mar (CSIC) in Barcelona under accession code ICMD 119/2006.

Results

The Mediterranean megalopa is described in detail. The morphological and meristic differences with Atlantic individuals are presented in Table I.

Liocarcinus depurator (Linnaeus, 1758) (Figures 1–9)

Lebour 1928, p 515, Plate VI, Figure 1; Ingle 1985, p 246; Ingle 1992, p 212, Figures 1.28d, 1.31g, 2.23a–g, 1.

Description of megalopa

Size. CL=3.02 ± 0.10 mm; CW=2.04 ± 0.12 mm (*n*=30).

Carapace (Figure 1A, B). Longer than broad, without spines. Rostrum horizontal and prominent, margin of the frontal region slightly raised, medial furrow shallow; a pair of prominent protogastric carinae. Posterior margin straight.

Antennule (Figure 1C). Peduncle three-segmented, with 4, 3, 2 setae, respectively. Endopod two-segmented with two subterminal and four terminal setae in distal segment.

Table I. Morphometrical and meristic differences in megalopae of *Liocarcinus depurator* from present and previous studies.

Feature	W Mediterranean (Catalonia) (present study)	NE Atlantic (Portugal) (present study)	NE Atlantic (British Isles) (Lebour 1928; Ingle 1985, 1992)
CL (mm)	3.02±0.10	2.76±0.10	2–2.01
CW (mm)	2.04±0.12	1.67±0.06	nd
Antennule: aesthetascs on exopod	0, 11, 9, 5	0, 12, 9, 5	0, 11, 10, 7
Antenna: no. of segments	7–8	7	8
Maxillule: setae on coxal endite	15–16	16	12
Maxilla			
Setae on coxal endite	7–8+4–5	8+4–5	6+6
Setae on scaphognathite	59–66	57–59	48
Pereopods 2–4: spines on dactyl	7, 7–8, 6–7	7, 7, 7	7, 8–9, 7–8
Pleopods: setae on pleopods	20–22, 22, 18–20, 17–18	20, 20–21, 19–20, 16–17	19, 18, 16–18, 15
Telson: setae on dorsal surface	4–6	4–6	4
Uropod			
Setae on protopod	0–2	1	0
Setae on exopod	10–11	10–11	8–10

nd, not described.

Exopod four-segmented, with 0, 10–12, 8–9 and 5 aesthetascs, respectively, and 0, 0, 2, 2 (one subterminal and one terminal) simple setae.

Antenna (Figure 2A). Peduncle three-segmented, with 2–4, 2, 2 setae, respectively. Flagellum seven- or eight-segmented (frequently segments 2 and 3 not completely segmented), with 0, (0), 4, 0–1, 4–5, 1, 4, 4–5 setae, respectively (usually 0, (0), 4, 0, 5, 1, 4, 5).

Mandible (Figure 2B). Palp two-segmented, with 11–13 (usually 12) sparsely plumose setae on distal segment.

Maxillule (Figure 2C). Coxal endite with 15–16 setae (seven cuspidate and eight to nine plumodenticulate). Basial endite with 28–31 setae (25–26 setae along posterior margin and three to five setae on inner lateral margin). Endopod unsegmented with four to six setae.

Maxilla (Figure 3). Coxal endite bilobed, with 7–8+4–5 setae. Basial endite bilobed, with 10–11+11–12 setae. Endopod unsegmented, with two to five plumose setae on its outer lateral margin. Exopod (scaphognathite) with 59–65 marginal plumose setae (mean value 61.9 ± 2.26) and four to six lateral setae.

First maxilliped (Figure 4). Epipod with 16–19 long simple setae. Coxal endite with 16–19 setae. Basial endite with 37–39 setae. Endopod unsegmented with one to two proximal plumose and four to five distal simple setae. Exopod three-segmented, proximal segment with five to seven distal plumose setae, distal segment with five to six long plumose terminal setae.

Second maxilliped (Figure 5). Epipod with one long simple seta. Coxa and basis not differentiated, with four setae. Endopod four-segmented with one to four simple setae on

Figure 1. *Liocarcinus depurator*, megalopa. (A, B) Carapace, lateral and dorsal views, respectively; (C) antennule. Scale bars: 1 mm (A, B); 0.2 mm (C).

proximal segment, one to two setae on the second, seven to eight plumodenticulate setae on third segment, nine (six cuspidate and three plumodenticulate) setae on distal segment. Exopod three-segmented, proximal segment with two to three short and thick setae, and distal segment with six to seven terminal plumose setae.

