

## VARIATION IN LARVAL MORPHOGENESIS WITHIN THE SOUTHERN CALIFORNIA BIGHT POPULATION OF *EUPHAUSIA PACIFICA* FROM WINTER THROUGH SUMMER, 1977-1978

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### ABSTRACT

Two dominant pathways of pleopod development were observed among young furciliae of *Euphausia pacifica* during the winter-summer of 1977-78, within the population of the Southern California Bight. The larvae that progressed through the shorter, more direct pathway, with one instar per stage within furcilia stages I and II, were generally most abundant in spring and early summer, when environmental conditions appeared optimal for larval development. The larvae that progressed through the longer pathway, with two instars within stage II and often within stage I, were generally most abundant during winter and late summer, when environmental conditions appeared sub-optimal. The degree of variation, apparently induced by environmental change during the nine-month survey period, suggests that patterns of pleopod development should not be used to characterize populations of *Euphausia* species without prior study of spatial and temporal variability in larval development across the range of a species. The apparent restriction of the capacity for marked variation in *Euphausia* pleopod development to one of three species groups, group III, supports the subgeneric classification based on adult morphology.

### RESUMEN

Se observó dos vías principales en el desarrollo de los pleópodos en furciliias juveniles de *Euphausia pacifica* durante el periodo invierno 1977-verano 1978, perteneciente a la población presente en la Bahía del Sur de California. Las larvas que siguieron la vía de desarrollo más breve y directa, con una muda por estadio entre los estadios furciliares I y II, fueron más abundantes en la primavera y comienzos de verano. En este período, las condiciones ambientales asociadas con el régimen estacional de surgencia parecían óptimas para el crecimiento y desarrollo larvario. Las larvas que siguieron la vía de desarrollo larga, con dos mudas durante el estadio II, y frecuentemente durante el estadio I, fueron más abundantes durante el invierno y a fines del verano cuando las condiciones ambien-

tales parecían subóptimas para el desarrollo larvario. El grado de variación dentro de la población de *E. pacifica* en la Bahía del Sur de California, aparentemente inducido por cambios ambientales durante los nueve meses estudiados, sugiere que los patrones de desarrollo de los pleópodos no deberían ser usados en la caracterización de poblaciones de *Euphausia* sin un estudio previo de la variabilidad espacial y temporal del desarrollo larvario para cada especie. La aparente restricción de la capacidad para marcada variación en el desarrollo de los pleópodos, dentro del género *Euphausia*, a uno de los tres grupos de especies, Grupo III, apoya su previa clasificación subgenérica basada en morfología adulta.

### INTRODUCTION

The course of larval development within the crustacean family Euphausiidae is generally well known (Gurney 1942; Mauchline and Fisher 1969; Mauchline 1980). There are three larval phases during ontogeny, and within phases one (nauplius) and two (calyptopis) the developmental sequence appears to be similar for all members of a species. In the third (furcilia) phase, however, there may be conspicuous variation in the addition and development of the five pairs of abdominal swimming appendages, or pleopods. The pleopods are added in sequence from anterior to posterior abdominal segments, with each pair appearing first as nonsetose rudiments which become setose and functional at the next molt (Fraser 1936; Mauchline and Fisher 1969). A larva may progress, for instance, during the course of three consecutive molts, from the final calyptopis stage, without pleopods, first to a form with 2 pairs of nonsetose pleopods, next to a form with 2 pairs of setose and 3 pairs of nonsetose pleopods, and finally to a form with the total complement of 5 pairs of setose pleopods.

The degree of pleopod development is a primary feature used to characterize the early furcilia stages of a species. Both number and relative abundance of forms within a stage may vary with respect to pleopod state, and the dominant forms in successive furcilia stages are presumed to indicate the most common pathway of development within a population (Fraser

1936). Both spatial and temporal variability in this aspect of euphausiid ontogeny have been discussed by, among others, Brinton and Townsend (in press), Makarov (1974), Makarov and Maslennikov (1981), and Mauchline (1980), who made the following observation: "A taxonomic group of species probably has a dominant pathway of development which is optimal for these species . . . and is used under optimal or near optimal environmental conditions for these species. When environmental conditions change, for example, later in the breeding season, and become less optimal for the species, the pathway of development changes in response to these conditions. This 'variant' pathway is probably not optimal for the species except possibly under the suboptimal environmental conditions."

Within the genus *Euphausia*, more than half of the described species—members of groups I and II of the three species groups established by Brinton (1975)—show little or no variation in this phase of larval development; members of group III may exhibit a variety of forms and dominant pathways. Endo and Komaki (1979) described the relative abundance of pleopod forms among furciliae in the Sea of Japan population of group III *E. pacifica*. The dominant forms and pathway of development differed from those previously described in the southern California population of the species (Boden 1950), and it appeared that the discrepancy might be evidence of intraspecific difference between the populations. The present study was prompted by the analysis of a sample of Southern California Bight *E. pacifica* larvae which showed a shift in dominant pathway of pleopod development from the one in Boden's sample. The appearance of two dominant pathways within one population of *E. pacifica* suggested that the apparent difference between the Japan Sea and southern California populations might be within the range of variation induced in this species by environmental change.

*Euphausia pacifica* inhabits the subarctic and transition zones of the North Pacific and ranges south in the California Current to 25°N (Brinton 1962a, 1967a, 1973). The biology of the population south of Point Conception, in the region of the Southern California Eddy, has been studied by Brinton (1976). He described the eddy as a reproductive refuge for this warm-temperate population, in which there is continuous larval recruitment of variable intensity. The maxima in spawning and recruitment coincide with events associated with seasonal upwelling in the area.

A study of the distribution of euphausiids in the California Current during the warm winter-spring of 1977-78 (Brinton 1981) found the southern California population of *E. pacifica* both diminished and re-

tracted northward in the winter, when ocean temperatures were 1°–2°C above average. The species became increasingly dense from May to July, apparently in a reproductive response to the development of coastal upwelling, and resumed its usual predominance among larger zooplankton in the area.

I selected the December 1977-August 1978 season for a study of variability of pleopod development during the furciliar phase within the Southern California Bight population of *E. pacifica*. It seemed likely that, if such variation were environmentally induced, a large number of forms within the genetic repertoire of the species might be expressed in response to the relatively wide range of environmental conditions during this period. The purpose of this paper is (1) to explore the type and extent of temporal variation in form of young furciliae, and (2) to compare the pattern of morphological variation with seasonal change in the larval environment and in abundance.

