Post-hatching development of the ornamental 'Red Cherry Shrimp' *Neocaridina davidi* (Bouvier, 1904) (Crustacea, Caridea, Atyidae) under laboratorial conditions

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Abstract

The 'Red Cherry shrimp', Neocaridina davidi is a small freshwater caridean shrimp living, originally, in various kinds of inland water bodies around Asian countries. This shrimp has reached several countries for ornamental use; however, basic information on the biology of the species is still scarce in the literature. Its early post embryonic development morphology has not yet been described. This paper focused on the production and the development of early post-hatching stages of N. davidi, its male secondary sexual features, observation of the gonads and the presence of females with embryos. The larval development of N. davidi was almost suppressed as noted by the presence of relatively large-sized eggs, first stage hatching as a decapodid; and the tail fans were present only from the 2nd post-hatching stage. A biological important consequence of the presence of this Red Cherry shrimp species in the Neotropics is its potential release into nature, which could cause its rapid dispersion affecting populations of other indigenous caridean freshwater shrimps.

Keywords: post-hatching stages, developmental time, Cherry shrimp, native, ornamental

Introduction

The genus *Neocaridina* Kubo (1938) has 23 species and 10 subspecies (De Grave & Fransen 2011). These freshwater shrimps are abundant in various kinds of inland water bodies (lakes, reservoirs, ponds, rivers and mountain streams) being distributed throughout Russia, China, Japan, Korea, Taiwan and Vietnam (Cai 1996; Liang 2004).

The atyid shrimp *Neocaridina davidi* (Bouvier, 1904), popularly known as 'Red Cherry shrimp' or 'RCS', is a small-size species (adults have approximate total lengths of 1.5–3.0 mm). Red Cherry shrimp are brightly coloured and widely reared for ornamental purposes. However, basic information on the biology of this species is still scarce in the literature.

The taxonomy of the Atyid from Asia is very difficult. They are documented in the literature under several synonyms and divisions of species into subspecies (Cai 1996; Liang 2002, 2004; Shih & Cai 2007). Klotz, Miesen, Hüllen and Herder (2013), describing an invasion of RCS in Germany, called it *N. davidi*. Considering the confusing and conflicting taxonomic status of the atyid shrimp, we sent some material for identification to an expert on Caridean taxonomy (Sammy De Grave, Oxford University Museum of Natural History). According to his analysis, our material (pictures and some specimens) belongs to *N. davidi* (Bouvier, 1904). Meanwhile, we compared our material with the original description (Kemp 1918) and also the figures from Klotz *et al.* (2013), which is consistent with the identification by De Grave.

The RCS have been selected by amateur raisers from specimens obtained in nature bearing a brownish colour and were cultured until the shrimp reached a red colour (Werner 2008). Subsequently, these crustaceans have reached several countries, mainly those in Neotropical regions, such as Argentina and Brazil for ornamental use. The success of RCS in the aquarium market is mainly due to the fact that this species is prolific, has a small size, and the supposed feeding on undesired algae, but non-feeding on vascular plants.

The early development of the atyid shrimp is very diverse with species showing common, abbreviated and completely suppressed type (Sollaud 1923; Lai & Shy 2009). Some authors have emphasized the importance of the egg's size and the larval morphology to classify the early development of Palaemonidae and Atvidae shrimps (Shokita 1981; Benzie 1982; Shy, Liou & Yu 1987). Following such arguments, Lai and Shy (2009) classified the early development into the following three categories: (1) the common type of early development has from 9 to 12 planktonic larval stages, and the pleopods of the first larval stage are not yet developed; (2) the abbreviated type has fewer (from 4 to 7) planktonic stages, and the pleopods of the first larval stage are still only rudiments and (3) the complete suppressed type has no planktonic larval stage, and the pleopods are well developed. Additionally, Lai and Shy (2009) indicate the following features for the complete suppressed type of development: freshly deposited eggs with sizes of 1.20×0.80 mm; pereiopods and pleopods completely developed; telson with 7-8 plumose setae; and benthic stages. Nevertheless, some variation could occur in species showing intermediate development.

Currently, there are two known species of the genus *Neocaridina* with respect to its early development; *Neocaridina denticulata* (De Haan, 1844) studied by Mizue and Iwamoto (1961), and *Neocaridina ishigakiensis* (Fujino & Shokita, 1975) originally described by Shokita (1976) as *Caridina denticulata ishigakiensis* (Fujino & Shokita, 1975).

Additionally, the descriptions of one subspecies, *Neocaridina denticulata denticulata* (De Haan, 1844), originally described as *Neocaridina denticulata sinensis* (Kemp 1918) by Yang and Ko (2003) are also available.

Detailed morphological descriptions are very important for relating form and function of the mouthparts of crustaceans. This is useful to understand the feeding requirements and preferences of different life phases of a given species, helping to define feeding protocols for both research and commercial cultivation (e.g. give or not food; if food should float or sink) (Cox & Johnston 2003; Epelbaum & Borisov 2006). Moreover, morphological knowledge of the early stages of development can allow separation of species that could be the same to the aquarium market, given the difficult identification of species of Neocaridina. In this study, we investigated N. davidi with respect to the number of young shrimp produced by parental females; the duration in days of the early posthatching stages; the time in days when it is possible to differentiate the sexes; the time when females begin to develop gonads and subsequently become ovigerous; and the incubation period and the size of eggs produced under laboratorial conditions. The complete morphology of the first three stages of N. davidi is illustrated and described in detail. Additionally, the main morphological changes occurring in male first and second pleopods are illustrated.

Material and methods

Broodstock and development of shrimp

Newly hatched individuals used in our experiments were obtained under laboratory conditions from breeding adults acquired in specialized aquarium shops (São Paulo, SP, Brazil). Two groups of reproducing adults with 30 females and 20 males were kept in aquariums $(25 \times 32 \times 15 \text{ cm})$ filled with 12 L of dechlorinated freshwater (pH 7), under continuous aeration to keep the dissolved oxygen concentration at $5-8 \text{ mg L}^{-1}$, and photoperiod 14 L:10 D (Jones 1997). The temperature was maintained at $25 \pm 1^{\circ}$ C provided by thermostat ATMAN (100 W). Java moss, Vesicularia dubyana (Brotherus, 1908), was used for shelter in the aquariums. Adults were daily fed ad libitum with TetraColor (TETRA®; Tetra GmbH, Herrenteich, Germany), whose approximate composition is: min crude protein 47.5%, min crude fat 6.5%, max crude fibre 2.0%, max moisture 6%, min phosphorus 1.5%, min ascorbic acid (vit C) 100 mg kg $^{-1}$, min omega 3-fatty acids 8000 mg kg⁻¹. This diet was previously tested and considered adequate to the species culture (Pantaleão, Barros-Alves, Tropea, Alves, Negreiros-Fransozo & López-Greco 2015). Water from the bottom of the aquariums was siphoned twice a week to remove the noningested food pieces and faeces, and to exchange the water. The aquariums were daily checked for detecting ovigerous females. Females carrying eggs were isolated in smaller aquariums of 2-L capacities each $(20 \times 10 \times 10 \text{ cm})$ under the same laboratory conditions as the reproducing adults until hatching. Ten females with embryos were used for the experiments.

