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PACIFICA OFF THE OREGON COAST

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Euphausia pacifica lives for a period of approximately one year, disappearing from the catches at a size of about 22-24 mm. Spawning, which occurs mainly inshore, extends from June through December, but generally is most prominent in the autumn months.

Average growth is calculated to be approximately 2.0 mm per month or 0.06 mm per day, with growth appearing to be faster during adolescent stages and somewhat slower during the older stages. These growth rates are several times greater than previous estimates for E. pacifica.

These studies were based on length measurements obtained from monthly vertical meter net collections from stations off Newport, Oregon over a four year period.

Size Structure and Growth Rate of Euphausia pacifica
off the Oregon Coast

by

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SIZE STRUCTURE AND GROWTH RATE OF EUPHAUSIA PACIFICA OFF THE OREGON COAST

INTRODUCTION

The Euphausiacea (class Crustacea), one of the most abundant groups of organisms in the ocean, play a prime role in the economy of the sea. In the pelagic regions of the ocean, euphausiids may represent a significant link between photosynthetic production of organic matter by phytoplankton and economically exploitable animal protein. For example, euphausiids are food for a variety of fishes such as the albacore (McHugh, 1952), salmon (Merkel, 1957), and sardine (Hand and Berner, 1959). They are also the main food for many baleen whales (Nemoto, 1957; Marr, 1962). In addition to their significance in marine food chains, euphausiids may contribute substantial amounts of organic detritus, such as molted exoskeletons, to the oceans (Lasker, 1964; Jerde and Lasker, 1966; Paranjape, 1967).

In the North Pacific and in the waters off the Oregon coast, Euphausia pacifica Hansen, 1911 is the most common and abundant euphausiid (Brinton, 1962a; Hebard, 1966). It is found in the Subarctic and Transitional water masses of the North Pacific as defined by Sverdrup, Johnson and Fleming (1942). Its range extends from North America to Asia in open oceanic and neritic waters. It is found as far north as 59°N and as far south as 25°N along the

California coast; the southern range is generally associated with the 9.5 C isotherm at 200 meters (Banner, 1949; Brinton, 1962a).

Of the voluminous literature on euphausiids, most deals primarily with taxonomy, distribution, or larval morphology (for example, see Lebour, 1926; Banner, 1949; Boden, Johnson, and Brinton, 1955; Brinton, 1962a). Some workers, though, have investigated life cycles and growth rates of euphausiids. Einarsson (1945) made growth estimates of several North Atlantic euphausiids and concluded that growth varies between species and from place to place within one species. The life cycle and growth of the Antarctic krill, Euphausia superba Dana, 1850, have been investigated by several authors (Ruud, 1932; Fraser, 1936; Bargmann, 1945; Marr, 1962). Ruud (1932) also gave brief life histories of other Antarctic euphausiids.

Several authors have attempted to describe the life cycle and growth rate of E. pacifica. Nemoto (1957) presented some growth data for E. pacifica and several other euphausiids common to the Japanese-Aleutian area. Ponomareva (1963), in her study of the distribution and ecology of euphausiids of the North Pacific, gave approximate estimates of growth of E. pacifica from plankton samples collected during the winter and spring. Lasker (1966) estimated the growth of E. pacifica reared in the laboratory and reported rates that were approximately twice Ponomareva's from field populations.

Because of the importance of growth rates for the estimation of secondary production and because of scanty and sometimes conflicting results on the growth of E. pacifica, this study was undertaken. My objectives are to examine the abundance, size structure, and growth rate of the E. pacifica population off Oregon.

METHODS AND MATERIALS

To estimate the growth rates of E. pacifica, attempts were made to sample the population at least once a month over a several year period. A total of 174 collections of euphausiids was made between June 1963 and July 1967 at stations located 15, 25, 45, and 65 miles off Newport, Oregon (designated NH-15, NH-25, etc.). Problems with weather, ship scheduling, etc. caused some irregularities in the sampling frequency. Nevertheless, all seasons of the year were sampled over the four year span of the study (Table 1). A one-meter diameter non-closing net with 0.571 mm mesh openings was used with a T.S.K. flowmeter placed in the mouth to measure the amount of water filtered.

Of the 174 samples, the first 20 were oblique tows and the other 154 were vertical tows. This change to vertical tows was made to insure equal sampling at all depths throughout a tow. Comparison of the catches of several paired oblique and vertical tows taken less than an hour apart indicated that oblique tows did not catch larger individuals of E. pacifica than vertical tows (Table 2). The largest carapace measured from all 20 oblique tows was about 6.9 mm, which is within the size range captured in vertical tows. Moreover, there appear to be no appreciable differences in the proportion of animals of different sizes in the samples.

Table 1. Sampling frequency at four stations off Newport, Oregon. X's indicate months samples were taken; open squares indicate no sample taken.

St.																															
NH-15				x	x	x	x		x					x	x		x					x	x				x		x		x
NH-25	x		x		x	x	x		x	x			x	x	x		x			x		x	x			x	x		x		x
NH-45	x	x	x		x	x	x		x	x	x		x	x			x	x	x	x		x	x		x	x	x		x		
NH-65	x	x	x				x		x	x			x	x			x		x	x		x			x	x	x		x	x	x
	06	07	08	09	10	11	12	01	02	03	04	05	06	07	08	09	10	11	12	01	02	03	04	05	06	07	08	09	10	11	12
	1963							1964														1965									

NH-15	x	x	x	x		x			x	x	x	x	x	x	x	x	x	x	x	
NH-25		x	x	x		x			x	x	x	x	x	x	x		x	x	x	
NH-45	x	x	x	x		x			x	x	x	x	x	x	x		x	x	x	
NH-65		x	x	x		x			x	x	x	x	x	x	x		x	x	x	
	01	02	03	04	05	06	07	08	09	10	11	12	01	02	03	04	05	06	07	
	1966												1967							

Table 2. Comparison of the percentages of different sizes of E. pacifica in three paired vertical and oblique tows.

		size groups (mm carapace length)																
		0.6	0.9	1.2	1.5	1.8	2.1	2.4	2.7	3.0	3.3	3.6	3.9	4.2	4.5	4.8	5.1	5.4
		0.9	1.2	1.5	1.8	2.1	2.4	2.7	3.0	3.3	3.6	3.9	4.2	4.5	4.8	5.1	5.4	5.7
Dec. 1963 NH-45	SM 459 vertical	4	2	8	-	14	28	25	14	2	-	-	-	2	-	-	-	-
	oblique	-	1	5	-	14	29	34	12	3	-	2	-	.5				
Dec. 1963 NH-25	SM 460 vertical	.5	-	5	-	12	34	33	12	3	-	.5	-	-	-	-	-	-
	oblique	-	+	3	-	7	26	39	21	3	-	1	+	+	-	-	+	-
Dec. 1963 NH-15	SM 461 vertical	-	-	-	-	15	28	15	28	-	-	15	-	-	-	-	-	-
	oblique	-	4	17	-	29	21	29	-	-	-	-	-	-	-	-	-	-

+ indicates negligible percentages

Euphausia pacifica captured in several 6-ft Isaacs-Kidd mid-water trawls and in vertical meter nets towed to a depth of 1000 m were also measured to see if larger individuals were avoiding the smaller vertical meter net or were found in deeper water. The largest specimens measured from the midwater trawls had a carapace length of approximately 6.8 mm, well within the maximum size caught with the vertical meter net. Also, six replicate vertical meter net samples taken within two days from depths of 200 m and 1000 m did not show appreciable size structure differences (Table 3). Therefore it appears that a representative euphausiid sample was caught in the upper 200 m. McGowan and Fraundorf (1966), studying the efficiency of various size zooplankton nets, believed that while euphausiids may avoid small nets (20, 40, and 60 cm diameter nets) they appear to be spatially distributed so that all nets manage to catch some individuals of all groups present. Thus, it appears that other sampling methods are obviously not better than the vertical meter net for sampling E. pacifica.