## METHODS

For his investigation of the population biology of southern California *E. pacifica*, Brinton (1976) delimited a study area south of Point Conception. The area is subdivided into inshore and offshore halves: the inshore portion is strongly affected by the coastal upwelling regime; the offshore section tends to be influenced by the southerly flow of the mainstream of the California Current. I selected the inshore area for the present study (Figure 1) because of the almost continuous presence of young larvae in these waters. A distributional atlas of euphausiid growth stages off southern California from 1953-56 (Brinton and Wyllie 1976) showed young (3-4 mm) furciliae of *E. pacifica* to be present 80%-100% of the time at inshore stations.

Zooplankton was collected at 27-33 stations within the study area during each of seven CalCOFI surveys of December 1977-August 1978 (Figure 1). Samples were obtained with two 0.71-m diameter bongo nets, one with a mesh width of 333  $\mu$  and the second of 505  $\mu$ , towed obliquely from 200 m; the cod ends of both nets were of 333- $\mu$  mesh. The euphausiids in all of the 505- $\mu$  net night samples from these surveys were identified and enumerated by E. Brinton and A. Townsend in the course of their research, and they have permitted me to use their unpublished data to calculate the average number/1000 m<sup>3</sup> per station of *E. pacifica* larvae less than 4.5 mm in total body length for each survey. The sampling, subsampling, and counting procedures are discussed, and estimates of sampling and counting variability provided, by Brinton (1979, 1981) and Brinton and Townsend (1981). The numbers of young larvae were grouped,

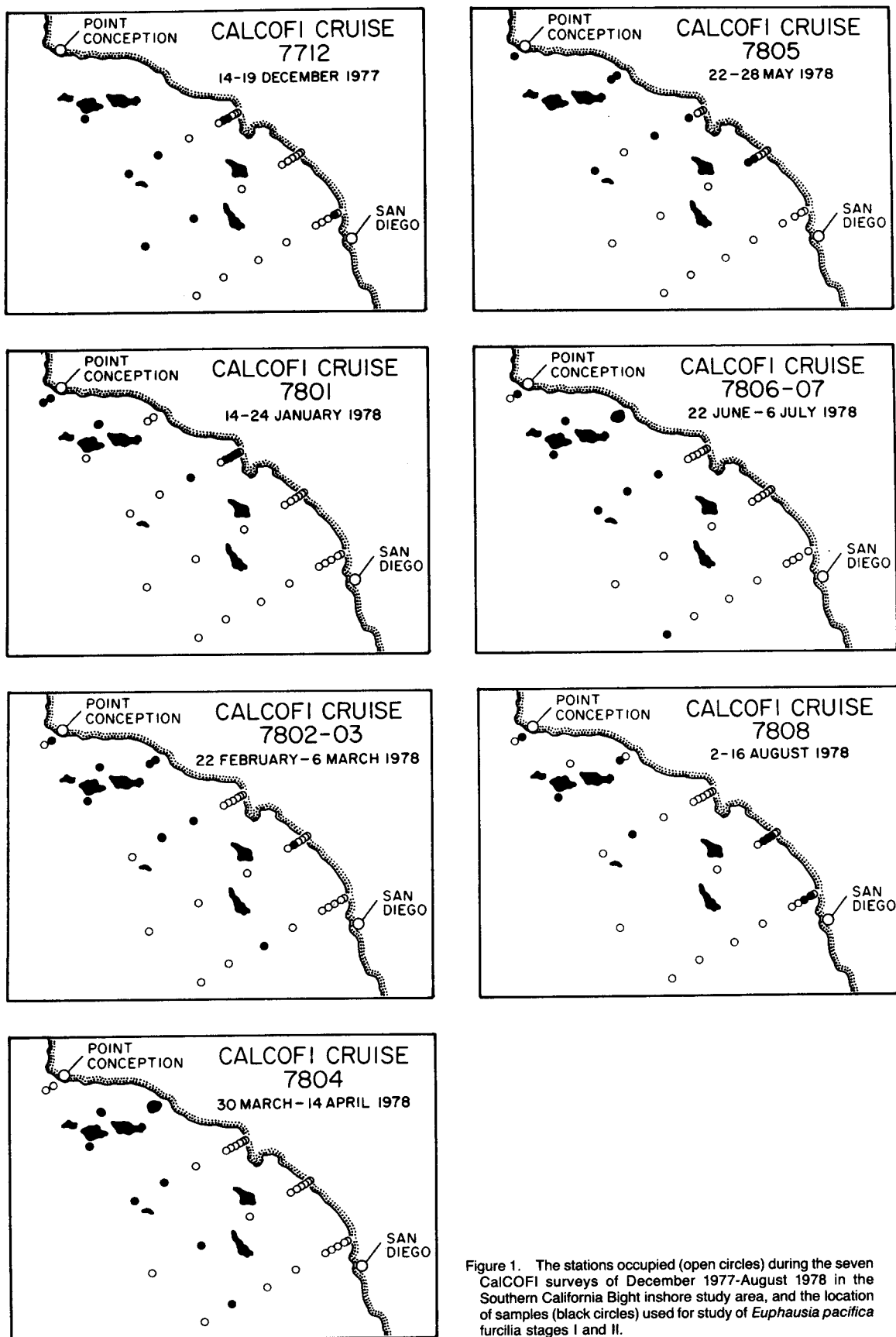


Figure 1. The stations occupied (open circles) during the seven CalCOFI surveys of December 1977-August 1978 in the Southern California Bight inshore study area, and the location of samples (black circles) used for study of *Euphausia pacifica* furcilia stages I and II.

when measured, by 1-mm increments of total body length, including the following stages: 1-2 mm, calyptopis stages I-III and a very few furcilia stage I; 3 mm, furcilia stages I-II; 4 mm, furcilia stage II and older larvae (A. Townsend, pers. comm., and author's data). Although absolute abundance of larvae smaller than 3 mm may be underestimated by a net with 505- $\mu$  mesh, the temporal change in relative abundance may be used as a measure of the recruitment of resident species to a population (Brinton and Townsend 1980).