Immediately after the early shrimp had hatched, reproductive females were removed from the aquaria, their brood counted and daily observed in order to register moults. Each day, food was offered *ad libitum* (approximately 2% of the average weight of the stage) (TetraColor TETRA[®], see above for details) and the water renewed partially to remove faeces and food remains. These young shrimp were maintained in the aquaria until the females born in the experiments had their first brood (i.e. about 3 months after hatching).

Categories of gonadal development following recommendations by Oh, Ma, Hartnoll and Suh (2003) were adopted to estimate when gonad development began in females. These authors suggested three stages of ovarian development as follows: Stage I, developing: thin, pale orange, filling one-third of the cephalothorax volume; Stage II, mature: orange, filling two-thirds of the cephalothorax volume; Stage III, ripe or almost ripe: deep orange, filling almost all of the cephalothorax. The time when it was possible to observe the gonads macroscopically in stage I was used to determine the period in days during which young females start developing gonads.

The time for the appearance of the embryos was estimated as the period in days from the hatch of females to spawning. After spawning, ovigerous females were maintained individually under the same laboratory conditions. Ten of these females were chilled in an ice-water bath before sacrifice, 1 day after spawning. Afterwards, the totality of embryos of each female was carefully stripped from the pleopods using a fine forcep and then counted. Subsequently, 20 eggs of each female were measured as length and width under a microscope (Leica ICC50 HD, Wetzlar, Germany) to investigate the size of initial eggs. The software LAS – Leica Application Suite, version 4.1.0, was used for image acquisition. We used females that were not sacrificed to estimate the egg incubation period, which was determined as the mean number of days from spawning to hatching.

General terminology of specialized cuticular structures verified in *N. davidi* post-hatching stages

In order to better represent the post-hatching morphology of the RCS, we studied the following cuticular structures: setae, spines, bristles and teeth (Pohle & Telford 1981; Watling 1989; Pohle, Mantelatto, Negreiros-Fransozo & Fransozo 1999; Garm 2004). Considering that there are many terms for these structures and they are not consistent in most of the papers dealing with Caridean early stages, we adopted those that best represented the structures observed in the obtained individuals during culture (Fig. 1), as follows:

Setae: the general seta structure shows a main part called the shaft with two broad outgrowth categories: setules and denticules.

Setules: vary in length, distribution and abundance; they are articulated at their base on the shaft. It can also have branches called setulettes.

Denticules: arise directly from the shaft, and they do not have articulation.

Simple seta: thin, smooth, sharp-tipped with prominent socket at the base; no outgrowth from the shaft; variable length and often bent distally.

Plumose seta: feather-like, annulus inconspicuous; flexible setules along almost entire length of the shaft and arranged in two opposite rows; setulettes present in the majority of setules. This kind of seta can vary with respect to the number and length of setules (sparsely plumose, densely plumose, very long setules); and also concerning its base (inflated base or not inflated).

Plumose natatory seta: it is a plumose seta, but characterized by an extremely long shaft with very conspicuous annuli. There is a variation of this kind of seta characterized by a long and fine shaft provided by two median proximal groups of setules in each side, and a row of setules arranged similarly in a plumose seta situated at the terminal portion of the shaft. In the present description, we call them plumose 'brush-like' seta.

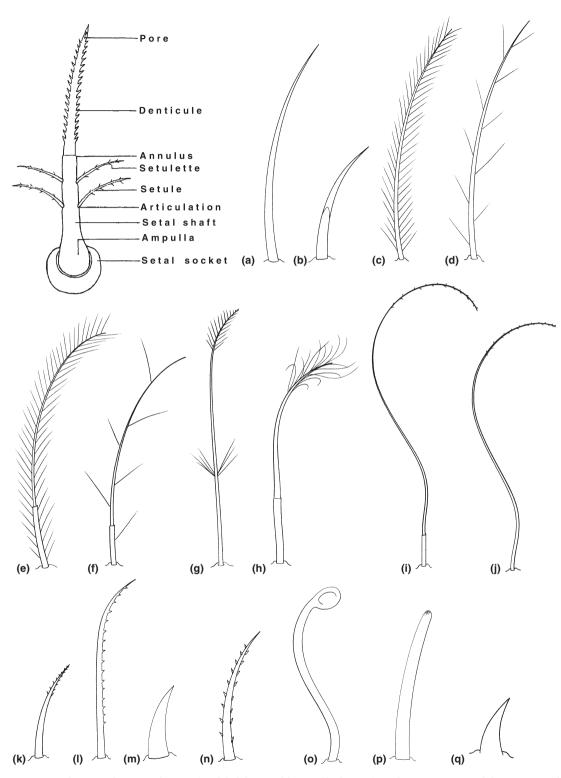


Figure 1 Schematic drawing of a seta (modified from Pohle & Telford 1981), and representation of the majority of outgrowths found in early post-hatching stages of *Neocaridina davidi*, as indicated by Pohle and Telford (1981), Watling (1989), and Garm (2004). (a, b) simple setae. (c–g) plumose setae. (h) pappose seta. (i, j) serrulate setae. (k–m) serrate setae. (n) cuspidate seta. (o) spoon-tipped seta. (p) aesthetascs. (q) spine (out of scale).

Pappose seta: with long, flexible setules, irregularly around shaft, from sparse to densely distributed setules. There is a variation of this kind of seta characterized by a fine and long shaft, annulus conspicuous and very flexible setules only around the terminal portion of the shaft. In the present description, we refer to it as pappose 'brush like' seta.

Serrate seta: shaft stout, no setules, naked preannularly; with denticules of different sizes, usually arranged in two rows at each side of the shaft.

