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MORPHOLOGICAL VARIABILITY IN LARVAL STAGES OF *NAUTICARIS MAGELLANICA* (A. MILNE EDWARDS, 1891) (DECAPODA: CARIDEA: HIPPOLYTIDAE) FROM SOUTH AMERICAN WATERS

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ABSTRACT

Of the three species of hippolytid shrimps known to occur in the southwestern Atlantic Ocean, *Nauticaris magellanica* (A. Milne Edwards, 1891) is the only representative of its genus. Zoeal larvae of *N. magellanica* were obtained from plankton samples taken by means of a plankton net in Argentine waters in the southwestern Atlantic Ocean during two expeditions carried out from onboard the RV WALTHER HERWIG and the RV SHINKAI MARU in 1978 and 1979, respectively. In the present work we distinguish and redescribe six zoeal stages of *N. magellanica* and compare our results with the previous description of larvae reared under laboratory conditions from a population off central southern Chile. Differences in size, number of setae on the appendages as well as in the development of the pereiopods are discussed from an ecological and biogeographical point of view.

The general knowledge of meroplanktonic larvae and their ecology is still limited, and taxonomists mainly focus on larval descriptions in order to facilitate studies on plankton ecology (e.g., Wehrtmann and Báez, 1997). However, due to the lack of larval descriptions it is hardly possible to work on a species level with decapod larvae. This is especially true for species inhabiting South American waters. Rearing larvae obtained from ovigerous females is the main method for analyses of larval development and allows a clear identification at the species level. In the history of larval research it has frequently been shown that larvae reared in the laboratory, and especially carideans, show a great variability in larval stages and morphology (Knowlton, 1974; Sandifer and Smith, 1979; Boschi, 1981; Criales and Anger, 1986; Wehrtmann, 1991). Published comparisons between decapod larvae reared in the laboratory and field-collected larvae do not exist, although laboratory observations give evidence that morphological variability might be a common pattern in nature, too. The amount of variability complicates the work of ecologists, and is one reason why scientists working on larval development and ecology mainly focus on autecological studies (e.g., Palma, 1994; Wehrtmann and Albornoz, 1998).

Nauticaris magellanica is the only representative of this genus inhabiting the coastal waters of southern South America (Holthuis, 1952; Méndez, 1981; Boschi et al., 1992). At the Pacific coast this shrimp is known to cover a geographical range of approximately 35° of latitude (Wehrtmann and Kattner, 1998), and therefore it is an ideal species for the study of ecological adaptations to different environmental conditions. It has been recorded from all parts of the Chilean coast (Retamal, 1981), except the South Patagonian Icefield (latitudinal range: 48°20′S to 51°30′S, Aniya and Skvarca, 1992; Mutschke et al., 1996), and is the most abundant shrimp associated with mussel raft cultures and holdfast of the kelp *Macrocystis pyrifera* (Aracena and López, 1973; Ojeda and Santelices, 1984). At the Atlantic coast, *N. magellanica* is known to occur from the coastal waters of Buenos Aires (Argentina) south to the Beagle Channel (Magellan region), as well as around the Falkland Islands/Islas Malvinas (Spivak, 1997; Boschi et al., 1992).

Wehrtmann and Albornoz (1998) provide a complete description of the larval development of *N. magellanica* reared from egg-carrying females obtained from a population collected from mussel raft culture (*Mytilus chilensis*) off central Chile (41°35′50″S, 72°42′53″W). Their work constitutes the first complete description for zoeal development in this genus. In our present study, we compare these larval descriptions with larvae of *N. magellanica* obtained from plankton samples taken in the southwestern Atlantic Ocean (37°35′S to 55°15′S; 53°40′W to 68°15′W), and discuss differences in size and morphology in relation to ecological adaptations and biogeographical separation.

Material and Methods

In the present work we provide information on the larval morphology of the hippolytid decapod *N. magellanica*. The material studied was collected in Argentine waters in the southwestern Atlantic Ocean (37°35′S to 55°15′S; 53°40′W to 68°15′W, see Fig. 1) during two expeditions carried out onboard the RV Walther Herwig and RV Shinkai Maru in 1978 (August to October) and 1979 (January to March), respectively (Ciechomski et al., 1979; Cousseau et al., 1979). Samples were collected by means of a Bongo net of 330 µm mesh size and were preserved in 3% formalin solution buffered with hexamethylenetetramine. Complete descriptions of the cruises and additional information on oceanographic measurements can be obtained from Ciechomski et al. (1979).

Carapace length (CL) was measured from the posterior edge of the orbital arch to the mid-dorsal posterior margin of the carapace; total length (TL) of the larvae was measured from the posterior margin of the orbital arch to the distal margin of the telson, excluding setae. The descriptions of larval stages represent an average of our observations. Nomenclature used for the differentiation of the larval phases and morphology corresponds to that suggested by Williamson (1960, 1968, 1982), Gurney (1942), Boschi (1981), Haynes (1978, 1981, 1985) and Albornoz and Wehrtmann (1997).

We compare our larval descriptions with that of Wehrtmann and Albornoz (1998) who reared larvae of *N. magellanica*, obtained from an adult population of a mussel raft culture (*M. chilensis*) in central southern Chile (41°35′50″S, 72°42′53″W).

Family Hippolytidae
Nauticaris magellanica (A. Milne Edwards, 1891)

Zoea I
TL = 2.2 ± 0.02 mm; CL = 0.6 ± 0.01 mm; n = 12

General Characteristics (Fig. 2A, B).—Eyes sessile; anterior and posterior part of carapace with small protuberances; rostrum acute and lightly curved down; one pair of pterygostomian spines present; supraorbital and antennal spines absent; 2nd abdominal segment without pleura; 6th abdominal segment continuous with telson.

Antennule (Fig. 2J).—Terminal region of external flagellum with three aesthetascs and one simple apical internal seta; internal flagellum with long plumodenticulate seta; protopodite long and without segmentation.

Antenna (Fig. 2K).—Exopodite with nine long plumose setae on internal margin (including tip) and two short external plumose setae; distal region divided in four segments; medium-internal margin of exopodite with small papilla; endopodite approximately two

