LARVAL DEVELOPMENT OF *EUPHAUSIA EXIMIA* (CRUSTACEA: EUPHAUSIACEA) WITH NOTES ON ITS VERTICAL DISTRIBUTION AND MORPHOLOGICAL DIVERGENCE BETWEEN POPULATIONS

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ABSTRACT

Larval development of *Euphausia eximia* includes the following stages: nauplius I-II, metanauplius, calyptopis I-III, and furcilia I-VI. The larvae are similar to those of congener *E. gibboides* but differ in both morphological detail and timing of developmental events.

A comparison of larvae of *E. eximia* from across the species' range showed significant differences in morphology between forms from the California Current terminus off Baja California and from the South Equatorial and Peru Currents. This variation may be evidence of genetic divergence between populations and perhaps indicates that the oxygen-deficient warm waters of the eastern tropical Pacific form an effective barrier between reproductive centers of the species. Significant differences in morphology were found as well during a preliminary survey of adults; the southern limit of the northern form of *E. eximia* was about latitude 2° north.

The vertical distribution of larval stages in day and night samples from two locations off Baja California and one in the South Equatorial Current showed development of diurnal vertical migration in the second half of the furcilia phase after acquisition of the full complement of setose abdominal pleopods. A "reverse" migration pattern was seen among calyptopes at two stations with the majority of larvae occurring in the surface stratum during the day and below the surface layer at night; larvae at the third station were found, both day and night, in the surface stratum until the onset of vertical migration. Variation in growth rate between areas within the range of each population may be correlated with relative abundance of food and duration of stay in food-rich surface waters.

Euphausia eximia Hansen is endemic to the eastern tropical Pacific, ranging from lat. 32°-34° N to 30° S and with areas of relative abundance in waters of the California Current terminus off Baja California and the Gulf of California, in the South Equatorial Current, and in the Peru Current (Brinton 1962; Antezana-Jeréz 1978). In a recent study of the horizontal and vertical distribution of euphausiids along a transect from ca. lat. 23° N, long. 115° W to lat. 3° S, long. 88° W, Brinton (1979) observed that *E. eximia* occurred sparsely between lat. 11° and 20° N but achieved high densities in the productive zones marginal to the oxygen-deficient portion of the eastern tropical Pacific. He noted that "Reproduction, as determined by presence of larvae, was not observed between 2° and 20° N; occurrences of juvenile and adult *E. eximia* in this zone, therefore, appear due to meridional advection from the northern (21° to 25° N) and equatorial population centers." This agreed with earlier observations of *E. eximia* in these areas (Brinton 1962).

Within the genus *Euphausia*, *E. eximia* is most closely related in adult morphology to *E. americana*, an Atlantic species, and to *E. krohnii*, found in both the Atlantic and Mediterranean (Mauchline and Fisher 1969). The larvae of *E. krohnii* have been described (Frost 1934; Casanova 1974) but those of *E. americana* have not yet been identified. The literature on larval development within the Euphausiacea has been reviewed by Gopalakrishnan (1973).

The purpose of this paper is to describe the larval development of *E. eximia* in the reproductive area of the California Current terminus population, to note the differences observed in morphology of larvae from the South Equatorial-Peru Current population and apparent variation within each population in rate of growth, and to provide information on the vertical distribution of larval stages.

METHODS

Larvae of *E. eximia* were sorted from preserved samples of plankton taken in the eastern Pacific (Figure 1) during Scripps Institution of Oceanog-

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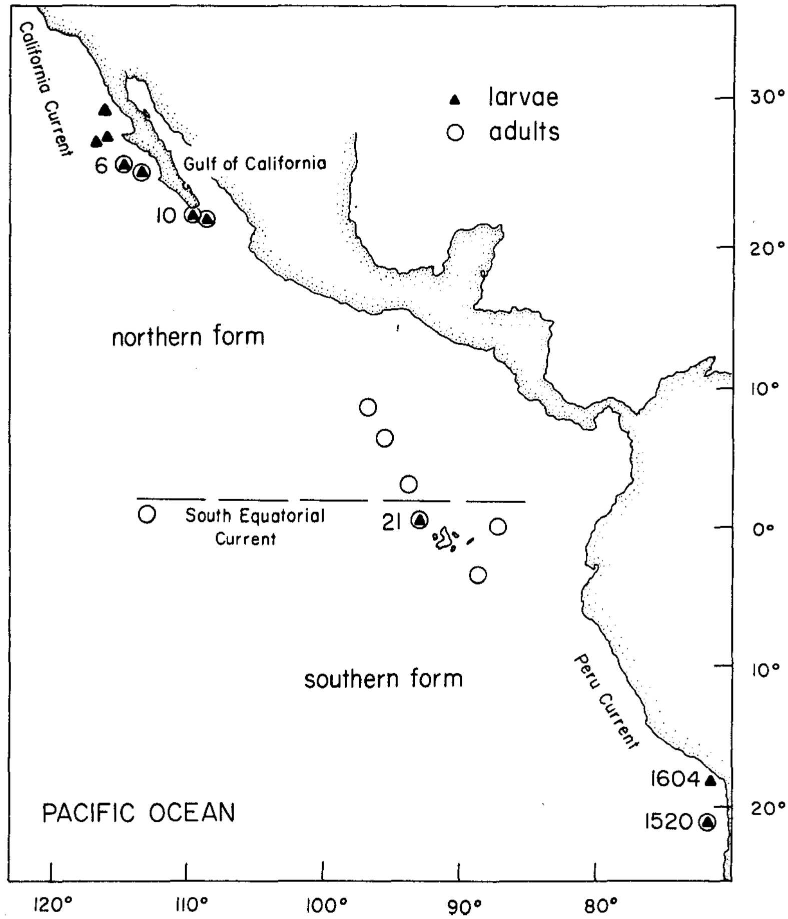

FIGURE 1.—Occurrence of northern and southern forms of *Euphausia eximia* in plankton samples from the eastern Pacific Ocean; Krill Expedition station numbers locate samples in which vertical distribution and growth of larvae were studied.

raphy Expeditions Krill, Aries, and Muddauber, and CalCOFI Cruise 5804. They were identified from an area off western Baja California in which *E. eximia* is consistently abundant and where closely related species (*E. mutica* and *E. recurva*), whose larvae we have identified, are rarely, if ever, present (Brinton 1967). At three locations (Stations 6, 10, and 21) larvae were counted as well in separate day and night series of tows taken across eight strata above 500 m on Krill Expedition (Brinton 1979) to investigate patterns of vertical distribution.

Larvae from each sample were grouped by size, information from length-frequency histograms, and degree of morphological differentiation into developmental stages which, to furcilia IV, were discrete and assumed to be separated by one molt. Furcilia V-VI and juvenile I were also presumed to be one intermolt although individual variation in growth and morphogenesis made boundaries less distinct. Altogether 2,210 individuals were measured and 347 dissected for study of appendages. Measurements were made with an ocular micrometer; the method was the same as that used in studies of species of the *E. gibboides* group (Knight 1975, 1978). In the comparison of growth rate between areas within each population larvae from Stations 1520 and 1604 were treated as one sample. Larvae were dissected in glycerine and at least 10 specimens of each stage were examined in detail. In the description of larval stages, the usual setation or condition noted is given in parentheses following the range observed. Drawings were prepared with the drawing attachment of a Wild M20 Microscope.[2]

The nomenclature used to describe larval morphology was modified from the studies cited above with respect to the mandible. It appears appropriate to refer to the dentate process near incisor

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

teeth of the right mandible as the lacinia mobilis (Weigmann-Haass 1977; Hessler[3]). In species of *Euphausia* I have examined in detail (*E. gibboides*, *E. sanzoi*, *E. fallax*, *E. pacifica*), in *Nematoscelis difficilis* (Gopalakrishnan 1973), and *Nyctiphanes couchii* (Le Roux 1976), the lacinia mobilis appeared only on the right mandible; it was found on the left mandible of *E. hanseni* by Weigmann-Haass (1977). Leg 1 is referred to as maxilliped through the furcilia phase.

Adults were sorted from a set of samples (Figure 1) for preliminary exploration of morphological differences between populations of *E. eximia*. The animals were sexed, measured to the nearest millimeter, and the armature of telson and inner process of segment 2 of antennular peduncle were inspected.

Gravid females of *E. eximia*, captured in nighttime plankton tows with a 1 m net from 200 m to the surface near Santa Catalina Island, were cultured aboard ship using the methods described by Lasker and Theilacker (1965). Larvae hatched from eggs spawned by one of the females were held through calyptopis I to confirm identification of early larval stages.

RESULTS

Observations of Reared Animals

Two gravid females spawned on the night of capture; they were 25.7 and 26.6 mm total length (TL) and shed 154 and 196 eggs. Their ovaries were blue before spawning and the embryos of the newly laid eggs were pale blue; the color faded before hatch. Of 154 eggs allowed to develop, 90% hatched and, at 17°-19° C room temperature, the duration of early larval stages was approximately as follows: 24 h for the egg; 24 h for nauplius I and II together; 48 h for the metanauplius. The first calyptopis appeared on the fourth day after spawn. These stages encounter similar temperatures in the surface waters off Baja California.

The spent female molted 6 days after spawning without shedding more eggs; a spermatophore was not found on the preserved female or her exuvia. Three other ovigerous females survived capture and molted twice, with 4 days between molts, without spawning; each shed a spermatophore with the exuvia during the first molt and the ovaries remained blue.

Description of Larval Stages

Larval development in the California Current population (northern form) of *Euphausia eximia* included the following stages: nauplius I and II; metanauplius; calyptopis phase, three stages; furcilia phase, six stages. The stage which followed furcilia VI usually (in 92% of 53 individuals) had the adult number of spines on the telson (one terminal and two pairs posterolateral) and is referred to here as juvenile I. The observed furcilia stages are listed in Table 1 along with the development of pleopods, telson, and antenna. Measurements of the calyptopis, furcilia, and juvenile stages are given in Tables 2 and 3.

TABLE 1.—Development of pleopods, telson spines, and antenna in furcilia I-VI and juvenile I in the northern and southern forms of *Euphausia eximia*; ' = pair nonsetose pleopods, " = pair setose pleopods.

Stage	Pleopod development	Telson spines: Terminal	Telson spines: Posterolateral	Form of antenna	Number of larvae: Northern form	Number of larvae: Southern form
Furcilia I	1'	7	3	Natatory	151	72
Furcilia II	1"4'	7	3	Natatory	132	80
Furcilia III	5"	7	3	Natatory	334	104
		6	3		0	9
		5	3		1	4
		4	3		0	3
		3	3		1	5
Furcilia IV	5"	6	3	Juvenile	2	0
		5	3		8	0
		4	3		16	0
		3	3		128	2
		2	3		85	5
		1	3		192	57
Furcilia V	5"	1	3	Juvenile	195	45
		1	2		0	1
Furcilia VI	5"	1	3	Juvenile	40	42
		1	2		19	25
Juvenile I	5"	1	3	Juvenile	4	0
		1	2		49	47

TABLE 2.—Measurements (millimeters) of metanauplius and calyptopis I-III in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Carapace width	Telson width
Metanauplius, n = 123:				
Range	0.46-0.51	—	0.33-0.39	—
Mean	0.49		0.35	
SD	0.01		0.01	
Calyptopis I, n = 127:				
Range	0.97-1.09	0.59-0.67	0.36-0.44	0.158-0.186
Mean	1.03	0.62	0.40	0.170
SD	0.02	0.02	0.01	0.006
Calyptopis II, n = 140:				
Range	1.58-1.76	0.75-0.81	0.40-0.46	0.195-0.242
Mean	1.67	0.78	0.43	0.224
SD	0.04	0.02	0.02	0.008
Calyptopis III, n = 140:				
Range	2.20-2.55	0.89-0.99	0.50-0.61	0.242-0.279
Mean	2.36	0.94	0.56	0.260
SD	0.06	0.02	0.02	0.009

[3]Robert R. Hessler, Professor of Oceanography, Scripps Institution of Oceanography, Univ. Calif., La Jolla, CA 92037, pers. commun. July 1978.

Although there is variation in timing of events with respect to stage, the form, setation, and development of appendages are very similar in larvae of congeners *E. gibboides* and *E. eximia*. The descriptions with figures of *E. gibboides* larvae (Knight 1975) may be consulted for morphology and development of appendages of *E. eximia* which are figured and discussed in detail here only when necessary to contribute information specific to *E. eximia*. The setations of maxillule, maxilla, and pleopods in larvae of *E. eximia* are given in Tables 4, 5, and 6.

