

Dimorphism and possible sex change in copepods of the family Calanidae

A. Fleminger

Marine Life Research Group, A-001, Scripps Institution of Oceanography; La Jolla, California 92093, USA

Abstract

Adult females of 14 of 25 species of the family Calanidae were found to be dimorphic with respect to the number of aesthetascs on the first antenna. The trithek morph, in which most antennal segments bear a complement of one aesthetasc and two setae, appears to be the typical female phenotype. The quadrithek morph is less common and, as in males, odd-numbered segments 2b, 3, 5, 7 and 9 carry quadritheks, i.e., two aesthetascs as well as two setae. Segment 21 in the quadrithek female bears an aesthetasc that is absent in the trithek female. Male antennal segments are distinguished from those of trithek and quadrithek females by pronounced morphological differences in aesthetasc shape and size as well as fusion of one or more pairs of antennal segments. The quadrithek morph usually comprised only a small proportion (<10%) of a local population. Quadrithek morphs were found in tropical and subtropical genera (*Cosmocalanus* and *Nannocalanus*), broadly ranging genera (*Calanoides*), as well as in cool-water lineages (*Calanus* s.s., *Calanus* s.l. *cristatus*, *C.* s.l. *plumchrus*, *C.* s.l. *propinquus* and *C.* s.l. *tonsus*). Maximum frequencies of quadrithek morphs (10 to 12%) in *Calanus pacificus californicus* occurred during the upwelling season from late winter into spring. No indication of sexual or antennal dimorphism was found in CV *C. pacificus californicus* sexed by examination of gonad and gonaduct. The quadrithek dimorph appears to be the product of sex change by the larger-sized late-juvenile potential male. The evolutionary and ecological significance of this presumptive hypothesis is that the larger-sized potential male reaching adulthood one or more weeks before maturation of genotypic females may increase its reproductive output by sex change in the course of the final molt to mature as a functional female. Given the sex-change hypothesis, morphogenesis of secondary sexual structures would appear to be controlled by androgenic-like secretions from the genital tract, as has been shown in malacostracans.

Introduction

Many species of the family Calanidae are colonizing opportunists whose populations rapidly increase when phytoplankton production increases seasonally (Longhurst, 1967; Binet and Suisse de Sainte Claire, 1975; Petit and Courties, 1976; Thiriot, 1978; Smith, 1982; Hirche, 1983). Moderate to highly skewed sex ratios are a familiar feature of these calanid populations (Marshall and Orr, 1955; Fulton, 1973; Tande and Hopkins, 1981; Miller *et al.*, 1984). The skewed ratios usually favor females and have been attributed to a wide variety of factors, the most familiar being earlier seasonal occurrence of males and shorter longevity of males (Marshall and Orr, 1955; Corkett and McLaren, 1978; Tande and Hopkins, 1981). Since predominance of females when growth conditions are optimal may maximize egg production (non-selectively), skewed sex ratios also have prompted speculation about sex change in free-living copepods (e.g. Battaglia, 1958, 1960, 1963; Conover, 1965; Heinle, 1970; Tande and Hopkins, 1981; Hopkins, 1982). Available evidence for sex change in copepods is not conclusive. Moreover, nothing definite is known of the mechanisms of sex determination in copepods. For animals in general, the sex of an individual may be determined (1) genetically, often by a chromosomal mechanism, or (2) epigenetically, under the influence of environmental factors. Within a given species of animal, some individuals may have genetically determined sex, and others may have environmentally determined sex.

The present paper demonstrates that populations of most calanid copepods include adult males and two morphological types of adult females, one of which has a first antenna resembling that of the male in the number of aesthetascs. The dimorphism between female types is abrupt, with no intermediate forms, and appears to be genetically founded.

Detailed analysis of the dimorphism suggests the following linked scheme of hypotheses:

(1) Sex determination within the Calanidae is largely, but not entirely, under genetic control.

(2) Environmental factors can induce change of the larger-sized males into functional females.

(3) Morphogenesis of secondary sexual characters is a response to hormones from secretory tissues probably associated with the gonad or gonaducts and differs in only minor details from sexual morphogenesis in the malacostacans (Charniaux-Cotton, 1960).

Although the present paper does not include direct evidence for sex change in calanid copepods, data to support the hypothesis were sought from two approaches. First, Barnes and Barnes (1953) and Woodhead and Riley (1957, 1959) suggested that *Calanus finmarchicus* and *C. helgolandicus* can be sexed in the Copepodid V larvae (CV) by the ratio of the cephalosome length to the width of the first pediger-bearing segment (ThI), although Conover (1965) found this ratio uninformative in *C. hyperboreus*. If the ratio correctly identifies the genetic sex of CV in some species, then the hypothetical scheme explaining males changing to females predicts that some CV will have male body proportions, but the developing gonad will be an ovary. The type of gonad an individual was forming at capture can be evaluated by staining and clearing techniques (Tande and Hopkins, 1981), and thus the comparison can be made. This is not a definitive test of the sex-change explanation, because the body proportions may be determined at the same time that the gonad differentiates under control by the same factors. However, it has been pursued and the results are reported.

Second, Ghiselin's (1974) model for sex change together with Charnov and Bull's (1977) model for environmental sex determination suggest that larger genetic males will be the ones most likely to switch sex, because as females they would produce an above-average number of eggs. Smaller males would best remain males, since the chances are they will mate with a larger female. For copepods, this leads to the prediction that if quadrithek females derive from the larger CV genetic males, the size distribution of adult males will be negatively skewed. Individuals smaller than the modal size will outnumber those larger. While methods for testing the significance of skewness lack power in the statistical sense, the bulk of size measurements in biological materials are positively skewed. Thus, recurring negative skewness for size of male copepods will enhance credence in the hypothesis of sex change in copepods.

Materials and methods

Specimens examined in this study came from many sampling sites, as listed in Table 1. Sources for samples were Scripps Institution of Oceanography, the Smithsonian Institution, National Museum of Natural History, the Smithsonian Oceanographic Sorting Center, the National Marine Fisheries Service, the Woods Hole Oceanographic Institution, the Canadian Oceanographic Sorting Center, the University of Tasmania, and the Institute of Oceanology, Moscow.

Specimens were selected at random except for the requirement that, where possible, all segments of the first antenna should be present. The material was stained following the tinting procedure of Judkins and Fleminger (1972), or in batch staining whereby tens to hundreds of specimens were washed in distilled water for 10 min, drained, immersed in 70% ethanol for 1 min, flooded with 1% chlorazol black in 70% ethanol for 1 min, flooded with distilled water, and rinsed a second time in distilled water. Stained specimens were transferred to glycerol on glass slides for dissection, analysis and storage. The first antennae were dissected for examination in ventral view at 250× magnification, and setae and aesthetascs were classified and recorded segment by segment.

Body measurements were taken from dorsal view at 25× magnification under a stereomicroscope equipped with a mechanical stage and an ocular micrometer (100 divisions, 1 division = 0.0379 mm); readings were taken to the closest one-half division (0.01895 mm). Prosoma length represents the straight-line distance from the apex of the forehead to the articulation between the fifth pediger-bearing segment and the first urosomal segment. Cephalosome length is the straight-line distance between the apex of the forehead and the posterior end of the mid-dorsal knob at the proximal end of the cephalon. ThI width is the maximum linear distance across the first pediger-bearing thoracic segment.

Seasonal changes in occurrence of trithek and quadrithek females of *Calanus pacificus californicus* were examined from samples collected in 1969 and 1978 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) at stations near Point Conception. Samples for 1969 were chosen because the eight samples spanned the entire year, and conditions were moderate throughout (Wyllie and Lynn, 1971). 1978 was chosen because, in that year, monthly samples were collected off Point Conception. Temperatures off Point Conception in the early months of 1978 were several degrees higher than normal, but dropped to average levels in late spring and summer (Brinton, 1981). *C. pacificus californicus* is abundant off Point Conception, probably in association with the large, cool-water plume that recurs in surface layers in spring (Fleminger, 1964, pp 49–50; Wyllie and Lynn, 1971, pp 53–56; Bowman and Johnson, 1973, pp 27–33; Bernstein *et al.*, 1977; Owen, 1980). Collecting was done by towing a 1 m plankton net (Smith, 1971) obliquely between 200 m and the surface. Adult females were selected at random, 100 or more per sample for 1969, 20 per sample for 1978. Specimens were stained with chlorazol black and the antennae were dissected. All setae and aesthetascs were recorded segment by segment from ventral view to determine the frequency of trithek and quadrithek morphs and the frequency of variation at individual sites.

Fifth copepodites of *Calanus pacificus californicus* were sorted randomly from January and May, 1969, Point Conception samples (CalCOFI 6901-Station 80.52 and 6905-Station 82.47, respectively), to evaluate the relation between the type of developing gonad and the ratio cephalo-

Table 1. Calanidae. Numbers examined for dimorphism in the first antenna, with geographical localities of specimens and frequencies of adults

Species	Locality	Date	Adult females		Adult males
			Trithek	Quadrithek	
<i>Calanoides acutus</i>	59°35'S; 24°41'W	21. V. 1963	4	1	0
	57°56'S; 27°38'W	28. V. 1963	0	0	1
	62°46'S; 128°12'W	3. XI. 1966	0	0	1
	62°20'S; 61°51'W	21. I. 1969	5	5	0
	62°00'S; 62°04'W	21. I. 1969	5	15	0
	60°02.1'S; 38°18.9'W	23. XI. 1983	8	2	0
<i>C. brevicornis</i>	19°21'N; 16°52'W	28. I. 1967	0	0	4
	18°30'N; 16°59'W	28. I. 1967	0	0	2
	09°19'N; 51°13'E	18. VIII. 1964	7	3	10
	~34°S; ~18°E	29. V. 1963	5	4	18
	17°30'N; 21°38'W	9. V. 1974	0	0	2
<i>C. carinatus</i>	39°38.8'S; 61°58.7'W	23. X. 1972	0	0	8
	36°19.4'S; 56°37.3'W	25. X. 1972	20	0	13
	22°06'S; 40°56.7'W	21. XII. 1972	8	2	1
<i>C. macrocarinatus</i>	28°20'S; 154°03'E	31. VII. 1967	5	15	1
	~43°20'S; ~148°16'E	16. XI. 1971	0	10	1
<i>C. patagoniensis</i>	33°05'S; 72°02'W	26. II. 1969	40	0	15
<i>C. philippinensis</i>	04°05.6'S; 133°34.5'E	5. VII. 1979	13	7	15
<i>Calanus</i> s.l. <i>cristatus</i>	53°57'N; 171°10.8'E	30. VIII. 1953	7	3	1
	53°32.4'N; 166°10.8'E	1. IX. 1953	0	0	3
	50°00'N; 135°00'W	11. IX. 1961	0	0	4
<i>C. s.l. hyperboreus</i>	Gulf of Maine	?	8	2	0
	37°09'N; 74°06'W	21. II. 1976	8	0	4
	Gulf of Maine	15. V. 1915	0	0	1
	Gulf of Maine	22. III. 1920	0	0	2
<i>C. s.l. plumchrus</i>	66°18'N; 168°30'W	24. VIII. 1949	0	0	5
	51°11'N; 173°24'W	21. VII. 1970	8	2	2
	58°21'N; 168°57'E	15. II. 1966	0	0	1
	39°56.4'N; 143°38.5'E	28. IX. 1953	9	1	0
<i>C. s.l. propinquus</i>	57°56'S; 27°38'W	28. V. 1963	0	0	4
	55°31'S; 126°28'W	29. X. 1966	0	0	2
	62°20'S; 61°51'W	21. I. 1969	1	0	1
	60°02.1'S; 38°18.9'W	23. XI. 1983	4	4	0
<i>C. s.l. simillimus</i>	56°26.3'S; 74°16.8'W	18. X. 1972	0	0	5
	57°43'S; 65°34'W	25. I. 1969	0	0	3
	57°31'S; 73°35'W	29. I. 1969	6	0	0
	59°22'S; 77°10'W	30. I. 1969	8	0	2
<i>C. s.l. tonsus</i>	44°20'S; 127°15'W	2. XII. 1957	10	0	0
	41°10'S; 142°43'W	26. VII. 1966	0	0	5
	42°31'S; 134°28'W	5. VIII. 1966	0	0	5
	42°06'S; 124°38'W	22. VIII. 1966	9	1	0
<i>C. s.s. chilensis</i>	33°10.5'S; 73°10'W	23. XII. 1957	5	0	0
	40°43'S; 74°34'W	14. I. 1969	5	0	0
	32°54'S; 72°00'W	26. II. 1969	5	0	15
	08°30'S; 80°37'W	13. VII. 1952	10	0	12
	12°24'S; 77°54'W	20. VII. 1952	10	0	6
<i>C. s.s. finmarchicus</i>	52°34'N; 44°29'W	5. IV. 1964	0	0	6
	52°37'N; 35°35'W	12. IV. 1964	0	0	10
	37°30'N; 74°30'W	23. VII. 1972	6	4	10
<i>C. s.s. glacialis</i>	49°27.4'N; 66°47.3'W	14. VI. 1971	0	0	16
	57°37.9'N; 155°57.3'E	6. X. 1952	9	1	0
<i>C. s.s. pacificus californicus</i>	34°24.5'N; 12°36.5'W	18. I. 1969	298	37	10
		18. II. 1969	89	11	0
		13. IV. 1969	90	10	0
		14. V. 1969	324	26	10