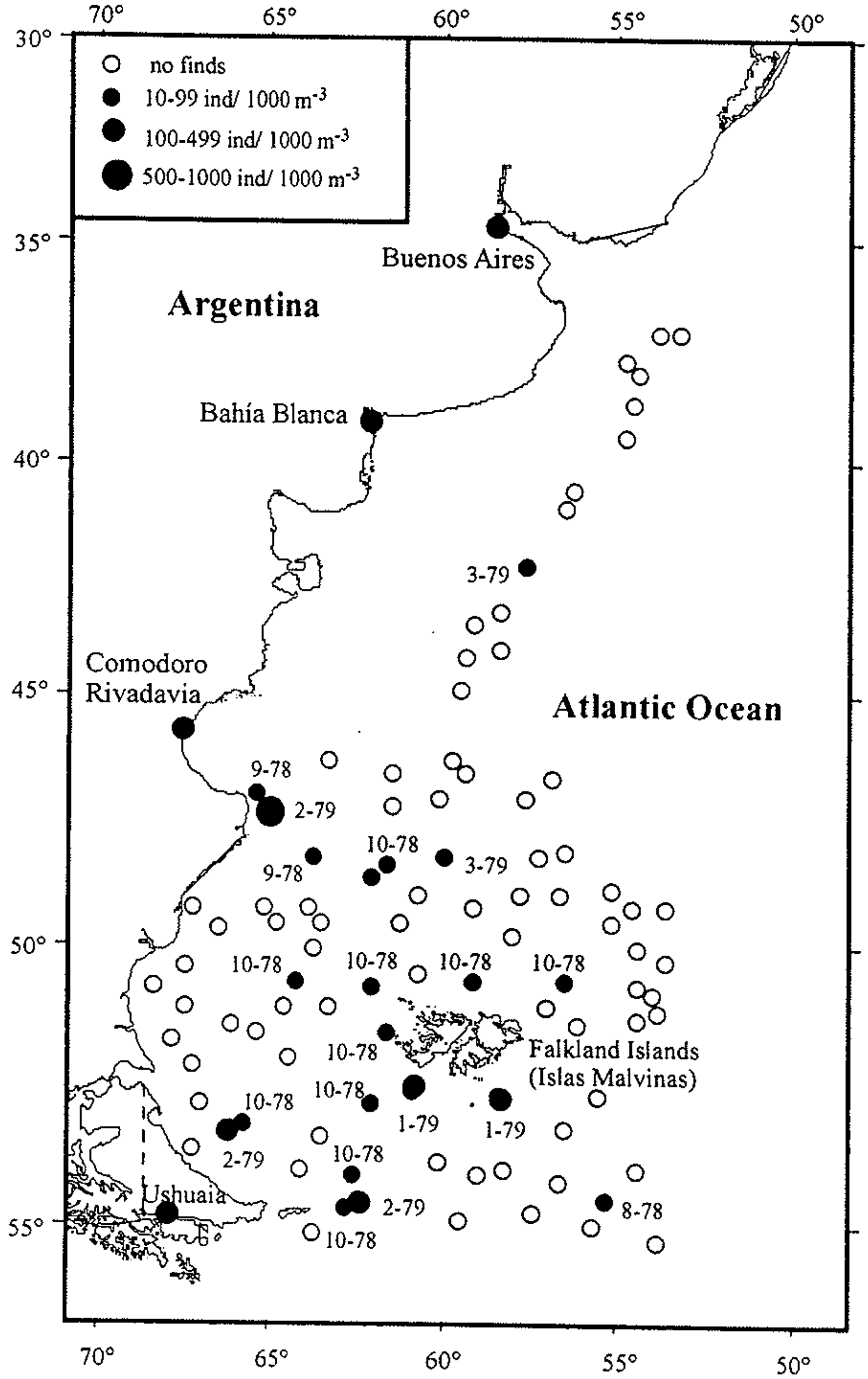

Figure 1. Sampling locations of larvae of *Nauticaris magellanica* in the southwestern Atlantic Ocean (Argentina) carried out onboard the RV Walther Herwig and the RV Shinkai Maru from August 1978 to March 1979 (sampling month and year as indicated by the numbers).

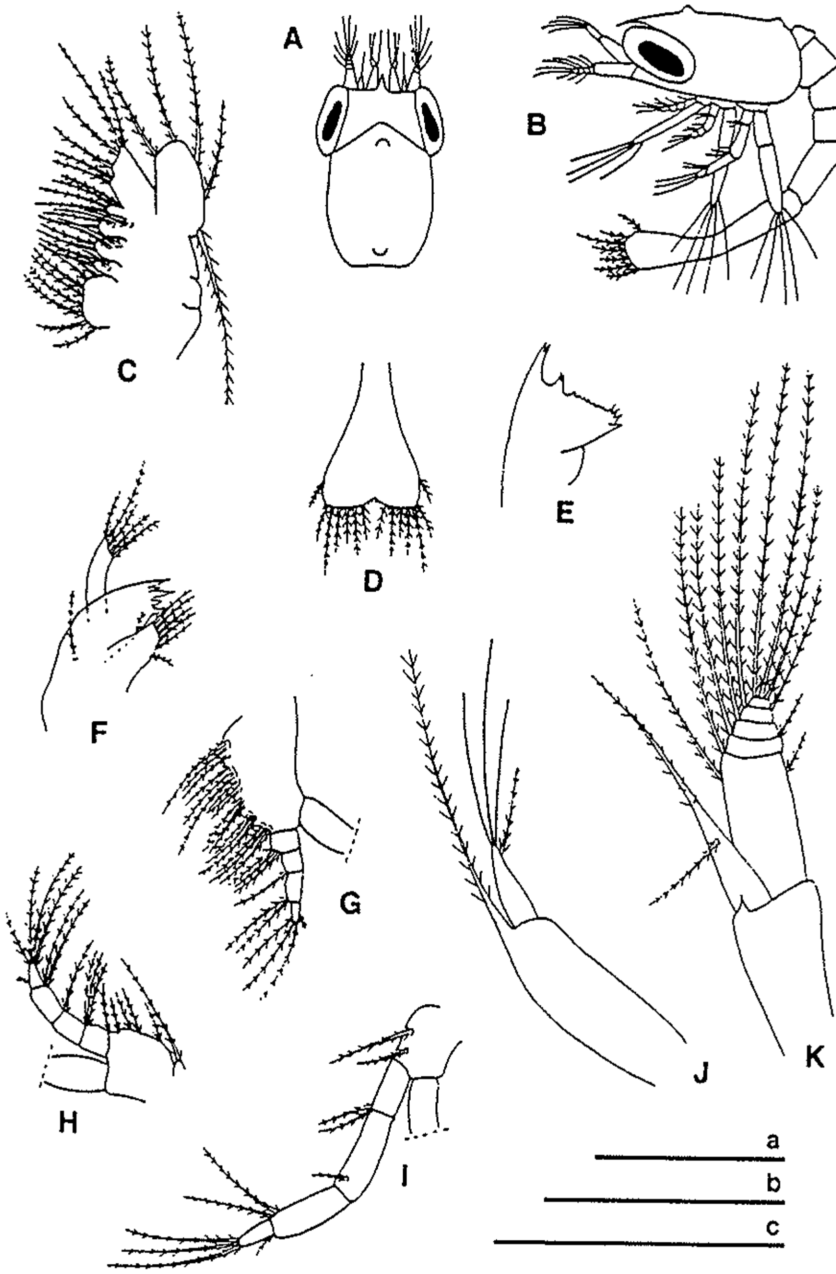

Figure 2. Zoea I. A: carapace with cephalic appendages, dorsal view; B: lateral view; C: maxilla; D: telson; E: mandible; F: maxillule; G: maxilliped I; H: maxilliped II; I: maxilliped III; J: antennule; K: antenna. Scale bars: a = 0.2 mm (C, E–F, J–K); b = 1 mm (A–B, D); c = 0.5 mm (G-I).

times larger than exopodite; with long plumose seta in medial position, distally bearing numerous denticles; protopodite with one small spine located on base of endopodite.

Mandible (Fig. 2E).—Incisor and molar processes present; incisor process bearing two strong terminal denticles; molar process with denticles and one protuberance.

Maxillule (Fig. 2F).—Endopodite with three plumodenticulate terminal setae and 12 subterminal setae; coxal endite with two long plumodenticulate and two short setae on lateral margin of endite, and three cuspidate setae on its distal part; internal margin with row of short, simple setae (microtrichia); basal endite with three spiniform setae, 2–3 spines with denticles and one serrate seta; protopodite with one plumose seta.

Maxilla (Fig. 2C).—Endopodite bilobed, with distal lobe longer, presenting 2, 1, 1, 2 plumodenticulate setae, from proximal to distal; proximal lobe with two plumodenticulate and one plumose setae; coxal endite with six plumose and three plumodenticulate setae on proximal lobe, and with two plumodenticulate and two plumose setae on distal lobe; basal endite with three plumodenticulate and one plumose setae on both proximal and distal lobe; scaphognathite with five plumose setae, one of which in apical region; internal margin of both endopodite and scaphognathite with row of small simple setae.