Serrulate or **finely serrate seta**: it is also used for very small, closely spaced serrations. There is a variation of this kind of seta characterized by an extremely fine, flexible and long shaft ornamented with one or two rows of denticules situated on the 1/3 length before its distal portion of the shaft.

Cuspidate seta: shaft cone shaped, short preannular shaft portion, prominent annular ring. Sometimes small and irregular denticules appear on the post-annular region.

Spoon-tipped seta: naked seta, but with a spoon tip shape (see Miller 1961).

Aestethasc seta: smooth, very delicate, length variable, tip blunt or round; it is a specialized setae only found in antennule of crustaceans.

Other cuticular outgrowths

Denticulettes, **Spinules**: minute, very sharp processes occurring in groups, usually on surfaces of some mouth appendages and telson.

Spine: stout outgrowth, with no evidence of articulation at the base as a socket in seta.

Cincinnuli: short rounded shaft, a curved and digitated tip region. It occurs in the endopods of the pleopods.

Microtrichia: extremely small, slender, flexible hair-like outgrowth usually aggregated on surface of basial endites of maxillipeds.

Descriptions of post-hatching stages

During rearing, the exuviae were conserved in a mixture of alcohol (70%) and glycerin in 1:1. The illustrations were performed from whole individuals and their exuviae. Observations, dissections and drawings were accomplished using a stereoscope and a light microscope equipped with *camera lucida* (Zeiss, SV6 and Axioskop 2 respectively). The carapace length (CL) of the young individuals was measured as the maximum length from the posterior margin of the ocular orbit to the poste-

rior margin of the carapace. All measurements were carried out using at least 10 individuals of each stage, and drawings were obtained from at least five different individuals from distinct parental females.

Illustrations and general descriptions were based on Benzie and de Silva (1983) and Pohle et al. (1999). Thus, the cuticular structure sequence is presented from the proximal to the distal part of the body or appendages. The present description of cuticular structures is limited to light microscopic observations. Comparisons of the first post-hatching stage of previously described species of Neocaridina are presented based on a review using original drawings and descriptions. For taxonomic and systematic reference we followed here De Grave and Fransen (2011). Vouchers of the parental females and post-hatching stages are deposited in the larvae collection of the Group of Studies on Crustacean Biology, Ecology and Culture (NEBECC) (access number: CA002).

Results

Production and development of N. davidi

The number of first post-hatching stages obtained from females varied between 10 and 67 individuals (27.5 ± 16.7) . Newly hatched individuals remained consistently near the bottom and in the Java moss, and they moulted after 1 day. These young shrimp did not search for food until stage III. The individuals developed during the subsequent stages (third stage onward), and growth was observed during each moult with body setation slightly increasing. Sexual dimorphism was not clear during the early stages. From stage S7 onwards, the sex could be determined despite its inconspicuous characteristic. Thus, measurements of stages S1 to S6 were provided for individual grouped, classified as 'non-sexed post-hatching stages' (Table 1). After S7, the sex was easily determined and each individual was measured and the data were categorized based on their sex.

Females with developing gonads were detected from stages S11 to S13. The gonads of the females began developing 30 days after hatching (36.6 ± 5.9 days). During the gonad development phase, the females did not moult. When the female gonads were fully developed (Stage III, ripe), the 'pre-mating moult' occurred and it was followed by mating. The first female with embryos was

	Duration (days, \pm SD)		Size (CL, mm \pm SD)		
Stages	Each stage	Accumulated from hatching	Non-sexed post-hatching stages	Females	Males
S1	1.00 ± 0.00	1.00 ± 0.00	0.83 ± 0.04		
S2	2.25 ± 0.45	3.25 ± 0.51	0.92 ± 0.05		
S3	2.63 ± 0.50	5.88 ± 0.64	1.01 ± 0.04		
S4	2.25 ± 0.45	8.13 ± 0.91	1.13 ± 0.05		
S5	2.50 ± 0.73	10.63 ± 0.99	1.32 ± 0.13		
S6	2.38 ± 0.50	13.01 ± 0.92	1.75 ± 0.13		
S7	2.63 ± 0.50	15.64 ± 1.35		1.89 ± 0.19	1.89 ± 0.32
S8	3.00 ± 0.55	18.64 ± 1.29		2.03 ± 0.23	2.12 ± 0.13
S9	3.50 ± 0.52	22.14 ± 1.63		2.14 ± 0.26	2.32 ± 0.21
S10	3.67 ± 0.78	25.81 ± 1.96		2.56 ± 0.25	2.56 ± 0.13
S11	3.67 ± 0.49	29.48 ± 2.48		3.00 ± 0.27	2.74 ± 0.31
S12	4.80 ± 0.79	34.28 ± 3.11		3.47 ± 0.55	3.60 ± 0.38
S13	5.40 ± 0.84	39.68 ± 2.82		4.19 ± 0.37	3.56 ± 0.41
S14	5.80 ± 0.79	45.48 ± 2.77			4.4
S15	4.75 ± 2.31	50.23 ± 3.53			4.76 ± 0.26
S16	3.67 ± 1.03	53.90 ± 4.94			5.17 ± 1.26

Table 1 Neocaridina davidi (Bouvier 1904). Duration (in days) of each stage (mean \pm standard deviation), accumulatedduration from hatching; and shrimps' size (CL in millimetres)

recorded 49 days after hatching (55.18 \pm 4.46). The egg incubation period varied between 16 and 19 days (17.5 \pm 1.07). The first females with embryos measured between 4.6 and 4.9 mm CL (4.74 \pm 0.15 mm CL), and they carried 43–60 (51.8 \pm 7.36) eggs. These eggs measured 0.71 \pm 0.02 mm in length and 1.03 \pm 0.04 mm in width.

The growth of the early life phase of *N. davidi* (Fig. 2) can be represented by the equation: DAH = 0.112S2 + 1.573S - 0.407 (R2 181 = 0.996); where DAH refers to days after hatching, S is the stage, and R2 is the determination coefficient.

Morphological descriptions of post-hatching stages of *N. davidi*

First stage (Fig. 3a–u)

Size: $CL = 0.82 \pm 0.04 \text{ mm}$ (*n* = 10 individuals).

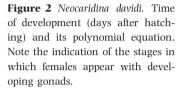
Carapace (Fig. 3a and b): spineless; rostrum slightly exceeding the eye stalks. Several round balls of yolk are visible in the median region of the carapace through the transparent exoskeleton. Rostrum with 3–4 small teeth dorsally, and 1 tooth, 1 simple seta and 1 plumose seta ventrally.