Because of shallow water at the inshore stations (approximately 120 m at NH-15 and 220 at NH-25), the maximum depth of tows varied at the different stations (Table 4). Variation of maximum depth probably affects results minimally because all samples were taken after dark when E. pacifica presumably had migrated to the upper 100 m (Brinton, 1967).

Table 3. Comparison of catches of E. pacifica in replicate 0-200 m and 0-1000 m vertical meter tows taken Nov. 1966, NH-65.
(percentage of total replicate samples)

	size groups (mm carapace length)																			
	0.6	0.9	1.2	1.5	1.8	2.1	2.4	2.7	3.0	3.3	3.6	3.9	4.2	4.5	4.8	5.1	5.4	5.7	6.0	6.3
	0.9	1.2	1.5	1.8	2.1	2.4	2.7	3.0	3.3	3.6	3.9	4.2	4.5	4.8	5.1	5.4	5.7	6.0	6.3	6.6
0-200 m tows	8	7	3	+	.5	11	26	15	6	6	5	3	4	1	1	.5	.5	+	+	+
0-1000 m tows	6	8	5	.5	3	14	24	20	6	4	4	1	2	-	1	-	-	-	-	-

+ indicates negligible percentages

Table 4. Maximum depths in meters of vertical meter net tows at four stations off Newport.

NH-15		NH-25	
number of samples	maximum depth	number of samples	maximum depth
14	40	2	75
4	50	1	100
1	60	1	110
5	70	1	125
2	75	16	130
9	80	1	180
		13	200
NH-45		NH-65	
number of samples	maximum depth	number of samples	maximum depth
41	200	40	200
		1	480

The entire plankton sample was preserved at sea with neutralized ten percent formalin. In the laboratory ashore all euphausiids were removed from each sample unless the number of euphausiids in a sample was very large (more than 200 individuals). In such cases the sample was usually divided in half with a Folsom Plankton Splitter and euphausiids were sorted from only one-half the sample.

The carapace length of each individual E. pacifica was measured to the nearest 0.1 mm from behind the eye to its posterior margin (see Figure 1). The smallest animals caught in our nets had carapace

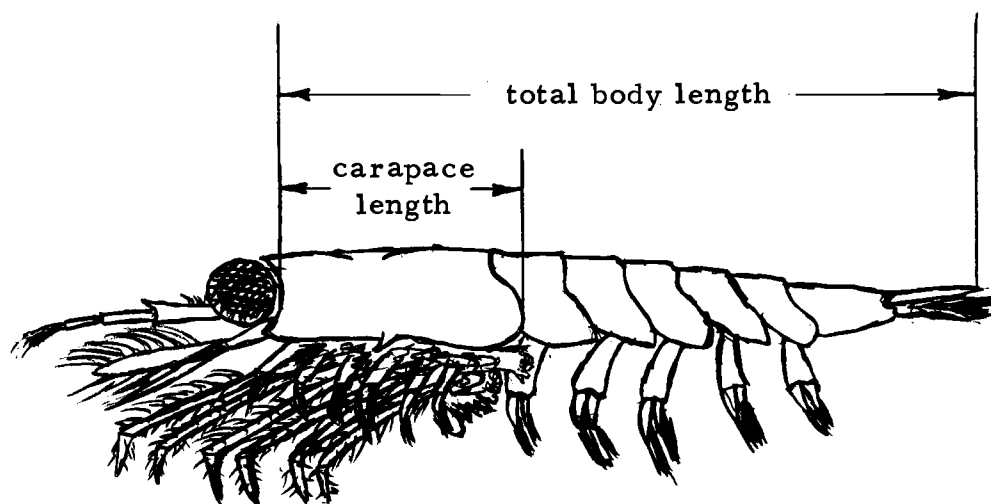


Figure 1. Length measurements of Euphausia pacifica.

lengths of 0.6 mm, and the largest had carapace lengths of about 7.5 mm. Every animal was then assigned to a 0.3 mm size group as described in Table 5. To be able to compare my data with others, total lengths (from the posterior of the eye to the tip of the telson) were also measured from several hundred, randomly selected individuals of various lengths. Total lengths corresponding to the 0.3 mm carapace length groups are shown in Table 5. Hereafter, measurements specified are total lengths unless otherwise stated.

Table 5. Corresponding carapace and body length measurements in millimeters.

carapace length	total length	variance ^a
0.6	2.6	-
0.9	3.8	.24
1.2	4.9	.30
1.5	6.0	3.73
1.8	7.0	.54
2.1	8.1	-
2.4	9.2	2.02
2.7	10.2	2.07
3.0	11.3	.26
3.3	12.3	.78
3.6	13.3	5.74
3.9	14.4	3.81
4.2	15.4	2.58
4.5	16.5	10.93
4.8	17.6	7.72
5.1	18.7	4.13
5.4	19.8	.76
5.7	20.9	.89
6.0	22.0	2.70
6.3	23.0	-
6.6	23.9	-
6.9	24.8	-

^aVariance (S^2) of total length.

RESULTS

Recruitment and Abundance

Off Oregon definite trends in larval recruitment can be seen over the four year period (Figure 2) despite the absence of samples from many months. Although young E. pacifica occurred almost all months of the year, the main period of recruitment extended over a restricted period, beginning sometimes as early as June (e.g. NH-15, 1966) and often ending as late as December (e.g. NH-15 and NH-25, 1966). The largest influx of larval forms occurred in the fall around October and November (see NH-25, 1963; NH-45, 1964; NH-15, 1966), but during some years recruitment was also prominent in the summer months (see all stations, 1965; NH-15, 1966; NH-25, 1964). Little or no recruitment was found during winter and spring.

These larval forms of E. pacifica entering the population were in the furcilia stage and were usually about seven mm or less, agreeing with Boden's (1950) size measurements of E. pacifica furcilia. Presumably spawning occurs 16-18 days before the first furcilia appear in the population (Ponomareva, 1963). The furcilia larvae are usually found within the upper 100 m of the water column (Ponomareva, 1963; Brinton, 1967).