Maxilliped I (Fig. 2G).—Coxopodite with six plumodenticulate setae; basipodite with 3, 3, 3, 3 plumodenticulate setae on internal margin; endopodite of four segments with 3, 1, 2 and 4 proximal and distal setae; exopodite with three plumose natatory terminal setae and 1 subterminal one.

Maxilliped II (Fig. 2H).—Coxopodite with one plumodenticulate seta on internal margin; basipodite with 2, 3, 3 plumodenticulate setae; endopodite of four segments with 3, 1, 2, and 4 proximal and distal setae, respectively, exopodite with three terminal plus two subterminal plumose natatory setae.

Maxilliped III (Fig. 2I).—Coxopodite without setae; basipodite with 1, 1, 2 plumodenticulate setae on internal margin; endopodite composed of four segments: distal one with three terminal and one subterminal setae; exopodite with three terminal and two subterminal plumose natatory setae.

Pereiopods.—Absent.

Abdomen (Fig. 2B).—With 5 segments, 6th segment continuous with telson; pleopods absent.

Uropods.—Absent.

Telson (Fig. 2D).—Subtriangular; with 7+7 spines with external pair located laterally; with pronounced median indentation.

Zoea II

TL = 2.9 ± 0.08 mm; CL = 0.7 ± 0.03 mm; n = 11

General Characteristics (Fig. 3A,B).—Eyes pedunculate; carapace with pair of pterygostomian and supraorbital spines, but lacking antennal spines; rostrum more pronounced and lightly curved down; 6th abdominal somite still continuous with telson.

Antennule (Fig. 3H).—Internal flagellum small and with one long plumodenticulate terminal seta; external flagellum with four aesthetascs and one seta; distal margin of protopodite with two short plumose setae.

Antenna (Fig. 3D).—Exopodite (including tip) with eight long and two short plumose setae; distal tip 4-segmented; internal medial margin of exopodite without papilla.

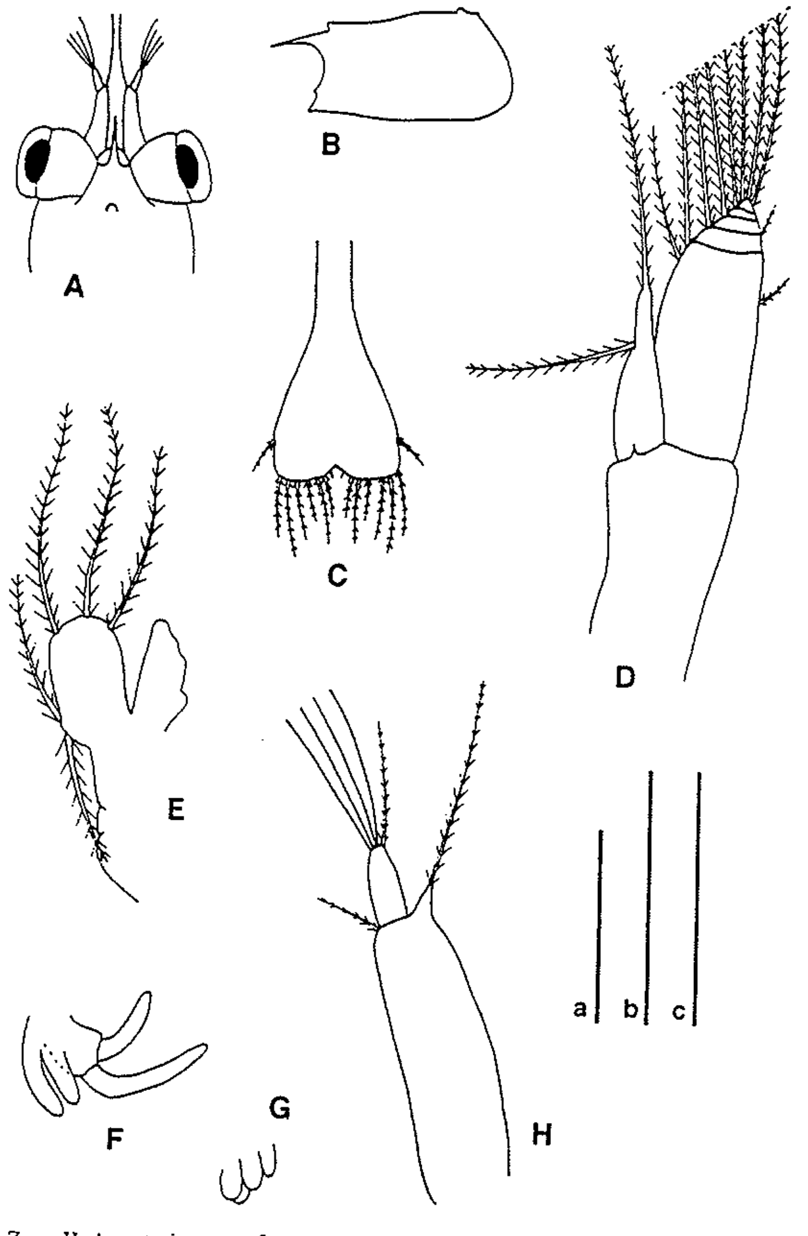

Figure 3. Zoea II. A: anterior part of carapace with cephalic appendages, dorsal view; B: carapace, lateral view; C: telson; D: antenna; E: maxilla; F: pereiopods I - II; G: pereiopods III – V; H: antennule. Scale bars: a = 0.2 mm (D–E, H); b = 1 mm (A–C); c = 0.5 mm (F–G).

Mandible.—Without changes.

Maxillule.—Coxal endite with seven setae; basal endite with five spines and two thinner ones; no other differences to previous stage.

Maxilla (Fig. 3E).—Proximal lobe of coxal endite with 11 plumose and four plumodenticulate setae; distal lobe with 2+2 plumodenticulate and plumose setae, respectively; proximal lobe of basal endite with 3+1 plumodenticulate and plumose setae, respectively; scaphognathite with four subterminal plus one apical plumose setae, one being apical; no other differences to previous stage.

Maxilliped I.—Coxopodite with eight plumodenticulate setae; basipodite with 3, 4, 4 and 3 proximal and distal setae, respectively; exopodite with four terminal and one subterminal plumose setae; no other differences to previous stage.

Maxilliped II.—Coxopodite with one plumodenticulate seta; endopodite 5-segmented, 1st one with one long plumose seta on internal margin, and 5th segment with six simple and serrate setae; exopodite with six plumose natatory setae; no other differences to previous stage.

Maxilliped III.—Coxopodite without setae; endopodite 5-segmented, 5th one with 3+1 setae; exopodite with six plumose natatory setae; no other differences to previous stage.

Pereiopods (Fig. 3F,G).—1st pereiopod biramous, semi-developed; 2nd and 3rd pereiopod biramous, rudimentary; 4th and 5th pereiopod rudimentary, represented by a small bud.

Abdomen.—As in previous stage.

Pleopods.—Absent

Uropods.—Absent.

Telson (Fig. 3C).—Subtriangular; posterior margin with 8+8 processes external pair laterally located, inner pair extremely short.

ZOEA III

TL = 3.9 ± 0.12 mm; CL = 1.0 ± 0.08 mm; n = 13

General Characteristics (Fig. 4A,B).—Carapace with one pair of supraorbital, antennal and pterigostomian spines; abdomen divided in six segments plus telson; rostrum slightly curved down.

Antennule (Fig. 4F).—Internal flagellum with one long plumose seta; protopodite 3-segmented; medial segment with two distal external setae; distal segment with one seta at basis of medial lobe; external flagellum with three aesthetascs and one seta.