Abdomen (Fig. 3a and b): six-segmented, with the sixth separated from the telson.

Telson (Fig. 3u): oval in shape, bearing eight plumose setae on each side of the posterior lateral margin, dorsal surface smooth. The first seta on lateral margin has setules only on the inferior border. The buds of uropods can be seen through the transparent cuticle.

Antennule (Fig. 3c): 3-segmented peduncle, proximal segment with very small and spiny stylocerite bearing three simple setae on latero-distal margin and a small knob-like apical spine. Four small plumose setae in angle located between stylocerite and basal segment. There is a simple seta on the median margin at the opposite side of the stylocerite. One, 3 and 3 plumose setae on ventromedian margin of basal, second and third segments of peduncle respectively. Dorsal margin of the peduncle with two small simple setae, two serrated setae and four plumose setae on basal segment, three serrated setae and two small simple setae on second segment, and one simple seta on the third segment. Ventral flagellum with six segments of similar size with 0, 2, 3, 0, 4 and 3 simple setae respectively. Dorsal flagellum with six segments, but the total length is shorter than the ventral flagellum. This flagellum has zero, two simple setae, three aestethascs, zero, three simple setae and four simple setae respectively.

Antenna (Fig. 3d): long, with the flagellum curved and reaching over back of the carapace.



Peduncle bearing three simple setae and one plumose seta. Flagellum with 42 segments, approximately, bearing sparse simple setae on it. Scaphocerite (exopod) with a large apical spine and three small simple setae on dorsal margin; ventral margin with 21 plumose setae.

Mandible (Fig. 3e): incisor process with three small teeth, median portion with three rows of fine simple setae (4 + 5 + 3), and molar process rounded and smooth. No palp.

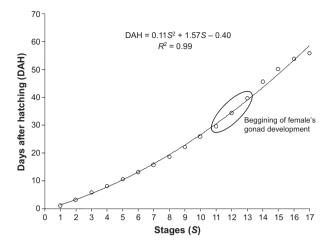
Maxillule (Fig. 3f): rudimentary. Unsegmented endopod with one very small spine distally. Basial endite with 10–11 short serrate setae. Coxal endite with three small spines.

Maxilla (Fig. 3g): Scaphognathite with four plumose setae on proximal portion, four serrulate setae apically and 30–31 plumose setae from median to distal portion. Endopod reduced. Basial endite with 14 min serrated setae on proximal lobe, and 6 min serrated setae on distal lobe. Coxal endite unilobed with 21 simple setae.

First maxilliped (Fig. 3h): biramous. Endopod reduced with one small plumose seta. Basial endite with approximately 18 serrated setae. Coxal endite with five simple setae. Exopod unsegmented, enlarged from proximal to one-third before the distal part; 17–18 plumose setae on enlarged part and one plumose and one small sparsely plumose setae on distal part. Epipod reduced and smooth.

Second maxilliped (Fig. 3i): biramous. Endopod fur-segmented, shorter than exopod, bearing 0, 0, 5, 11 small serrated setae. Exopod long with four long terminal plumose setae. Epipod reduced and smooth.

Third maxilliped (Fig. 3j): biramous. Endopod four-segmented, first and second segment with six



and eight simple setae, respectively; third segment with 2 simple setae, 1 plumose setae and 14 (3 + 5 + 3 + 3) cuspidate setae; and fourth segment with three fine simple setae and three short and enlarge serrated setae. Exopod shorter than endopod, bearing four long terminal plumose and one small simple seta. Epipod as a small bud.

Pereiopods (Fig. 3k–o): 1st and 2nd chelate, 5-segmented, former shorter than later. Both chelipeds bear very small simple setae on the tip of the dactylus and propodus, and some sparse simple setae on all segments. A slender serrulated seta present on the dorsal margin of the basis, which is common for all pereiopods except for the fifth. The dactylus of the third, fourth and fifth pereiopods is provided with a terminal claw and 2, 2 and 6 small and strong serrated setae respectively. Third, fourth and fifth pereiopods with some serrated setae on ventral margin of merus, carpus and propodus.

Pleopods (Fig. 3p–t): all five biramous and bearing a simple setae on protopod. Exopods with 10, 11, 10, 10 and 10 plumose setae. The second and the fifth pairs also have one simple seta on the distal margin of the exopod. Endopods with 3, 6, 7, 7 and 6 plumose setae on terminal margin. The fifth pleopod also has one plumose seta on its proximal margin. All the endopods of pleopods, except for the first, have a fully developed appendix interna with four cincinnuli each.

Second stage (Fig. 4a–p)

Size: $CL = 0.91 \pm 0.05 \text{ mm} (n = 10 \text{ individuals}).$

Carapace (Fig. 4a and b): similar to the previous stage, but rostrum has seven teeth on dorsal margin, one tooth, one simple seta and one plumose seta on ventral margin.

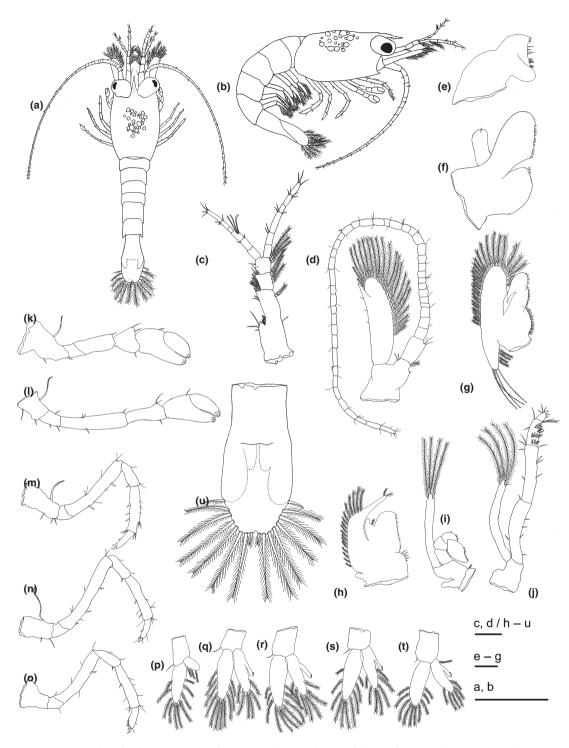


Figure 3 Neocaridina davidi. First post-hatching stage. (a) Dorsal view. (b) Lateral view. (c) Antennule. (d) Antenna. (e) Mandible. (f) Maxillule. (g) Maxilla. (h–j) 1st to 3rd Maxillipeds. (k–o) 1st to 5th Pereiopods. (p–t) 1st to 5th Pleopods. (u) Telson (Scale bars – c, d/h - u = 0.1 mm; e-g = 0.1 mm; a, b = 1 mm).

