DESCRIPTION OF LARVAE OF THE NORTHERN SHRIMP, *PANDALUS BOREALIS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

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ABSTRACT

Northern shrimp, *Pandalus borealis*, were reared in situ in Kachemak Bay, Alaska, from Stage I (first zoeal) through Stage VIII (second juvenile). Each of the six larval stages and first juvenile stage is described and illustrated, and a brief description is given for the second juvenile stage. Apparently larvae of *P. borealis* in Alaska waters have at least one less stage than larvae of *P. borealis* in either British Columbia, Greenland, or Japan waters. Of the known larvae of the North Pacific Ocean, larvae of *P. borealis* are most similar morphologically to larvae of *P. goniurus* but are separable from them by being slightly larger in size and, in zoeal Stages I-III, by bearing more setae on certain appendages, particularly the antennal scale and certain mouth parts. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*. The criterion of the lack of an outer seta on the maxillule for distinguishing zoeae of *Pandalus* from certain other Caridea is shown to be invalid.

In 1972 the National Marine Fisheries Service began studies on the early life history of pandalid shrimp in Alaska waters with the initial objective of describing in detail laboratory-reared larvae of each pandalid species previously unverified. Two previous reports have described larvae of *Pandalus hypsinotus* Brandt reared in the laboratory (Haynes 1976) and *P. goniurus* Stimpson reared in situ in Kachemak Bay, Alaska (Haynes 1978). This report describes and illustrates each of the six larval stages and the first juvenile stage of northern shrimp, *P. borealis* Krøyer, and compares the stages obtained from rearing in situ with descriptions of pandalid shrimp larvae given by other authors. A brief description of the second juvenile stage is included.

MATERIALS AND METHODS

Rearing techniques were identical in all respects to those described in an earlier report on *P. goniurus* (Haynes 1978). Briefly, the technique consists of obtaining Stage I larvae of known parentage in the laboratory, then rearing the larvae in flasks submerged at sea. Larvae from plankton were also reared in flasks at sea in an identical manner beginning with Stage I. Larvae reared in flasks were compared with larvae from plankton for verification of sequence of stage and larval morphology.

Because the paired appendages of the larvae are symmetrical, only one member (the left) is figured. An exception is the mandibles which are drawn in pairs. Orientation of surface of appendages in the figures is given in the figure legends. The figures of the appendages are in part schematic and represent typical setal counts. Variability in setation or segmentation of paired appendages, such as the difference in number of carpal joints between the left and right second pereopods in the megalopa, is mentioned in the text. Carapace length refers to the straight-line distance from posterior margin of orbit to middorsal posterior margin of carapace. Total body length refers to the distance from tip of rostrum to posterior margin of telson, not including telson spines. Terminology, methods of measuring, techniques of illustration, and nomenclature of gills and appendages follow Haynes (1976). Comparison of larvae from plankton with cast skins from flasks was facilitated by first clearing the larvae in 10% KOH. For clarity, setules on setae are usually omitted but spinulose setae are shown.

STAGE I ZOEA

Mean total length of Stage I (Figure 1A) 6.7 mm (range 6.5-7.3 mm; 25 specimens). Live specimens characterized by orange color; conspicuous chromatophores throughout cephalothorax re-

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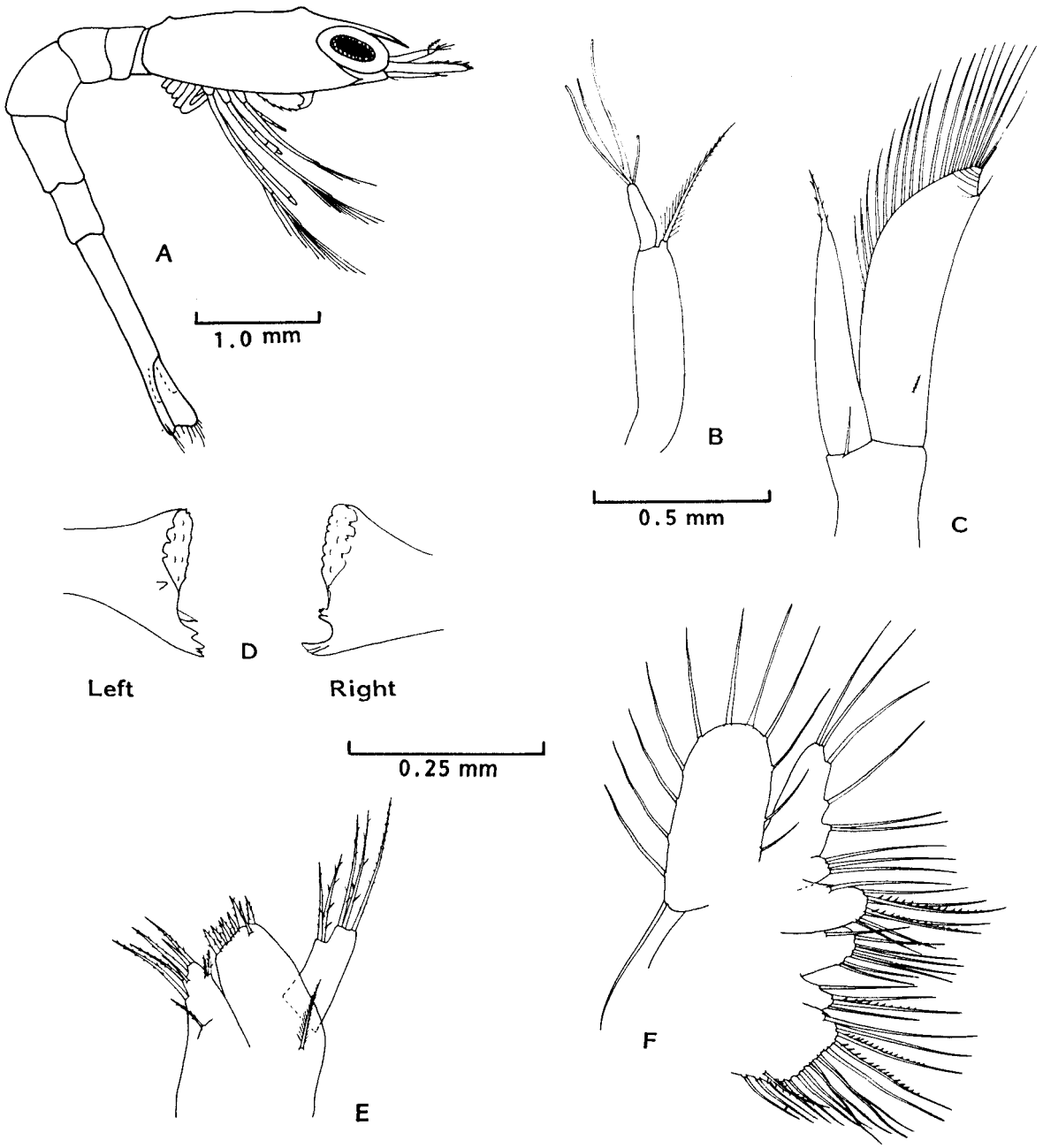
gion, especially in mouth parts; large chromatophore near tip of antennal scale, at base of telson, and at front of eye; smaller but distinct chromatophores on maxillipeds; ventral surface of each abdominal somite tinged orange; faint greenish hue at base of pereopods. Rostrum slender, spiniform, without teeth, about one-third length of carapace, projecting horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller, rounded prominence near posterior edge. These two prominences occur in all zoeal stages. Pterygostomian spines present but usually hidden by sessile eyes. Three or four mi-



nute spinules along ventral margin of carapace immediately posterior to pterygostomian spine (spinules not shown in Figure 1A). These spinules usually occur in all zoeal stages but may vary in number from two to five not only between stages but among individuals within a given stage.

ANTENNULE (Figure 1B).—First antenna, or antennule, consists of simple unsegmented tubular basal portion with heavily plumose seta terminally and distal conical projection with four aesthetascs: one long, one short, and two of intermediate length.

