

**Abstract.**—The megalopal stage of *Cancer oregonensis* Dana is described from both laboratory-reared and naturally occurring populations in the Puget Sound Basin. It is compared with megalopae from natural populations of *C. productus* Randall collected in the same locale. Because megalopal characters of *C. productus* from these northern populations were found to differ significantly from those described by Trask (1970) for a California population, a redescription of the megalopa of *C. productus* based on the present collections is included. A key to the local megalopae of *Cancer* species, based on gross morphology, is presented.

# A Comparative Study of the Megalopal Stages of *Cancer oregonensis* Dana and *C. productus* Randall (Decapoda: Brachyura: Cancridae) from the Northeastern Pacific

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The brachyuran crab genus *Cancer* Linnaeus is recognized throughout the world because of the major contributions of some of its species to commercial fisheries. Of the 13 Recent species reported in the Eastern Pacific (Nations 1975), four species, *C. gracilis* Dana, *C. magister* Dana, *C. oregonensis* Dana, and *C. productus* Randall, coexist in the Puget Sound Basin of Washington and British Columbia (Orensanz and Gallucci 1988). A fifth species, *C. branneri* Rathbun, has also been reported from the region (e.g., Rathbun 1904 [as *C. gibbosulus* DeHaan], 1930; Schmitt 1921 [as *C. gibbosulus*]; Kozloff 1974, 1987; Hart 1982). However, the only verified occurrences of *C. branneri* have been those cited by Rathbun (1904) for a single male from Port Althorp, Alaska (Natl. Mus. Nat. Hist., USNM 12516), and

a second single male from Ucluelet, west coast of Vancouver Island, B.C. (USNM 40078). A specimen from Vancouver Island identified as *C. branneri* (Calif. Acad. Sci., CAS 015782) has proved to be *C. oregonensis* (personal examination). All subsequent records of *C. branneri* from the northeastern Pacific, north of the Oregon coast, are merely range listings based upon this early Rathbun material.

Of the four species indigenous to Puget Sound, *Cancer magister* (Dun-  
geness crab) is the most thoroughly studied because of its commercial significance. However, catch records throughout its range exhibit considerable interannual fluctuations (Botsford 1986). Because of these fluctuations, fishery biologists have begun to examine the life history and larval dynamics of *C. magister* (e.g., Lough 1976, Reilly 1983). These studies suggested that larval and postlarval

stages may hold the clue to periodic changes in the strength of year-classes. *Cancer* species pass through five larval (zoeal) and one postlarval (megalopal) stage. The megalopal stage represents the transition between the planktonic zoeae and the benthic adult. As the zoeae provide a major food source for several fish species (Garth and Abbott 1980), it is probable that the assessment of abundance of megalopae will provide the most reliable information on annual recruitment for commercial species. Therefore, it is essential that megalopae of the four species can be distinguished in mixed plankton tows. Information on the megalopal development of *C. magister*, *C. productus*, and *C. gracilis* are available; this is the first description of the megalopae of *C. oregonensis*.

Iwata and Konishi (1981) suggested that the setal formulae for the antenna and the endopod of the third maxilliped would permit specific identifications of the megalopae of several *Cancer* species, including *C. magister* and *C. productus*; however, their evaluation was made only from the published data available. Quintana and Saelzer (1986), in their summary of megalopal characters of *Cancer* species, remarked that endopodal setation of the third maxilliped was variable among species and very difficult to determine. They instead placed emphasis upon the setation of the epipod of the second maxilliped. Unfortunately, there often are considerable discrepancies between published descriptions of the same species. For example, Anderson (1978) emphasized the significance of the antennal setation in distinguishing megalopae of *C. anthonyi* Rathbun from *C. productus*. However, his setal count for *C. anthonyi* differed appreciably from that illustrated, but not specified, by Trask (1974) in his description of this species.

At least some morphological variation in larval characters may be attributed to differing geographic areas (Wencker et al. 1983, Shirley et al. 1987). We initially compared megalopae of *C. oregonensis* with megalopae of *C. productus* collected from Puget Sound. However, when we then compared the local *C. productus* megalopae with the description of megalopae from California (Trask 1970), we found substantive differences. Therefore, we have compared laboratory-reared and locally captured population of *C. oregonensis* megalopae with northern populations of *C. productus* megalopae and have redescribed the latter. From these descriptions, together with the descriptions provided by Poole (1966) for the megalopae of *C. magister* and Ally (1975) for *C. gracilis* megalopae, we have prepared a key to the megalopae of the northern populations of the four *Cancer* species.