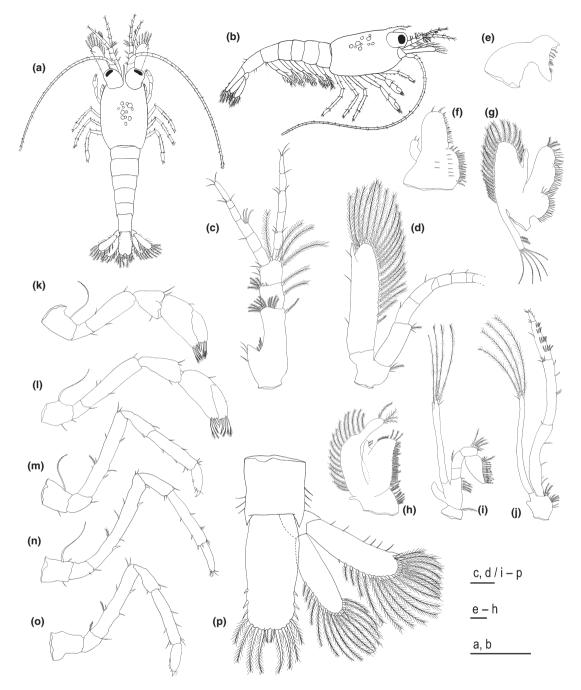


Figure 4 *Neocaridina davidi.* Second post-hatching stage. (a) Dorsal view. (b) Lateral view. (c) Antennule. (d) Antenna. (e) Mandible. (f) Maxillule, (g) Maxilla. (h–j) 1st to 3rd Maxillipeds. (k–o) 1st to 5th Pereiopods. (p) Telson and uropods (scale bars – c, d/i-p = 0.1 mm; e–g = 0.05 mm; a, b = 1 mm).

Abdomen (Fig. 4a and b): some small simple setae present on fifth and sixth somite as illustrated.

Telson (Fig. 4p): longer than wide bearing three serrated setae, five plumose setae and two fine simple setae on its postero-lateral margin. Surface smooth.

Antennule (Fig. 4c): Peduncle 3-segmented, proximal segment with a stylocerite bearing three simple setae on laterodistal margin; and four small plumose setae in angle between stylocerite and basal segment. Proximal segment also has subterminal plumose setae, 10 terminal plumose setae and one serrated seta. Second segment with two lateral plumose setae, four terminal plumose setae and third serrated setae. Third segment with four terminal plumose setae and four (2 + 2) simple setae. Ventral flagellum six-segmented with 0, 3, 0, 3, 1 and 3 simple setae. Dorsal flagellum six-segmented with 0, 1, 0, 0 3 and 3 simple setae respectively. Three aestethascs present on ventral margin of third segment.

Antenna (Fig. 4d): Peduncle bearing one plumose seta and two simple setae. Flagellum with approximately 49 segments, bearing one plumose and two simple setae on first segment, sparse simple setae on other segments. Scaphocerite with a large apical spine and three small simple setae on dorsal margin; ventral margin with 22 plumose setae.

Mandible (Fig. 4e): incisor process with three teeth, median portion with three rows of setae bearing three plumose setae, seven simple setae and four simple setae; molar process rounded and smooth. No palp.

Maxillule (Fig. 4f): unsegmented endopod with one small spine and one simple seta, distally. Basial endite with two plumose setae distally, 13–15 short serrated setae, two to three plumose and two to three serrated (Fig. 1k) setae marginally; coxal endite with two small plumose setae, 18–20 median plumose setae marginally and six to seven serrated setae, eight spines on its surface.

Maxilla (Fig. 4g): Scaphognathite with two plumose setae proximally, four serrulate setae apically, and 27–29 plumose setae along median to distal. Endopod reduced. Basial endite with approximately 28 simple setae on proximal lobe; approximately nine simple setae and three plumose setae on distal lobe. Coxal endite unilobed with approximately 30 simple setae.

First maxilliped (Fig. 4h): biramous. Endopod reduced with two small plumose setae. Basial endite with microtrichia on dorsal margin, third plumose setae on terminal end and five sparsely plumose setae on median margin; several small spoon-tipped setae on median margin. Coxal endite with 11 plumose setae. Exopod similar to previous stage with 16 plumose setae on enlarged part, three sparsely plumose and one plumose seta on distal part. Epipod very reduced.

Second maxilliped (Fig. 4i): biramous. Protopod with one simple seta and four plumose setae. Endopod four-segmented bearing zero, one plumose seta, four plumose setae and two simple setae, and three plumose and 16–20 plumose brush-like setae respectively. Exopod long with four long terminal plumose and one simple seta. Epipod reduced and smooth.

Third maxilliped (Fig. 4j): biramous. Protopod with five simple and six plumose setae. Endopod 4-segmented with 5, 8, 3 and 2 simple setae and 4 serrated setae. Third segment has 16 (5 + 5 + 3 + 3) cuspidate setae. Exopod shorter than endopod, bearing four long terminal plumose and one simple seta. Epipod as a small bud.

Pereiopods (Fig. 4k–o): both chelipeds similar as in previous stages, except for the presence of several serrated and pappose brush-like setae on tips of dactylus and propodus. Some sparse simple setae present on all segments. Dactylus of third, fourth and fifth pereiopods with a claw and 2, 1 and 5 small and strong serrated setae. Third and fourth pereiopods with one plumose seta on dorsal margin of merus; fifth pereiopod with one plumose seta on dorsal margin of ischium and merus. Third, fourth and fifth pereopods with some serrated setae on ventral margin of merus, carpus and propodus.

Pleopods (not illustrated): very similar to previous stage.

Uropods (Fig. 4p): biramous. Exopod with five simple setae on its dorsal margin; and one terminal spine, three simple setae, 16–20 plumose setae and one small seta distributed along postero-ventral margin. Endopod with 14–17 plumose setae and one simple seta along postero-ventral margin.