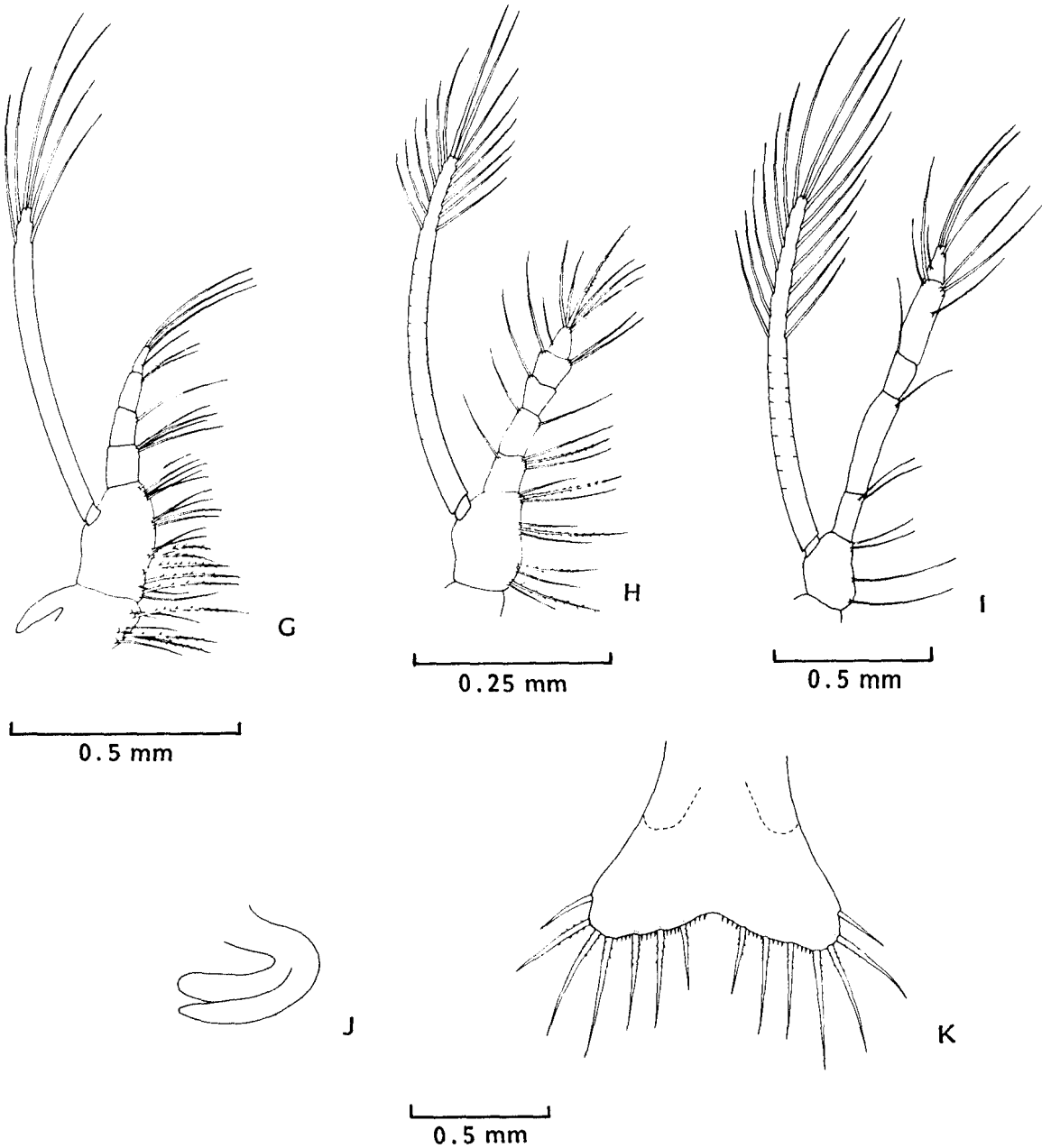


FIGURE 1.—Stage I zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, second pereopod, lateral; K, telson, dorsal.

ANTENNA (Figure 1C).—Second antenna, or antenna, consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, and tipped by spinulose spine. Antennal scale distally divided into six joints (the two proximal joints incomplete) and fringed with 19 heavily plumose setae along terminal and inner margins; small seta occurs on outer margin at base of joints and another proximally near outer margin. Protopodite bears spinous seta at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 1D).—Without palps in this and all succeeding zoeal stages. Incisor process of left mandible bears four teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) whereas right mandible bears two immobile premolar denticles. Truncated molar process of left mandible bears subterminal tooth that occurs throughout all zoeal stages.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and endopodite. Coxopodite (proximal lobe) bears stout seta near base, and eight spinulose spines terminally. Basipodite (median lobe) bears nine spinulose spines on terminal margin and large setose seta proximally. Endopodite originates from lateral margin of basipodite; bears three terminal and two subterminal setae, three of them sparsely plumose and remaining two spinulose.

MAXILLA (Figure 1F).—Second maxilla, or maxilla, bears platelike exopodite (scaphognathite) with 11 long, evenly spaced plumose setae along outer margin and one slightly longer and thicker seta at the slightly expanded proximal end. Endopodite gives indication of four partly fused segments and bears nine large plumose setae. Coxopodite and basipodite bilobed. Coxopodite bears 21 setae, 4 on distal lobe and 17 on proximal lobe. Basipodite bears eight setae on each lobe. Five setae, three on coxopodite (one on distal lobe and two on proximal lobe) and two on distal lobe of basipodite, bear row of little spines along entire length. An additional seta on proximal lobe of coxopodite is especially spinulose.

FIRST MAXILLIPED (Figure 1G).—Most heavily setose of natatory appendages. Protopodite fully segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment, 9 of them spinulose. Endopodite distinctly four-segmented; setation formula 4, 2, 1, 4. Exopodite a longer slender ramus segmented at base; bears two terminal and three or four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite bisegmented; distal segment bears 10 sparsely plumose setae, no setae evident on proximal segment. Endopodite distinctly five-segmented, fourth segment expanded laterally; setation formula 7, 3, 1, 2, 4. A seta on segments 1 and 5 of endopodite and three setae on protopodite especially spinulose. Exopodite with 2 terminal and 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five-segmented; nearly as long as exopodite; setation formula 4, 5, 1, 1, 2. Exopodite with 2 terminal and 14 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3.

PLEOPODS.—Absent.

TELSON (Figure 1K).—Not segmented from sixth abdominal somite; slightly emarginate posteriorly; bears 7 + 7 densely plumose setae. Fourth pair of setae longest, about one-half width of telson. Minute spinules at base of each seta. Larger spinules along terminal margin between bases of four inner pairs and on setae themselves but rarely on seventh pair. Uropods visible and enclosed. No anal spine.

STAGE II ZOEA

Mean total length of Stage II (Figure 2A) 7.5 mm (range 6.7-8.2 mm; 25 specimens). Chromatophore color and pattern essentially identical to Stage I, except chromatophores larger and color more pronounced, especially in mouth parts. Rostrum still without teeth and not curved downward as sometimes in Stage I. Carapace with prominent supraorbital spine and clearly visible antennal and pterygostomian spines. These three

spines persist through all remaining zoeal stages. Epipodite of first maxilliped slightly larger than in Stage I but still not bilobed; pleurobranchiae present as primordial buds.

ANTENNULE (Figure 2B).—Three-segmented; bears large outer and smaller inner flagellum on terminal margin. Flagella not segmented. Inner flagellum conical, bears one long spine terminally. Outer flagellum bears two groups of aesthetascs: one group terminally consisting of eight aesthetascs, two of them larger than remaining six, and a pair of aesthetascs on inner margin. A small budlike projection (not shown in Figure 2B)

