LIFE CYCLE OF THE MARINE CALANOID COPEPOD *ACARTIA CALIFORNIENSIS* TRINAST REARED UNDER LABORATORY CONDITIONS

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ABSTRACT

For the first time the entire life cycle of 6 naupliar and 5 copepodid stages and 1 adult stage of the marine calanoid copepod *Acartia californiensis* Trinast is described and illustrated. The account includes setation and segmentation for all stages. Specimens from Estero de Punta Banda, Baja California, México, were reared under laboratory conditions (17°C ± 1°C and 35 ‰).

The sexual differences found in the structure of appendages, in the urosome, fifth swimming legs, and first antenna were only in the sixth copepodid stage (adult). Comparative anatomical measurements such as total length and prosome/urosome ratio were also recorded.

RESUMEN

Se describe, por primera vez, el ciclo de vida completo del copépodo calanoídeo marino *Acartia californiensis* Trinast, a partir de especímenes cultivados bajo condiciones de laboratorio (17°C ± 1°C y 35 ‰) provenientes del Estero de Punta Banda, Baja California, México. La descripción incluye la setación y segmentación de todos los estadíos de desarrollo.

En base a los resultados de la descripción, las diferencias sexuales en la estructuración de los apéndices, en el urosoma, quinta pata natatoria y anténula, sólo fueron encontradas en el estadío adulto (C-VI). También se registraron datos anatómicos comparativos como longitud total y razón prosoma/urosoma.

INTRODUCTION

In most investigations of copepod population dynamics, a production estimate has been approached through study of the populations' life cycles, for example, cohort analysis (Landry 1976). For the sake of simplicity, however, naupliar stages (Yablonskaya 1962; Heinle 1966; Parsons et al. 1969) and copepodid stages (Greze and Baldina 1964) have often been grouped as single units.

Several authors have observed that naupliar larvae of marine copepods belonging to the same genus are remarkably similar, and sometimes identical. Examples are *Acartia longiremis* Lilljeborg, *A. bifilosa* Giesbrecht, and *A. clausi* Giesbrecht (Oberg 1906; Gurney 1932), and *A. tonsa* Dana and *A. californiensis* Trinast (Trinast 1976; Pace 1978; Johnson 1981).

According to Johnson (1934) there are two main reasons for studying the life cycle of copepods. First, from a taxonomic point of view, knowing larval development will help reveal the natural relationships among adult organisms. Second, in order to better understand their importance in the ocean's economy, it is necessary to know the organisms accurately, to distinguish all their developmental stages, and to ascertain the habits and requirements of each.

Life cycles have been described for at least 106 copepod species, but almost all of the descriptions are incomplete. Björnberg (1972) also described the partial life cycles of 21 more species. The descriptions are incomplete because it is difficult to collect all developmental stages of copepods in nature and to keep them in culture.

Acartia, the only genus in the family Acartiidae, contains about 79 described species belonging to the 8 subgenera proposed by Steuer (1923); undoubtedly, new species are yet to be described. This genus is widely distributed and recorded in all oceans (Subbaraju 1967). It occurs in coastal waters, especially estuaries (Uye 1982). However, larvae of only 13 of the 79 species have been described.

Acartia californiensis Trinast (subgenus *Acanthacartia:* group Rostrata of Steuer 1923) was described by Trinast (1976). It is endemic to the northeastern Pacific and apparently restricted to estuaries and coastal lagoons (Figure 1). According to Johnson (1981), *A. californiensis* extends north to Yaquina Bay, Oregon. On the California coast, this species has been recorded from San Francisco Bay (Johnson 1981), Elkhorn Slough in Monterey Bay (Pace 1978), Newport Bay in Los Angeles (Trinast 1976), and Laguna Peñasquitos and Mission Bay in San Diego (Fleminger, pers. comm.). It has also been observed in abundance at Estero de Punta Banda in Bahía de Todos Santos in Ensenada, Baja California (Trujillo-Ortíz, unpublished data), Laguna de Guerrero Negro, Baja California Sur (Fleminger, pers. comm.), and Laguna

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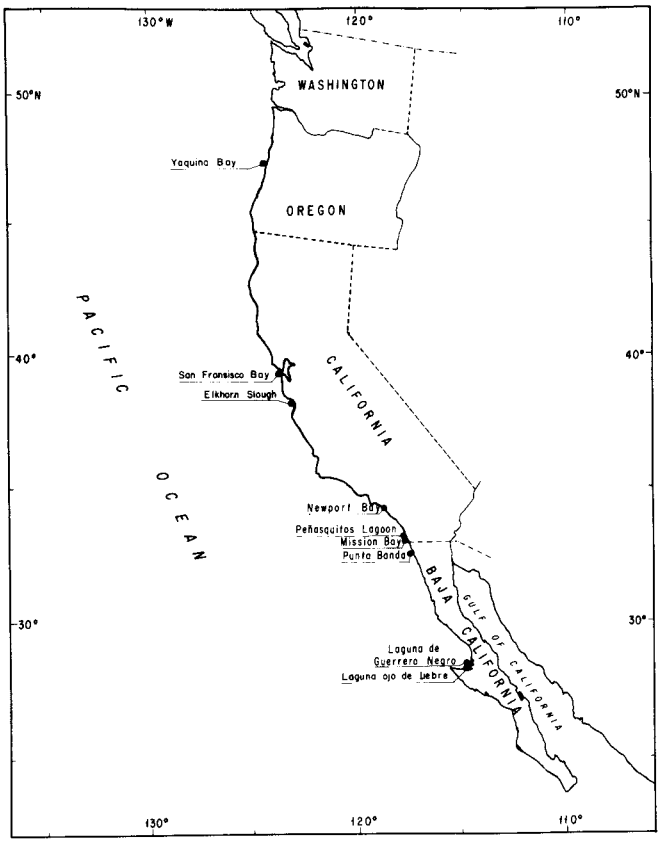

Figure 1. Known geographical distribution of *Acartia californiensis*.

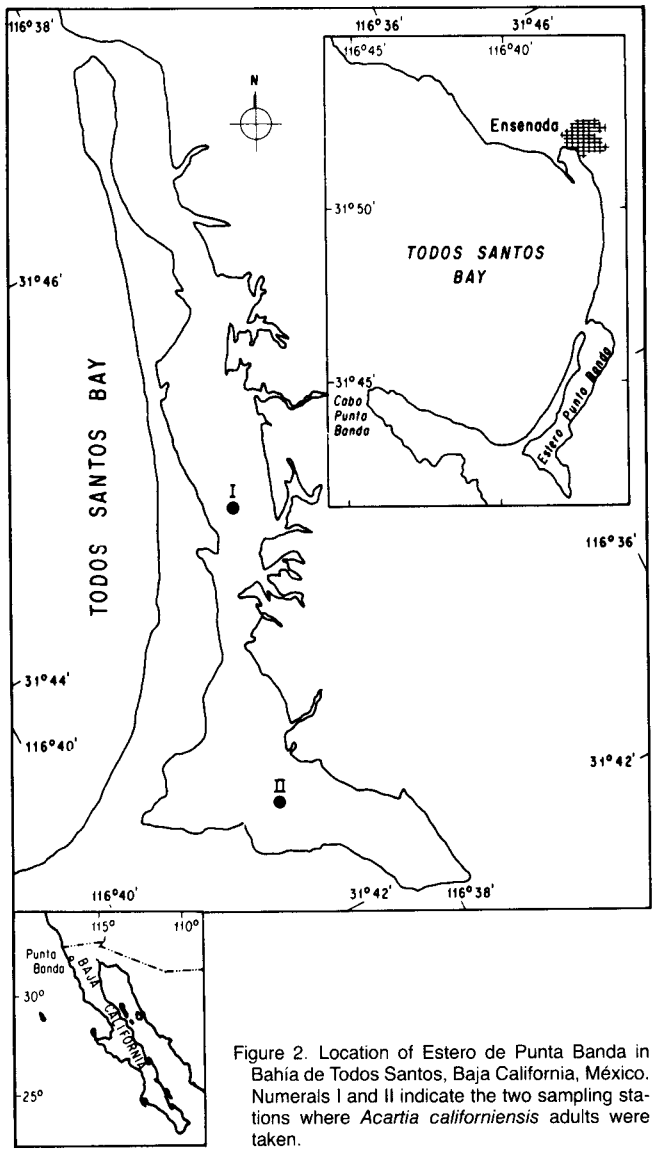

Figure 2. Location of Estero de Punta Banda in Bahía de Todos Santos, Baja California, México. Numerals I and II indicate the two sampling stations where *Acartia californiensis* adults were taken.

Ojo de Liebre, Baja California Sur (Trujillo-Ortíz, unpublished data).

The biology of *Acartia californiensis* is practically unknown. Pace (1978) studied its distribution, abundance, and rates of fecundity and growth in Elkhorn Slough in Monterey Bay; Johnson (1980) studied the effects of temperature and salinity on production and hatching of dormant eggs in Yaquina Bay; and Johnson (1981) studied population dynamics and cohort persistence in Yaquina Bay. Zimmerman (1972), Frolander et al. (1973), Johnson (1974), Johnson and Miller (1974), and Miller et al. (1977) had already worked with *A. californiensis*, but because of its close resemblance to *A. tonsa*, and because it had not yet been described as a separate species, they mistook it for *A. tonsa*. They considered it a smaller ecophenotypic variant of the larger offshore *A. tonsa*, present in the northerly Davidson Current during the winter. In other studies Trinast (1975) called it *Acartia* n. sp., and Uye and Fleminger (1976) *Acartia* sp. I.

MATERIALS AND METHODS

Sampling Site

Adult specimens of both sexes were collected from populations in the inner and middle regions of Estero de Punta Banda (Figure 2). Estero de Punta Banda is a coastal lagoon located between 31°42′–31°47′N and 116°37′–116°40′W in the southwestern end of Bahía de Todos Santos about 13 km south of the city of Ensenada on the Pacific coast of Baja California.