## Materials and methods

Samples from naturally occurring populations of megalopae of *Cancer oregonensis* and *C. productus* were collected from two broad regions within the Puget Sound Basin. The first region included 16 sites in the Strait of Georgia, British Columbia; the second consisted of 17 sites in the Strait of Juan de Fuca, Washington. Supplemental samples were also collected near Anacortes, Washington. Monthly sampling took place over a period of 5 months, May through September, 1987. Each sampling cruise consisted of nightly trawling with an otter neuston sampler (Mason and Phillips 1986) over a 3-day period. Megalopae were transferred to the laboratory and isolated in compartmented trays and maintained in a constant temperature unit (CTU) at 15°C in filtered seawater of 31‰. The megalopae were changed daily into fresh seawater, and newly-hatched *Artemia salina* (Linnaeus) nauplii were provided as nourishment. Exuviae were preserved in 70% ethyl alcohol. First crab instars were used to confirm species identifications. Twelve exuviae of each species were stained using 1% chorazol black in equal parts phenol and lactic acid; mouthparts and appendages were dissected and mounted in polyvinyl alcohol lactophenol. Morphological characters were then described and illustrations were made with the aid of a camera lucida mounted on a Wild M-5 stereomicroscope. An additional 42 exuviae of *C. oregonensis* and 48 exuviae of *C. productus* were examined for significant morphological characters not requiring dissection. Laboratory-reared megalopae of *C. oregonensis* were obtained from rearing studies. Six of the laboratory-reared megalopae were stained and dissected following the above procedure and an additional ten specimens were examined for gross morphology. Setal counts for all appendages are cited from proximal to distal.

## Results

The megalopal stage of *Cancer oregonensis* is described from specimens collected from naturally occurring populations, and its morphological characters are compared with those of laboratory-reared individuals. Megalopae of *C. productus* from naturally occurring populations were similarly examined, and their morphological characters are compared with those described by Trask (1970) for a California population of this species (Table 1). Because a number of significant character differences exist between the populations, a redescription of *C. productus* megalopae, based on the northern populations, is included.

Abbreviations used in the text are defined as follows: TL: Total length, measured from the tip of the rostrum to the midpoint of the telson; CL: Carapace length, measured from the tip of the rostrum to the posterior midpoint of the carapace.

### Description: *Cancer oregonensis* Dana

TL 5.6–6.2 mm, CL 2.5–3.8 mm.

**Carapace (Fig. 2A)** Considerably longer than broad, lacking setae; lateral knobs usually absent, but with pair of gastric protuberances. Rostrum well developed. Dorsal spine projecting posteriorly over first two abdominal somites. Rostral region broad, with ventromedial tubercle. Eyes well developed, corneae slightly dilated.

**Antennule (Fig. 1A)** Biramous; peduncle 3-segmented, proximal segment broadly expanded and with 6–14 scattered setae, penultimate segment with 4 or 5 submarginal setae distally, ultimate segment with 2 or 3 setae. Exopod 4-segmented, basal segment naked, 2nd segment with 7–13 aesthetascs, 3rd with 6–9 aesthetascs and 2 or 3 submarginal setae, 4th with 3–5 aesthetascs, 1 distomarginal seta and 1 terminal seta. Endopod indistinctly 2-segmented, proximal segment naked, distal segment with 2 or 3 marginal and 3 or 4 terminal setae.

**Antenna (Fig. 1B)** Peduncle 3-segmented, flagellum with 8 articles; setal formula varying from 3, 2, 4, 0, 0, 3, 0, 3, 0, 4, 3 to 6, 3, 5, 0, 1, 4, 0, 5, 1, 4, 4.

**Mandible (Fig. 1C)** Molar and incisor processes not distinguishable. Mandibular palp 2-segmented, proximal segment naked, distal segment with 9–11 marginal setae.

**Maxillule (Figure 1D)** Endopod indistinctly 2-segmented, proximal segment with or without 1 marginal seta basally, distal segment with 1 or 2 terminal setae. Coxal endite with 13–16 setae. Basal endite with 23–29 total setae/spines including 4 or 5 distinct marginal setae basally.

**Maxilla (Fig. 1E)** Endopod broad basally, with 4–6 naked setae on outer margin in proximal half. Coxal endite with 3–6 terminal and 1–3 subterminal plumose setae on proximal lobe, 2–5 terminal and 1–3 subterminal plumose setae on distal lobe. Basal endite with 8–10 terminal and 1 or 2 subterminal plumose setae on proximal lobe and 8–11 terminal and 1 or 2 subterminal plumose setae on distal lobe. Scaphognathite with 68–85 marginal and 4 or 5 scattered surface setae (not shown in illustration).

**First maxilliped (Fig. 1F)** Epipod with 14–17 marginal or submarginal setae. Exopod 2-segmented, proximal segment with 2–4 plumose marginal setae distally, distal segment with 3–6 terminal plumose setae. Endopod 1-segmented with 1–3 marginal setae basally, 3–5 setae distally and 1 short terminal seta. Coxal endite with 15–20 setae. Basal endite with 26–35 setae.