Third stage (Fig. 5a–u)

Size: CL = 1.01 ± 0.04 mm (*n* = 10 individuals).

Carapace (Fig. 5a and b): similar to previous stage, but rostrum with eight dorsal teeth; one plumose seta and one tooth on ventral margin.

Abdomen (Fig. 5a and b): similar to previous stage, except for third somite, which is larger than others.

Telson (Fig. 5u): longer than wide with 5 + 5 plumose setae on posterior margin. Three serrated setae on each side of postero-lateral margin.

Antennule (Fig. 5c): Peduncle similar to previous stage. Proximal segment has one lateral and subterminal, and one lateral and terminal plumose setae; 11 terminal plumose setae and two serrated setae. Second segment with three lateral plumose setae and one simple seta; two terminal plumose setae and one simple seta and four

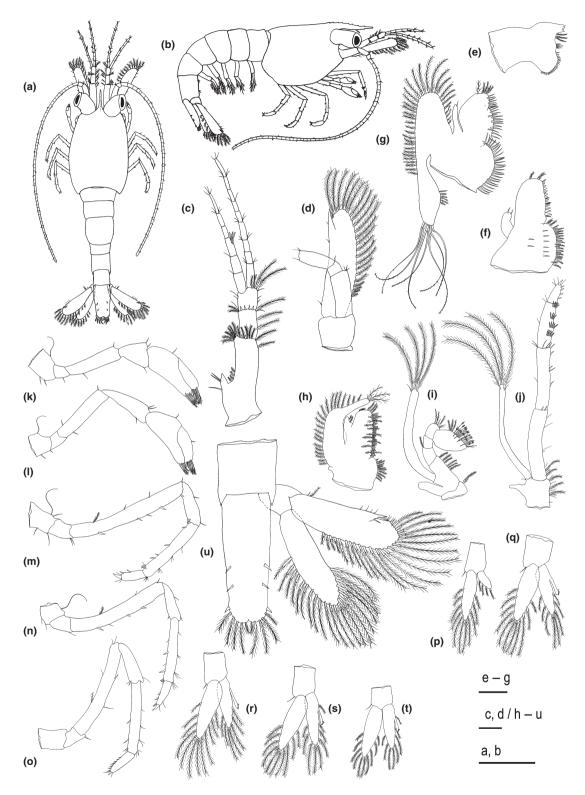


Figure 5 *Neocaridina davidi.* Third post-hatching stage. (a) Dorsal view. (b) Lateral view. (c) Antennule. (d) Antenna. (e) Mandible. (f) Maxillule. (g) Maxilla. (h–j) 1st to 3rd Maxillipeds. (k–o) 1st to 5th Pereiopods. (p–t) 1st to 5th Pleopods. (u) Telson and uropods (scale bars – e-g = 0.1 mm; c, d/h-u = 0.1 mm; a, b = 1 mm).

terminal serrated setae. Third segment with four terminal setae (two short) and five simple setae. Ventral flagellum nine-segmented with 4, 0, 4, 4, 0, 2, 0, 4 and 3 simple setae. Dorsal flagellum sixsegmented with 1, 1, 0, 0, 4 and 4 simple setae respectively. Three short aestethascs present on ventral margin of third segment.

Antenna (Fig. 5d): Peduncle smooth. Flagellum with 56–59 segments bearing three simple setae on first segment, and other segments with sparse simple setae. Scaphocerite with a large apical spine and three small simple setae on dorsal margin; ventral margin with one simple seta and 22–24 plumose setae.

Mandible (Fig. 5e): incisor process with four teeth, median portion with two rows of setae bearing three plumose and five simple setae; molar process rounded with 25–27 serrated setae. No palp.

Maxillule (Fig. 5f): similar to previous stage.

Maxilla (Fig. 5g): Scaphognathite with six plumose setae proximally, seven serrulate setae apically, and 34–35 plumose setae from median to distal. Endopod reduced with one simple seta. Basial endite with approximately 40 simple setae on proximal lobe; and approximately 10–12 simple setae, four plumose setae and one sparsely plumose seta on distal lobe. Coxal endite unilobed with 40–43 simple setae.

First Maxilliped (Fig. 5h): Endopod reduced with 1–2 small plumose setae. Basial endite with microtrichia on dorsal margin, three plumose setae on terminal end; approximately two rows of 16–18 plumose setae each on median margin; approximately 70 spoon-tipped setae distributed in 4 rows. Coxal endite with 11 plumose setae. Exopod unsegmented, similar to previous stage with 19–20 plumose setae on enlarged part and three to five sparsely plumose setae on distal part. Epipod very reduced.

Second Maxilliped (Fig. 5i): Protopod with sixto seven plumose setae. Endopod four-segmented bearing one plumose seta on first segment; no seta on second segment; three plumose and three simple setae on third segment; threeplumose setae and two rows of 11–13 plumose brush-like setae each and one row of five to six plumose setae. Exopod long with four long terminal plumose and one simple seta. Epipod reduced and smooth.

Third Maxilliped (Fig. 5j): Protopod with eight simple setae and six plumose setae. Endopod foursegmented. First segment with two plumose, six simple and two serrated setae; second segment with 11 simple setae; third segment with three simple and four rows of 5-6, 5-6, 4 and 3-4 cuspidate setae; fourth segment with four simple and five serrated setae. Exopod with four long terminal plumose and one simple seta. Epipod represented by a bud.

Pereiopods (Fig. 5k–o): similar to previous stage. Dactylus of last three pereiopods with a claw and 2, 2 and 7 small and strong serrated setae. Fifth pereiopod has no plumose setae on ischium. Third, fourth and fifth pereopods with some serrated setae on ventral margin of merus, carpus and propodus.

Pleopods (Fig. 5p-t): similar to previous stages. but the seta number can vary. All five pleopods have one simple seta on protopod. Last four pleopods with appendix interna and four cincinnulli. First pleopod with four and 11 plumose setae on endopod and exopod respectively. Second pleopod with eight plumose setae and one simple seta on endopod, and 11 plumose setae and one simple seta on exopod. Third pleopod with 7 and 12 plumose setae on endopod and exopod respectively. Fourth pleopod with 8 and 10 plumose setae on endopod and exopod respectively; one plumose seta on proximal portion of endopod. Fifth pleopod with 7 and 10 plumose setae on endopod and exopod respectively; one plumose seta on proximal region of endopod.