Collection of Samples

Zooplankton sampling was done with a 0.5-m-diameter standard plankton net of Nitex 202-μm-mesh monofilament screen cloth (nylon) hauled obliquely for 3 minutes at 1-2 knots at the two stations in Estero de Punta Banda. Hauls were circular, with the net beside the boat in order to avoid water disturbance caused by the propeller. Sampling depth varied according to bottom topography.

Two hauls were performed at each station: I kept one sample alive, and preserved the other with 5% for-

maldehyde buffered with sodium borate (borax) for subsequent analysis.

The live samples were deposited in ice chests containing water from the site. I added 37 mg•l^{-1} EDTA (Bernhard 1957; Carrillo Barros-Gómez et al. 1974; Azcárate-Capriles 1980) and 6.25 mg•l^{-1} G-penicillin (Neunes and Pongolini 1965; Azcárate-Capriles 1980) to the water samples in order to keep the copepods healthy during transport to the laboratory.

Precipitated material (feces and dead phytoplankton and zooplankton) was siphoned out. Oxygen was provided through a controlled air system. After 5 hours, I transferred samples from the ice chests into 500-ml beakers. Because *Acartia californiensis* is positively photoactive to light, I used a lamp to concentrate the organisms for separation. I took aliquots with Pasteur pipettes and transferred them to glass Petri dishes. To facilitate the identification of adults of *A. californiensis*, I added a few drops of 0.1% MS-222 marine solution to the dishes to anesthetize the copepods and stop their movement.

I placed selected specimens of *A. californiensis* into 1000-ml beakers containing seawater previously filtered in 3-, 5-, and 10-μm polypropylene Kuno cartridges and UV-sterilized. To this water I added 37 mg•l^{-1} of EDTA.

Culturing Method

I selected 600 *A. californiensis* individuals in a ratio of 3 males per female to enhance fecundity. I transferred these organisms to two culture towers (10-liter polyethylene bags, 65 cm tall and 17 cm in diameter). Each tower contained 29 individuals per liter, or one individual per 35 ml, of water (Urry 1965; Corkett and Urry 1968). Each tower (Figure 3) had a simple conical drain valve at the bottom, an opening mechanism in the top for adding food, and an oxygen-supply line extending into the top 10 cm of the water column.

Every 5 days I added food consisting of an equal mixture of the chrysomonid *Isochrysis tahitiana* and the microflagellate *Tetraselmis* sp. kept in the "f/2" culturing medium of Guillard (1975), concentrated at 75 x 10^3 cells per ml. A Fushs-Rosenthal hemocytometer was used to count the cells to maintain the desired concentration, after the method of Corkett and Urry (1968).

I used Houde's (1978) method to maintain the phytoplankton concentration. Water was changed weekly through a PVC cylinder (11.5 cm in diameter and 12.5 cm long) provided with a Nytex 40-μm monofilament screen cloth (nylon) attached to the end.

Laboratory temperature was kept constant at 17°C ± 1°C; the air conditioning system was equipped with an electrostatic filter. Twelve 75W fluorescent cool-white tubes were arranged horizontally 10 cm from the towers to provide light. Water salinity was 35‰.

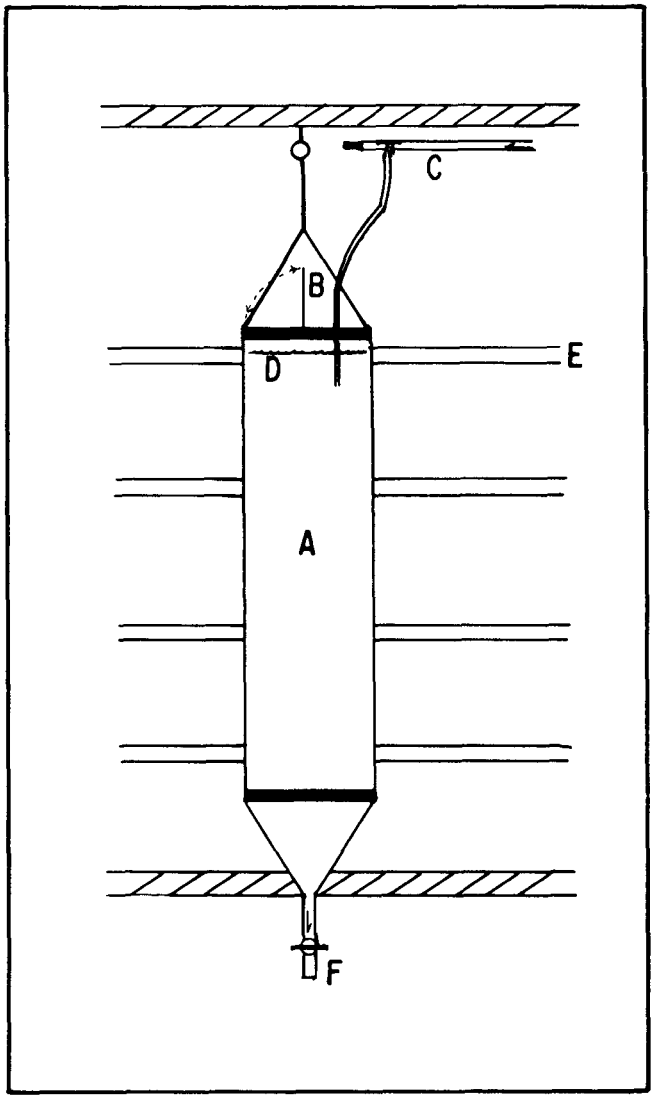

Figure 3. Culturing device: *A*, polyethylene bag (tower); *B*, opening mechanism; *C*, air-supply line; *D*, water level; *E*, fluorescent cool-white tube; *F*, conical drain valve.

Taxonomic Considerations

The characteristics chosen to identify the different naupliar stages in cultivated and preserved samples include: number of setae in the segments of the antennule; number and pattern of spines in the caudal armature; presence of other appendages such as maxillule, maxilla, maxilliped, buds of swimming legs (pereiopods); and body size. I used an ocular micrometer to measure 30 specimens dorsally and laterally from the anterior end of the cephalosome (head) to the end of the caudal armature. I chose a subsample of 10 specimens for dissection. These were cleared with 100% lactic acid for a week. I made naupliar dissections directly in

a drop of lactic acid under a dissecting microscope at magnifications of 50 and 100 ×.

In the copepodid stages, I counted the abdominal segments (urosome) and number of swimming legs; the urosome also served for sex determination. The measurements in these stages were the same as in the naupliar stages, except that the furcal setae were not included in the body length. Prosome (cephalosome and metasome or thorax) and urosome length, and prosome/urosome ratios were also recorded. The number of copepodids measured varied from 43 (copepodid V, female) to 83 (copepodid I).

I used a 70% alcoholic chlorazol black E (CBE) solution to stain copepodids (10 of each stage) from preserved samples, in the depressions of a Boerer chamber. The sequence was as follows: (1) 2 baths of distilled water, 2-3 minutes each to eliminate excess formaldehyde; (2) a 35% alcohol solution bath for 2-3 minutes to dehydrate partially; (3) a 70% alcohol solution bath for 3 minutes to complete dehydration; (4) a bath of CBE in 70% alcohol for 1-2 minutes; (5) the same steps in reverse order (without the fourth); (6) microdissection in a glycerin drop on microscope slide. This procedure is my modification of that of Omori and Fleminger (1976).

I made microdissections of the copepodid stages in drops of glycerin under a dissecting microscope at magnifications of 25 and 50 ×. I used sharpened 000 entomological needles for all dissections. As the appendages were dissected off, I arranged them in natural sequence in glycerin drops on microscope slides and covered them with no. 1 round cover slips. For additional information on this method, refer to Pantin (1964), Griffiths et al. (1976), and Omori and Fleminger (1976).

All drawings were made with the aid of a camera lucida mounted in a compound microscope. I observed naupliar stages and their appendages at 400 ×. For the copepodid stages, I observed complete specimens at 250 ×, and their appendages at 400 ×.

RESULTS

Egg

The egg of *Acartia californiensis* (Figure 4a) is spherical, 0.075 ± 0.002 mm in diameter, $n = 30$ eggs, range 0.069-0.083 mm, SD ± 0.01 mm. The eggs are granular and clear yellow-brown or yellow-green. Three concentric membranes can be clearly distinguished. The outer membrane is thin, has no fuzz, and usually bears protuberances that make it appear irregular. In fertile eggs, cell differentation is often visible. When hatching, the nauplius emerges, and the remainder of the egg tends to remain spherical. The middle membrane is also thin and flexible, and sometimes it partially collapses toward the outer membrane, causing the inner space between them to vary as embryonic development progresses. The inner membrane covers and protects the first naupliar stage during its development.

The newly laid eggs are small and capsular. They immediately sink to the bottom and gradually swell until they become completely spherical.

Naupliar Stages

During postembryonic development, six naupliar stages are evident. Average naupliar length is about 2.1 times its width. The body is not significantly curved laterally. All naupliar stages are oval anteriorly, and narrow toward the caudal armature. There is an anteroventral pigment spot, generally red, also known as the naupliar eye. The posterior-inner part is tan, and the body is generally clear and translucent but slightly yellow-green. A small internal lipid body is usually present posteroventrally in most of the naupliar stages, and is clearly visible. In lateral view (Figure 5), the labrum is clearly evident in all naupliar stages; in addition, there are short, thin setules in the labrum's inferior margin.

The most important distinguishing characters of the naupliar stages of *Acartia californiensis* are as follows.

Nauplius I (Table 1; Figures 4b, 5a, 6a, 7a, 8a). Average length of 30 specimens was 0.095 ± 0.004 mm, range 0.081-0.113 mm, SD ± 0.01 mm. Caudal armature has 2 terminal sensory setae and transverse row of setules. First nauplius only slightly resembles adult, except for oval-shaped labrum bearing setules at bottom margin, and rudimentary antennule, antenna, and mandible.

After the first molt, the nauplii enlarge slightly, and the antennule, antenna, and mandible become more specialized.

