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Larval Stages of Euphausiids with Descriptions of Those of *Thysanoessa longipes* BRANDT

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Abstract

Numerous forms of furcilia larvae of euphausiids are classified into 9 stages, instead of the previously suggested 3 or 4 stages. The number of the variously differentiated pleopods and the terminal spines on the tip of the telson, which are easy to examine, are taken into account and formulated into new stage names. The previous simple classifications are advantageous in common application to many species but may be disadvantageous in distinguishing interspecific differences in the developmental pathways. Using our finer classification, the interspecific difference between *Euphausia pacifica* HANSEN and *Thysanoessa longipes* BRANDT in the Japan Sea, and the intraspecific difference between the Japan Sea and south Californian populations of *E. pacifica* are described.

Because larval stages of *T. longipes* have not yet been reported, their descriptions are given.

I. Introduction

It is known that the development and differentiation in the external morphology of the euphausiid larvae can be followed by a few general rules (*cf.* MAUCHLINE and FISHER 1969). (1) The larva develops from an egg to the furcilia stage through 2 stages of nauplius, 1 stage of metanauplius and 3 stages of calyptopis. After several molts during the furcilia stages, the larva grows to the juvenile stage which is morphologically identical to the adult except for the secondary sexual characters. (2) Development and differentiation of the swimming legs or pleopods, which do not appear in the calyptopis stages, progress from anterior pairs to posterior pairs in the furcilia stages. This differentiation occurs discretely; non-setose primitive pleopod appears at first, and following molt, it always becomes setose. Differentiation of the setose pleopods from the non-setose ones requires one molt. (3) The number of terminal spines on the tip of the telson is constant throughout early furcilia stages, but decreases during late furcilia stages; a pair of spines usually disappear after each molt.

On the other hand, the number of the pairs of non-setose pleopods which appear

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first in the early furcilia stages is so variable that developmental pathways of the pleopods are inevitably numerous. Among these pathways, the "dominant pathway" which can be traced through the subsequent dominant forms occured in high frequency, is usually recognized (*e.g.* FRASER 1936). Since the dominant forms vary

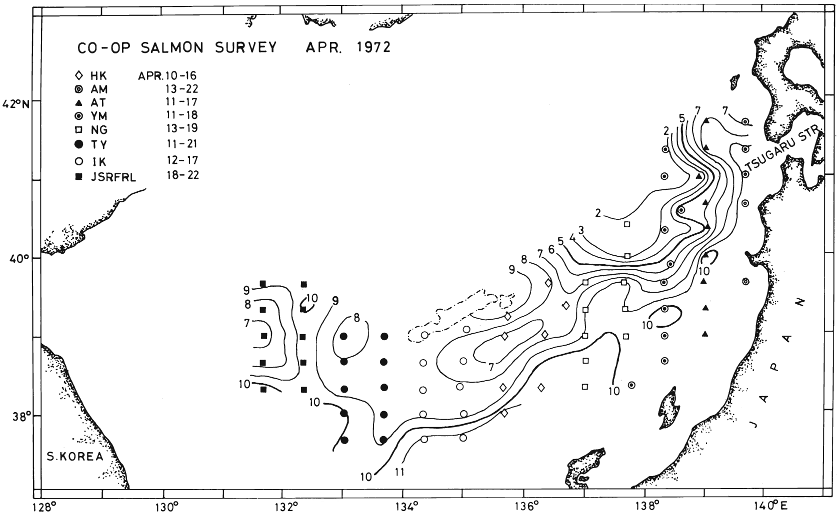

Fig. 1. Location of stations in April, 1972. Isotherms indicate water temperature (°C) at 50 m depth. All samplings were performed within 13 days with cooperation of 8 institutions. For abbreviations of the names of respective institutions, HK, AM, *etc*, see text.