continued on p. 276

Table 1 (continued)

Species	Locality	Date	Adult females		Adult males
			Trithek	Quadrithek	
	34°24.5'N; 120°36.5'W	21. VII. 1969	95	5	0
		30. VIII. 1969	93	7	0
		22. X. 1969	98	2	0
		26. XI. 1969	95	5	0
		24. I. 1978	17	3	10
	34°26'N; 120°32.5'W	6. III. 1978	19	1	10
		14. IV. 1978	18	2	0
		22. V. 1978	19	1	0
		6. VII. 1978	19	1	0
		<i>Canthocalanus pauper</i>	12°15'S; 124°09'E	1. I. 1973	10
16°25.5'N; 98°42'W	1. XI. 1978		60	0	10
06°03'S; 167°44'E	VII. 1946		0	0	4
<i>Cosmocalanus caroli</i> + <i>C. darwini</i>	11°58'N; 55°11'E	26. VIII. 1964	0	0	1
	07°26'N; 89°31'W	30. VI. 1952	16	0	5
	18°16'S; 95°05'W	27. XI. 1960	0	0	1
	02°12'S; 166°39'E	VII. 1946	6	4	7
<i>Mesocalanus lighti</i>	30°20.5'N; 119°27.5'W	10. VII. 1958	1	0	3
	16°07'S; 165°13'W	11. I. 1953	8	0	2
	16°26'S; 132°58'W	29. X. 1969	6	0	3
	34°06'N; 140°00'W	8. VIII. 1964	14	0	0
<i>M. tenuicornis</i>	35°57'N; 127°12'W	18. IV. 1958	4	0	3
	34°24.5'N; 120°36.5'W	26. XI. 1969	2	0	5
	37°05'N; 131°30'E	27. IV. 1966	7	0	6
	40°19'N; 150°00'W	25. VIII. 1955	10	0	0
	39°30'S; 74°09'W	13. I. 1969	3	0	2
<i>Nannocalanus minor</i>	47°28.2'N; 10°26'W	29. VI. 1967	0	0	4
	16°26'S; 132°58'W	29. X. 1969	13	2	5
	07°26'S; 89°31'W	30. VI. 1952	0	0	3
<i>Neocalanus gracilis</i>	47°28.2'N; 10°26.2'W	6. III. 1978	1	0	0
	07°47'S; 121°17'E	26. X. 1960	0	0	6
	13°44'N; 112°05'E	1. VI. 1960	0	0	7
	27°27'N; 155°00'W	12. IX. 1964	8	0	0
	06°03'S; 167°44'E	VII. 1946	8	0	0
<i>N. robustior</i>	07°47'S; 121°17'E	26. X. 1960	0	0	1
	16°26'S; 132°58'W	29. X. 1969	15	0	3
	18°16'S; 95°05'W	27. XI. 1960	0	0	11
<i>Undinula vulgaris</i>	07°25'S; 12°34'W	2. VII. 1963	0	0	2
	09°33'N; 84°37'W	8. XI. 1965	10	0	0
	10°37'N; 79°39'E	1. V. 1960	10	0	0
	17°00.15'N; 61°45.8'W	8. VIII. 1976	20	0	8

some length:ThI width. Gonads and gonaducts in CV stage were examined by staining in borax carmine for at least 2 wk (according to Tande and Hopkins, 1981). The specimens were then dehydrated in ethanol and mounted in terpineol, which serves as clearing agent and temporary mounting medium. Measurements were made as described above.

Adult males and quadrithek females of *Calanus pacificus californicus* also were sorted from these samples to evaluate the prediction that their size distributions may be skewed to smaller sizes. Skewness was measured by the statistic suggested by Simpson *et al.* (1960, p. 143):

$$Sk = \frac{3(\text{mean} - \text{median})}{SD}$$

In a symmetrical distribution, mean and median are equal, and $Sk=0$. In right-skewed distributions, the mean is larger than the median, and Sk is positive; in left-skewed distributions, Sk is negative.

Arrangement, morphometrics and morphology of antennal setae and aesthetascs may provide considerable information of systematic value, but only broad morphological types were used in the present study. Setae and aesthetascs are often broken, and ornamentation such as plumosity or fleshy lobes may be broken or lost. However, even severely damaged aesthetascs can be distinguished from setae by their swollen outline and thin walls, and examination of a large series of specimens confirms the regularity in patterns of these elements.

Two different generic systems have been proposed for Calanidae, one by Brodsky (1967, 1972) and the other by Bradford and Jillett (1974). This is not the place to discuss their respective strengths and weaknesses but, on the basis of new morphologic studies and a cladistic analysis of calanid lineages (Fleminger, unpublished data), I find Brodsky's views largely unacceptable. I also have substantive disagreements with Bradford and Jillett's view of *Calanus* and *Neocalanus*; I find their concepts of these genera to be polyphyletic. Accordingly, in this report I restrict use of *Neocalanus* to *N. gracilis* and *N. robustior*, and I use *Calanus sensu lato* for taxa whose generic status is in my view as yet unresolved (i.e., *C. s.l. cristatus*, *C. s.l. hyperboreus*, *C. s.l. plumchrus*, *C. s.l. propinquus*, *C. s.l. simillimus*, and *C. s.l. tonsus*). I use *Calanus sensu stricto* for the various species of the *Calanus finmarchicus* complex (i.e., *chilensis*, *finmarchicus*, *glacialis*, *pacificus*, *orientalis*, *sinicus*, *australis*, *helgolandicus*, *marshallae*). I retain *Nannocalanus* and use remaining genera as proposed by Bradford and Jillett (1974, i.e., *Calanoides*, *Canthocalanus*, *Cosmocalanus*, *Mesocalanus*, and *Undinula*).

Results

General morphology of the calanid first antenna

The first antenna in the CV and adult female calanids contains 25 articulated segments. Enumeration of the segments begins with the most proximal following Giesbrecht (1892). In the female (Fig. 2C), Segments 1 and 2 are always separate. Segment 2 bears three clusters of setae and aesthetascs, each cluster containing two setae and one aesthetasc. Segment 2 is probably a compound of three primitive segments formed by fusion of articulations and distinguished here by letters 2a, 2b and 2c. In the adult male (Fig. 2A), Segments 1 and 2 are always fused into a compound segment, 1-2, and the cluster on Site 2b contains two setae and two aesthetascs. Other sets of fused segments occur in the males in some genera, as noted in Table 2. In each case these fusions are easily recognized, since the number and position of the setae and aesthetascs remain the same as in those taxa without secondary fusions. In both sexes, the articulation between Segments 8 and 9 is modified by partial fusion (Bowman, 1978).

The first antenna bears an array of receptor organs of two morphological and functional classes: (1) setae, and (2) aesthetascs. Setae are relatively slender, flexible organs, usually tapering to a fine point and often bearing a single or paired row of fine hairs, thereby conveying the appearance of a feather (Gurney, 1931, p. 38). They are assumed to perform primarily as mechanoreceptors (Strickler and Bal, 1973; Friedman, 1980; Haury *et al.*, 1980). Aesthetascs, or sense clubs, are thin-walled pegs filled with dendrites of bipolar neurons (Laverack, 1968) that serve as chemoreceptors (Griffiths and Frost, 1976; Ache, 1982; Bush and Laverack, 1982; McLaughlin, 1982). Both setae and aesthetascs occur in several morphologically distinctive forms

and, as noted by Gurney (1931, p. 38), are remarkably constant in both structure and position. Each regularly occupies particular sites on particular segments throughout the family. Within each taxon, differences in arrangement and size of setae and aesthetascs among the proximal, middle and distal sectors of the first antenna suggest that these sectors receive different ranges as well as directionality of chemical and mechanical signals (Friedman, 1980).

Morphological types of setae and aesthetascs

Four types of antennal setae may be recognized among the Calanidae. Most common, Type 1, are smooth-surfaced, acuminate filaments varying from shorter than the bearing segment to more than ten times its length (Fig. 1D), and located anteriorly on the segment. Type 2 are short, coniform processes (Fig. 1E) always found on the anterior, distal end of Segment 8 and in many species on Segment 12. Type 3 are pseudo-annulated setae bearing spike-like setules (Fig. 1F) located on Segments 22, 23 and 24. Type 4 are short and with a more or less capitate apex, usually filled with lipid-like globules (Fig. 1G). They occur only in adult males on one or more of the following segments depending upon the species: fused Segment 1-2, Segment 7, and Segment 9. The capitate, Type 4 setae, occupy the distal position that is filled by a Type 1 seta in the female and in the CV stage.