Nauplius II (Table 1; Figures 4c, 5b, 6b, 7b, 8b). Average length of 30 specimens was 0.116 ± 0.002 mm, range 0.111-0.123 mm, SD ± 0.004. Body is egg-shaped. The 2 terminal sensory setae of the caudal armature (Figures 4c, 5b) are longer than in the previous stage; one is ventral, the other dorsal. The labrum is oval, with setules in the lower margin. Posteroventrally the body has a transverse row of fine setae.

Nauplius III (Table 1; Figures 4d, 5c, 6c, 7c, 8c). Average length of 30 specimens was 0.137 ± 0.003 mm, range 0.127-0.147 mm, SD ± 0.007. The body remains egg-shaped. The caudal armature now consists of 2 ventral spines with slightly toothed margins (saw-type), 2 sensorial setae that have the same appearance as in the previous stage, and a transverse row of fine setae. Posteroventrally the body has 2 transverse rows of setae.

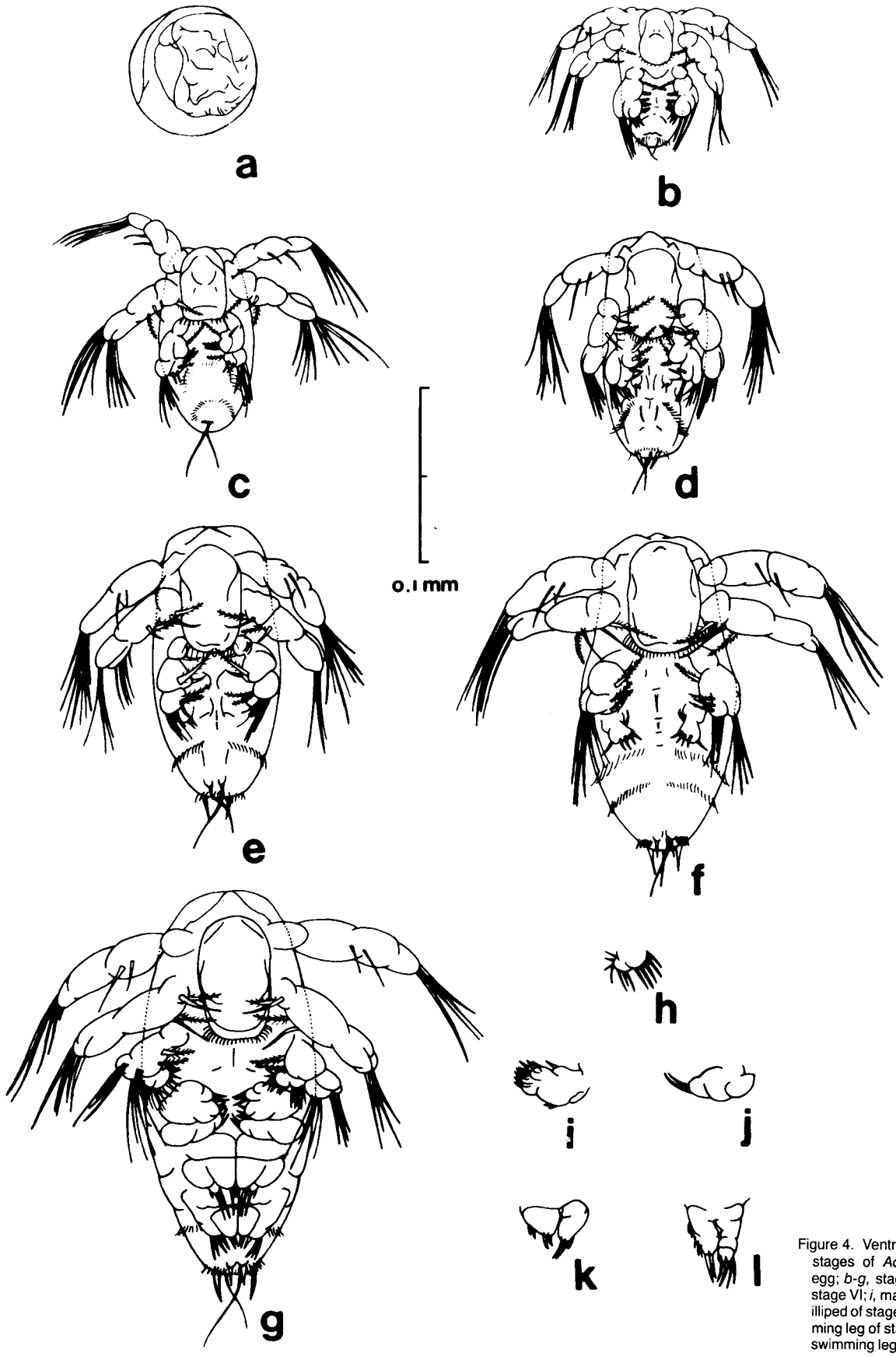

Figure 4. Ventral views of the naupliar stages of *Acartia californiensis*: *a*, egg; *b-g*, stages I-VI; *h*, maxillule of stage VI; *i*, maxilla of stage VI; *j*, maxilliped of stage VI; *k*, bud of first swimming leg of stage VI; *l*, bud of second swimming leg of stage VI.

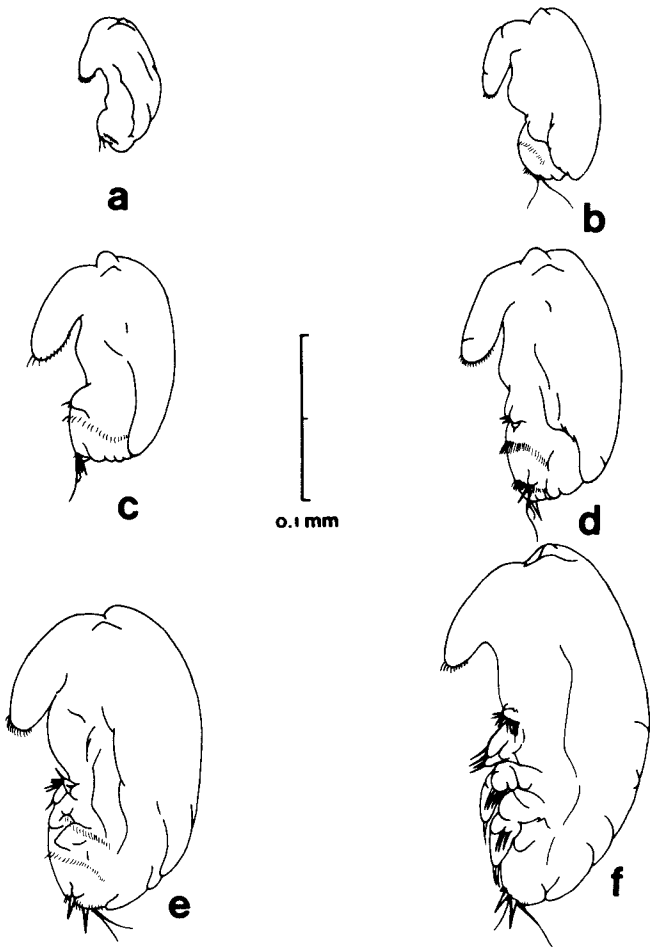

Figure 5. Lateral views of naupliar stages I-VI of *Acartia californiensis*.

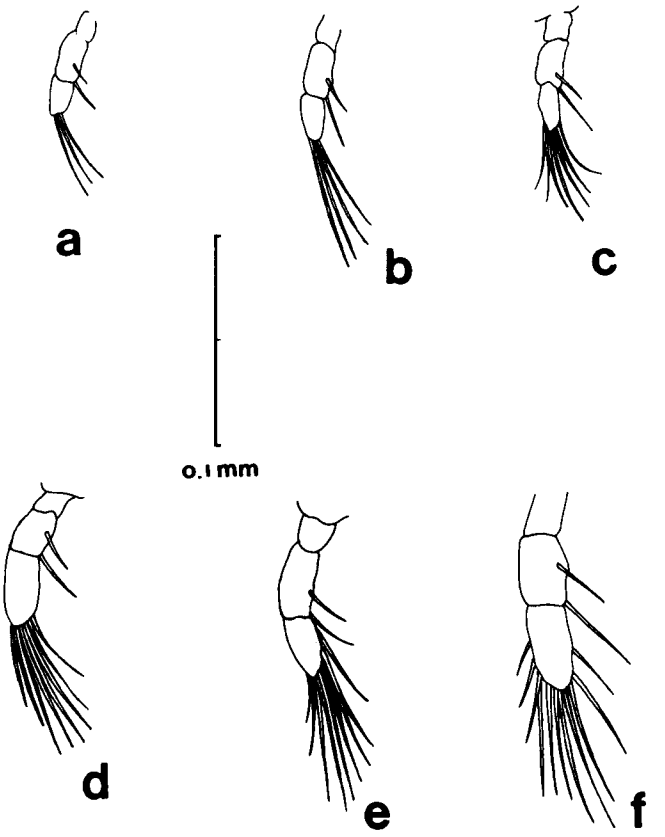

Figure 6. Antennules of naupliar stages I-VI of *Acartia californiensis*.

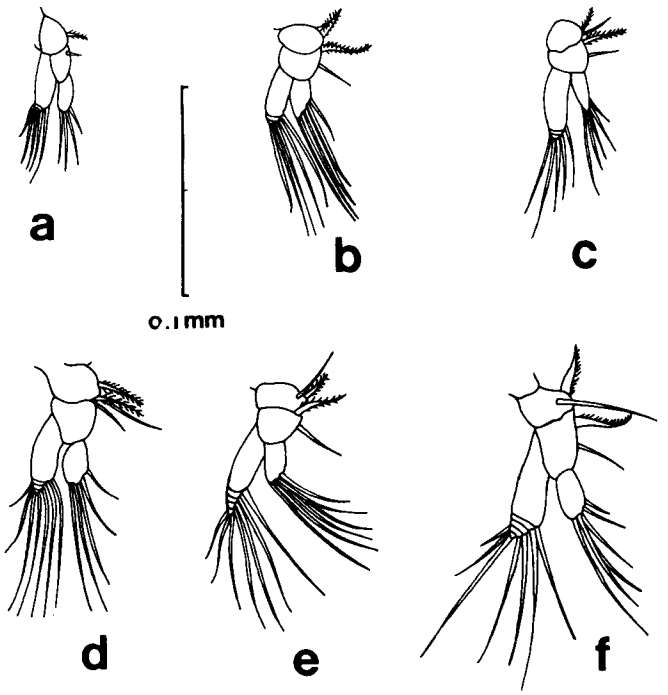

Figure 7. Antennae of naupliar stages I-VI of *Acartia californiensis*.