Catch curves (length vs. number summed over all seasons,

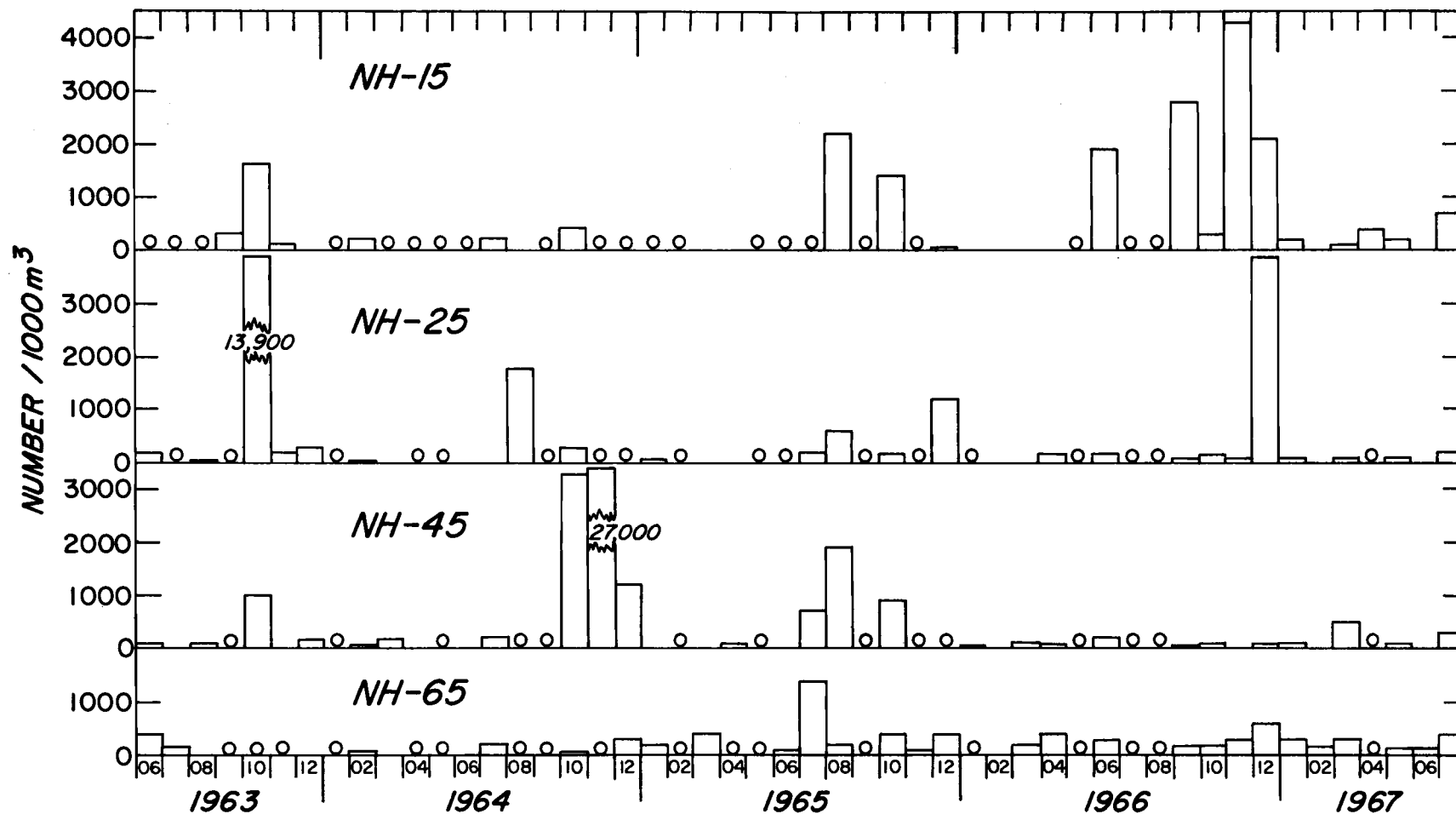


Figure 2. Recruitment graph for four stations off Newport, Oregon.
 "0" means no sample taken that month

Figure 3) show that E. pacifica is much more abundant inshore (15 and 25 mile stations) than offshore (65 miles and beyond. Some samples were taken from stations further than 65 miles offshore, but data are not presented here). Large individuals (larger than 15 mm) were rare at NH-65 and those stations further offshore. Larval forms were also uncommon at those offshore stations compared to the inshore stations (Figure 2). Brinton (1962b) also found that E. pacifica was more abundant inshore than offshore off the California coast.

If euphausiid populations were not uniformly distributed throughout the entire depth of tows, catches per m^3 may not be comparable between tows to different depths. For example, if all E. pacifica were present only in the upper 50 m of the water column, a 200 m tow would underestimate abundance in terms of no./ m^3 compared to inshore-station tows more nearly confined to the upper 50 m because three-quarters of the tow (the lower 150 m) would be filtering water but catching no euphausiids. Since the depth at inshore stations did not permit 200 m tows, catches per m^3 in tows confined to the upper 50 m could be four times higher than those to 200 m. The differences between inshore and offshore catches, however, are too large (approximately ten times) to be explained by differences in sampling depths (Figure 3). Also, abundance estimates at NH-45 were intermediate between inshore and offshore estimates. This

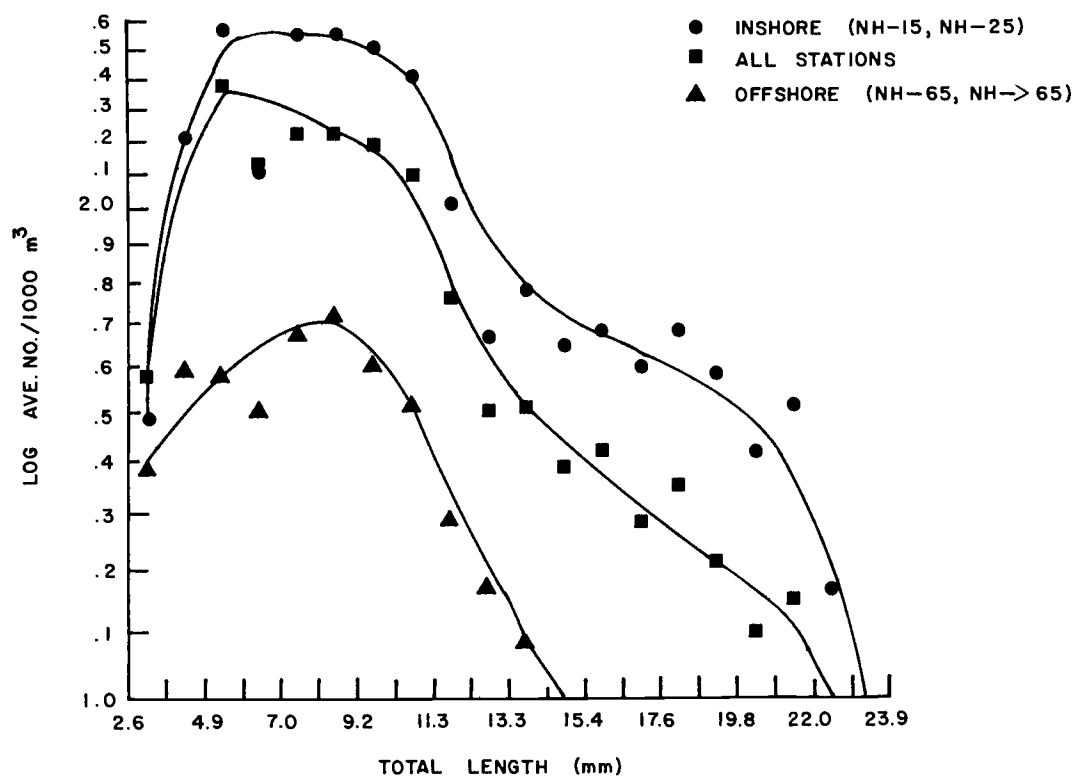


Figure 3. Catch curves. Logarithm of the average number of *E. pacifica* caught per 1000m³ seawater for all samples taken over all seasons of the year

represents further evidence that there is a significant difference in inshore and offshore abundance of E. pacifica populations, since all tows at NH-45 were to 200 m as were the offshore tows. Similarly, Hebard (1966) found that E. pacifica was mainly found inshore and reported "a drastic decrease in abundance of euphausiids occurred between NH-25 and NH-45. At NH-45 and beyond, the abundance remained rather low."

The shape of the catch curves (Figure 3) indicates that not all larval forms below 6.0 mm length are retained by my nets. The gradual decrease in numbers as the individuals grow above 6 mm length suggests that I am probably dealing with only one population off the Oregon coast. The rapid decrease in abundance in the 11-14 mm length range, which corresponds approximately to the winter months, may represent high mortality or large scale advection of this size group from the area. Hebard (1966) believed that during the winter advection was mainly inshore due to prevailing southwesterly winds. However, during the summer prevailing winds are from the north and surface current direction is often offshore. Since large adult E. pacifica are found in low numbers at offshore stations and spawning appears to be predominately an inshore phenomenon, larval and adolescent forms may be carried here by these local offshore currents during summer months rather than spawned here.