For this study, the number of pairs and state (nonsetose or setose) of pleopods on *E. pacifica* furciliae with fewer than 5 setose pairs were counted in 8-9 samples from each of the seven surveys (Figure 1); 25%, 50%, or 100% of the sample was examined, depending on the density of larvae. If only one pleopod was present on an abdominal segment, it was counted as a pair; it was often difficult to determine whether the asymmetry was due to absence or breakage of the appendage. Both day and night samples were counted because the bulk of the larvae of *E. pacifica*, and most probably the young furciliae lacking a full complement of setose pleopods, remain above 150 m (Brinton 1967b; Youngbluth 1976).

I have followed Boden (1950) in assigning the various larval forms of *E. pacifica* to furcilia stages I (FI) and II (FII) and have added the pleopod state in parenthesis to describe the forms within each stage (Table 1). A pair of nonsetose (ns) pleopods is indicated by the symbol ', a pair of setose (s) pleopods by ''': for instance, a form with 2 pairs of setose and 3 pairs of nonsetose pleopods in furcilia stage II would be described as FII(2''3').

In presenting the data, I subdivided stage FII (s + ns) into forms with 5 pairs of pleopods and those with fewer than 5 pairs, which would require at least one more instar within furcilia stage II to achieve stage III, a form with 5 pairs of setose pleopods. There may

be one or more instars in both stages FI and FII, and in predicting the pathway of pleopod development I assumed that a pair of nonsetose pleopods appears on an abdominal segment at one molt and becomes setose at the subsequent molt (Fraser 1936; Endo and Komaki 1979; Mauchline 1980). The various pathways of pleopod development may be inferred from Table 1. A calyptopis III larva, without pleopods, may molt to a form of furcilia I with 0-5 pairs of nonsetose pleopods; the form selected is presumed to place certain limits on the ensuing forms. For example, an FI larva with 3 pairs of nonsetose pleopods might develop by the following pathways requiring 3 and 2 molts, respectively, to achieve the stage III condition:

$$\begin{aligned} & \text{FI}(3')\text{---FII}(3''1')\text{---FII}(4''1')\text{---FII}(5'') \\ & \text{FI}(3')\text{---FII}(3''2'')\text{---FIII}(5'') \end{aligned}$$

The total body lengths of the dominant forms in furcilia stages I(ns) and II(s + ns) were measured in dorsal view along the midline from the anterior margin of rostral plate to the posterior margin of telson excluding terminal spines. The larvae were measured, to the nearest 0.04 mm, by ocular micrometer with the 25  $\times$  objective of a stereomicroscope. The average lengths of the dominant forms are based on the sum of measurements of individuals from surveys of January, February/March, May, and June/July 1978.

Seasonal change in the larval environment was represented by the temporal variation in temperature ( $^{\circ}\text{C}$ ) at 10 m, representative of the mixed layer and hence of the larval habitat (Brinton 1979), and in surface chlorophyll *a* ( $\mu\text{g}/\text{l}$ ). Measurements of surface chlorophyll are believed to correlate significantly with integrated chlorophyll and primary production in the euphotic zone of the California Current (Peláez and Guan 1982).

The percent similarity index (PSI), which expresses the degree to which one sample resembles another with respect to proportions of species (McGowan and Miller 1980), was used to determine the degree of similarity between the percent frequency distributions of pleopod forms within stages FI and FII in the seven survey samples, and the samples of *Euphausia pacifica* described by Boden (1950) and Endo and Komaki (1979). PSI values range from 0 (no forms in common) to 100 (all forms in common with identical proportions), and in these comparisons PSI values  $> 60$  were believed to indicate a strong similarity between samples.

Seasonal patterns of variation in dominant larval forms, numbers of larvae, temperature, and chlorophyll *a* in the inshore area were compared using ranked values for each category. The agreement between pairs and sets of ranks was assessed using Kendall's tau coefficient of correlation and coefficient of concordance *W* (Tate and Clelland 1957).

TABLE 1  
 Symmetrical States of Pleopod Development  
 within Furcilia Stages I and II

Furcilia I		Furcilia II				
(0)	(ns)	(s + ns)			= 5 pairs	
		<5 pairs				
0	1'	1''	<u>1''1'</u>	<u>1''2'</u>	<u>1''3'</u>	<u>1''4'</u>
	2'	2''	2''1'	<u>2''2'</u>		<u>2''3'</u>
	3'	3''	<u>3''1'</u>			<u>3''2'</u>
	4'	4''				<u>4''1'</u>
	5'					

The underlined forms were present in the Southern California Bight population of *Euphausia pacifica* within the inshore study area during December 1977-August 1978.

' = pair nonsetose (ns) pleopods, '' = pair setose (s) pleopods.

TABLE 2  
 Percent Similarity Indices for the Frequency of Pleopod Forms within Furcilia Stages I and II  
 in the 1977-78 Southern California Bight Population of *Euphausia pacifica*

FI	January	February/ March	April	May	June/ July	August
December	90.05	42.10	52.30	61.20	27.95	80.85
January	—	41.05	51.25	62.15	25.40	81.80
February/March		—	89.80	49.70	79.35	57.95
April			—	47.10	74.15	63.15
May				—	34.65	66.85
June/July					—	38.90
				<i>Mean</i>	<i>Median</i>	<i>Range</i>
Within group A (February/March, April, June/July)				81.10	79.35	74.15-89.90
Within group B (December, January, May, August)				73.95	73.85	61.20-90.95
Between groups A and B				44.29	44.60	25.40-57.95

FII	January	February/ March	April	May	June/ July	August
December	88.85	37.40	48.50	71.85	24.00	79.15
January	—	29.55	45.25	69.70	17.15	74.90
February/March		—	67.40	36.25	83.70	45.85
April			—	45.45	54.90	55.05
May				—	21.65	85.30
June/July					—	31.25
				<i>Mean</i>	<i>Median</i>	<i>Range</i>
Within group A (February/March, April, June/July)				68.67	67.40	54.90-83.70
Within group B (December, January, May, August)				78.29	77.03	69.70-88.85
Between groups A and B				36.45	36.85	17.15-55.05

## RESULTS

### *Temporal Variation in Form within Furcilia Stages I and II*

There was temporal variation both in dominant pathways of pleopod development and in the number of forms in furcilia stage II within the inshore population of *E. pacifica*. The percent frequencies of pleopod forms within stages FI and FII in samples from the seven CalCOFI surveys from December 1977–August 1978 are shown in Figure 2. I calculated percent similarity indices (PSI) for these frequency distributions (Table 2), and distinguished two groups—A (February/March, April, June/July) and B (December, January, May, August)—in which the indices were more similar between members of a group than between members of different groups. The mean PSI was considerably higher within than between survey groups in stages FI and FII. Within group A, the PSI between April and June/July surveys in stage FII was relatively low because of the abundance of form FII(1'4'), and within group B the May survey was least similar to the other surveys in stage FI because of the abundance of forms FI(3') and (4').