TABLE 3.—Measurements (millimeters) of furcilia I-VI and juvenile I in the northern form of *Euphausia eximia*.

Stage	Total length	Carapace length	Telson width
Furcilia I, *n* = 151:			
Range	2.87-3.19	0.81-0.87	0.232-0.270
Mean	3.02	0.84	0.250
SD	0.07	0.02	0.009
Furcilia II, *n* = 132:			
Range	3.41-3.84	0.89-1.01	0.195-0.232
Mean	3.59	0.94	0.219
SD	0.09	0.02	0.009
Furcilia III, *n* = 183:			
Range	3.84-4.46	0.97-1.13	0.158-0.214
Mean	4.13	1.05	0.188
SD	0.12	0.03	0.010
Furcilia IV, *n* = 269:			
Range	4.08-4.97	1.07-1.25	0.149-0.195
Mean	4.60	1.16	0.167
SD	0.15	0.03	0.008
Furcilia V, *n* = 158:			
Range	4.52-5.66	1.13-1.39	0.121-0.177
Mean	5.13	1.26	0.153
SD	0.23	0.05	0.008
Furcilia VI, *n* = 58:			
Range	5.09-6.06	1.19-1.45	0.112-0.158
Mean	5.55	1.34	0.138
SD	0.23	0.06	0.009
Juvenile I, *n* = 53:			
Range	5.45-6.79	1.35-1.64	0.112-0.149
Mean	6.15	1.49	0.131
SD	0.32	0.07	0.007

EGGS.—Perivitelline space relatively small, 50 spawned eggs with the following measurements: Outer diameter, 0.38-0.46 mm; mean, 0.45 mm; SD, 0.02 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.06 mm; SD, 0.01 mm. Eighty-five eggs from the plankton differed slightly: Outer diameter, 0.40-0.48 mm; mean, 0.45 mm; SD, 0.01 mm. Perivitelline space, 0.03-0.07 mm; mean, 0.05 mm; SD, 0.01 mm.

NAUPLIUS I AND II.—Body ovoid, as figured for *E. gibboides*, with one pair long posterior spines in nauplius I and a second short outer pair in nauplius II; both stages with 3 pairs of functional appendages—antennule, antenna, and mandible. Seven hatched nauplius I larvae with the following dimensions: Length, 0.38-0.41 mm; mean, 0.39 mm; SD, 0.02 mm. Width, 0.25-0.27 mm; mean, 0.26 mm; SD, 0.01 mm.

TABLE 4.—Development of maxillule in the northern form of *Euphausia eximia*; exopod with 4 setae and endopod with 2 medial and 3 terminal setae in all stages; () = usual condition.

	Endopod		Basal endite setae			Pseudexopod	
Stage	Segments	Lateral seta	Medial	Proximal	Coxal endite setae	Presence	Anterior seta
Calyptopis I	2	0	3	0	7	–	0
Calyptopis II-III	2	0	5	0	7	–	0
Furcilia I	2	0	6-7(7)	0	8	–	0
Furcilia II	2	0	7	0-1(1)	8	–	0
Furcilia III	2	0	9	1	8-9(8)	–	0
Furcilia IV	1-2	0-1(0)	8-10(9)	1	8-9(9)	–	0
Furcilia V	1	1	8-10(9-10)	1-2(1)	8-9(9)	–/+(+)	0
Furcilia VI	1	1	9-13(10)	1-2	9-10(9)	+	0
Juvenile I	1	1	10-12(10-11)	1-2(2)	9-11(10)	+	0-1

TABLE 5.—Setation of maxilla in the northern form of *Euphausia eximia*; medial lobe five with 3 setae in all stages; () = usual condition.

			Medial lobes			
Stage	Exopod	Endopod	1	2	3	4
Calyptopis I-III	1	3	8	4	4	4
Furcilia I	1	3	8	4	4-5 (5)	4
Furcilia II	1	3	8	4	4-5 (5)	4
Furcilia III	1	3	8	4	5-6 (5)	4-5 (4)
Furcilia IV	1	3	8	4-6 (4)	5-6 (6)	5
Furcilia V	1	3	8	4-6 (5-6)	6-7 (6)	5-6 (5)
Furcilia VI	1-3 (1-2)	3-4	8	5-6 (6)	6-7 (6)	5-6 (6)
Juvenile I	2-6 (2-5)	3-6 (4)	8-9 (8)	6	6-9 (7)	6-7 (6)

METANAUPLIUS (FIGURES 2A, 3A).—Rostral hood of carapace fringed with spines, 3 pairs on anterior margin relatively long, a fourth anterolateral pair sometimes somewhat longer than surrounding spines; usually 3 shorter spines between medial pair of long spines, tiny spines rarely interspersed; other small spines variable in number. Dorsal crest high, rounded, with 2 small spines (frequently broken or bent in preserved

TABLE 6.—Setation of pleopods in the northern form of *Euphausia eximia*; () = usual condition.

	Pleopod I		Pleopod 2		Pleopod 3		Pleopod 4		Pleopod 5	
Stage	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod	Exopod	Endopod
Furcilia I	0	0	—	—	—	—	—	—	—	—
Furcilia II	6	1	0	0	0	0	0	0	0	0
Furcilia III	6-8(6)	2	6	1	6	1	6	1	6	1
Furcilia IV	7-8(8)	2-4(3-4)	8-9(8)	2-3(2)	8	2-3(2)	7-8(8)	2-3(2)	6-8(7-8)	2
Furcilia V	8-10(9)	4-6(4)	8-10(9)	4-5(4)	8-10(9)	3-5(4)	8-10(9)	4	7-9(8)	3-4(4)
Furcilia VI	9-11(10)	4-6(6)	9-11(10)	4-6(6)	9-11(10)	5-6	9-11(9-10)	4-6(5-6)	8-10(8-9)	4-5(4)
Juvenile I[1]	10-13(11)	5-7(6)	11-12(11)	6-7(6)	11-12(11)	6-7(6)	10-12(11)	6-7(6)	9-11(9)	4-6(5)

[1]In juvenile I, 11, 13, and 7% of pleopods 1, 2, and 3 with 1 seta proximal to appendix interna on endopod in 30 individuals.

specimens). Small pair of papillae on anterior margin of body beneath carapace; Fraser (1936) described papillae as frontal sensory organs.

Antennule and antenna functional, mandible reduced, buds of maxillule, maxilla, and maxilliped present.

Abdomen short, posterior margin with 5 pairs of spines; relatively long third pair articulated with telson, shorter spines fused. The long spine is plumose in *E. gibboides* but appears nearly smooth (with tiny serrations sometimes visible) in *E. eximia*.

CALYPTOPIS I (FIGURES 2B, 3B).—Rostral hood of carapace fringed with spines curving medially on anterior margin and posteriorly on posterolateral curve of hood; posterior margin of carapace produced into small dorsal spine; dorsal crest without spines. Striated body of photophore visible in developing compound eye, ocular papillae situated medially slightly below anterior margin of eye.

Mandibles (Figure 4a) with asymmetrical median armature and with anterolateral process but without lateral knob seen in species of the *E. gibboides* group (lateral knob is not found in any stage of *E. eximia*); anterolateral process, representing palp (Gurney 1942), decreases in size until furcilia V.

Maxillule and maxilla functional.

Maxilliped (Figure 5a) with form and setation as in *E. gibboides*: coxa with 4 setae on inner margin and 1 seta on posterior face; basis with 5 setae on inner margin and 1 distal submarginal seta, 1 marginal seta noticeably stout; endopod 2-segmented, proximal segment with 3 setae, 2 marginal and 1 submarginal, 1 marginal seta small and stout, distal segment with 4 terminal setae; exopod with 4 terminal setae and 1 lateral seta near articulation with basis. In *E. gibboides* the stout setae of endopod segment 1 and basis are nearly equal in length.

Abdomen unsegmented.

Telson (Figure 6a) with 1 pair lateral, 3 pairs posterolateral, and 6 terminal spines, middle posterolateral spine slightly longer than other spines.

CALYPTOPIS II (FIGURES 2C, 3C).—Carapace with lateral margins of rostral hood curved ventrally around body so that in dorsal view marginal spines are visible only on anterior margin of carapace.

Maxilliped with stout seta of endopod segment 1 and basis now about equal in length, as figured for calyptopis III (Figure 5b).

Abdomen with 5 segments.

Telson (Figure 6b) with 7 terminal spines, middle posterolateral spine relatively long, armature of telson spines as in *E. gibboides*.

CALPYTOPIS III (FIGURES 2D, 3D).—Carapace still with marginal spines of rostral hood visible in dorsal view only on anterior margin which extends well beyond eyes; lateral margins with denticle. Pigment sometimes visible in developing compound eyes; ocular papillae small, set farther out on eyestalk.

Maxilliped (Figure 5b) endopod with 5 setae on terminal segment unlike species of *E. gibboides* group which retain 4 setae in this stage, coxa with 6 setae.

Abdomen with 6 segments, sixth segment with pair of biramous uropods.

FURCILIA I (FIGURES 7A, 8A).—Carapace with rectangular rostral plate fringed with marginal spines which curve toward small median spine or denticle; posterior margin with dorsal spine. Eyes movable, pigmented, with rounded contour in furcilia stages (Figure 8d) unlike lobed contour of *E. gibboides* eye.

Bud of leg 2 present.

Abdomen with one pair nonsetose pleopods on segment 1.

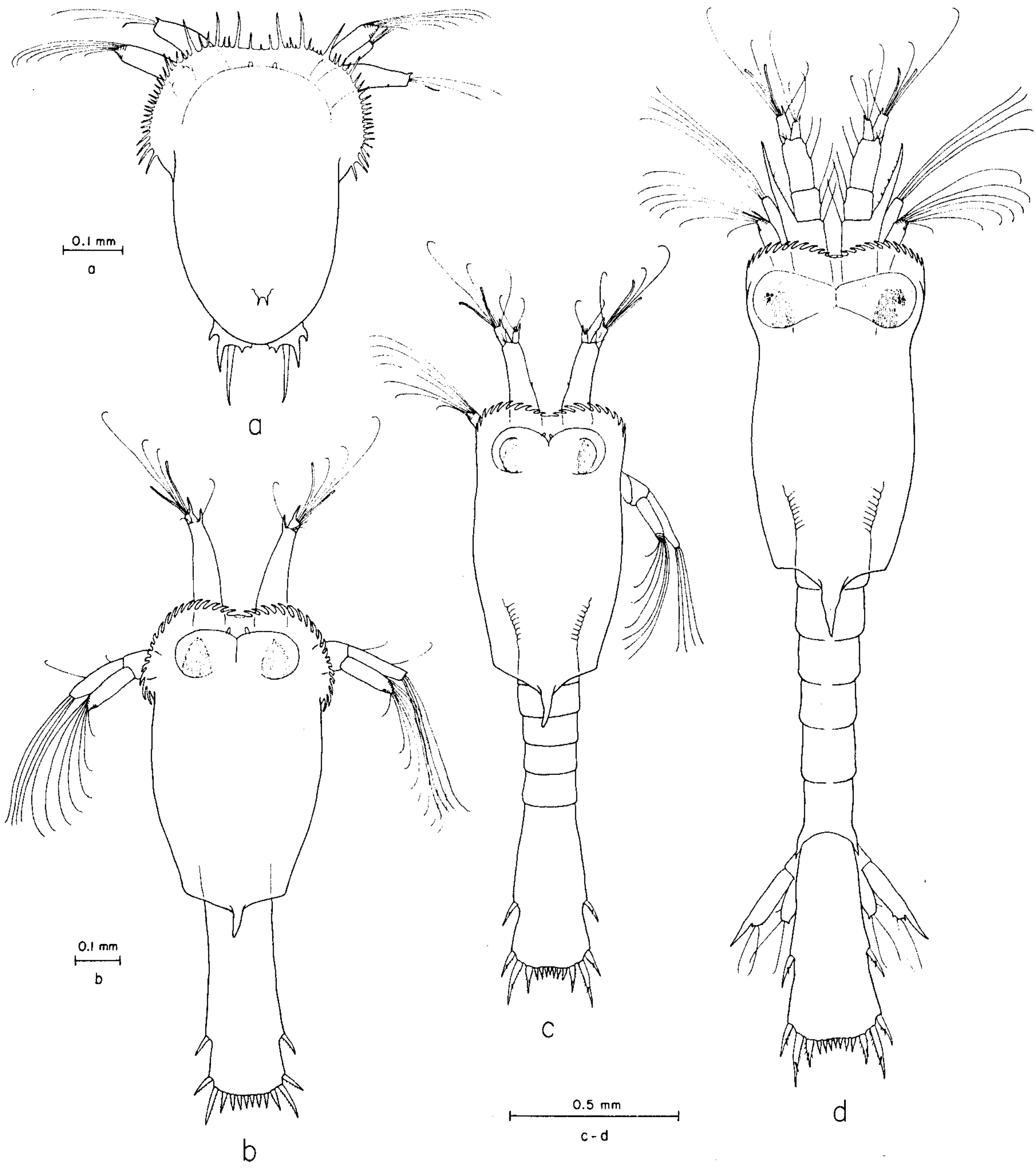

FIGURE 2.—*Euphausia eximia*, northern form, dorsal view: a, metanauplius; b-d, calyptopis I-III.