Another problem in estimating abundance of zooplankton is

patchy distribution, both spatially and temporally. Currents move these patches so that the same portion of a population is rarely, if ever, susceptible to capture during consecutive sampling periods at one station. Cushing (1962) found that replicate tows can vary 200-300% in areas where there is high variability in oceanographic conditions such as compensation depth, mixing depth, etc. Wiebe and Holland (1968) noted that field estimates of replicate tows varied up to several hundred percent. Off Oregon replicate vertical meter net tows and 6-ft midwater trawls showed high coefficients of dispersion, s^2/\bar{x} (Blackman, 1942), where s^2 is variance and \bar{x} is the mean (Table 6). The high coefficients of dispersion obtained here suggest a very high degree of patchiness, since values approximating unity indicate a random distribution.

Growth Rate

Due to the extended spawning season and patchiness of E. pacifica, the interpretation of growth based on changes in size structure of the population was sometimes rather difficult. In an attempt to clarify the growth picture, the data were presented in several different forms: (1) modal progressions of size-frequency histograms for each year class, (2) modified vertical histograms over all four years, (3) progression of means for each year class separately, and (4) means of all year classes for all stations condensed into one life

Table 6. Day-night differences, numbers, coefficients of dispersion, and maximum size (mm carapace) among catches in replicate tows of adult E. pacifica.

Gear	Date	depth meters	No. day	samples night	DAY			NIGHT		
					no. / 1000 m ³ (mean \pm std. dev.)	coef. disp.	max. size	no. / 1000 m ³ (mean \pm std. dev.)	coef. disp.	max. size
VMN	19NOV66	0-200	-	6	-			424 \pm 247	144	6.5
VMN	21NOV66	0-1000	6	5	176 \pm 255	369	5.2	248 \pm 102	42	5.9
VMN	18DEC66	0-1000	6	6	54 \pm 36	24	5.6	88 \pm 71	57	5.8
VMN	12FEB67	0-1000	5	5	9 \pm 6	4	-	10 \pm 7	5	-
VMN	13FEB67	0-200	-	4	-			28 \pm 14	7	5.1
6 'MT	17DEC66	0-1000	3	4	5 \pm 3	2	5.5	42 \pm 17	7	5.7
6 'MT	12FEB67	0-200	-	3	-			82 \pm 15	3	6.2
6 'MT	13FEB67	0-1000	2	2	10 \pm 12	14	6.2	14 \pm 8	4	6.3
6 'MT	14FEB67	0-200	3	7	16 \pm 13	10	6.3	102 \pm 61	36	6.8

cycle period. These methods are clearly not independent of each other in that the same data are used in the various methods.

These various methods led generally to the same conclusions, namely that E. pacifica lives for a period of one year or slightly longer and is absent from samples of the population after a size of about 22-24 mm total length. Although the growth rates derived from these different methods do not agree completely, differences that do exist can usually be explained.

Modal progressions of size-frequency histograms at individual stations were difficult to follow over a period of more than several months. To obtain an "average" picture over a longer period of time, data from all four stations were combined. When this was done, modal progressions of year classes over a full year were sometimes quite evident.

Two examples of growth based on monthly size-frequency histograms of two year classes are presented in Figure 4A and 4B. The growth of individuals recruited in the fall of 1965 (Figure 4A) is illustrated by the shift of modes through June 1966. This mode then disappears from the catches at a size of about 21-23 mm. Some recruitment is indicated during the spring and summer months of 1966 (Figure 4A). Another modal progression can be followed from the fall of 1966 through April 1967 (Figure 4B). A few large animals caught in June 1967 may represent a remnant of this modal group.

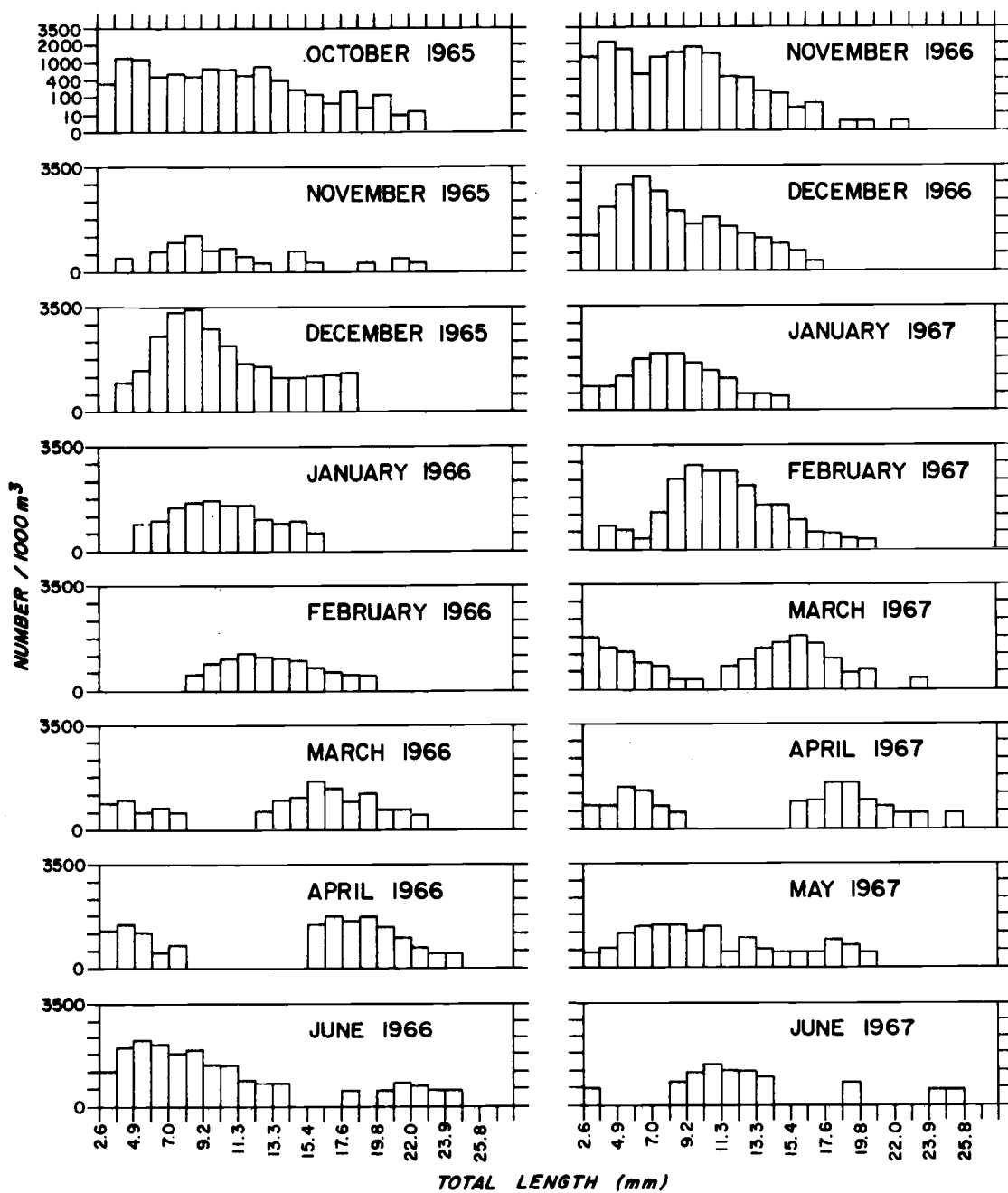


Figure 4A. Size-frequency distribution of *E. pacifica* from all four stations off Newport Oregon for the 1965 year class

Figure 4B. Size-frequency distribution of *E. pacifica* from all four stations off Newport Oregon for the 1966 year class

As in the previous year, early spring recruitment is represented quite clearly with its own modal progression. Year classes 1963 and 1964 (not shown here) also showed very similar trends.