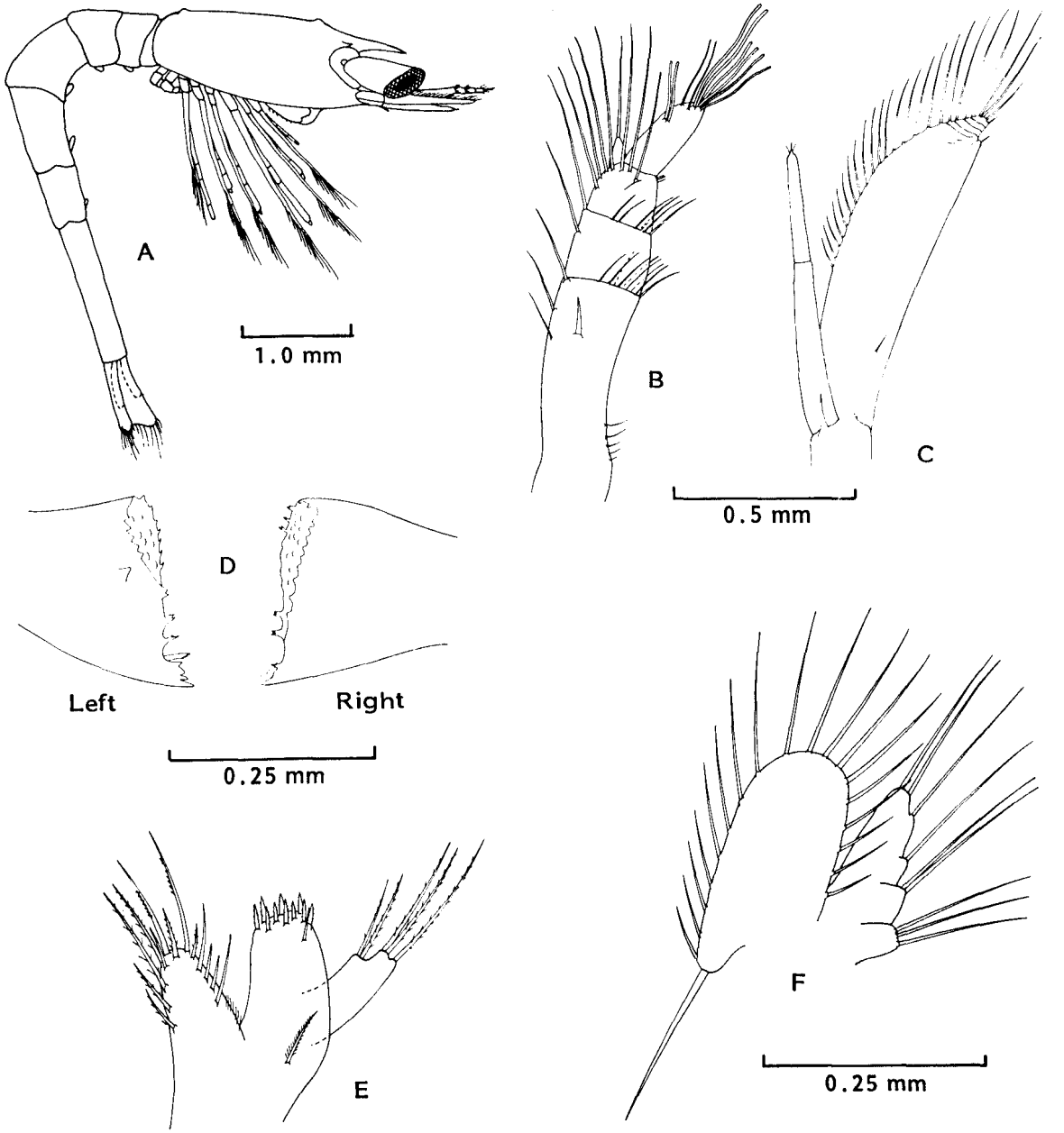


FIGURE 2.—Stage II zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla (exopodite and endopodite), dorsal.

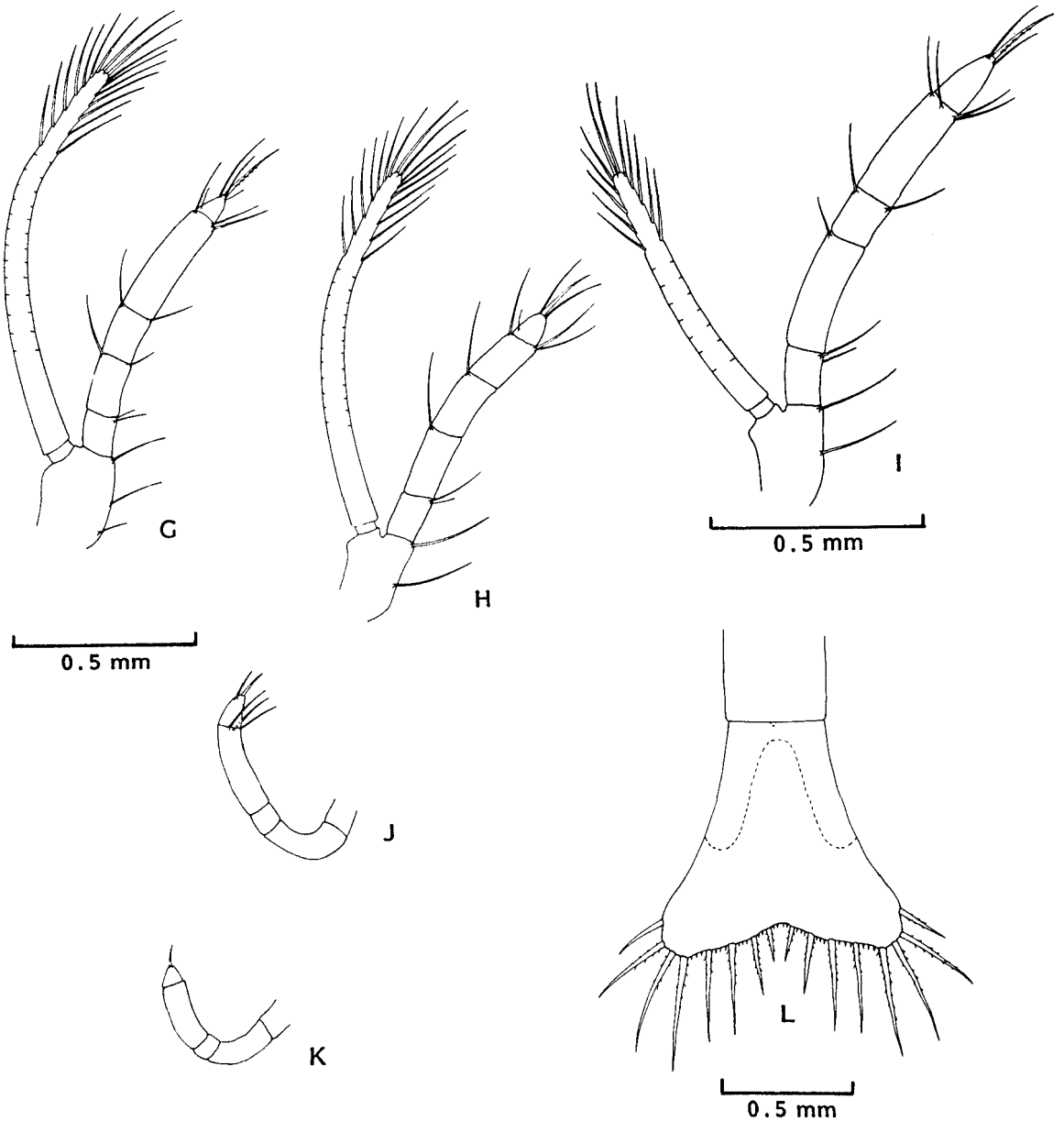


FIGURE 2.—Stage II zoea of *Pandalus borealis*: G, first pereopod, lateral; H, second pereopod, lateral; I, third pereopod, lateral; J, fourth pereopod, lateral; K, fifth pereopod, lateral; L, telson, dorsal.

originates at base of flagella and bears five simple setae. Proximal segment of antennule usually bears five setae laterally near slightly expanded base, three plumose setae laterally and distally, about nine dorsally curving but smaller plumose setae around distal joint, and large spine projecting slightly downward from ventral surface. Second segment bears two plumose setae laterally and about six dorsally curving plumose setae around distal joint. Third segment bears seven plumose setae laterally, about four of them originating ventrally, and three simple setae laterally at base of outer flagellum.

ANTENNA (Figure 2C).—Flagellum two-segmented, still shorter than scale, styliform, and tipped by two small simple setae and short spine. Antennal scale fringed with 25 or 26 long, thin, plumose setae along terminal and inner margins; still has six joints distally but only the three most distal joints complete. Protopodite bears minute spine at base of scale in addition to conspicuous spine at base of flagellum.

MANDIBLES (Figure 2D).—More massive than in Stage I. Incisor processes of both mandibles bear additional tooth. Both mandibles bear additional denticles and molar processes more developed. Lacinia mobilis of left mandible consists of single spinous denticle. Curved lip of truncated end of molar process of right mandible more developed than in Stage I.

MAXILLULE (Figure 2E).—Coxopodite bears 12-15 spines and row of fine hairs proximally; spinules on two of the terminal spines of coxopodite resemble a row of teeth. Basipodite and endopodite essentially unchanged from Stage I, except basipodite bears two additional spinulose spines.

MAXILLA (Figure 2F, exopodite and endopodite).—Exopodite similar in shape to Stage I except more distinctly expanded proximally; bears 17-19 marginal plumose setae in addition to plumose seta at proximal end. Endopodite unchanged from Stage I. Coxopodite bears 3 setae on distal lobe and 17-19 on proximal lobe. Each lobe of basipodite bears additional seta.

