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Studies on the *provenzanoi* and other pagurid groups: VI. Larval and early juvenile stages of *Pagurus ochotensis* Brandt (Decapoda; Anomura; Paguridae) from a northeastern Pacific population, reared under laboratory conditions

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Zoeal, megalopal, and early juvenile stages of *Pagurus ochotensis* (Brandt, 1851) from a northeastern Pacific population are described from laboratory-reared individuals. Zoeal and megalopal development in this population is compared with that described for a population of this species from Hokkaido, Japan. First and second juvenile crab stages of this species are described for the first time. The nearly identical developmental morphology of the two populations supports the earlier synonymy of the northeastern Pacific species, *Pagurus alaskensis* (Benedict) with *P. ochotensis*.

KEYWORDS: Decapoda, Crustacea, Anomura, Paguridae, *Pagurus*, larval stages, NE Pacific.

Introduction

Benedict (1892, 1901) was the first to categorize hermit crab species as belonging to a particular type or group in his descriptions of two species from Alaskan waters that he referred to the '*bernhardus*' type. In her survey of North Pacific hermit crabs, McLaughlin (1974) reviewed the taxonomic status of the three species of this *bernhardus* group occurring in North Pacific waters, i.e. *P. alaskensis* (Benedict), *P. aleuticus* (Benedict), and *P. armatus* (Dana), and concluded that *P. alaskensis* was synonymous with the Asian species *P. ochotensis* (Brandt, 1851). Larval development of *P. ochotensis* from Japanese waters has been recently described (Quintana and Iwata, 1987). We have now reared larvae from a female of a Puget Sound, Washington population from hatching through the second juvenile stage. Zoeal and megalopal development in this population is described, illustrated and compared with these developmental stages in the Japanese population. Early crab stages of this species are described for the first time.

Materials and methods

An ovigerous female of *P. ochotensis* was collected at a depth of 30·5 m off Waldron Island, San Juan Archipelago, Washington on 18 March 1989. Upon return to the laboratory at the Shannon Point Marine Center, the crab was isolated in a glass culture dish with approximately 2000 ml of natural sea water. The dish was then placed in a sea-table with circulating sea water, with the temperature maintained at approximately

12°C. More than 300 larvae hatched on 2 April 1989. Approximately 50 prezoeae were preserved within 1–2 h of hatching; 146 zoeal stage I larvae were placed in individual compartments in 24-compartmented plastic trays each with *ca* 50 ml of natural sea water (salinity of 29–31‰); the remainder were maintained in mass culture dishes, each with *ca* 500 ml of sea water and 25–30 larvae. Trays and mass culture dishes were kept in a constant temperature unit (CTU) at 12 ± 1°C, without light, during the entire rearing period. At the megalopal stage, surviving larvae from the mass culture dishes were transferred to rearing trays to replace larvae that had died during the zoeal stages. These larvae were used in the morphological study, but were not included in computations of megalopal and juvenile survival. Each larva, including the supplemental megalopae, was assigned an individual identification number so that its moults could be recorded accurately. Water was changed daily and the larvae were provided with a diet of freshly hatched *Artemia* nauplii. Methodology, as well as terminology for the descriptions, follows that of McLaughlin and Gore (1988). Descriptions are based on moults and on preserved and living stages observed throughout development. Zoeal appendages are described from proximal to distal. *N* refers to the number of individuals of the initial 146 reported for each stage that survived through that stage and successfully molted to the next; *n* refers to the number of individuals measured and/or dissected. Carapace length (CL) is as measured with an ocular micrometer, from the rostral tip to the posterior midpoint of the carapace; total specimen length (TL) is as measured from the tip of the rostrum to the midpoint of the telson margin, excluding the telsonal processes; length of the cephalothoracic shield of megalopae and juveniles (SL) is as measured from the tip of the rostrum to the mid-point of the cervical groove. Neither interference phase nor electron microscopes were available at the time of this study; consequently no attempt has been made to define or compare setal morphology at these levels (c.f. Quintana and Iwata, 1987; Ingle, 1990). Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, USA.

Description of larvae

Prezoea

The prezoeal body was covered initially with thin cuticle which was shed within 1–2 h of hatching. The rostrum was poorly developed and mouth parts and maxillipeds were non-functional. Terminal telsonal processes were well developed; however, the abdomen and telson were curved under the body as in the prehatching posture. The fifth abdominal somite was appreciably shorter than observed in first day zoeae I.

Zoea I

Size. CL = 1·52–1·67 mm; TL = 2·75–3·02; $n = 32$.

Duration. 6–8 days; $N = 112$.

Carapace (Fig. 1A). Rostrum broad proximally, narrowing to elongate slender spinose projection, over-reaching antennal scaphocerite; posterolateral angles of carapace produced as moderately short spines; eyes sessile.

Abdomen (Fig. 1A). Five somites and telson, first somite with 4 minute spinules on posterodorsal margin, somites 2–4 each with 3 pairs of spines on posterodorsal margin, outermost pair frequently quite small, spine pairs progressively increasing in size from anterior to posterior somites, posterolateral margins each with small spine, fifth somite with 2 pairs of strong spines on posterodorsal margin and elongate pair of posterolateral spines.

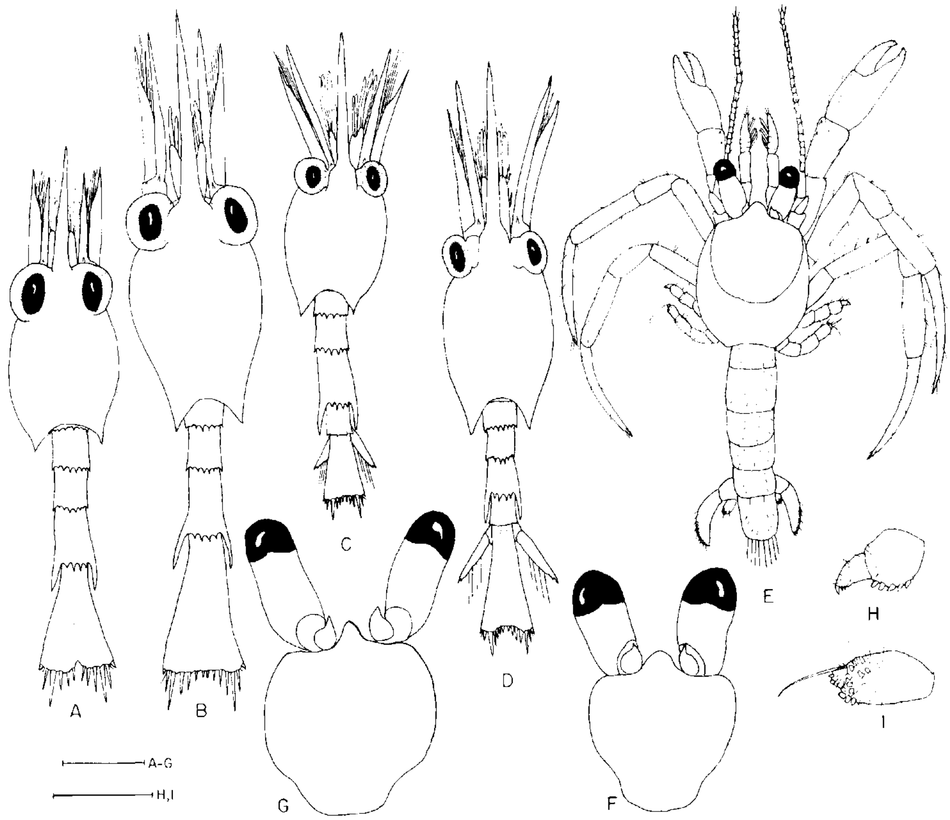

FIG. 1. *Pagurus ochotensis*: A. Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1 carapace and ocular peduncles; G, Crab 2 carapace and ocular peduncles; H, Crab 1 fourth pereopodal propodus and dactyl; I, Crab 1 fifth pereopodal propodus and dactyl. Scales equal 1·0 mm (C, D); 0·5 mm (A, B, E–G); 0·25 mm (H, I).

Telson (Fig. 2A). Fused with sixth somite; elongate, somewhat fan-shaped posteriorly; posterior margin with small median cleft and 7+7 processes (1, ii, 3–7), outermost an unarmed, but weakly articulated spine (1), second an anomuran hair (ii), third through seventh articulated, plumodenticulate spines or setae (3–7), of which fourth is longest, approximately three-fourths telson width at terminal margin; anal spine present.

Antennule (Fig. 3A). Subcylindrical, indistinctly bilobed, one-third to one-quarter length of antenna; 2 aesthetascs and 2 short setae terminally, occasionally also additional longer terminal seta; 1 long plumose terminal seta on endopodal bud.

Antenna (Fig. 4A). Scaphocerite slightly over-reaching endopod, with strong distal spine, outer margin straight and unarmed, inner margin convex and with 6 or 7 plumose setae and occasionally also 1 or 2 short, simple setae; endopod fused to protopod, naked; protopod with strong spine armed with tiny denticles at base of endopodal junction.

Mandible (Fig. 5A). Asymmetrical dentate; incisor processes each with 1 strong tooth and several smaller teeth; molar processes serrate and with tuberculate ridges and few acute or blunt teeth; no palp bud.

FIG. 2. *Pagurus ochotensis*: telson and tailfan. A. Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2 telson and uropodal endopods; H, Crab 2 left uropodal exopod; I, Crab 2 right uropodal exopod. Scale equals 0·25 mm.