Antenna (Fig. 4E).—Distal region 2-segmented; external spine well developed, without external setae, internal margin (including tip) with 11 setae; endopodite (including terminal spine) as long as exopodite.

Mandible.—Similar to previous stages.

Maxillule.—Coxal endite with three cuspidate setae, two long plumodenticulate and 2–3 plumodenticulate fine and short setae; basal endite with one spiniform seta, five spines armed with spinules, and two serrate setae; no other differences to previous stage.

Maxilla (Fig. 4D).—Proximal lobe of coxal endite with 13 plumose and four plumodenticulate setae; distal lobe with two plumodenticulate and two plumose setae; proximal and distal lobe of basal endite with four plumodenticulate and one plumose setae, respectively; scaphognathite with 10 subapical plus one apical plumose setae, one being apical.

Maxilliped I.—Basipodite with 3, 4, 4, 4 plumodenticulate setae; coxopodite with eight setae; no other differences to previous stage.

Maxilliped II.—Without changes compared to previous stage.

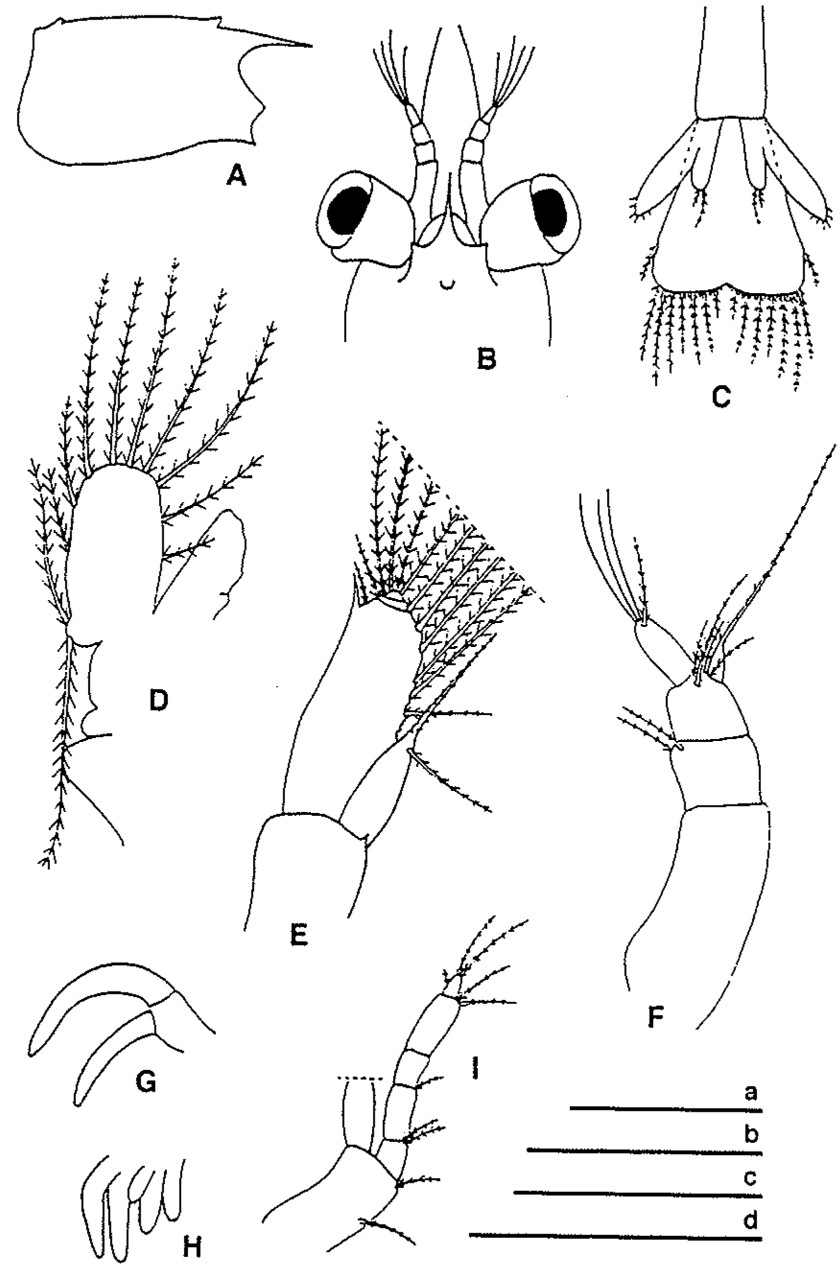

Figure 4. Zoea III. A: carapace, lateral view; B: anterior part of carapace with cephalic appendages; C: uropods and telson; D: maxilla; E: antenna; F: antennule; G: pereiopod II; H: pereiopods III – V; I: pereiopod I. Scale bars: a = 0.2 mm (D); b = 1 mm (A–C); c = 0.5 mm (G–I); d = 0.5 mm (E–F).

Maxilliped III.—Endopodite with 4+1 setae on distal segment; exopodite with eight plumose setae; no other differences to previous stage.

Pereiopods (Fig. 4G,H,I).—First pereiopod completely developed; exopodite with eight plumose natatory setae; basipodite with two setae; endopodite 5-segmented with 2, 1, 0, 2 and 3 proximal and distal setae, respectively, without cheliped; 2nd pereiopod present as biramous buds; pereiopods 3 and 4, biramous, less developed; pereiopods 4 and 5, uniramous, represented as simple buds.

Abdomen.—With 6 segments, 6th segment with one pair of spines on its posterolateral margin.

Pleopods.—Absent.

Uropods (Fig. 4C).—Biramous, developing; exopodite with six short simple setae on its margin, forming tail fan; endopodite with two plumose setae, terminal one three times as long as subterminal one.

Telson (Fig. 4C).—With 8+8 posterior processes, external pair located laterally.

ZOEA IV

TL = 4.03 ± 0.25 mm; CL = 1.03 ± 0.05 mm; n = 16

General Characteristics (Fig. 5A,C).—Eyes pedunculate, laterally oriented; carapace wider than in previous stages; carapace with one pair of supra-orbital, sub-orbital and pterygostomian spines; abdomen 6-segmented, second abdominal segment with developing pleura.

Antennule (Fig. 5D).—Protopodite 3-segmented, stilocerite with three distal setae and two external plumose setae and one internal seta; medial segment with two plumose internal and external setae, respectively; distal segment with one large distal plumodenticulate seta, and one smaller external one; external flagellum with three aesthetascs and one plumose seta; internal flagellum one third the size of external flagellum, with one plumodenticulate seta, as long as external flagellum (including setae).

Antenna (Fig. 5 E).—Endopodite with long plumose setae; endopodite half as long as exopodite; no other differences to previous stage.

Mandible.—Without palp; no other differences to previous stage.

Maxillule.—Coxal endite with nine setae; basal endite with nine spines and one spiniform seta; no other differences to previous stage.

Maxilla (Fig. 5F).—Proximal and distal lobes of coxal endite with 14 and four setae, respectively; basal endites with seven setae, each; scaphognathite with 17 marginal plumose setae, one being apical.

Maxilliped I.—Basipodite with 3, 5, 6, 4 plumodenticulate setae; coxopodite with eight setae; exopodite with six plumose setae; no other differences to previous stage.

Maxilliped II.—Endopodite of five well separated segments; carpus with one external plumose seta; exopodite with six natatory plumose setae; no other differences to previous stage.

Maxilliped III.—Exopodite with eight natatory plumose setae; no other differences from previous stage.

Pereiopod I (Fig. 5G).—Well developed; exopodite with nine natatory plumose setae; caxopodite with two plumose setae; endopodite 5-segmented with 1, 0, 0, one and two plumose setae.