Aesthetascs appear in three forms. Category 1 are slender, vermiform processes (Fig. 1A) located on most

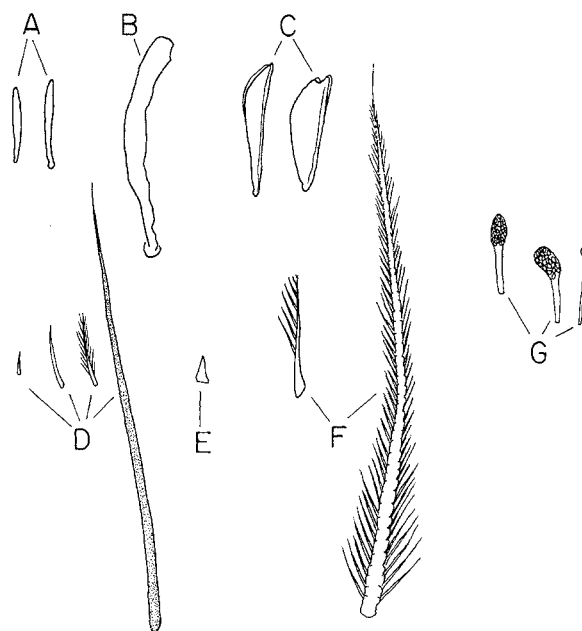


Fig. 1. Aesthetascs and setae on the first antenna of Calanidae. (A) Vermiform aesthetascs on trithek females and immature copepods; (B) digitiform aesthetasc on adult males; (C) scale-like aesthetasc on adult males; (D) type 1 seta, spiniform; (E) type 2 seta, acuminated; (F) type 3 setae, pseudo-annulated with spike-like setules; (G) type 4 setae with capitate apex

Table 2. Calanidae. Number of setae (Set) and aesthetascs (Aes) per antennule segment in the Calanidae genera examined. Bracketed segments are completely fused; Segments 8 and 9 are incompletely fused. Individual segments with similar numbers of Set and Aes are grouped together

Segment	Females									
	Trithek					Quadrithek				
	<i>Calanus</i> s.l. <i>Calanus</i> s.s <i>Canthocalanus</i> <i>Cosmocalanus</i> <i>Nannocalanus</i> <i>Undinula</i>		<i>Calanoides</i>		<i>Mesocalanus</i> <i>Neocalanus</i>		<i>Calanus</i> s.l. <i>Calanus</i> s.s <i>Canthocalanus</i> <i>Cosmocalanus</i> <i>Mesocalanus</i> <i>Nannocalanus</i> <i>Neocalanus</i> <i>Undinula</i>		<i>Calanoides</i>	
	Set	Aes	Set	Aes	Set	Aes	Set	Aes	Set	Aes
1	3	1	3	1	3	1	3	1	3	1
2a	2	1	2	0 or 1	2	1	2	1	2	0 or 1
2b	2	1	2	1	2	1	2	2	2	1 or 2
2c	2	1	2	1	2	1	2	1	2	1
3	2	1	2	1	2	1	2	2	2	2
4	2	1	2	1	2	1	2	1	2	1
5	2	1	2	1	2	1	2	2	2	2
6	2	1	2	1	2	1	2	1	2	1
7	2	1	2	1	2	1	2	2	2	2
8	2	1	2	1	2	1	2	1	2	1
9	2	1	2	1	2	1	2	2	2	2
10	2	1	1 or 2	1	2	1	2	1	1	1
11, 12, 14, 16, 18	2	1	2	1	2	1	2	1	2	1
13	2	1	1 or 2	1	2	1	2	1	1 or 2	1
15	2	1	1 or 2	1	2	1	2	1	1 or 2	1
17	2	1	1 or 2	1	2	1	2	1	1 or 2	1
19	2	1	1	1	2	1	2	1	1	1
20	1	1	1	1	1	1	1	1	1	1
21	1	0	1	0 or 1	1	1	1	1	1	1
22, 23	2	1	2	1	2	1	2	1	2	1
24	2	0	2	0	2	0	2	0	2	0
25	5	2	5	2	5	2	5	2	5	2

segments of the female antenna. Category 2 are digitiform, irregularly swollen or pinched along their length, and rounded at the apex (Fig. 1B). They occur on Segments 1 through 9 in males. Category 3, occurring in males on Segments 10 to 23, vary structurally in fine detail among the genera, but all have a central cuticular keel articulating proximally with the antero-distal corner of the segment and extending to the succeeding antennal segment (Fig. 1C). A "fleshy" layer covers the keel and extends as dorsal and ventral lamellae over the length of the Category 3 aesthetasc. These lamellae may be fused over the entire length of the aesthetasc or may separate at the distal end. The "fleshy" layer is fragile and often is partially to totally eroded by capturing nets or during storage in formaldehyde.

Arrangement of setae and aesthetascs

In all 25 species studied, most or all of the adult females had a trithek arrangement (i.e., one proximal seta, a distal seta,

and a distal aesthetasc on each segment of the first antenna except Segments 1 and 20 to 25 (Table 2, Figs. 2–4). Segment 1 bears three setae and one aesthetasc. Segment 2, apparently a fusion of three segments, bears three such tritheks in Positions 2a, 2b and 2c. Segments 20 and 21 each lack one seta and the latter usually lacks the aesthetasc as well. Segments 22 and 23 have only one seta and one aesthetasc anteriorly and one posteriorly positioned, plumose, pseudo-annulated seta (Type 3). Segment 24 has two setae similar to those of Segment 23 but no aesthetasc. Segment 25 bears four relatively short setae, one minute seta and two aesthetascs (Figs. 3 and 4). It may be derived from the fusion of two or more segments.

The first antenna of adult males exhibits alternation of trithek and quadrithek combinations, the latter consisting of two setae and two aesthetascs and occurring on Segments 2b, 3, 5, 7 and 9. Segments 2a, 2c, 4, 6, 8, and 10 through 19 bear tritheks as in the female. Segment 21 bears one seta and one aesthetasc in the male. The remaining segments carry the same numbers and types of setae and aesthetascs as found in the female (Table 2).

Table 2 (continued)

Segment	Males													
	<i>Calanus</i> s.l. (<i>pars</i>) <i>Calanus</i> s.s. <i>Undinula</i>		<i>Calanoides</i>		<i>Calanus</i> s.l. <i>propinquus</i> <i>C. s.l. simillimus</i>		<i>Cosmocalanus</i> <i>Nannocalanus</i>		<i>Mesocalanus</i>		<i>Neocalanus</i>		<i>Canthocalanus</i>	
	Set	Aes	Set	Aes	Set	Aes	Set	Aes	Set	Aes	Set	Aes	Set	Aes
1	3	1	3	1	3	1	1	1	3	1	1	1	3	1
2a	2	1	2	1	2	1	2	1	2	1	2	1	2	1
2b	2	2	2	2	2	2	2	2	2	2	2	2	2	2
2c	2	1	2	1	2	1	2	1	2	1	2	1	2	1
3	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	2	1	2	1	2	1	2	1	2	1	2	1	2	1
5	2	2	2	2	2	2	2	2	2	2	2	2	2	2
6	2	1	2	1	2	1	2	1	2	1 or 2	2	1	2	1
7	2	2	2	2	2	2	2	2	2	2	2	2	2	2
8	2	1	2	1	2	1	2	1	2	1	2	1	2	1
9	2	2	2	2	2	2	2	2	2	2	2	2	2	2
10	2	1	1	1	2	1	2	1	2	1	2	1	2	1
11-19	2	1	1	1	2	1	2	1	2	1	2	1	2	1
20	1	1	1	1	1	1	1	1	1	1	1	1	1	1
21	1	1	1	1	1	1	1	1	1	1	1	1	1	0
22, 23	2	1	2	1	2	1	2	1	2	1	2	1	2	1
24	2	0	2	0	2	0	2	0	2	0	2	0	2	0
25	5	2	5	2	5	2	5	2	5	2	5	2	5	2

Table 3. *Calanus* s.s. Antennule segmentation, setation and aesthetasc. Individual segments with similar numbers of setae and aesthetascs are grouped together. Setae: Set, setiform; Spi, spiniform; Plu, plumose and pseudoannulated; Cap, capitata. Aesthetascs: Ver, vermiform; Dig, digitiform; Sca, scale-like

Segment	Females						Males		
	Trithek morph			Quadrithek morph			Setae	Aesthetascs	
	Setae No., types	Aesthetascs No., types	Sum	Setae No., types	Aesthetascs No., types	Sum	No., types	No., types	Sum
1	3	1	4	3	1	4	3	1	4
2a	2	1	3	2	1	3	2	1	3
2b	2 } Set	1	3	2 } Set	2	4	1 Set, 1 Cap	2	4
2c, 4, 6	2	1	3	2	1	3	2 } Set	1	3
3, 5	2	1	3	2	2	4	2 } Set	2 } Dig	4
7	2	1 Ver	3	2	2	4	1 Set, 1 Cap	2	4
8	1 Set, 1 Spi	1	3	1 Set, 1 Spi	1 Ver	3	1 Set, 1 Spi	1	3
9	2 } Set	1	3	2 } Set	2	4	1 Set, 1 Cap	2	4
10, 11	2	1	3	2	1	3	2 Set	1	3
12	1 Set, 1 Spi	1	3	1 Set, 1 Spi	1	3	1 Set, 1 Spi	1	3
13-19	2	1	3	2	1	3	2	1	3
20	1 } Set	1	2	1 } Set	1	2	1 } Set	1 } Sca	2
21	1	0	1	1	1	2	1	1	2
22, 23	1 Set, 1 Plu	1	3	1 Set, 1 Plu	1	3	1 Set, 1 Plu	1	3
24	1 Set, 1 Plu	0	2	1 Set, 1 Plu	0	2	1 Set, 1 Plu	0	2
25	5 Set	2	7	5 Set	2 Ver	7	5 Set	2 Dig	7

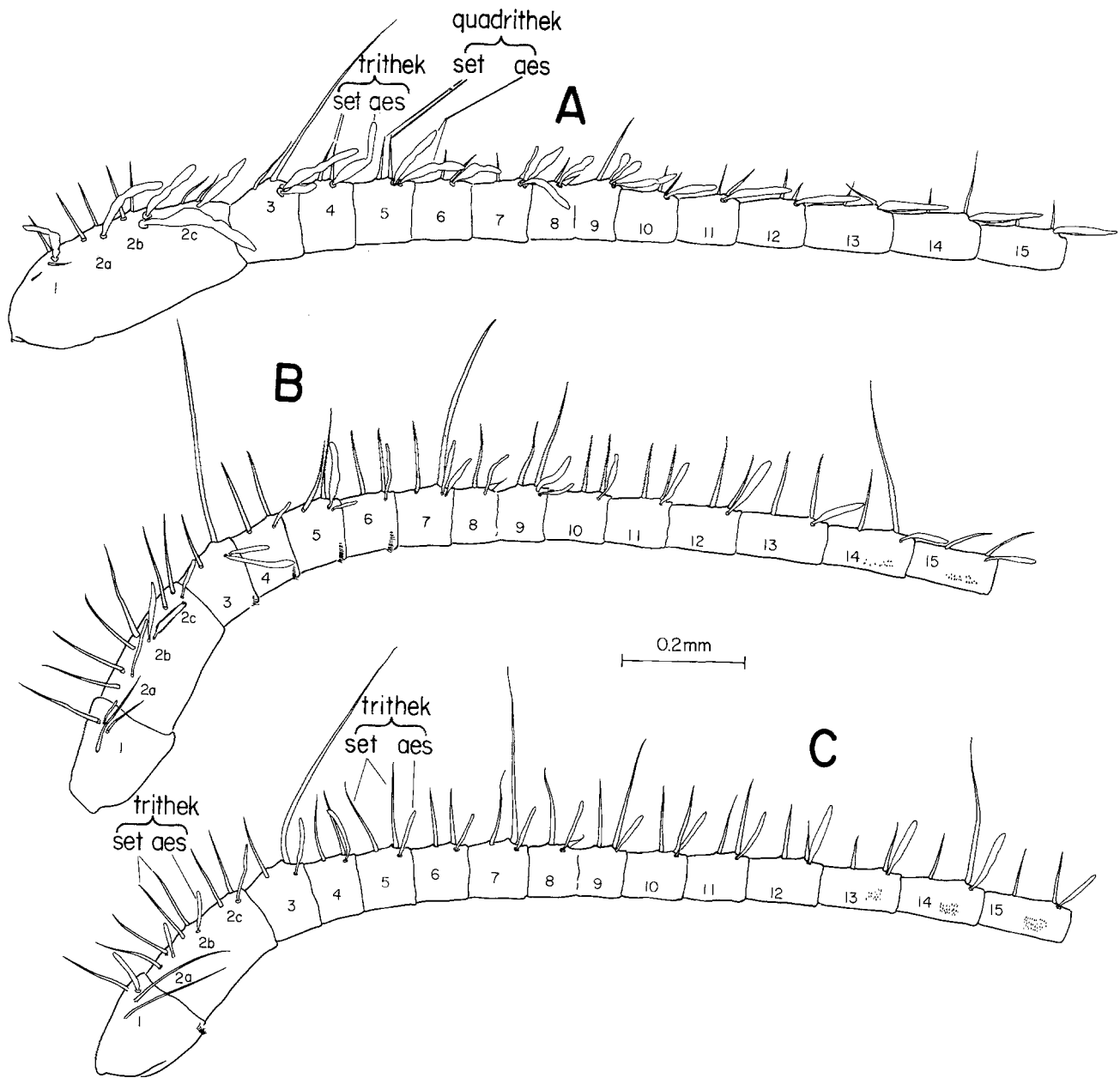


Fig. 2. *Calanus pacificus californicus*. Left antenna of adults, ventral view, Segments 1–15. (A) Male, with trithek grouping on Segment 4 and quadrithek groupings on Segment 5; (B) quadrithek female; (C) trithek female, with trithek groupings on Segments 2 b and 5 delineated. Set: seta; aes: aesthetasc

In females, distal setae on Segments 3, 7, 9, 14, 21 and 24 tend to be longer than the other anterior setae, but lengths vary among the species studied. All the setae and the scale-like male aesthetascs are articulated and rotate through about 90° from normal to the antenna surface to flat against it.