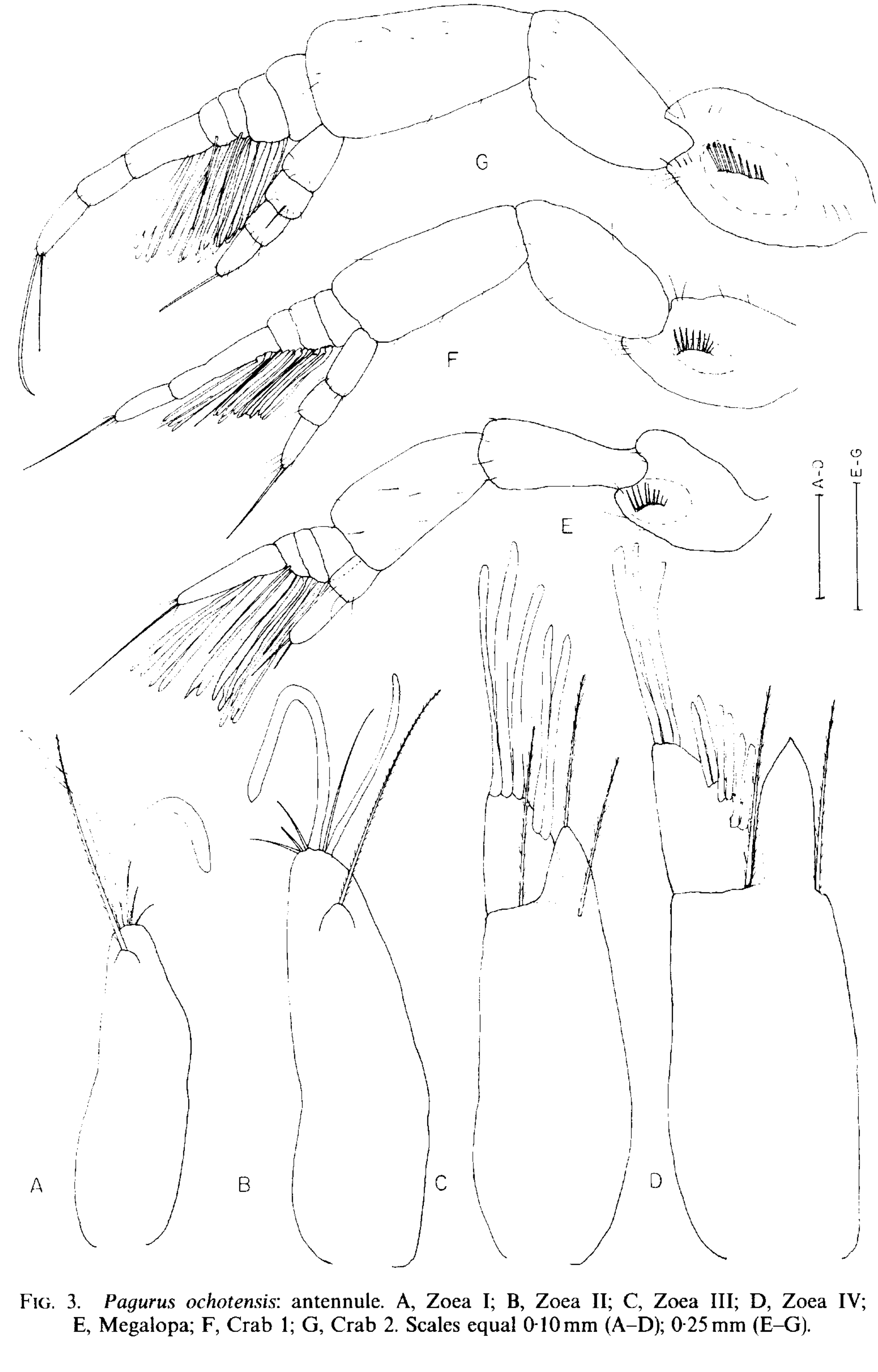

FIG. 3. *Pagurus ochotensis*: antennule. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scales equal 0·10 mm (A–D); 0·25 mm (E–G).

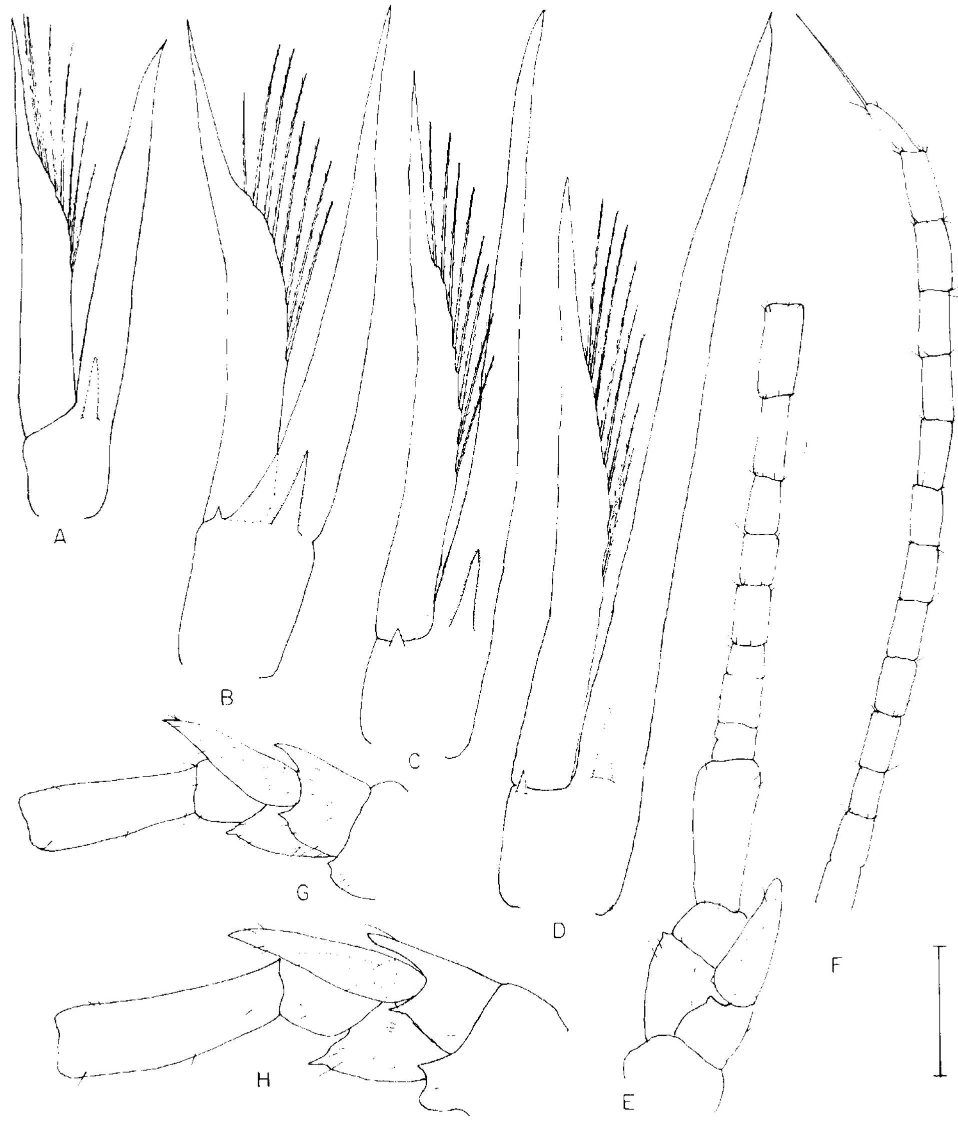

FIG. 4. *Pagurus ochotensis*: antenna. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, distal portion of megalopal antennal flagellum; G, Crab 1; H, Crab 2. Scale equals 0·25 mm.

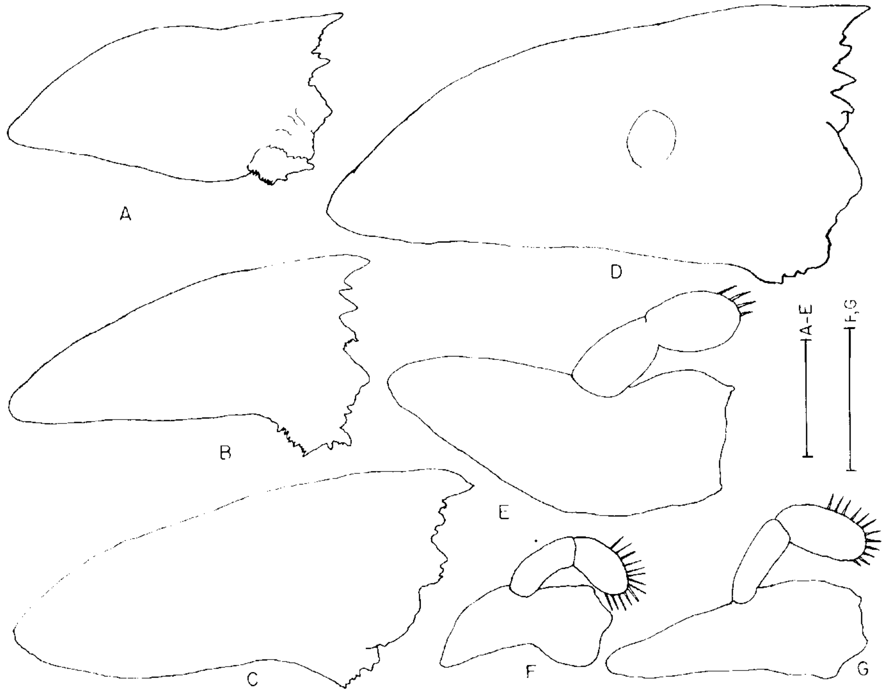

Fig. 5. *Pagurus ochotensis*: mandible. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scales equal 0·10 mm (A–E); 0·25 mm (F, G).