MAXILLIPEDS.—Essentially identical to Stage I but bear additional setae as follows. On first maxilliped, protopodite bears 8-10 setae on proximal segment and 19-21 on distal segment; endopodite bears 4, rarely 5, setae on proximal segment; exopodite bears 7 or 8 natatory setae rather than 5 or 6 as in Stage I; no change in epipodite. On second maxilliped, protopodite bears seta on proximal segment and 8-10 setae on distal segment; exopodite bears 14 lateral natatory setae in addition to the 2 terminal setae. On third maxilliped, endopodite bears additional seta terminally on dactylopodite, 2 additional setae on propodite, and additional seta on carpopodite, setation formula 5, 7, 3, 1, 2; exopodite bears 16 lateral natatory setae in addition to 2 terminal setae. No gill buds on second or third maxillipeds.

FIRST PEREOPOD (Figure 2G).—Protopodite bears three setae. Endopodite functionally developed; five-segmented, terminating in simple conical dactylopodite; setation formula 5, 3, 2, 2, 2. Exopodite, longest among pereopods, bears 2 terminal and 14 lateral natatory setae.

SECOND PEREOPOD (Figure 2H).—Protopodite bears two setae. Endopodite similar to first pereopod except shorter; setation formula 4, 3, 1, 1, 2. Exopodite bears 2 terminal and 13 or 14 lateral natatory setae.

THIRD PEREOPOD (Figure 2I).—Protopodite bears two setae. Endopodite one-fourth to one-third longer than exopodite; dactylopodite slightly longer than in first two pereopods; setation formula 3, 4, 2, 1, 2. Exopodite noticeably shorter than exopodites of first and second pereopods and bears 2 terminal and 9 or 10 lateral natatory setae.

FOURTH PEREOPOD (Figure 2J).—Endopodite five-segmented but still poorly developed and directed under body somewhat anteriorly as in Stage I (Figure 2A); dactylopodite and propodite bear two setae and three setae, respectively. No exopodite.

FIFTH PEREOPOD (Figure 2K).—Similar to fourth pereopod but shorter and dactylopodite tipped with single seta. No exopodite.

PLEOPODS (Figure 2A).—Present as distinct buds.

TELSON (Figure 2L).—Similar in shape to Stage I but distinctly jointed from sixth abdominal somite; bears 8 + 8 densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

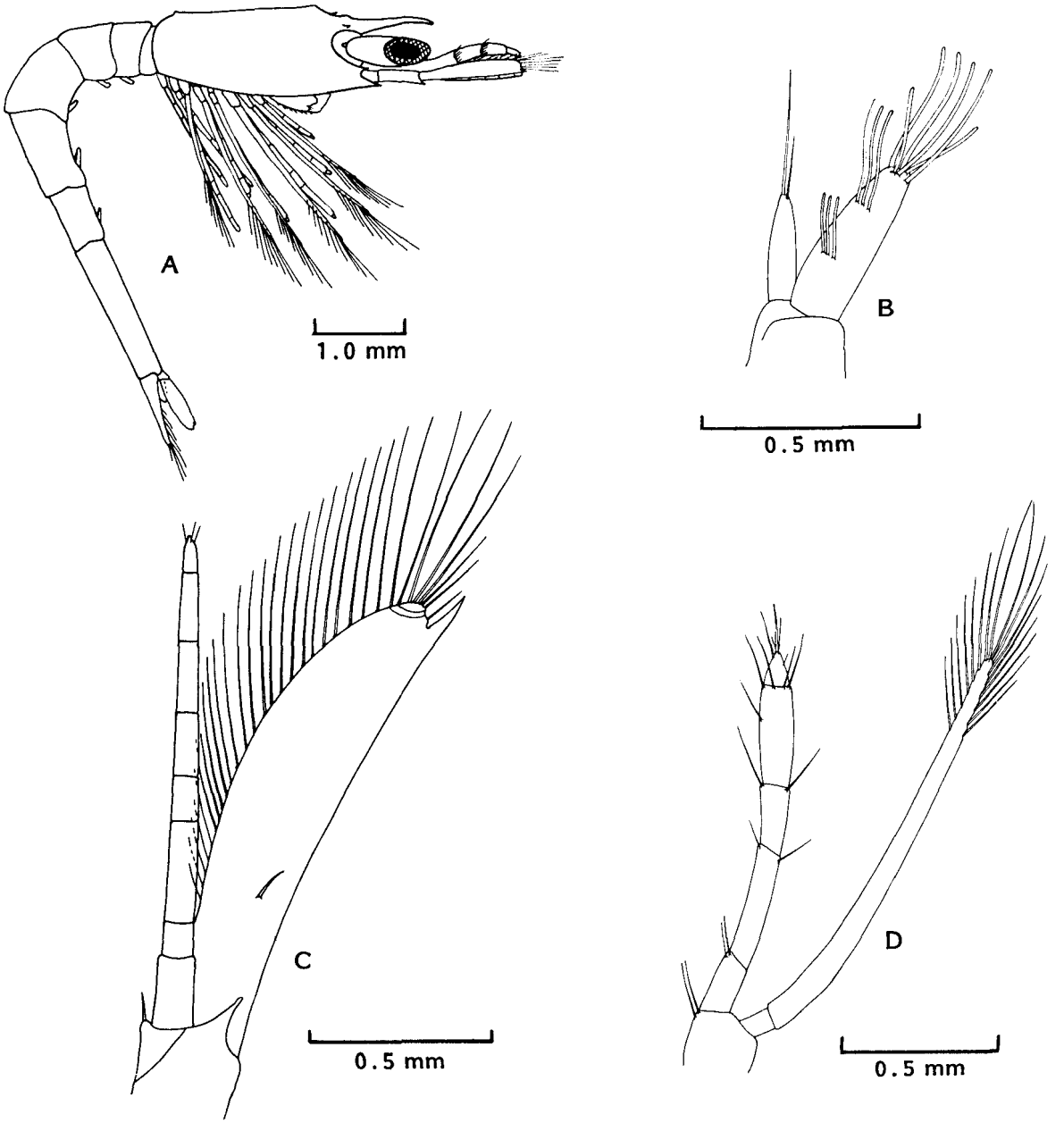
Mean total length of Stage III 9.5 mm (range 9.0-10.0 mm; 10 specimens). From this stage on, zoeae gradually become more orange and color pattern not useful in identifying a given stage. Rostrum (Figure 3A) projects horizontally but curves slightly downward at tip; bears one or two teeth at base. Epipodite of first maxilliped bilobed; pleurobranchiae present as small buds.

ANTENNULE (Figure 3B, inner and outer

flagella).—Flagella not segmented. Inner flagellum about one-half length of outer flagellum, bearing stiff seta at base of terminal spine. Outer flagellum bears four long and two shorter aesthetascs terminally and two groups of three aesthetascs each proximally.

ANTENNA (Figure 3C).—Flagellum eight-segmented, about equal in length to scale, tipped by three short setae and remnant of terminal spine. Antennal scale narrower than in Stage II and fringed with about 30 plumose setae; two complete joints at tip. Spine on protopodite at base of scale considerably larger than in Stage II.

MAXILLIPEDS.—Change in form and setation of maxillipeds from Stage III on is slight and consists primarily of second maxilliped becoming



curved as in adult and its propodite slightly widened, third maxilliped becoming shaped as in adult, and natatory setae on exopodites of second and third maxillipeds increasing in number to usually 20 in Stage V.

FIRST PEREOPOD (Figure 3D).—Has begun to acquire adult shape, particularly in widened propodite and carpopodite segments.

SECOND PEREOPOD (Figure 3E).—Similar to Stage II except distal joint of propodite projects slightly anteriorly.

THIRD, FOURTH (Figure 3F), AND FIFTH PEREOPODS.—Endopodites similar; like first pereopod have begun to acquire adult shape, especially in lengthened dactylopodite and widened propodite. Ischiopodite articulates somewhat laterally with meropodite.

PLEOPODS (Figure 3G, second pleopod).—Bilobed, unsegmented, and without setae.

TELSON (Figure 3H).—Endopodite not fully developed; about one-third length of exopodite and bearing several setae along lateral and posterior margins. Uropods free. Anal spine clearly visible.