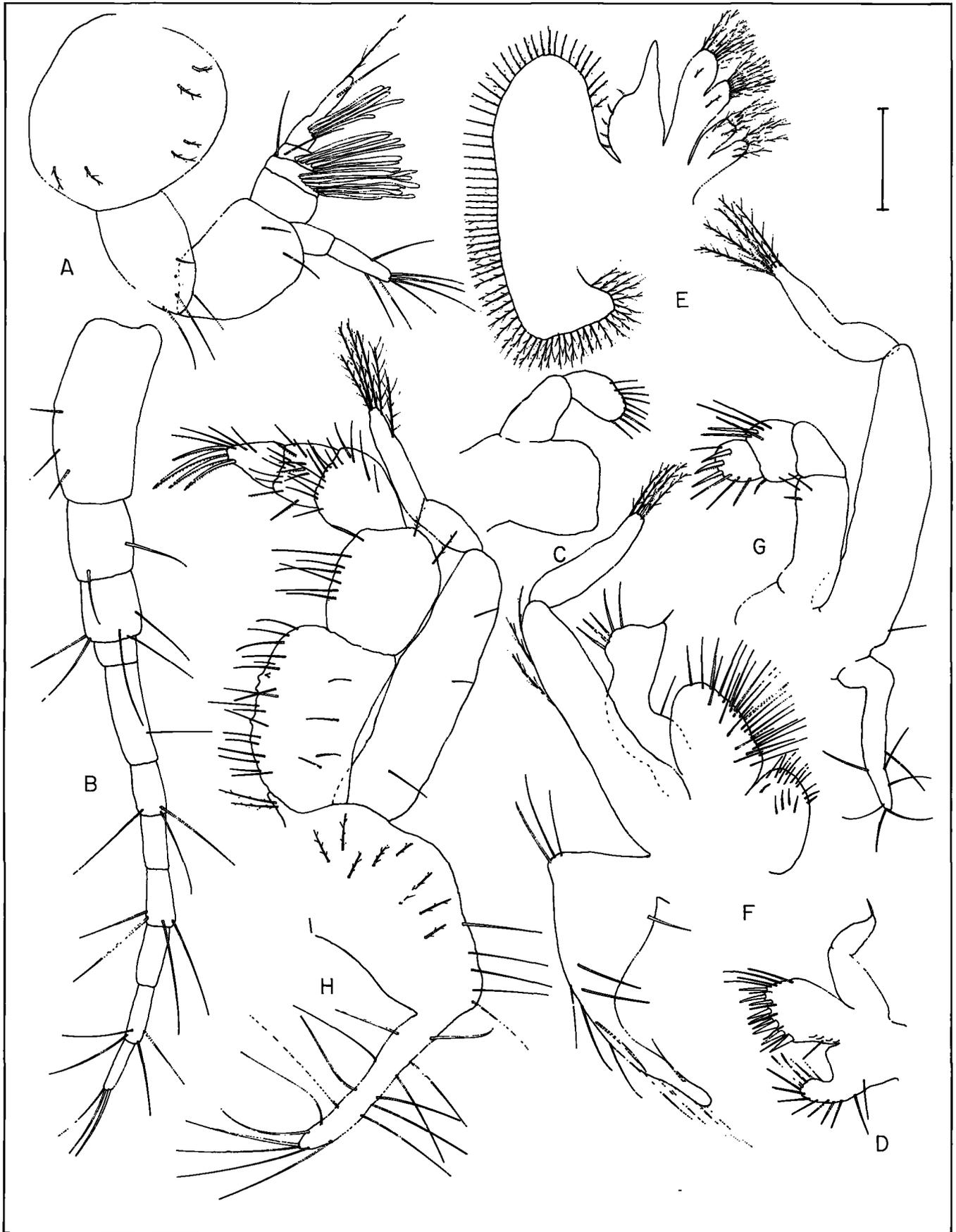
**Second maxilliped (Fig. 1G)** Epipod with 6–9 marginal setae; protopod with 1–5 setae. Exopod 2-segmented, proximal segment with 1 or 2 short marginal spine-like setae, distal segment with 3–5 terminal plumose setae. Endopod 4-segmented, merus with 1–4 submarginal setae distally, carpus unarmed or with 1 or 2 marginal setae distally, propodus with 6–9 setae distally, dactyl with 8–11 marginal and submarginal setae, some distinctly serrate.