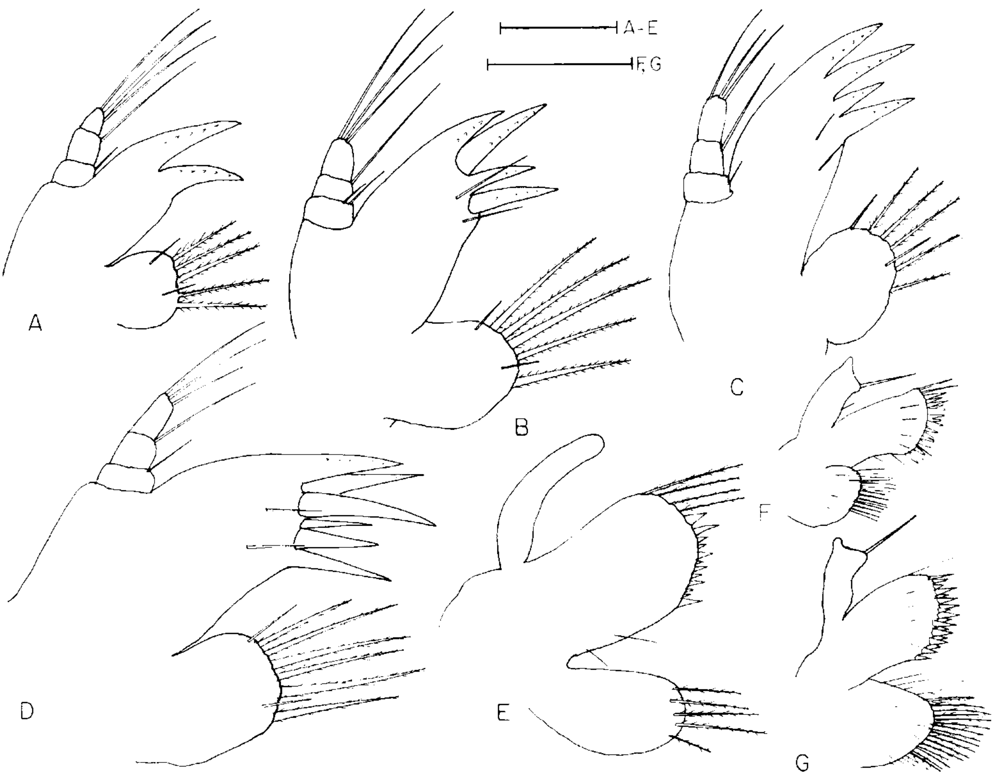

Fig. 6. *Pagurus ochotensis*: maxillule. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scales equal 0·10 mm (A–E); 0·25 mm (F, G).

Maxillule (Fig. 6A). Endopod 3-segmented, setal formula 1 or rarely 2, 1, 3, all simple setae; coxal endite with 5 marginal plumose setae or 1 naked and 4 plumose setae and 2 short simple setae submarginally; basal endite with 2 strong teeth, each armed with 2–5 small denticles.

Maxilla (Fig. 7A). Endopod bilobed, proximal lobe with 2 or 3 plumose marginal setae, distal lobe with 3 or 4 plumose marginal setae; coxal and basal endites also bilobed, coxal endite with 5 or less frequently 6 marginal and 1 submarginal plumose setae on proximal lobe, 3 marginal and 1 submarginal plumose setae on distal lobe; basal endite with 4 and 3 marginal plumose setae on proximal and distal lobes

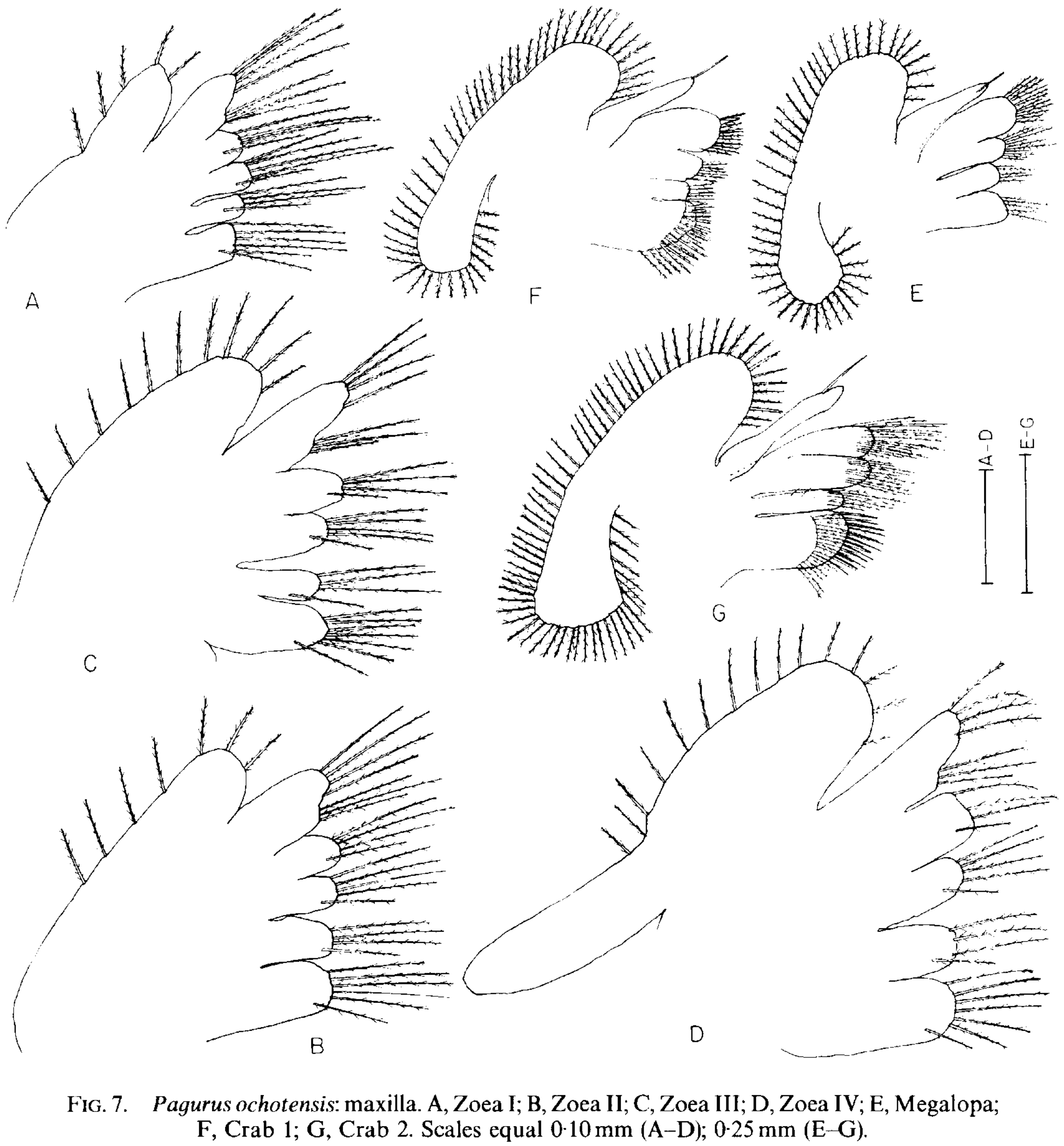

FIG. 7. *Pagurus ochotensis*: maxilla. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scales equal 0·10 mm (A–D); 0·25 mm (E–G).

respectively and also 1 submarginal plumose seta on each lobe; scaphognathite fused to protopod proximally, distal lobe with 5 short plumose marginal setae.

Maxilliped 1 (Fig. 8A). No coxopodal setae apparent; basipod with setal formula progressing distally 1 or 2, 2, 3, 2 (rarely) or 3; endopod 5-segmented, setation of segments 1–5 (proximal to distal): 3, 2, 1, 2, 4+I (Roman numeral denoting posterolateral seta), plus additional fine setae on lateral margins of first three proximal segments; exopod indistinctly 2-segmented, with 4 terminal natatory setae.

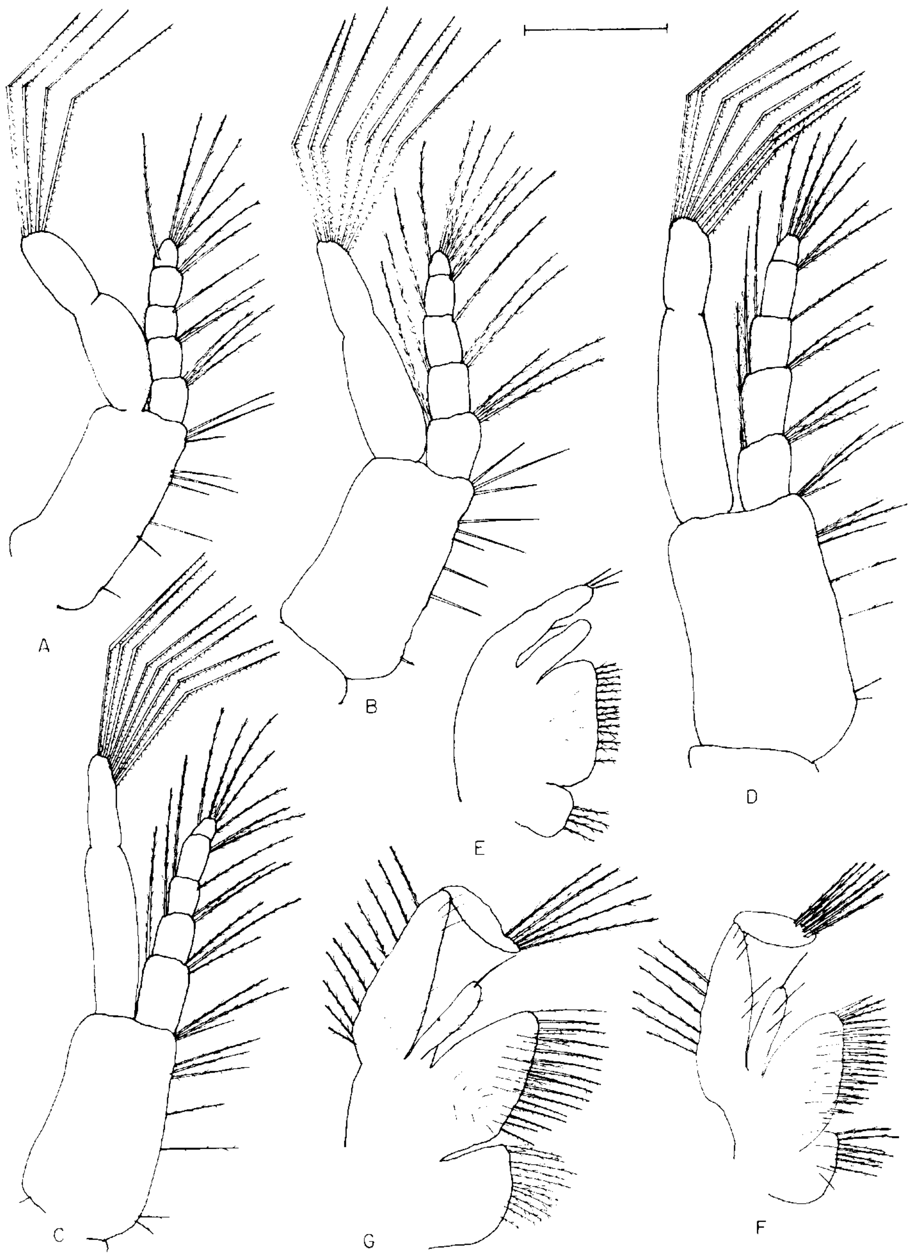

FIG. 8. *Pagurus ochotensis*: first maxilliped. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scale equals 0·25 mm.