Table 7 summarizes the growth rates computed by this method of plotting all size-frequency data and following the modes of the various year classes. These growth rates vary from 1.6 to 2.9 mm per month. The growth rate may be fastest at young ages since year classes 1963 and 1964 had the slowest average rates (1.6 and 2.1 mm/month) and were calculated over a longer time period, whereas year classes 1966 and 1967 are represented over the shortest periods of time and had the fastest average rates (2.9 and 2.6 mm/month). This slowing down of growth at the larger sizes is apparent in Figure 4A where the growth rate from January to March was about 3.2 mm/month, while from March to June it was about 2.0 mm/month.

A modified histogram plot, again with all four stations combined, presents all the data for four years in Figure 5. These plots are distorted by the constraint that there had to be at least 50 individuals per 1000 m^3 of water within one size group to be plotted and concentrations above $5000/1000\text{ m}^3$ were plotted only as $5000/1000\text{ m}^3$. Although larger individuals, not being as abundant as smaller sizes, sometimes did not meet the $50\text{ individuals}/1000\text{ m}^3$ minimum, the largest sizes caught (22-23 mm) are represented on this plot. This method has the advantage of being able to follow the main modes of

Table 7. Average growth rate measurements by various presentations.

year class	recruitment month	number months followed	GROWTH RATES mm/month		
			modal progression	modes of Fig. 5	means of Fig. 6
1963	09	10	1.61	1.87	1.63
1964	10	9	1.99	1.95	1.86
1965	10	8	2.09 ^a	2.16	2.00
1966	11	5	2.88 ^a	2.51	2.41
1967	03	3 ^b	2.57	2.50	2.47

^a Illustrated in Figure 4A and 4B.

^b Sampling program was discontinued after this time.

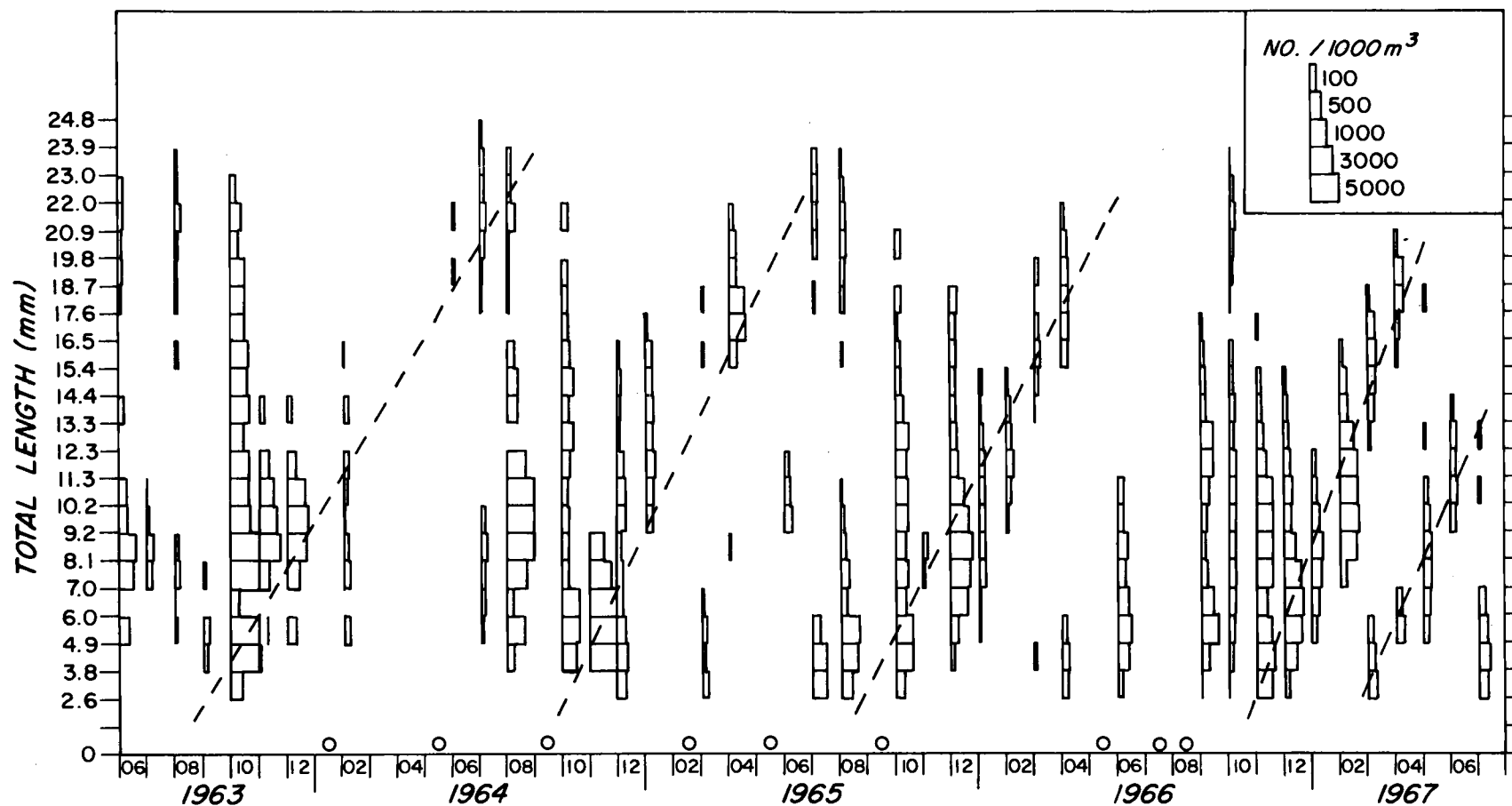


Figure 5. Monthly histograms of abundance in relation to size with time from all four stations combined. At least 50 individuals per 1000 m³ seawater for a single size group were needed to be plotted. Dotted lines represent average growth of individual year classes. "0" means no sample taken from any station during that month

different sizes throughout the four year period.

All four years represented in Figure 5 show some similarity. The main recruitment pulses are in the fall and summer and the maximum size attained is approximately 22-23 mm length. It is only after a period of about one year, late in the next summer or fall, that these maximum size individuals disappear from the population.

Dashed lines connect sequences of modes that are thought to represent average growth. These lines should not be interpreted as actual growth curves, but simply as trend marks to call attention to the sequence of modes. The slope can only be interpreted as average growth over the entire sequence of modes. The lines for the 1965 and 1966 year classes are based on the same modes that are given in Figure 4. These estimates of average growth rate ranged from 1.8 mm/month to 2.5 mm/month, with an average of about 2.1 mm/month (Table 7). This agreed well with the growth estimates from modal progressions of size-frequency histograms from each year class as illustrated in Figure 4. Again, the highest rates were calculated for shorter periods of time for young euphausiids when growth may be faster. A bias with this method of calculating growth rate lies in selecting consecutive months and giving less importance to modes in June through September that do not comprise modal sequences.