Third maxilliped (Figure 6). Epipod elongated with 10–12 long setae. Coxa and basis not differentiated with 20–25 setae. Endopod five-segmented, ischium inner margin with three or four teeth (crista dentata) and 28–30 setae; merus with 13–17 setae; carpus with 9–11 setae; propodus with 12–14 serrate setae; dactylus with 10–11 serrate setae, respectively. Exopod three-segmented, proximal segment with one or two setae, and distal segment with five to seven terminal plumose setae.

Pereiopods (Figure 7A–G). All segments well differentiated. Pereiopod 1 (chelipeds) with one ischial spine; pereopods 2–4 with one coxal spine. Dactyls of pereopods 2–4 with 7, 7–8, 6–7 small spines on the inner margin. Dactyl of pereopod 5 with three long subterminal setae.

Figure 2. *Liocarcinus depurator*, megalopa. (A) Antenna; (B) mandibular palp; (C) maxillule. Scale bars: 0.5 mm (A); 0.2 mm (B, C).

Sternum (Figure 7H). Maxillipeds and cheliped sternites fused with 4–6+2+6–8 setae plus one medial small process. Sternites of pereopods 2–4 with 1–2, 1, 1 setae.

Abdomen (Figure 8A, B). Six somites, broader than long, with well-developed tergites. Setation on somites as figured.

Pleopods (Figure 8C, D). Well developed and biramous; endopod unsegmented, inner margin with 3, 3, 4, 4 subterminal coupling hooks, respectively. Exopod unsegmented with 20–22, 22, 18–20, 17–18 long marginal natatory setae, respectively.

Uropods (Figure 9F, G). Uropods two-segmented, proximal segment (protopod) with zero to two (usually one) plumose setae, and distal segment (exopod) with 10–11 long marginal plumose setae, respectively.

Figure 3. *Liocarcinus depurator*, megalopa. Maxilla. Scale bar: 0.2 mm.

Telson (Figure 9A–E). Broader than long; dorsal surface with four to six simple setae (see Figure 9A–E), and a pair of setae on lateral margin, and a pair of setae on ventral surface.

Discussion

Geographically related intraspecific variability is often recorded in marine decapod crustaceans (e.g. Tully and Hillis 1995; Rebach and Wowor 1997; Defeo and Cardoso 2004). Within the family Portunidae, some of these studies encompass variability in morphometrics, genetics and/or reproductive characteristics (e.g. Clark et al. 2001; Davis et al. 2003; Chang and Hsu 2004). In particular, interpopulation variability in *Liocarcinus depurator* has been recorded concerning genetics (Mantovani et al. 1992; Passamonti et al. 1997), carapace shape and morphometrics (Rufino et al. 2004a, 2006), or distribution characteristics (Rufino et al. 2005).

This study has shown that the western Mediterranean megalopae of *Liocarcinus depurator* collected from the plankton show important differences in morphometric and meristic features from previous descriptions (Table I), namely (1) larger carapace length; (2) lower setation of the distal segment of the antennular exopod; (3) articulation between antennal flagellum segments 2–3 usually not present; (4) much higher setation of the scaphognathite margin; (5) larger number of setae in pleopods; (6) basal segment of the uropod with usually one seta; (7) mean higher number of setae on the uropod exopods.

Figure 4. *Liocarcinus depurator*, megalopa. First maxilliped. Scale bar: 0.2 mm.

Additionally, high intrapopulation variability in setation is found in planktonic Mediterranean megalopae. Thus, some setation patterns are more frequent than others, as in the typical antennal flagellum setation (0, 4, 0, 5, 1, 4, 5), but differences from this pattern can be found; also, the uropod protopod bears one seta in 82% of the individuals examined. However, setation variability is not found in some appendages, such as the antennular endopod (two+four simple setae), the distal segment of the antennular exopod (five aesthetascs), and the dactyl of the second maxilliped endopod (six cuspidate and three plumodenticulate setae).