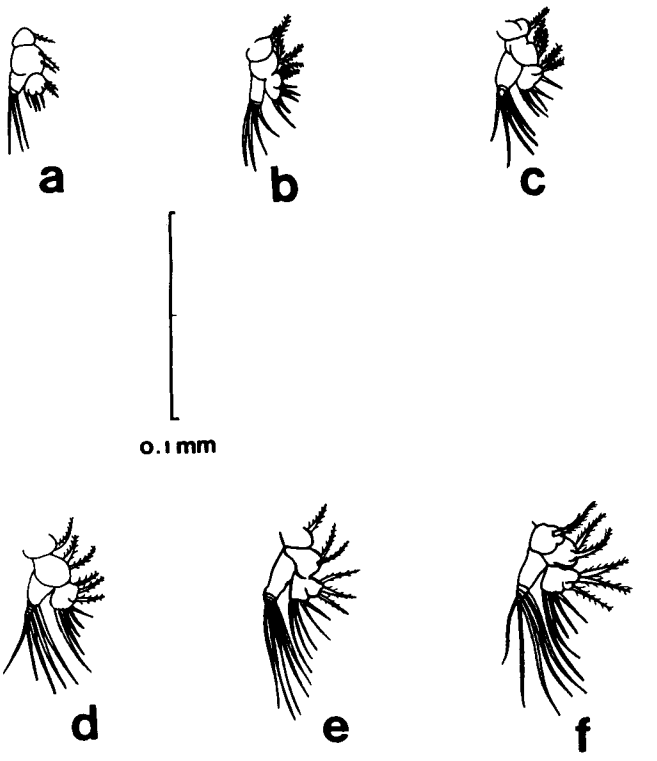

Figure 8. Mandibles of naupliar stages I-VI of *Acartia californiensis*.

TABLE 1
Setae, Spines, and Masticatory Processes on Appendages of Naupliar Stages of *Acartia californiensis*

Stage	N I	N II	N III	N IV	N V	N VI
Total average length (mm)	0.095 ± 0.004	0.116 ± 0.002	0.137 ± 0.003	0.167 ± 0.003	0.198 ± 0.003	0.229 ± 0.003
Range (mm)	0.081–0.113	0.111–0.123	0.127–0.147	0.157–0.176	0.189–0.208	0.218–0.240
Antennule (Fig. 6)						
No. segments	3	3	3	3	3	3
No. setae	5	6	8-9	9-10	10-11	12-13
Proximal segment	0	0	0	0	0	0
Medial segment	2	2	2	2	2	2
Distal segment	3	4	6-7	7-8	8-9	10-11
Antenna (Fig. 7)						
Coxopod	1sp	1sp	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp
Basiopod	1	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp	1 + 1sp
Endopod	4	5	5	5	6	6
Exopod	5	5	5	7	7	7
Mandible (Fig. 8)						
Coxopod	1pm	1pm	1pm	1pm	1pm	1pm
Basiopod	2pm	2pm	2pm	2pm	2pm	2pm
Endopod	2pm:4	2pm:5	2pm:5	3pm:5	2pm:1pm:5	2pm:1pm:5
Exopod	3	4	5	5	5	5
Maxillule (Figs. 4,5)						
External lobe I			1	1	1	5
External lobe II			0	0	0	0
Exopod			0	0	0	0
Internal lobe I			1	2	1	2
Internal lobe II			0	0	4	5
Internal lobe III						
Basiopod						
Endopod						
Maxilla (Figs. 4,5)						
Lobe I						0
Lobe II						2
Lobe III						4
Lobe IV						4
Lobe V						1
Endopod						0
Maxilliped (Figs. 4,5)						
Coxopod						2
Lobe I						0
Lobe II						0
Lobe III						0
Basiopod						0
Endopod						0
Caudal armature (Figs. 4,5)						
Sensory setae	2	2	2	2	2	2
Dorsal terminal spines	0	0	0	2	2	2
Ventral terminal spines	0	0	2	2	2	2
Bristles	1	1	1	1	1	1
Leg I (Figs. 4,5)						
Coxopod						0
Basiopod						0
Endopod 1						2S + 2
2						0
3						0
Exopod 1						2S
2						0
3						0

TABLE 1 (continued)
Setae, Spines, and Masticatory Processes on Appendages of Naupliar Stages of *Acartia californiensis*

Stage	N I	N II	N III	N IV	N V	N VI
Total average length (mm)	0.095 ± 0.004	0.116 ± 0.002	0.137 ± 0.003	0.167 ± 0.003	0.198 ± 0.003	0.229 ± 0.003
Range (mm)	0.081–0.113	0.111–0.123	0.127–0.147	0.157–0.176	0.189–0.208	0.218–0.240
Leg II (Figs. 4,5)						
Coxopod						0
Basiopod						0
Endopod 1						2S+5
2						0
3						0
Exopod 1						2S+5
2						0
3						0

Main designations are according to Owre and Foyo (1967) and Björnberg (1972). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, S = spine, pm = masticatory process.

Nauplius IV (Table 1; Figures 4e, 5d, 6d, 7d, 8d). Average length of 30 specimens was 0.167±0.003 mm, range 0.157-0.176 mm, SD±0.007. Body is oval. The caudal armature is larger than in naupliar stage III, and has 2 terminal spines with toothed margins, 2 anterior sensory setae, a new pair of ventral spines, and a fine, transverse row of setules.

Nauplius V (Table 1; Figures 4f, 5e, 6e, 7e, 8e). Average length of 30 specimens was 0.198±0.003 mm, range 0.189-0.208 mm, SD±0.007. The caudal armature is a small transverse row of small setae: 4 spines remain as in naupliar stage IV (2 ventral strong and small, 2 large dorsal, terminally toothed); there are also 2 sensorial setae. Oval labrum has an inferior margin with setules.

Nauplius VI (Table 1; Figures 4g-l, 5f, 6f, 7f, 8f). Average length of 30 specimens was 0.229±0.003 mm, range 0.218-0.240 mm, SD±0.008. Until this last naupliar stage the body remains oval. In lateral view (Figure 5f), there is a clear differentiation of 5 segments that are well delimited. The oval labrum has setules on its inferior margin. The caudal armature is the same as in nauplius stage V.

Copepodid and Adult Stages

The final naupliar stage metamorphoses into the first of six copepodids. When the individual reaches copepodid stage I, as the direct result of a drastic change in structure, it is a miniature adult, except that it has only two pairs of functional swimming legs. A new pair of legs is added in each successive molt until copepodid IV. From that stage until the adult form (copepodid VI), no new swimming legs are added; instead, the sexually modified fifth pair of legs develops in the adult form.

During the copepodid stages, males increase 2.23 times in average body length to reach the adult stage; females increase 2.62 times. From copepodid IV on, the sex of each individual is evident.

The most important characters of the copepodid stages of *Acartia californiensis* are as follows:

Copepodid I (Table 2; Figures 9a, 10a, 11a, 12a, 13a, 14a, 15a, 16a, 17a, 18a). Average length of 83 specimens (including caudal furca, omitting furcal setae here and in all subsequent copepodid stages) was 0.385±0.004 mm, range 0.347-0.443 mm, SD±0.017, average prosome/urosome ratio 3.75:1. The cephalosome occupies about 60% of the prosome length. The metasome has 4 segments: the first two have functional swimming legs; the third, in some cases, has biramous buds of the third pair of swimming legs; and the fourth lacks appendages. The urosome has one segment. In the caudal furca each ramus is longer than it is wide (1:0.76) and has 4 plumose setae, of which the inner one is shortest. The appendages, in general, are very similar to each other but not identical to those of the adult. With maturation, the appendages enlarge and specialize by acquiring such ornamental structures as setae and spines. The rostrum bears two filaments.

Copepodid II (Table 2; Figures 9b, 10b, 11b, 12b, 13b, 14b, 15b, 16b, 17b, 18b, 19a). Average length of 82 specimens (including caudal furca) was 0.469±0.003 mm, range 0.424-0.500 mm, SD±0.017, average prosome/urosome ratio 4.02:1. The cephalosome occupies 54% of prosome length; it has 2 rostral filaments. The metasome has 4 segments, of which the first 3 have functional swimming legs and the fourth lacks appendages. The urosome has 2 segments. Each ramus of caudal furca has 5 plumose setae; both the outer and inner setae are short. In some cases buds of the fourth biramous legs are present.