Using a method described by Hasselblad (1966), means of

population size modes within single samples were calculated. These means, which generally agreed with the modes of the various collections, were then plotted for the months of the four year sampling period. The main disadvantage of this procedure is that abundance, or the number of euphausiids constituting a mode, is not taken into consideration. Thus, means of less abundant large euphausiids are given as much weight as means of the very abundant small sizes. The means from all stations are plotted on Figure 6 to provide growth estimates for each year class. Dashed lines, again, connect consecutive monthly means used in calculating average growth. Growth estimates by this method varied from 1.6 mm/month to 2.4 mm/month with an average of about 1.9 mm/month (Table 7). Fastest growth rates, as before, were calculated over a short adolescent period. The means of the smaller sizes are probably slightly overestimated since catch curves (Figure 3) indicate escapement from my nets of individuals below 6 mm. This may result in a slight underestimation of growth rates.

All the means in Figure 6 were combined into one plot (Figure 7) for all year classes and stations in order to compare the array of all means with the growth trends shown in Figure 6. When two means were from the same month, placement of each mean into its proper part of the life cycle of Figure 7 was arbitrary. However, these means usually differed widely and no problem was encountered in

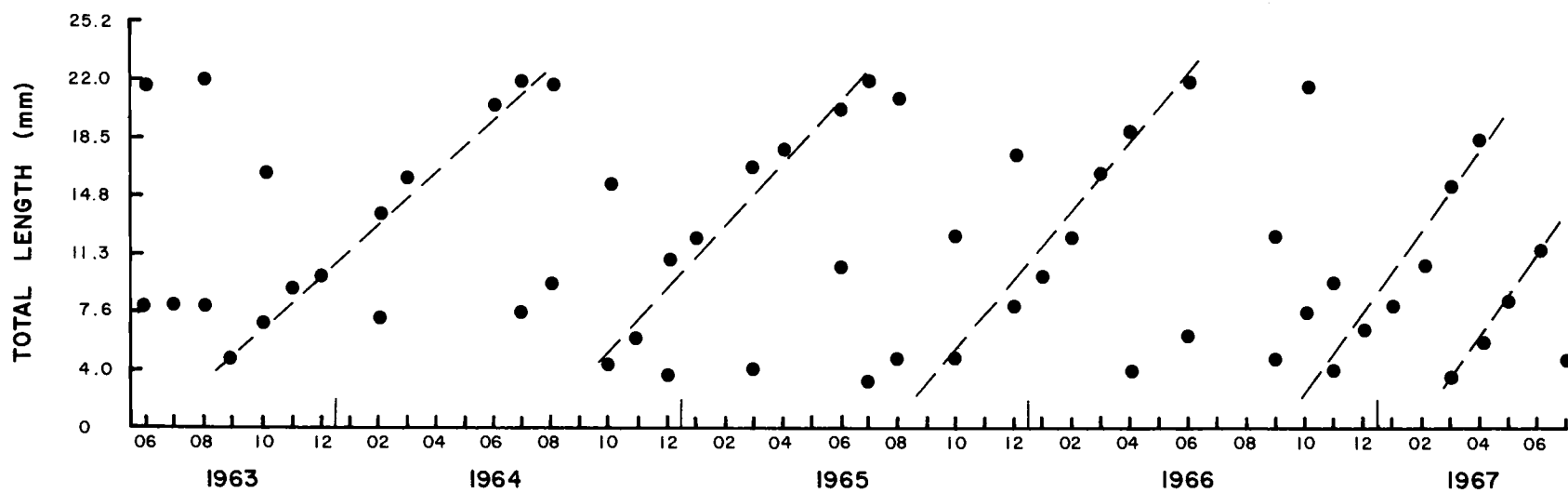


Figure 6. Means from samples of all four stations totaled together. Dotted lines represent average growth trends of year classes.

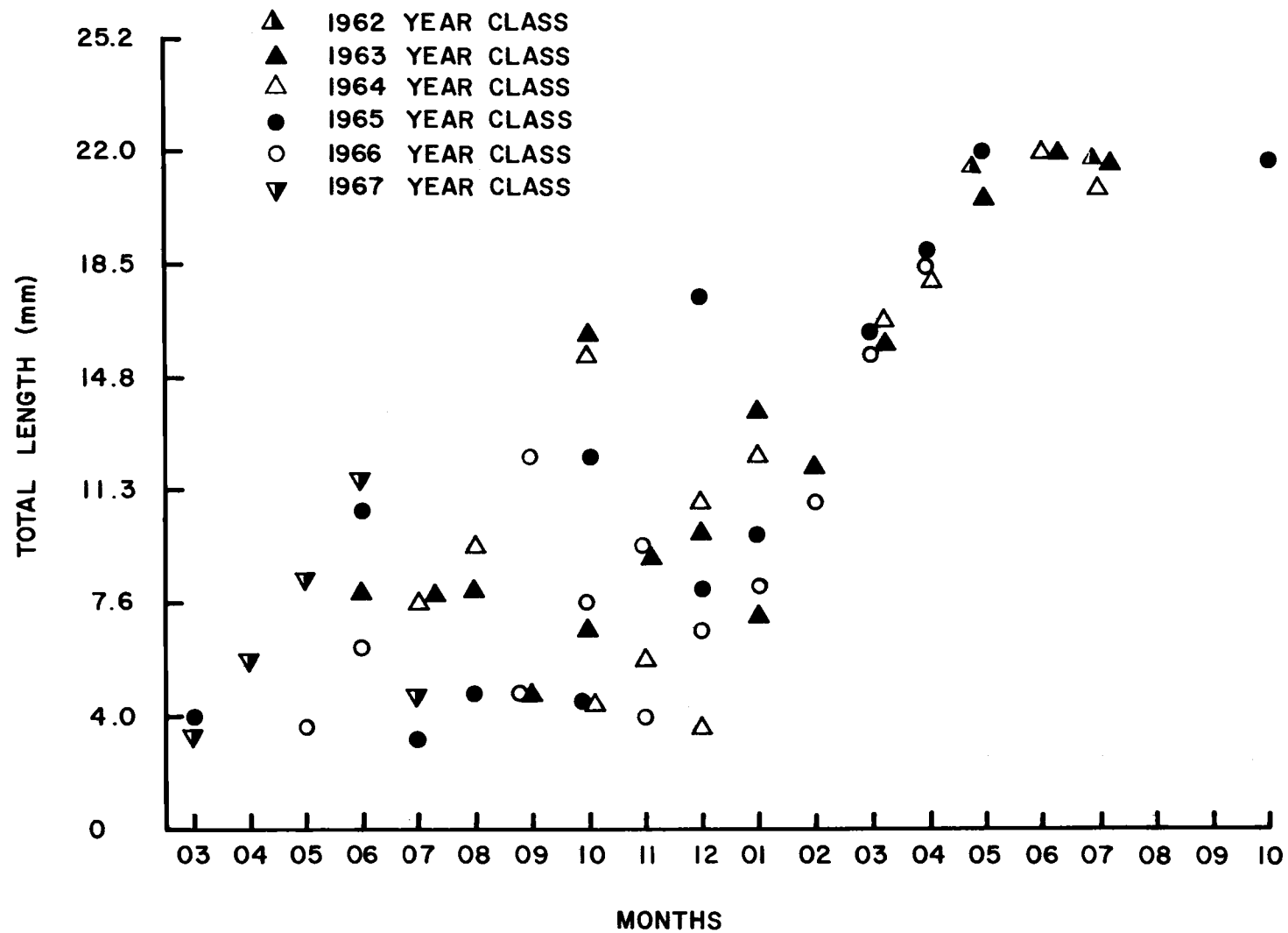


Figure 7. Monthly population means taken over a four year period from all stations totaled together

placing them into early or late stages in the life cycle. Assuming growth is constant throughout the life cycle, a line by least squares was fitted to the points. The slope of this line gives a much lower estimate of growth (1.0 mm/month) than individual modal progressions (about 2.0 mm/month, see Table 7). This difference is mainly caused by the smaller spring and early summer recruitment pulses that were not included in the growth estimates provided by the fall recruitment pulses. By plotting all the data as in Figure 7, equal weight is, of course, given to all the means. Since there are many more points plotted for smaller size groups because of prolonged recruitment, more weight is given to these small sizes and less weight given to large individuals. This causes an underestimation of growth for animals that survive a full year life cycle. Many of the spring and early summer recruitment modes may pass out of the population because of either mortality or advection and hence never reach an adult size in the sampling area.