FURCILIA II (FIGURES 7B, 8B).—Carapace with narrower rostral plate and larger median spine, posterior margin without dorsal spine.

Maxilliped endopod with 5 or 6 (5) setae on distal segment.

Leg 2 endopod with 3-5 (4) segments, 1 or 2 (2) terminal setae, and variable marginal setation; exopod nonsetose; gill with two lobes; developing photophore may be visible.

Leg 3 unsegmented, nonsetose, with bud of exopod and bifid gill bud.

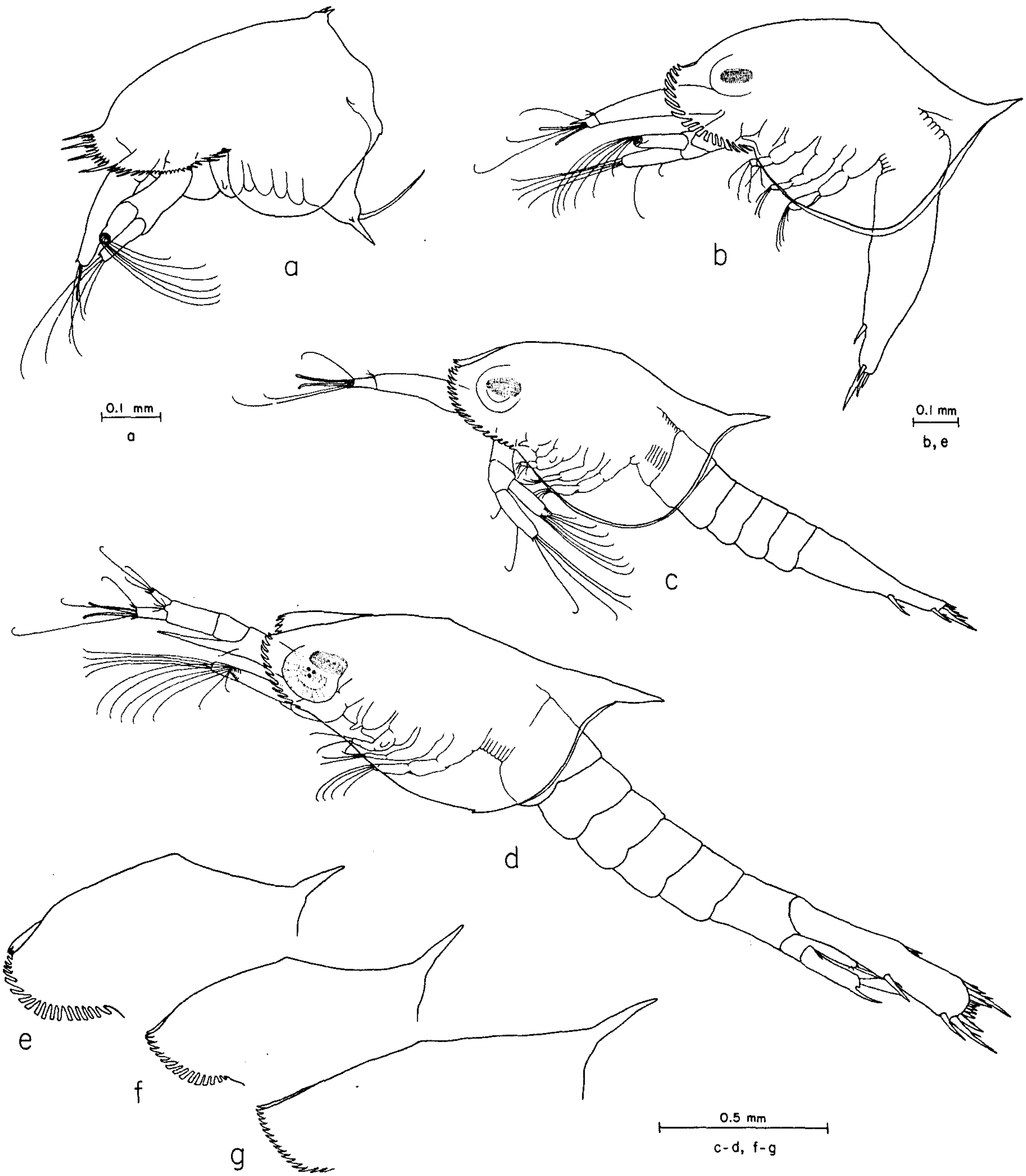

FIGURE 3.—*Euphausia eximia*, lateral view. Northern form: a, metanauplius; b-d, calyptopis I-III. Southern form: e-g, calyptopis I-III.

Buds of legs 4 and 7 sometimes present.

Abdomen with one pair setose pleopods on segment 1 and 4 pairs nonsetose pleopods on segments 2-5; photophore on segment 1 pigmented, photophore of segment 4 sometimes forming.

FURCILIA III (FIGURES 7C, 8C).—Carapace with rostrum narrower and lengthening.

Antennule with flagella lengthening, often 2-segmented; 1 of 2 aesthetes on outer ramus bifurcate distally as in *E. gibboides* furcilia III.

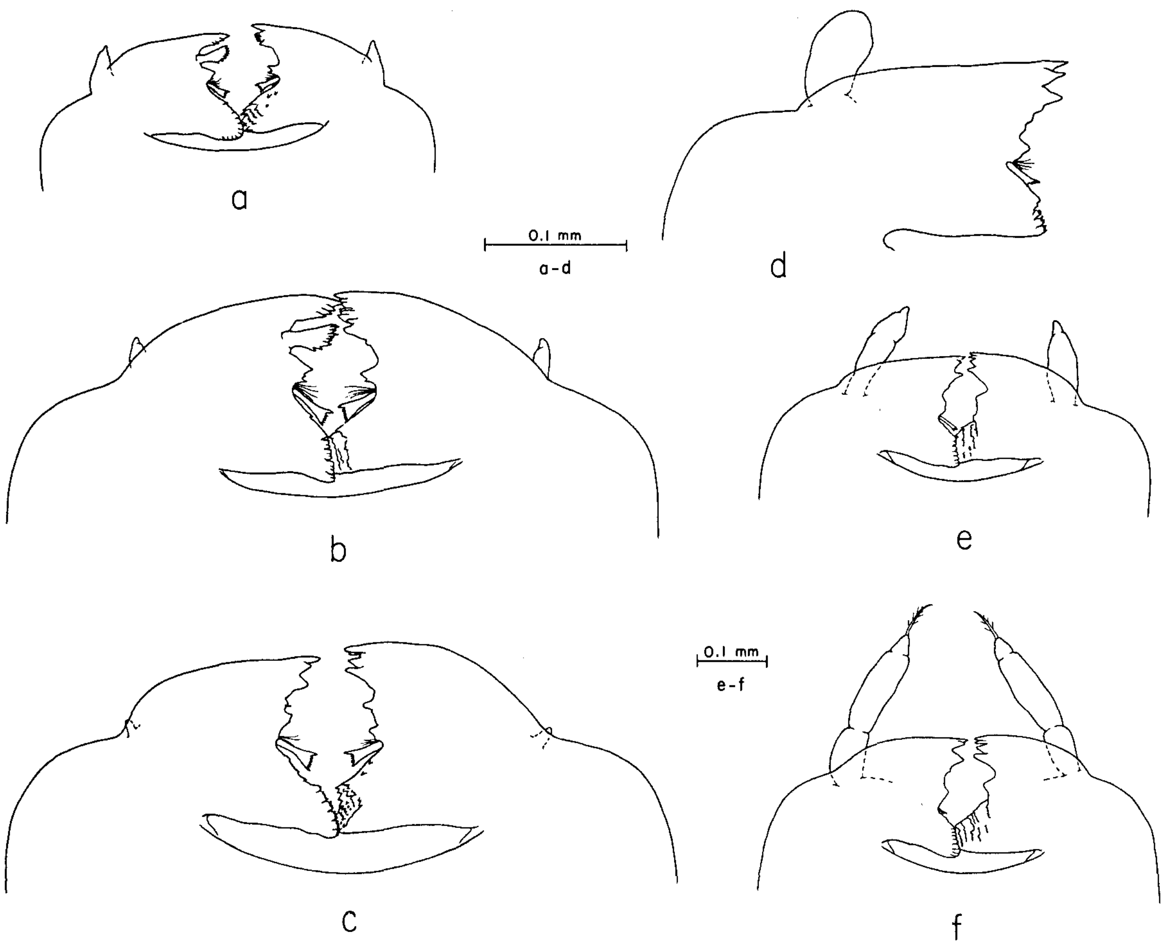

FIGURE 4.—*Euphausia eximia*, northern form. Mandible, posterior view: a, calyptopis I; b-e, furcilia III-VI; f, juvenile I.

Maxilliped endopod with 5 or 6 setae on distal segment.

Leg 2 endopod 5-segmented with more than 2 terminal setae; exopod with 2-4 (3) setae; gill sometimes with bud of third lobe; photophore pigmented.

Leg 3 endopod 5-segmented with 2 terminal setae and variable marginal setation; exopod with 0 or 1 (0) seta; gill with bud of third lobe.

Leg 4 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose; gill with two lobes.

Leg 5 rudimentary, sometimes with buds of exopod and gill.

Leg 7 with bifid gill and developing photophore visible.

Bud of leg 8 sometimes present.

Abdomen with 5 pairs setose pleopods; photophores pigmented on segments 1 and 4 and forming on segment 2.

Telson (Figure 6f) still usually with 7 terminal spines and 3 pairs posterolateral spines (2 of 336 larvae varied with 3 and 5 terminal spines); telson of next instar sometimes visible beneath cuticle, the following percentages (in parentheses) of terminal spines were observed among 293 furcilia III larvae: 7(1.0), 6(0.3), 5(1.4), 4(2.4), 3(30.4), 2(15.7), 1(48.8). The setation pattern on inner margins of middle and innermost posterolateral spines differs from *E. gibboides*; the middle spine has 3 stronger spinules separated by small spinules and inner spine bears several spinules distally.

FURCILIA IV (FIGURES 7D, 9A).—Carapace with a few small spines on lateral margins of rostrum and stronger median spine.

Antennular flagella with 8 or 9 segments, one of the paired aesthetes on outer ramus no longer bifurcate.