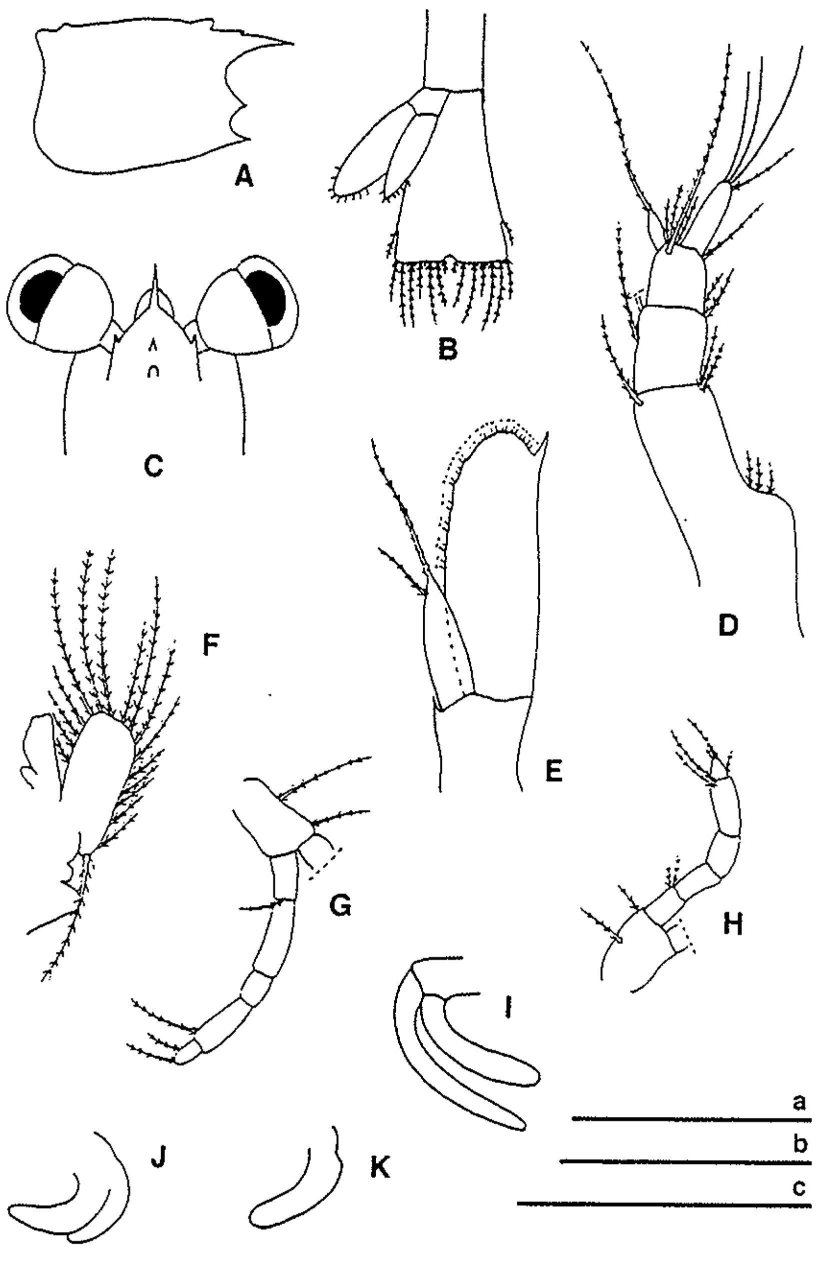

Figure 5. Zoea IV. A: carapace, lateral view; B: uropods and telson; C: anterior part of carapace with cephalic appendages, dorsal view; D: antennule; E: antenna; F: maxilla; G: pereiopod I; H: pereiopod II; I: pereiopod III; J: pereiopod IV; K: pereiopod V. Scale bars: a = 1 mm (A–C); b = 0.5 mm (G–K); c = 0.5 mm (D–F).

Pereiopod II (Fig. 5H).—Developed; exopodite with six natatory plumose setae; coxopodite with two plumose setae; endopodite 5-segmented with 2, 0, 0, 2 and 3 plumose setae.

Pereiopod III (Fig. 5I).—Rudimentary, biramous.

Pereiopod IV (Fig. 5J).—Present as biramous buds.

Pereiopod V (Fig. 5K).—Simple buds.

Pleopods.—Absent.

Uropods (Fig. 5B).—Well developed, biramous; endouropod with seven short marginal setae; exouropod with nine short marginal setae.

Telson (Fig. 5B).—Longer than wide; with 8+8 posterior processes; external pair being located at distal quarter.

Zoea V

TL = 4.68 ± 0.45 mm; CL = 1.1 ± 0.05 mm; n = 6

General Characteristics (Fig. 6A,B).—Eyes pedunculate; carapace with one pair of dorsal spines on base of rostrum; rostrum generally more pronounced and straight; one pair of suborbital, antennal and pterygostomian spines.

Antennule (Fig. 6E).—Antennal peduncle 3-segmented; stylerocerite with one terminal plumose and 8 plumose setae; basal segment with one internal and six plumose external setae; medial segment with three external and two internal plumose setae; distal medial lobe with four plumodenticulate setae; external flagellum with two subterminal and three terminal aesthetascs and one apical plumose seta.

Antenna (Fig. 6F).—Exopodite with 18 long plumose setae; endopodite half as long as exopodite; lateral setae absent; no other differences to previous stage.

Mandible.—Without palp; no other major differences to previous stage.

Maxillule.—Coxal endite with 13 plumose setae; basal endite with 10 spines and two setae; external seta reduced; no other differences to previous stage.

Maxilla (Fig. 6C).—Proximal lobe of coxal endite with 10 plumose and six plumodenticulate setae; distal lobe with two plumodenticulate and two plumose setae; proximal and distal lobe of basal endite with six and seven plumodenticulate setae, respectively; each one with an additional plumose setae; scaphognathite with 26 marginal setae, one apical and one terminal flagellum.

Maxilliped I.—Coxopodite with eight plumodenticulate setae; basipodite with 4, 5, 5 and 6 plumodenticulate setae; no other differences to previous stage.

Maxilliped II.—Without changes.

Maxilliped III.—Without changes.

Pereiopod I.—Exopodite with 11 natatory plumose setae; endopodite as in previous stage.

Pereiopod II.—Endopodite as in pereiopod I; basipodite with two simple setae; exopodite with 10 natatory plumose setae.

Pereiopod III (Fig. 6G).—Well developed; endopodite 5-segmented with 0, 0, 1, 1, 1 plumose setae; exopodite simple, shorter than endopodite, without setae.

Pereiopod IV (Fig. 6H).—Biramous, rudimentary.

Pereiopod V (Fig. 6I).—Present as simple buds.

Pleopods.—Absent.