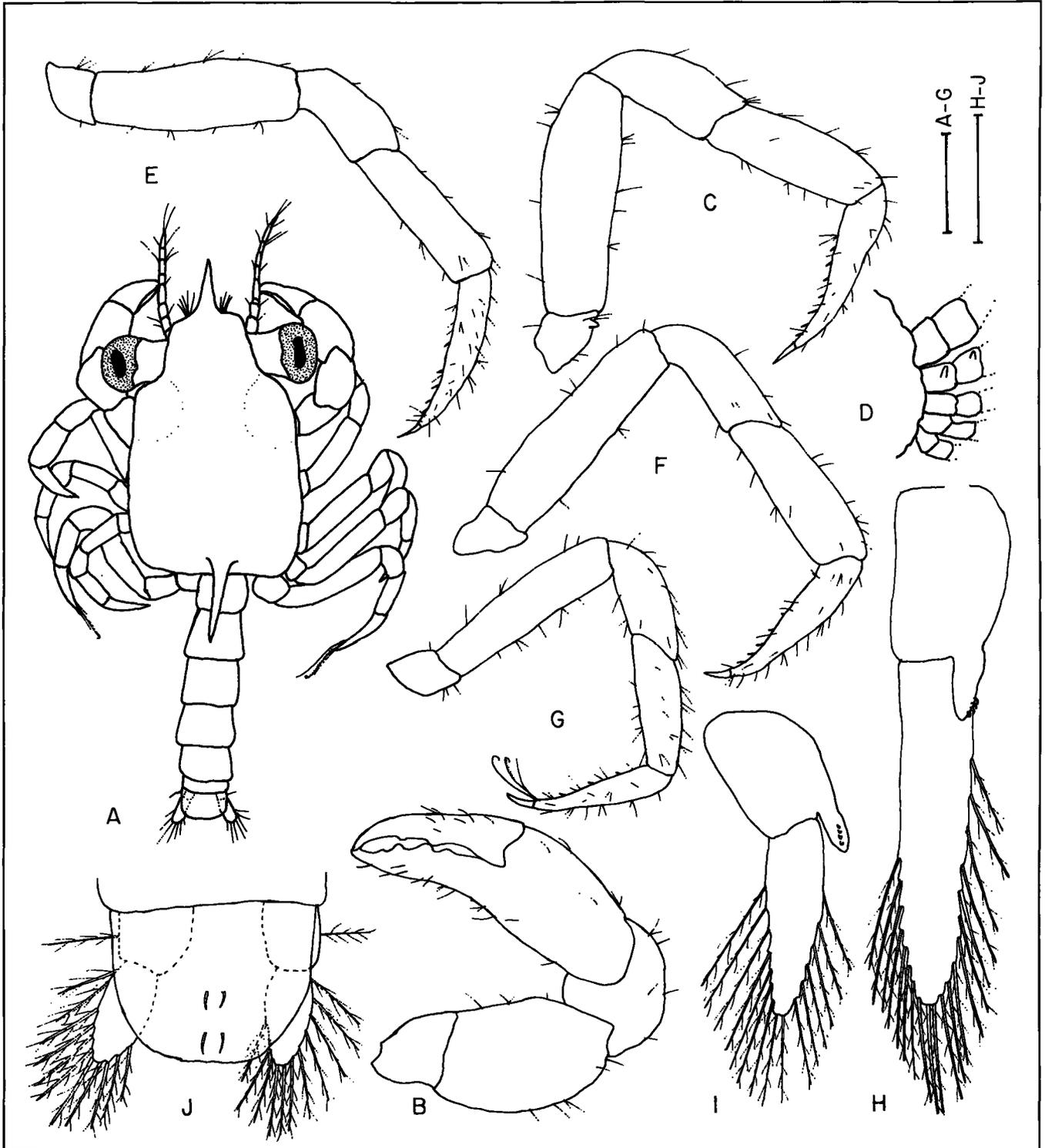
**Third maxilliped (Fig. 1H)** Epipod with 17–21 marginal setae; protopod with numerous scattered setae on surface. Exopod 2-segmented, proximal segment with 3–5 submarginal setae, distal segment with 4–8 terminal plumose setae. Endopod 5-segmented, ischium with inner margin somewhat denticulate, 24–32 marginal and/or submarginal and surface setae, merus with 9–13 setae, carpus with 14–19 setae, propodus with 12–18 simple and serrate setae, dactyl with 7–9 simple or serrate setae and 1 or 2 distinctly toothed bristles.

**Pereopods (Figs. 2B, C, E–G)** Segments of all pereopods with scattered short setae. Cheliped with ventral surface of ischium unarmed; cutting edge of fixed finger with 3 or 4 teeth, cutting edge of dactyl with 2–4 teeth. Second pereopod with coxa and ischium each armed with acute process on ventrodorsal margin (Fig. 2D), latter 1/3 size of former; dactyl with 6 or 7 spines on ventral margin. Third, 4th and 5th pereopods lacking coxal and ischial processes. Dactyls with 4–8, 5–7 and 3 or 4 spines on ventral margins respectively; dactyl of 5th also with 3 terminal setae.

**Abdomen and pleopods (Figs. 2A, 2H, I)** Abdomen 6-segmented, segments unarmed. Second through 5th pleopods with 3–5, 4 or 5, 3 or 4, and 4 hooks respectively on appendix internae. Exopods with 20–22, 19–22, 17–22, and 17–19 plumose setae respectively. Uropods 2-segmented, peduncle with 1 marginal plumose seta, exopod with 11–13 plumose setae, endopod absent.

**Telson (Fig. 2J)** Dorsal surface with 3 or 4 pairs of short setae in midline distally, terminal margin slightly rounded, without marginal setae.



