

POPULATION BIOLOGY OF *EUPHAUSIA PACIFICA* OFF SOUTHERN CALIFORNIA

EDWARD BRINTON¹

ABSTRACT

Euphausia pacifica was observed with respect to reproduction, growth and development of cohorts, and successions in population structure and biomass during 4 yr, 1953-56. The southern California eddy and its upwelling regime serve as a reproduction refuge for a warm-temperate population of this euphausiid. Three size classes spawn there during a year—the largest in April-June, an intermediate in June-February, and small, newly mature females usually in August-January. There were year-to-year differences.

The largest densities of larvae were observed about a month after egg peaks (one survey later) or appeared coincident with them. In 1953 there was strong spring recruitment, abruptly subsiding with an early decline in upwelling—the index of environmental enrichment used. During 1954 only one substantial cohort was recorded, in June at the height of a poor upwelling season. In 1955 repeated spawning occurred during the long upwelling season, but recruitment after July was poor. The year of most intense upwelling, 1956, yielded three strong cohorts—the last, July-October, being exceptionally strong. Smallest larvae were usually in 12°-16°C waters. Ripe females were concentrated at high densities at these same temperatures during August-March but were distributed over a broader range at 10.5°-19°C during April-July.

Growth was estimated to be about 3 mm body length per month, slowing during September-January or after about 17 mm. Females appeared to grow slower in breeding seasons. Maturity can be at 11 mm, but reproduction is not general until 15-16 mm. Here, maximum size was 21 mm after about 7 mo for early-year recruits and a year for summer recruits. Survival rates appeared higher in the latter. Growth rates were similar to those reported for *E. pacifica* off Oregon and higher than in the subarctic Pacific. Survivorship was lowest for furcilia larvae, increased in juvenile and young adult phases, then decreased after reproduction became regular. Slowed growth and increased survivorship at life interphases appeared to cause regular frequency and biomass maxima at lengths of 7, 10-12, and 15 mm. Sex ratio favored females. Males apparently accomplished multiple fertilizations.

Euphausia pacifica Hansen is a temperate North Pacific euphausiid crustacean, composing a substantial part of the zooplankton of the North Pacific Drift, lat. 40°-50°N, and ranging southward along the coast of North America as far as lat. 25°N (Brinton 1962a). In the cooler part of the California Current, it occurs in association with the euphausiids *Nematoscelis difficilis* and *Thysanoessa gregaria*. Depth ranges of the three species overlap daily as *E. pacifica* and *N. difficilis* engage in distinctive vertical migrations while *T. gregaria* does not migrate (Brinton 1967a). Horizontal ranges are sufficiently similar so that these species, together with *E. gibboides*, were considered the euphausiids of a California Current-Transition Zone plankton assemblage (Brinton 1962a).

Euphausia pacifica performs extensive vertical migrations. Off California it lives at daytime depths of 200-400 m, entering the surface layer at

night. It is an omnivore (Lasker 1966) and possesses thoracic food-gathering limbs which are nearly uniform in length and in setation of the filtering screens.

Euphausia pacifica is usually the most abundant euphausiid. Its maximum densities are often centered relatively near to the coast of California. The low-latitude part of the population of *E. pacifica* is the object of this study. Aspects of its life history have been observed in the more typically temperate regime to the north of lat. 40°N (Nemoto 1957; Ponomareva 1963; Smiles and Percy 1971) where environmental characteristics show stronger seasonality than to the south. The extent to which the downstream portion of this distributional range is maintained by local processes has not been previously investigated.

The study was organized in relation to existing knowledge of the physical-chemical characteristics of the area and of the species distributions.

Surveys of the region of the California Current since 1949 have provided a reservoir of hydrographic data and plankton samples that lend

¹ Scripps Institution of Oceanography, La Jolla, CA 98093.

themselves to time-series studies of biological and environmental developments. The CalCOFI (California Cooperative Oceanic Fisheries Investigations) Atlas series (Numbers 1-24) presented varied material, including euphausiid distributions derived from the program. Charts of distributions of *E. pacifica* based on the data that are the subject of the present analysis are included in Brinton and Wyllie (in press). Smith (1971) described the distribution of zooplankton biomass.

Description of the Study Area

The southern California eddy is the southernmost area in which *E. pacifica* is still both abundant (commonly 10-1,000 individuals beneath 1 m² of sea = 10-1,000 mg wet weight) and dominant among the larger zooplankters (Brinton 1967a, b). The eddy may be considered bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. Its east-west extent is about 250 km; beyond its western limits, flow is consistently from the north and apparently contributes relatively little water and biota to the eddy.