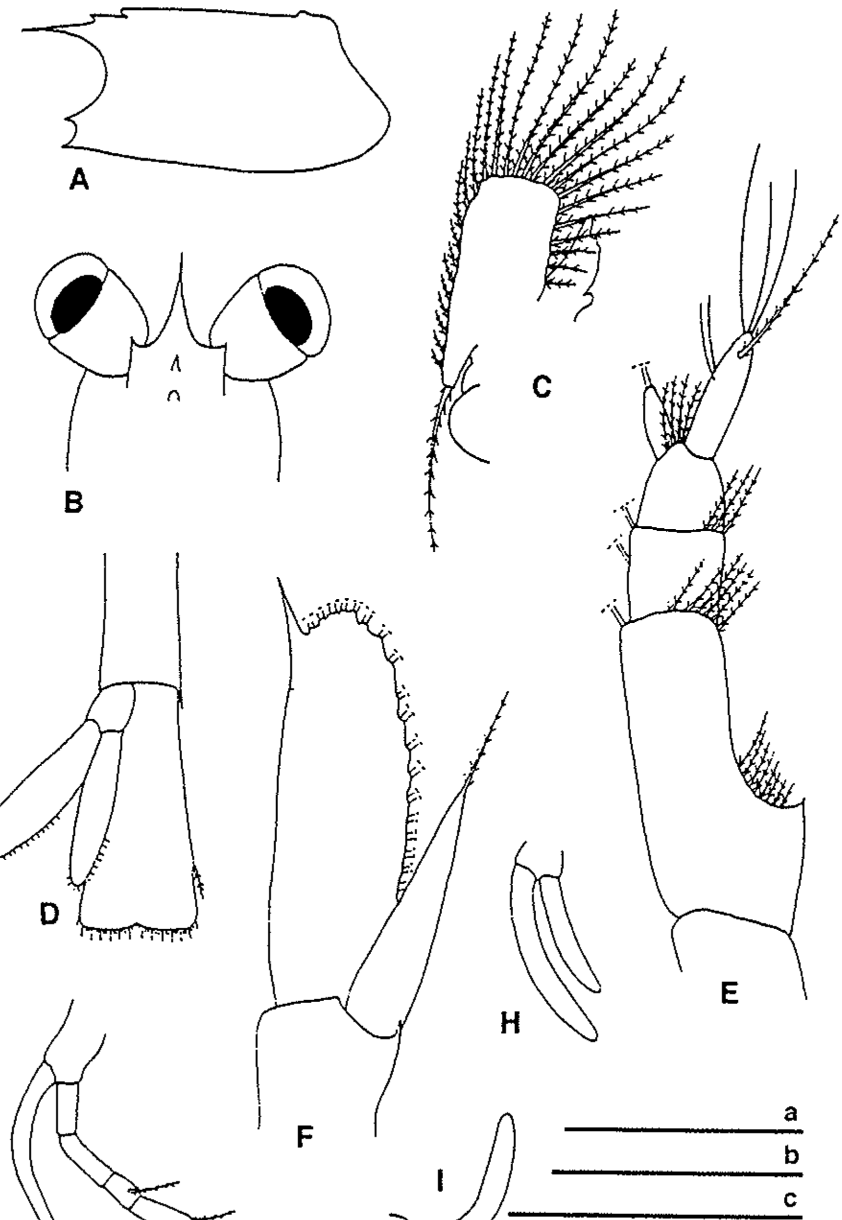

Figure 6. Zoea V. A: carapace. Lateral view; B: anterior part of carapace with cephalic appendages, dorsál view; C: scaphognathite of maxilla; D: uropods and telson; E: antennule; F: antenna; G: pereiopod III; H: pereiopod IV; I: pereiopod V. Scale bars: a = 1 mm (A–B, D); b = 0.5 mm (G–I); c = 0.5 mm (C, E–F).

Uropods (Fig. 6D).—Endouropod with 11 marginal setae; exouropod with 18 marginal setae; external terminal margin with 1 short spine.

Telson (Fig. 6D).—Posterior margin with 8+8 spines, external pair being located at distal quarter; telson longer, with nearly parallel lateral margins.

Zoea VI

TL = 5.9 ± 0.28 mm; CL = 1.5 ± 0.15 mm; n = 8

General Characteristics (Fig. 7A,B).—Carapace with dorsal medial spine at rostral base; eyes pedunculate; carapace with one pair of dorsal spines on base of rostrum; rostrum generally more pronounced and straight; one pair of suborbital, antennal and pterygostomian spines.

Antennule (Fig. 7F).—Basal segment with eight distal external plumose setae and four marginal internal ones; stylocerite with seven plumose setae; medial segment with five distal external plumose setae and two marginal internal setae; distal segment with one marginal internal plumose seta and two large setae at base of medial lobe, the last bearing five setae; internal flagellum with one large plumodenticulate seta; external flagellum with 2, 3 and 3 proximal and distal aesthetascs, respectively, and one subterminal distal seta.

Antenna (Fig. 7E).—Exopodite with 20 long plumose setae; endopodite with two segments, basal one smaller, with one small subterminal spine.

Mandible.—Without palp; no other differences to previous stage.

Maxillule.—Coxal endite with 17 plumose setae; basal endite with 12 spines and three aesthetascs; no other differences to previous stage.

Maxilla (Fig. 7D).—Endopodite as in previous stage; proximal and distal lobe of coxal endite with 20+4 plumose setae, respectively; basal endite with nine plumodenticulate setae; scaphognathite with 36 marginal plumose setae.

Maxilliped I.—Basipodite with 4, 6, 7 and 6 plumodenticulate setae; no other differences to previous stage.

Maxilliped II.—Basipodite with 1, 2, 1, 3 and 3 plumose setae; exopodite with eight natatory plumose setae; no other differences from stages 4 and 5.

Maxilliped III.—Exopodite with 12 natatory plumose setae; carpus with one external and one internal seta; no other major differences.

Pereiopod I (Fig. 7G).—Basipodite with two simple setae; endopodite of five segments with 2, 1 and 1 setae on segments 1–3, respectively; propodus as long as dactylus, with one medial external plumose seta and two distal internal ones; dactylus with one strong terminal spine and two plumose setae.

Pereiopod II (Fig. 7H).—Basipodite with two simple setae; endopodite 5-segmented with 2, 1, and 1 setae on segments 1–3; propodus with two internal plumose setae; dactylus with one strong terminal spine and three plumose setae; exopodite with 16 natatory plumose setae.

Pereiopod III (Fig. 7I).—Basipodite as in pereiopod I and II; endopodite of five segments with 2, 1, 2, 6 and 1 setae; dactylus with one strong terminal spine and 1 small internal one; exopodite with 14 natatory plumose setae.

