SIZE STRUCTURE AND GROWTH RATE OF Euphausia pacifica OFF THE OREGON COAST'

MICHAEL C. SMILES, JR.,² AND WILLIAM G. PEARCY³

ABSTRACT

Euphausia pacifica (Hansen) off Oregon has a maximum life expectancy of about 1 year. During this time it grows rapidly to a length of 22-24 mm. Furcilia larvae were found throughout the year but were most abundant during the autumn months. The population density and the proportion of juveniles was higher within 25 miles of the coast than in offshore oceanic waters.

Growth rates off Oregon are about twice those previously reported for this species from other regions. Spawning also appears to be later in the year. All these features may be explained by the high primary production which is extended throughout the summer by coastal upwelling and by the lack of wide seasonal fluctuations of water temperatures along the Oregon coast.

Euphausia pacifica is one of the most abundant euphausiids in the North Pacific Ocean. Dense populations are found in Subarctic and Transitional waters (Brinton, 1962a; Ponomareva. 1963) and off the Oregon coast (Hebard, 1966: Osterberg, Pearcy, and Kujala, 1964; Pearcy and Osterberg, 1967).

Euphausiids are important food for many marine carnivores (see Mauchline and Fisher. 1969, and Ponomareva. 1963, for reviews), and Euphausia pacifica is no exception. It is preved upon by salmon (Ito, 1964), baleen whales (Nemoto, 1957, 1959; Osterberg et al, 1964), herring (Ponomareva, 1963), sardine and mackerel (Nakai et al, 1957, as cited by Ponomareva. 1963: Komaki, 1967), rockfish (Pereyra, Pearcy, and Carvey, 1969), pasiphaeid and sergestid shrimp (Renfro and Pearcy, 1966), pandalid shrimp (Pearcy, 1970), and myctophid fishes (Tyler, 1970).

Studies on the growth of several species of euphausiids are reviewed in the monograph by Mauchline and Fisher (1969). Data on the

Manuscript received September 1970.

FISHERY BULLETIN: VOL. 69, NO. 1, 1971.

growth and life history of E. pacifica are limited. Nemoto (1957) presented some growth data for E, pacifica from the Japanese-Aleutian area. Ponomareva (1963), in her study on the distribution and ecology of euphausiids of the North Pacific, estimated the growth of E. pacifica from plankton samples collected during the winter and spring. Lasker (1966) determined the growth of E. pacifica reared in the laboratory. Preliminary growth rates of E. pacifica based on some of our data were also presented by Small (1967).

Because growth rates are needed to understand the ecology and energetics of a species. we undertook this study on the abundance, size structure, and growth rate of E, pacifica off Oregon.

COLLECTION METHODS

We made a total of 174 collections using 1-m mouth diameter plankton nets between June 1963 and July 1967 at stations located 15, 25, 45, and 65 miles off Newport, Oreg. In addition, 25 collections were obtained from stations 85-285 miles off Newport. These provided samples of E. pacifica for all seasons of the year over a 4-year period. Nets had 0.571-mm mesh openings and were used with a flowmeter placed in

¹ This research was supported by the National Science

Foundation (GB-5494) and the Atomic Energy Com-mission (AT(45-1)-1750; RLO 1750-50). ^a Formerly, Department of Oceanography, Oregon State University; present address: Biology Depart-ment, State University of New York, Farmingdale, N.Y. 11735.

³ Department of Oceanography, Oregon State University, Corvallis, Oreg. 97331.

the mouth to measure the amount of water filtered.

The first 20 samples were from oblique tows, and the other 154 were from vertical tows. This change to vertical tows was made to ensure equal sampling at all depths throughout a tow. Comparison of the catches of several oblique and vertical tows taken during the same night indicated little difference in the number and size of *E. pacifica* per unit volume filtered.

Because euphausiids may avoid nets in the daytime, all tows were taken during nighttime when visual avoidance would be minimal (Brinton, 1967). This is also a period when *E. pacifica* presumably has migrated into the upper 100 m of the water column. *E. pacifica* captured in several 6-ft Isaacs-Kidd midwater trawls were measured to see if large euphausiids that were possibly avoiding the small vertical meter net could be captured. There was no indication that the maximum size of trawl-caught was larger than meter net-caught euphausiids.