The sluggish circulation off southern California evidently permits substantial autonomy for the resident populations. The currents are commonly 5-10 cm/s and rarely as much as 25 cm/s, both at the surface and at 200 m depth (Wyllie 1966). Direction of flow sometimes reverses between these two levels. These are, respectively, the night and day depth levels occupied by vertically migrating *E. pacifica* (juvenile and adult) in the area; larvae remain near the surface day and night (Brinton 1967a).

Circulation of the eddy is cyclonic. Within it, therefore, there is upward transport of enriched water. The center of the eddy (no surface flow) is, on the average, near San Nicholas Island (lat. 33°15'N, long. 119°30'W), 100 km off the midpoint of the southern California coast. The study area was centered here. Farther east, mean flow is northwesterly along the coast. To the west, flow is southeasterly, angling toward the coast near lat. 30°N.

About 150 km south of Point Conception, mean geostrophic flow approaches 135°, averaging 10 cm/s. A parcel of water entering the eddy from the northwest would, at that speed, take 100 days to move around the eddy back to Point Conception, flow permitting. Average velocities within the eddy are much less. Places where substantial

advection takes place across margins of the area are determinable from the flow diagrams in a relative sense. Northerly surface flow into and out of the area is characteristic of winter months when the Davidson Countercurrent is developed. Southerly flow into or through the western part of the area is usually strongest in April-July. The eddy persisted in almost all of the months studied.

Upwelling enhances the temperate character of the area during spring and summer, usually intensifying during April-June (Bakun 1973) when annual temperature minima are usually found. It is responsible for much of the local nutrient enrichment (Reid et al. 1958). Seasonal periodicity is evident when water temperature is averaged for the area of the eddy as a whole: August-October is generally warmest and January-April coolest (Anonymous 1963). The area contains a scatter of islands which provide substantial shoal grounds, regarded off Oregon to be areas best suited for *E. pacifica* (Smiles and Pearcy 1971). Such islands also provide topography for the formation of downstream eddies which are enrichment centers (Uda and Ishino 1958). They also serve as centers of upwelling. Here, upwelling is less dependent on the direction of the wind than on its intensity. However, the coast from Point Conception eastward remains the main focus of upwelling during the period of prevailing northwest winds, February-June. According to the indices derived by Bakun from extrapolated atmospheric pressure gradients at the sea surface, upwelling off southern California is the most intense to be found in the California Current.

For this initial life-history study, the period chosen (1953-56) was one of generally stable oceanic climate and hydrographic conditions, compared with the years immediately following, which included times of more extreme fluctuations in temperature and flow characteristics. During 2 of the 4 yr, 1955 and 1956, upwelling was inferred by Bakun (1973) to be more intense than the 1946-71 mean; however, during 1954 it was less, and during 1953 upwelling commenced early but barely achieved the June peak of mean intensity and was greatly diminished in the summer months.

Thus it was anticipated that the study period would yield observations of low annual variability in the population of *E. pacifica*, thereby providing a baseline against which eventually to measure events in years of known extremes in ocean climate, e.g., 1957-59 (Brinton 1960).

Previous Investigations

In addition to the observations on the life history of *E. pacifica* (Nemoto 1957; Ponomareva 1963; Smiles and Pearcy 1971), aspects of the energy budget and physiology of this species have been studied. Lasker (1964, 1966) measured moulting frequency, feeding rates, respiration and carbon utilization by specimens maintained in the laboratory, and observed growth rate in juveniles and adults. Fowler et al. (1971) considered effects of temperature and size on moulting. Small et al. (1966) measured respiration at different temperatures and discussed energy flow, while Small (1967) further examined energy flow. Paranjape (1967) made observations on moulting and respiration. Aspects of depth-habitat and pressure in relation to respiration were considered by Small and Hebard (1967), Pearcy and Small (1968), and Childress (1971). Gilfillan (1972) studied oxygen uptake in relation to laboratory controlled temperatures and salinities.

Total oocytes in a large female were counted by Ponomareva (1963). Clutch size estimates and the vertical distribution of different age groups were given in Brinton (1962b and 1967a, respectively).