Maxilliped 2 (Fig. 9A). No coxopodal setae; basipod with 1 simple marginal seta, 1 strong spine-like process with marginal spinules and 1 plumose seta at inner distal angle; endopod 4-segmented, proximal 3 segments each with 1 strong spine-like process armed with marginal spinules and 1 plumose seta, distal segment with 4+1 plumose setae; exopod indistinctly 2-segmented, with 4 terminal natatory setae.

Maxilliped 3 (Fig. 10A). Exopod unsegmented, terminating acutely or with minute bifurcation.

Colour. Zoeae transparent overall with red and yellow chromatophores as follows: red chromatophores on carapace over gut and laterally at level of first maxillipeds, at bases of mandibles, maxillules and maxillae; yellow chromatophore beneath carapace over gut; corneae black and turquoise.

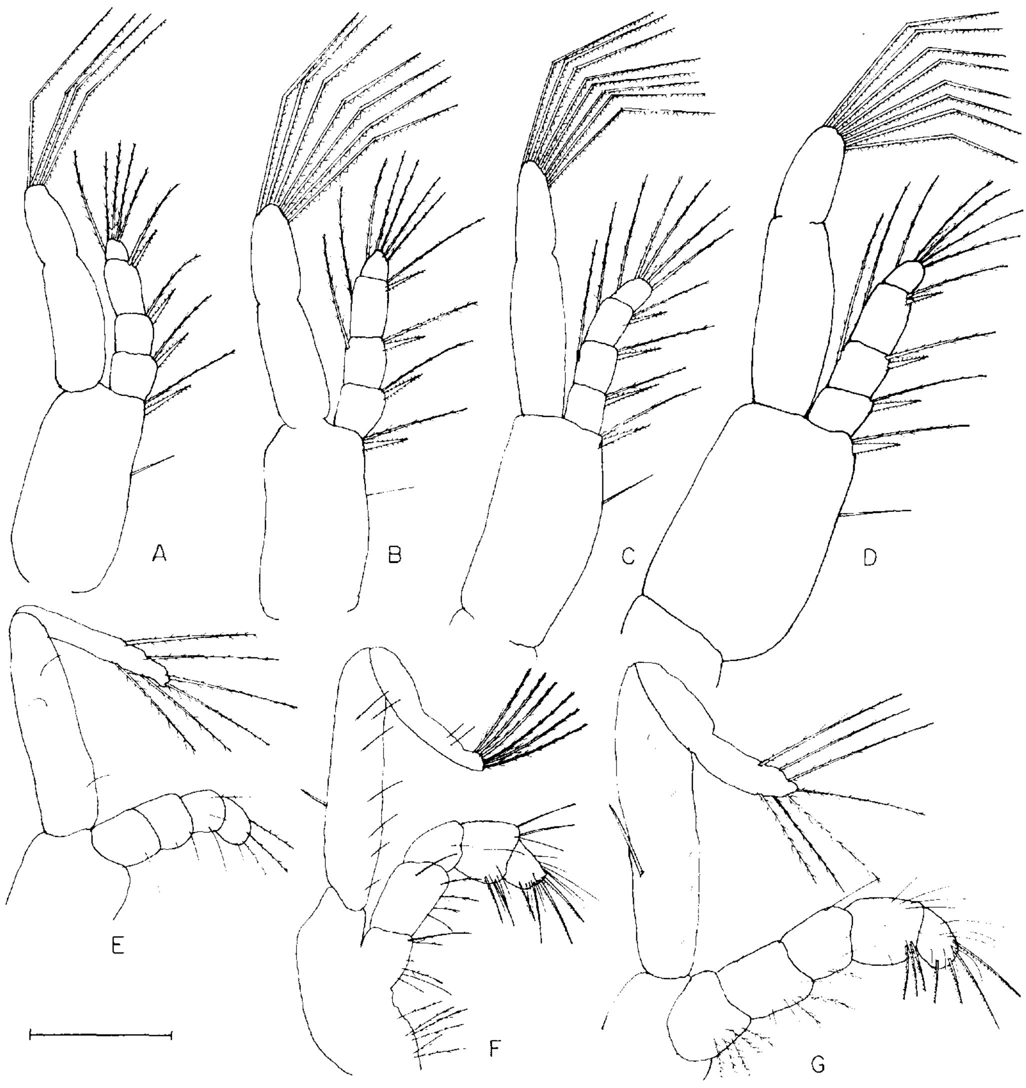

FIG. 9. *Pagurus ochotensis*: second maxilliped. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scale equals 0·25 mm.

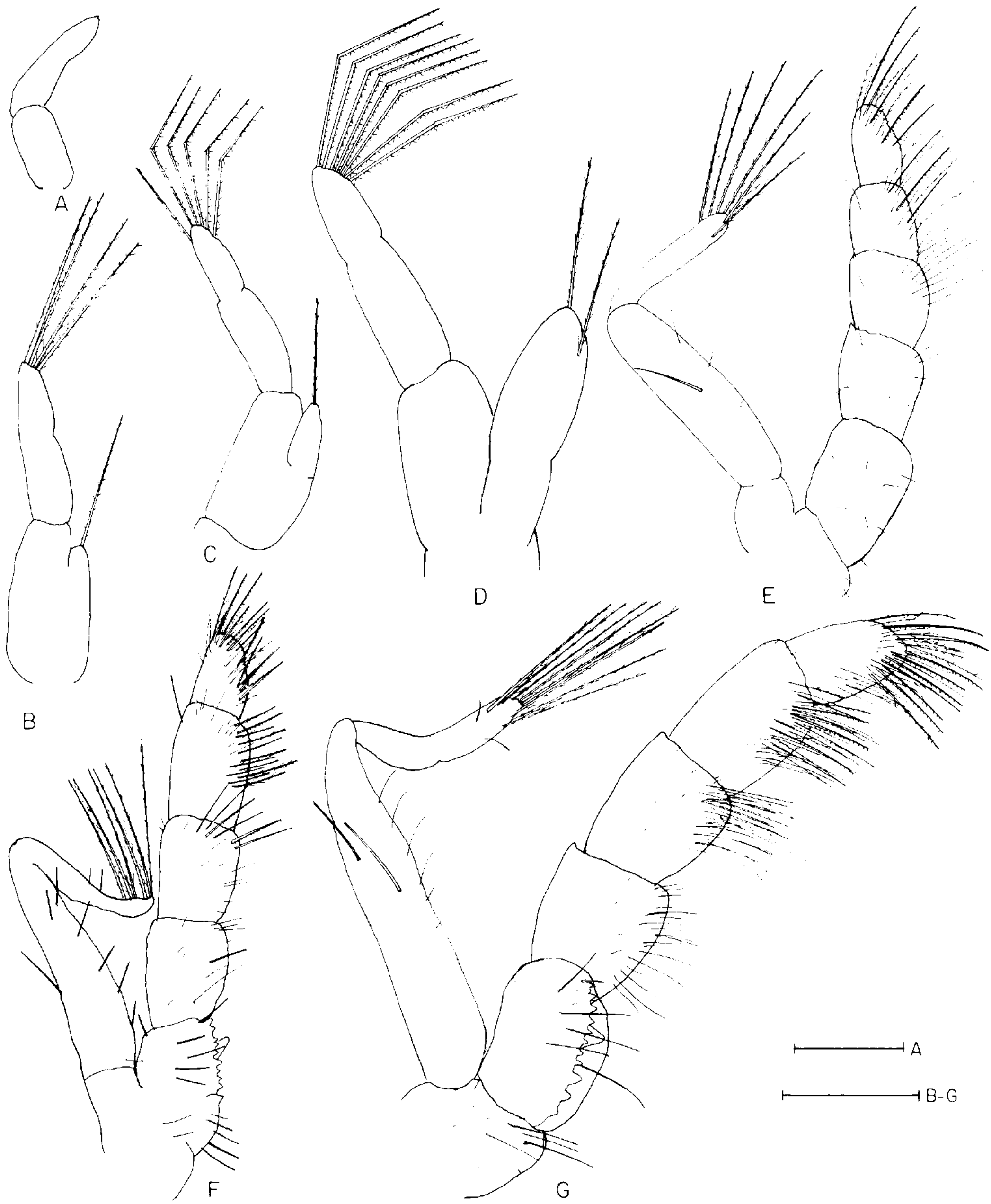

FIG. 10. *Pagurus ochotensis*: third maxilliped. A, Zoea I; B, Zoea II; C, Zoea III; D, Zoea IV; E, Megalopa; F, Crab 1; G, Crab 2. Scales equal 0·10 mm (A); 0·25 mm (B–G).

Zoea II

Size. CL = 1·80–2·42 mm; TL = 3·83–4·52 mm; $n = 26$.

Duration. 5–7 days; $N = 95$.

Carapace (Fig. 1B). Larger, otherwise unchanged; eyes stalked.

Abdomen (Fig. 1B). Spines of posterodorsal margin of first somite usually absent, spines of second reduced; spination of somites 3–5 unchanged from previous stage, or with outermost pair minute.

Telson (Fig. 2B). Still fused with sixth somite; posterior marginal formula now 8 + 8 (1, ii, 3–8) with addition of shortest median spines, fourth pair still $\geqslant$ one-half telson width; median cleft obsolete; anal spine absent.

Antennule (Fig. 3B). Still weakly bilobed, with 2 or occasionally 3 terminal aesthetascs and 2–4 short to moderately long, simple setae; 1 long, terminal plumose seta on developing endopal bud.

Antenna (Fig. 4B). Scaphocerite still with prominent distal spine, inner margin with 7 or 8 plumose setae and frequently 1 more distal simple seta; endopod equalling or slightly exceeding length of scaphocerite, naked; protopod now with additional small spine near junction of scaphocerite.