Copepodid III (Table 2; Figures 9c, 10c, 11c, 12c, 13c, 14c, 15c, 16c, 17c, 18c, 19b, 20a). Average length

TABLE 2
Anatomical Characteristics of Copepodid Stages of *Acartia californiensis*

Stage	C I	C II	C III	C IV	
				Male	Female
Total average length (mm)	0.385 ± 0.004	0.469 ± 0.003	0.577 ± 0.005	0.656 ± 0.005	0.700 ± 0.007
Range (mm)	0.347–0.443	0.424–0.500	0.519–0.635	0.597–0.674	0.635–0.751
Prosome/urosome ratio	3.75:1	4.02:1	4.03:1	3.99:1	3.54:1
Antennule (Fig. 11)					
No. segments	11	14	16	17	17
Antenna (Fig. 12)					
Coxopod	1sp	1sp	1sp	1sp	
Basiopod	4	5	6	7	
Endopod	7(2+5)	8	11	11(6+5)	
Exopod	8	8	8	8(5+3)	
Mandible (Fig. 13)					
Coxopod: gnathobase	6t	7t	8t	8t	
Basiopod	1+sm	1+sm	1+sm	1+sm	
Endopod	2:6	2:7	2:7	2:8	
Exopod	6	6	6	6	
Maxillule (Fig. 14)					
External lobe I	4	6	8	9	
External lobe II	1	1	1	1	
Exopod	2	2	2	2	
Internal lobe I	7	7	7	7	
Internal lobe II	3	3	3	3	
Internal lobe III	1	1	1	1	
Basiopod	sm	sm	sm	sm	
Endopod	5	5	5	5	
Maxilla (Fig. 15)					
Lobe I	2	2	2	2	
Lobe II	1	1	1	2	
Lobe III	1	1	1	1	
Lobe IV	1	2	2	2	
Lobe V	1	1	2	1	
Endopod	4	4	4	5	
Maxilliped (Fig. 16)					
Coxopod	0	0	0	0	
Lobe I	1	1	1	1	
Lobe II	2	3	3	3	
Lobe III	1	1	1	1	
Basiopod	0	1	1	1	
Endopod	3	4	4(1:1:2)	5(1:1:1:2)	

Main designations are according to Owre and Foyo (1967). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, t = tooth, sm = micro setule, S = spine, Se = external spine, St = terminal (apical) spine.

of 71 specimens (including caudal furca) was 0.577 ± 0.005 mm, range 0.519-0.635 mm, SD ± 0.02, average prosome/urosome ratio 4.03:1. The cephalosome occupies nearly 52% of the total length of the prosome. Metasome has 4 segments, each with a pair of functional swimming legs. The caudal furca has 6 setae; the same number occurs in the following copepodid stages. Forehead has 2 rostral filaments.

Copepodid IV, male (Table 2; Figures 9d, 10d, 11d, 12d, 13d, 14d, 15d, 16d, 17d, 18d, 19c, 20b, 21a). Average length of 75 specimens (including caudal furca) was 0.656 ± 0.005 mm, range 0.597-0.674 mm, SD ± 0.02, average prosome/urosome ratio 3.99:1. From this stage on, sexes are easily distinguishable. The cephalosome occupies nearly 51% of the total length of the prosome. Each of the 4 metasomal segments has a pair of swimming legs; the posteriormost segment also has the two-jointed fifth pair of legs, which is symmetrical. The urosome has 3 abdominal segments. The caudal furca has 2 furcal rami with 6 plumose setae each, as in the previous copepodid stage. The innermost seta is the shortest. The species has two rostral filaments.

C V		C VI	
Male	Female	Male	Female
0.759 ± 0.009	0.818 ± 0.016	0.859 ± 0.008	1.008 ± 0.009
0.693–0.809	0.712–0.924	0.770–0.924	0.924–1.097
3.13:1	3.3:1	2.93:1	3.35:1
17	17	17	17
1sp		1sp	
9		9	
13(6+7)		14(3:4:7)	
8(5+3)		8	
9t		10t	
1+sm		1+sm	
2:8		2:9	
6(1:1:1:3)		6	
9		9	
1		1	
2		2	
7		7	
3		3	
1		1	
sm		sm	
5		5	
2		3	
2		2	
1		2	
2		1	
1		1	
5		4	
0		0	
1		1	
3		3	
1		1	
1		1	
5(1:1:1:2)		6(1:1:1:3)	

Table 2 continued on next page.

Copepodid IV, female (Table 2; Figures 9e, 10e, 11e, 13e, 14e, 15e, 16e, 17e, 18e, 19d, 20c, 21b). Average length of 66 specimens (including caudal furca) was 0.700 ± 0.007 mm, range 0.635-0.751 mm, SD ± 0.027, average prosome/urosome ratio 3.54:1. Female has the same general characteristics as the corresponding male stage, except that the urosome has 2 segments. The fifth pair of legs is symmetrical.

Copepodid V, male (Table 2; Figures 9f, 10f, 11f, 12f, 13f, 14f, 15f, 16f, 17f, 18f, 19e, 20d, 21c). Average length of 59 specimens (including caudal furca) was 0.759 ± 0.009 mm, range 0.693-0.809 mm,

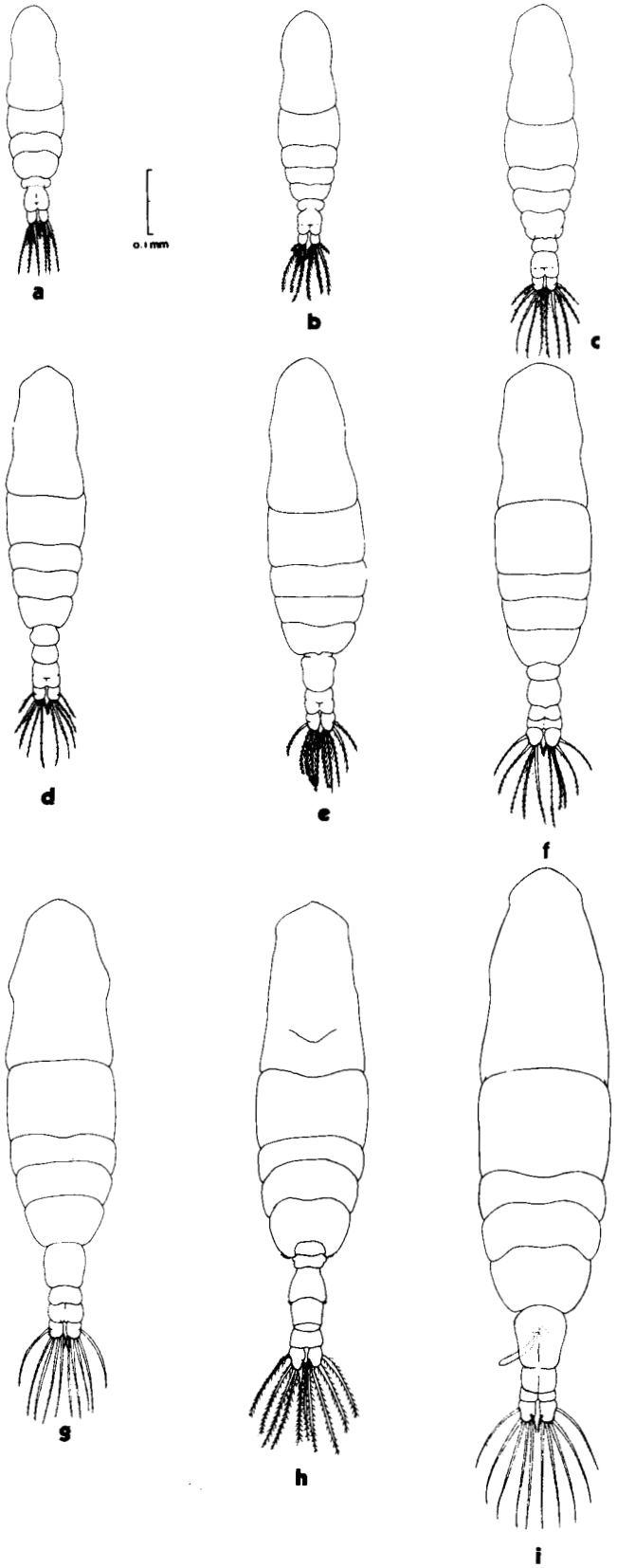

Figure 9. Dorsal views of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female, with spermatophore.

TABLE 2 (continued)
Anatomical Characteristics of Copepodid Stages of *Acartia californiensis*

Stage	C I	C II	C III	C IV	
				Male	Female
Total average length (mm)	0.385 ± 0.004	0.469 ± 0.003	0.577 ± 0.005	0.656 ± 0.005	0.700 ± 0.007
Range (mm)	0.347–0.443	0.424–0.500	0.519–0.635	0.597–0.674	0.635–0.751
Prosome/urosome ratio	3.75:1	4.02:1	4.03:1	3.99:1	3.54:1
Leg I (Fig. 17)					
Coxopod					
Basiopod					
Endopod 1	1	1	1	1	
2	6	6	6	6	
3	0	0	0	0	
Exopod 1	1	1	2	2	
2	0*	0*	0*	0*	
3	2+1Se+1+1St+3	2+1Se+1+1St+4	2+1Se+1+1St+4	2+1Se+1+1St+4	
Leg II (Fig. 18)					
Coxopod					
Basiopod					
Endopod 1	1	1	2	2	
2	5	5	5	6	
3	0	0	0	0	
Exopod 1	1Se+1	1Se+1	1Se+1	1Se+1	
2	0*	0*	1Se+1	1Se+1	
3	1Se+1St+3	1Se+1St+4	1Se+1St+4	1Se+1St+4	
Leg III (Fig. 19)					
Coxopod					
Basiopod					
Endopod 1	0	1	2	2	
2	0	4	5	6	
3	0	0	0	0	
Exopod 1	0	1Se	1Se	1Se+1	
2	0	0*	0*	1Se+1	
3	0	1Se+1St+3	1Se+1St+4	1Se+1St+4	
Leg IV (Fig. 20)					
Coxopod					
Basiopod					
Endopod 1			1	2	
2			4	5	
3			0	0	
Exopod 1			1Se	1Se	
2			0*	1Se+1	
3			1Se+1St+3	1Se+1St+4	
Leg V (Fig. 21)					
Coxopod				1	0
Basiopod				0	0
Right leg				1:1+1S	1:0
Left leg				1:1+1S	1:0

Main designations are according to Owre and Foyo (1967). Special designations of appendage armature are: arabic numerals = setae, sp = plumose seta, t = tooth, sm = micro setule, S = spine, Se = external spine, St = terminal (apical) spine, * = segment not defined.

SD ± 0.035, average prosome/urosome ratio 3.13:1. The cephalosome occupies nearly 46% of the prosome's length. The metasome has 4 segments; each one has a pair of swimming legs; the posteriormost segment also bears the two-jointed fifth pair of swimming legs, which is asymmetrical. The urosome has 4 segments. Each furcal ramus has 6 plumose setae; the innermost is shortest. This stage has 2 rostral filaments.