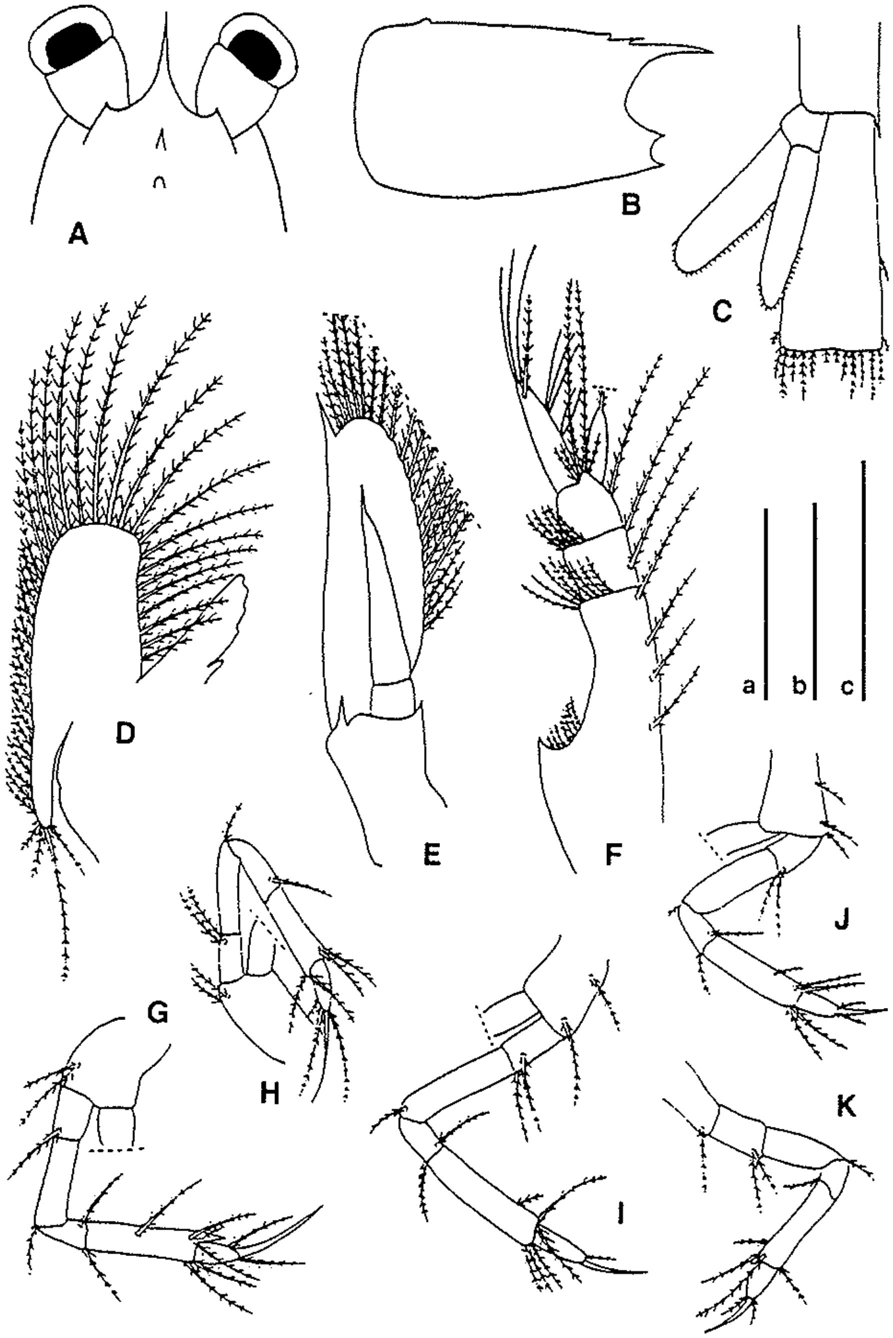

Figure 7. Zoea VI. A: anterior part of carapace with cephalic appendages, dorsal view; B: carapace, lateral view; C: uropods and telson; D: scaphognathite of maxilla; E: antenna; F: antennule; G: pereiopod I; H: pereiopod II; I: pereiopod III; J: pereiopod IV; K: pereiopod V. Scale bars: a = 1 mm (A–C); b = 0.5 mm (E–K); c = 0.5 mm (D).

Pereiopod IV (Fig. 7J).—Basipodite with three setae; endopodite of five segments with 2, 1, 2, 5 and 2 distal and proximal setae, respectively; dactylus with one strong terminal spine; exopodite with 12 pairs of plumose setae.

Pereiopod V (Fig. 7K).—Uniramous; endopodite of five segments with 2, 1, 1, 4 and 2 proximal and distal setae, respectively; dactylus with one strong terminal spine; basipodite with one plumose seta.

Pleopods.—Rudimentary buds in segments 2–5.

Uropods (Fig. 7C).—Endouropod with 21 marginal setae; exouropod with well developed external spine and 25 marginal setae; no other differences to previous stage.

Telson (Fig. 7C).—Lateral margins almost parallel; posterior margin with 8+8 processes, lateral pair located at distal third.

Discussion

The main two issues addressed by the morphological comparisons in the herein presented work are (1) differences between two populations from Chilean Pacific coastal waters and the southwestern Atlantic (see methods), being geographically separated by the Chilean South Patagonian Icefield (SPI), and (2) differences between laboratory-reared and field-collected larvae.

(1) *N. magellanica* is one of the most widely distributed hippolytid shrimps of South America with a geographical range of approximately 35° of latitude (Wehrtmann and Kattner, 1998), and the only of its genus which is known to occur in Chilean as well as in Argentine waters (Retamal, 1981; Boschi et al., 1981, 1992; Arntz et al., 1996; Spivak, 1997; Wehrtmann and Albornoz, 1998). Larvae of the two populations compared in this study are geographically separated by the Chilean South Patagonian Icefield (Campos de Hielo Sur; Warren and Sugden, 1993) which extends about 460 km along the Chilean Pacific coast, and where *N. magellanica* was shown to be absent. In fact, only eight decapod species have been recorded in the SPI yet, contributing less than 5% of the Chilean decapod fauna in general (Mutschke et al., 1996; see also Retamal, 1981). This faunal impoverishment in decapods was discussed to be due to lower average temperatures, salinity as well as sediment input and ice impact due to glaciers (cf U.S. Navy, 1982; Peters and Breeman, 1993; Sievers et al., 1996). *N. magellanica* is one of the most abundant shrimps on the continental slope of southern South America. An aggregation of older larval stages in potential coastal recruitment habitats was observed during our investigations, whereas early zoeae were found widely distributed in the open sea (Fig. 1).

Hippolytid larvae obtained during our investigation were clearly identified as belonging to *N. magellanica*. Apart from some differences (Table 1), the general scheme and morphological features correspond the larval description of Wehrtmann and Albornoz (1998). Only two other hippolytid species (*Chorismus tuberculatus*, *Chorismus antarcticus*) are known to occur in our sampling area in the southwestern Atlantic, and they can easily be distinguished from the studied species (see Gurney, 1937; Thatje and Bacardit, 2000). Distinctive characters distinguishing *N. magellanica* from the latter two hippolytid species are:

- Zoea I with small rostral spine.
- Margins of carapace smooth, reduced supraorbital spines and pterigostomian spines present.

Table 1. Differences in morphological characters (average observations) of *Nauticaris magellanica* between a population off central Chile (according to Wehrtmann and Albornoz, 1998) and the present investigation performed in the southwestern Atlantic Ocean. Pacific population (Chile) = Pacific. Southwestern Atlantic population (Argentina) = Atlantic. No difference = (–).

	Zoea I		Zoea II		Zoea III	
Character	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Mean TL	1.40 mm	2.2 mm	1.85 mm	2.9 mm	2.25 mm	3.9 mm
Mean CL	0.30 mm	0.6 mm	0.04 mm	0.7 mm	0.47 mm	1.0 mm
Rostrum	-	-	-	-	-	-
Antennule	-	-	External Flagellum with 3 aesthetascs + 1 seta	External Flagellum with 4 aesthetascs + 1 seta	-	-
Antenna	Exopodite with 7+2 setae	Exopodite with 9+2 setae	-	-	-	-
Maxillule	Endopodite with 3+2 setae	Endopodite with 3+12 setae	Coxal endite with 7+4 setae	Coxal endite with 11+4 setae	-	-
Maxilla	-	-	-	-	Coxal endite with 8+4 setae	Coxal endite with 13+4 setae
Maxilliped I	Endopodite with 3,1,3,1 setae	Endopodite with 3,1,2,4 setae	-	-	-	-

Table 1. Continued.

Character	Zoea I		Zoea II		Zoea III	
	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Maxilliped II	Basipodite with 1,2,3,3 setae; expo-dite with 5+2 setae	Basipodite with 2,3,3,0 setae; expo-dite with 3+2 setae	-	-	-	-
Maxilliped III	-	-	-	-	Expodite with 7 setae Endopodite with 1,0,0,2,4 setae	Expodite with 8 setae Endopodite with 2,1,0,2,3 setae
Pereiopod I	rudimentarious buds	absent	-	-		
Pereiopod II	rudimentarious buds	absent	-	-	-	-
Pereiopod III	-	-	absent	rudimentarious bud	-	-
Pereiopod IV	-	-	-	-	absent	uniramous simple buds
Pereiopod V	-	-	-	-	absent	uniramous simple buds
Pleopods	-	-	-	-	-	-
Uropods	-	-	developing buds visible	-	-	-
Telson	-	-	-	-	-	-

Table 1. Continued.