The mean percent frequency of pleopod forms for survey groups A and B is presented in Table 3. Features characterizing furcilia stages I and II within the two groups are summarized in Table 4.

The relative abundance of forms in group A indicated that most larvae required only two instars to

advance through furcilia stages I and II to the stage III form having 5 pairs of setose pleopods, and that FI(2')–FII(2'3') and FI(1')–FII(1'4') were the dominant and subdominant pathways of pleopod development. The abundance of forms within group B, on the other hand, indicated that most larvae required at least two instars within stage II to achieve stage III, and that FI(1')–FII(1'3')–FII(4'1') was the most common pathway. Two instars were often required within stage FI also, in the B surveys, with FI(0) preceding FI(ns) to progress, probably, to FI(3') or FI(4'). The mean percent frequency for the seven surveys (Figure 2) illustrates the degree of variability, with respect to the number of forms expressed within each stage, and the two dominant developmental modes within the population, FI(2')–FII(2'3') and FI(1')–FII(1'3')–FII(4'1').

The total body lengths of *Euphausia pacifica* furciliae in the two dominant pathways of pleopod development are presented in Table 5. The growth factors (expressed as mean size in stage divided by the size in preceding stage) at the molt from FI–FII in pathways A and B, and from instar 1–2 with FII in the B pathway, are compared in Table 6. Average total length and average growth factor are larger among larvae in the more direct A pathway. There is a significant difference ( $p = < 0.01$ ) between mean body lengths of forms FI(1') and FI(2') and between FII(1'3') and FII(2'3') presumed to be comparable instars.

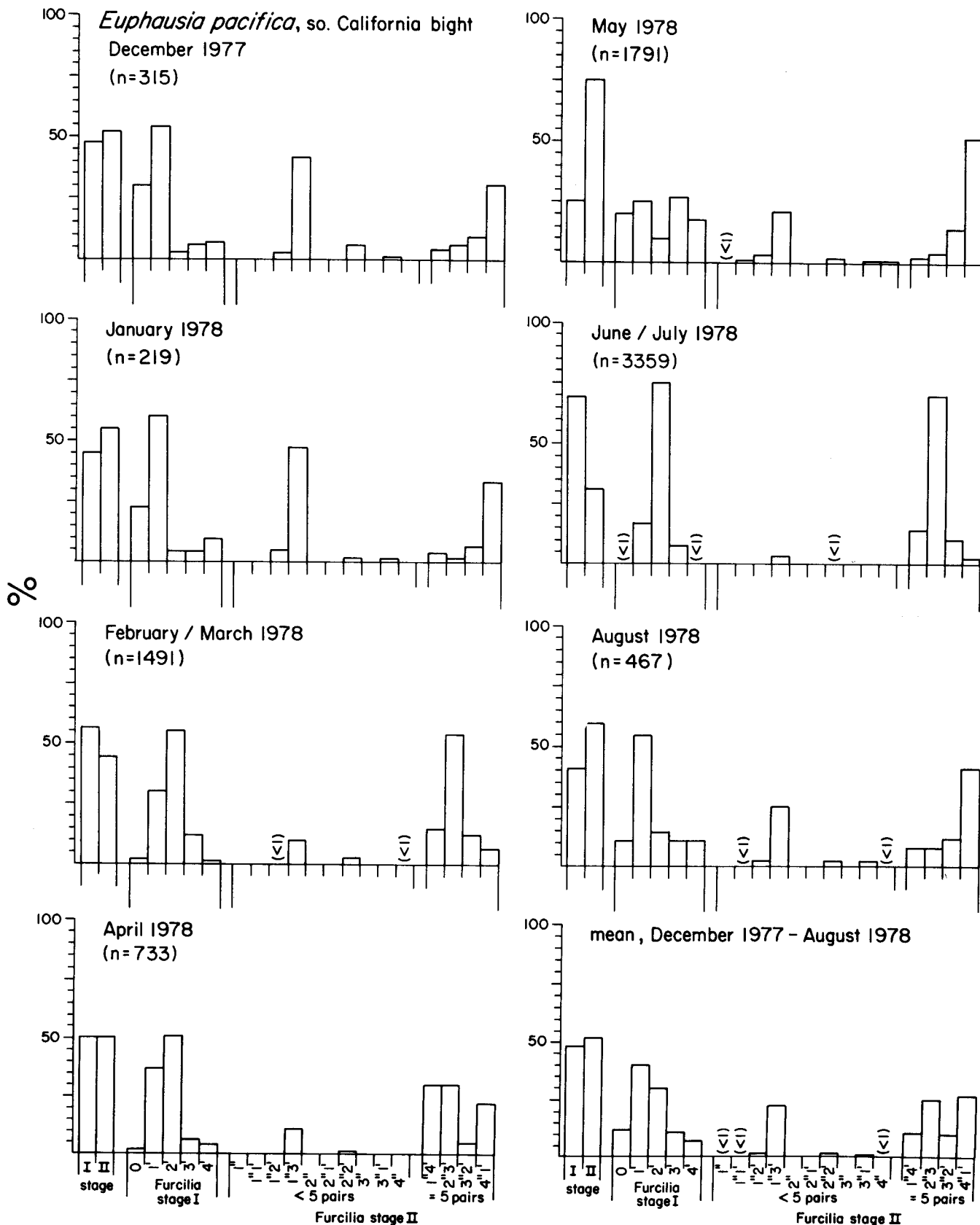


Figure 2. The relative abundance of furcilia stages I and II and percent frequency of pleopod forms within each stage in the Southern California Bight population of *Euphausia pacifica* sampled by seven CalCOFI surveys.