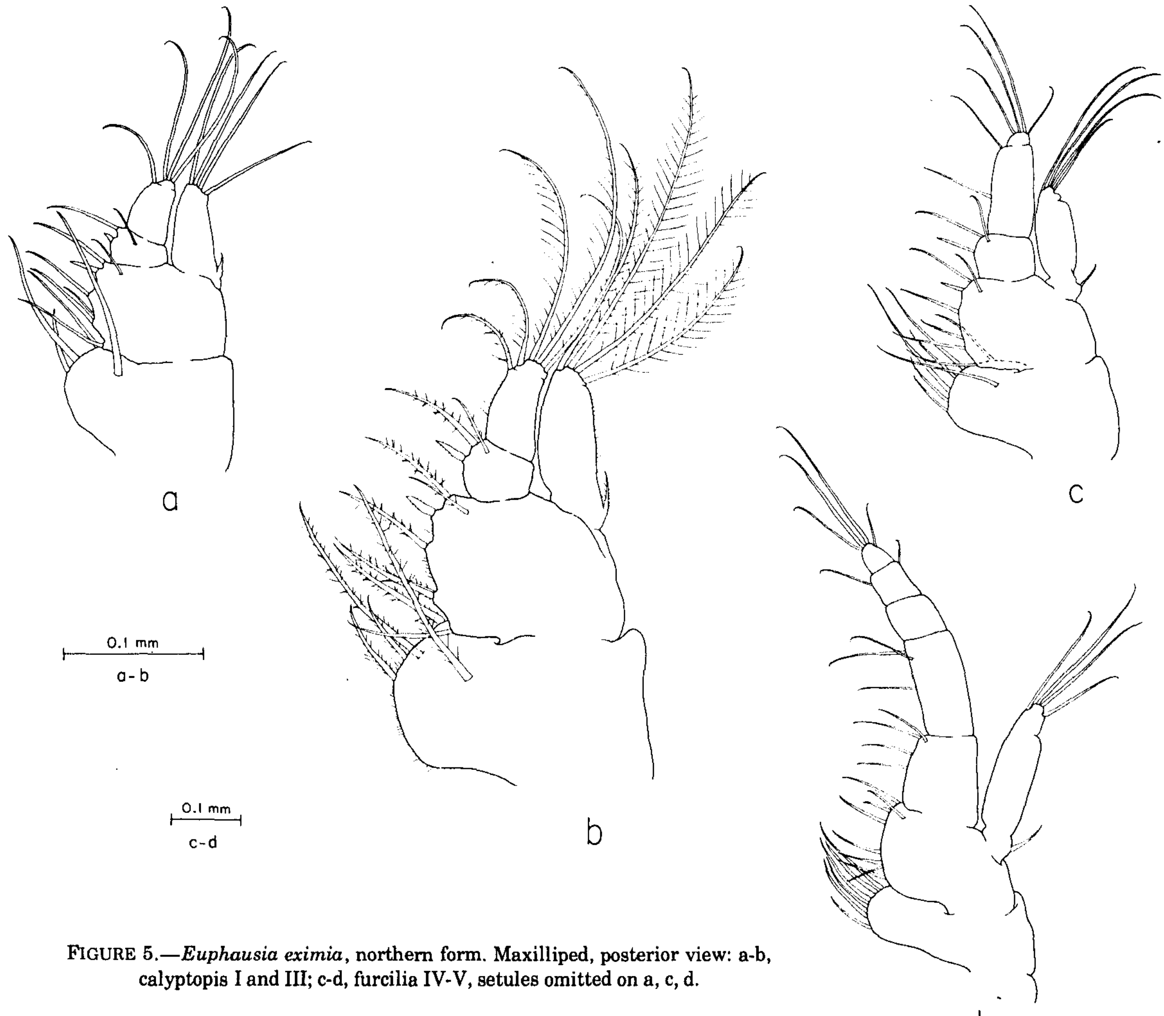

FIGURE 5.—*Euphausia eximia*, northern form. Maxilliped, posterior view: a-b, calyptopis I and III; c-d, furcilia IV-V, setules omitted on a, c, d.

Antenna (Figure 10a) modified from natatory to juvenile form, scale (exopod) with 11-13 (12) setae, flagellum (endopod) with 4-6 (4) segments, 2 or 3 (2) peduncular and 2-4 (2) flagellar.

Mandible (Figure 4c) modified with fewer, somewhat broader incisor teeth and lacinia mobilis missing or very much reduced; anterolateral process very small.

Maxilliped (Figure 5c) with 5 or 6 (6) setae on distal segments of lengthening endopod; basis and coxa with 6-8 (6-7) setae.

Leg 2 exopod with 5 or 6 (5) setae, gill with three lobes.

Leg 3 endopod with >2 terminal setae, exopod with 4-6 (5) setae; gill with three lobes, rarely with bud of fourth lobe.

Leg 4 endopod 5-segmented with 2-5 (2) terminal setae, exopod with 0-4 (0-2) setae; gill with small third lobe.

Leg 5 endopod usually unsegmented (ca. 3 segments occasionally seen) with 0-2 (0-1) terminal setae; exopod nonsetose; gill sometimes with bud of third lobe.

Leg 6 rudimentary with exopod bud and 2 or 3 gill buds.

Leg 7 with lightly pigmented photophore and three-lobed gill; leg 8 with three gill lobes.

Abdomen with photophores pigmented on segments 1, 2, and 4, and sometimes forming on segment 3.

Telson (Figure 6g) with 6-1 terminal spines and 3 pairs posterolateral spines (Table 1), 45% of 431 furcilia IV with 1 and 30% with 3 terminal spines (frequencies similar to those observed on developing telson of furcilia IV in premolt furcilia III); telson of next instar when forming beneath cuticle with 1 terminal and 3 pairs posterolateral spines. Inner margin of innermost posterolateral spine with series of strong spinules and shorter spinules interspersed. A second pair of lateral spines, or a

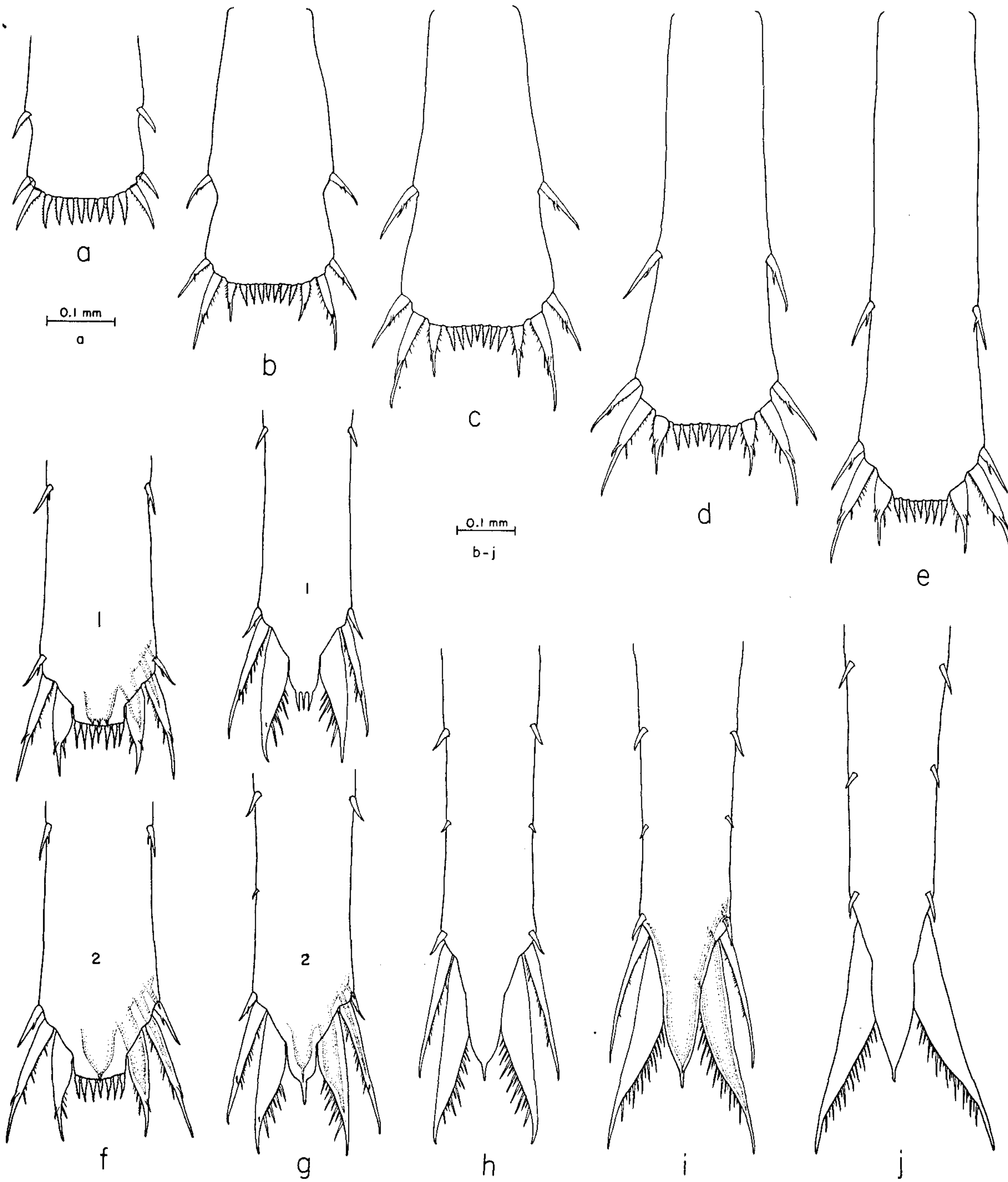

FIGURE 6.—*Euphausia eximia*, northern form. Telson, dorsal view: a-c, calyptopis I-III; d-e, furcilia I-II; f, furcilia III, 1-premolt to 3 terminal spines, 2-premolt to 1 terminal spine; g, furcilia IV, 1-with 3 terminal spines, 2-with 1 terminal spine; h-i, furcilia V-VI; j, juvenile I.

single additional spine on one side only, was found on 48% of 87 larvae examined for this feature.

FURCILIA V (FIGURES 7E, 9B).—Carapace with or without a few tiny lateral denticles on rostrum.

Antennule with lateral spine of peduncle segment 1 slightly longer than or equal to length of

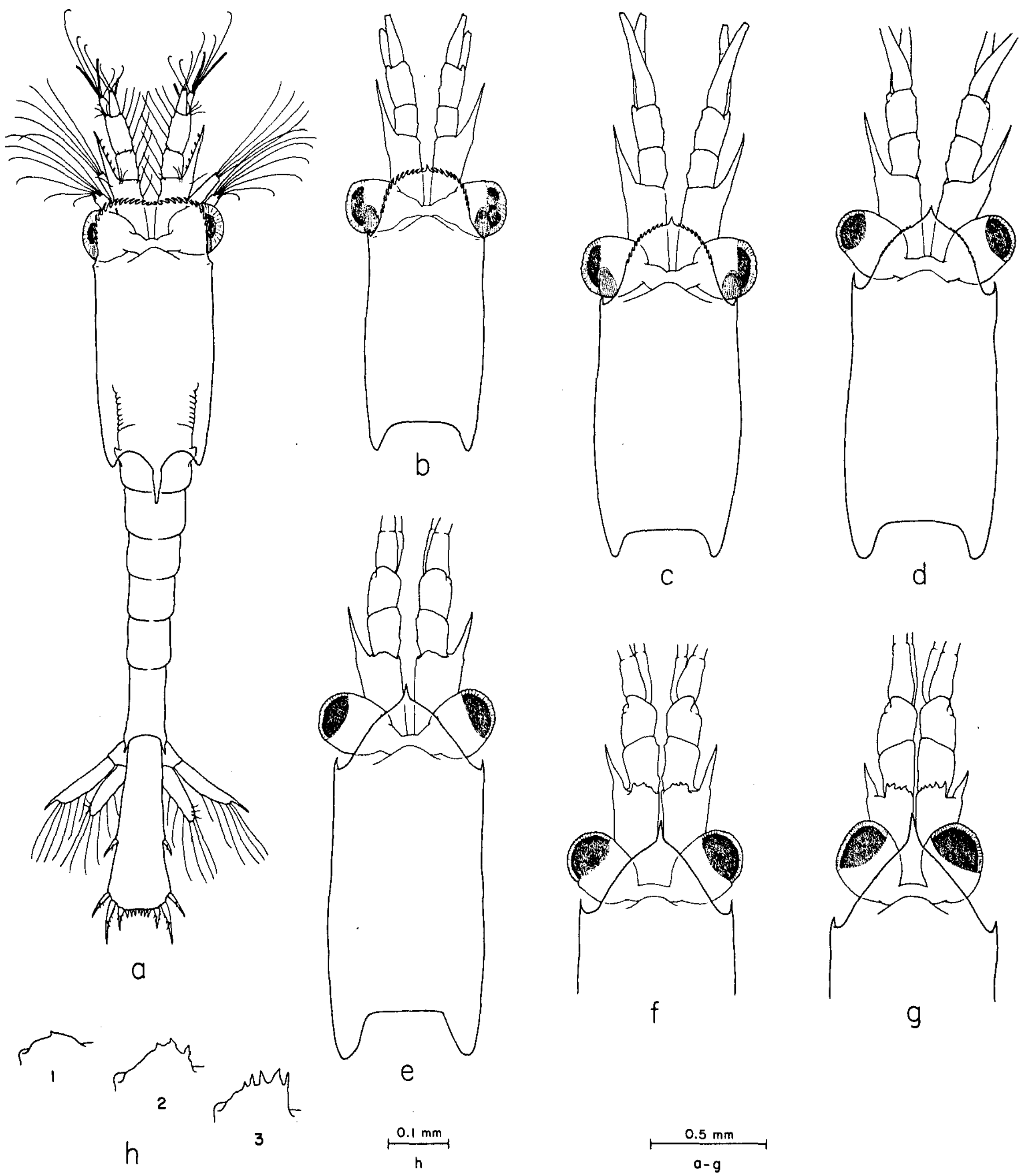

FIGURE 7.—*Euphausia eximia*, northern form, dorsal view: a-f, furcilia I-VI; g, juvenile I; h1-3, typical development of dorsal lappet on segment 1 of antennular peduncle in furcilia V-VI and juvenile I

segment 2, sometimes small variable rudiment of dorsal lappet present on segment 1 of peduncle with margin smooth or extended into 1 or 2 small knobs (Figure 7h-1); no specimens with flagella intact.