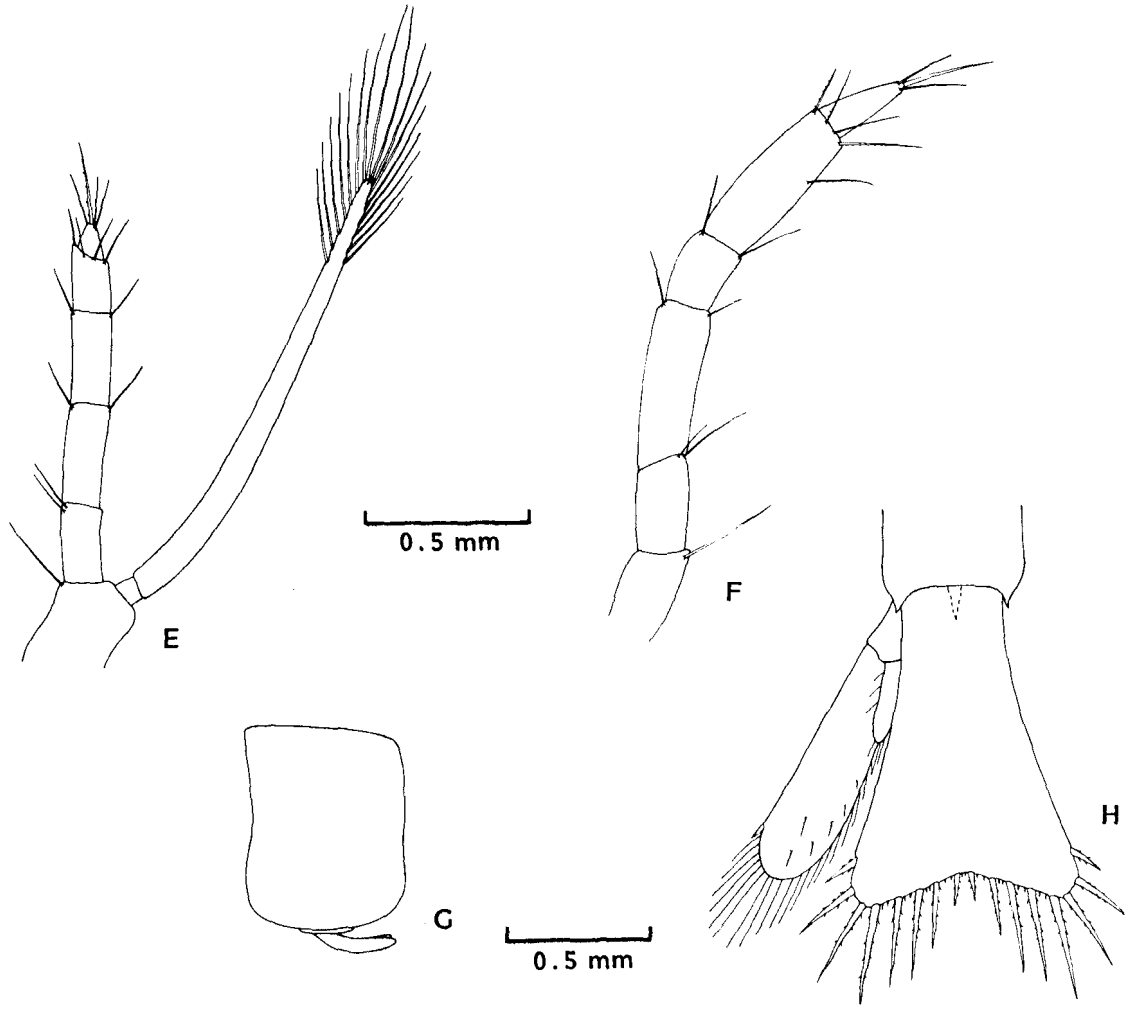


FIGURE 3.—Stage III zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod, lateral; E, second pereopod, lateral; F, fourth pereopod, lateral; G, second abdominal somite and pleopod, right side; H, telson, dorsal.

STAGE IV ZOEA

Mean total length of Stage IV 13.0 mm (range 12.6-13.2 mm; 10 specimens). Rostrum (Figure 4A) bears four to eight but usually six teeth dorsally, no teeth ventrally; tip not bifid. No change in epipodite of first maxilliped or pleurobranchiae except slight increase in size. Epipodite on second maxilliped present as small bud. No mastigobranchiae.

ANTENNULE (Figure 4B, inner and outer

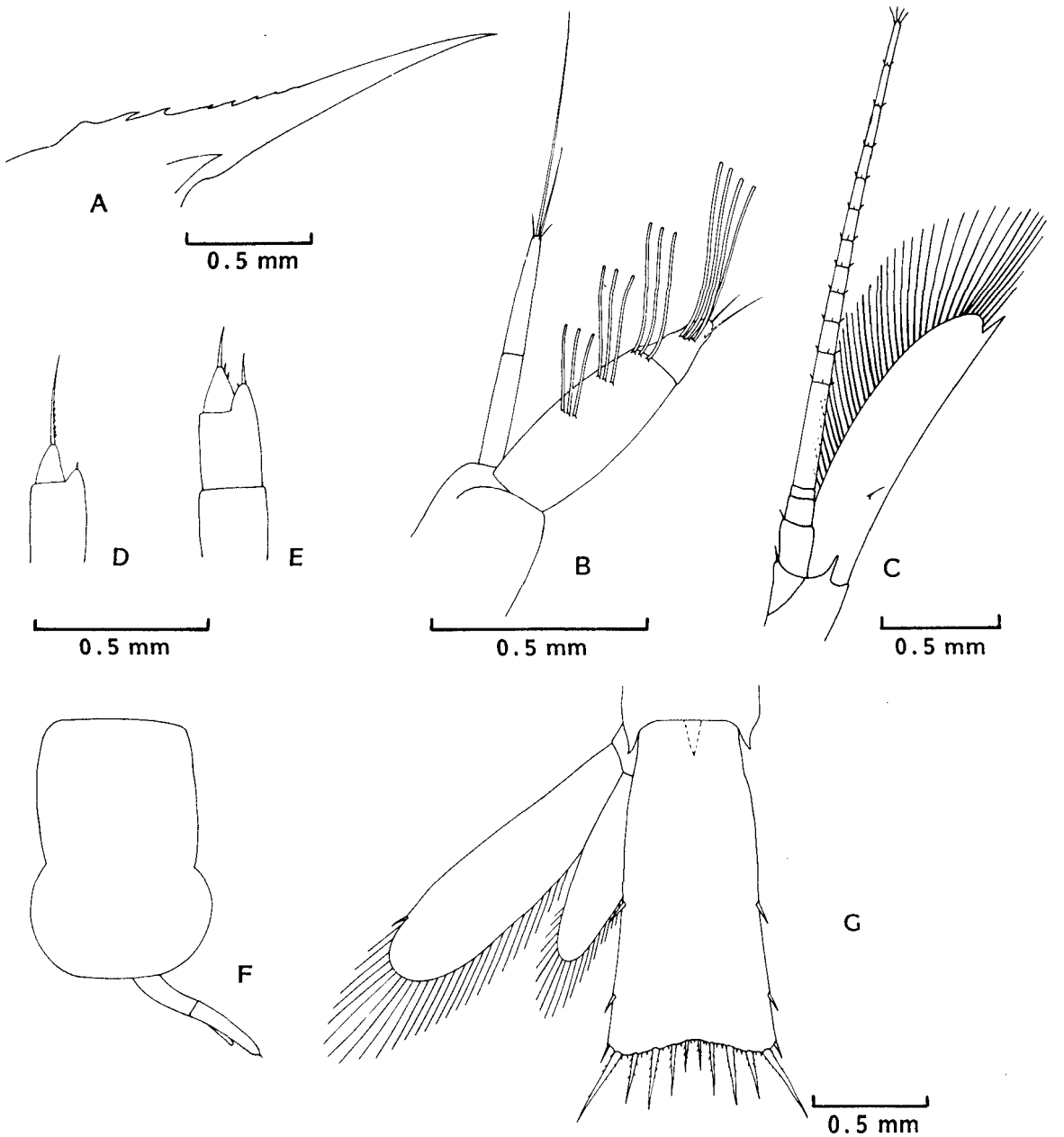


FIGURE 4.—Stage IV zoea of *Pandalus borealis*: A, rostrum, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod (distal segments only), lateral; E, second pereopod (distal segments only), lateral; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

flagella).—Flagella two-segmented. Inner flagellum nearly as long as outer flagellum. Outer flagellum bears four aesthetascs and two spines terminally and three groups of three aesthetascs each on proximal segment.

ANTENNA (Figure 4C).—Flagellum 15-segmented; 1.5-2 times length of scale, extending past tips of plumose setae fringing antennal scale. Antennal scale without joints at tip. Other than increase in size, changes in antennal scale from Stage IV onward are negligible.

FIRST PEREOPOD (Figure 4D).—Distal joint of propodite projected anteriorly and tipped with small spine.

SECOND PEREOPOD (Figure 4E).—Distal joint of propodite projected anteriorly to about one-half length of dactylopodite; projection tipped by two spines, one terminal and other subterminal and much shorter. Dactylopodite bears one terminal spine and two considerably shorter subterminal spines.