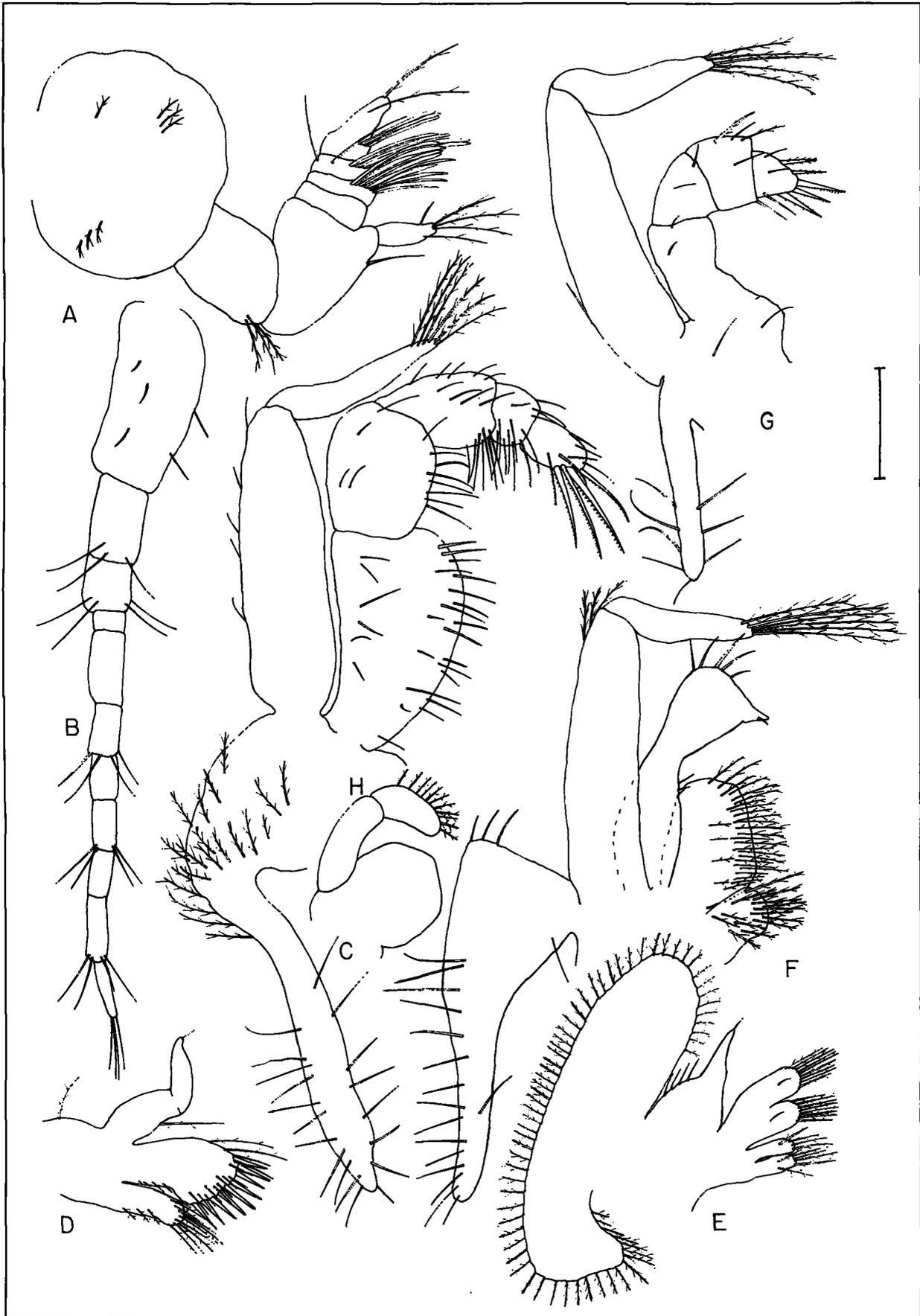


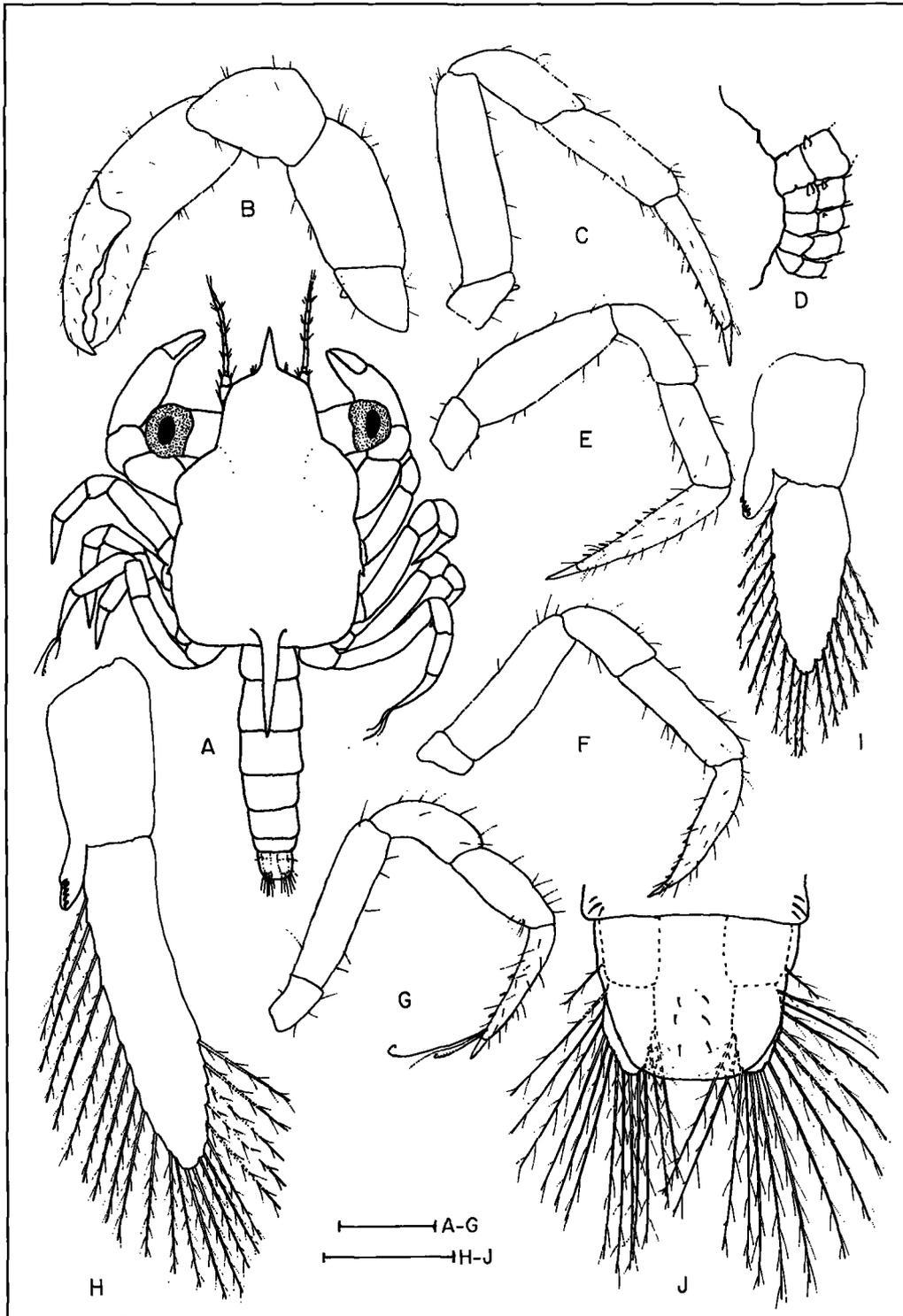
**Figure 1**

Megalopa of *Cancer oregonensis* Dana from Puget Sound Basin. (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped; (H) 3rd maxilliped. Scale 0.1 mm.

**Figure 2**

Megalopa of *Cancer oregonensis* Dana from Puget Sound Basin. (A) whole animal (dorsal view); (B) cheliped; (C) 2nd pereopod; (D) coxae and bases (ventral view); (E) 3rd pereopod; (F) 4th pereopod; (G) 5th pereopod; (H) 2nd pleopod; (I) 5th pleopod; (J) telson and uropods. Scales 1.0 mm (A), 0.5 mm (B-G), and 0.1 mm (H-J).





**Figure 4**

Megalopa of *Cancer productus* Randall for Puget Sound Basin. (A) whole animal (dorsal view); (B) cheliped; (C) 2nd pereopod; (D) coxae and bases (ventral view); (E) 3rd pereopod; (F) 4th pereopod; (G) 5th pereopod; (H) 2nd pleopod; (I) 5th pleopod; (J) telson and uropods. Scales 1.0 mm (A), 0.5 mm (B-G), and 0.1 mm (H-J).

**Figure 3**

Megalopa of *Cancer productus* Randall from Puget Sound Basin. (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) 1st maxilliped; (G) 2nd maxilliped; (H) 3rd maxilliped. Scale 0.1 mm.