Mandible (Fig. 5B). Larger and with some denticles more acute, but generally as in stage I.

Maxillule (Fig. 6B). Endopod now with 1 or 2 simple setae on basal segment; coxal endite with 5 plumose marginal setae and 2 simple submarginal setae; basal endite with 4 strong teeth each armed with several denticles and 2 submarginal simple setae.

Maxilla (Fig. 7B). Setation of endopod and endites unchanged from previous stage; scaphognathite usually with 7 short plumose setae, occasionally as few as 5 or as many as 9.

Maxilliped 1 (Fig. 8B). Protopodal setation unchanged; endopodal setation now 3 + I, 2 + I, 1 + I, 2, 4 + I; exopod with 7 or 8 terminal natatory setae.

Maxilliped 2 (Fig. 9B). Protopodal setation unchanged; endopodal setal formula now 2, 2 + I, 2 + I, 4 + I; exopod with 7 or 8 terminal natatory setae.

Maxilliped 3 (Fig. 10B). Exopod indistinctly 2-segmented, usually with 4, occasionally with 6 or 7 terminal plumose setae; endopodal bud with 1 terminal plumose seta.

Colour. Changed from stage I by addition of red chromatophores anteriorly and posteriorly on either side of midgut.

Zoea III

Size. CL = 2·33–3·14 mm; TL = 4·92–5·53 mm; $n = 25$.

Duration. 6–11 days; $N = 49$.

Carapace (Fig. 1C). Larger but generally as in previous stages; chelae and pereopod buds apparent posteriorly beneath carapace.

Abdomen (Fig. 1C). Somite 2 with posterodorsal spines usually absent, spines of somites 3 and 4 reduced; fifth somite still with elongate pair of posterolateral spines; sixth somite now clearly delineated and with small spine at posterolateral angles; uniramous uropods present, inner margins of exopods each with 4 plumose setae or 1 simple and 3 plumose setae, usually small spine or spinule and occasionally also simple seta distally, terminating in strong bifid spine.

Telson (Fig. 2C). No longer fused to sixth somite, otherwise unchanged.

Antennule (Fig. 3C). Exopod with 3 or rarely 4 terminal and 2 subterminal aesthetascs; endopod approximately two-thirds length of exopod, with 1 terminal plumose seta; protopod with 1 or less frequently 2 plumose setae at exopodal junction.

Antenna (Fig. 4C). Endopod overreaching scaphocerite by very little to approximately one-eighth own length; scaphocerite still with 7 or 8 plumose setae.

Mandible (Fig. 5C). Larger but little changed from previous stage.

Maxillule (Fig. 6C). Setation of endopod simple or weakly plumose; no other changes from previous stage.

Maxilla (Fig. 7C). Proximal lobe of coxal endite now with 6 marginal and 1 submarginal plumose setae; no changes in endopod or basal endite; scaphognathite with proximal lobe still fused posteriorly, distal lobe now with 9–12 marginal plumose setae and often 1 or 2 short setae distally on still fused posterior lobe.

Maxilliped 1 (Fig. 8C). Protopod and endopod unchanged from previous stage; exopod with 8 terminal natatory setae.

Maxilliped 2 (Fig. 9C). Protopod and endopod unchanged from previous stage; exopod with 8 terminal natatory setae.

Maxilliped 3 (Fig. 10C). Endopod bud better developed, with 1 terminal seta; exopod with 6 or 7 terminal setae.

Colour. As in previous stage but with addition of orange and red chromatophores visible on developing chelae.

Zoea IV

Size. CL = 3·30–4·12 mm; TL = 5·82–7·04 mm; $n = 36$.

Duration. 9–21 days; $N = 30$.

Carapace (Fig. 1D). Larger but otherwise unchanged; rostrum still longer than antenna. Pereopod buds larger, fingers of chelae well formed.

Abdomen (Fig. 1D). Armature of abdominal somites unchanged from previous stage. Uropods with endopod present but fused to protopod and without setae; exopod still with 4 plumose setae, sometimes now without spinule on inner margin distally and occasionally 1 additional simple seta proximally, terminating in 1 very strong spine and adjacent bifid spine. Pleopod buds present on somites 2–5.

Telson (Fig. 2D). Basically unchanged from previous stage; however, fourth telsonal process frequently now shorter than half telson width.

Antennule (Fig. 3D). Exopod now with 3 terminal and 2·5–3 pairs of subterminal aesthetascs, frequently also with 1 terminal seta; endopod naked but with acute tip; protopod with 2 long plumose setae at endopodal junction.

Antenna (Fig. 4D). Scaphocerite with 8 plumose setae and occasionally 1 shorter simple seta distally; endopod now one-seventh to one-fifth longer than scaphocerite.

Mandible (Fig. 5D). Larger, but dentition generally similar to previous stage; palp bud present, but frequently quite small.

Maxillule (Fig. 6D). Endopod unchanged; basal endite now with 6 (or very rarely 5) teeth, 1 or 2 usually appreciably smaller and lacking accessory denticles; coxal endite with 5 or 6 plumose marginal setae and 2 submarginal simple setae.

Maxilla (Fig. 7D). Setation of endopod and endites unchanged from previous stage; proximal lobe of scaphognathite no longer fused to protopod, elongate and usually with 1 or 2 plumose setae distally, distal lobe with 12–16 marginal plumose setae.

Maxilliped 1 (Fig. 8D). Unchanged.

Maxilliped 2 (Fig. 9D). Unchanged.

Maxilliped 3 (Fig. 10D). Endopod larger, with 1 terminal and 1 subterminal plumose seta; exopod now with 8 terminal setae.

Colour. Red chromatophore pattern unchanged from previous stage; 1 additional yellow chromatophore on carapace anteriorly near base of rostral keel.

Megalopa

Size. SL = 0·67–0·92; CL = 1·01–1·58; $n = 23$.

Duration. 9–17 days; $N = 27$.

Carapace (Fig. 1E). Shield two-thirds to three-fifths total carapace length, slightly longer than broad; rostrum produced, often reaching to tip of moderately well-developed ocular acicles, bluntly rounded. Ocular peduncles short, corneae slightly dilated.

Abdomen (Fig. 1E). With 6 somites, unarmed but with few scattered setae on dorsal and ventral surfaces; symmetrically paired, biramous pleopods (Fig. 11A–D) on somites 2–5, exopods well developed, setal formulae progressing posteriorly 10 or 11 (second and third), 9–11 (fourth) and 9 or 10 (fifth), endopods each with appendix interna of 2 small apical hooks.

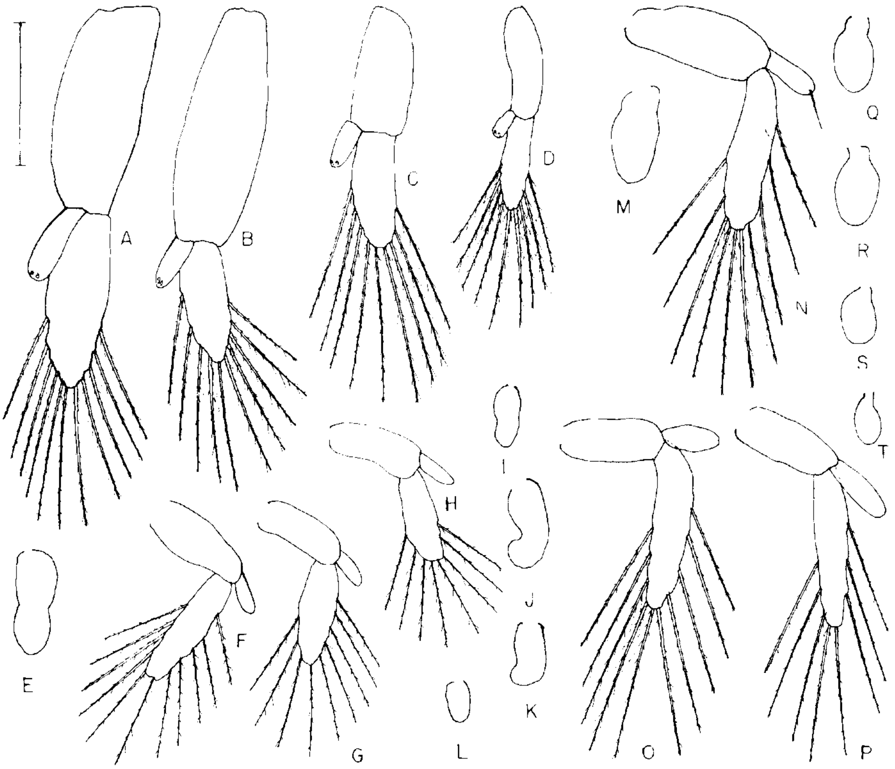

FIG. 11. *Pagurus ochotensis*: pleopods. A, Megalopa right second; B, Megalopa right third; C, Megalopa right fourth; D, Megalopa right fifth; E, Crab 1 left second; F, Crab 1 left third; G, Crab 1 left fourth; H, Crab 1 left fifth; I, Crab 1 right second; J, Crab 1 right third; K, Crab 1 right fourth; L, Crab 1 right fifth; M, Crab 2 left second; N, Crab 2 left third; O, Crab 2 left fourth; P, Crab 2 left fifth; Q, Crab 2 right second; R, Crab 2 right third; S, Crab 2 right fourth; T, Crab 2 right fifth. Scale equals 0·25 mm.

Tail fan (Fig. 2E). Telson with few short setae on dorsal surface as illustrated; posterior margin straight or slightly convex, setal formula 4+4; uropods biramous, slightly asymmetrical (left larger); protopods each with acute spine at posteromesial angle; exopods each with 9–14 corneous scales posterolaterally and several simple and plumose setae on lateral margins, mesial margins each with 3 or 4 long plumose setae; endopods small, each with 5–7 corneous scales and 2 or 3 short setae.

Antennule (Fig. 3E). Biramous, peduncle 3-segmented, over-reaching ocular peduncles, basal segment with row of stiff bristles at site of developing statocyst, few setae distally and ventrally, penultimate segment with few short setae distally, ultimate segment with scattered setae; exopod (upper ramus) 4-segmented, aesthetascs and setae progressing distally 0, 4 pairs, 2 pairs plus 1 long seta, 2 pairs plus 1 long and 3 or 4 short terminal setae; endopod (lower ramus) 2-segmented, basal segment with 3–5 short setae distally, terminal segment with 3–5 terminal setae and often 2 or 3 additional subterminal setae.