The Atlantic megalopae of *Liocarcinus depurator* collected from the plankton showed intermediate morphological characters between Mediterranean megalopae and previous laboratory descriptions (Table I). Carapace length was significantly shorter than in Mediterranean megalopae (Student's *t* test; $t = -6.335$; $P < 0.01$), but larger than the 2 mm reported by Ingle (1992) and Lebour (1928). The megalopae studied by Ingle (1992) were laboratory-reared from ovigerous females collected in Strangford Lough, Ireland. Since larvae collected from the plankton are generally larger than those obtained from rearing experiments in laboratory conditions (Mene 1987; DeBrosse et al. 1989; Veloso and Calazans 1992; González-Gordillo and Rodríguez 2000; Wehrtmann and Albornoz 2003), this size difference could be attributed to the rearing conditions. However, Lebour's

Figure 5. *Liocarcinus depurator*, megalopa. Second maxilliped. Scale bar: 0.2 mm.

(1928) megalopae, which also measured 2 mm in carapace length, were obtained from late-stage zoeae collected directly from the plankton off Plymouth and thus, the size of the megalopae would be much less influenced, if at all, by laboratory conditions. This would imply that the size of megalopae found in the British Sea area would certainly be smaller than western Mediterranean and Portuguese ones.

Also, the number of plumose marginal setae of the scaphognathite of Portuguese Atlantic megalopae is lower than in the Mediterranean, but higher than in descriptions of laboratory-reared specimens. However, most setation features are more similar to those of Mediterranean megalopae than to those from previous laboratory descriptions (Table I).

Figure 6. *Liocarcinus depurator*, megalopa. Third maxilliped. Scale bar: 0.2 mm.

Geographical differences in decapod crustacean morphology may be attributed to genetic and/or ecological factors. Plastic responses to the environment have been demonstrated in many species of decapod larvae (Anger 2001). Thus, variability in the development and

Figure 7. *Liocarcinus depurator*, megalopa. (A–E) Pereiopods 1–5; (F) dactyl of the first pereopod; (G) dactyl of pereopod 5; (H) sternum. Scale bars: 0.5 mm.

morphology of zoeae has been found in relation to different temperature regimes (Shirley et al. 1987; Barria et al. 2005). Morphological plasticity in larval brachyura is not as pronounced as in the Caridea (Anger 2001), but is commonly found in species that have relatively many zoeal stages (Montú et al. 1990). DeBrosse et al. (1990) reported morphological differences between offshore and inshore megalopae of *Cancer magister* which may reflect different hydrographic features of the region. Kornienko and Korn (2004) also found differences in megalopae of the spider crab *Pugettia quadridens* (de Haan, 1850) from different areas. Armendariz (2005) also reported morphological differences

Figure 8. *Liocarcinus depurator*, megalopa. (A, B) Abdomen, lateral and dorsal views, respectively; (C) first pleopod; (D) pleopod 4. Scale bars: 0.3 mm.

between megalopae of *Uca uruguayensis* (Nobili, 1901) collected from Argentinian plankton material and megalopae reared in the laboratory from ovigerous females collected in Brazil.

Some studies suggested that morphological variability is lower in larvae obtained from the plankton than those reared in laboratory conditions, hypothesizing that natural selection in the field eliminates less viable morphs, thereby reducing the morphological variability among the remaining larvae (Fincham 1979; Wehrtmann and Albornoz 2003). However, larval developmental variability in decapods does exist in the natural environment and could be interpreted as an adaptative strategy for enhancing survival in the largely variable pelagic environments (Sandifer and Smith 1979; Montú et al. 1990; Anger 2001).

Figure 9. *Liocarcinus depurator*, megalopa. (A-E) Variety of telson, dorsal view; (F, G) uropods. Scale bars: 0.3 mm.

Taking into account the information presented above, one of the main conclusions reached is that it is necessary to study the morphology of larval stages directly collected from the plankton whenever possible, at least in parallel with larval rearing in the laboratory to confirm important characters in relation to inter- and intrapopulation variability, especially so in species with a large geographical distribution. This study has shown that, even in morphological characters considered conservative, meristic variation may be found. This information will be important for phylogenetic and phylogeographic studies as well as to elaborate useful identification keys. Concerning the species studied, the portunid crab *Liocarcinus depurator*, the present work provides additional information concerning the

occurrence of geographical differences between Atlantic and Mediterranean populations (Mantovani et al. 1992; Passamonti et al. 1997; Rufino et al. 2004a, 2005, 2006).

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