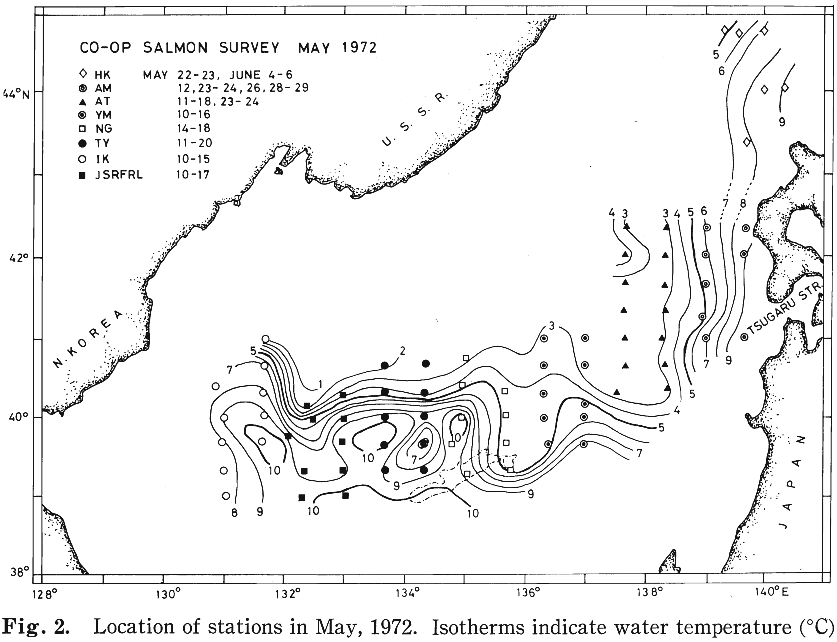

Fig. 2. Location of stations in May, 1972. Isotherms indicate water temperature (°C) at 50 m depth. All samplings were performed within 28 days with cooperation of 8 institutions. For abbreviations of the names of respective institutions, HK, AM, *etc*, see text.

from species to species, the stages themselves have been newly named in each species.

SHEARD (1953), MAUCHLINE (1959) and SOULIER (1965b) classified furcilia forms into only 3 or 4 stages or phases. Simple classifications are advantageous in common application to many species. However, such classifications may result in the omission of several intermediate stages and, in turn, are disadvantageous in differentiating subtle variation in developmental pathways between different species and often between different populations of the same species. Finer classification of stages or phases is needed.

In this paper, we divide all forms of furcilia larvae of *T. longipes* and *E. pacifica* collected in the Japan Sea into 9 practical stages. These were theoretically deduced from the three general rules mentioned above. The validity of our classification is discussed in the close examination of the larval development of euphausiids.

II. Materials and Methods

The samples examined were gathered by various institutions that participated in the Cooperative Salmon Survey near the polar front in the Japan Sea in April and May, 1972. The institutions involved were Hokkaido Central (HK), Aomori (AM), Akita (AT), Yamagata (YM), Niigata (NG), Toyama (TY) and Ishikawa (IK) Prefectural Fisheries Experimental Stations and the Japan Sea Regional Fisheries Research Laboratory (JSRFRL) of the Fisheries Agency of Japan. Stations where the samples were collected and dates of samplings are shown in Figs. 1 and 2, along with water temperature at the level of 50 m depth (NAGAHARA unpublished). As shown in Figs. 1 and 2, both April and May samples were collected synoptically over wide sea areas around the polar front.

The North Pacific Standard net, (45 cm in diameter, 180 cm long, 0.35 mm mesh aperture) was hauled vertically from 150 m depth to the surface at all stations. Since the flow-meter was not always available, an empirical linear regression equation,

$$v = 0.351 \times l - 24.11,$$

derived by MORIOKA and KOMAKI (unpublished) was used to compute the volume of water filtered (v in m^3) from the length of wire paid out (l in m).

Eggs, larvae, juveniles and adults of all euphausiids were identified and enumerated. Body length, from behind the eye to the posterior end of the sixth abdominal segment, was measured on every specimen using a Kogakusha® micrometer (precision, ± 0.01 mm). For comparison with previous data, total length, from the anterior end of the rostrum to the posterior end of the telson, was also measured.

III. Results

Euphausiids which had been recored from the Japan Sea are *Euphausia pacifica* HANSEN, *Pseudeuphausia latifrons* (G. O. SARS) HANSEN, *Thysanoessa inermis* (KRØYER) HANSEN, *T. longipes* BRANDT and *T. raschii* (M. SARS) HANSEN (PONOMAREVA 1955, KOMAKI and MATSUE 1958). Recently ARAKI (1971) found *E. diomedeae* ORTMANN, *E. nana* BRINTON, *Nematoscelis gracilis* HANSEN, *Stylocheiron affine* HANSEN and *T. gregaria* G. O. SARS as well as previously reported species except *T. raschii*. *T. inermis* and *T. raschii* were reported to be found abundantly in the northern coastal waters, *T. gregaria* was in the limited area around the western entrance of the Tsugaru Straits, and *E. diomedeae*, *E. nana*, *N. gracilis*, *P. latifrons* and *S. affine* were in the warm Tsushima current intruding from the south. *E. pacifica* and *T. longipes* are most dominant in the central Japan Sea (PONOMAREVA 1955, KOMAKI and MATSUE 1958, ARAKI 1971). In this investigation, adult forms collected included only the latter two species, probably because the samplings were restricted to the polar front regions in spring.