Antenna (Fig. 4E). With supernumerary segment clearly delineated; second segment with dorsolateral distal angle produced, terminating subacutely, dorsomesial distal angle with small spine; third segment with small spine at ventrodistal margin and few scattered setae, fourth and fifth segments also with few setae; acicle terminating subacutely; flagellum with 20–26 segments, setal formula highly variable, first article without setae, subsequent articles each usually with 1–7 short setae, terminal article with 4 or 5 short setae and 1 or 2 long terminal setae.

Mandible (Fig. 5E). Reduced, simple; palp indistinctly 2-segmented, terminal segment with 4–6 short stiff setae.

Maxillule (Fig. 6E). Endopod unsegmented, naked; coxal endite with 5 or 6 plumose marginal and frequently 1 or 2 submarginal setae; basal endite with 10–15 small marginal teeth, 3 or 4 long plumose marginal setae and 1 or 2 simple setae.

Maxilla (Fig. 7E). Endopod unsegmented, broadened basally and with 1 subterminal simple seta; coxal endite with 5–7 plumose setae on proximal lobe and 4–6 on distal lobe; basal endite with 10–12 plumose setae on proximal lobe and 11–15 on distal lobe; scaphognathite with 46–49 marginal plumose setae.

Maxilliped 1 (Fig. 8E). Exopod indistinctly 2-segmented, with 3 or 4 terminal simple setae and 1 short simple seta on mesial margin; endopod unsegmented, naked or with 1 short simple seta; coxal endite with 4–6 plumose setae, basal endite with 12–15 marginal plumose setae and few simple setae submarginally.

Maxilliped 2 (Fig. 9E). Exopod 2-segmented, proximal segment with 2 or 3 short setae on outer surface, distal segment usually with 6, occasionally only with 4, plumose setae; endopod 4-segmented, all segments with few setae as illustrated.

Maxilliped 3 (Fig. 10E). Exopod 2-segmented, distal segment usually with 6, occasionally only with 4, plumose setae, proximal segment with 1 long stiff seta medially and 2 or 3 short setae near mesial margin; endopod 5-segmented, ultimate and penultimate segments each with numerous setae, some serrate or denticulate, remaining segments with setae generally as illustrated, merus occasionally with small spinule at dorsodistal margin, ischium with crista dentata sometimes indicated by single small tooth.

Gills. Arthrobranch buds present on second to fourth pereopods.

Pereopods (Figs 1H, I and 12A, C, E, G, I, L). Chelipeds (Fig. 12A, C) unequal, right appreciably larger. Merus of right cheliped unarmed or with small spine at ventrolateral distal angle; carpus with 2 or 3 spines on dorsomesial margin; chela unarmed but occasionally with scattered low protuberances on dorsal surface, cutting

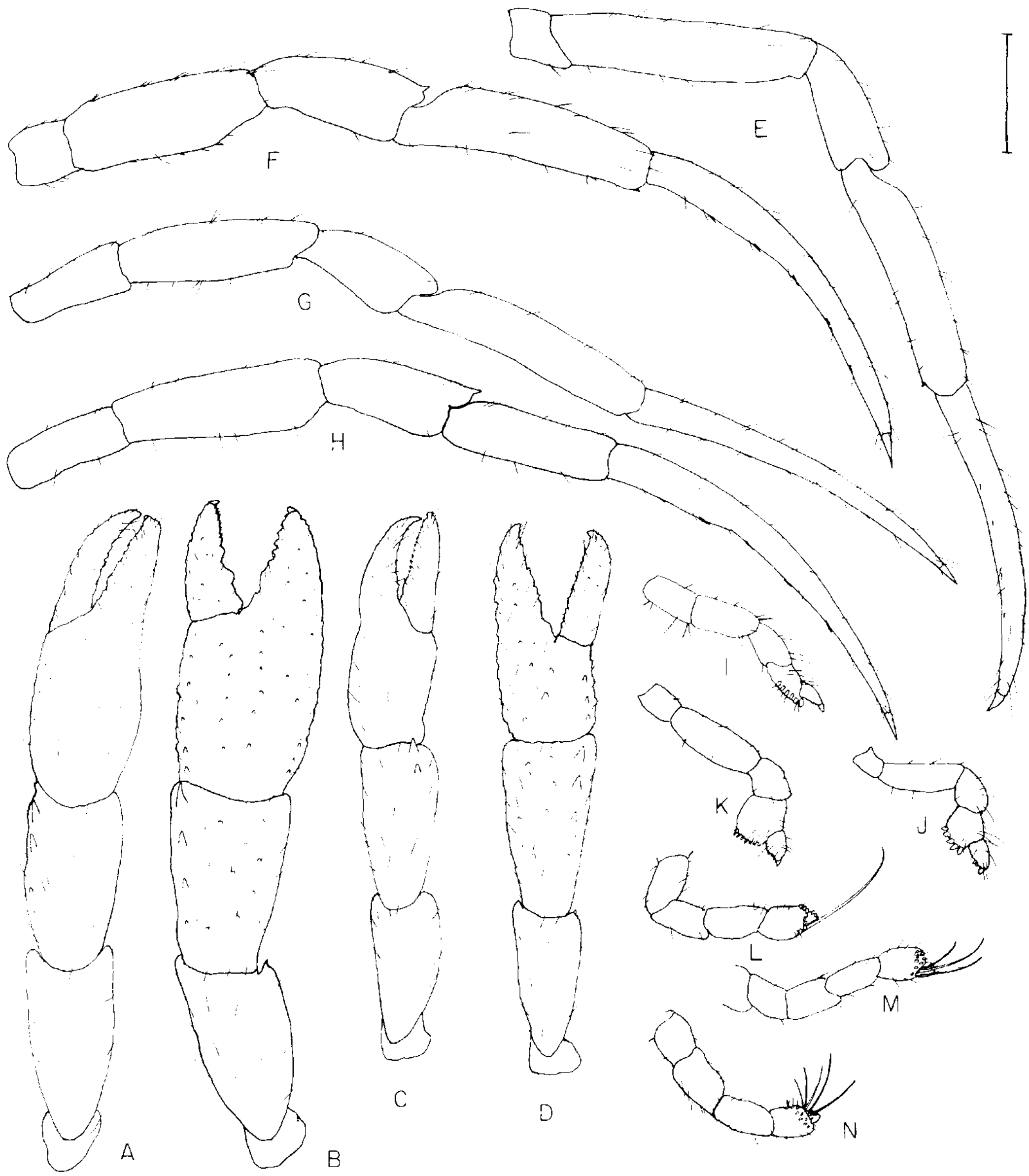

FIG. 12. *Pagurus ochotensis*: chelipeds and pereopods. A, Megalopa right cheliped; B, Crab 2 right cheliped; C, Megalopa left cheliped; D, Crab 2 left cheliped; E, Megalopa right second pereopod; F, Crab 2 right second pereopod; G, Megalopa right third pereopod; H, Crab 2 right third pereopod; I, Megalopa right fourth pereopod; J, Crab 1 right fourth pereopod; K, Crab 2 right fourth pereopod; L, Megalopa right fifth pereopod; M, Crab 1 right fifth pereopod; N, Crab 2 right fifth pereopod. Scale equals 0·5 mm.

edges of dactyl and fixed fingers with few small teeth; all segments with scattered setae. Merus and chela of left cheliped unarmed; carpus with 2 or occasionally 3 spines on dorsomesial margin; cutting edge of dactyl with several corneous teeth, cutting edge of fixed finger with 2 or 3 small calcareous teeth proximally. Ambulatory legs (Fig. 12E, G) with long dactyls, each with 4 or 5 widely spaced corneous spinules near ventral margin; propodi each with 1 or 2 small corneous spinules on ventral margins; all segments with scattered setae. Fourth pereopods (Figs 1H and 12I) with 2 or 3 corneous scales on dactyl at base of claw, 4–6 corneous scales on propodus. Fifth pereopods (Figs 1H and 12L) with 17–20 corneous scales on propodus and 3–5 on dactyl, propodus also with 1 very long curved seta and several short and moderately long setae; all segments with scattered short setae.

Colour. Transparent shield and posterior carapace flecked with red. Ocular peduncles translucent but with red spots, corneae black with yellow flecks. Antennular peduncles translucent but with red flecks, flagella light bluish-purple. Antennal flagella light yellow. Chelae and carpi of chelipeds translucent but with flecks of red, meri bluish-purple. Dactyls, propodi and carpi of ambulatory legs bluish-purple, meri translucent but usually with 1 or 2 red flecks.

First crab stage

Size. SL = 0·82–1·11 mm; CL = 1·53–2·10 mm; $n = 15$.

Duration. 20–48 days, $N = 14$.

Carapace (Fig. 1F). Shield usually slightly broader than long; rostrum broad, obtusely rounded, not over-reaching ocular acicles. Ocular peduncles shorter than shield, corneae slightly dilated. Ocular acicles with terminal spine and occasionally 1 or 2 dorsal setae.

Abdomen. Abdomen slightly twisted, segmentation marked only by transverse fibrils, with scattered setae on dorsal, lateral and ventral surfaces. Pleopods (Fig. 11E–L) of second abdominal somite both uniramous, reduced, right pleopods of somites 3–5 also uniramous and markedly reduced, left pleopods of somites 3–5 biramous, exopods with 10 or 11, 9 or 10, and 8 or 9 plumose setae respectively, endopods reduced, naked.

Telson and uropods (Fig. 2F). Telson with anterior lobes usually only faintly indicated by transverse suture, lateral margins with several long, stiff setae, dorsal and ventral surfaces with scattered setae more numerous ventrally, terminal margin deeply indented, almost V-shaped, armed with 3–5 spines on either side of midline; asymmetry of uropods more pronounced; protopods now with 1 or 2 spines at posteromesial angle; exopods with 14–20 corneous spines and numerous setae on posterolateral margins, mesial margins with few short setae; endopods each with 8 or 9 corneous spines and few setae.