	Zoea IV		Zoea V		Zoea VI	
Character	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Mean TL	2.64 mm	4.03 mm	2.88 mm	4.68 mm	3.17 mm	5.9 mm
Mean CL	0.56 mm	1.03 mm	0.61 mm	1.1 mm	0.64 mm	1.5 mm
Rostrum	-	-	with 2 simple setae	no setae	with 2 simple setae	no setae
Antennule	External Flagellum with 4 aesthetascs + 2 seta	External Flagellum with 3 aesthetascs + 1 seta	-	-	External Flagellum with 4 aesthetascs + 2 seta	External Flagellum with 8 aesthetascs + 1 seta
Antenna	-	-	-	-	-	-
Maxillule	-	-	-	-	-	-
Maxilla	-	-	-	-	Scaphognathite with 18–25 setae	Scaphognathite with 36 setae
Maxilliped I	-	-	Coxopodite with 10 setae; basipodite with 4,5,6,4 setae	Coxopodite with 8 setae; basipodite with 4,5,5,6 setae	Basipodite with 4,6,6,6 setae Basipodite with 1,1,1,1,0 setae	Basipodite with 4,6,7,6 setae Basipodite with 1,2,1,3,3 setae
Maxilliped II	-	-	-	-		

Table 1. Continued.

Character	Zoea IV		Zoea V		Zoea VI	
	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Maxilliped III	-	-	-	-	-	-
Pereiopod I	Caxopodite without setae; endopodite with 0,0,0,0,5 setae	Caxopodite with 2 setae; endopodite with 1,0,0,1,2 setae	-	-	-	-
Pereiopod II	-	-	-	-	Exopodite with 13 setae	Exopodite with 14 setae
Pereiopod III	-	-	Endopodite with 8–9 setae	Endopodite without setae	Endopodite with 11–12 setae	Endopodite with 14 setae
Pereiopod IV	-	-	-	-	Exopodite with 8–9 setae	Exopodite with 12 setae
Pereiopod V	absent	simple buds	-	-	-	-
Pleopods	-	-	-	-	absent	Buds in segments 2–5
Uropods	-	-	-	-	Endouropod with 11–18 setae; exouropod with 16–22 setae	Endouropod with 21 setae; exouropod with 25 setae
Telson	-	-	-	-	-	-

- Maxillule with external seta.
- Exopodites present on pereiopods 1-4.
- Somites 4 and 5 without lateral spines.
- No anal spine.
- Posterior margin of telson straight in all stages, with 7+7 posterior processes, lateral pair located at distal third.

Due to the absence of complete larval descriptions of species other than *N. magellanica*, it is not possible to point out general characters which separate this genus from other genera of the Hippolytidae. At least for the southwestern Atlantic, the above mentioned characteristics allow a clear separation from the other hippolytid shrimps.

In the case of *N. magellanica*, morphological variability can be discussed as an ecological strategy and adaptation to changing environmental conditions. Most obvious differences in larval morphology of *N. magellanica* occurred in total larval length, being over 1.5 times bigger in the southwestern Atlantic as compared to the material studied by Wehrtmann and Albornoz (1998) from northern Chile (Table 1). Wehrtmann and Kattner (1998) observed a latitudinal increase in egg-size of *N. magellanica* at the Chilean Pacific coast which, in addition to the increase in larval size, confirms part of the reproductive theories for marine benthic invertebrates postulated by Thorson (1936, 1950), later known as "Thorson's rule" which was originally related to latitudinal changes in temperature. However, this rule has been discussed controversially during the last decade (Pearse et al., 1991; Hoegh-Guldberg and Pearse, 1995), but was often testified to be valid at least in gastropods and decapods (e.g., Thorson, 1950; Gorny et al., 1993; Clarke, 1993; Thatje et al., in review). Waters of northern Chile show higher, and greater fluctuating temperatures (winter/summer 14–24°C) than the southwestern Atlantic (winter/summer 4–10°C) (e.g., Medeiros and Kjerfve, 1988; Peters and Breeman, 1993), thus may explain the necessity of energy saving strategies by developing big-sized eggs and first zoeae, and a shorten planktonic larval development in the Atlantic population of *N. magellanica*. The early determination of the pereiopods III to V from Zoea II to IV, respectively (Table 1), supports this view towards a more abbreviated larval development in the southwestern Atlantic in contrast to northern Chile (Clarke, 1987, 1993).

Apart from larval size, main features characterizing larvae of *N. magellanica*, such as the rostrum, telson and uropods, did not show strong variability (Table 1), and therefore larvae of both compared populations may in some cases show identical morphology. However, we are not sufficiently able to explain the great observed variability in the number of setae, especially on thoracopods (Table 1), between both compared populations, just using terms of functional morphology or ecological adaptation. Future investigations need to confirm, if such variability is a common pattern in the larval development of other species, too, or if these basic morphological differences are a hint at a species split-off of two geographically separated populations of *N. magellanica* (for discussion see also Thatje and Bacardit, 2000).

(2) Rearing larvae under laboratory conditions was often proposed to be the best method for analyzing developmental pathways in marine invertebrates, mainly, because it allows a clear relation of larvae to the species. Variability in both larval morphology and the number of larval instars before metamorphosis has been described since first complete laboratory culturing of decapod development succeeded (Boyd and Johnson, 1963; Campodonico and Guzmán, 1981; Gore and Scotto, 1982), and was shown to be especially conspicuous in a variety of caridean shrimps (e.g., Knowlton, 1974; Christiansen

and Anger, 1990; Wehrtmann, 1991). Published comparisons between laboratory-reared and field-collected larvae do not exist, although larval variability is generally assumed to occur in nature, too, and to be an important factor in the development of carideans, enhancing survival and dispersal of larvae (e.g., Fincham and Figueras, 1986; Villamar and Brusca, 1988; Wehrtmann, 1991).

Wehrtmann and Albornoz (1998) described nine zoeal stages with the number of instars extending up to eleven in laboratory-reared larvae of *N. magellanica,* whereas our field-collected larvae divided into only six clear zoeal stages. It was frequently shown that caridean morphogenesis is affected by distinctive biotic and abiotic factors such as temperature, salinity and food availability (e.g., Villamar and Brusca, 1988; Christiansen and Anger, 1990). These factors are hardly possible to control in rearing experiments, because in most cases species ecology is rather unknown and mass-culturing is proposed to provide finally at least some juveniles. This may also be one reason why mortality rates in larvae cultures are in most cases dramatically high. However, if we assume that great variability in larval instars in laboratory cultures appears to be a reaction to physical and chemical stress, biased by unstable rearing conditions, and resulting in different developmental pathways in one culture (compare with Wehrtmann and Albornoz, 1998), why does larval development seem to be less variable in nature?

One possibility explaining these circumstances might be that the ability of meroplanktonic larvae, especially early developmental stages, to move actively is rather limited. Larvae are tied to water masses they are released to, and therefore distribution over greater distances is realized by transport by means of currents (for discussion see Banse, 1955; Dooley, 1977; Thatje et al., 1999), and for this reason environmental conditions can be more stable than in artificial rearing experiments. Developmental pathways may not necessarily depend on flexibility in larval instars, but in the case of changes in environmental conditions, such as mixture of water masses, food deficiency or changes in temperature and salinity, this flexibility is an evolutional and ecological strategy which enhances survival and allows distribution of larvae over greater distances.

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