PLEOPODS (Figure 4F, second pleopod).—Segmented; length of second pair of pleopods about one-half height of second abdominal somite. Exopodite usually bears one to four small setae terminally and endopodite sometimes bears single seta terminally. Appendices internae not present.

TELSON (Figure 4G).—Endopodite of uropod about two-thirds length of exopodite and fringed with about 20 setae. Lateral margins of telson nearly parallel but slightly divergent posteriorly and bear two spines each. Posterior margin still slightly emarginate; bears 6 + 6 spines, the outermost (sixth) pair usually without spinules.

STAGE V ZOEA

Mean total length of Stage V 16.0 mm (range 15.2-17.1 mm; 10 specimens). Rostrum (Figure 5A) with 9-12 dorsal teeth, bifid tip, and usually 4, but sometimes 5, partially developed ventral teeth. Pleurobranchiae curve somewhat anteriorly and edges minutely lobulate. Mastigobranchiae occur as minute buds on protopodite of third maxilliped and pereopods 1-4.

ANTENNULE (Figure 5B, flagella only).—Inner flagellum four-segmented. Outer flagellum four- or five-segmented; bears six groups of three aesthetascs each. Each segment bears at least one seta but number and location of setae somewhat variable.

ANTENNA (Figure 5C).—Flagellum 2-3 times length of scale.

FIRST PEREOPOD (Figure 5D, distal segments only).—Projection of propodite at least one-half length of dactylopodite; bears two small spines, one terminally and one subterminally. Dactylopodite bears small spine subterminally in addition to terminal spine.

SECOND PEREOPOD (Figure 5E, distal segments only).—Chela well formed. Terminal spine of propodite shorter and stouter than in Stage IV. Dactylopodite bears five spines, the distal two especially stout. Carpopodite usually at least partially segmented.

PLEOPODS (Figure 5F, second pleopod).—Second pair of pleopods about equal in length to height of second abdominal somite; outer flagellum fringed with 11 or 12 plumose setae, inner flagellum with about 8 setae. Appendices internae usually present on pleopods 2-5; tips sometimes bear a few cincinnuli.

TELSON (Figure 5G).—Lateral margins of telson essentially parallel and bear two spines each. Posterior margin straight or slightly emarginate, bearing 6 + 6 spines. Uropods similar in shape to adult; no evidence of transverse hinge of exopodite.

STAGE VI (MEGALOPA)

Mean total length of Stage VI 18.5 mm (range 17.4-20.2 mm, 5 specimens). Rostrum (Figure 6A) shaped as in adult; bears 13-15 dorsal teeth in addition to distinct bifid tip, and 6 or 7 distinct ventral teeth. Usually one or two setae between dorsal teeth. Carapace lacks supraorbital spine. Exopodites on maxillipeds and pereopods 1-3 reduced. Pleurobranchiae and mastigobranchiae shaped as in adult. Inner and outer flagella of antennule eight- to nine-segmented and five-segmented, respectively. Flagellum of antenna about 6 times length of antennal scale. Mandibles still without palps. Chaelae of first and second pereopods shaped as in adult; carpal joints of left

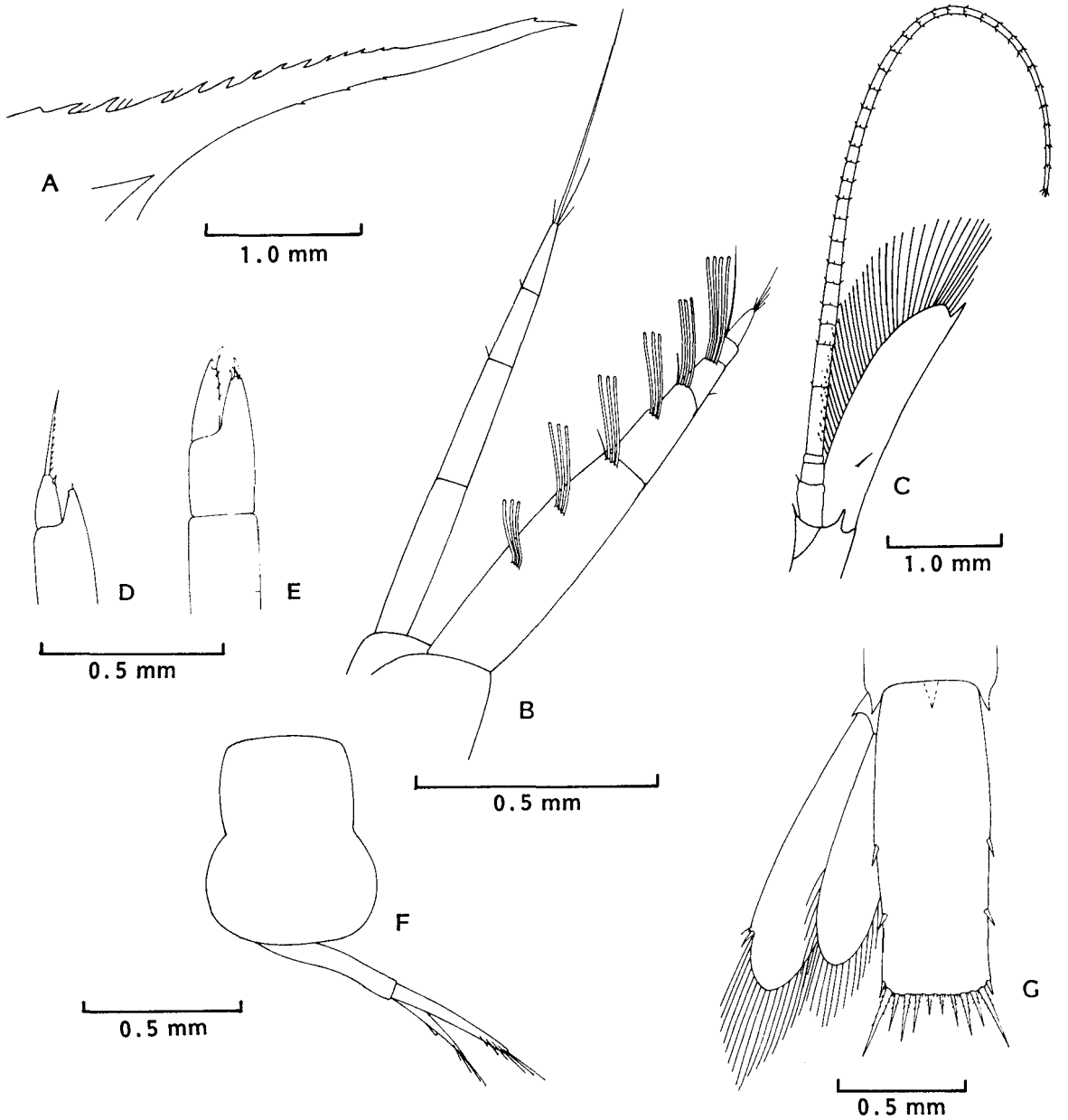


FIGURE 5.—Stage V zoea of *Pandalus borealis*: A, rostrum, right side; B, antennule (flagella only), ventral; C, antenna, ventral; D, first pereopod (distal segments only), dorsal; E, second pereopod (distal segments only), dorsal; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

and right second pereopods 20-25 and 10-13, respectively. Pleopodal setae extend along entire lateral margins of both flagella; tips of appendices internae bear several distinct cincinnuli. Length of second pair of pereopods, excluding setae, 1.5-2 times height of second abdominal segment. Telson (Figure 6B) shows, for first time, shape and spination similar to adult; lateral margins converge posteriorly but widen slightly at junction with posterior margin; typically four spines on each lateral margin but in this stage and Stages VII and VIII one lateral spine often lacking. Posterior margin of telson rounded but not as much as in Stage VII; bears 3 + 3 stout spines and sometimes

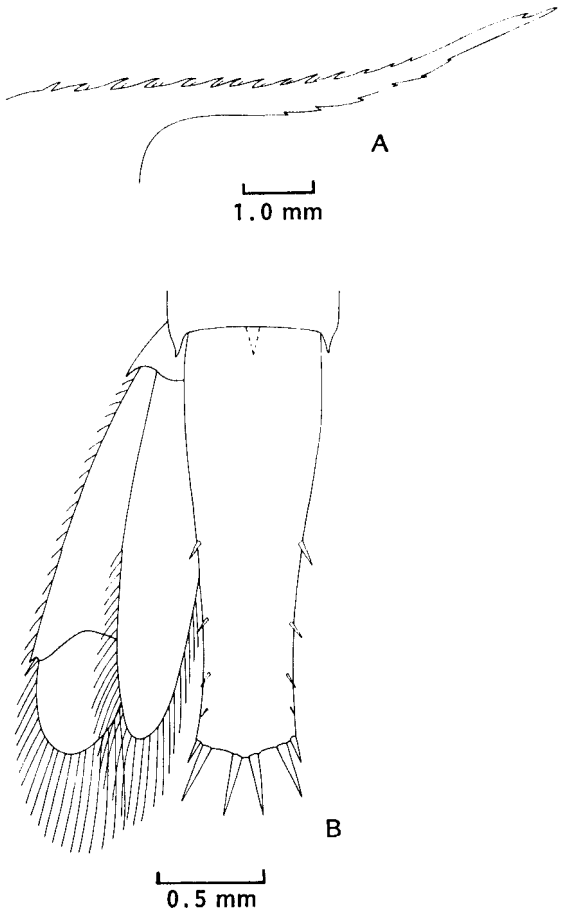


FIGURE 6.—Stage VI (megalopa) of *Pandalus borealis*: A, rostrum, right side; B, telson, dorsal.

remnants of a spine or two from Stage V. Transverse hinge of exopodite of uropod complete.