Limitations of the Study

Understanding the population biology of an oceanic species depends in large part upon the extent to which a representative part of the population can be representatively sampled. In the planktonic environment, currents not only tend to transport the organisms across an observer's horizon, but also cause relative horizontal displacement of life stages because, in many species, the various stages of development live at different depths and experience different horizontal transport. This is true of euphausiids. Species undergoing both ontogenetic and daily vertical migrations, such as *E. pacifica*, are further subject to differential horizontal transport. Thus, water movement is a variable which complicates any plan for temporal continuity in sampling a population. The area covered and the time spent in carrying out an assessment of a population does not need to be great if the waters are restricted geographically and if growth and development of the population is measurable between successive assessments. Clearly, a gyre of circulation, such as the eddy lying off southern California, may be expected to harbor elements of a population that

persists locally. This study area has proven practical in size according to the logistics of CalCOFI.

MATERIALS AND METHODS

Samples were obtained by oblique tows, 0-140 m depth (except where the water was shallower), using the CalCOFI standard net, 1-m mouth diameter and 0.55-mm mesh width (Ahlstrom 1948). The mesh width of the cod end and of a 40-cm section in front of it was 0.25 mm. The volume of water strained through a net was determined with a TSK (Tsurumi-Seiki Kosakusho) flowmeter.² Most volumes were in the range of 300-400 m³. The net was towed at about 75 cm/s. The 1953-56 cruises provided month-to-month data, including more frequent surveys off southern California in late 1955 (four in September, three in November). Station positions and collecting data together with displacement volumes of the plankton samples are from annual listings of CalCOFI plankton sampling 1953-56 (South Pacific Fishery Investigations 1954, 1955, 1956; Thrailkill 1957).

Specimens smaller than 3 mm in length are able to pass through the meshes of the net and therefore were not representatively sampled. Smaller specimens (2 mm) are nevertheless retained by the fine meshes of the cod end of the net and counts of these are included as indicative of the presence of the small calyptopis larvae. Free floating eggs of *E. pacifica* are not retained by this net. Estimates of egg production are derived from examination of the ripe females sampled, as described in the discussion of fecundity below.

A total of 819 samples from 48 cruises, 5301 (January 1953) through 5612 (December 1956), were examined (Figure 4d). Only nighttime samples were used since juveniles and adults are not representatively sampled in the daytime, owing to vertical migration and avoidance of the net (Brinton 1967a). Between 7 and 43 nighttime samples were collected in the study area during each cruise. "Night" was considered to be the period from 1 h after sunset to 1 h before sunrise. A few sunrise and sunset samples were analysed if they were collected under overcast skies. A sample marginal to, but outside of, the area was studied when such a sample was from a locality nearer to the closest boundary of the area than any of the

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sampled localities within the area. Thus, some samples from station lines 77 (northern) and 97 (southern), or designated 80.80 (western), were occasionally used.

The samples were examined in the following manner. An aliquot containing 100-200 *E. pacifica* was counted; the specimens were measured to the nearest millimeter of body length (tip of frontal plate to tip of telson); adults were sexed; and the degree to which the reproductive products were developed was recorded. If, for adults (specimens >10.5 mm in length), the initial aliquot contained fewer than three specimens of any particular length, a second aliquot of equal size was examined for specimens of that size or larger. In this way, increasingly large fractions of the sample were examined for specimens of those length intervals which were progressively determined to be fewest in the sample. This procedure made it possible to count the rarer, large specimens with a degree of accuracy comparable with that to which the consistently more abundant small specimens were counted. Usually, the entire sample was examined for specimens of more than 14-mm body length. This procedure was facilitated by the use of the Folsom plankton splitter which, through successive splitting operations, provides aliquots of $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, . . . $1/n$. All counts were standardized for 1,000 m³ of water strained by the net.

After standardization, the counts for a sample (station) were weighted according to the proportion of the survey area represented by that station. When the nearest area surrounding the station was equal to a 65 × 65 km square (a usual spacing for CalCOFI stations), the weighting factor was 1.0. When areas represented by stations were greater or less than 65 × 65 km, weighting factors were proportionally greater or less than 1.0. The study area was equal to 19 65 × 65 km squares. Therefore the sum of the weighted abundances (for each size of *E. pacifica*) was divided by 19, providing a mean standardized abundance for the area for the given survey. (The night stations were not at the same localities on each cruise, though tracks followed by the vessels were generally repeated. Furthermore, as is to be expected, clusters of day stations tend to alternate with clusters of night stations. Unsampled parts of the area are expected to be better represented by samples from stations nearest to that unsampled part than by samples from more distant localities.)