The generality of the pattern and arrangement of setae and aesthetascs is seen in comparison of the antennules of *Calanoides* and *Calanus* s.s., the two genera representing the most recent end points of separate evolutionary sequences within the family (Fleminger, in preparation). Despite the considerable taxonomic distance separating the two genera, differences in the first antennae are rather

small, with some *Calanoides* species deviating from the *Calanus* female trithek arrangement as follows: Segment 2 a may lack an aesthetasc and Segments 10, 13, 15, 17 and 19 may lack a seta (Figs. 2–4, Table 2). The distribution of the various types of setae and aesthetascs in *Calanus* is shown in Table 3.

The typical trithek arrangement in females of other genera, the alternating trithek-quadrithek arrangement in males, and the sets of fused segments in males are listed in Table 2. Examples of the male antennal Segments 1 through 12 are illustrated in Figs. 5 and 6. Marked differences in the size and proportion of the segments and their appendages notwithstanding, they show the same pattern of setae

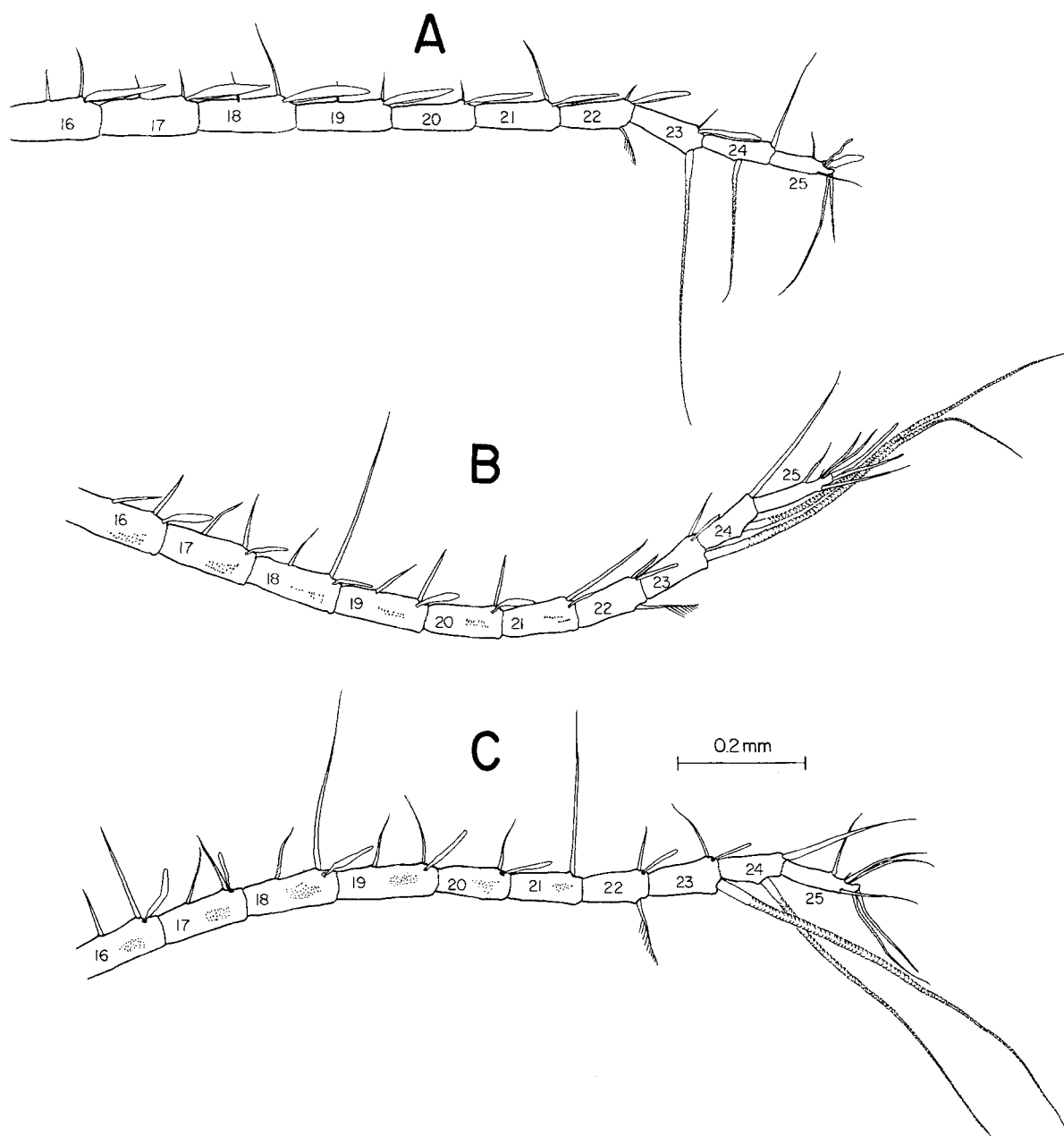


Fig. 3. *Calanus pacificus californicus*. Left antenna of adults, ventral view, Segments 16–25. (A) Male; (B) quadrithek female; (C) trithek female

and aesthetascs characterizing all taxa within the Calanidae and the Megacalanidae, the former family's phylogenetically closest known outgroup.

Dimorphism in the female first antenna

In all 25 of the species studied, the trithek arrangement of appendages on all antennal segments (Tables 2 and 3) is typical in the female, but in 15 species a male-like arrangement (alternating quadritheks and tritheks) was found. This "quadrithek" arrangement usually occurred in 5 to 10% of females pooled among samples for each species.

All setae and aesthetascs of quadrithek females resemble those of the trithek females: aesthetascs are all vermi-

form, and the capitate setae, scale-like aesthetascs and swollen aesthetascs found in the adult male are lacking. Examples of both types of female first antennae are shown in Figs. 2–4, and the complete arrangement of setae and aesthetascs in quadrithek females is included in Tables 2 and 3. When one considers the small size of the samples for most of the species examined, failure to find quadrithek morphs in eight of the species does not mean they never occur.

Apart from the occurrence of fully quadrithek females, deviations from the trithek pattern are infrequent and never extensive. Table 4 shows that single anomalies occur more often in *Calanoides* than in other calanid genera. Table 5 shows the result of an extensive search for anomalies in *Calanus pacificus californicus* collected in winter and spring. Very small deviations in aesthetasc number

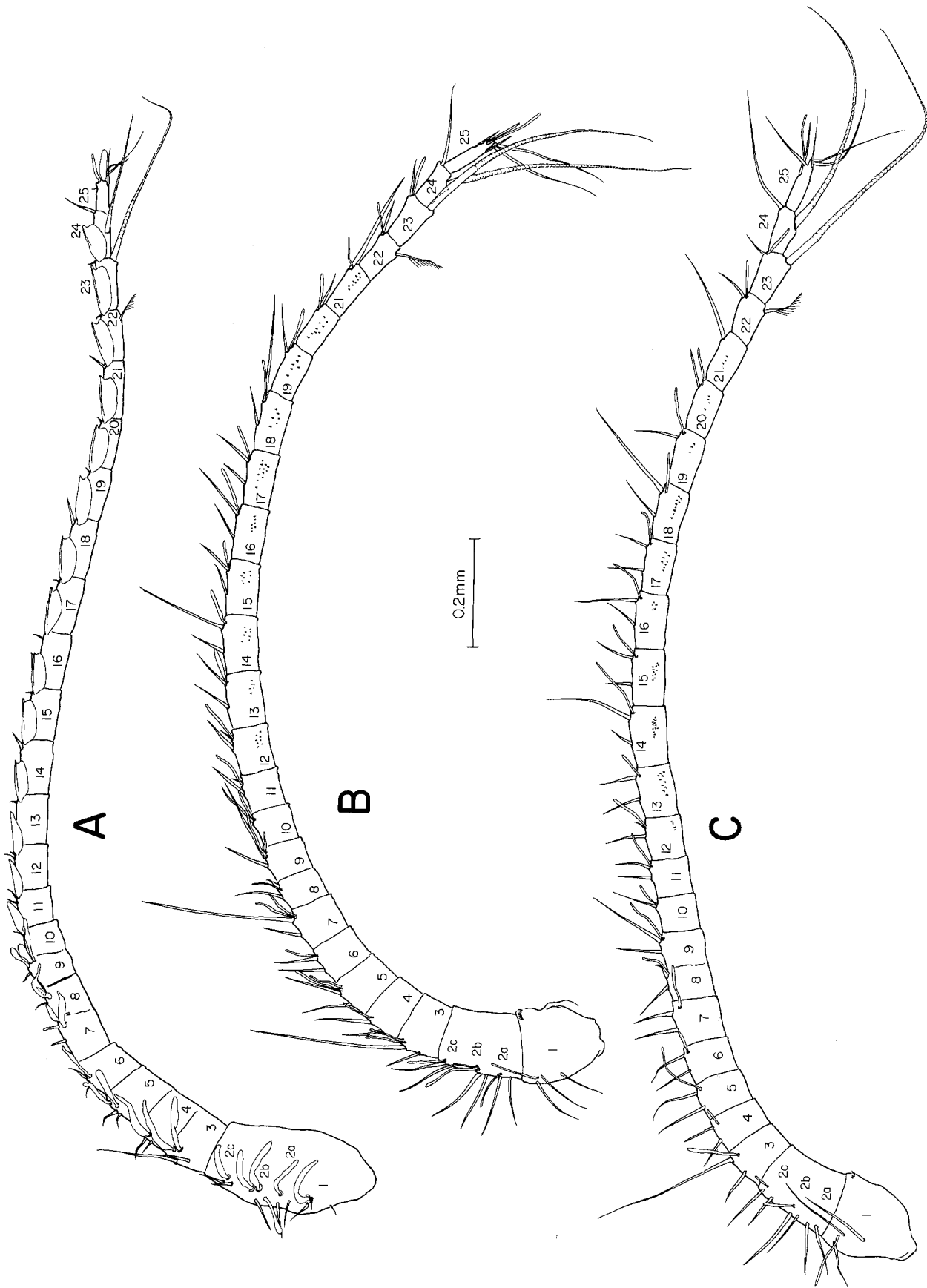


Fig. 4. *Calanoides philippinensis*. Left antenna of adults, ventral view. (A) Male; (B) quadrithek female; (C) trithek female