The maximum depth of our tows was usually 200 m. Because 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, tows were taken to 1000 m with both the midwater trawls and vertical meter nets. These deeper tows, however, did not contain any larger animals. Twelve vertical meter net samples from depths of 200 m or 1000 m to the surface did not show appreciable differences in size structure. Therefore, we assumed that a representative sample of the *E. pacifica* population was caught in the upper 200 m at night.

The entire plankton sample was preserved at sea in neutralized 10 % Formalin. In the laboratory ashore, all euphausiids were removed from each sample unless the number of euphausiids was large (more than 200 individuals). In such cases the sample was usually divided in half with a Folsom plankton splitter (Mc-Ewen, Johnson, and Folsom, 1954), and euphausiids were sorted from only one-half the sample. Males and females were not differentiated.

The length of each individual E. pacifica was measured to the nearest 0.1 mm from behind

the eye to the posterior margin of the carapace, and each animal was then assigned to a 0.3-mm size-group. Total lengths (from the posterior of the eye to the tip of the telson) were also measured from randomly selected individuals of various lengths to enable comparisons of our data with those of others. A least squares fit of 146 comparisons gave the equation:

$$Y = 2.54 \ X + 0.66$$

where Y = total length and X = carapace length. The variance was 248.19. Our measurements are all given as total lengths.

RESULTS

RECRUITMENT AND ABUNDANCE

Although larval *E. pacifica* occurred during almost all months of the year, definite trends in abundance were evident over the 4-year period (Fig. 1). Larvae were usually most abundant between October and December. During some years recruitment began as early as June and was also prominent in the summer months. No major concentrations of larvae were found during winter or spring.

These larval forms of E. pacifica were furcilia of about 7 mm or less, agreeing with Boden's (1950) size measurements and description of E. pacifica furcilia. Furcilia are found 16-18 days after spawning, usually within the upper 100 m of the water column (Ponomareva, 1963; Brinton, 1967).

Catch curves (Fig. 2) show the average number of different size-groups of E. pacifica collected during the entire study. All sizes of E. pacifica were much more abundant per m³ inshore over the continental shelf than in oceanic offshore waters. Individuals larger than 15 mm were rare at station 65 miles or farther offshore. Our finding that larvae were less abundant at offshore than inshore stations agrees with Brinton (1962b), who also noted that E. pacifica was more abundant inshore than offshore of California. Thus, despite the wide oceanic distribution of E. pacifica, the density of near-



FIGURE 1.—Number of furcilia of *E. pacifica* collected at four stations off Newport, Oregon (NH-15, 25, 45, 65) during 1963-67. "0" indicates no sample taken for that month.



FIGURE 2.—Catch curves: the logarithm of the average number of various sizes of *E. pacifica* caught per 10^3 m³ for all samples during the study.

shore populations may be considerably higher than offshore populations in the same region.

Although inshore tows were generally made

only to 50 m and 130 m at the 15- and 25-mile stations respectively because of depth of water, euphausiid abundance at these stations was approximately 10 times greater than at offshore stations. This difference is too great to be explained by the differences in sampling depths even assuming that all euphausiids were concentrated in the upper 50 m at night.

GROWTH RATE

The extended spawning season and variability of catches of *E. pacifica* made interpretation of growth difficult. Three related methods, all based on progressions of size-frequency histograms, generally gave similar growth rates (Table 1) and led to the same conclusion: *E. pacifica* lives for a period of about 1 year and attains a maximum size of about 22-24 mm total length. We tenuously assumed for all these analyses that we sampled the same population, or populations with similar age structures and growth rates.

Two illustrations of growth based on monthly

TABLE 1.—Summary of average growth rate estimated from the progression of modes or means (see Figs. 3 and 4).

Year class	Recruitment month	Number months followed	Growth rates		
			Modes (Fig. 3 for 1965 and 1966 year classes)	Modes (Fig. 4)	Means
		4	M	m/month -	
1963	09	10	1.6	1.9	1.6
1964	10	9	2.0	2.0	1.9
1965	10	8	2.1	2.2	2.0
1966	11	5	2.9	2.5	2.4
1967	03	3	2.6	2.5	2.5

size-frequency histograms of all stations combined (Fig. 3) illustrate the increasing modal lengths between December and June for the 1965 and 1966 year classes. Recruitment of small *E. pacifica* is also obvious during the spring of 1966 and 1967 and also shows a shift in modes with time. The 1963 and 1964 year classes (not shown here) showed similar trends.