Antennal scale with 13-16 (14-15) setae and

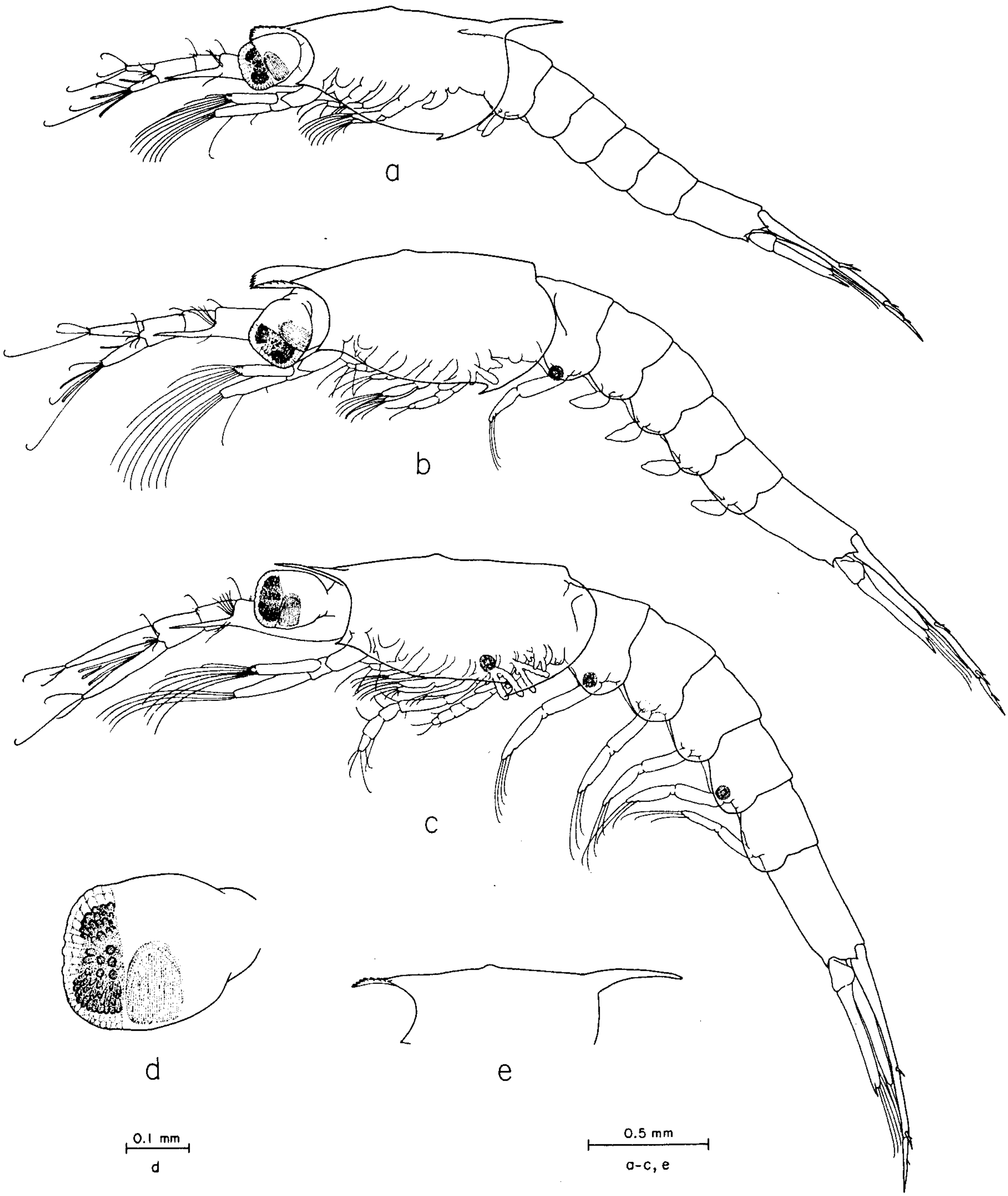

FIGURE 8.—*Euphausia eximia*, lateral view. Northern form: a-c, furcilia I-III; d, eye of furcilia II. Southern form: e, carapace of furcilia I.

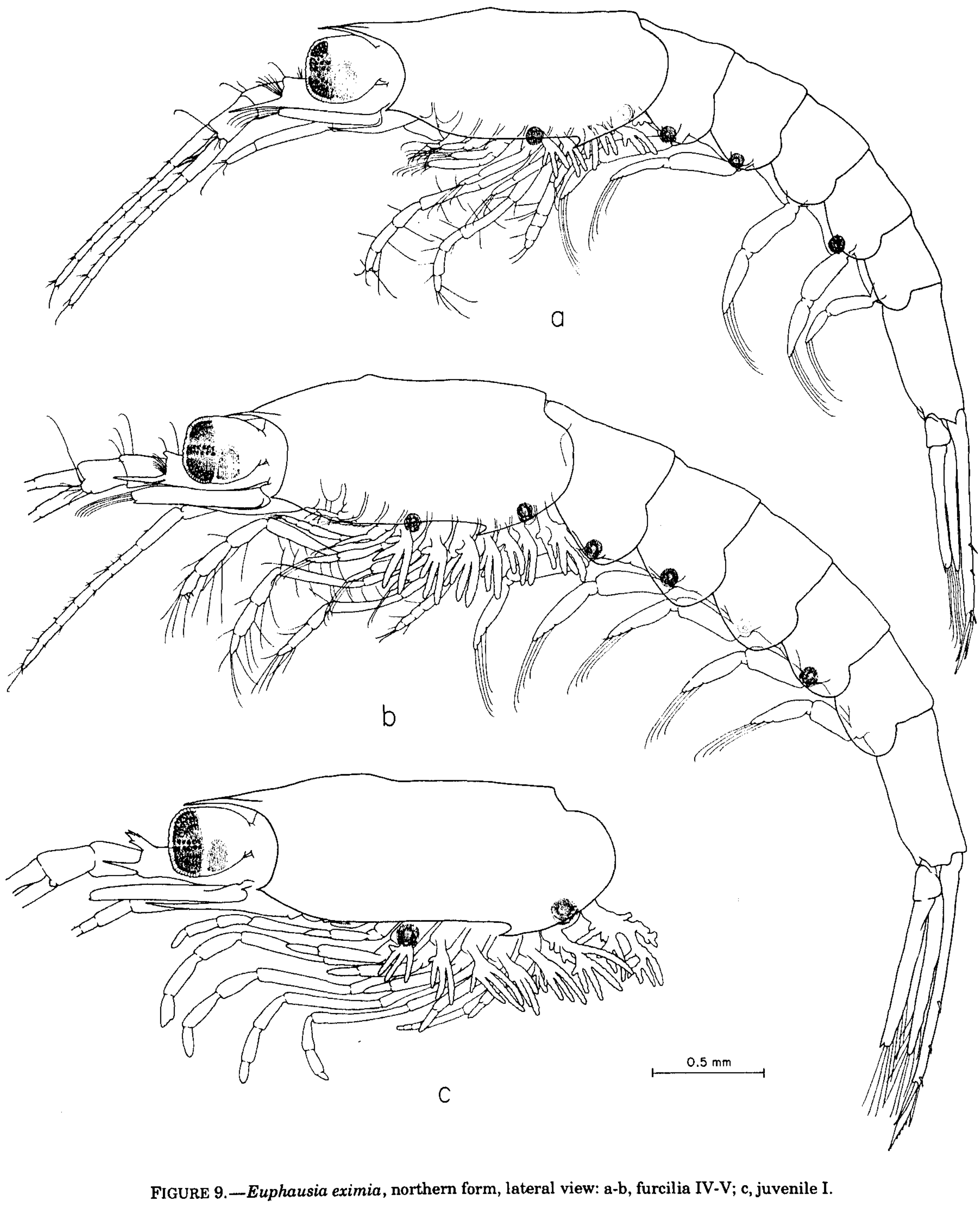

FIGURE 9.—*Euphausia eximia*, northern form, lateral view: a-b, furcilia IV-V; c, juvenile I.

flagellum usually with 12 segments, 3 peduncular and 7-10 (9) flagellar (Figure 10b).

Mandible (Figure 4d) without remnant of lacinia mobilis, palp lengthening.

Maxilliped (Figure 5d) with endopod now about equal in length to knee of leg 2, basis with 7-9 (8), and coxa with 6-8 (6) setae and usually without long seta on posterior face.

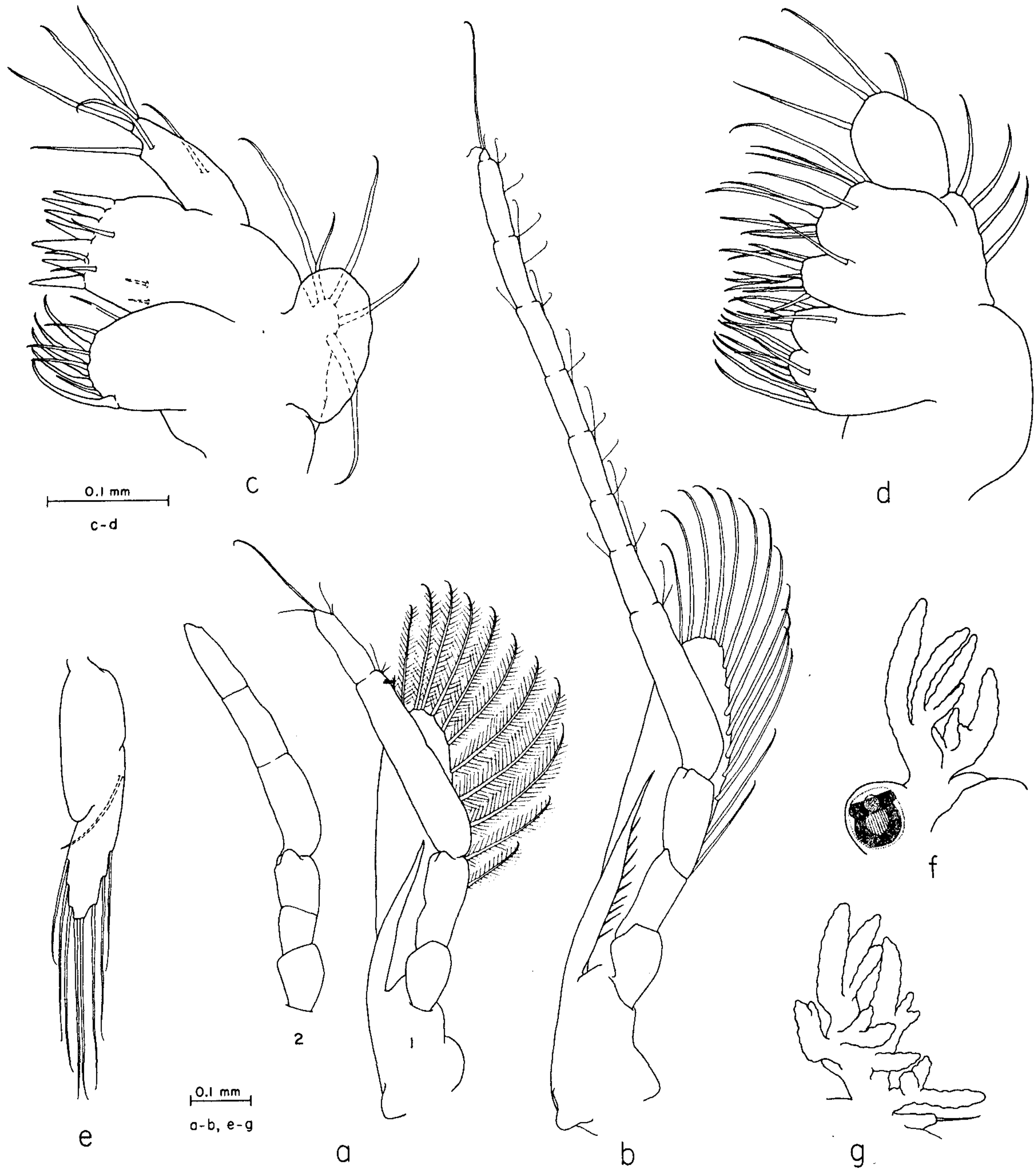

FIGURE 10.—*Euphausia eximia*, northern form. Antenna, ventral view: a 1-2, furcilia IV with variation in segmentation of endopod; b, furcilia V. Maxillule and maxilla, posterior view: c-d, juvenile I. Leg 2 exopod and legs 7-8: e-g, juvenile I (setules omitted in b-e).