Copepodid V, female (Table 2; Figures 9g, 10g, 11g, 12g, 13g, 14g, 15g, 16g, 17g, 18g, 19f, 20e, 21d). Average length of 43 specimens (including caudal furca) was 0.818 ± 0.016 mm, range 0.712-0.924 mm, SD ± 0.053, average prosome/urosome ratio 3.3:1.

C V		C VI	
Male	Female	Male	Female
0.759 ± 0.009	0.818 ± 0.016	0.859 ± 0.008	1.008 ± 0.009
0.693–0.809	0.712–0.924	0.770–0.924	0.924–1.097
3.13:1	3.3:1	2.93:1	3.35:1
1		1	
6		6	
0		0	
2		2	
2*		2	
1 + 1Se + 1 + 1St + 4		1 + 1Se + 1 + 1St + 4	
2		2	
6		7	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
2		2	
7		7	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
3		3	
6		6	
0		0	
1Se + 1		1Se + 1	
1Se + 1		1Se + 1	
1Se + 1St + 5		1Se + 1St + 5	
1sp	0	0	0
0	0	1sp	0
2s:1S	1:1St	1S:1S:2-3	1sp:1St
0:1S	1:1St	0:0:2S	1sp:1St

The female is larger than corresponding stage of male (mean ratio 1:0.87). The cephalosome is approximately 46% as long as the prosome, and has 2 rostral filaments. In general, the female has the same characteristics as the male, except that urosome has 3 segments, of which the first is larger. The fifth swimming legs are symmetrical.

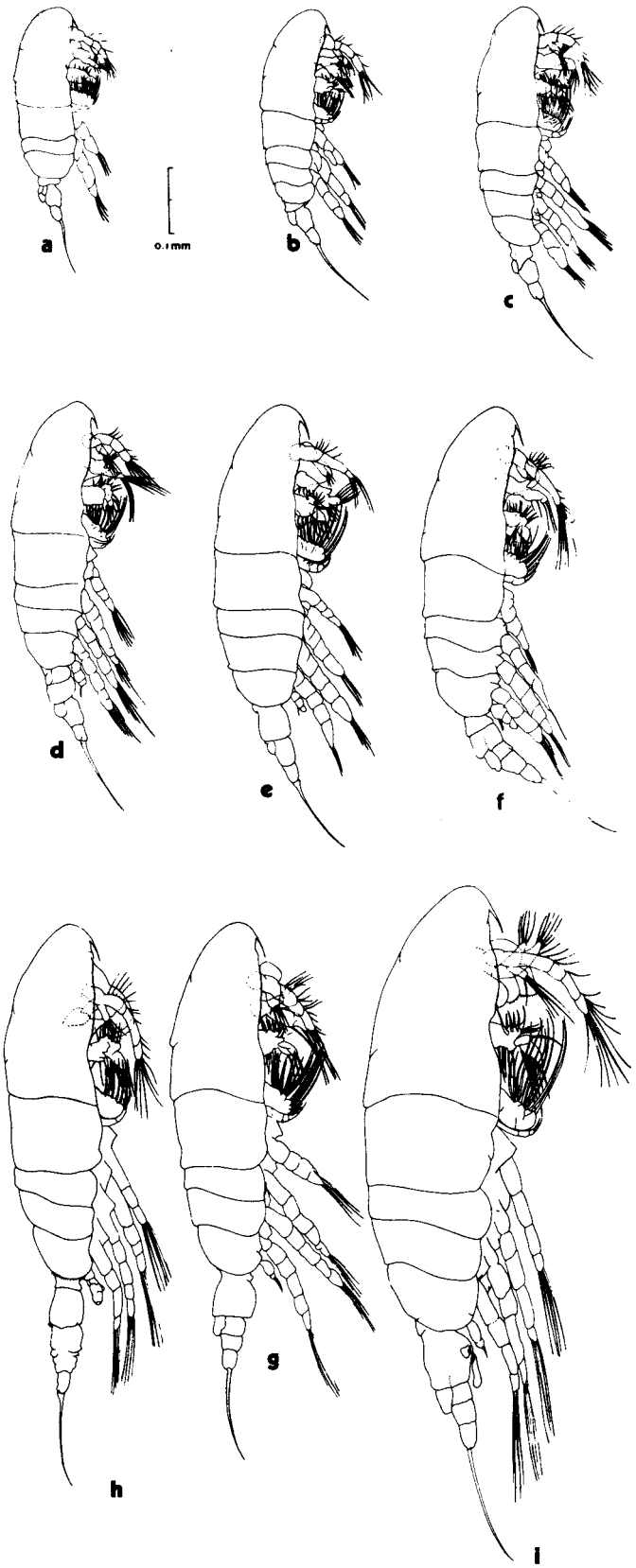

Figure 10. Lateral views of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female, with spermatophore.

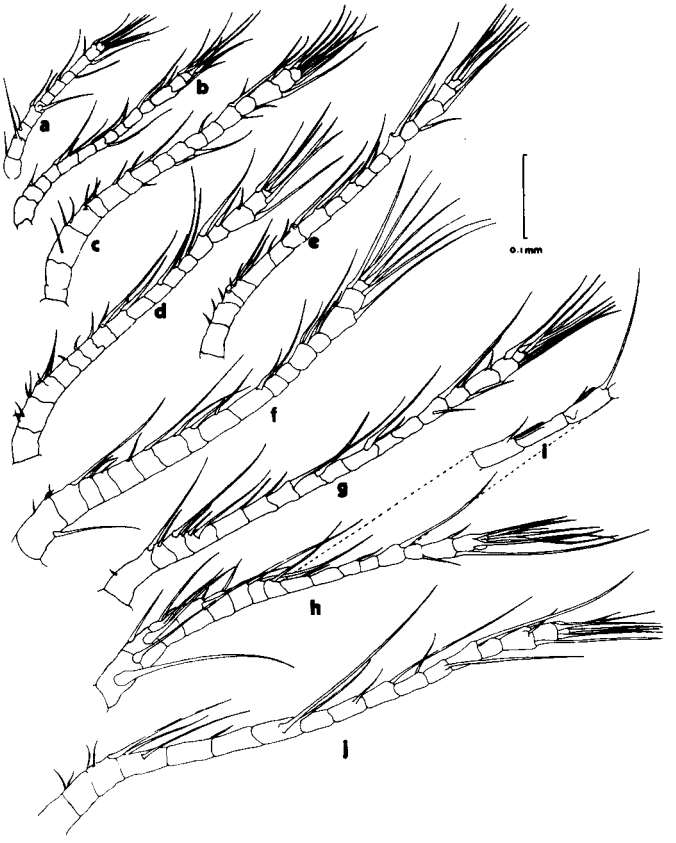

Figure 11. Antennules of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male left; *(i)* stage VI, male right; *(j)* stage VI, female.

Copepodid VI, male (Table 2; Figures 9h, 10h, 11h, 12h, 13h, 14h, 15h, 16h-i, 17h, 18h, 19g, 20f, 21e). Average length of 59 specimens (including caudal furca) was 0.859 ± 0.008 mm, range 0.770-0.924 mm, SD ± 0.036, average prosome/urosome ratio 2.93:1. The prosome has 6 segments. The cephalosome is approximately 50% as long as the prosome; it has 2 rostral filaments. The metasome has 4 segments. The urosome has 5 abdominal segments. Furcal rami have 6 plumose setae (the innermost is the smallest). The fifth legs are uniramous and asymmetrical.

Copepodid VI, female (Table 2; Figures 9i, 10i, 11i, 12i, 13i, 14i, 15i, 16i, 17i, 18i, 19h, 20g, 21f). Average length of 73 specimens (including caudal furca) was 1.008 ± 0.009 mm, range 0.924-1.097 mm, SD ± 0.04, average prosome/urosome ratio 3.35:1. The female is longer than the same male stage (average ratio 1:0.82). The cephalosome is nearly 46% as long as the prosome; it has 2 rostral filaments. This stage has the same general characteristics as the corresponding male stage, except that the urosome has 3 segments: the first one (genital) is longer than it is wide, and the third one (anal) is shorter and lacks spines and setae. The caudal furcal rami are longer than they are wide. The fifth legs are uniramous and symmetrical.

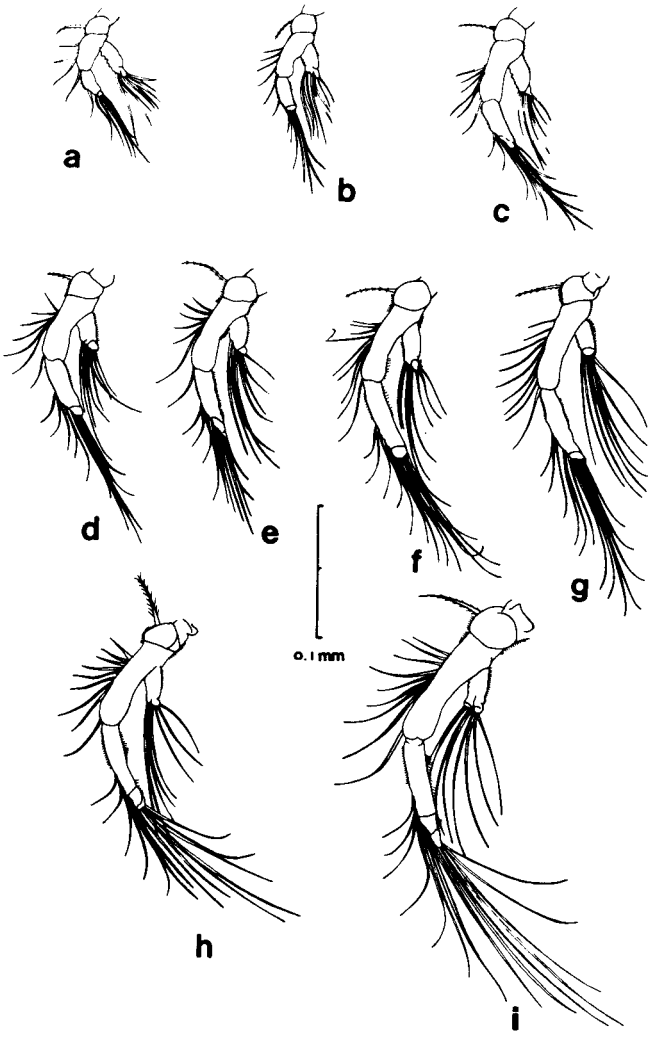

Figure 12. Antennae of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

DISCUSSION

This work describes for the first time the life cycle of the marine calanoid copepod *Acartia californiensis* Trinast from specimens reared in the laboratory. The life cycles of only 13 species of the genus *Acartia* have been described previously, and most of these descriptions are incomplete. There is a close morphological similarity between *A. californiensis* and *A. tonsa* Dana, especially in the adult stage, as well as, to a lesser extent, with *A. clausi* Giesbrecht, *A. bifilosa* Giesbrecht, and *A. iseana* Ito. It is possible that the juvenile stages of the latter four species are very similar to those of *A. californiensis*. However, published descriptions of their life cycles (except for *A. iseana*) are inadequate for further comparison and discussion of possible relationships.