In addition, larvae of 2 species were also found. Referring to BODEN (1950) one of the larval forms was identified as *E. pacifica*. The other was likely to be one of *E. nana*, *N. gracilis* or *T. longipes* larvae of which are not described yet. Because any adult of *E. nana* or *N. gracilis* was not collected, it is reasonably suggested that no larvae of *E. nana* and *N. gracilis* were detected in this investigation. If larvae of *E. nana* were collected, they might be easily distinguished from its allied *E. pacifica* larvae by body size. These suggest that the larval forms collected, other than those of *E. pacifica* were of *T. longipes*.

These latter larvae could also be distinguished morphologically from others. The first calyptopis of almost all euphausiid species bear 6 terminal spines on the tip of the telson. This increases to 7 at the second calyptopis stage, but doesn't change till the later furcilia stages. In fact, in the present larvae, the number of terminal spines is also 6, but remains constant throughout first calyptopis to early furcilia stages. Reduction in number takes place at the later stages. No larvae collected other than those of *E. pacifica* bear 7 spines. Only *Stylocheiron suhmii* is reported to follow the same way (LEBOUR 1926a, b) but this species does not inhabit the Japan Sea. By these facts, the present larvae is identified as *T. longipes*.

Because development of pleopods and reduction of the terminal spines on the telson progress in regular manner, and because these appendages and spines can be easily examined, we took them as practical criteria into account in the classification of furcilia larvae. All possible forms of the furcilia stages bearing a different number of pleopods and spines are listed in the first column of Table 1. N and S mean non-setose primitive pleopods and setose pleopods, respectively. Figures affixed to the letters indicate the number of pairs of these pleopods. Thus the formula F(0) indicates a furcilia larva without pleopods and F(2S3N) indicates a larva with

Table 1. Furcilia forms and stages of *Euphausia pacifica* and *Thysanoessa longipes* in the Japan Sea. Those of *E. pacifica* in southern California waters reported by BODEN (1950) are also tabulated.

Form	Stage	Frequency of Occurrence				
		E. pacifica			*T. longipes*	
		April	May	BODEN[a]	April	May
F(0)	F(0)	713	15	3	116	401
F(1N)	F(n)	411	20	9	7	12
F(2N)	F(n)	97	7	19	1	12
F(3N)	F(n)	45	3	14	4	15
F(4N)	F(n)	24	2	–	6	28
F(5N)	F(5N)	1	–	–	15	43
F(1S)	F(sn)	8	–	–	–	–
F(1S1N)	F(sn)	65	–	–	–	1
F(1S2N)	F(sn)	98	3	–	–	1
F(1S3N)	F(sn)	210	7	4	–	1
F(2S)	F(sn)	1	–	–	–	–
F(2S1N)	F(sn)	10	–	–	–	–
F(2S2N)	F(sn)	59	2	–	–	1
F(3S)	F(sn)	–	–	–	–	1
F(3S1N)	F(sn)	35	–	–	–	–
F(4S)	F(sn)	11	–	–	–	–
F(1S4N)	F(SN)	42	8	8	–	3
F(2S3N)	F(SN)	45	3	39	1	5
F(3S2N)	F(SN)	73	6	29	3	8
F(4S1N)	F(SN)	266	12	8	3	16
F(7Tsp)	F(7Tsp)	515	40	242	–	–
F(6Tsp)	F(6Tsp)	20	2	2	20	83
F(5Tsp)	F(5Tsp)	270	17	49	–	–
F(4Tsp)	F(4Tsp)	12	1	6	8	12
F(3Tsp)	F(3Tsp)	92	9	36	1	1
F(2Tsp)	F(2Tsp)	7	2	3	1	1
F(1Tsp)	F(1Tsp)	111	21	29	–	2

[a] Rearranged from BODEN (1950).

pleopods the first two pairs of which are setose, but the last three are non-setose. The formulae F(7Tsp), F(6Tsp), *etc* are used to denote furcilia larvae which bear respective number of the terminal spines on the telson, and carry 5 pairs of developed setose pleopods.

In most euphausiid species, sequential reduction of the terminal telsal spines seems to be a constant feature, but the reduction does not occur until the larva with developed setose pleopods molts. The known exceptions are *Nematoscelis difficilis*, *N. gracilis* (GOPALAKRISHNAN 1973), *N. megalops* (FROST 1935), *N. microps* (GURNEY 1947, GOPALAKRISHNAN 1973), *N. microps-N. atlantica* (CASANOVA-SOULIER 1968), *N. tenella* (GOPALAKRISHNAN 1973), *P. latifrons* (TATTERSALL 1936) and *P. sinica* (WANG

1965). In these cases the reduction occurs before all 5 pairs of pleopods become setose.