	Puget Sound Basin (Present study)	California (Trask 1979)
<b>Setal formulae</b>		
Antenna		
peduncle plus flagellum	3, 2, 4, 0, 0, 4, 0, 4, 0, 3, 4 to 6, 3, 5, 0, 0, 5, 0, 5, 0, 4, 5	5, 4, 4, 0, 0, 3, 2, 3, 1, 3, 5
Maxilla		
scaphognathite	62-72	62-64
First maxilliped		
basal endite	28-38	38-40
coxal endite	15-19	9
Third maxilliped		
epipodite	20-29	13
exopod	5 or 6 + 5-9	-/+6
endopod		
segment 1	25-30	26*
segment 2	11-14	10*
segment 3	12-17	19*
segment 4	12-16	12*
segment 5	9-12	23*
Pleopodal exopod		
2nd	20-22	21
3rd	21 or 22	19
4th	20-23	19
5th	18-22	19
<b>Armature</b>		
Cheliped	Ischial process	-
2nd pereopod	Coxal, ischial processes	-
-Not reported.		
* Derived from figure.		

### Redescription: *Cancer productus* Randall

TL 5.6-6.4 mm, CL 3.1-3.6 mm.

**Carapace (Fig. 4A)** Considerably longer than broad, naked, lateral spines reduced to small, sometimes indistinct knobs, pair of gastric prominences present. Rostrum well developed and with ventromedial tubercle, dorsal spine projecting posteriorly over 1st and 2nd abdominal somites. Eyes well developed, corneae slightly dilated.