Changes occurring during naupliar development of *Acartia californiensis* are: an increase in body length;

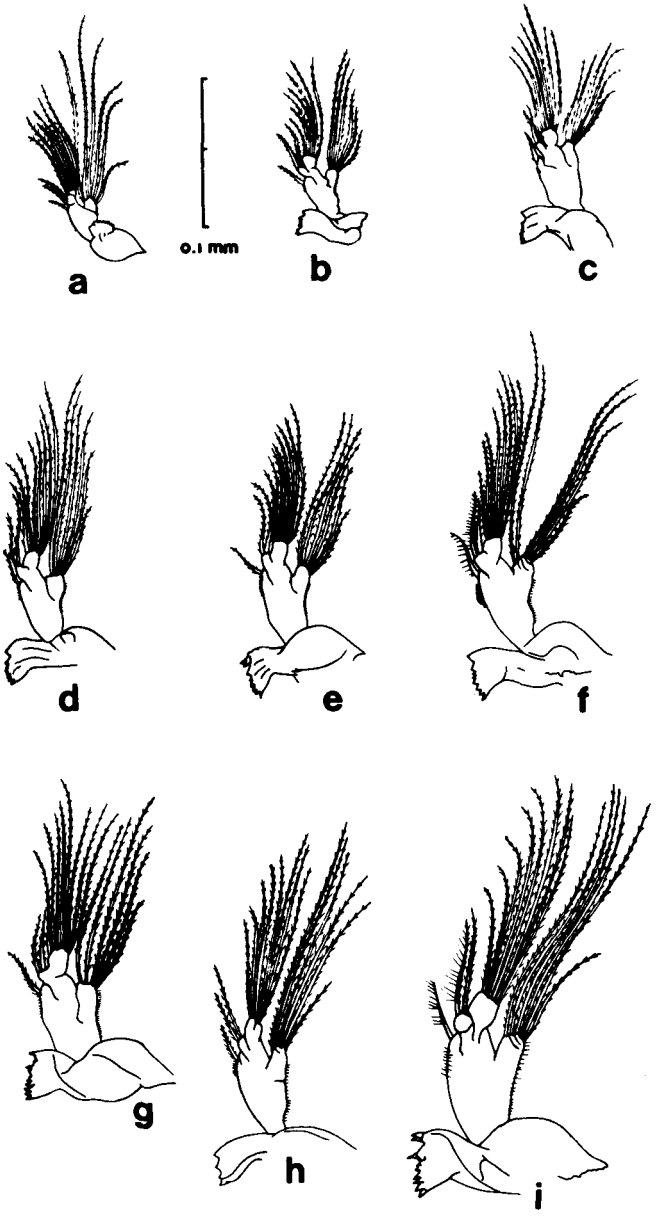

Figure 13. Mandibles of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

an increase in the number of setae of the distal segment of the antennule; an increase in the setation of the antenna and mandible; and an increase in the number of elements in the caudal armature until naupliar stage IV. The next stages (V and VI), remain the same except for the addition of new pairs of appendages, as follows: maxillule during naupliar stage III; maxilla and maxilliped (buds) during naupliar stage V; and first and second pairs (buds) of swimming legs during naupliar stage VI.

In the copepodid development stages, which are morphologically different from the naupliar stages and essentially miniature versions of the adult stages, body

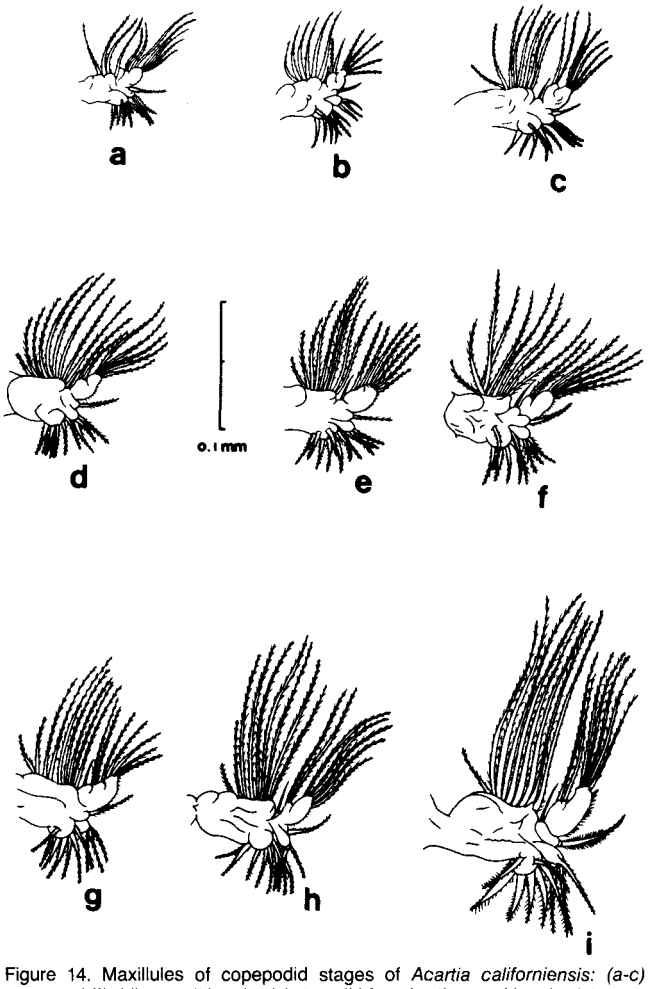

Figure 14. Maxillules of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

size increases until copepodid stage III. At this stage it becomes possible to differentiate sexes, either by size or number of urosome segments, as well as by the presence and structure of the fifth pair of swimming legs. The female always increases more in size than the male.

At first, there are two pairs of swimming legs. Then, in each successive copepodid stage until stage IV, a new pair of swimming legs is added. Copepodid stages V and VI do not add swimming legs.

Acartia californiensis—like other neritic-estuarine species of the genus *Acartia*, such as *A. tonsa* (Zillioux and Wilson 1966; Zillioux 1969; Heinle 1969, 1970), *A. clausi* (Corkett 1968; Zillioux 1969), and *A. grani* (Vilela 1972)—proved able to live and breed for several generations under simple laboratory culturing conditions.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of the late Martin Wiggo Johnson (Sept. 30, 1893–Nov. 28,

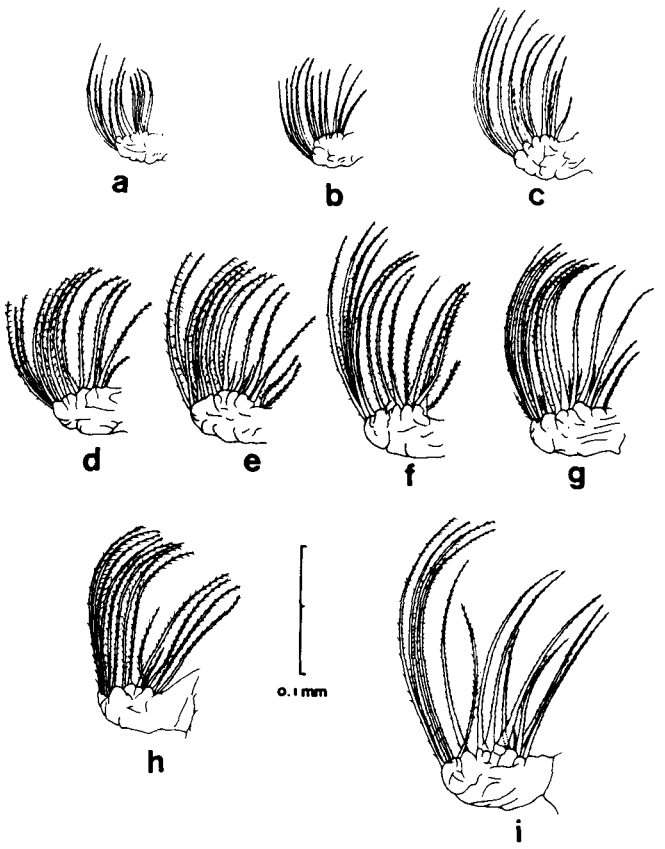

Figure 15. Maxillae of copepodid of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