According to the general rules cited earlier, the third calyptopis should molt to either of the furcilia forms, expressed by F(0), F(1N), F(2N), F(3N), F(4N) or F(5N). And F(0) should molt to F(1N)–F(5N). From F(1N), larvae molt to F(1S)–F(1S4N) and from F(5N) to F(6Tsp) or F(7Tsp). While larvae of most species bear 7 terminal spines [F(7Tsp)], species such as *T. longipes* have 6 spines [F(6Tsp)].

Conclusively, along these moltings it is suggested that all possible forms of furcilia larvae can be combined into the 9 practical stages. Although close description of *T. longipes* larvae are given below, the characteristics of these 9 stages are summarized as follows:

Stage F(0): larvae without pleopods,
Stage F(n): larvae with non-setose pleopods less than 5 pairs,
Stage F(5N): larvae with 5 pairs of non-setose pleopods,
Stage F(sn): larvae with both non-setose and setose pleopods less than 5 pairs,
Stage F(SN): larvae with 5 pairs of non-setose and setose pleopods,
Stage F(6Tsp) or F(7Tsp): larvae with 5 pairs of setose pleopods and 6 or 7 terminal spines on the tip of the telson,
Stage F(4Tsp) or F(5Tsp): larvae the spine number of which is reduced from 6 or 7 to 4 or 5,
Stage F(2Tsp) or F(3Tsp): larvae with 2 or 3 terminal spines,
Stage F(1Tsp): larvae with only 1 spine.

In these formulae capital letters (N) or (SN) indicate that all 5 pairs of their pleopods will be setose in the next stage after one molt, and small letter (n) or (sn) indicate that more than one pair of pleopods will remain non-setose after following one molt. These formulae make it possible to describe morphological characteristics of different forms of furcilia larvae through numbering of the pleopods and the telsal spines that are quite easily examinable.

IV. Discussion

Table 1 shows the individual numbers of various forms of *T. longipes* and *E. pacifica* which occurred in the Japan Sea, with those reported by Boden (1950) on *E. pacifica* in southern California waters. The dominant pathway of *E. pacifica* in southern California waters is likely to be

F(2N)⟶F(2S3N)⟶F(7Tsp)⟶F(5Tsp)⟶F(3Tsp)⟶F(1Tsp)

and/or

F(3N)⟶F(3S2N)⟶F(7Tsp)⟶F(5Tsp)⟶F(3Tsp)⟶F(1Tsp).

However, early steps in the dominant pathway of the Japan Sea population seems to be very different;

F(0)⟶F(1N)⟶F(1S3N)⟶F(4S1N)⟶F(7Tsp)⟶F(5Tsp)⟶F(3Tsp)⟶ F(1Tsp).

According to BODEN (1950), the form F(0) is absorbed together with the forms F(1N)–F(3N) into a single Furcilia I stage, and F(1S3N) and F(4S1N) are absorbed together with other forms which bear mixed setose and non-setose pleopods into a Furcilia II stage. However, as mentioned above, each of the three forms F(0), F(1S3N) and F(4S1N) are clearly independent stages in the Japan Sea population. If the BODEN's scheme is followed, there will be a single pathway common to both the Japan Sea and the California populations, that is,

Furcilia I⟶F. II⟶F. III⟶F. IV⟶F. V⟶F. VI⟶F. VII.

In our classification, the pathways of the southern California and the Japan Sea populations can be expressed separately as follows;

S. California: F(n)⟶F(SN)⟶F(7Tsp)⟶F(5Tsp)⟶F(3Tsp)⟶F(1Tsp)

and

Japan Sea: F(0)⟶F(n)⟶F(sn)⟶F(SN)⟶F(7Tsp)⟶F(5Tsp)⟶
F(3Tsp)⟶F(1Tsp),

respectively. Thus, the differences in the dominant pathway between the two populations can be revealed only by our new scheme of classification. The main results of consequence are two additional intermediate steps, F(0) and F(sn), introduced into the Japan Sea population.

During early stages, *T. longipes* develops through the same dominant pathway as the other *Thysanoessa* species such as *T. gregaria* (EINARSSON 1945, GURNEY 1947, SHEARD 1953, BARY 1956), *T. inermis* (EINARSSON 1945), *T. longicaudata* (LEBOUR 1926c, EINARSSON 1945, SOULIER 1965a), *T. raschii* (EINARSSON 1945, MAUCHLINE 1965); namely

F(0)⟶F(5N)⟶F(6Tsp) or F(7Tsp).

The previously reported dominant pathway of other *Thysanoessa* species ends with F(7Tsp), but *T. longipes* ends with F(6Tsp) (Table 1). This should be expressed in our classification as

F(0)⟶F(5N)⟶F(6Tsp), [or F(7Tsp) in all other species].

In the previous classifications F(0) can not be distinguished from F(5N), and F(6Tsp) from F(7Tsp).