STAGES VII AND VIII (JUVENILES)

Mean total length of Stage VII (first juvenile) 18.4 mm (range 15.1-21.0 mm; 5 specimens). Usually two setae between most rostral teeth. Carapace without supraorbital spine. Arthrobranchiae on third maxilliped and pereopods 1-4 present as minute buds. Mandibular palp present for first time; three-segmented. Inner and outer flagella of antennule each 11- to 13-segmented. Exopodites on maxillipeds and pereopods 1-3 remnant. Third abdominal somite sometimes bears minute spine on middorsal posterior margin. Carpal joints of left and right second pereopods 28-30 and 14-17, respectively. Lateral margins of telson (Figure 7) typically bear 5 + 5 spines; posterior margin rounded as in adult.

Mean total length of Stage VIII (second juvenile) 21.6 mm (range 19.0-23.6 mm; 8 specimens). Morphological differences between Stages VII and VIII slight. Most notable features of Stage VIII: at least three or four setae between most rostral spines; complete lack of exopodites on third maxilliped and pereopods 1-3; inner and outer flagella of antennule each 15- to 16-segmented; lateral margins of telson typically bear 6 + 6 spines.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The first description of larvae ascribed to *Pandalus borealis* was given by Sars (1900), based on specimens collected from plankton. Berkeley (1931) showed that Sars' larvae could not be *P. borealis*; almost simultaneously Lebour (1930) showed that they were *Caridion gordoni* (Bate). Sars' "post-larval" specimen, however, is considered by both Lebour and Berkeley to be correctly identified as *P. borealis*. As far as can be compared, my Stage VI (megalopa) and Sars' "post-larval" specimen are essentially identical except for the

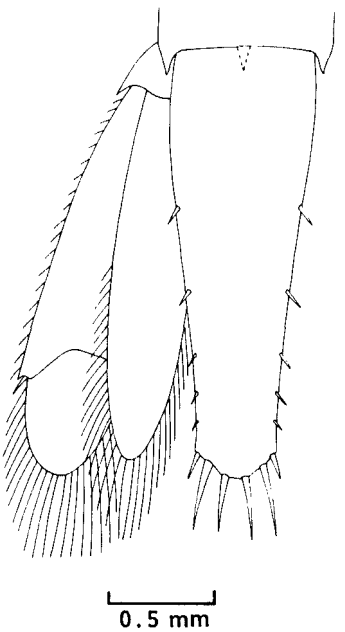


FIGURE 7.—Stage VII (first juvenile) of *Pandalus borealis*: telson, dorsal.

rostral tip, which in my larva is bifid but in Sars' is styliform, and the chela of the first pereopod, which is completely developed in my larva but not in Sars'.

Stephensen (1912) described zoeal Stages I to V from plankton that he provisionally identified as "*P. propinquus* (?)" and Stage III zoeae (1916) as "*Spirontocaris*-larva No. 4." Berkeley (1931) noted the close similarity of the "*P. propinquus* (?)" specimens to zoeae of *P. borealis* from British Columbia waters. Stephensen (1935) later decided that both "*P. propinquus* (?)" and "*Spirontocaris*-larva No. 4" were actually zoeae of *P. borealis*. He also compared his zoeae with fragments of a specimen identified by Krøyer as *Dymas typus* and decided Krøyer's specimen was a Stage IV zoea of *P. borealis*.

Comparing the description and figures of Stephensen's (1912) zoeae and mine in general for each stage, my zoeae are slightly more advanced than Stephensen's. In my Stage I zoeae the antennal scale bears 19 plumose setae; the basipodite and coxopodite of the maxillule bear 9 + 1 and 9 spines, respectively; the endopodite of the first maxilliped is segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 6, 14, and 16 natatory setae, respectively. In Stephensen's Stage I zoeae the antennal scale bears only eight or nine plumose setae; the basipodite and coxopodite of the maxillule bear five and six spines, respectively; the endopodite of the first maxilliped is not segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 4, 10, and 10 natatory setae, respectively. In Stage II, the relative difference in number of setae and spines between my zoeae and Stephensen's remains essentially the same, except in my zoeae the exopodites of pereopods 1, 2, and 3 bear 16, 16, and 12 setae, respectively, whereas in Stephensen's zoeae they each bear 18 setae. In Stage III, the rostrum of my zoeae bears only a single tooth and the antennal flagellum is eight-jointed, but in Stephensen's zoeae the rostrum bears as many as three teeth and the antennal flagellum is not jointed. In Stage IV, the rostrum of my zoeae bears six or seven teeth, the antennal flagellum is 15-segmented, and the telson bears eight pairs of spines whereas in Stephensen's zoeae the rostrum bears only four teeth, the antennal flagellum is still unsegmented, and the telson bears only seven pairs of spines. In Stage V, the most obvious difference is that the pleopods are segmented in my zoeae but not in Stephensen's.

In his 1916 report, Stephensen described an additional larva which he considered the sixth stage of *P. propinquus* G. O. Sars; later (1935) he decided it was *P. borealis*. According to Stephensen, this stage closely resembles his Stage V zoeae, differing primarily in the left second pereopod being considerably longer than the right, and, for both second pereopods, the joint at the distal end of the carpopodite being complete. In my larvae, morphological change from Stage V to Stage VI is sufficiently pronounced that I consider the sixth stage to be the megalopa. If Stephensen was correct in assuming his specimen to be a sixth stage zoea, then *P. borealis* in Greenland waters has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

In her classic study of pandalid larvae from British Columbia waters, Berkeley (1931) described and figured *P. borealis* Stage I zoeae reared in the laboratory and Stages II-VI collected from plankton. Her larvae follow a pattern of development similar to my larvae but each stage is less well developed. For instance, she described the antennal flagellum in her Stage I zoeae as tipped by a simple seta whereas in my zoeae it is tipped by a spinulose spine, and she neither figured nor described the spinous seta which my zoeae bear on the protopodite at the base of the flagellum. Also, the exopodite of the maxilla of her Stage I zoeae bears 8-10 long simple setae and has no trace of a proximal expansion whereas in my zoeae the exopodite of the maxilla bears 11 long plumose setae as well as one longer, thicker seta at the proximal end which is slightly expanded. In Stage II, the outer flagellum of the antennule of Berkeley's zoeae is figured as bearing only three aesthetascs distally whereas my zoeae bear eight. The proximal expansion of the exopodite of the maxilla is "just appearing" in Berkeley's Stage II but in mine it is distinctly expanded. Moreover, she described the telson as being still indistinctly segmented from the sixth abdominal somite but in my zoeae it is always distinctly segmented at Stage II. Berkeley's Stage III zoeae are essentially identical to mine as far as can be determined from her description. Her Stage IV zoeae have four small teeth at the base of the rostrum, the pleopods are without joints, and there is no epipodite on the second maxilliped. In my Stage IV zoeae, the rostrum usually has six teeth, the pleopods are jointed, and an epipodite occurs on the second maxilliped. In Stage V, the rostral tip of Berkeley's zoeae is still styliform. There is no evidence

from either her description or figure of ventral teeth on the rostrum, and the pleopods have not yet developed appendices internae. In my Stage V zoeae the rostral tip always bears at least a protuberance indicative of the bifid tooth, and pleopods 2-5 bear at least partially developed appendices internae. In contrast to my Stage VI, the megalopa, Berkeley's Stage VI is still typically zoeal: there is still no mention of ventral rostral teeth, the carapace still bears a supraorbital spine, the carpopodites of the second pereopods are not segmented, and the telson bears three pairs of lateral spines (not including the sixth terminal pair) and terminal setal pairs 2-4 have begun to degenerate.