Females were classified as 1) with ripe eggs

(Mauchline's [1968] egg phase IV) and with attached spermatophore, 2) with ripe eggs and no spermatophore, 3) with ripening eggs (approx. Mauchline's phase II), or 4) ovary weakly developed. Adult males were categorized as 1) with ripe spermatophores, either protruding or internal, or 2) without ripe spermatophores.

Biomass was calculated using abundance at each body length (1-mm increment). Values are in terms of wet displacement volume (wet weight) of *E. pacifica*, given per body length increment in Miller (1966). The following conversion factors from Lasker (1966) may be applied:

Dry weight	= 17.2% of wet weight
Carbon	= 42 ± 1.7% of dry weight
Carbon	= 7.2% of wet weight

RESULTS

Southern California Eddy in Relation to the Rest of the California Current

October 1955 data (cruise 5510) illustrated characteristics of flow and temperature in the current, and occurrences of *E. pacifica* larvae (Figure 1a-c). These were general to fall-winter 1953-56 and placed the southern California area in broader geographical perspective. At that time the landward portion of the current, slow and cool, supported five centers of recruitment of *E. pacifica* (Figure 1c): 1) off San Francisco, probably related to the September peak off Oregon observed by Smiles and Pearcy (1971), 2) north of Point Conception, 3) southern California, 4) Point Colnett (lat. 31°N), and 5) Point Canoa (lat. 29°N). The three centers off California were then associated with current reversals while the two centers off Baja California were places where upwelling was conspicuous. A Punta Eugenia center, farther south (lat. 27°-28°N), usually supports *E. pacifica* earlier, during the local peak of spring coastal upwelling, May-June.

Direction and intensity of coastal flow tends to vary on a seasonal basis. During cruise 5510 and through ensuing fall and winter months, coastal currents off California provided means of northerly transport for portions of southern populations. During spring and summer, intensified southerly currents off northern California are expected to bring elements of the northern population into the southern California area via the offshore route west of Point Conception, diverting shoreward near lat. 32°N.