During later steps, consequently, the successive reduction in the number of terminal telsal spines in *T. longipes* proceeds along the unique pathway starting from 6;

F(6Tsp)⟶F(4Tsp)⟶F(2Tsp)⟶F(1Tsp).

It has been reported for many species that the dominant pathway is variable even in the same species with time and place (FRASER 1936, EINARSSON 1945, SHEARD 1953, MAUCHLINE 1959, 1965, SOULIER 1965b, MAKAROV 1974). LE ROUX (1973, 1974) shows experimentally on *Meganyctiphanes norvegica* and *Nyctiphanes couchii* that the pathway as well as growth rate changes with feeding mode; the dominant pathway of a strain feeding on phytoplankton is different from that of the strain supplied with zooplankton. Therefore, as we have seen in *E. pacifica*, the larval development of a species in a certain place and time including the present data is not always identical with different populations of the same species. If any simplified classifications are applied, such a difference may be overlooked. Nine stages proposed here, however, can well describe the inter- and intraspecific differences.

V. Descriptions of *T. longipes* larvae

Eggs, nauplii and metanauplii of *T. longipes* were not encountered in the present plankton samples. Since the diameter of eggs of *T. longipes* is 0.99–1.05 mm (PONOMAREVA 1959), the eggs would have been collected by the net used (0.35 mm in mesh aperture), if they were distributed in the upper 150 m. The spawning and development in early stages of this species possibly takes place in the depths (KOMAKI 1976). The larvae from calyptopis I to post-furcilia or juvenile are described below.

In furcilia stages, forms F(0), F(5N), F(6Tsp), F(4Tsp), F(2Tsp) and F(1Tsp) are dominant in the Japan Sea, and all stages are slender as in larvae of other *Thysanoessa* species.

(1) Calyptopis stages

Calyptopis I (Fig. 3)

The carapace without lateral denticles is hood-shaped. The antennular peduncle consists of one segment. Antenna, mandible, maxillule, maxilla and the first thoracic limb are also present. Abdomen is cylindrical and unsegmented, furnished with 6 terminal spines and three pairs of lateral spines on posterior end. On the ventral side of the abdomen, one pair of short spines exists. Total length: 0.96–1.30 mm.

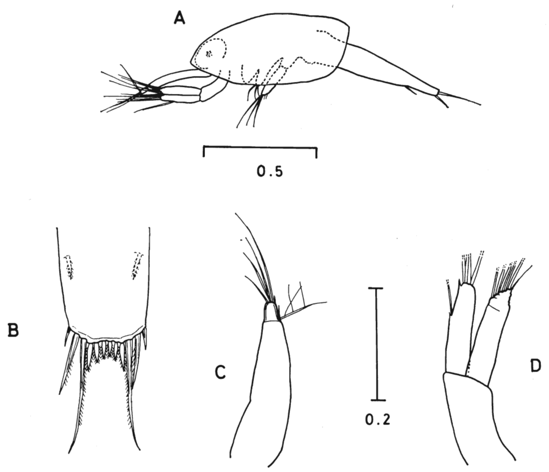

Fig. 3. *Thysanoessa longipes*, calyptopis I. A: whole animal, lateral view; B: telson, dorsal view; C: antennule; D: antenna. Scale in mm.

Calyptopis II (Fig. 4)

The carapace is of the same shape as in the previous stage, but in side view the posterior margin is a little more pointed, the tip of which reaches behind the posterior margin of the lateral parts, as in the case of *T. longicaudata* (EINARSSON 1945).

The abdomen has six segments developed. The terminal segment shows indications of uropods. It is armed with six terminal spines as in the previous stage. Total length: 1.43–1.93 mm.

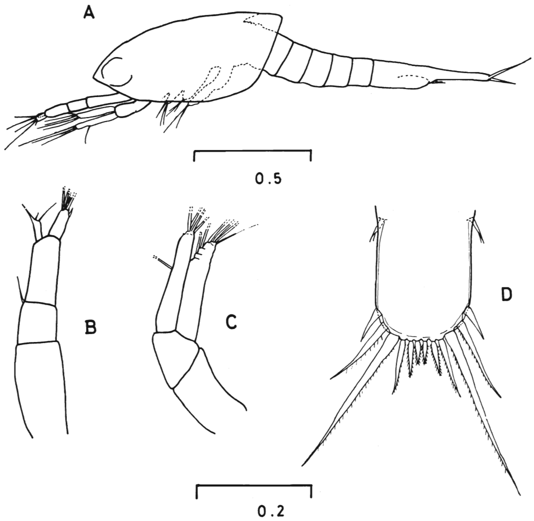

Fig. 4. *Thysanoessa longipes*, calyptopis II. A: whole animal, lateral view; B: antennule; C: antenna; D: telson, dorsal view. Scale in mm.