Uropods (Fig. 5u): Exopod with five simple and one plumose setae on dorsal margin; one spine and two serrated setae terminally; rounded by 22–24 plumose setae. Some small setae hair-like and plumose setae present between terminal spines and the set of plumose setae. Endopod with 20–23 plumose setae.

From the third post-hatching stage on, there are slight alterations in shape and setation. Most of these changes are related to the size and number of setae. The main appendages that show significant alterations are the first and second pleopods of the male specimens.

Morphological description of male pleopods from the 6th to 12th stages of *N. davidi* (Fig. 6)

First pleopod

The exopod of the first pleopod from the 6th to the 12th post-hatching stages has 17 plumose setae; 25 plumose and 1 simple seta; 25 plumose and 1 simple seta; 24 plumose and 2 simple setae; 26 plumose and 1 simple seta; 28 plumose and 4

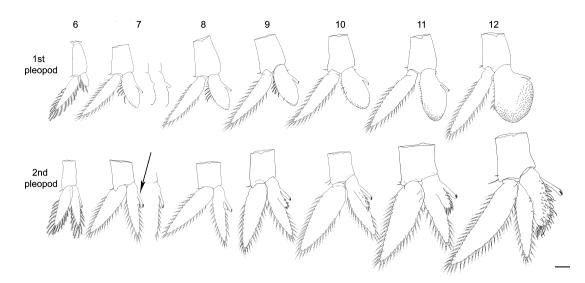


Figure 6 *Neocaridina davidi.* Morphology of first and second pleopods of males from the 6th to 12th post-hatching stages. Black arrow indicates the first appearance of the appendix masculina (scale bar = 1 mm).

simple setae; and 31 plumose and 1 simple seta respectively.

The first pleopod acquires an increase of setae on the endopod and the appearance of the appendix interna from the sixth to the seventh posthatching stage (Fig. 6), i.e. from 5 to 7-8 small plumose setae. The shape of the appendix interna is variable during the seventh stage. In the next five stages, the number of plumose setae on the endopod is reduced, with four to five plumose and two to three simple setae in the eight stage, five to six plumose setae and one to two simple setae in the ninth stage, and only simple setae in the 10th, 11th, 12th stages. In the 11th post-hatching stage, the endopod becomes enlarged with several spinules on its terminal margin, whereas in the next stage the endopod is already rounded with innumerous spinules on its terminal margin, reaching a similar shape as the adult male.

Regarding the female first pleopod (except for small variations in the amount of setae) there is no difference at the exopod. However, the endopod of the female lacks the characteristic internal appendage and small spines of the male. The numbers of the plumose setae and the simple setae on the endopods of females gradually increase throughout the stages.

Second pleopod

The exopod of the second pleopod from the 6th to the 12th stages has 16 plumose setae; 24 plumose setae; 26 plumose and 1 simple seta; 24

plumose and 1 simple seta; 29 plumose setae; 31 plumose and 1 simple seta; and 43 plumose and 2 simple setae respectively.

The endopod of the second pleopod remains slightly growing with 13 plumose setae and one simple seta in the sixth post-hatching stage. From the seventh stage onwards there are 17, 19, 17, 17, 17 and 24 plumose setae, respectively, on the endopod of the pleopods. The appendix interna has 6, 8, 5-6, 9, 10, 10 and 12 cincinnuli, respectively from the 6th to 12th stages. The appendix masculina appears from the seventh as one small plumose seta situated between the appendix interna and the endopod. This appendage grows as the development advances and the number of setae also changes as follows: two simple setae in the eight stage, nine simple setae in the ninth stage, 15 simple setae in the 10th and 11th stages, and approximately 40 simple setae in the 12th stage.

For females, except for small variations in the amount of setae and the absence of an appendix masculina, there are no differences on the exopod and the endopod respectively.

Discussion

The carideans of the genus *Neocaridina* (family Atyidae) are commonly sold in the aquarium trade in South American countries, mainly, Argentina and Brazil. The species of this genus are native to Asian countries. In Taiwan, for instance, there are

atyid shrimps (about three centimeters in length), which typically inhabit clean freshwater areas, are omnivorous and are primary consumers (Lai & Shy 2009).

The present confirmation of the larval development beginning directly by the decapodid stage for *N. davidi* is of significant interest not only for ornamental aquaculture purposes but also because the species has morphological features associated with highly abbreviated development. These characteristics include a relatively large freshly deposited egg ($\cong 1.0 \times 0.8$ mm), completely developed pereiopods and pleopods, and spatulated telson with 8 + 8 setae; the uropod appears in the second stage. This last feature follows the general pattern observed for the direct development species throughout the Caridea (Benzie & de Silva 1983).

Complete suppression of larval development is shown by many landlocked species of *Caridina* H. Milne Edwards, 1837, the largest genus of the Atyidae (290 species), and probably by all of the 30 species and subspecies of the genus *Neocaridina*, the second largest genus of the Atyidae (De Grave & Fransen 2011; Vogt 2013). As an example of the genus *Neocaridina*, *N. davidi* hatches as a decapodid with well-developed appendages, eyes and sensory setae on the antennae, but no free uropod, very similar to *N. ishigakiensis* (Fujino & Shokita, 1975), that is endemic to the Ryukyu Islands, Japan (Shokita 1976).

The morphological characters that differentiate the first post-hatching stage previously described for species and subspecies of the genus *Neocaridina* are presented in Table 2. Considering the available descriptions for early life stages of various *Neocaridina* species, all species share the following features: antennular peduncle three-segmented; mandible with developed incisor and molar processes; maxilla with palp like endopod; exopod of second maxilliped with four setae; pleopods with variable number of setae on both exopod and endopod; and no appendix interna on the first pleopod.

Nevertheless, after a detailed comparison among all appendages, we found some characters in the studied *N. davidi* that are not shared among other known *Neocaridina* species. Among those features, the most important set of characters to distinguish the material of this study are: the number of teeth on the rostrum (four dorsal and one ventral); antennular flagellum with six segments; first maxilliped with both exopod and endopod bearing 19–20 and one plumose seta respectively; and telson with only 8 + 8 plumose setae.

The observed increase in the density and robustess of the mouth parts setation, along with an increase in the in the size of mouthparts between the early and late stages suggests the capacity for a dietary shift (Cox & Johnston 2003). This fact, together with the presence of yolk in the cephalothorax of the first two stages of development, indicates that young *N. davidi* have facultative lecithotrophy. They can complete these early phase without food. However, despite the shrimp not searching for ration up to the third stage, we cannot ensure that they do not feed on these early stages, because they may have fed on material (e.g. biofilm and detritus) from Java moss.