Antennule (Fig. 3F). Larger than previous stage; exopod now 5-segmented, penultimate segment rarely with incomplete median suture, aesthetasc pairs now 0, 3, 3, 2, 2 plus 1 long seta on fourth segment and occasionally also on fifth, 1 long and 3 or 4 short terminal setae.

Antenna (Fig. 4F). Larger and with peduncular spines slightly more prominent, but generally unchanged from previous stage; flagellum now with 27–31 segments, setal formula still highly variable.

Mandible (Fig. 5F). Adult morphology more apparent; palp clearly 2-segmented or occasionally indistinctly 3-segmented, terminal segment with 10–13 short setae.

Maxillule (Fig. 6F). Endopod with 1 short seta on inner margin in proximal half, internal lobe provided with 1 long simple seta, external lobe somewhat produced; coxal endite with 12–15 marginal and 4–6 submarginal setae; basal endite with double row of small marginal teeth, 1 or 2 marginal setae and 4 or 5 submarginal setae.

Maxilla (Fig. 7F). Proximal lobe of coxal endite now with double row of plumose setae, distal lobe with few additional setae on surface, lobes of basal endite also with few additional setae; endoped unchanged; scaphognathite now with 45–52 marginal plumose setae.

Maxilliped 1 (Fig. 8F). Exopod 2-segmented, proximal segment with 6 plumose setae on lateral margin, 4 or 5 setae submarginally near mesial margin, distal segment with 5 or 6 plumose setae; endopod with 1 terminal setae and 1 or 2 setae submarginally near mesial margin; coxal endite with 5 or 6 marginal plumose setae and 2 or 3 submarginal simple or plumose setae; basal endite with marginal row of 15–21 plumose or denticulate setae and 2 submarginal rows of simple or weakly plumose setae.

Maxilliped 2 (Fig. 9F). Exopod with 6 plumose setae on distal segment, proximal segment with short, thick lateral seta and several setae on surface mesially; endopod incompletely 5-segmented, ultimate and penultimate segments each with few denticulate setae and several simple and/or plumose setae, proximal segments with scattered setae as illustrated.

Maxilliped 3 (Fig. 10F). Exopod with few additional setae on proximal lobe, routinely now with 6 terminal setae; endopod with crista dentata now clearly developing, usually consisting of 8–10 teeth and well-developed accessory tooth; dactyl and propodus each with numerous serrate and denticulate setae, carpus with few denticulate setae and scattered simple and plumose setae, merus with few setae and often small spine at dorsodistal margin.

Gills. Pleurobranch of fourth pereopod moderately well-developed; well-developed arthrobranchs on fourth and third pereopods, moderately well developed arthrobranchs on second pereopods and developing arthrobranchs on chelae, arthrobranch buds apparent on third maxillipeds.

Pereopods (Fig. 12J, M). Chelipeds little changed from previous stage. Carpi of second pereopods now occasionally with small spine at dorsodistal margin; dactyls of second and third now each with 5 corneous spinules near ventral margin. Fourth pereopods with 5–7 corneous scales on propodus and 2–4 on dactyl. Propodi of fifth pereopods now with 2 or 3 long curved setae and several shorter setae.

Colour. Shield now red marginally. Ocular peduncles light orange, corneae yellow. Antennular peduncles now light orange. Antennal flagella orange. Chelae or chelipeds white, carpi and meri whitish and with patches of red. Dactyls of ambulatory legs, still bluish-purple, propodi, carpi and meri with streaks of red.

Second crab stage

Size. $SL = 1{\cdot}02–1{\cdot}20$ mm; $CL = 1{\cdot}52–2{\cdot}13$ mm; $n = 12$.

Duration. 21 days for juvenile surviving to crab stage 3; $N = 1$.

Carapace (Fig. 1G). Shield now usually as long as broad, lateral projections not yet delineated; rostrum narrower than in previous stage, still terminally rounded. Ocular peduncles now two-thirds to three-quarter shield length; cornea with little if any dilation.

Abdomen. Noticeably twisted; segmentation still indicated by transverse fibrils. Pleopods (Fig. 11M–T) with both right and left of second abdominal somite generally unchanged from previous stage, right pleopods of somites 3–5 rudimentary, left pleopod 3 with 10–12 plumose setae on well-developed exopod, often 1 simple seta on endopod, left pleopods 4 and 5 with 10 or 11 and 9 or 10 plumose setae respectively, endopods naked.

Telson and uropods (Fig. 2G). Transverse suture of telson now more distinctly discernible; anterior lobes with 2 or 3 long marginal setae and few short setae on dorsal and ventral surfaces; posterior lobes with 2 or 3 long and 1 or 2 short setae on lateral margins, dorsal and ventral surfaces with scattered short setae, more numerous on ventral surface, terminal margin strongly concave or V-shaped, but without medium cleft, 4 small spines marginally on either side of midline. Uropods increasingly asymmetrical; protopods now with 2 or 3 spines at dorsomesial angles; left exopod with usually single row of 20–23 corneous scales and few setae on posterolateral margin, right with double row of 7–14 corneous scales and numerous setae, mesial margins with several setae; endopods now 8–13 corneous scales.

Antennule (Fig. 3G). Peduncle longer and segments with few additional scattered setae; exopod usually still 5-segmented, occasionally 7-segmented, aesthetascs formula 3, 3, 2, 2 or 3, 3, 3, 2, antipenultimate often with additional 2 or 3 short setae near distal margin, penultimate segment also with 2–4 short setae distally, ultimate segment with 1 long curved setae and 4–6 shorter terminal setae, 1 or 2 additional short setae on ventral surface; endopod 3- or 4-segmented, each segment with several short setae distally, ultimate segment also still with 1 long terminal seta.

Antenna (Fig. 4G). Peduncle increased in size and with ventral lobe of first segment better developed; flagellum with 25–27 segments, setal formula still highly variable.

Mandible (Fig. 5G). Larger but generally as in previous stage; palp still 2-segmented or indistinctly 3-segmented, distal segment with 11–14 short setae, frequently in double row distally.

Maxillule (Fig. 6G). Endopod with 1 or less frequently 2 long setae on internal lobe, external lobe better developed; coxal endite with 12–15 marginal setae, basal endite with 19–25 marginal denticulate teeth, 2–5 simple marginal setae and 4–7 submarginal short setae.

Maxilla (Fig. 7G). Larger than in previous stage; endopod unchanged; endites with few additional setae; scaphognathite with 51–56 plumose setae.

Maxilliped 1 (Fig. 8G). Exopod still 2-segmented, basal segment now with 6–10 plumose setae on lateral margin, few setae on surface and on mesial margin, distal segment still with 5 or 6 plumose setae; endopod with 1 or 2 additional setae on mesial margin; coxal and basal endites with 9 or 10 and 21–23 setae, respectively.

Maxilliped 2 (Fig. 9G). Flagellum of exopod now with 7 or 8 plumose setae; endopod clearly 5-segmented, setation as illustrated.

Maxilliped 3 (Fig. 10G). Flagellum of exopod now with 8 plumose setae; endopod with 9–12 teeth on crista dentata, merus with small spine at dorso-distal margin, setation as illustrated.

Gills. Increased in size and complexity.

Pereopods (Fig. 12B, D, F, H, K, N). Right cheliped now routinely with spine at ventrolateral distal angle of merus; carpus with 3 or 4 spines on dorsomesial margin and scattered small spines or tubercles on dorsal surface; chela with few small spines on dorsomesial and dorsolateral margins, dorsal surface with 2 irregular small spinules or tubercles in midline and few scattered on surface of fixed finger; armature of cutting edges of dactyl and fixed finger stronger. Left cheliped with small spine at ventromesial distal angle of merus; carpus with row of 3 or 4 spines on dorsomesial margin and few scattered spinules or tubercles on dorsal surface; chela with row of small spines on ventromesial margin and scattered small spines or tubercles on dorsal surface; cutting edge of dactyl with row of corneous teeth, cutting edge of fixed finger with row of small weakly calcified teeth. Ambulatory legs each now with small spine at dorsodistal angle of carpus; propodi with 2 or 3 corneous spinules ventrally; dactyls still each with 5 corneous spinules near ventral margin. Propodi and dactyls of fourth pereopods now with few more corneous scales. Propodi of fifth pereopods now with 5 or 6 long curved setae.

Results

Very few differences in developmental morphology were found between the Japanese and Puget Sound populations of *P. ochotensis*. These findings are in sharp contrast to the disparities reported recently in the larval development of hermit crabs from different populations and/or year classes (e.g. Tirmizi and Siddiqui, 1980; Konishi and Quintana, 1988; McLaughlin *et al.*, 1988; Siddiqui *et al.*, 1991). Perhaps the most significant difference between larvae of the two populations is the presence of a small posterolateral spine on the sixth abdominal somite in stages III and IV in the Puget Sound larvae that is not mentioned for the Japanese larvae. Other than minor variations in setation the only other differences observed are the length ratio of the antennal endopod to scaphocerite and the number of aesthetascs of the antennule in the later zoeal and megalopal stages (Table 1). In the majority of earlier larval studies antennal proportions are given only in terms of the length/width ratio of the scaphocerite, as the breadth of this structure does appear to have phylogenetic significance (e.g. MacDonald *et al.*, 1957; Roberts, 1970). Quintana and Iwata (1987) illustrate antennal development through all stages, but do not give actual ratios. It is probable that intraspecific variation accounts for the differences indicated. Intraspecific variation in aesthetascs has been reported for several pagurid species (e.g. Nyblade, 1970; MacMillan, 1971) and has been found in the juvenile stages of our Puget Sound material; thus we assume that the differences observed between the two populations similarly reflect such variation.

A comparison of stage duration and larval survival between the Japanese population and the Puget Sound population (Fig. 13) shows substantially greater differences. In the Japanese study the total time required to complete the four zoeal stages was only 20–24 days. Puget Sound larvae began moulting to megalopae on the 26th day and with 1 aberrant individual that ultimately died in stage IV, the last several had moulted by the 39th day. Temperature differences alone could account for the more rapid development of the Japanese larvae since they were reared at 18°C. By contrast, our larvae were reared at 12 ± 1°C. Quintana and Iwata (1988) reported similar delays in moulting in a second *Pagurus* species raised at only 13–14°C. However, significant differences in stage durations have been found among simultaneously hatched larvae from different females within a single population (Bidle and McLaughlin, 1992). Quintana and Iwata (1988) reported approximately 40% survival to the megalopal stage; no megalopae moulted to the first crab stage. In our study only about 25% reached the megalopal stage; however, most of these moulted to crab stage 1 and several reached crab stage 2. A single individual moulted to crab stage 3 and survived for 33 days.