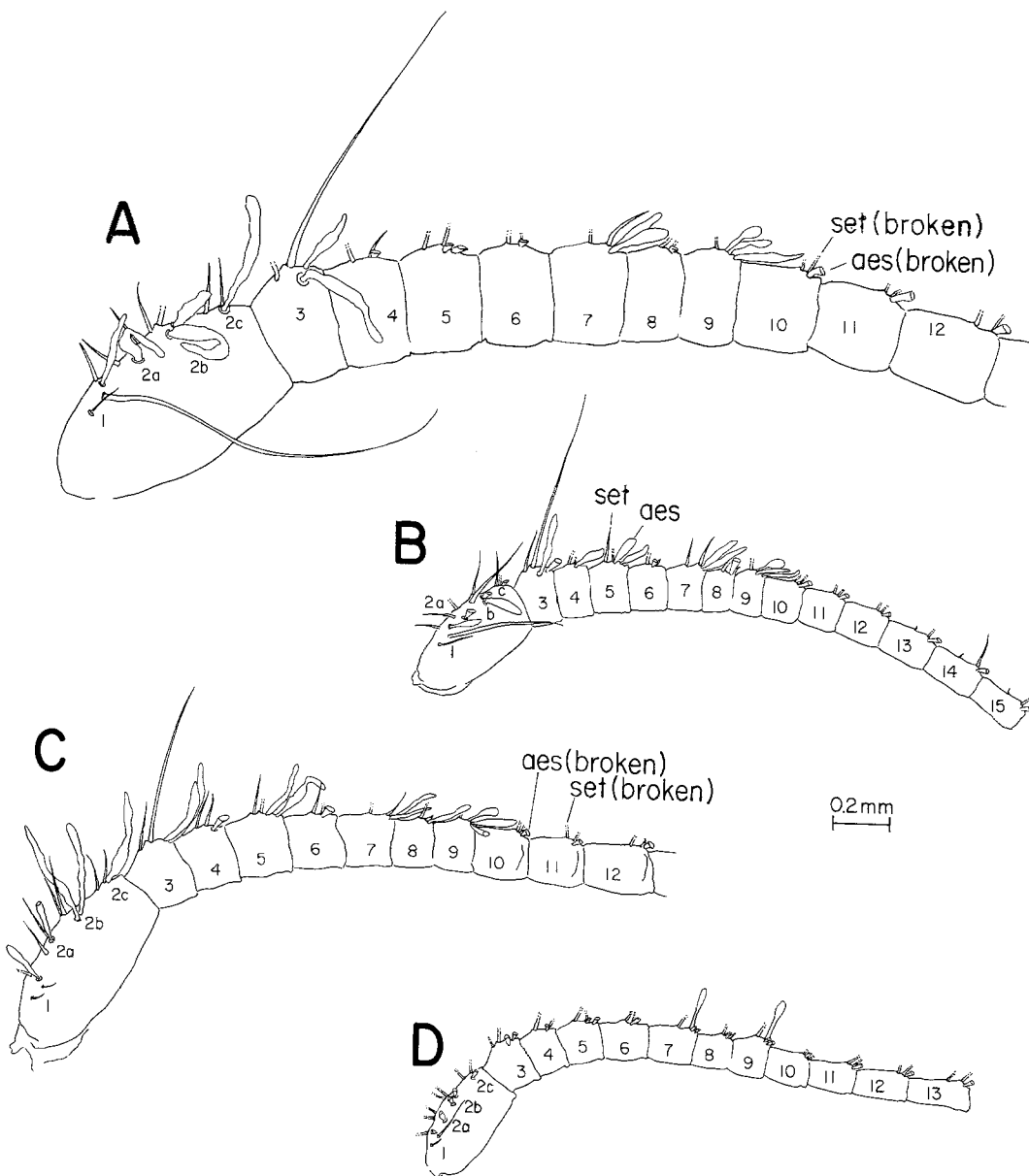


Fig. 5. Left first antenna of adult male Calanidae, proximal segments, ventral view. (A) *Calanus* s.l. *cristatus*; (B) *Calanus* s.l. *plumchrus*; (C) *Calanus* s.l. *hyperboreus*; (D) *Calanus* s.l. *tonsus*. Broken appendages shown incomplete as in specimen, aesthetasc (aes) truncate, with slightly to strongly flaring distal end and thin wall; setae (set) slender, without flared end and with thicker wall

occurred in 19 of 200 specimens. No anomaly in any species or specimen approached the full quadrithek condition. Variation in the number of setae occurred in less than 1% of specimens and was limited to a unilateral loss or additional seta on one segment. There are no intermediate degrees of anomaly in armamentation of the female first antenna. Among quadrithek females observed, necessarily a smaller sample, there were no additional anomalies in antennal appendages.

Routine observations throughout the study showed that the morphology of the reproductive system was normal in both trithek and quadrithek females: both morphs showed an advanced state of ovarian development and oviducts filled with eggs. The seminal receptacles

always appeared to be filled with sperm, and the antrum and the cover plate were similar in both morphs. In sum, except for the antennae, no differences in sexual morphology were noted between the trithek and quadrithek females.

Temporal variation in frequency of dimorphs

In samples taken near Point Conception in both 1969 and 1978, quadritheks were more abundant in winter and early spring, their numbers diminishing through midsummer to a low in autumn (Fig. 7, Table 6). Quadrithek frequency, prosome length, and population density all tended to be

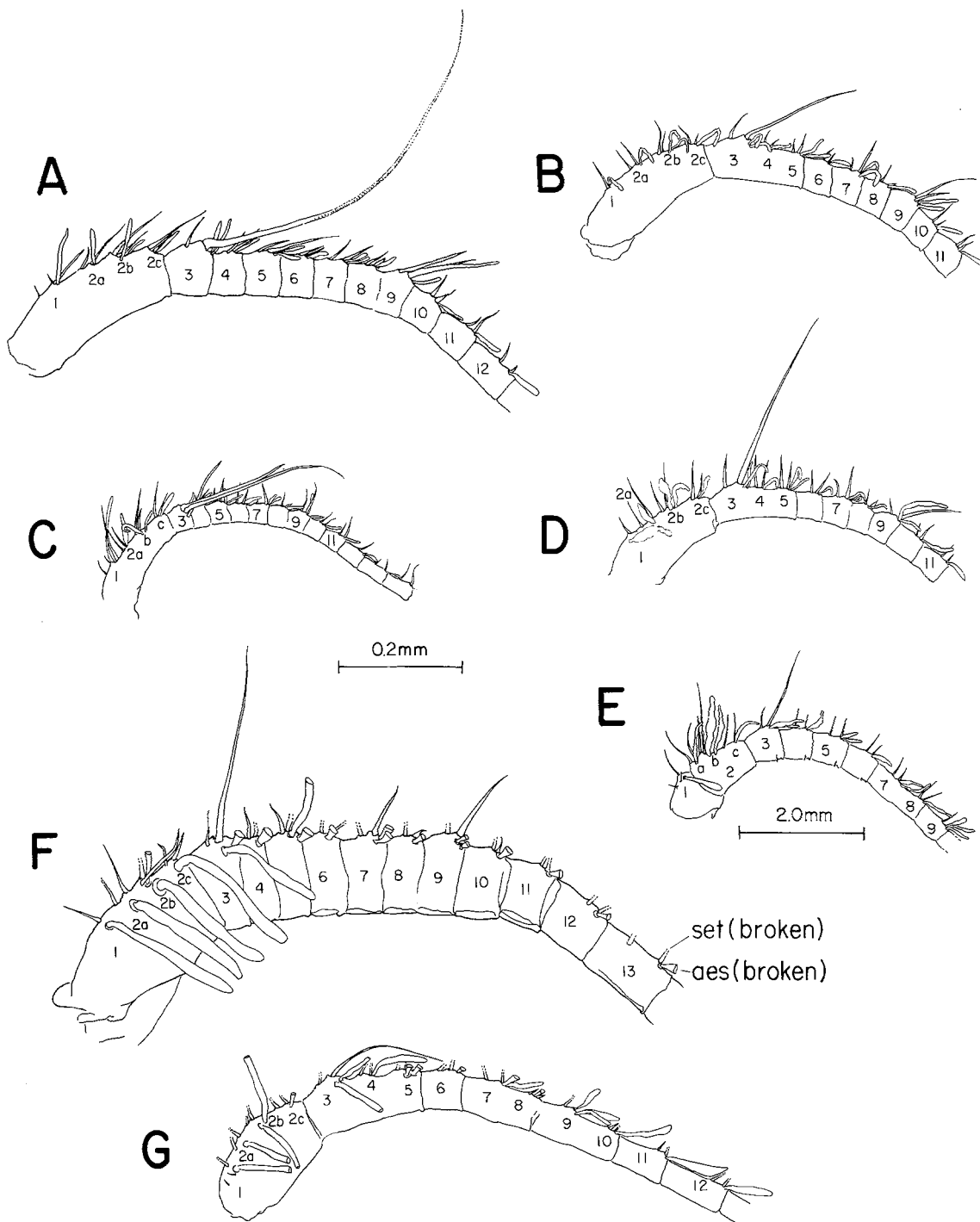


Fig. 6. Left first antenna of adult male Calanidae, proximal segments, ventral view. (A) *Undinula vulgaris*; (B) *Cosmocalanus darwini*; (C) *Canthocalanus pauper*; (D) *Nannocalanus minor*; (E) *Megacalanus princeps*; (F) *Neocalanus robustior*; (G) *Mesocalanus tenuicornis*

high at temperatures below 14 °C. At temperatures above 14 °C, quadrithek frequency, size, and population density tended to be low (Table 6).