TABLE 3  
 Percent Frequency of Pleopod Forms within Furcilia Stages I and II of *Euphausia pacifica* in Survey Groups A and B

Stage	Pleopod Form	Group A		Group B	
		(Feb./Mar., Apr., June/July)		(Dec., Jan., May, Aug.)	
		Mean	Range	Mean	Range
FI	0	1.3	0.2- 1.9	20.6	10.5-29.6
	1'	28.0	16.9-36.8	48.2	25.0-60.2
	2'	60.3	51.0-75.2	7.8	3.3-14.1
	3'	8.6	6.0-12.3	12.0	4.1-27.1
	4'	1.7	0.1- 4.4	11.3	7.2-18.3
FII	<5 pairs				
	1''	0	0	<0.1	0 - 0.1
	1''1'	0	0	0.3	0 - 0.8
	1''2'	<0.1	0 - 0.1	3.3	2.5- 5.0
	1''3'	8.0	2.9-11.2	33.6	20.9-47.1
	2''2'	1.4	0.4- 2.6	2.6	1.6- 5.5
	3''1'	0	0	1.5	1.0- 2.2
	4''	<0.1	0 - 0.1	0.3	0 - 0.7
	= 5 pairs				
	1''4'	19.8	14.2-30.3	4.6	2.4- 8.0
	2''3'	51.4	30.3-70.1	4.6	1.6- 7.6
	3''2'	9.1	4.9-12.2	10.2	5.8-13.7
	4''1'	10.4	2.3-22.4	39.1	30.7-52.0
No. larvae		5583		2792	

**Temporal Variation in Dominant Forms within Furcilia Stages I and II in Relation to the Environment and Larval Abundance**

Temporal fluctuation in dominant pathways of pleopod development, depicted by the change in percent frequency of form FI(2') within stage FI representing the A pathway, was compared with coincident changes in (1) mean and range of temperature and chlorophyll *a* values in the larval environment, and (2) mean number/1000 m<sup>3</sup> of larvae 1-2, 3, and 4 mm in body length in the inshore study area (Figure 3).

The mean temperature was 1°-2°C above the seasonal average from December to May, and average during the June/July and August surveys (Brinton 1981). The maximum chlorophyll *a* values increased with the onset of coastal upwelling, and both maximum and mean values peaked, along with the temperature minimum, in June/July (Figure 3a). There was a significant negative correlation between ranked mini-

TABLE 4  
 Features Characterizing Furcilia Stages I and II in Survey Groups

Stage	Survey group	
	A	B
FI(0)	0.2-2% of FI	11-30% of FI
FI(ns), Dominant form	FI(2')	FI(1')
FII(s + ns), No. of forms	6-8	8-11
No. with <5 pairs of pleopods	3-13% of FII	28-55% of FII
Dominant form	FII(2''3')	FII(1''3') and FII(4''1')

TABLE 5  
 Total Body Lengths of *Euphausia pacifica* Furcillae in the Dominant Pathways of Pleopod Development

Stage	Path-way	Pleopod form	Body length, mm			
			Mean	Range	SD	n
FI	B	1'	2.74	2.46-2.95	0.10	95
	A	2'	2.87	2.63-3.11	0.10	76
FII	B	1''3'	3.16	2.87-3.43	0.13	67
	A	2''3'	3.42	3.15-3.60	0.08	59
	B	4''1'	3.52	3.19-4.04	0.17	59

Larvae were measured in a sample pooled from surveys of January, February/March, May, and August 1978.

imum temperature and maximum chlorophyll *a* values for the seven surveys (Kendall's tau = -0.90, *p* = 0.01).

The mean numbers of young *E. pacifica* showed continuous production of 1-2-mm larvae with two peaks in abundance, the first in February/March and the second, and by far the larger, in June/July (Figure 3d), when the environment, with respect to tempera-

TABLE 6  
 Growth Factors\* of *Euphausia pacifica* Furcillae in the Dominant Pathways of Pleopod Development

Molt	Path-way	Pleopod form	Growth factor
FI-FII	A	2'-2''3'	1.19
	B	1'-1''3'	1.15
FII, instar 1-2	B	1''3'-4''1'	1.11

\*Expressed as mean size in stage divided by the mean size in preceding stage.

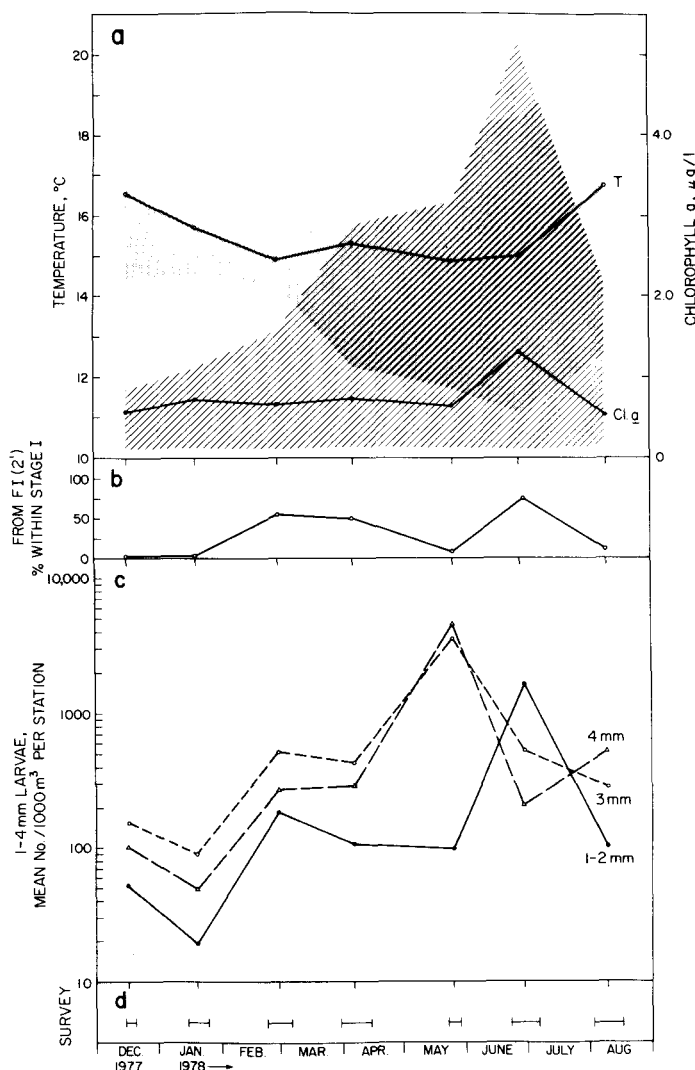


Figure 3. Temporal variation in the larval environment, the dominant pathways of pleopod development, and larval abundance of the Southern California Bight population of *Euphausia pacifica* sampled by seven CalCOFI surveys, depicted by:  
 a. mean and range of 10-m temperature (°C) ( $n = 27-33$ ) and surface chlorophyll *a* ( $\mu\text{g/l}$ ) ( $n = 4-16$ );  
 b. percentage of form FI(2') within stage FI representing the group A pathway;  
 c. mean number/1000 m<sup>3</sup> of 1-4-mm larvae by 1-mm increments ( $n = 11-22$ );  
 d. duration of survey.