Calyptopis III (Fig. 5)

In this stage, the carapace covers the eyes. The antennular peduncle has three segments, and the proximal one has developed a spine that reaches almost to the end of the third segment. Uropods are free. Total length: 1.89–2.54 mm.

(2) Furcilia stages

Stage F(0) (Fig. 6)

In this stage there are no pleopods. The frontal plate of the carapace is pointed as in *T. macrura* (RUSTAD 1930). The lateral margins of the carapace have no conspicuous denticle, but when greatly magnified, a very delicate spine is sometimes observed. Eyes are free with long eyestalks. The antennular spine extends to about the middle of the third segment of the antennular peduncle. Total length: 2.28–3.20 mm.

Stage F(5N) (Fig. 7)

In this stage there are five pairs of non-setose pleopods. The second thoracic limb shows

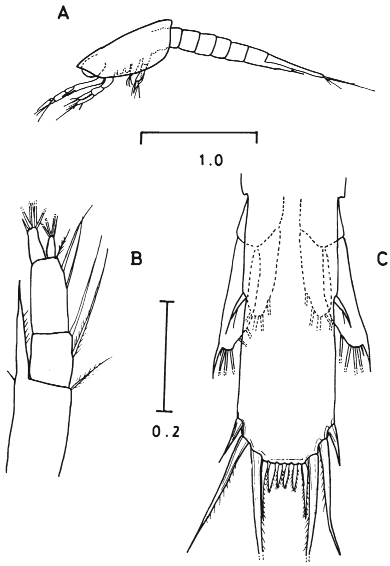

Fig. 5. *Thysanoessa longipes*, calyptopis III. A: whole animal, lateral view; B: antennule; C: telson, dorsal view. Scale in mm.

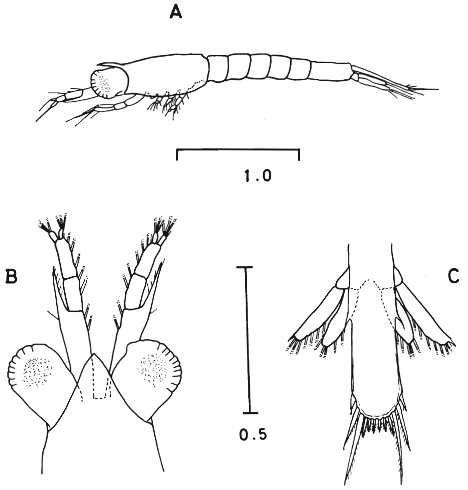

Fig. 6. *Thysanoessa longipes*, stage F(0). A: whole animal, lateral view; B: front part, dorsal view; C: telson, dorsal view. Scale in mm.

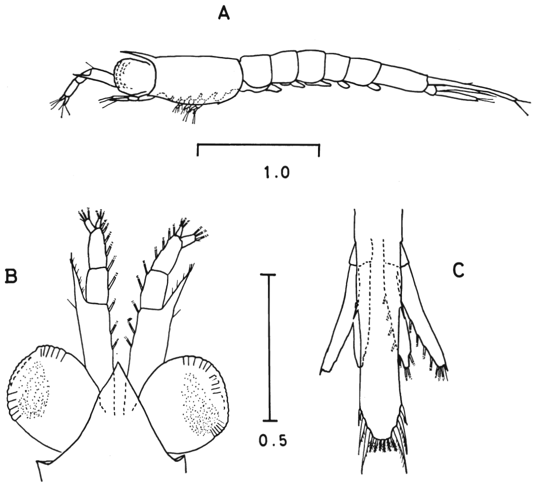

Fig. 7. *Thysanoessa longipes*, stage F(5N). A: whole animal, lateral view; B: front part, dorsal view; C: telson, dorsal view. Scale in mm.

further development. There are conspicuous denticles at the lateral margins of the carapace. Total length: 3.02–3.48 mm.

Stage F(6Tsp) (Fig. 8)

In this stage there are five setose pleopods, and the antennal endopodite is unsegmented. The third thoracic limbs show further development. The telson has six terminal spines. Total length: 3.11–4.82 mm.