Prosome proportions in CV and adult stages

No significant differences were found in the ratio cephalosome length:ThI width between CV developing ovaries and CV developing testes in either January or May

samples from off Point Conception (Fig. 8, Table 7). This is counter to previous results on another species, *Calanus finmarchicus* (Barnes and Barnes, 1953; Woodhead and Riley, 1957, 1959). Obviously this ratio has no great utility for predicting sex at CV in *C. pacificus californicus*. Moreover, it leads to no conclusion about the possible derivation of quadrithek females from genetic males. First antennae of these CV uniformly bore setae and aesthetascs in the CVI trithek arrangement, irrespective of sex as indicated

Table 4. Calanidae. Number of individuals with aesthetasc number varying from those typical of trithek and quadrithek morphs. No trithek morph had more than one anomaly. No quadrithek morph or male had one or more anomalies

Taxon	Trithek morphs		Quadrithek morphs lacking anomalies	Males, lacking anomalies
	lacking anomalies	one unilateral anomaly		
<i>Calanoides acutus</i>	21	1	23	2
<i>C. brevicornis</i>	9	3	7	18
<i>C. carinatus</i>	26	2	2	14
<i>C. macrocarinatus</i>	2	3	25	2
<i>C. patagoniensis</i>	36	4	0	15
<i>C. philippinensis</i>	9	4	7	15
<i>Calanus</i> s.l. <i>cristatus</i>	7	0	3	8
<i>C.</i> s.l. <i>hyperboreus</i>	16	0	2	7
<i>C.</i> s.l. <i>plumchrus</i>	17	0	3	8
<i>C.</i> s.l. <i>propinquus</i>	5	0	4	7
<i>C.</i> s.l. <i>simillimus</i>	14	0	0	10
<i>C.</i> s.l. <i>tonsus</i>	19	0	1	10
<i>Calanus</i> s.s. <i>chilensis</i>	45	0	0	33
<i>C.</i> s.s. <i>finmarchicus</i>	6	0	4	10
<i>C.</i> s.s. <i>glacialis</i>	9	0	1	16
<i>Canthocalanus pauper</i>	67	3	0	16
<i>Cosmocalanus caroli</i> + <i>C. darwini</i>	22	0	4	13
<i>Mesocalanus lighti</i>	29	0	0	8
<i>M. tenuicornis</i>	26	0	0	16
<i>Nannocalanus minor</i>	13	0	2	12
<i>Neocalanus gracilis</i>	17	0	0	13
<i>N. robustior</i>	15	0	0	15
<i>Undinula vulgaris</i>	40	0	0	10

Table 5. *Calanus pacificus californicus*. Aesthetasc variability in the first antenna of the trithek females. Number of aesthetascs deviating from one per antennal segment. In all instances of deviations, two aesthetascs were observed; 17 specimens displayed one unilateral deviation, 2 specimens displayed one bilateral deviation. L, left, R, right

CalCOFI sample	No. of specimens	Segment								All other segments	
		2b		3		7		9			
		L	R	L	R	L	R	L	R	L	R
Jan. 1969 80.52	100	5	1	1	0	0	1	1	0	0	0
May 1969 82.47	100	4	2	1	1	0	1	2	1	0	0

by gonad morphology. Frequency distributions of prosome length for sexed CV are shown in Figs. 9 and 10, and summary statistics are presented in Table 8. Male and female CVs were of comparable size.

Slightly more than half of CVs had an undifferentiated gonad (cells minute, length less than that of ThI, genital ducts paired and thin, no anterior diverticulum, as in Fig. 2a of Tande and Hopkins, 1981). Males were almost one-third of CVs, females were about one-tenth, and the remainder had no detectable gonad. The proportions are consonant with the males developing more rapidly, as

observed for *Calanus finmarchicus* by Tande and Hopkins. The ovary and anterior diverticulum, filled with enlarged ova, may appear fully ripe in CV, so that newly molted females probably can spawn very quickly after receiving sperm.

Cephalosome length:ThI width ratios were also determined for adults sorted from the same January and May samples. The means and distributions for trithek and quadrithek females were not significantly different, but both differed from males (Figs. 11 and 12; Table 7). Females of both types were more rotund than males. In

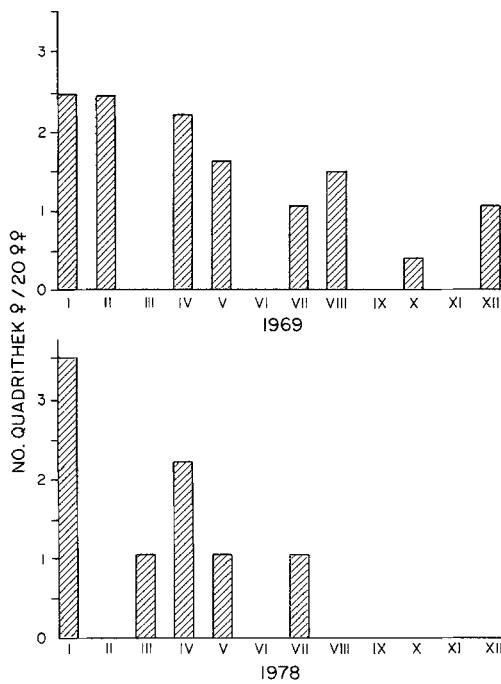


Fig. 7. *Calanus pacificus californicus*. Number of quadritheks females per 20 adult females in standard CalCOFI net tows hauled obliquely from 200 m to the surface at CalCOFI Stations 80.52 and 82.47 off Point Conception, California, USA. Estimates of quadritheks for the 1969 samples are based on examination of 100 or more individuals per sample; estimates for the 1978 samples are based on 20 individuals per sample

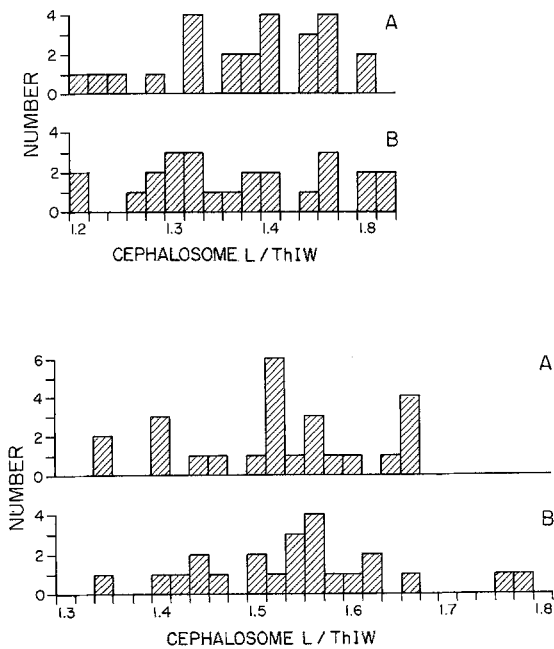


Fig. 8. *Calanus pacificus californicus*. Frequency distribution of ratio length of cephalosome to width of Th1 (first pedigerous segment) in CV; ordinate gives no. of specimens. Upper two histograms: data from January 1969, Station 80.52, (A) male CV, $\bar{x} = 1.3844 \pm 0.0346$ (95% confidence limits), $N = 25$; (B) female CV, $\bar{x} = 1.3748 \pm 0.0395$ (95% CL), $N = 25$. Lower two histograms: data from May 1969, Station 82.47, (A) male CV, $\bar{x} = 1.5304 \pm 0.0398$ (95% CL), $N = 25$; (B) female CV, $\bar{x} = 1.5252 \pm 0.0491$ (95% CL), $N = 25$

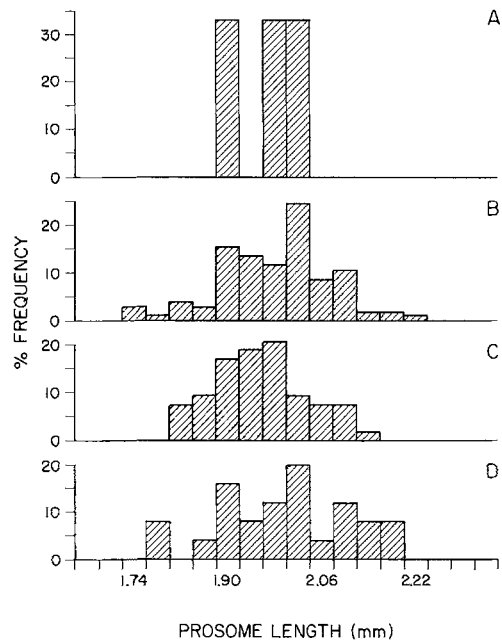


Fig. 9. *Calanus pacificus californicus*. Frequency distribution of prosome length in CV. Data from January 1969, Station 80.52. (A) With no discernible gonad; (B) with undifferentiated gonad, $\bar{x} = 1.9732 \pm 0.0177$ mm (95% CL), $N = 103$; (C) with testis, $\bar{x} = 1.9874 \pm 0.0211$ mm (95% CL), $N = 53$; (D) with ovary, $\bar{x} = 1.9876 \pm 0.044$ mm (95% CL) $N = 25$

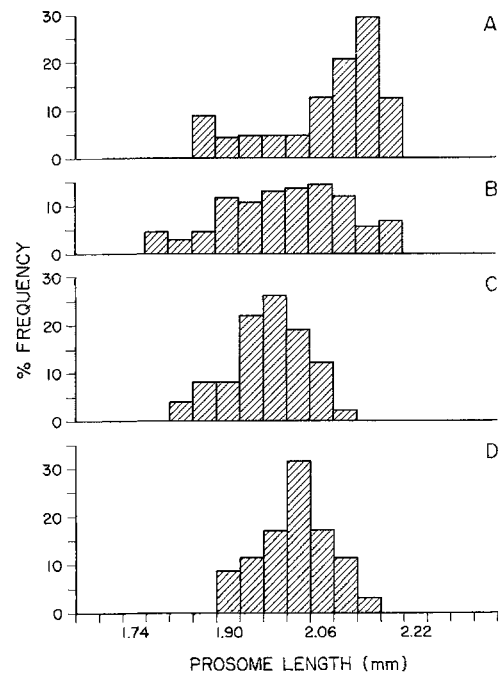


Fig. 10. *Calanus pacificus californicus*. Frequency distribution of prosome length in CV. Data from May 1969, Station 82.47. (A) With no discernible gonad, $\bar{x} = 2.0593 \pm 0.0389$ mm (95% CL), $N = 24$; (B) with undifferentiated gonad, $\bar{x} = 1.9913 \pm 0.014$ mm (95% CL), $N = 175$; (C) with testis, $\bar{x} = 1.9618 \pm 0.0122$ mm (95% CL), $N = 99$; (D) with ovary, $\bar{x} = 2.0025 \pm 0.0193$ mm (95% CL), $N = 35$

Table 6. *Calanus pacificus californicus* off Point Conception. Abundance of quadritheks, prosome length \pm 95% confidence limits (CL) and population density as a function of season

Month	Station	T at 10 m (°C)	(N)	Quadritheks (no. per 20 specimens)	Prosome length (mm)		No. m ⁻³		% adult ♀ in sample
					$\bar{x} \pm 95\%$ CL	Range	CII-V	adult	
1969									
Jan.	80.52	13.03	(298)	2.48	2.5304 \pm 0.0148	2.12 – 2.843	33.5	36.1	46.6
Feb.	80.52	13.27	(100)	2.47	2.4396 \pm 0.0247	2.084 – 2.767	19.5	13.2	67.9
Apr.	80.52	11.37	(100)	2.22	2.5742 \pm 0.0263	2.312 – 2.843	84.5	105.1	47.4
May	82.47	11.98	(324)	1.60	2.5238 \pm 0.0128	2.236 – 2.843	133.4	29.5	51.1
July	80.52	15.66	(100)	1.05	2.3619 \pm 0.0249	2.047 – 2.653	6.4	2.4	71.4
Aug.	80.52	14.95	(100)	1.51	2.301 \pm 0.0208	2.084 – 2.577	2.2	4.8	39.7
Oct.	80.52	13.49	(100)	0.41	2.31 \pm 0.0214	2.047 – 2.577	3.0	2.1	48.2
Dec.	80.52	15.58	(100)	1.05	2.3085 \pm 0.0287	1.933 – 2.653	0.4	2.5	79.1
1978									
Jan.	80.51	15.18	(20)	3.53	2.355 \pm 0.0493	2.17 – 2.56	1.2	13.6	91.4
Mar.	80.51	14.66	(20)	1.05	2.50 \pm 0.0758	2.21 – 2.80	0.5	7.8	17.2
Apr.	80.51	12.42	(20)	2.22	2.539 \pm 0.0585	2.25 – 2.72	4.1	14.3	76.2
May	80.51	11.73	(20)	1.05	2.504 \pm 0.0731	2.29 – 2.91	703.9	233.7	68.9
July	80.51	11.23	(20)	1.05	2.413 \pm 0.0715	2.02 – 2.76	17.6	15.9	89.3