ture and chlorophyll *a* abundance, appeared optimal for larval survival. The pattern is consistent with this population's reproductive cycle; Brinton (1976) observed pulses in recruitment at a 2- to 3-month frequency with maxima in periods of temperature minima during seasonal upwelling. The fluctuation in abundance of 3- and 4-mm larvae was similar to that of younger stages through April but differed from May to August. A relatively high density of predominantly older larvae developed in May: 75% of the total number of FI and FII larvae were in stage FII (Figure 2), and within FII, 52% were in the second instar form FII(4'1'). In June/July, on the other hand, during

peak production of 1-2-mm larvae, 70% of total FI-FII larvae were in stage FI.

The direct A pathway of pleopod development, with relatively larger larvae in FI and instar 1 of FII, was dominant during surveys of February/March, April, and June/July, with the maximum percent frequency in June/July (Figure 3b). The longer B pathway, with smaller larvae, on average, in comparable instars predominated in December, January, May, and August.

The pattern of dominance by the A pathway of development in FI-FII generally coincided with the abundance pattern of recently hatched 1-2-mm larvae in the seven samples of inshore *E. pacifica*; there was a significant correlation between the ranked percent frequency of form FI(2'), depicting the A pathway, and mean numbers of young larvae (Kendall's tau = +90,  $p = 0.01$ ). The first pulse in dominance of the A path and in recruitment corresponded with the decrease in temperature and increase in range of chlorophyll *a* values of February/March, whereas peaks in dominance of FI(2') and in number of 1-2-mm larvae coincided with the highest mean and maximum chlorophyll *a* values of June/July and hence, presumably, with the greatest abundance of larval food; the agreement between ranks for these categories was significant (Kendall's coefficient of concordance  $W$ ,  $p < 0.01$ ).

The alternate B pathway of pleopod development was predominant during periods with relatively high mean temperatures and/or low chlorophyll *a* values (December, January, and August) or with a relatively high density of older and larger larvae (May). Reversion to the B path in May, a period of moderate temperature and abundant chlorophyll *a*, presumably reflected a change in the quality of the larval habitat, perhaps a reduction in the supply of appropriate food by the increasing number of late furcilia larvae.

Ross (1981) found that among larvae of *E. pacifica* reared in the laboratory at 12°C, the median duration of calytopis stages I, II, and III, and furcilia stages I and II was 3.5, 4.0, 5.5, 5.5, and 4.5 days. Larval euphausiids begin to feed in the first calytopis stage, and the body length and form in furcilia stage I may be influenced by the variation in increments at three molts during a period of about 13 days, perhaps particularly by the accumulation of reserves within calytopis stage III during the 6 days before the molt to stage FI. At the higher mean temperatures of the inshore area, the duration of these stages might be slightly less; a decrease in intermolt duration with an increase in temperature has been observed in laboratory culture of euphausiid larvae by Ross (1981) and Le Roux (1974).



The duration of surveys ranged from 6-15 days with a mean duration of 12.1 days; the interval between surveys ranged from 25-39 days with an average interval of 28.1 days, about five times the median duration of the third calyptopis instar. It appeared reasonable, therefore, to relate the pattern of development in furcilia stages I and II to the environmental conditions within the study area during the periods when the furciliae were collected.

### *Inferences from Observations*

In general, the following trends in furciliar development within the Southern California Bight population of *E. pacifica* from winter-summer 1977-78 may be inferred: (1) dominance of a short, direct pathway of pleopod development—i.e., FI(2')–FII(2''3'')—was most pronounced, and variability with respect to the number of forms in furcilia stage II was reduced, when conditions in the larval environment appeared optimal for growth and development (June/July) and there was maximum production of young (1-2 mm) larvae; (2) dominance of a longer path—i.e., FI(1')–FII(1''3'')–FII(4''1'')—was most pronounced, and the number of forms in stage II increased, when conditions appeared suboptimal for larval growth (December, January, and August) and production of young larvae was minimal.

### DISCUSSION

Food and temperature are considered the primary extrinsic factors influencing molt increment and intermolt period, the two components of crustacean growth (Hartnoll 1982). In general, a diet of insufficient quantity or suboptimal quality depresses growth by reducing the increment and lengthening the duration of the intermolt. Both effects may occur together, and one or the other may predominate. An increase in temperature may decrease the increment, but usually the predominant effect is a decrease in intermolt duration, which results in an accelerated rate of growth.

Le Roux (1974) explored the effects of varied diet and temperature on the larval growth and morphogenesis of the euphausiid *Meganyctiphanes norvegica*, a species which can vary the development of pleopods. He found that the duration of intermolt was influenced primarily by temperature, whereas both the increment and morphogenesis were affected most strongly by the quality and quantity of food: with a poor diet, the increment decreased with age, morphogenesis was retarded, and the number of pathways of pleopod development, as well as variability in number of forms, increased. In general, the temporal variation in morphogenesis among *E. pacifica* furciliae in the inshore Southern California Bight popula-

tion from December 1977-August 1978 is consistent with these observations. The indirect B pathway of pleopod development dominated when a decrease in the food supply, as in December and January, might be expected to reduce the increment, decrease morphogenesis per molt, and increase the number of instars required to achieve a given stage of development. The more direct A pathway dominated when an increase in the abundance of food, as in June/July, might be expected to increase both increment and morphogenesis per molt, and reduce the number of instars required to reach a comparable stage of development. The apparent decrease in increment, with predominance of the B pathway in May, might reflect a decrease in the quality of larval food associated with the relatively high density of 3-4-mm larvae. In a study of regional relationships between development and growth of larval Antarctic krill, *E. superba* (Brinton and Townsend, in press), the widest variety of pleopod forms in furcilia stages I and II, and most indirect developmental pathways, were associated with a range of relatively low to moderate chlorophyll values and very high larval densities.