Facultative lecitotophy can be considered as a phenotypic plasticity of the species that allows utilization of the volk during periods or places with low food supply. In species that show facultative lecitotrophy, early stages contain a large quantity of yolk, but when food is available, they accumulate additional reserves of energy which can be advantageous in unpredictable nutritional conditions (Anger 1995; Pantaleão et al. 2015). Additionally, Pantaleão et al. (2015), studying the nutritional vulnerability of N. davidi in the initial stages (first and third post-embryonic stages). demonstrated that despite the exposure of the young shrimp to starvation they can moult normally, the periods of feeding restriction negatively affected growth and survival of juveniles exposed to starvation immediately after hatching. Similarly, some newly hatched Lysmata Risso, 1816 larvae can indeed moult to the next zoeal stage under starvation, but the nutritional stress imposed is later reflected in a prolonged larval development and by an increase in mortality at metamorphosis (Calado, Figueiredo, Rosa, Nunes & Narciso 2005).

The interest in the culturing of ornamental fish and invertebrates is growing continuously. It is recognized as a feasible alternative to the reduced harvests of specimens from the wild (Tlusty 2002). As mentioned by the same author, the first benefit of ornamental aquaculture focuses on species conservation, and the production of species that are difficult to obtain from the wild, for instance, rare animals or those that are abundant, but rare in the trade (see other examples in Tlusty 2002). Another benefit of ornamental aquaculture is minimizing the harm of wild harvesting using destructive methods. Additionally, many colour varieties

Table 2 Morphological characters of the first post-hatching stage described for species and subspecies of the genus Neo-	
caridina Kubo, 1938	

Characters	<i>N. denticulata</i> Mizue and Iwamoto (1961)	<i>Caridina denticulata ishigakiensis*</i> Shokita (1976)	<i>Neocaridina denticulata sinensis</i> * Yang and Ko (2003)	<i>Neocaridina davidi</i> Present study
Carapace				
Rostrum	Variable number of teeth both dorsal and ventrally	Smooth	8 dorsomedian teeth	4 dorsomedian and 1 ventromedian sp
Inner flagellum	6 segments	7 segments	8 segments	6 segments
Outer flagellum	5 segments	5 segments	5 segments	6 segments
Antenna				
Scaphocerite	1 distolateral sp + 19 ps	1 distolateral sp + 20 ps	1 distolateral sp + 20 ps	1 distolateral sp + 3 ss + 21 ps
Maxillule				
Endopod	1 sp	1 sp	Smooth	1 sp
Coxal endite	Several ss	2 ps + several ss	3 dc	3 sp
Basial endite	12 st	Several sp	10 dc	10–11 st
Maxilla				
Scaphognathite	Several ps	Approximately 32 ps	29 ps	30–31 ps
Terminal process	3 long + several setae	3 long + 3 short ss	4 long + 3 short ps	4 long sr + 4 short ps
Coxal endite	Several setae	Several ss	22 short ps	20 ss
Basial endite	Bilobed; several setae on both lobes	Bilobed; 13, 3 dc	Bilobed; 13, 7 dc	Bilobed; 14, 6 st
First maxilliped				
Exopod	Several ps and ss	16 ps + 4 ss	21 ps	19–20 ps
Endopod	4 setae	2 setae	3 ps	1 ps
Coxal endite	Several ps	1 seta	2 short ps	5 st
Basial endite	Several setae	Several sp	24 dc	18 st
Second maxilliped				
Endopod	4-segmented	4-segmented	4-segmented; 2, 0, 0, 12 dc	4-segmented; 0, 0, 5 and 11 st
Third maxilliped				
Endopod	3-segmented	3-segmented	4-segmented	4-segmented
Epipod	Absent	A small bud	A small bud	A small bud
Pereiopods	Dactylus of 3rd, 4th and 5th with 2, 2 and 5 sp on inferior margin	Dactylus of 3rd, 4th and 5th with 2, 2 and 5 sp on inferior margin	Dactylus of 3rd, 4th and 5th with 2, 2 and 6 sp on inferior margin	Dactylus of 3rd, 4th and 5th with 2, 2 and 6 st on inferior margin
Telson	8 + 8 ps	8 + 8 ps	8 + 8 ps. 6 pairs of dorsomedian ss	8 + 8 ps

*Neocaridina denticulata sinensis = Neocaridina denticulata denticulata; Caridina denticulata ishigakiensis = Neocaridina ishigakiensis, according to De Grave and Fransen (2011).

ss, simple seta; ps, plumose seta; st, serrate seta; sr, serrulate seta; sp, spine; dc, denticles.

and body types can be produced in ornamental aquaculture to increase marketing. The Atyid shrimps have also been growing in popularity in the aquarium industry as they are small, possess beautiful colours and eat nuisance algae that grow in aquaria (Heerbrandt & Lin 2006).

The presence of *N. davidi* and any other atyid shrimp with similar features in South America can be problematic in the near future, considering their prolific reproduction and small size, which could hinder their identification in nature for their control. As mentioned by Turkmen and Karadal (2012), the aquarium ornamental trade in Turkey has an important risk of invasion mechanisms at post-importation stages. The RCSs are considered invasive also in other regions such as in Chinese waters, where they replace other shrimp species. In this case, shrimp dispersal by humans is considered as the likely pathway of introduction (Englund & Cai 1999). Werner (2008) includes the distance between the nearest water body and the aquarium ornamental store as a potential risk of invasion of this species. Thus, in this sense, the adoption of this species for industrial production should proceed with caution to ensure that the immediate benefit does not result in impending risks. According to Klotz *et al.* (2013), *N. davidi* might affect native aquatic invertebrates by competitive interactions as verified in Germany, where it invaded a temperate downstream habitat of the River Rhine drainage system.

In this study, we demonstrated some biological features of RCS: extremely abbreviated and fast development and easy adaptation to captivity. These features, apart from making the commercial cultivation extremely viable, because the species can be fed with artificial ration throughout the life cycle, demonstrate that *N. davidi* could be used as a model for scientific use in studies of reproduction, ecotoxicology and neuro-physiology, for instance. Additionally, the morphology of the early stages of close related decapods is usually very similar. Detailed descriptions are therefore necessary to allow the identification of these commercially exploited species, many times using a combination of several anatomical characters.

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