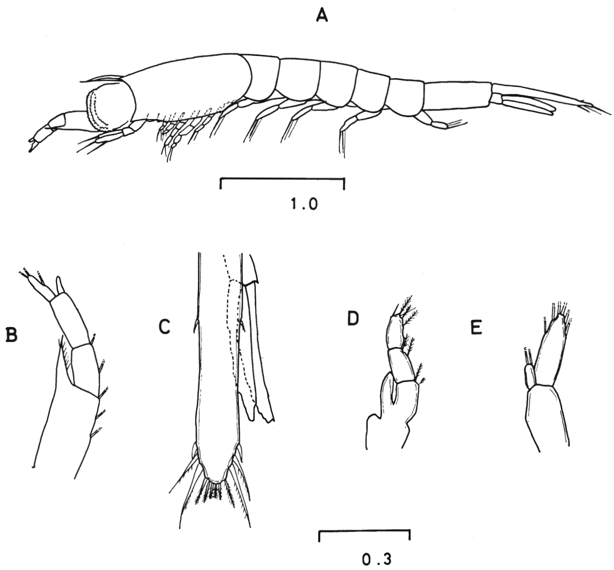

Fig. 8. *Thysanoessa longipes*, stage F(6Tsp). A: whole animal, lateral view; B: antennule; C: telson, dorsal view; D: third thoracic leg; E: first pleopod. Scale in mm.

Stage F(4Tsp) (Fig. 9)

The telson has four terminal spines. Total length: 4.42–5.15 mm.

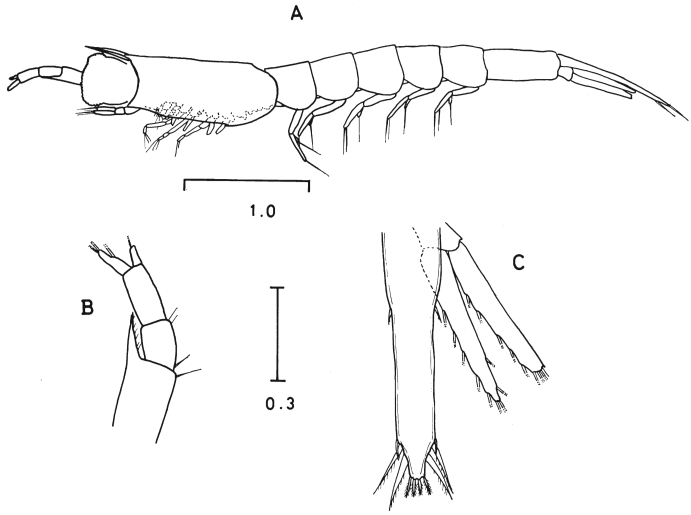

Fig. 9. *Thysanoessa longipes*, stage F(4Tsp). A: whole animal, lateral view; B: antennule; C: telson, dorsal view. Scale in mm.

Stage F(2Tsp) (Fig. 10)

In this stage the telson has two terminal spines, two pairs of long lateral spines and one pair of short lateral spines. The antennular endopodite shows a sign of segmentation. The antennal endopodite is two-segmented, and the exopodite is

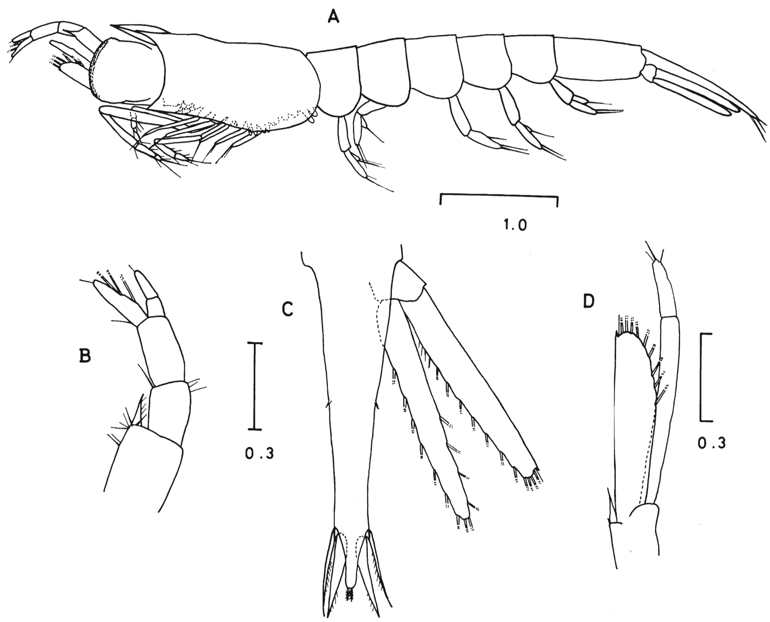

Fig. 10. *Thysanoessa longipes*, stage F(2Tsp). A: whole animal, lateral view; B: antennule; C: telson, dorsal view; D: antenna. Scale in mm.