### *Geographical Variation in Morphology of Furcilia Stages I and II*

Larval forms in furcilia stages I and II of *Euphausia pacifica* have been described in populations of the Sea of Japan (Endo and Komaki 1979) and the Strait of Georgia (Heath 1977), and in a spring-summer sample of the population off southern California (Boden 1950). The percent frequency distribution of forms enumerated by Boden, calculated from his data, is shown in Figure 4. The FI(2')–FII(2''3'') pathway of pleopod development predominated, as in group A surveys, and the relative abundance of each form is within the range of variability observed in this study except for FI(3') and FII(3''2''); this pathway was subdominant in the 1950 spring-summer sample. The PSI between the frequency distribution of forms within FI and FII in Boden's sample and in the group A survey mean is relatively high (Table 7): above 70 in both stages and within the range of group A indices in FI and FII, which indicates a strong similarity between the two samples of the species in southern California waters.

Heath (1977) presented a frequency distribution of pleopod forms among *E. pacifica* furciliae in Saanich Inlet, British Columbia, during May-June 1975, in which the dominant forms were again FI(2') and FII(2''3''). The sample differed from the California population in the relatively small number of forms in FII(s + ns)—5 only—and in abundance of form FI(5'). This form was not encountered in the Southern

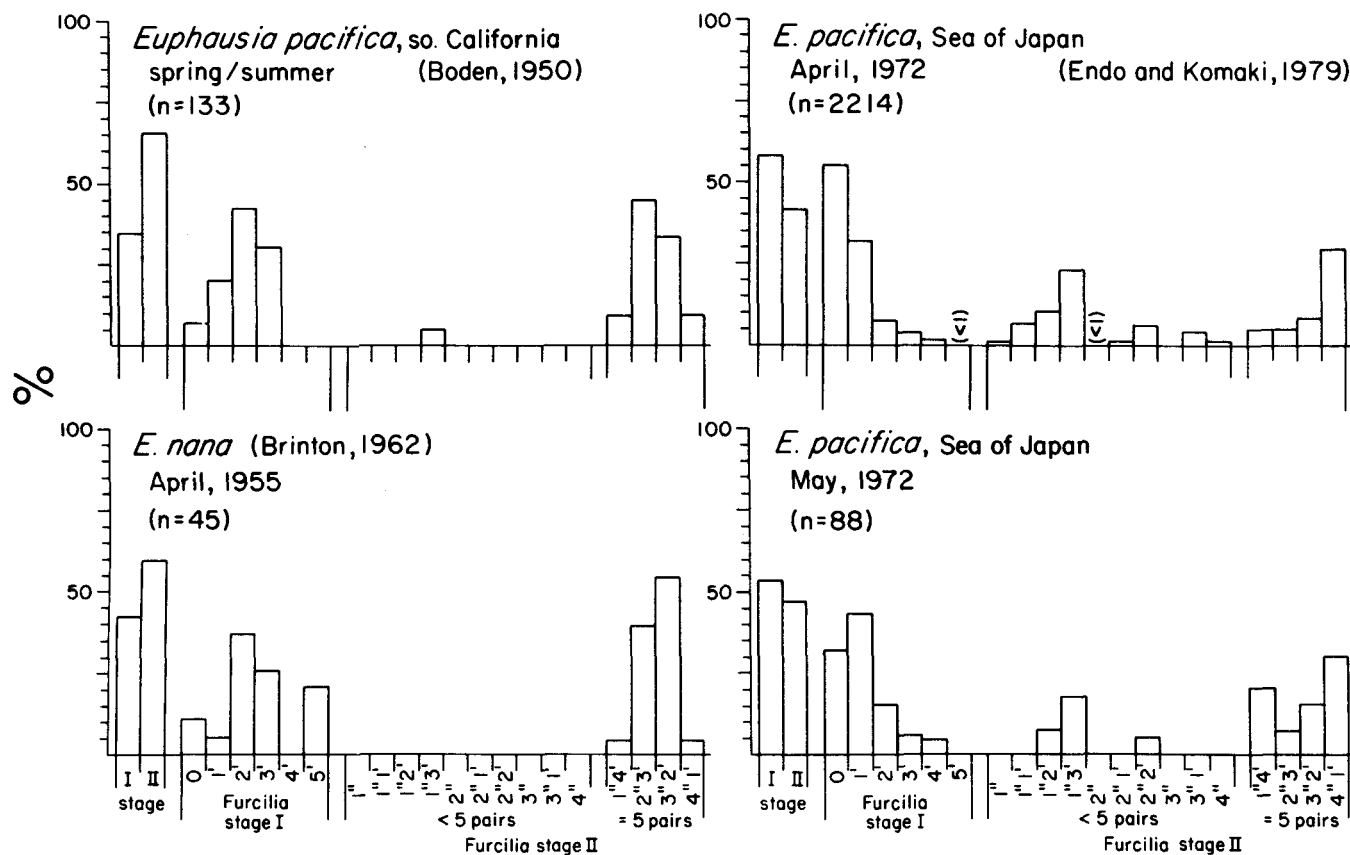


Figure 4. The relative abundance of furcilia stages I and II and percent frequency of pleopod forms within each stage for (upper left) *Euphausia pacifica* from southern California; (upper and lower right) *E. pacifica* from the Sea of Japan; and (lower left) *E. nana*.

TABLE 7  
 Percent Similarity Indices for the Frequency of Pleopod Forms within Furcilia Stages I and II

	<i>E. pacifica</i>					<i>E. nana</i> <sup>a</sup>
	So. California			Sea of Japan <sup>b</sup>		
	Group A mean	Group B mean	Boden sample <sup>c</sup>	April	May	
<b>FI</b>						
<i>E. pacifica</i>						
So. California						
Group A mean	—	47.30	72.15	42.05	52.15	52.05
Group B mean		—	46.30	65.15	81.50	35.45
Boden sample			—	37.70	47.95	61.95
Sea of Japan						
April				—	76.55	26.70
May					—	36.85
<b>FII</b>						
<i>E. pacifica</i>						
So. California						
Group A mean	—	38.00	76.05	37.10	54.15	55.20
Group B mean		—	32.95	75.60	70.15	22.40
Boden sample			—	30.95	43.10	79.15
Sea of Japan						
April				—	75.45	20.40
May					—	28.05

<sup>a</sup>Brinton (1962)

<sup>b</sup>Endo and Komaki (1979)

<sup>c</sup>Boden (1950)

California Bight inshore area during the study period but was seen occasionally to the northwest, which suggests that there might be a latitudinal trend in its contribution to stage FI.