A modified histogram plot (Fig. 4) was used to show the data for all 4 years and all 4 stations together. The advantage of this method is that one can follow the main modes of different sizes throughout the 4-year period. A disadvantage is that these plots are distorted by the arbitrary constraints that (1) at least 50 individuals per 103 m³ of water within one size-group had to be present for plotting and (2) concentrations above 5000/103 m³ were plotted only as 5000/103 m³. All of the years represented in Figure 4 show some similarity. The main recruitment pulses are in the fall and summer, and the maximum size attained is approximately 22-24 mm length. After about 1 year, late in the second summer or fall, these large individuals disappeared from our collections. Interestingly, many of the modes that were composed of small euphausiids during the spring and early summer disappeared or were undiscernible by the fall. Either these individuals were subjected to higher mortality than the fall recruits or were transported out of the area. Apparently they made no major contribution to the local adult population.

Average lengths of size modes were also calculated for each collection using the computer techniques described by Hasselblad (1966). The means were generally close to the values for the modal lengths of various collections shown in Figures 3 and 4 and, therefore, are not illustrated here but are given in Table 1.

Our estimates of the growth of E. pacifica by all these methods are summarized in Table 1. As expected, estimates are similar for the same year classes. Growth varied from 1.6 to 2.9 mm per month among year classes, averaging about 2.0 mm per month. Growth rates were fastest for young stages. Year-classes 1963 and 1964 had slower average rates (1.6 and 2.0 mm/ month) and were calculated over a longer period. Year-classes 1966 and 1967, on the other hand, were represented for the shortest periods of time and had the fastest average rates (2.9 and 2.6 mm/month). This deceleration of growth at the larger sizes is also apparent in Figure 3 where the growth rate from January to March 1966 was about 3.2 mm/month, while from March to June it was about 2.0 mm/month.

Our estimates are biased in several ways. They favored the recruitment pulses of the fall because the smaller modes of young that appeared earlier (June through September) did not comprise a good series of modal sequences. Moreover, the modes and means of the smaller sizes of *E. pacifica* are probably slightly overestimated since catch curves (Fig. 2) indicate escapement from our nets of individuals below 6 mm. This may cause an underestimation of growth rates.

DISCUSSION

Generalized growth curves of E. pacifica for three regions of the North Pacific are contrasted in Figure 5. On the basis of bimodal size-frequency distributions of winter and spring samples, Ponomareva (1963) concluded that E. pacifica lives for a period of 2 years. She found predominantly 8 and 14-15 mm individuals in the winter and 12-13 mm (her 1year olds) and 19 mm (2-year olds) in the spring. Off Oregon not only were 12-13 mm individuals rare or absent in spring samples, but also 13-14 mm individuals, the size that Ponomareva would expect to find in the summer and fall, were absent. Moreover, our data, unlike Ponomareva's, show no large seasonal fluctuations of growth with retarded growth of the 13-14 mm sizes



FIGURE 3.—Size frequency distributions of E. pacifica from all stations for the 1965 year class (left) and the 1966 year class (right).



FIGURE 4.--Size frequency histograms for all stations, 1963-67. Dashed lines are an estimate of average growth of individual year classes. "0" indicates no samples for that month.



FIGURE 5.—Comparison of generalized growth curves of *E. pacifica*.

in the summer and fall. Nemoto (1957 and personal communication) believes that E. pacifica grows rapidly, reaching a length of 17-18 mm after 1 year. Many individuals spawn after 1 year and then may continue to live for another year, reaching a maximum of 22 mm after 2 years. We find no convincing evidence, however, for continuation of large adults through a second year. Large euphausiids disappeared from our samples by the winter (Fig. 4).

Thus our results indicate a faster growth rate and shorter life cycle than those of Ponomareva and Nemoto for the northwestern Pacific but a similar maximum size. Our growth rates off Oregon averaged 0.065 mm/day for the entire life span, about twice those for the other field studies of *E. pacifica*. Maximum rates for rapidly growing juveniles were 0.095 mm/day. These rates are higher than Lasker's (1966) maximum rates for juvenile *E. pacifica* reared in the laboratory, suggesting that growth in nature may exceed "optimal" conditions in the laboratory.