Leg 2 exopod with 6 or 7 (6) setae, 1 of 28 appendages examined with additional proximal seta on inner margin common in furcilia VI and juvenile I (Figure 10e); gill sometimes with bud of fourth lobe.

Leg 3 exopod with 5-7 (6) setae, 1 of 34 appendages examined with proximal seta as on leg 2 exopod; gill sometimes with bud of fourth lobe.

Leg 4 endopod setose; exopod with 4-6 (5) setae; gill sometimes with bud of fourth lobe.

Leg 5 endopod with 4 or 5 (5) segments and 1-5 (2) terminal setae; exopod with 0-5 (0-2) setae; gill with bud of third lobe.

Leg 6 endopod unsegmented with 0 or 1 (0) terminal seta; exopod nonsetose and gill with two or three lobes.

Legs 7 and 8 with more than three gill lobes.

Abdomen with pigmented photophores on segments 1, 2, and 4, photophore on segment 3 sometimes with visible structure and some pigment.

Telson (Figure 6h) with 1 terminal and 3 pairs of posterolateral spines; telson of next instar when visible beneath cuticle with only 2 pairs posterolateral spines in 38% of 77 larvae; 97% of 71 furcilia V with 2 pairs lateral spines.

FURCILIA VI (FIGURE 7F).—Carapace with smooth lateral margins on well-developed rostrum.

Antennule with lateral spine about equal or less than length of peduncle segment 2, dorsal lappet of segment 1 with small knob or few spines (Figure 7h-2).

Antennal scale with 15-18 (16) setae; flagella no longer intact in preserved specimens.

Mandibles (Figure 4e) with palp relatively long, usually unsegmented, sometimes constricted into 2 or 3 weakly defined segments; 1 of 18 furcilia VI with 1 terminal seta on 2-segmented palp; slender terminally dentate plate near molar area of each mandible reduced, sometimes missing on left mandible.

Maxilliped continues to lengthen to juvenile form, endopod 5-segmented and setose, exopod still with 1 proximal and 4 distal setae, coxa without long seta on posterior face.

Leg 2 exopod with 6-8 (6-7) setae, 14 of 17 appendages examined with additional proximal seta on inner margin (Figure 10e); gill with four lobes.

Leg 3 exopod with 6-8 (6) setae, 22 of 24 appendages with proximal seta; gill with four lobes.

Leg 4 exopod with 6 or 7 (6) setae, 4 of 21 appendages with proximal seta; gill with four lobes.

Leg 5 endopod 5-segmented and setose; exopod with 4-6 (5) setae; gill with four lobes.

Leg 6 endopod with 0-5 (0-3) segments and 0-2 (1) terminal setae; exopod with 0-3 (0) setae; gill with four or more lobes.

Legs 7 and 8 with branching gill lobes, rudiment of leg 7 sometimes with terminal seta (Figure 10f).

Abdomen with photophores pigmented on segments 1-4.

Telson (Figure 6i) with 3 or 2 (in 32% of 59 larvae) pairs of posterolateral spines, developing telson of next instar when visible beneath cuticle with 2 pairs posterolateral spines in 18 of 19 larvae; 94% of 52 furcilia VI with 2 pairs of lateral spines.

JUVENILE I (FIGURES 7G, 9C).—Carapace with lengthening rostrum.

Antennule with lateral spine from slightly less than to about one-third the length of peduncle segment 2, lappet with 3-6 spines (Figure 7h-3).

Antennal scale with 16-19 (18) setae.

Mandibles (Figure 4f) with palp usually three-segmented, sometimes with 1 terminal seta and 0-3 lateral setae on segment 2, median armature as in furcilia VI.

Maxillule without or with seta on anterior margin of pseudexopod and maxilla with increasing numbers of setae on endopod and exopod (Tables 4, 5; Figure 10 c-d).

Leg 1 (maxilliped) exopod with 4-7 (4) setae.

Leg 2 exopod (Figure 10e) with 6-8 (8) setae, all with additional proximal seta on inner margin; gill with four lobes.

Leg 3 exopod with 6-8 (8) setae plus proximal seta on inner margin; gill with four lobes.

Leg 4 exopod with 6-8 (6-7) setae, 12 of 20 appendages with proximal seta; gill with four lobes.

Leg 5 exopod with 5-8 (6-7) setae, 3 of 17 appendages with proximal seta; gill with four lobes.

Leg 6 endopod with 4 or 5 (5) segments and 2-4 (2) terminal setae; exopod with 2-6 (2-3) setae; gill many branched.

Legs 7 and 8 (Figure 10f-g) rudiments each with terminal seta and ramified gills.

Telson (Figure 6j) usually with 2 pairs posterolateral and 2 pairs lateral spines (in 92% and 98% of 53 larvae).

In *E. eximia*, as in *E. gibboides*, the reduction in number of terminal telson spines appears not to be a reliable single guide to recognition of developmental stages in furcilia IV-VI but rather only one of a group of features that characterize these stages. Furcilia IV of *E. eximia*, as delimited in this study, had a variable number of terminal spines which overlapped with the number of terminal telson spines in furcilia III and V. Furcilia IV differed from furcilia III, however, in the following features: modification of both antenna and mandible; segmentation of antennular flagellum; setation of exopods of legs 2 and 3; setation and segmentation of leg 4 endopod; and setation of pleopods 2-5. Furcilia IV was separated from furcilia V by the segmentation of antennal flagella, maxilliped endopod, and leg 5 endopod; and endopod setation of pleopods 2-5, with small overlap on pleopod 3 only. Grouping of stages by terminal telson spine number would not be supported by these characters and if, for instance, all larvae with 1 terminal and 3 pairs posterolateral telson spines were grouped together, the range in size within the stage would become uncomfortably large, more than twice that of furcilia III and almost twice that in furcilia V. Variability in reduction of posterolateral spines was seen in furcilia VI and rarely in juvenile I.

The number of telson spines did relate to variation in size within a stage. For instance, furcilia III larvae that would molt from 7 to 3 terminal spines were 0.04 mm smaller on the average than those that would molt from 7 to 1 terminal spine and in furcilia IV, larvae with 3 terminal spines were 0.08 mm smaller on the average than those with 1 terminal spine. Variation in morphology within a stage was assessed in a sample of larvae from one location, as by midfurcilia phase there was a noticeable difference in rate of development between areas within the range of the population. It may be seen, for example, in a comparison of the length of larval stages at two locations in the California Current terminus (Figure 11) that, although they were smaller on the average, furcilia VI larvae from Station 10 in the mouth of the Gulf of California were within the size range of juvenile I of the slower growing larvae from Station 6 off western Baja California. The patterns of telson spine reduction in furcilia III-VI and juvenile I at these two locations, shown in Table 7, exemplify variation within the stages which appears to reflect the difference in rate of growth and morphogenesis.

South Pacific Population

Larvae from two areas within the southern range of *E. eximia* (Figure 1) were compared with larvae from the California Current terminus and, although the populations were generally similar, discrepancies were discovered. The most conspicuous differences proved to be in the armature of the telson. Among larvae in the South Equatorial and Peru Current population (southern form), the middle posterolateral spine was longer relative to the other two posterolateral spines and the majority of larvae had one pair of lateral spines only in all stages (Figure 12, Table 8); northern form larvae had 2 pairs of lateral telson spines from furcilia V. Furcilia III was slightly more variable in number of terminal telson spines while furcilia IV was less variable (Table 1). The carapace differed also with relatively longer posterodorsal spines from calyptopis I to furcilia I (Figures 3e-g, 8e) and sometimes with slightly larger and more persistant marginal spines.

Development of appendages was usually similar in the two forms. The lateral spine of the antennule was sometimes shorter and the lappet less developed in southern form furcilia VI and the setation of maxillule basal endite differed: 20, 62, and 75% of larvae examined had acquired 2 setae on the proximal margin of endite in furcilia V, VI, and juvenile I among northern form larvae while only 0, 2, and 17% of southern form larvae had a second seta in these stages.

Southern form larvae were smaller on the average in the furcilia phase but, as in the California Current terminus, differences in growth per stage between areas within the range of the population were noted. Developmental stages of *E. eximia* from the Peru Current (Stations 1520/1604) were larger on the average than those from the South

TABLE 7.—Pattern of telson spine reduction in furcilia III-VI and juvenile I in the northern form of *Euphausia eximia* at two locations (Stations 6 and 10) in the California Current terminus. Values indicate percentage with telson armature in stage.

		Terminal + posterolateral telson spines								
Stage	Stn	7+3	6+3	5+3	4+3	3+3	2+3	1+3	1+2	*n*
Furcilia	6	100.0	—	—	—	—	—	—	—	280
III	10	97.0	—	1.5	—	1.5	—	—	—	68
Furcilia	6	—	0.7	2.9	5.1	36.7	21.1	33.5	—	275
IV	10	—	—	—	—	15.1	19.0	65.9	—	126
Furcilia	6	—	—	—	—	—	—	100.0	—	41
V	10	—	—	—	—	—	—	100.0	—	97
Furcilia	6	—	—	—	—	—	—	92.9	7.1	14
VI	10	—	—	—	—	—	—	21.4	78.6	14
Juvenile	6	—	—	—	—	—	—	25.0	75.0	12
I	10	—	—	—	—	—	—	—	100.0	24

TABLE 8.—Number of pairs of lateral telson spines in furcilia IV-VI, juvenile I, and adult in northern and southern forms of *Euphausia eximia*. Values indicate percentage with telson armature in stage.