In the fall and early winter the means of Figure 7 are extremely variable. This is the result of the prolonged recruitment of these animals. The animals spawned during the summer have grown by the time the fall recruitment pulse occurs. Thus, these two (or more) recruitment periods produce the large scatter of means for this time of the year. Reduction of this variability in the later stages of the life cycle is due in part to the reduction in the number and size of modes at

older stages. It may also indicate that animals spawned in the fall have a faster growth rate at this time of year than spring and summer spawned animals and that by the summer these groups merge into one size group. Another possibility is that the spring and summer spawned euphausiids, due to their smaller recruitment pulse, do not make major contributions to the adult populations at our stations.

To summarize, E. pacifica appears to live for about a period of one year or slightly longer, to spawn in the summer and fall months, and to disappear from the population at about 23-24 mm late in the next summer. Growth rates determined by the following modal progressions of year classes averaged about 2.0 mm/month or 0.06 mm/day. Growth is probably fastest at larval and adolescent stages (up to 3.0 mm/month), and then slows down as the animals become older.

DISCUSSION

In an attempt to study the growth of E. pacifica off Oregon, I had to make several assumptions: (1) There is one large, self-sustaining population of this organism off the Oregon coast. Catch curves (Figure 3) present no contrary evidence, nor did Brinton (1962a) find evidence of discrete sub-populations in his study of this species in the northeastern Pacific. (2) Large adult euphausiids do not avoid the plankton gear at night to any significant extent. Since there is evidence that euphausiids may avoid nets in the daytime by visual perception (Brinton, 1967), all tows were taken during nighttime hours when visual avoidance would be minimal. Although avoidance due to some other factor is impossible to measure, maximum sizes of my E. pacifica were similar to those found by others (Nemoto, 1957; Ponomareva, 1963). (3) The entire population is represented in the upper 200 m. Ponomareva (1963) suggested that E. pacifica adults inhabit the 200-500 m layer in their second winter and no longer migrate daily to the surface, but my tows taken to 1000 m with the midwater trawls and vertical meter nets (Tables 3 and 6) did not contain any larger animals off Oregon in this deeper layer.

In an attempt to review certain aspects of the life history of E. pacifica, I will first discuss spawning and how it is related to

swarming, temperature, and productivity. Then I will compare my findings on life span and growth with those of other authors.

Until the present time, there was general agreement that spawning occurs in the spring and early summer. Ponomareva (1963) concluded that E. pacifica spawns in June in the Far Eastern Pacific. Nemoto (1957) also suggested that this species spawns in "spring or early summer" off Japan. Barham (1957) found in Monterey Bay, California that "increase in the catches of the immature forms suggests that the summer months . . . were a period of recruitment for the E. pacifica populations." In contrast to the earlier workers cited above, I found the main pulses of recruitment of young, hence spawning, to be in the fall off Oregon.

Barham (1957) observed swarming, or the presence of tremendous numbers of E. pacifica at the surface in broad daylight, during the spring. This swarming is believed to be associated with spawning activities or some sort of maturation or reproductive drives (Barham, 1957; Zelickman, 1961; Ponomareva, 1963; Komaki, 1967). Komaki (1967) also found swarming to occur mainly in the spring, but in higher latitudes swarming occurred later in the season. For example, at 41°N swarming occurred from May to September, suggesting a protracted breeding period for E. pacifica such as I found off Oregon. Indeed, Brinton (personal communication) found larval recruitment of E. pacifica almost throughout the year off California.

Ponomareva (1963) cited an example in the Yellow Sea where E. pacifica reproduces twice a year, at the end of March and the end of July, with protracted breeding periods. She did not mention if individuals reproduce once or twice during a single year.

Komaki (1967) believed that favorable conditions for swarming may be related to certain oceanographic conditions, namely the approach and the mixing of offshore cold water masses to the inshore areas. In this same sense, coastal upwelling with its influx of cold water during the summer months may provide similar conditions off Oregon. From temperature profiles off Oregon, spawning periods of E. pacifica appear to be associated with the 9 C isotherm intruding into the upper 40 meters or less. On many occasions, however, this isotherm intrudes but no spawning or swarming was apparent, so it appears that an influx of cold water may be only one of several factors required for favorable spawning conditions off Oregon.

Ponomareva (1963) believed that the synchronism of euphausiid swarms with dense phytoplankton blooms is probably important since phytoplankton is necessary for proper development of genital products and provides a rich food supply for newly hatched larvae. Anderson (1964) discovered that high phytoplankton productivity and high standing stocks persisted for the entire summer in inshore Oregon waters, presumably because of upwelling, while offshore oceanic waters had the typical summer productivity minimum. Small and Curl (in

preparation) found that chlorophyll a concentrations averaged over all seasons were highest inshore and steadily decreased offshore; average chlorophyll a in mg per m³ of water in the photic zone graded from 1.10 at 25 miles offshore to 0.71 at 65 miles offshore. These seasonal and inshore-offshore gradients in phytoplankton off the Oregon coast correlate well with my findings on the spawning of E. pacifica: spawning, generally an inshore phenomenon, was protracted over the summer and fall months. Thus, upwelling and high primary productivity are probably correlated with reproductive success.

The density of the phytoplankton crop may affect the growth as well as the reproduction of euphausiids. Ruud (1932) and Bargmann (1945) concluded that the supply of food, mainly diatoms, is the main factor affecting growth of E. superba. Maximum growth coincided with times of phytoplankton maxima, and minimum growth, with phytoplankton minima. Off Oregon, juvenile euphausiids, most abundant during summer and fall, may grow more rapidly than larger individuals, but pronounced seasonal variations in growth rates were not obvious.

Only a few data are available on the life span and growth of E. pacifica. Ponomareva (1963) concluded that E. pacifica lives for a period of two years. She cites three reasons for this conclusion: (1) The presence of adults of two size groups, (2) disappearance of the largest specimens soon after spawning, and (3) the formation of

sexual products only once a year. None of these reasons is proof of a two year life cycle. Only the first reason warrants further discussion. Ponomareva found that in winter the 8 mm and 14-15 mm long specimens predominate, while in the spring the 12-13 mm (her one year olds) and 19 mm long groups predominate. Off Oregon not only were 12-13 mm animals rare or absent in spring samples, but also adults of 13-14 mm, which according to Ponomareva should be found in the summer and fall, were absent. Figure 8 compares generalized growth patterns proposed by Ponomareva with my findings.

Ponomareva's model is based only on winter and spring samples. My data show no retarded growth for the 13-14 mm sizes in the summer and fall months as is indicated in Ponomareva's model. Also, her two year old adults are about the same size as what I believe are euphausiids one year of age. Hence, there seems to be no pattern in my data that conforms to her size groups through a two year life cycle.