Although our estimates of the growth of *E.* pacifica are higher than previously reported, they approximate the estimates for several other species of euphausiids. A length of about 22 mm after 1 year was also found by Mauchline (1966) for *Thysanoessa raschii*; by Ruud (1936), Mauchline (1960), and Einarsson (1945) for *Meganyctiphanes norvegica*; by Einarsson (1945) for *Thysanopoda acutifrons*; by Ruud

(1932), Bargmann (1945), and Marr (1962) for Euphausia superba; and by Baker (1959) for Euphausia triacantha. Most of these species have a maximum life expectancy of 2 years, reproduce each year, and grow slowly during the winter. Other species are known to have a life expectancy of 1 year (Mauchline and Fisher, 1969).

Development, growth, and sexual maturity of the same species of euphausiid are known to vary among geographic populations (Einarsson, 1945: Nemoto, 1957; Ponomareva, 1963; Mauchline and Fisher, 1969). Mauchline and Fisher (1969) stress that this variability is probably directly related to differences in food and temperature. Hence, the rapid growth of E. pacifica off Oregon may be related to the high productivity of the region and the lack of large seasonal temperature fluctuations in nearshore waters.

Small, Curl. and Glooschenko' report high values for primary productivity in the coastal waters off Oregon. Curl and Small⁵ found that standing stocks of chlorophyll-a averaged highest inshore and steadily decreased offshore. High production and stocks persist through the summer, the upwelling season, in inshore waters. whereas offshore waters have a typical summer productivity minimum (Anderson, 1964), Note that those seasonal and inshore-offshore gradients in phytoplankton are correlated in time and place with the spawning of E. pacifica off Oregon, mostly inshore and protracted over the summer and fall months. Ponomareva (1963) believes that phytoplankton is not only important as food for euphausiid larvae, but also may be necessary in the diet for development of reproductive products of E. pacifica.

Water temperatures along the Oregon coast are fairly uniform throughout the year and lack the extremes found along the eastern coasts of continents at similar latitudes. Advection of cool water to the surface (upwelling) during the summer and warm water toward shore dur-

ing the winter moderates the usual seasonal variations. Pattullo, Burt, and Kulm (1969) observed that the seasonal range of heat content was twice as large offshore as inshore (within 65 miles) of the Oregon coast. The absence of severe winter temperatures may help to explain the rapid growth of E. pacifica throughout the year off Oregon. Conversely the slow and seasonally variable growth of E. pacifica found by Ponomareva (1963) was in the Far Eastern Seas of Asia where temperatures are often lower and where thermal variations are greater. The fact that E. pacifica is the only widespread euphausiid that spawns in the summer, when the phytoplankton bloom was almost over, indicates that this boreal species may be poorly adapted to the cold marginal Far Eastern Seas (Ponomareva, 1963).

The main pulses of larvae, hence spawning, of E. pacifica were in the fall, and not in the spring and summer as found by Ponomareva (1963), Nemoto (1957) off Japan, and Barham (1957) in Monterey Bay, Calif. Brinton (personal communication) notes larval recruitment throughout the year off Southern California. The later spawning off Oregon, like the rapid growth, may again be related to the prolonged production cycle caused by upwelling off Oregon and the moderate fall and winter water temperatures.

ACKNOWLEDGMENTS

We are grateful to J. Mauchline for his suggestions and to T. Nemoto for providing his growth curve for E. pacifica.

LITERATURE CITED

ANDERSON, GEORGE C.

1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnol. Oceanogr. 9(3): 284-302.

BAKER, A. DE C. 1959. The distribution and life history of Euphausia triacantha Holt and Tatersall. Discovery Rep. 29: 309-340.

BARGMANN, HELENE E.

1945. The development and life-history of adolescent and adult krill, Euphausia superba. Discovery Rep. 23: 103-176.

⁴ L. F. Small, H. Curl, Jr., and W. A. Glooschenko. Seasonal primary production in a region of upwelling. III. Effects of solar radiation and upwelling on daily production. Unpublished MS. ⁶ H. Curl, Jr., and L. F. Small. MS.

BARHAM, ERIC GEORGE.

- 1957. The ecology of sonic scattering layers in the Monterey Bay area, California. Ph.D. Thesis, Stanford Univ. 192 p. Univ. Microfilms, Ann Arbor, Mich. Publ. 21, 564.
- BODEN, BRIAN P.
 - 1950. The post-naupliar stages of the crustacean *Euphausia pacifica*. Trans. Amer. Microsc. Soc. 69(4): 373-386.
- BRINTON, EDWARD.
 - 1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. Univ. Calif. 8(12): 51-270.
 - 1962b. Variable factors affecting the apparent range and estimated concentrations of euphausiids in the North Pacific. Pac. Sci. 16(4): 374-408.
 - 1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12(3): 451-483.