Table 7. *Calanus pacificus californicus*. Ratio of cephalosome length to width of first pediger-bearing segment (Ceph L:ThI W) in CV and adults. Values are means \pm 95% confidence limits

Month (1969)	Station	Stage	Sex	N	Cephalosome length (mm)	ThI width (mm)	Ceph L:ThI W
Jan.	80.52	CV	♂	25	0.9346 \pm 0.0156	0.677 \pm 0.0177	1.3844 \pm 0.0346
		CV	♀	25	0.9263 \pm 0.0175	0.676 \pm 0.021	1.3748 \pm 0.0395
May	82.47	CV	♂	25	0.9202 \pm 0.0172	0.6025 \pm 0.0154	1.5304 \pm 0.0398
		CV	♀	25	0.9308 \pm 0.016	0.6153 \pm 0.0206	1.5252 \pm 0.0491
Jan.	80.52	adult	♂	25	1.1507 \pm 0.0270	0.7550 \pm 0.0180	1.5374 \pm 0.0319
		adult	♀ quadritheks	25	1.1545 \pm 0.0194	0.8710 \pm 0.0252	1.329 \pm 0.0259
		adult	♀ tritheks	25	1.1492 \pm 0.0255	0.8582 \pm 0.0258	1.3377 \pm 0.0295
May	82.47	adult	♂	25	1.1218 \pm 0.0175	0.7002 \pm 0.0137	1.6001 \pm 0.0248
		adult	♀ quadritheks	25	1.1416 \pm 0.0204	0.7808 \pm 0.0163	1.4644 \pm 0.0306
		adult	♀ tritheks	25	1.1704 \pm 0.0236	0.8142 \pm 0.0197	1.4392 \pm 0.0211

Table 8. *Calanus pacificus californicus*. CV and adult prosome length (mean \pm 95% confidence limits). State of gonad: 0 = gonad absent; u = gonad undifferentiated; ♂ = testis; ♀ = ovary. % F: % frequency

Month (1969)	Station	Stage	State of gonad	N	% F	Prosome length (mm)
Jan.	80.52	CV	0	3	1.6	1.958
		CV	u	103	56.0	1.9732 \pm 0.0177
		CV	♂	53	28.8	1.9874 \pm 0.0211
		CV	♀	25	13.6	1.9876 \pm 0.044
May	82.47	CV	0	24	7.2	2.0593 \pm 0.0389
		CV	u	175	52.5	1.9913 \pm 0.0146
		CV	♂	99	29.7	1.9618 \pm 0.0122
		CV	♀	35	10.5	2.0025 \pm 0.0199
Jan.	80.52	adult	♂	120		2.2269 \pm 0.0163
		adult	♀ quadritheks	37		2.5549 \pm 0.0372
		adult	♀ tritheks	298		2.5304 \pm 0.0148
May	82.47	adult	♂	100		2.205 \pm 0.0158
		adult	♀ quadritheks	25		2.4387 \pm 0.0436
		adult	♀ tritheks	324		2.5238 \pm 0.0128

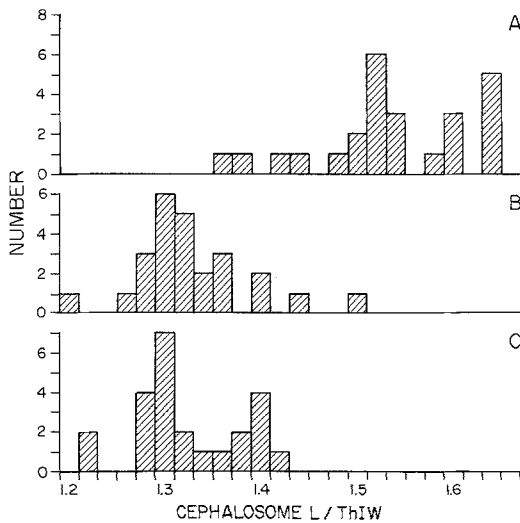


Fig. 11. *Calanus pacificus californicus*. Frequency distribution of ratio length of cephalosome to width of ThI (ThIW) in adults. Data from January 1969, Station 80.52. (A) Male, $\bar{x} = 1.5374 \pm 0.0319$ (95% CL), $N = 25$; (B) quadrithek female, $\bar{x} = 1.329 \pm 0.0259$ (95% CL), $N = 26$; (C) trithek female, $\bar{x} = 1.3377 \pm 0.0295$ (95% CL), $N = 25$

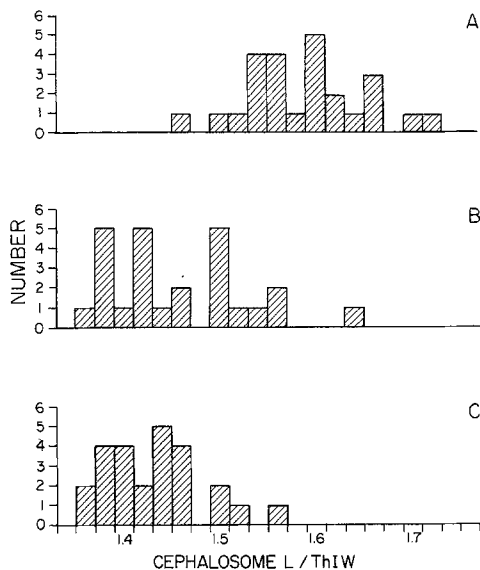


Fig. 12. *Calanus pacificus californicus*. Frequency distribution of ratio length of cephalosome to width of ThI in adults. Data from May 1969, Station 82.47. (A) Male, $\bar{x} = 1.60 \pm 0.0248$ (95% CL), $N = 25$; (B) quadrithek female, $\bar{x} = 1.4644 \pm 0.0306$ (95% CL), $N = 25$; (C) trithek female, $\bar{x} = 1.4392 \pm 0.0211$ (95% CL), $N = 25$

both CV and CVI stages the ratio was larger in May, caused primarily by the consistently greater width of ThI in the January population (Table 7). Females were larger than males (Figs. 13 and 14, Table 8) in both seasons. Trithek and quadrithek females were not appreciably different in size in January, while in May there were slightly more large specimens among tritheks than among quadritheks. Thus, on the whole, size and body form of adult females did not have interesting correspondences with the dimorphism of antennal appendages.

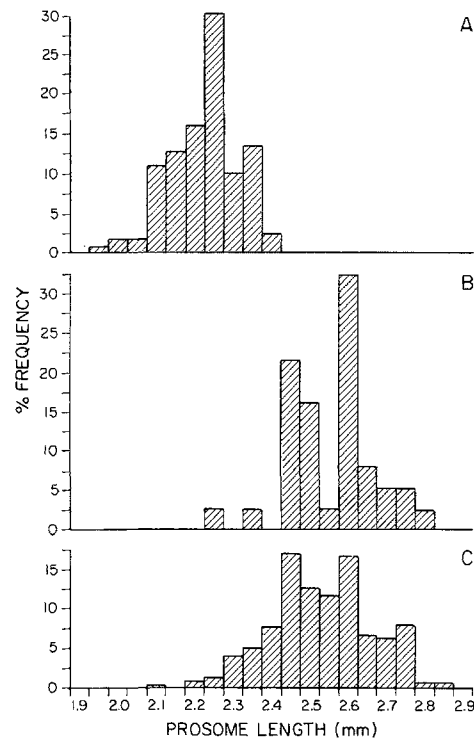


Fig. 13. *Calanus pacificus californicus*. Frequency distribution of prosome length of adults. Data from January 1969, Station 80.52. (A) Male, $\bar{x} = 2.2269 \pm 0.0163$ mm (95% CL), $N = 120$; (B) quadrithek female, $\bar{x} = 2.5549 \pm 0.0372$ mm (95% CL), $N = 37$; (C) trithek female, $\bar{x} = 2.5304 \pm 0.0148$ mm (95% CL), $N = 298$

Table 9. *Calanus pacificus californicus*. Coefficients of skewness (Sk) for distribution of prosome length in adults

Station	Sex	Sk coeff.
Jan. 1969 80.52	♂	-0.437
	♀ quadrithek	-0.5957
	♀ trithek	-0.2052
May 1969 82.47	♂	-1.1654
	♀ quadrithek	-0.3371
	♀ trithek	+0.5734

Consistent with the prediction that male distributions will be negatively skewed if quadrithek females derive from the larger sizes of genetic males, values of the statistic Sk were negative and large for prosome length of males collected in January and May (Table 9). The hypothetical scheme for production of quadrithek females by sex change predicts that trithek females should include all genetic females and suggests their skewness in size will approach zero or be positive: exactly as found (Table 9). Both samples of quadrithek females had modest, negative

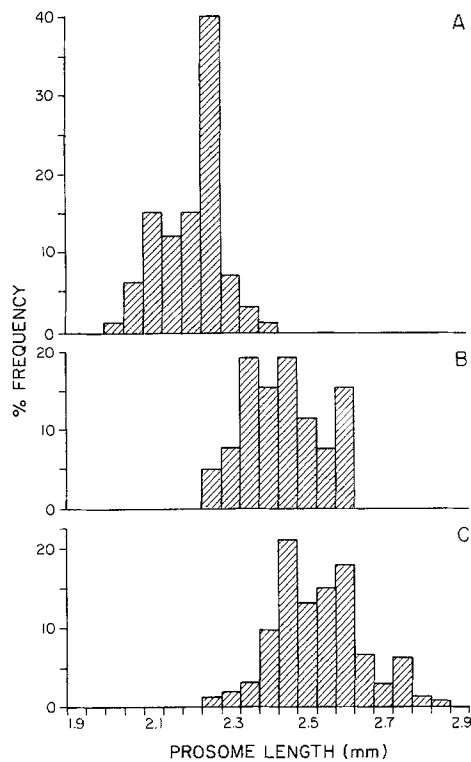


Fig. 14. *Calanus pacificus californicus*. Frequency distribution of prosome length of adults. Data from May 1969, Station 82.47. (A) Male, $\bar{x} = 2.205 \pm 0.0158$ mm (95% CL), $N = 100$; (B) quadrithek female, $\bar{x} = 2.4387 \pm 0.0436$ mm (95% CL), $N = 26$; (C) trithek female, $\bar{x} = 2.5238 \pm 0.0128$ mm (95% CL), $N = 324$

values of S_k , but sample sizes were unreliably small for statistical significance. Differential mortality or some form of nonlinear differential growth pattern could also lead to skew.

Discussion

Documented cases of polymorphism in planktonic calanoids are not common (e.g. Johnson, 1961, 1964; Bowman, 1965; Fleminger, 1967; Ferrari, 1984). The quadrithek-trithek dimorphism of the female first antenna in the Calanidae is unusual because it appears in at least half the species of a generically diverse family. However, no function for the quadrithek arrangement in the female is readily apparent. Whereas in the male the pairs of aesthetascs in quadritheks are swollen and probably function to detect female pheromones (Griffiths and Frost, 1976), the additional aesthetascs of quadrithek females are not swollen and resemble both the others and those of trithek females. Since quadrithek females mate in the same fashion as trithek females, apparently soon after molting from CV and before hardening of the exoskeleton (Fleminger, unpublished observations), males presumably find them in the same way and they require no special olfactory

capability. Thus, the sensory specialization represented by the quadrithek pattern in males is probably not fully developed in quadrithek females.