Although my data do not fit her proposed growth cycle, her data can be integrated into mine. For example, her 12-13 mm spring animals do not lie along my typical growth curve as do most of her other size groups (Figure 8). However, this could easily be explained by later spawning, say in October or November, which does, of course, occur off Oregon. The problem, thus, may be the extended spawning of E. pacifica. Ponomareva assumed spawning occurred only in the

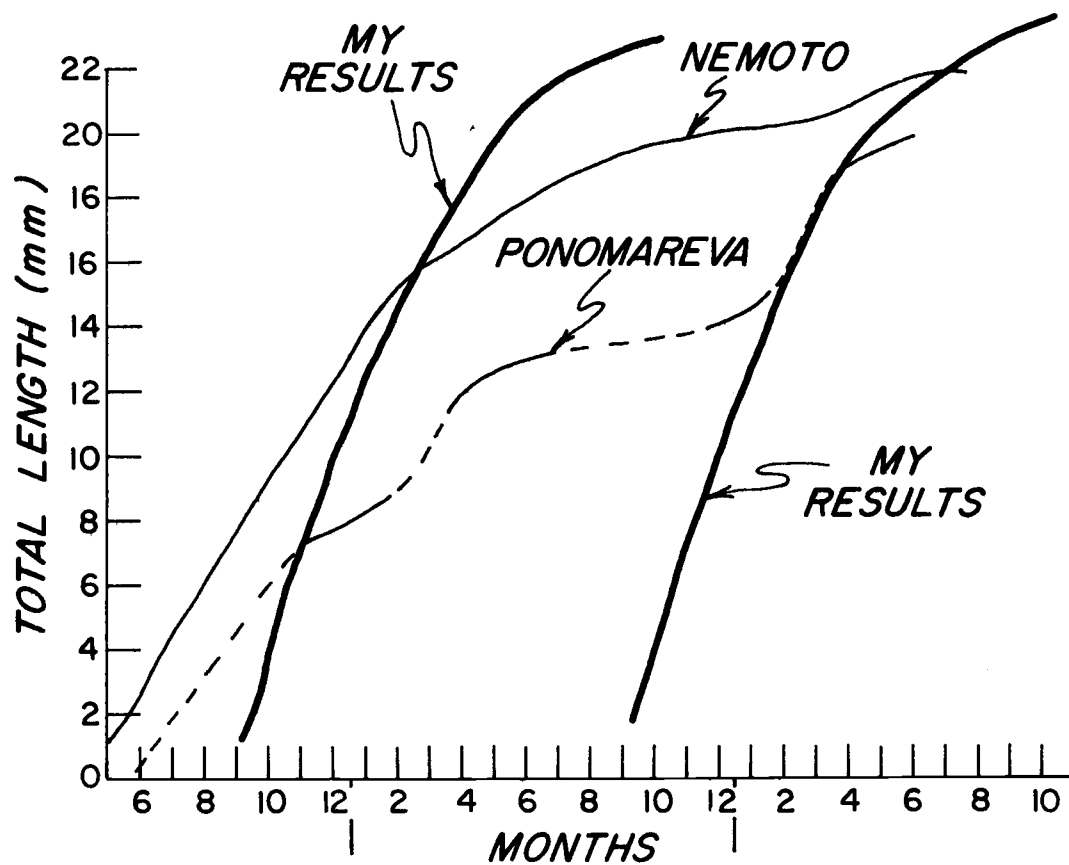


Figure 8. Comparison of growth models of *E. pacifica* as described by Ponomareva (1963) and Nemoto (personal communication) with one described in this paper. Solid portions of the line in Ponomareva's model are based on actual samples.

month of June, whereas the protracted spawning that I found could cause wide variance in modal sizes for a single month (see Figure 7). Thus, if samples are not taken regularly over a several year period, one could easily be misled in interpreting life cycles from field samples.

Nemoto (1957 and personal communication) believes that E. pacifica spawns in the spring and grows very rapidly reaching a length of 17-18 mm after one year (Figure 8). Many individuals spawn after this time and then continue to live for another year reaching a maximum length of about 22 mm and spawning for a second time at the age of two years. Nemoto, though, feels that growth this second year is very slow and sizes from one year up are not easily discernible. The data from Nemoto's 1957 paper are very scanty being from only summer samples with only 15 specimens at most in any one mm size group. In my data, however, there does not appear to be a continuation of large adults through a second year. During winter months the large adult euphausiids have disappeared from my samples (Figure 5).

Barham (1957) also believed that E. pacifica "very likely" has a life cycle of two years. His general impressions from sorting euphausiids over a four year period were that even-numbered years were generally dominated by large adults, whereas the odd-numbered years were characterized by a predominance of adolescent forms. This pattern was not observed in my data.

From Ponomareva's field data, growth rates (assuming them to be constant) were about 0.025 mm/day over the two year period. However, adolescents appeared to grow faster and averaged about 0.044 mm/day. Lasker (1965 and 1966) found maximum laboratory rates for juveniles of 4.5 to 8.5 mm sizes to be as rapid as 0.048 mm/day. Following modes of fall recruitment pulses, my calculations of average growth rate were about 0.065 mm/day with a maximum rate as high as 0.095 in early stages of development.

Small (1967) reported average growth of E. pacifica in terms of weight to be approximately 0.0104 mg/day. Small, however, found no significant difference in growth in weight between small and large euphausiids. This implies that growth in terms of length slows down as the animals become larger, since weight is generally related to the cube of the length. Following modes of length-frequency histograms that Small originally used to measure his growth rate, I calculated growth to be about 0.04-0.05 mm/day.

Euphausia superba lives for two years (Ruud, 1932; Fraser, 1936; Bargmann, 1945; Marr, 1962) with varying growth rates over this two year cycle. Growth is very fast during spring months and very slow during winter months. The maximum spring growth rate of 0.27 mm/day was calculated by Ruud (1932). However, his average rate over the two year cycle was 0.085 mm/day. Marr (1962) found an average growth rate to be 0.048 mm/day over the first year,

0.076 mm/day over the second year, and an average of 0.069 mm/day over the two years. Thus, my growth rate for E. pacifica over one year is approximately the same as that calculated for E. superba over two years. Therefore, E. superba grows to about twice the size of E. pacifica in twice the time.

Any universal conclusions or generalizations about euphausiid growth may be impossible since differences in growth in different years and different geographic areas may possibly be explained by environmental differences such as food availability and temperature. It is very possible that other factors, which have not yet been investigated, may also play important roles in affecting growth. Einarsson (1945) found that growth appeared more rapid in warmer parts of the sea and generalized that growth not only varies between species but also from place to place within one species.

The problem of whether E. pacifica lives for one or two years may be an example of Chamberlain's (1897) so called "ruling theory." Since previous work on euphausiids, mainly E. superba, showed a two year life cycle, it may have become assumed that most euphausiids live for two years (the ruling theory). Thus, there was the tendency to magnify phenomena agreeing with the theory and to fit the facts to the theory. Subsequently, these reports were published and accepted. While I do not mean to say or to imply that my conclusions are right and the others are wrong, I do think that a careful reevaluation of

past conclusions and methods is sorely needed in the area of field population growth studies.

SUMMARY

1. Off the Oregon coast E. pacifica appeared to have a very protracted spawning period. It may commence as early as March and continue through December. However, the main pulses of larval recruitment were generally in the summer and especially in the fall.
2. Euphausia pacifica lives for a period of about one year and passes out of the population at a size of about 22-24 mm. Thus, these animals reach sexual maturity within one year.
3. The average growth rates calculated by following progressive monthly modes were approximately 0.065 mm/day. However, it appeared that growth was somewhat faster at the younger sizes and slowed down as they became fully mature adults.
4. Spawning was generally an inshore phenomenon. Euphausiids were most abundant at the inshore stations and became progressively less abundant offshore.

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