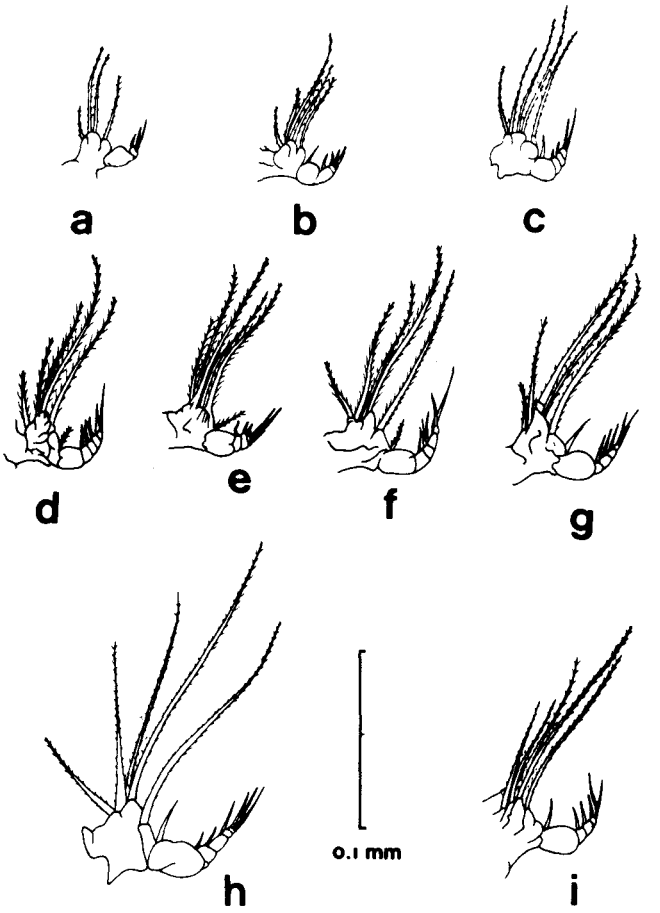

Figure 16. Maxillipeds of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

1984), whose accomplishments in marine biology focused on the distribution and life history of marine crustaceans and planktonic organisms.

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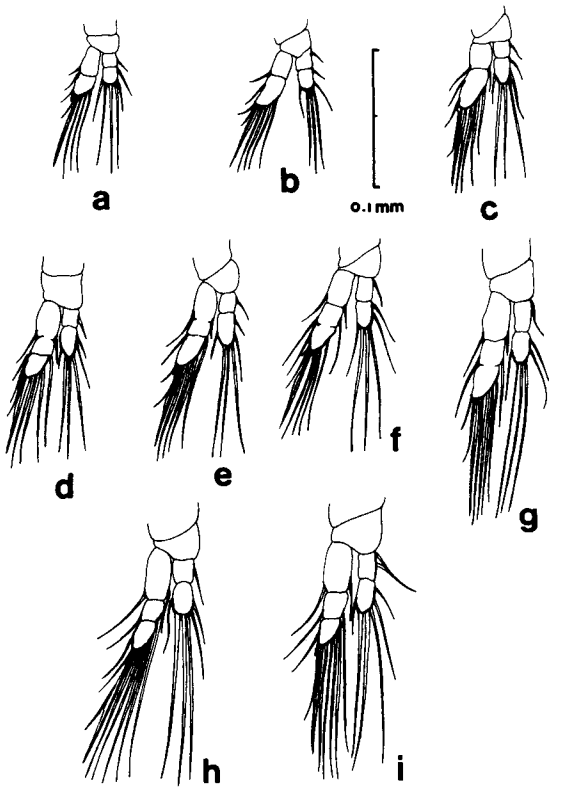

Figure 17. Leg I of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

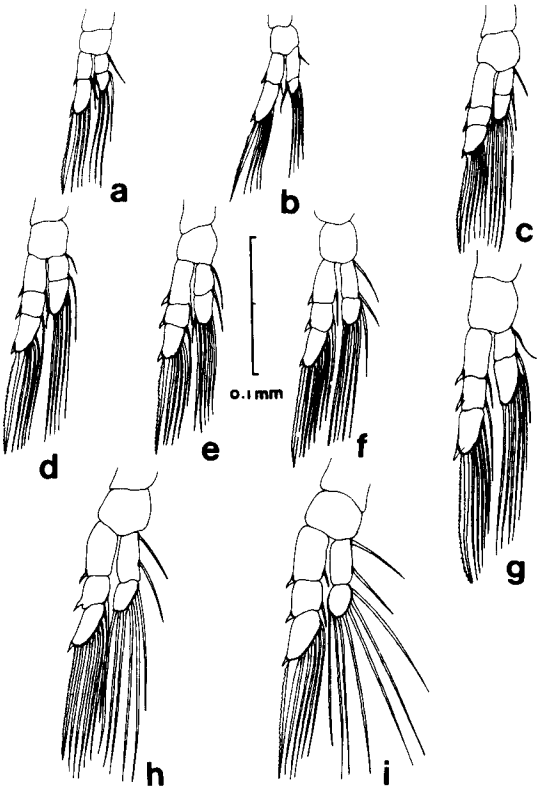

Figure 18. Leg II of copepodid stages of *Acartia californiensis: (a-c)* stages I-III; *(d)* stage IV, male; *(e)* stage IV, female; *(f)* stage V, male; *(g)* stage V, female; *(h)* stage VI, male; *(i)* stage VI, female.

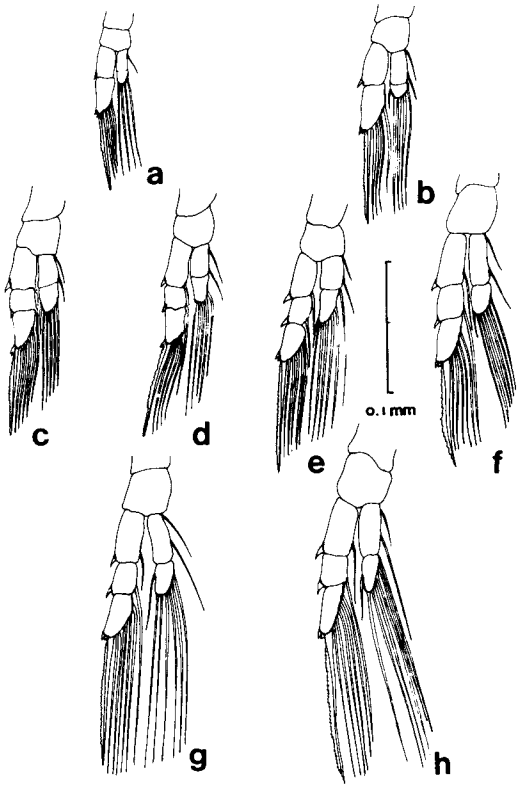

Figure 19. Leg III of copepodid stages of *Acartia californiensis: (a-b)* stages II-III; *(c)* stage IV, male; *(d)* stage IV, female; *(e)* stage V, male; *(f)* stage V, female; *(g)* stage VI, male; *(h)* stage VI, female.

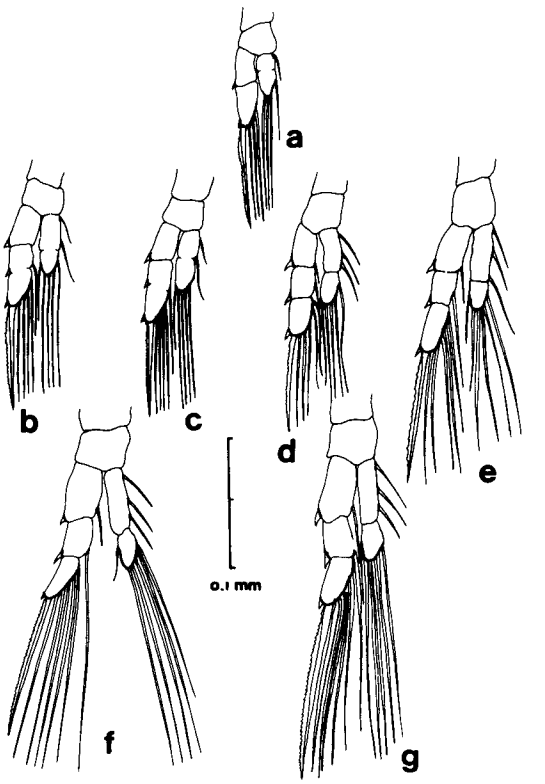

Figure 20. Leg IV of copepodid stages of *Acartia californiensis: (a)* stage III; *(b)* stage IV, male; *(c)* stage IV, female; *(d)* stage V, male; *(e)* stage V, female; *(f)* stage VI, male; *(g)* stage VI, female.

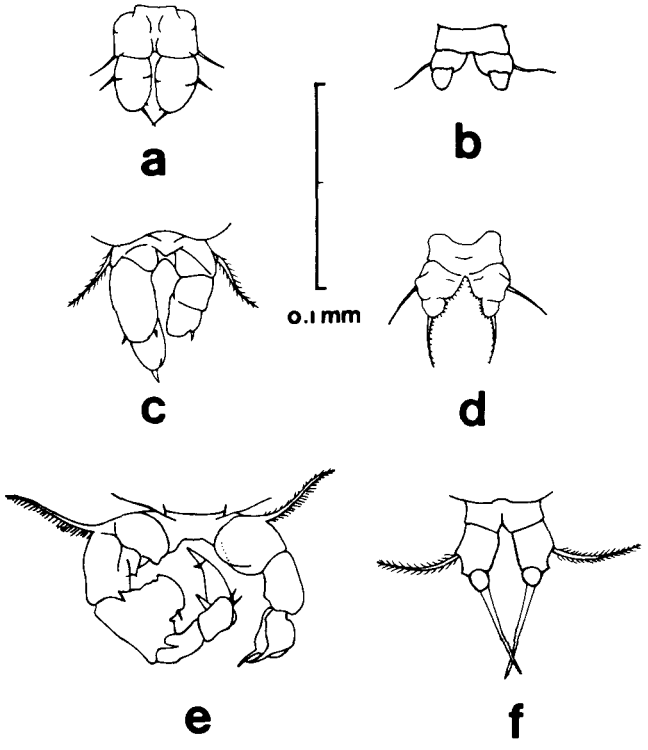

Figure 21. Leg V of copepodid stages of *Acartia californiensis: (a)* stage IV, male; *(b)* stage IV, female; *(c)* stage V, male; *(d)* stage V, female; *(e)* stage VI, male; *(f)* stage VI, female.

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