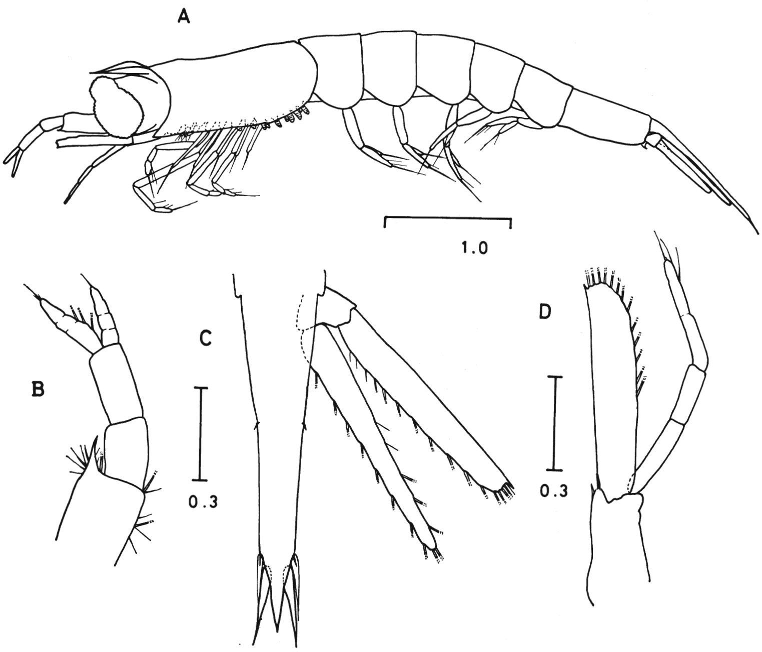

Fig. 11. *Thysanoessa longipes*, stage F(1Tsp). A: whole animal, lateral view; B: antennule; C: telson, dorsal view; D: antenna. Scale in mm.

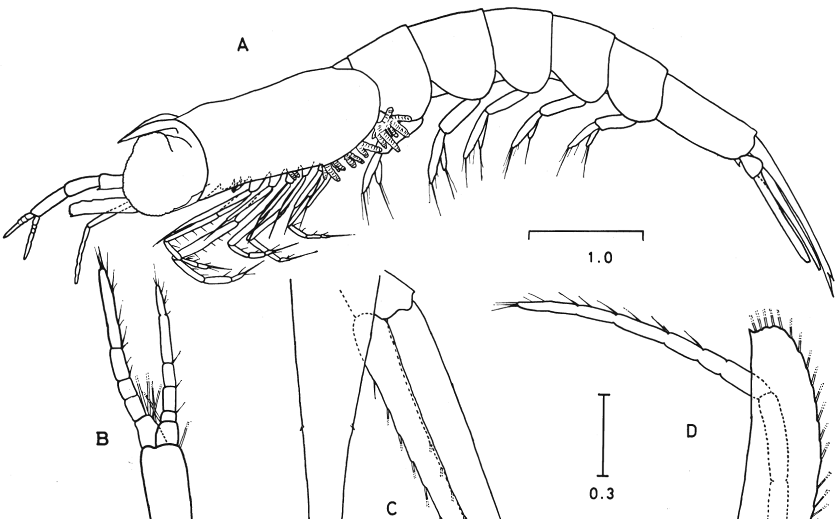

Fig. 12. *Thysanoessa longipes*, post-furcilia. A: whole animal, lateral view; B: antennule; C: telson, dorsal view; D: antenna. Scale in mm.

beginning to show the scale form. The antennular spine is as long as the second peduncular segment. Total length: 4.98 mm (one specimen).

Stage F(1Tsp) (Fig. 11)

In this stage the number of the terminal spines are reduced to one. Total length: 5.15 mm (one specimen).

(3) Post-furcilia or juvenile (Fig. 12)

In this stage the telson has one pair of long lateral spines and one pair of short lateral spines. The antennular spine is very short. There was no intact specimen to be measured.

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オキアミ類フルシリア期幼生のステージ区分と *Thysanoessa longipes* BRANDT 幼生の記載

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要約

オキアミ類幼生のフルシリア期では脱皮するごとに胸脚や腹脚が発生すると共に，尾節の末端刺の数が漸次減少するため，様々な形態の幼生が混在する．従来フルシリア期の一般的なステージ区分はわずかに3～4つのステージに分ける方法がとられてきた．このような簡略化されたステージ区分法は多くの種に共通して適用されうる利点を有するが，反面発生経路の種による違いを明らかにすることができないという欠点を有する．この欠点を補うために，本研究では脱皮に即してフルシリア期を9つのステージに区分する方法を新しく提唱した．これにより日本海における優占種 *Euphausia pacifica* HANSEN と *Thysanoessa longipes* BRANDT との種間による発生経路の違いを論ずると共に，日本海と南カリフォルニア沖の両海域に出現した *E. pacifica* の発生経路の個体群間での違いを指摘することでこの区分法の妥当性を示すことができた．

また *T. longipes* の幼生の記載はまだなされていないので各ステージごとに形態記述を行なつた．