Quadrithek females exhibit the male phenotype in the number and arrangement of antennal aesthetascs, all other obvious female qualities notwithstanding. The lack of intergrades between the trithek and quadrithek females suggests they are separated by a genetic difference. I saw no indication suggesting that parasitism or disease is responsible for the dimorphism, and the high frequency of quadrithek females rules out an origin from repetitive, ordinary mutations. Given these facts, I postulate that quadrithek females derive from genotypic males in which the gonad develops as an ovary. The final, phenotypic sex in this scheme is affected by environmental factors, or possibly by internal factors relating to conditions developed in diapause, which modify the hormonal control of morphogenesis of sexual characters.

To suggest that switching from the genotypic sex occurs in copepods is not new, but it derives here from the new observations on female dimorphism. Inferences from experimental and field studies have led a number of workers to suspect that environmental factors may affect sex determination in copepods (e.g. Coker, 1938; Cattley, 1948; Egami, 1951; Metzler, 1955, 1957; Battaglia, 1958, 1960, 1963, 1965; Mednikov, 1961; Igarashi, 1964 a, b; Conover, 1965; Monakov, 1965; Vacquier and Belser, 1965; Heinle, 1970; Katona, 1970; Williams and Wallace, 1975; Grigg *et al.*, 1981; Hopkins, 1982). Environmental factors suggested by these authors as influencing sex determination include nutrition, temperature, pressure, population density, and parasitism. Definitive proof that copepods can switch from their genotypic sex to the opposite sex has proved elusive because there is no demonstration of the sex-determination mechanisms and growth by molting precludes finding an individual in transition. While both males and females appear to derive from diploid zygotes (Harding, 1963; Goswami and Goswami, 1972, 1974; Colomera and Lazzaretto-Colomera, 1978; Vaas and Pesch, 1984), there is no unequivocal evidence of heterochromosomal sex determination (but see below). The possibility of arrhenotoky (haploid males), which occurs in some crustaceans (Bull, 1983, p. 145 ff), has not been ruled out altogether for copepods, but it is certainly not usual.

Sex change is moderately frequent in crustaceans (Charniaux-Cotton, 1960), and it is most readily proved in the instances of sequential hermaphroditism which occur in forms with less determinate growth than characterizes the copepods (e.g. Wenner, 1972; Charnov, 1979). Moreover, sex change and sequential hermaphroditism are common in animals generally (Policansky, 1982), and much recent theoretical work has considered the selective process by which it arises and becomes a feature of the phenology of a species (Ghiselin, 1974; Warner, 1975; Charnov and Bull, 1977; Charnov, 1982; Bull, 1983).

A hypothetical selective process can be suggested within the framework of this body of theory predicting that change of a fraction of genetic males to functional

females frequently could be of advantage among the Calanidae. This derives from the facts that male calanids mature more quickly than females, and, more importantly, tend to emerge from diapause stages first. Thus, there are periods when the males of a generation are mature but there are few, if any, adult females with which they can breed. Males that can switch to female function and retain part of the male lead in maturation timing will "capture" all or part of the early reproductive output of the population for that generation. Because they reproduce first, their descendants will be disproportionately abundant in the population at the end of the breeding season, no matter how many generations that includes. When genetic females become mature later in the season, the advantage of switching will be reduced or lost. At that time, switching males would lose out on mating, as males mate with the now abundant genotypic females. Moreover, switching males would lose the potential for multiple matings to give them genetic representation in the offspring of many females. I have demonstrated (Fig. 7) that near Point Conception the season of greatest abundance of quadrithek females of *Calanus pacificus californicus* is January, the time of emergence of the population from its diapause phase. Thus, if quadrithek females are indeed produced by sexual switching, they occur at the period when an excess of males will be most certain, a requirement of the theory. Switching could respond to environmental factors usually associated with seasons of male dominance: for example, colder conditions or the composition and quantity of food organisms in the case of Point Conception waters. Alternatively, switching could be a specific feature of emergence from the fall-early winter diapause phase.

It seems likely that switching of sex would be most favored for the largest size classes of genetic males, and the negatively-skewed size-distribution of males (Table 9) agrees with the notion that larger male CV may have been lost from the distribution at maturation. This suggestion follows the general model of environmental sex switching of Charnov and Bull (1977) and incorporates Ghiselin's (1974) idea that sex switching will be favored for the larger individuals of a given genotypic sex when size is of greater adaptive value for the opposite sex than for the genotypic one. Female calanoid copepods of larger size produce more eggs per clutch (Corkett and McLaren, 1969, 1978; Durbin *et al.*, 1983; Maly, 1983) and certainly more eggs overall, whereas no great importance of size is apparent in males. In fact, there are examples that appear to reflect selection pressures driving males of some species to an unusually small size (Fleminger, 1967). Egg size varies over a narrow range in typical calanoid species (Marshall and Orr, 1955; Corkett and McLaren, 1978), so ovarian development and fecundity may be expected to vary directly with the size or volume of the prosome, a relationship previously noted by McLaren (1965), although fecundity is known also to vary directly with food ration (Marshall and Orr, 1952; Mullin and Brooks, 1967; Paffenhöfer, 1970; Harris and Paffenhöfer, 1976; Paffenhöfer and Harris, 1976; Heinle *et al.*, 1977; Gatten *et al.*, 1980). All

these facts point to sex switching being more advantageous for large genetic males than for small ones.

The proposal of Barnes and Barnes (1953) and of Woodhead and Riley (1957, 1959) that sex of CV individuals of *Calanus finmarchicus* can be determined from the ratio cephalothorax length:ThI width has not been borne out by my study of *C. pacificus californicus*. With respect to the study by Grigg *et al.* (1981) on prosome length in CV or CVI *Calanus* spp., their data are unsuitable for comparison, since it is self-evident that one of their species pertains to a mixture of two species, namely *C. finmarchicus* and *C. glacialis*. Thus, it has not yet been possible to demonstrate that CVs identifiable as genetic males have switched sex by evaluating their developing gonads. This does not, however, weaken the hypothesis that quadrithek females develop from genetic males.

The sex-modification hypothesis raises questions concerning the nature of sex determination in the Calanidae. Little is known in the form of established facts. Some view sex determination in copepods as being largely influenced by a polygenic system and modifiable by environmental factors (Ginsburger-Vogel and Charniaux-Cotton, 1982; Hedgecock *et al.*, 1982), so that progeny are commonly of one sex, individual sex conversion possible, and sex ratios often deviate from 1:1. In polygenic sex determination, individuals of either sex in dioecious species are regarded as possessing the genes necessary for realizing both male and female morphogenesis, and the genetic system controlling the final phenotypic sex is modifiable by environmental sex determination (Bull, 1983). Other workers claim to have distinguished sex chromosomes from autosomes, males usually being the purported heterogametic sex in centropagids, pontellids, acartiids and tortanids (Goswami and Goswami, 1972, 1974; Colombero and Lazzaretto-Colombero, 1978). However, sex chromosomes were not found in eurytemorids (Vaas and Pesch 1984), and there is uncertainty about their presence in *Calanus* spp. (Harding, 1963). Given the dominant position of calanoid copepods in the pelagic ecology of lakes and oceans, this problem is important.

Some experimental leads are already available. First, S. Marshall (unpublished report) conducted a series of experiments at S.I.O. in 1972 on the effect of different types of food on the sex ratios of *Calanus pacificus californicus*. She collected CIIIs, CIVs and CVs at sea and kept them in the laboratory until the adult molt or death. She found that females dominated among the survivors: CVs raised to adulthood yielded about 25% males ($N=148$) and CIIIs 0% males ($N=55$). In her view, the low percentage cannot be explained by differential mortality of immature males. She writes, "It is obvious that in spite of its genetic constitution the sex of *Calanus* spp. can be altered at a later stage of development probably by nutritional factors." Nutrition influencing sex determination of *Calanus* spp. has been suggested by others as well (Mednikov, 1961; Conover, 1965; Corkett and McLaren, 1978; Tande and Hopkins, 1981).

Second, in the morphogenesis of sexual characters in malacostracan crustaceans, it is well established that male

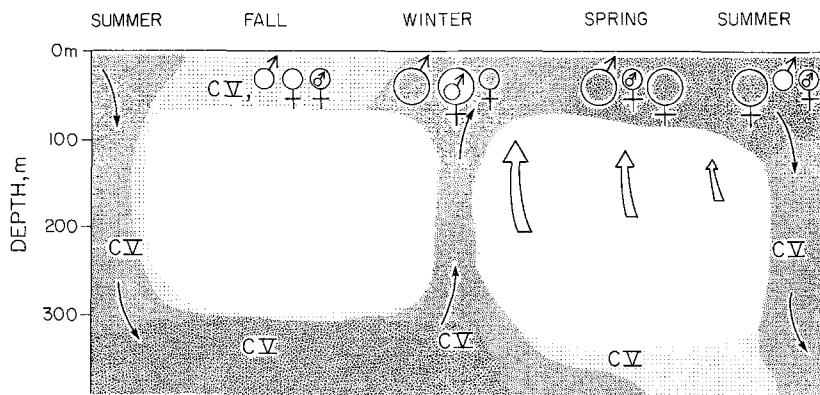


Fig. 15. *Calanus pacificus californicus*. Schematic view of seasonal changes in vertical distribution and relative abundance of males, females and Copepodite V larvae (CV) in California Current off Point Conception. Larger sized symbols represent much greater numbers than smaller symbols. ♀: quadrithek females; ♂: trithek females. Open arrows depict periods of coastal upwelling, size of arrow indicating relative intensity. Shading depicts usual relative abundance of *C. pacificus californicus* population. Wider or heavier shading indicates larger numbers than narrower or lighter shading. Black arrows show direction of seasonal vertical movement of the copepods

morphology develops in response to secretions from the androgenic gland (Charniaux-Cotton, 1960; Ginsburger-Vogel and Charniaux-Cotton, 1982). Removal of an androgenic gland experimentally or by parasites results in loss of secondary sexual characters. In copepods, as in malacostracans, parasitic castration has a similar impact (Sewell, 1929; Callan, 1940; Cattley, 1948; Marshall and Orr, 1955; Shen and Bai, 1956; Bayly, 1963; Williams and Wallace, 1975; Corkett and McLaren, 1978; Fleminger, unpublished observations on Pontellidae). While no androgenic gland has been reported in copepods, there are patches of secretory cells (that could well be androgenic) along the length of the vas deferens (Park, 1966; P. Blades-Eckelbarger, personal correspondence). Carlisle and Pitman (1961) showed long ago that the general physiology of molting in copepods is not greatly different from that in larger crustaceans. It is, therefore, unlikely that control of sexual development is radically different.

The seasonal role of quadritheks

Available facts suggest the following seasonal cycle for *Calanus pacificus* in the California Current off Point Conception (Fig. 15). In midwinter, following the onset of upwelling, most of the deeply submerged Copepodid V larvae appear to end their diapause and rise to the mixed layer to join the portion of the Copepodid V population that failed to enter diapause in the previous summer and fall. Males mature first and are initially much more abundant than the trithek females. Simultaneously, the number of functional females increases as some of the genotypic Copepodid V males molt and change sex, becoming quadrithek Copepodid VI females. At this time of few females, quadritheks have a greater likelihood of contributing to the next generation than early males, many of whom probably die without ever mating. Trithek females gradually increase in numbers during spring, eliminating the advantage to sex-switching males while providing a positive advantage to males that fertilize two or more females. From the middle of spring through the summer, trithek females usually greatly outnumber males; quadrithek females show a relative decline that may be

proportional to the reduction in males. Later in summer, Copepodid V larvae begin to dominate, although the population is greatly reduced in the mixed layer, the great majority submerging and entering diapause at roughly 300 to 450 m depth and remaining there until the next upwelling season sometime in winter.

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