**Antennule (Fig. 3A)** Biramous; peduncle 3-segmented, proximal segment broadly expanded and with 6-14 scattered setae, penultimate segment with 3-5 distal plumose setae, ultimate segment with 1 seta. Exopod 4-segmented, basal segment naked, 2nd segment with 7-12 aesthetascs, 3rd segment with 5-9 aesthetascs and 2 or 3 marginal setae, 4th segment with 3-5 aesthetascs, 1 submarginal and 1 terminal seta. Endopod indistinctly 2-segmented, proximal segment naked, distal segment with 2 marginal and 3 or 4 terminal plumose setae.

**Antenna (Fig. 3B)** Peduncle 3-segmented; flagellum with 8 articles; setal formula varying from 4, 2, 4, 0, 0, 4, 0, 4, 0, 3, 4 to 6, 3, 4, 0, 0, 5, 0, 5, 0, 4, 5.

**Mandible (Fig. 3C)** Molar and incisor processes not distinguishable. Mandibular palp 2-segmented, proximal segment naked, distal segment with 10-12 marginal setae.

**Maxillule (Fig. 3D)** Endopod indistinctly 2-segmented, proximal segment with 1 or 2 marginal setae, distal segment with 0-2 terminal setae. Coxal endite with 10-19 setae. Basal endite with 22-24 terminal setae/spines and 4 or 5 marginal setae basally.

**Maxilla (Fig. 3E)** Endopod expanded basally and with 4 marginal setae in proximal half, 1 short terminal seta. Proximal lobe of coxal endite with 2-4 terminal and 1 or 2 subterminal plumose setae, distal lobe with 2-5 terminal and 2 or 3 subterminal plumose setae. Proximal lobe of basal endite with 9 or 10 terminal and 1-3 subterminal plumose setae, distal lobe with 8 or 9 terminal and 1 subterminal plumose setae. Scaphognathite

with 62–72 marginal setae and 3–5 scattered surface setae (not shown in illustration).

**First maxilliped (Fig. 3F)** Epipod with 12–20 marginal and/or submarginal setae. Exopod 2-segmented, proximal segment with 3 or 4 marginal plumose setae distally, distal segment with 4–6 terminal plumose setae. Endopod with 1–3 marginal setae basally and 4–7 distally, 1 terminal seta; coxal endite with 15–19 plumose setae; basal endite with 28–38 plumose setae.

**Second maxilliped (Fig. 3G)** Epipod with 6–10 marginal setae; protopod with 1–7 scattered setae. Exopod 2-segmented, proximal segment with 1 or 2 marginal, short spine-like setae, distal segment with 4 or 5 terminal plumose setae. Endopod 4-segmented, merus with 2–6 setae, carpus with 2 or 3 setae, propodus with 5–9 setae, dactyl with 3–5 submarginal setae and 4–6 terminal serrate setae.

**Third maxilliped (Fig. 3H)** Epipod with 20–29 marginal setae. Protopod with 21–32 scattered plumose setae. Exopod 2-segmented, proximal segment with 5 or 6 marginal setae, distal segment with 5–9 terminal plumose setae. Endopod 5-segmented, ischium with 25–30 setae, merus with 11–14 setae, carpus with 12–17 setae, propodus with 12–16 setae, dactyl with 9–12 setae and 0–2 distinctly toothed bristles.

**Pereopods (Figs. 4B, C, E–G)** Segments of all pereopods with scattered short setae. Cheliped with ischium armed with acute spine on ventrodistal margin, cutting edge of fixed finger and dactyl each with 2–4 teeth. Second pereopod with coxa and ischium each armed with acute spine on distoventral margin (4D), ischial spine smaller than coxal spine, dactyl with 5–7 spines on ventral margin. Third pereopod with ischium frequently armed with minute process on ventrodistal margin, dactyl with 6 or 7 spines on ventral margin. Fourth and 5th pereopods with coxae and ischia unarmed, dactyls with 5–7 and 2–4 spines on ventral margin respectively; dactyl of fifth also with 3 terminal setae.

**Abdomen and pleopods (Figs. 3A, 4H, I)** Abdomen six-segmented. Second pleopod with 3–5 and 3rd through 5th each with 3 or 4 hooks on appendix interna. Exopods with 20–22, 21 or 22, 20–23, 18–22 plumose setae respectively. Uropods 2-segmented, peduncle naked or with 1 basal marginal plumose seta. Exopod with 12–13 plumose setae, endopod absent.

**Telson (Fig. 4J)** Dorsal surface with 3 or 4 pairs of short setae in midline distally, terminal margin usually slightly rounded, without marginal setae.

## Discussion

Of concern to field biologists is the fact that larval studies primarily report characters found in specimens reared under laboratory conditions. Even though environmental conditions have been varied to ascertain their influence on larval development, there often remains a question as to the similarities of characters reported for these laboratory-reared organisms and those that would be found in naturally occurring populations of the same species. Although the megalopal characters of *Cancer oregonensis* and *C. productus* reported in this study were based upon specimens collected from naturally occurring populations, counts for some characters of *C. oregonensis* have been compared with counts derived from laboratory-reared animals. No appreciable differences were found between the two populations; however, in carapace length, the laboratory-reared individuals fell in the lower half of the length-frequency curve determined for the natural population.