Endo and Komaki (1979) described the larval forms of *E. pacifica* in the Sea of Japan during April and May 1972, and found the dominant pathway of pleopod development to be FI(0)–FI(1')–FII(1''3')–FII(4''1'). The percent frequency of forms within furcilia stages I and II, as delimited in my study, was calculated from their data (Figure 4); the relative abundance of forms proved generally similar to that in group B surveys (Table 3). The frequency distribution of forms in the two samples from the Sea of Japan and the mean distribution of forms of California *E. pacifica* in survey groups A and B were compared by percent similarity index (Table 7). In both stages, the PSI between the group B mean and one of the two Japan Sea samples was slightly higher than the PSI between April and May surveys within the Sea of Japan, and all were within the range of group B indices in FI-II, indicating a strong similarity between the populations in the B pattern of pleopod development and variety of forms.

In these data, the Japan Sea population exceeds the California population in abundance of FI(0), presence of FI(5'), and in number and relative abundance of forms in FII. It differs from both North American populations in lacking dominance of the short FI(2')–FII(2''3') pathway of pleopod development, and this disparity might be evidence of divergence between the widely separated populations of the species. However, the degree of variation presumably induced by environmental change within the inshore southern California population during the nine-month survey period suggests that the pattern of pleopod development should not be used to characterize populations of *E. pacifica* without prior study of spatial and temporal variability in larval morphogenesis across the range of the species.

#### **Variation in Early Furciliar Development within *Euphausia* Species Group III**

Furciliar development has been described in 24 of the 31 species constituting the genus *Euphausia* (Mauchline 1980). The 31 species have been grouped by features of adult morphology into three assemblages (Brinton 1975). Variation in development of pleopods seems very rare in species groups I and II but is found in several species of group III, which includes IIIa, *E. mucronata*, *E. lamelligera*, *E. sibogae*, *E. distinguenda*; IIIb, *E. tenera*; and IIIc, *E. pacifica*, *E. nana*, *E. lucens*, *E. vallentini*, *E. frigida*, *E. superba*, *E. crystallorophias*. Brinton (1979) observed that spe-

cies of the group III lineage are adapted to environments that tend to vary in productivity, both temporally and spatially, compared with the central water masses of midlatitudes, i.e., eastern boundary currents, zones of equatorial divergence, or temperate to polar latitudes.

In addition to *E. pacifica*, three of these group III species—*E. superba* and *E. nana*, also of subgroup c, and *E. mucronata* of subgroup a—are known to vary considerably in pleopod development. These four species may also be related by their expression of form FI(2'), and related FII(s + ns) forms, which appear to be absent or very rare in other *Euphausia* species: FI(2') constituted 0.2% of 661 larvae in stage FI(ns) of group I species *E. sanzoi* (Knight 1976), but has not been recorded in other described species.

The pleopod development of Antarctic *E. superba* has been discussed at length by Fraser (1936), Makarov (1974), Makarov and Maslennikov (1981), and Brinton and Townsend (in press). The species resembles *E. pacifica* in range of variability in furcilia stages I and II but differs in dominance of pathways FI(4')–FII(4''1') and FI(5')–FII(5''); a form with 5 pairs of setose pleopods is not conventionally included in furcilia stage II of *E. pacifica* (Boden 1950).

*Euphausia nana*, with limited distribution south of Japan and in the East China Sea, is closely related to *E. pacifica* (Brinton 1962b); the frequency of forms in furcilia stages I and II sampled in April 1955, calculated from Brinton's data, is shown in Figure 4. Although it appears that *E. nana* may lack forms with fewer than 5 pairs of pleopods in FII(s + ns), the dominant pathways are similar to California *E. pacifica* sampled by Boden (1950) and the group A surveys of this study. Percent similarity indices between the frequency distributions of FI and FII forms in group A and B survey means, the Boden sample, and *E. nana* (Table 7) show only a moderate, < 60, similarity between *E. nana* and the group A mean, but a relatively strong, > 60, similarity between *E. nana* and Boden's sample. Both share subdominance of FI(3') and dominance or subdominance of FII(3''2'), a less important pathway in the southern California population of *E. pacifica* during December 1977–August 1978. In this sample, *E. nana* does not resemble the described neighboring population of *E. pacifica* in the Sea of Japan in either dominance or number of forms; the PSI between FI and FII forms of *E. nana* and the April sample of Sea of Japan *E. pacifica* were the lowest observed (Table 7).

*Euphausia mucronata* inhabits the Peru-Chile Current and may be considered the South American counterpart of California Current *E. pacifica*. Antezana (1978) studied the larval growth and development of

*E. mucronata* in both laboratory and field samples. The two dominant pathways he described for the field population, FI(2')-FII(2''3'') and FI(1')-FII(1''3'')-FII(4''1''), correspond to the dominant modes of southern California *E. pacifica*. *E. mucronata* may be somewhat less variable: FI(0) was not present and there were fewer forms of FII(s + ns). The growth factors from FI-FII in the A and B pathways of California *E. pacifica*, and from instar 1-2 within FII in the B pathway, were very similar to the growth factors in the same stages and pathways of *E. mucronata*. Antezana found that a greater number of molts, and minimal morphological change between molts, were associated with less growth per molt in the laboratory. He hypothesized that, in the field, dominance of the short FI(2')-FII(2''3'') path would indicate optimal conditions for larval growth, while dominance of the longer FI(1')-FII(1''3'')-FII(4''1'') path would reflect a sub-optimal environment. The results of this study support his hypothesis.

The close correspondence between the boundary current populations of *E. pacifica* and *E. mucronata* in variability of both habitat and larval development is consistent with the observed correlation within the family Euphausiidae between the relative stability of a species's environment and pattern of furciliar development (Mauchline and Fisher 1969). Antezana (1978) inferred that a species such as *E. mucronata*, with a high degree of plasticity in larval development, was well suited to a habitat like the Peru-Chile Current, which is characterized by a diversity of water masses and strong upwelling; the inference applies equally to southern California *E. pacifica*.

The apparent restriction of the capacity for marked variation in larval pleopod development to species of group III supports the subgeneric classification of adults (Brinton 1975). When the complete description of larval development within the genus permits comparison, the further association of species by type of dominance and variation, and by use of form FI(2'), may convey information about specific relationships within the species groups.

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