The only published account of juvenile development in species assigned to the *bernhardus* group is that of *Pagurus bernhardus* (Linnaeus) by Carvacho (1988). Although specific differences can be detected (e.g. initial development of the lateral

Table 1. Differences in zoeal and megalopal development in *Pagurus ochotensis* from Puget Sound (PS) and Japan.†

Character	Stage I		Stage II		Stage III		Stage IV		Stage M	
	PS	Japan	PS	Japan	PS	Japan	PS	Japan	PS	Japan
Abdominal somite 6 posterolateral spine	—	—	—		present	absent	present	absent	—	—
Antennule aesthetascs (paired)	2	2	2	2	3 or 4+2	4+2	3+2+2+1·5−2	4+2+2+2	4, 2, 2	5, 4, 3
Antenna endopod/exopod	approximately equal	approximately equal	slightly longer	approximately 1/5 longer	approximately 1/8 longer	approximately 1/4 longer	approximately 1/4 longer	approximately 1/3 longer	20–25-segment flagellum	21-segment flagellum
Maxillule										
Endopod	1 or 2, 1, 3	2, 1, 3	1 or 2, 1, 3	2, 1, 3	1 or 2, 1, 3	2, 1, 3	1 or 2, 1, 3	2, 1, 3	0	0
Endite (c)	5+2	6+1	5+2	6+1	5+2	6+1	7+1	7+1	5	8
Endite (b)	2(t)	2(t), 1(s)	4(t), 2(s)	4(t), 2(s)	4(t), 2(s)	4(t), 2(s)	6(t), 2(s)	6(t), 2(s)	12(t), 5(s)	14(t), 7(s)
Maxilla										
Endite (c)	5–6+1, 3+1	6+1, 3+1	5–6+1, 3+1	6+1, 3+1	5+1, 3+1	6+1, 3+1	6+1, 3+1	6+1, 3+1	5–6, 5	5, 5
Endite (b)	4+1, 3+1	3+1, 3+1	4+1, 3+1	4+1, 3+1	4+1, 3+1	4+1, 3+1	4+1, 3+1	4+1, 3+1	10–11, 11–13	10, 12
Scaphognath.	5	5	6–9	7	9–12	11	12–16	15	46–49	40–41
MXP1 basis	9–10	9	9–10	10	9–10	10	9–10	10	—	—
UROPOD exopod				—	4–4+1	4+1	4–4+1	5	9–12+7–8	12–13+7–8

† Derived from text and/or figures (Quintana and Iwata, 1987). t, Teeth; s, setae; —, not applicable or not yet developed.

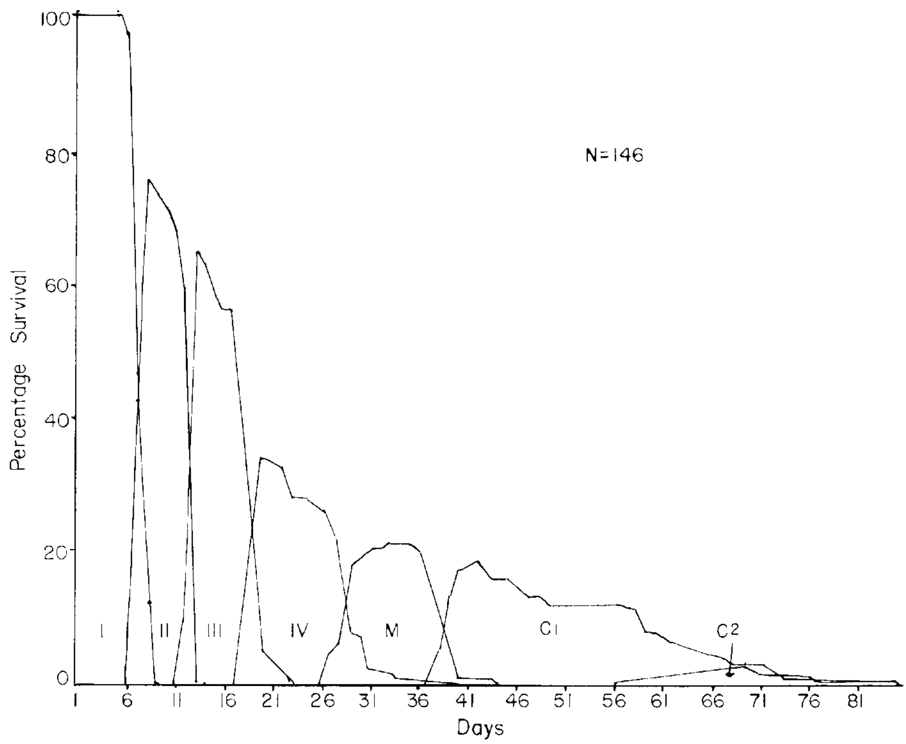

FIG. 13. Percentage survival of *Pagurus ochotensis* from Puget Sound reared under laboratory conditions. N = number of zoeae reared individually.

projections of the shield in crab stage 1 in *P. bernhardus*) the pattern of development in most characters appears to be quite similar, and in contrast to the early juvenile stages of another northeastern Pacific species, *P. kennerlyi* (Stimpson) as described by McLaughlin *et al.* (1989). In the first crab stage the antennal flagellum consists of 21 or 22 (rarely 18–24) articles in *P. bernhardus*, 29–31 in *P. ochotensis*, but only 16 in *P. kennerlyi*. Internal and external lobes of the maxillule are developed more weakly in the latter species than in either of the two *bernhardus* group species. Number of marginal setae on the scaphognathite exceeds 40 in both *P. bernhardus* (45) and *P. ochotensis* (46–48). Only 32–38 are reported for *P. kennerlyi*. Perhaps the most striking difference is seen the pleopods. Transition from megalopa to adult is accompanied by the loss of pleopods on the right side of the abdomen in all but those species having paired pleopods and/or gonopods in adults. This loss is not uniform and is quite possibly of phylogenetic significance (see McLaughlin *et al.* (1989) for review). In the first crab stage of both *P. bernhardus* and *P. ochotensis* the left pleopod of the second abdominal somite is markedly reduced. In contrast, the left second of *P. kennerlyi*, albeit now uniramous, still is provided with several terminal setae on the 2-segmented exopod. Carvacho (1988) makes no mention of right-side pleopods in *P. bernhardus*, so presumably they are vestigial or absent at this stage. Rudimentary right second through fifth pleopods are present in *P. ochotensis* in both the first and second crab stages. In contrast, the right pleopods are uniramous and reduced but still appreciably better developed in crab stage 1 in *P. kennerlyi*; however, they are vestigial or entirely absent in crab stage 2. In the single individual of *P. ochotensis* that moulted to crab stage 3, vestigial pleopods are still visible on both sides of the second somite and on somites 3–5 on the right.

Remarks

Characters by which two primary larval groups of hermit crabs could be distinguished were proposed by MacDonald *et al.* (1957). As additional larval data became available a third group (c.f. Pike and Williamson, 1960) and then a fourth group (c.f. Roberts, 1970) were added. Character overlap among the groups was sufficiently great that, with one exception, no single character could be used to define a group. That exception pertained to group C in which the fourth telsonal process was articulated with the telson in zoeal stages III and IV. In the other three groups this process reportedly was always fused. Quintana and Iwata (1987) assigned *P. ochotensis* to larval group A, but called attention to the presumably distinctive character in *P. ochotensis* of an articulated fourth telsonal process in all zoeal stages. However, occurrence of an articulated telson in the later zoeal stages is not unique to this species. As Roberts (1973), Gore and Scotto (1983), and McLaughlin *et al.* (1989) have pointed out, an articulated fourth process also occurs is several other *Pagurus* species that have been assigned to larval group A. Perhaps more significant is the apparent articulation of the first telsonal process in all zoeal stages in both the Japanese and Puget Sound populations of *P. ochotensis*. A first telsonal process fused to the telson is typical of larvae of the Paguridae (Dechancé, 1962). In fact Gore and Scotto (1983) cited an articulated first telsonal process as one of the characters by which the larvae of *Phimochirus holthuisi* (Provenzano) could be distinguished from other pagurid larvae. However, a similar condition is reported in *Pagurus armatus* (Dana) and *P. bernhardus* by McLaughlin and Gore (1992), and the implication of articulation of this process in *P. caurinus* Hart is noted by Bidle and McLaughlin (1992).

Larval development has played a significant role in distinguishing among closely related adult taxa. Lebour (1930), for example, described a new species of the shrimp genus *Caridion* after finding its development significantly different from a species with which it had formerly been confounded. MacMillan (1971) compared the larval development of *Pagurus samuelis* (Stimpson) from California with the development of the presumably same species from Japan and found sufficient differences to suggest that two species were involved. Subsequently, McLaughlin (1976) redescribed the Japanese taxon as *Pagurus geminus* McLaughlin. Konishi and Quintana (1988) compared laboratory-reared larvae of *P. middendorffii* Brandt with larvae presumed to be of that species described by Kurata (1964) from the plankton. Differences were such that Konishi and Quintana (1988) concluded that two distinct species were involved. In contrast, few, if any, differences, at least in setal morphology, have been observed among certain closely related brachyuran species (e.g. Christiansen, 1973; Clark, 1983, 1984). The comparison made by McLaughlin and Gore (1992) among the larvae and megalopae of four species of the *bernhardus* group showed minor differences in setal formulae, and no single character could be used to distinguish among the larvae. However, when a suite of characters (32 per larval stage) was considered, interspecific differences were confirmed. No such differences could be found between the Japanese and eastern North Pacific populations of *P. ochotensis*. These nearly identical morphological patterns provide supporting evidence that McLaughlin's proposition (1974) of the synonymy of *P. alaskensis* (northeastern Pacific) and *P. ochotensis* (Japan) was correct.

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