As previously indicated, a number of differences between the megalopae of *C. productus* examined in this study and those described by Trask (1970) have been observed. Most obvious are the differences in setal formulae for the coxal endite of the first maxilliped and the epipod of the third maxilliped. Differences in antennal setation were also observed; however, Trask did not give a range for the number of setae occurring on each article, thus overlap between *C. oregonensis* and *C. productus* remains a possibility. Trask described the endopod of the 3rd maxilliped as four-segmented; however, five segments are clearly illustrated (1970, Fig. 7i). Quintana and Saelzer (1986) suggested that if the apparently contradictory descriptions of the megalopal stage of *Cancer anthonyi* Rathbun presented by Trask (1974) and Anderson (1978) were based on correct identifications and observations, geographical differences probably accounted for the great differences in the setation reported. A similar situation may account for the differences in *C. productus* megalopae.

Although Quintana and Saelzer (1986) recommend the use of the antennal setation, as well as the setation of the epipods of the maxillipeds, for distinguishing between *Cancer* megalopae, these characters cannot be used to separate Puget Sound populations with any degree of reliability. The antennal setation found in *C. oregonensis* overlaps that reported for *C. gracilis*; only the setae of the antepenultimate article differ between *C. oregonensis* and *C. productus*. The setation reported for *C. magister* that we have determined from the figure presented by Poole (1966, Fig. 6C) differs from counts made for northern specimens. With the exceptions of larger numbers of setae on the epipods

of the first and second maxillipeds of *C. magister*, setal numbers for the maxillipedal epipods overlap among all four local species.

In his description of the larval development of *Cancer magister*, Poole stated that the megalopa possessed five abdominal segments and a telson, and this number was repeated by both Ingle (1981) and Iwata and Konishi (1981) in their reviews of megalopal characters of *Cancer* species. As all other described larvae possess a six-segmented abdomen, this single character would be expected to provide a very simple and easy means for recognizing megalopae of *C. magister*. Poole's (1966) description of the megalopae was based on two specimens collected from Drakes Bay, California; however, Poole indicated that he had compared these individuals with laboratory-reared specimens. He noted no significant differences. His figure (1966: fig 6A) indicates no suture between the sixth abdominal somite and the telson, and he refers to the uropods as the "pleopods of the telson." Unless a major, and evolutionarily significant, variation occurs in the postlarvae of this species over its range, Poole's description is incorrect. We have examined a substantial number of *C. magister* megalopae from the Puget Sound Basin, and in all cases the sixth abdominal somite is clearly separated from the telson by a well marked suture; the uropods arise, as in other megalopae, from the distal margin of the sixth somite.

Megalopae of *Cancer* have been broadly grouped by Orensanz and Gallucci (1988) into the size categories small, medium, and large. In the species of local interest, *C. gracilis* is grouped among those species with small megalopae: *C. oregonensis* and *C. productus* in the medium-sized group and *C. magister* as the single representative in the large category. However, Orensanz and Gallucci have reported a bimodal recruitment of *C. magister*, with the late-summer megalopae being of considerably smaller size. Thus the use of size in distinguishing *C. magister* from other local species may be less reliable during certain periods of the year than previously assumed. The megalopae of *C. oregonensis* and *C. productus* are morphologically very close and no definitive means of distinguishing between the two species at this stage has been available. During the course of this study an apparently constant and easily recognizable character has been found that will distinguish *C. productus* from *C. oregonensis*, i.e., the presence in the former species of an acute process on the ventral surface of the ischium of the cheliped (Fig. 4D) that is absent in the latter species (Fig. 2D). In fact, the absence of a spine or process on the ischium of the cheliped distinguishes *C. oregonensis* megalopae from all three of the other local species. Poole (1966) described a spine only on the "basi-ischipoidite of the first walking leg" of *C. magister*; however, in our northern

populations we have found that a strong, acute spine is present on the ventrodiscal margin on the ischium of the cheliped and on the ventrodiscal margin of the coxa of the 2nd and 3rd pereopods. Ally (1975) reports a spine ("hook") on the ventral surface of the ischium of the cheliped in *C. gracilis*. We have not been able to examine local megalopae of this species; therefore, in preparing the following key to the local species, we have relied on the completeness and accuracy of Ally's description.

#### Key to the megalopae of northern populations of *Cancer*

- 1 No spine or process on ventrodiscal surface/  
margin of ischium of cheliped . . . . *C. oregonensis*  
Acute spine or process on ventrodiscal  
surface/margin of ischium of cheliped . . . . . 2
- 2 Megalopae of small size (<3.0 mm); 2nd and  
3rd pereopods lacking coxal spine or process  
on ventrodiscal surface . . . . . *C. gracilis*  
Megalopae of medium to large size (<4.0  
mm); 2nd pereopod with coxal spine or  
process on ventrodiscal surface . . . . . 3
- 3 Megalopae with acute spine on ventrodiscal  
surface of coxa of 3rd pereopod . . . . *C. magister*  
Megalopae usually without process, or rarely  
with very small process on ventrodiscal sur-  
face of coxa of 3rd pereopod . . . . . *C. productus*

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