Berkeley (1931) also mentioned a *P. borealis* larva she obtained from plankton that, according to her, corresponds to the sixth stage of *P. danae* Stimpson and is similar to that described by Sars (1900) as the "post-larval" stage of *P. borealis*. Berkeley's sixth stage and Sars' "post-larval" stage are typically nonzoeal as indicated by the lack of supraorbital spines, segmentation of the carpopodites of the second pereopods, degeneration of the pereopodal and third maxilliped exopodites, and the typically adult shape and spination of the telson. Because this stage would be at least the seventh stage, it appears that *P. borealis* in British Columbia waters, as well as Greenland waters (Stephensen 1916), has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

The preceding comparisons show that Berkeley's zoeae were less well developed at each given stage than mine and an additional stage or two was probably necessary for her zoeae to reach the megalopa stage. An apparent contradiction to this delayed development is the lack of segmentation of the antennal scale in the early stages of Berkeley's zoeae. As shown by Haynes (1976), however, Berkeley was mistaken in this regard and her specimens undoubtedly possessed a segmented scale in the early stages.

The only other description of larvae of *P. borealis* known to me is that of Kurata (1964) who, like Berkeley (1931), obtained Stage I zoeae in the laboratory from known parentage but Stages II-VII from plankton. Kurata's zoeae are essentially identical to mine through Stage V, except the rostrum of Kurata's Stage V zoeae is identical to the rostrum of my Stage IV zoeae. Kurata's Stage VI corresponds to my Stage V, but his Stage VII possesses characteristics intermediate between my Stages V and VI. For instance, in Kurata's Stage VII the exopodites on pereopods 1-3 and the third maxilliped have not begun to degenerate nor are the carpopodites segmented whereas in my Stage VI (megalopa) the exopodites on pereopods 1-3 and the third maxilliped are reduced and the carpopodites of the left and right second pereopods are segmented. Also, the lateral spination and shape of the telson of Kurata's Stage VII are typical of postzoeae but posteriorly the telson bears 6 + 6 spines, a typically zoeal characteristic. By studying Stage VII individuals just prior to molting, Kurata found that Stage VIII individuals possessed a distinct mandibular palp and degeneration of posterior telson spines 2-4. He concluded that Stage VII was the last zoeal stage and Stage VIII the first postzoea, or megalopa.

According to Lebour (1930), the lack of an outer seta on the maxillule in zoeae of *Pandalus* is one criterion for distinguishing this genus from certain other Caridea. Pike and Williamson (1964), however, found the seta consistently present in early stages of British species of *Pandalus*. Occurrence of the seta in Stage I zoeae has been reported by Gurney (1942) for *Pandalus montagui* Leach and *P. stenolepis* Rathbun; by Kurata (1955, 1964) for *P. borealis* and *P. kessleri* Czerniavski; and Modin and Cox (1967) for *P. jordani* Rathbun. I have consistently found the seta in the early stages of *P. hypsinotus*, *P. goniurus*, and *P. borealis*. Lebour's suggestion that the lack of the seta is a distinguishing criterion for zoeae of *Pandalus* should, therefore, be disregarded.

In addition to *P. borealis*, larvae have been described, at least in part, for nine other species of pandalids from the North Pacific Ocean: *P. goniurus, P. jordani, P. platyceros* Brandt, *P. danae, P. kessleri, P. hypsinotus, P. stenolepis, Pandalopsis dispar* Rathbun, and *P. coccinata* Urita. Of these nine species, larvae of *Pandalus stenolepis, P. jordani,* and *P. goniurus* are most like larvae of *P. borealis*, being characterized by exopodites on pereopods 1-3 rather than only on pereopods 1 and 2 and by poorly developed pereopods in Stage I. Zoeae of *P. stenolepis* were described by Needler (1938). Based on her descriptions, zoeae of *P. stenolepis* are readily distinguished from zoeae of *P. borealis* by 1) the shape and spination of the rostrum, which in Stage I *P. stenolepis* is about as long as the carapace and projects upward rather than downward as in *P. borealis*, and 2) the fringed posterior edge of the abdominal somites and the serrated margins of

the carapace, both of which persist to Stage V in *P. stenolepis* but never occur in *P. borealis*.

Larvae of *P. jordani* have been described from specimens reared in the laboratory. Compared with development of similar species, Modin and Cox (1967) and Lee (1969) obtained more stages (11-13 and at least 8, respectively) than expected for larvae of *P. jordani* from plankton. Because of the possibility of these extra stages, only Stage I zoeae of *P. borealis* and *P. jordani* can be compared. Upon hatching, zoeae of *P. borealis* are slightly more developed than zoeae of *P. jordani*. For instance, in Stage I *P. jordani*, the exopodites of maxillipeds 1, 2, and 3 bear 4, 9-11, and 11 or 12 natatory setae, respectively; the left mandible bears no lacinia mobilis; the basipodite of the maxillule bears six spines terminally; and the scaphognathite of the maxilla bears seven to nine setae along its outer margin. In Stage I *P. borealis*, maxillipeds 1, 2, and 3 bear 5 or 6, 13 or 14, and 16 natatory setae, respectively; the left mandible bears a single lacinia mobilis; the basipodite of the maxillule bears 9 spines terminally; and the scaphognathite of the maxilla bears 12 setae along its outer margin. Beyond Stage I, the most distinguishing difference between zoeae of *P. jordani* and *P. borealis* seems to be the development of the rostral tip which in zoeae of *P. jordani* remains acuminate but in zoeae of *P. borealis* becomes bifid in later stages.

In an earlier report (Haynes 1978), I described larvae of *P. goniurus* reared in the same manner as larvae of *P. borealis* described here. Larvae of both species are morphologically similar, especially in early stages, and often occur together in plankton. To facilitate identification of larvae of these two species, the most readily observable morphological differences are listed by stage in Table 1. Larvae of *P. goniurus* are characteristically smaller than those of *P. borealis* and in

TABLE 1.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska.

Stage and characteristic	*P. borealis*	*P. goniurus*
Stage I zoea:		
Mean total length (mm)	6.7 (range 6.5-7.3; 25 specimens)	4.0 (range 3.7-4.2; 10 specimens)
No. of plumose setae fringing antennal scale	19	9
No. of spines terminally on basipodite of maxillule	9	5
No. of plumose setae on scaphognathite (in addition to single proximal seta)	11	4
No. of nataory setae on exopodites:		
Maxillipeds 1, 2, 3,	5-6, 13-14, 16	4, 8, 12
Stage II zoea:		
Mean total length (mm)	7.5 (range 6.7-8.2; 25 specimens)	5.9 (range 4.5-5.3; 10 specimens)
No. of plumose setae fringing antennal scale	About 25	About 19
No. of natatory setae on exopodites:		
Maxillipeds 1, 2, 3,	7, 16, 18	6, 12, 14
Pereopods 1, 2, 3,	16, 16, 12	12, 8, 8
Stage III zoea:		
Mean total length (mm)	9.5 (range 9.0-10.0; 10 specimens)	6.2 (range 6.0-6.6; 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	About 30 setae	About 20 setae
Stage IV zoea:		
Mean total length (mm)	13.0 (range 12.6-13.2; 10 specimens)	7.7 (range 6.8-8.3; 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	About 1½ × scale, extending past tips of plumose setae	Longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	Projected anteriorly about ½ length of dactylopodite	Projected anteriorly only slightly
Pleopods	Segmented, pleopod 2 about ½ height of abdominal somite	Unsegmented, pleopod 2 about 1/3 height of abdominal somite
Stage V zoea:		
Mean total length (mm)	16.0 (range 15.2-17.1; 10 specimens)	10.3 (range 8.2-11.3; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 4-5 partially developed ventral teeth	5-6 dorsal teeth; tip not bifid (but may show slight protuberance); no ventral teeth
Chela of pereopod 2	Fully formed	Not fully formed, propodite extension about ½ length of dactylopodite
Pleopods	With appendices internae; fringed with plumose setae; pleopod 2 as long or longer than height of abdominal somite	Without appendices internae; 2-4 simple setae terminally; pleopod 2 about 2/3 height of abdominal somite
Stage VI (megalopa):		
Mean total length (mm)	18.5 (range 17.4-20.2; 5 specimens)	13.8 (range 11.1-15.8; 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Stages I-III the number of setae on certain appendages, particularly the antennal scale and certain mouthparts, is fewer than for zoeae of *P. borealis*. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*.

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