		Pairs of lateral telson spines				
Stage	Form	1	2	3	4	*n*
Furcilia IV	Northern	51.7	48.3	—	—	87
	Southern	98.4	1.6	—	—	61
Furcilia V	Northern	2.8	97.2	—	—	71
	Southern	97.9	2.1	—	—	48
Furcilia VI	Northern	5.8	94.2	—	—	52
	Southern	100.0	—	—	—	67
Juvenile I	Northern	1.8	98.2	—	—	55
	Southern	95.0	5.0	—	—	60
Adult	Northern	5.6	85.7	7.9	0.8	126
	Southern	97.5	2.5	—	—	121

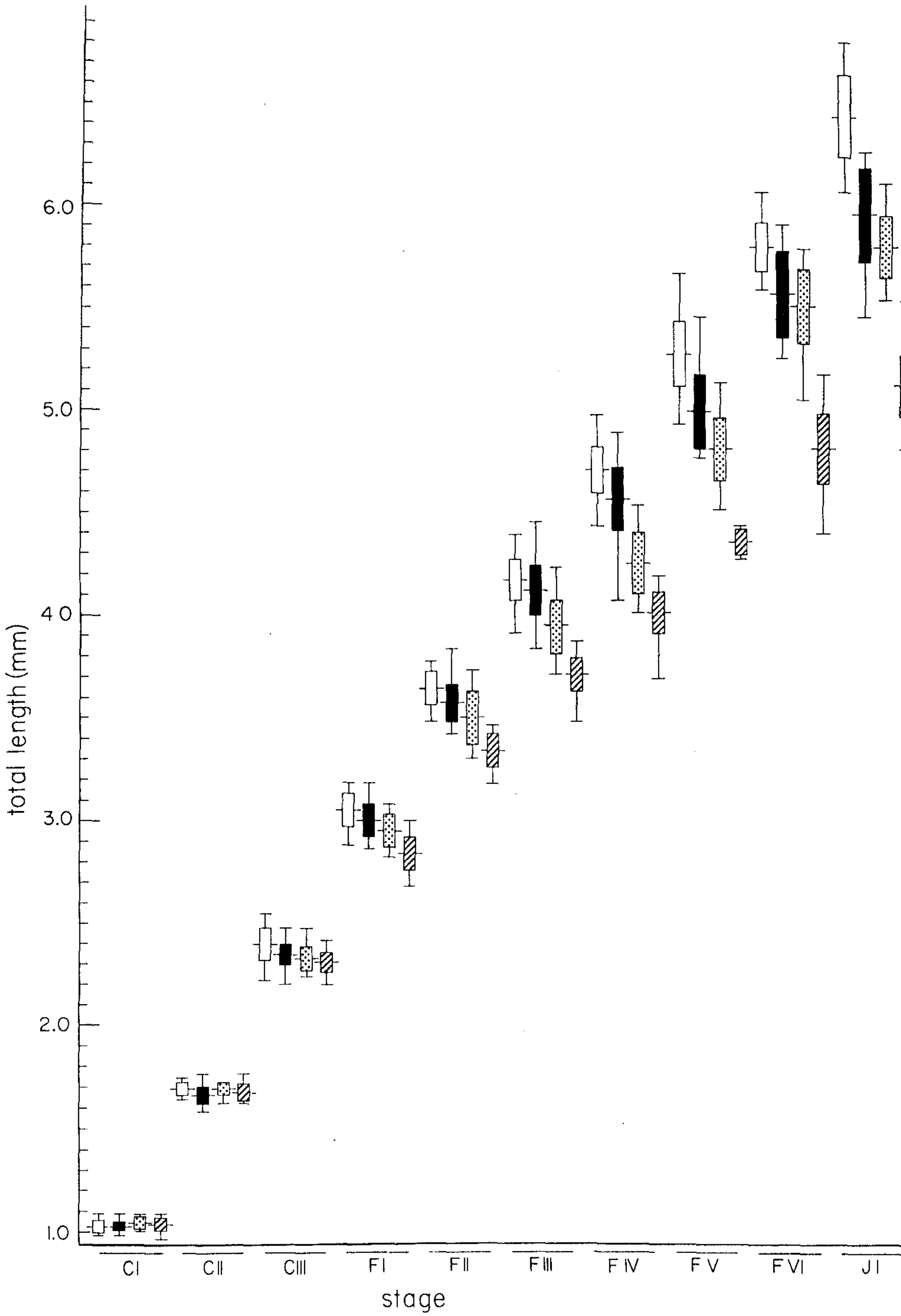

FIGURE 11.—Length of developmental stages of northern and southern forms of *Euphausia eximia* at four locations: mouth of Gulf of California, Station 10 (white); west of Baja California, Station 6 (black); Peru Current, Stations 1520/1604 (dots); South Equatorial Current, Station 21 (diagonal lines); vertical lines indicate range, horizontal lines indicate mean, and rectangles indicate sample standard deviations.

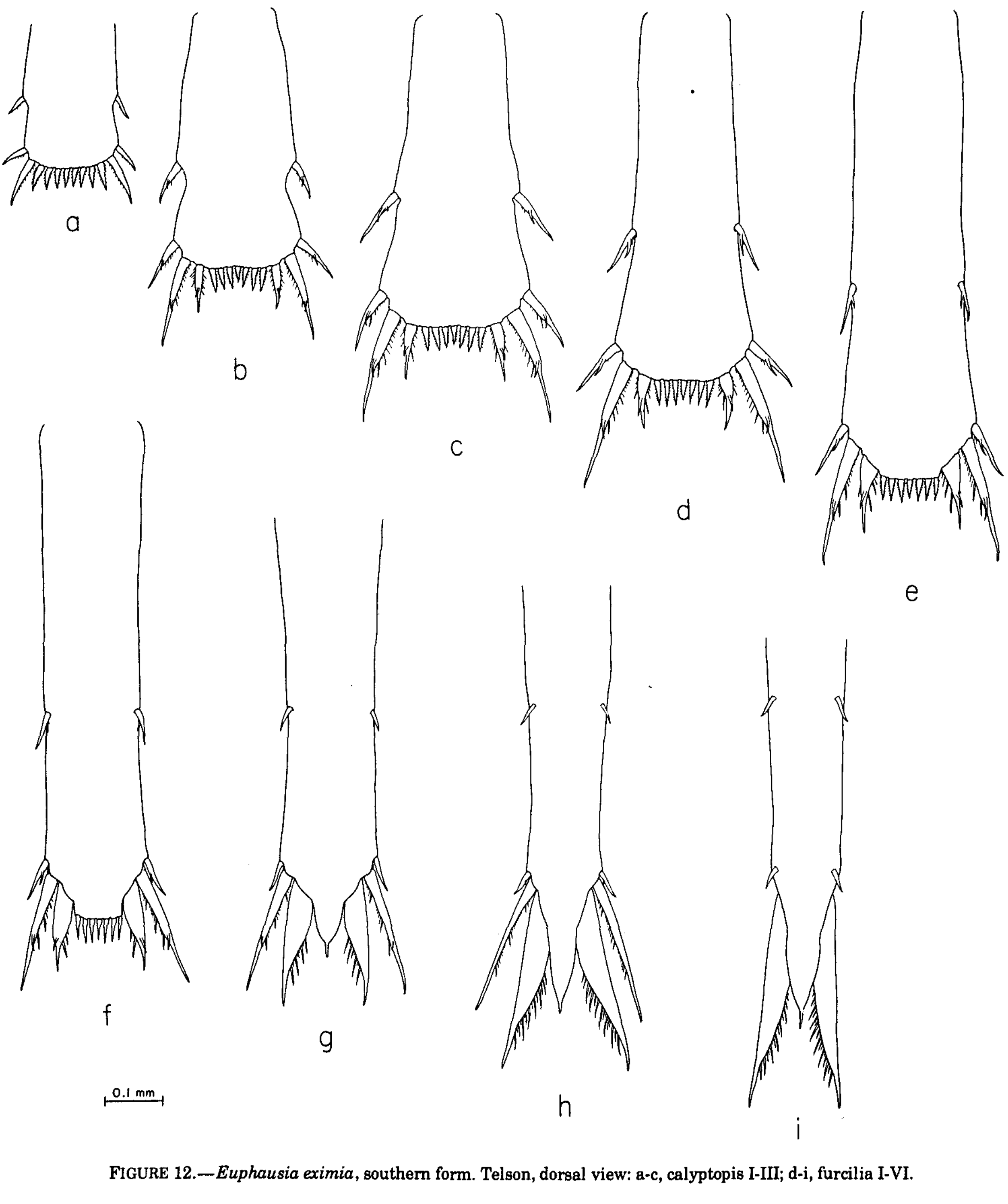

FIGURE 12.—*Euphausia eximia*, southern form. Telson, dorsal view: a-c, calyptopis I-III; d-i, furcilia I-VI.

Equatorial Current (Station 21). The lengths of larvae from these two locations are compared in Figure 11 (there were few furcilia V at Station 21 and consequently a small range in total length of this stage). Proportions of carapace length and telson width to total length were, on the average, as in northern form larval stages.

Because of the differences encountered between northern and southern form larvae, a preliminary survey of a few adult morphological characters was carried out on samples of *E. eximia* from across the species' range. Variation in number of pairs of lateral telson spines was found to persist in the adult (Table 8) and a discrepancy in the armature of antennular peduncle, described and photographed by Roger (1967) in equatorial *E. eximia*, was found as well. The inner process of antennular peduncle segment 2 had 1 or 2 spines in the northern form and 1-5 spines in southern form adults (Table 9) and the number of spines was related to size. Northern form adults <21 mm TL had 1 spine only; 1 or 2 spines were found only on the largest animals of 21-27 mm. Southern form *E. eximia* of 12-18 mm length had 1-4 spines but animals >18 mm had 2-5 spines; 1 spine was not seen on the larger adults. Armature of the process was often asymmetrical.

The differences between populations of *E. eximia* in frequency of numbers of lateral spine pairs on the telson of furcilia V-VI and adult, and in armature of adult antennular peduncle segment 2 proved highly significant ($P = <0.005$) in chi-square analyses.

TABLE 9.—Number of spines on inner process of antennular peduncle segment 2 in adults of the northern and southern forms of *Euphausia eximia*. Values indicate percentage with armature in form.

	Number of spines on inner process, antennular peduncle segment 2					
Form	1	2	3	4	5	Number
Northern	93.2	6.8	—	—	—	117
Southern	21.2	33.9	33.1	11.0	0.8	118

Vertical Distribution

When larvae were sorted for taxonomic study, they were also counted at three stations in day and night series of vertical samples taken during Krill Expedition (Brinton 1979). The data obtained are presented in Tables 10-12.

At Station 6, west of Baja California in the California Current (Table 10), the distribution of eggs corresponded with the nighttime range of adults indicating that the majority of female *E. eximia* had spawned in the surface waters during the night. The highest concentration of metanauplii was found in the layer below the surface, reflecting sinking of eggs prior to hatching (Mauchline and Fisher (1969) note that eggs of *Thysanoessa raschii* and *Meganyctiphanes norvegica* sank at 5.5-7.5 m/h in water of 33.3‰ and 15° C). The majority of calyptopes and early furcilia stages were in the surface layer during the day, sinking to strata beneath at night. The pattern shifted gradually in midfurcilia phase and from furcilia III, the stage when all pleopods are setose, the larvae moved deeper in the daytime and toward the surface at night, and developed stronger migrating capability with increasing size.

The larval population structure and distribution pattern varied at Station 10 in the mouth of the Gulf of California (Table 11). No eggs were found and larvae were most abundant in early furcilia stages instead of in the metanauplius and calyptopis phases. The metanauplii were seen at the surface, and there was no evidence of nightly

TABLE 10.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off western Baja California (Station 6) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	97.2	26.2	99.6	99.9	100.0	99.3	95.0	67.7	51.4	40.5	—	—
43-86	2.4	73.6	0.3	—	—	—	5.0	16.5	18.0	33.1	60.0	—
86-129	—	0.1	—	—	—	—	—	12.8	14.9	13.5	—	—
129-172	—	—	—	—	—	—	—	3.0	15.7	10.8	40.0	—
182-275	0.3	(<0.1)	0.1	0.1	—	—	—	—	—	—	—	100.0
275-368	0.1	0.2	—	—	—	—	—	—	—	—	—	—
368-461	—	—	(<0.1)	0.1	—	0.7	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	3,283	10,593	7,510	3,835	991	288	100	436	255	37	5	28
Night:												
0-43	88.1	5.7	1.3	1.5	3.8	0.7	0.8	11.1	48.8	50.0	77.8	69.1
43-86	8.4	79.5	70.7	54.5	41.1	52.9	70.7	74.4	51.2	50.0	22.2	15.6
86-129	3.5	14.8	28.0	44.0	55.0	46.4	28.4	14.5	—	—	—	15.3
129-172	—	—	—	—	0.1	0.1	0.1	—	—	—	—	—
182-275	—	—	—	—	—	—	—	—	—	—	—	—
275-368	—	—	—	—	—	—	—	—	—	—	—	—
368-461	—	—	—	—	—	—	—	—	—	—	—	—
461-554	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	143	5,402	4,380	2,089	4,018	1,180	874	379	125	18	9	392

TABLE 11.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the California Current terminus off the mouth of the Gulf of California (Station 10) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-43	—	—	99.7	99.8	99.9	99.8	99.8	99.3	79.0	33.2	41.2	—
43-136	—	—	0.3	0.2	0.1	0.2	0.2	0.7	21.0	61.8	45.1	—
136-229	—	—	—	—	—	—	—	12.8	14.9	13.5	—	—
229-322	—	—	—	—	—	—	—	—	—	—	7.8	—
322-415	—	—	—	—	—	—	—	—	—	—	—	100.0
No./1,000 m³	—	—	1,021	2,083	3,439	5,522	5,567	1,751	376	382	51	72
Night:												
0-43	—	100.0	100.0	100.0	100.0	99.9	99.8	96.9	93.3	100.0	100.0	72.2
43-86	—	—	—	—	—	0.1	0.2	3.1	6.7	—	—	27.8
86-129	—	—	—	—	—	—	—	—	—	—	—	—
129-222	—	—	—	—	—	—	—	—	—	—	—	—
222-315	—	—	—	—	—	—	—	—	—	—	—	—
315-408	—	—	—	—	—	—	—	—	—	—	—	—
408-501	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	—	249	79	1,223	3,464	4,260	4,508	1,651	416	150	11	126

TABLE 12.—Vertical distribution (percentage of stage at depth) of larvae and adults of *Euphausia eximia* in day and night samples from the South Equatorial Current (Station 21) and number/1,000 m³ in each stage.