EINARSSON, HERMANN.

1945. Euphausiacea. 1. North Atlantic species. Dana Rep. Carlsberg Found. 27, 1-185.

HASSELBLAD, VICTOR.

1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8(8): 431-444.

HEBARD, J. F.

1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis. 85 p.

ITO, JUN.

1964. Food and feeding habit of Pacific salmon (genus Oncorhynchus) in their oceanic life. Bull. Hokkaido Reg. Fish. Lab. 29: 85-97.

KOMAKI, YUZO.

1967. On the surface swarming of euphausiid crustaceans. Pac. Sci. 21(4): 433-448.

LASKER, REUBEN.

1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Bd. Can. 23(9): 1291-1317.

MARR, JAMES.

1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Rep. 32: 33-464.

- 1960. The biology of the euphausiid crustacean, Meganyctiphanes norvegica (M. Sars). Proc. Roy. Soc. Edinburgh, Sect. B. (Biol.) 67: 141-179.
- 1966. The biology of *Thysanoessa raschii* (M. Sars), with a comparison of its diet with that of *Meganyctiphanes norvegica* (M. Sars). *In* Harold Barnes (editor), Some contemporary studies in marine science, p. 493-510. George Allen and Unwin Ltd., London.

MAUCHLINE, JOHN, AND LEONARD R. FISHER.

1969. The biology of euphausiids. In Frederick S. Russell and Maurice Yonge (editors), Advances in marine biology. Vol. 7, 454 p. MCEWEN, G. F., M. W. JOHNSON, AND TH. R. FOLSOM. 1954. A statistical analysis of performance of the Folsom plankton sample splitter, based on test observations. Arch. Meteorol. Geophys. Bioklimatol., Ser. A. 7: 502-527.

NEMOTO, TAKAHISA.

- 1957. Foods of baleen whales in the northern Pacific. Sci. Rep. Whales Res. Inst. 12: 33-90.
- 1959. Food of baleen whales with reference to whale movements. Sci. Rep. Whales Res. Inst. 14: 149-290.
- OSTERBERG, CHARLES, WILLIAM PEARCY, AND NORMAN KUJALA.

1964. Gamma emitters in a fin whale. Nature (London) 204 (4962) : 1006-1007.

- PATTULLO, JUNE G., WAYNE V. BURT, AND SALLY A. KULM.
 - 1969. Oceanic heat content off Oregon: Its variations and their causes. Limnol. Oceanogr. 14(2): 279-287.

PEARCY, WILLIAM G.

1970. Vertical migration of the ocean shrimp, *Pandalus jordani*: A feeding and dispersal mechanism. Calif. Fish Game 56(2): 125-129.

PEARCY, WILLIAM G., AND CHARLES L. OSTERBERG.

1967. Depth, diel, seasonal, and geographic variations in zinc-65 of midwater animals of Oregon. Int. J. Oceanol. Limnol. 1(2): 103-116.

- PEREYRA, WALTER T., WILLIAM G. PEARCY, AND FORREST E. CARVEY, JR.
 - 1969. Sebastodes flavidus, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Bd. Can. 26(8): 2211-2215.

PONOMAREVA, LARISA NATAL'EVNA.

1963. Euphausiids of the North Pacific, their distribution and ecology. Akad. Nauk SSSR Inst. Okeanol. (Translated by Israel Program for Scientific Translations, Jerusalem 1966, IPST catalog no. 1368, 154 p.)

RENFRO, WILLIAM C., AND WILLIAM G. PEARCY.

1966. Food and feeding apparatus of two pelagic shrimps. J. Fish. Res. Bd. Can. 23(12): 1971-1975.

- 1932. On the biology of southern Euphausiidae. Hvalradets Skr. 2. 105 p.
- 1936. Euphausiacea. Rep. Dan. Oceanogr. Exped. 1908-1910 Mediter. Adjacent Seas 2D6(Biol.), 86 p.

SMALL, LAWRENCE F.

1967. Energy flow in Euphausia pacifica. Nature (London) 215(5400): 515-516.

Tyler, H. R., Jr.

1970. The feeding habits of three species of lanternfishes (Myctophidae) off Central Oregon. Master's Thesis, Oregon State Univ., Corvallis. 64 p.

MAUCHLINE, J.

RUUD, JOHN T.