			Calyptopis			Furcilia						
Depth (m)	Eggs	Metanauplius	I	II	III	I	II	III	IV	V	VI	Adult
Day:												
0-37	10.2	—	73.4	58.5	48.1	30.3	11.1	14.1	13.1	28.1	—	—
37-75	41.2	20.6	14.7	31.8	36.9	48.6	56.2	45.7	34.0	—	—	—
75-112	27.5	58.8	—	0.4	—	0.8	7.0	10.5	20.0	—	13.6	—
112-150	20.8	20.1	11.9	9.3	14.7	20.3	25.7	29.7	31.9	34.4	9.1	—
150-227	0.1	0.3	—	—	—	—	—	—	—	—	—	—
227-305	0.2	0.2	—	—	0.3	—	—	—	0.9	37.5	77.3	36.1
305-382	0.1	—	—	—	—	—	—	—	—	—	—	63.9
382-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	35,600	2,184	1,734	2,144	1,285	650	844	1,330	429	32	66	391
Night:												
0-36	21.7	—	25.7	31.9	34.5	35.4	20.4	6.4	16.8	—	19.9	45.1
36-72	20.1	—	59.3	62.1	60.1	51.0	49.1	49.1	50.4	100.0	80.1	39.8
72-108	56.2	98.0	14.1	5.9	5.3	13.3	30.5	43.9	32.8	—	—	15.1
108-144	0.5	—	—	—	—	0.3	—	—	—	—	—	—
144-223	1.4	2.0	0.8	0.1	—	—	—	—	—	—	—	—
223-302	(<0.1)	—	—	—	—	—	—	—	—	—	—	—
302-381	(<0.1)	—	—	—	—	—	—	—	—	—	—	—
381-460	—	—	—	—	—	—	—	—	—	—	—	—
No./1,000 m³	4,478	653	1,605	2,784	2,331	933	407	328	125	25	312	11,388

sinking of calyptopes and early furcilia larvae; almost the entire population remained in the surface layer until furcilia III. Diurnal vertical migration again developed in the last half of the furcilia phase.

The pattern of vertical distribution at Station 21 in the South Equatorial Current (Table 12) had features in common with the distribution observed at Station 6 but was less clearly defined. The position of the calyptopes reflected a developmental ascent from the depth at which eggs had hatched; calyptopis I was more abundant in the surface layer during the day than at night, and there was also some evidence of nighttime sinking in calyptopis II and III. In the furcilia phase the pattern of vertical migration was modified in that the larvae appeared to avoid the surface 0-35 m stratum to some extent. The population structure differed with calyptopis II being the most abundant larval stage.

The differences in larval vertical distribution appeared not to be related to time of sampling; in the upper 150-200 m, where most of the larvae were found, the three night samples were taken between 0000 and 0030 and the day samples in midafternoon (1600) at Stations 6 and 21 and midmorning (0800-0900) at Station 10 (Brinton 1979, figure 3).

DISCUSSION

The species of *Euphausia* were separated into groups, characterized by adult armature of carapace, abdomen, antennule, and petasma, by

Brinton (1975). Among species which have two lateral denticles on the carapace (group IA), *E. eximia* is most closely related to *E. krohnii* and *E. americana* by the conspicuous pectinate dorsal lappet on the first segment of the antennular peduncle. The larvae of *E. krohnii* have been described from the North Atlantic and Mediterranean by Frost (1934) and Casanova (1974) and, while it is not possible to compare the species in detail, the development of *E. eximia* appears to be very similar to that of the North Atlantic population of *E. krohnii*. The timing of acquisition of pigmentation in abdominal photophores may differ; Frost notes that all are pigmented in furcilia III but this condition was not normally seen in *E. eximia* until furcilia V. Development of the distinctive antennular lappet appears to begin at about the same stage (in furcilia V of *E. eximia* at 4.5-5.7 mm TL and in 5.9-6.1 mm larvae of North Atlantic *E. krohnii*) and with variable form. According to Soulier (1963) the lappet of Mediterranean *E. krohnii* develops in a fixed pattern, and >2 spines are not seen until 10 mm TL. There was greater variability in number of telson spines in furcilia IV of *E. eximia*, and one more stage in the furcilia phase, than noted by Casanova (1974) in *E. krohnii* from the Mediterranean. Larvae of the California Current population of *E. eximia* were intermediate in size between the large North Atlantic larvae of *E. krohnii* and the smaller Mediterranean population, while larvae of *E. eximia* from the South Equatorial Current tended to be similar in overall length to Mediterranean *E. krohnii*.

Larval forms appear to be very similar within *Euphausia* species group IA which, besides *E. eximia*, *E. krohnii*, and *E. americana*, includes *E. recurva*, *E. mutica*, *E. brevis*, and *E. diomedeae*. Their larvae share the following characters: spines on anterior margin of carapace in metanauplius, calyptopis phase, and early furcilia stages; a posterodorsal spine on carapace in calyptopis I-III and furcilia I; telson with middle posterolateral spine relatively long until midfurcilia phase; and a fixed pattern of pleopod development which progresses from 1 pair nonsetose to 1 pair setose plus 4 pair nonsetose, and finally to 5 pairs setose pleopods. Talbot (1974) noted variation in number of telson spines developing beneath the cuticle of furcilia III in *E. recurva-mutica* of the Agulhas Current, and Casanova (1974) described timing of events among larvae of *E. brevis* (e.g., modification of antenna and mandible, and development of legs), which is similar to the pattern discerned in *E. eximia*.

Developmental events may vary considerably, however, between the species groups of *Euphausia*. *Euphausia eximia* (group IA) and *E. gibboides* (group IB) differ in several details, some of which are listed in Table 13, although they share all the general features of group IA larvae except pattern of pleopod development. Larvae of *E. gibboides* are larger than those of *E. eximia*, on the average, in the metanauplius and calyptopis phases but they are similar in the furcilia phase due to a slightly higher rate of growth per stage in furciliae of *E. eximia*. The telson is wider in *E. gibboides* from calyptopis I through furcilia I, and the carapace is wider from calyptopis I-III, than in *E. eximia*, with no overlap in range of measurements.

The morphological differences observed within *E. eximia*, between larvae from the California Current terminus and the South Equatorial-Peru Current populations, appear related to the geographical separation of reproductive centers described by Brinton (1979) in his study of the distributional adaptations of euphausiids to the oxygen-deficient eastern tropical Pacific. He found that *E. eximia* achieved the highest densities (>500 beneath 1 m^2) in the South Equatorial Current and across the California Current-eastern tropical Pacific transition off Baja California, the productive zones marginal to the low oxygen waters. The species occurred consistently across a transect of the eastern tropical Pacific but only

TABLE 13.—Some differences in larval development of *Euphausia eximia* and *E. gibboides*.

Feature	*E. eximia*	*E. gibboides*
Pleopods: pattern of development from furcilia I (′ = nonsetose, ″ = setose)	1′ → 1″4′ → 5″	1′ → 1″3′ → 4″1′ → 5″
Telson: dominant pattern of terminal spine reduction from furcilia III to VI	7 → 3/1 → 1 → 1	7 → 5 → 3 → 1
innermost posterolateral spine, inner margin	With spinules	With distal spinule only from furcilia III
number of lateral spines	2 pairs from furcilia V	1 pair
Carapace: stage when anterior median spine develops	Furcilia I	Furcilia V-VI
Antennule: stage when dorsal lappet develops	Furcilia V-VI	Juvenile
Antenna: stage when modified to juvenile form	Furcilia IV	Furcilia V
Mandible: stage when modified to juvenile form	Furcilia IV	Furcilia VI
lateral knob in calyptopis phase	Absent	Present

sparsely (<4 under 1 m^2) from lat. 11° to 20° N where the surface temperature exceeded 26° C and lowest middepth O_2 values were <0.05 ml/l through a stratum of 600 m, and where water of westerly origin entered with the Equatorial Countercurrent. Larvae were not observed between lat. 2° and 20° N.

The significant difference in frequency of numbers of lateral telson spines on late furciliae of the California Current and the South Equatorial and Peru Currents may be evidence of the development of reproductive isolation between the two populations. The larval evidence was corroborated by a preliminary survey of adult *E. eximia* which showed a significant difference between populations in the armature of both telson and antennular peduncle. A more thorough examination of adult morphology is necessary, however, for an evaluation of the divergence within the species. The distribution of northern and southern forms observed (Figure 1) suggests that juveniles and adults of *E. eximia* are carried from the species' reproductive center off Baja California into the oxygen-deficient warm waters of the eastern tropical Pacific which may form an effective barrier between the reproductive areas of the two populations.

Variation in size of larvae at the same stage of development (Figure 11) between areas sampled within each population may be related to the amount of food available among other factors. Le Roux (1974), investigating the effects of diet and temperature on the larval development of *Meganyctiphanes norvegica*, demonstrated that rhythm of molt, growth, and morphogenesis were influenced by quality and quantity of food. With excess food, an elevation in temperature caused an acceleration in rate of molt but not precocious differentiation and reduction of the number of larval stages; the larvae were found to be a little smaller in a given stage at the higher temperature due to a decrease in growth per molt.

The relationship of surface temperature to size among *E. eximia* larvae studied was not consistent. Relatively smaller larvae were found at the higher temperature within the South Equatorial-Peru Current population (22° and 16° C at Stations 21 and 1520/1604) but in cooler waters of the California Current (18° and 24° C at Stations 6 and 10). There was a direct correlation of size with abundance of food, however, among California Current larvae; the volume of zooplankton biomass was very low at Station 6 but relatively high at Station 10 (Brinton 1979) reflecting displacement upward of recently upwelled waters with high concentrations of nutrients and probably, with relatively green waters, abundant food for larval forms. The larger size of larvae from Station 10 may also be related to their position in the water column; numbers of calyptopes and early furcilia at Station 6 sank below the surface stratum at night while those at Station 10 remained almost entirely day and night in the food-rich surface layer. Data on biomass and on larval vertical distribution were not available for Stations in the Peru Current for comparison with those in the South Equatorial Current.

Most species of euphausiids studied show indications of some downward daytime vertical migration from calyptopis II (Mauchline and Fisher 1969) but at Stations 6 and 21 (Tables 9, 11) the position of *E. eximia* calyptopes in day and night samples appeared to indicate a reverse pattern of movement. After a presumed developmental ascent from the depths at which nauplii hatched from sinking eggs, the majority of calyptopis I were found in the surface layer in the daytime and in deeper strata at night. The pattern continued through furcilia III at Station 6 and through calyptopis III, to some extent, at Station 21. As noted above, most larvae at Station 10 were found in the surface stratum in both day and night samples through furcilia II; the lack of nighttime sinking in early stages may be related to the shoaling of low oxygen water and upwelling conditions observed in the area (Brinton 1979).

The position of calyptopis I in the day-night series at Stations 6 and 21 suggests that the larvae were drawn to the surface layer by positive phototaxis. Sulkin (1973), working with two species of xanthid brachyurans, showed that, in the absence of light, the distribution of larvae varied with ontogeny; the four zoeal and one megalopa stage assumed a differential vertical distribution due to forces of gravity and hydrostatic pressure as well as different sinking rates, with early stages near the surface. In assessing the influence of light on depth regulation in the same species, Sulkin (1975) suggested that the observed positive phototaxis superimposed a diurnal vertical migration on the basic pattern of differential ontogenetic vertical distribution. Larvae of *E. eximia* appear to show a similar response during the calyptopis phase with modification of their behavior during ontogeny as furcilia develop a pattern of vertical migration similar to that of the adult.

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