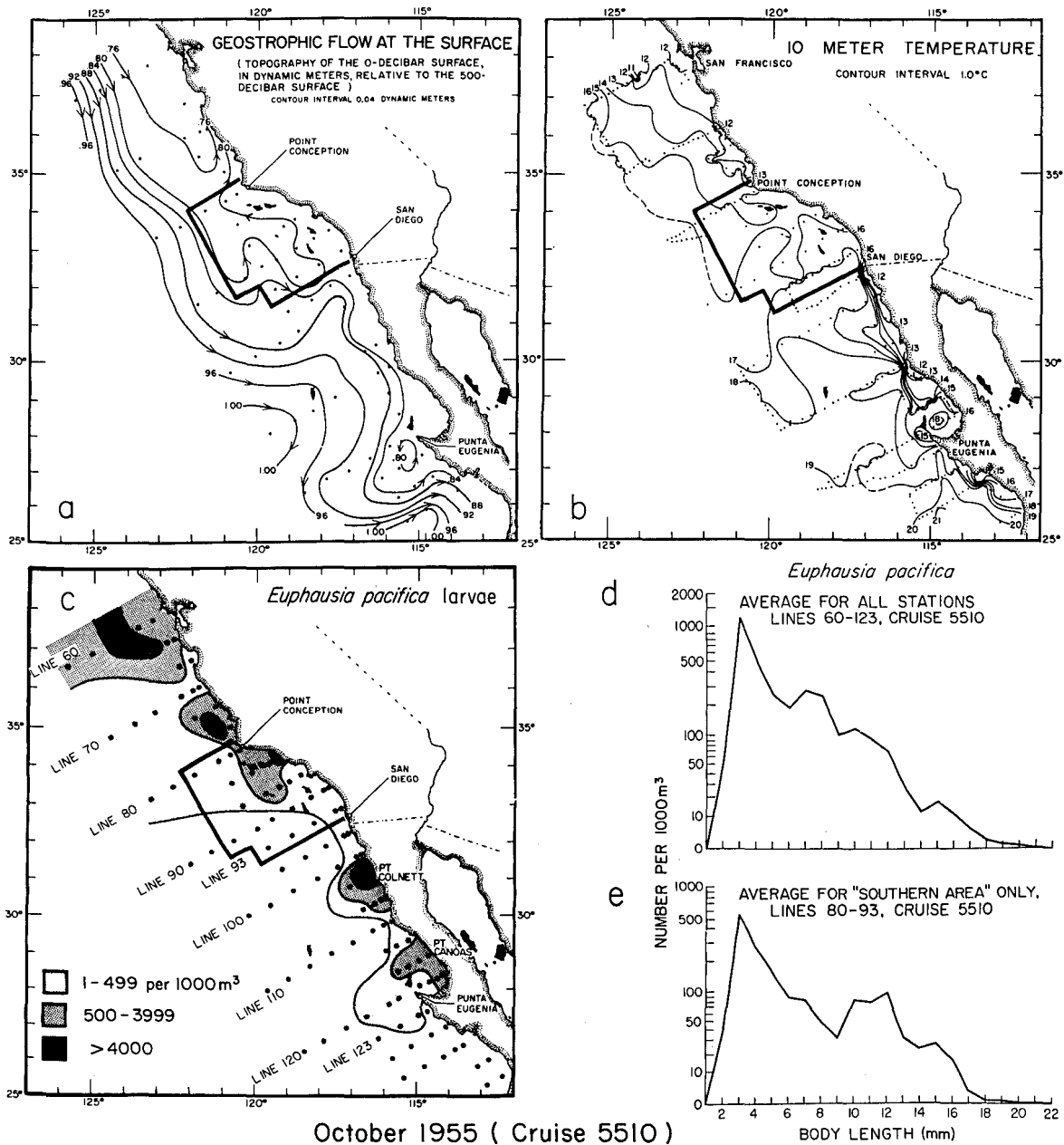


FIGURE 1.—October 1955 data (cruise 5510). a, Surface streamlines showing areas of current reversals off California and b, 10-m temperatures indicating upwelling centers along Baja California, both associated with c, aggregations of *Euphausia pacifica* larvae. Length-frequency distributions of *E. pacifica* are averages for d, all nighttime stations and e, stations within southern California area.

The length-frequency (L-F) diagram for *E. pacifica* in the California Current as a whole (cruise 5510) shows four modes present in the overall population: 3-4 mm (larvae), 7-8 mm, 10-12 mm, and 15-16 mm (Figure 1d). Time progressions in such modes are used below to estimate popula-

tion development, including growth and mortality. The southern California part of the population is characterized by small (10-12 mm) and large adults (15-16 mm). It will be shown below that each of these two October 1955 modes is distinguishable within a month-to-month L-F sequence of cohort

development; the 10-12 mm group, most characteristic of the southern California area in Figure 1e, was of a cohort which remained locally dominant from its inception in July 1955 until January 1956.

The 7-8, 9-12, and 15-16 mm modes are described below as being common to *E. pacifica* because they are at body lengths at which life-phase changes and growth slows; therefore frequencies of those sizes increase, particularly during fall-winter periods of reduced food supply.

L-F curves for individual stations show the clear 7-8 mm mode along an "offshore" north-south track (Figure 2a, c) in the axis of the fastest part of the current (Figure 1a). It dominates the 9-10 mm mode as the transect, following the steamlines, angles shoreward along the southern edge of the southern California area, until lat. 35.5°N (station 97.50) where the 7-8 mm mode becomes inconspicuous and the 9-10 mm mode assumes dominance. Thus offshore, where southerly population transport would be expected on the basis of the observed current, dissipation of the L-F characteristic of the northern population takes place along the western limit of the study area. This is considered evidence that such transport then contributed little to the area's population, relative to more nearshore, local contributions.

Individual stations along a "nearshore" north-south transect (Figure 2b) showed a dense heterogeneous population of *E. pacifica* off San Francisco (station 63.55, lat. 37°N). Off central California (stations 70.55, 77.55), 7-8 mm juveniles became conspicuous (cf. Figure 3). Farther south, particularly in the southern California area (stations 83.51-90.28), 7-10 mm individuals were much reduced in numbers, while the frequency of the 11-12 mm size increased, appearing as a clear L-F mode. In October, larvae were few off northernmost Baja California where oceanic water typically moves eastward compressing shoreward the faunistic connection of the southern California area to more southern upwelling centers. To the south along the Mexican coast, the 11-12 mm mode characteristic of the study area reappeared, coincident with areas of production of larvae. Farthest south (off Punta Eugenia; stations 120.45, 123.40), modes were at 9-10 mm and at 3-mm larvae. These 9-10 mm specimens may be poorly nourished individuals, corresponding in age to 11-12 mm individuals occupying the area immediately to the north—an area which appears relatively fertile with respect to production of larvae. The same

relationship was observed locally off northernmost Baja California; there the population having a 9-10 mm mode included few larvae (Figure 1c) and occupied an easterly incursion of oceanic water (Figure 1a), being bounded on the north and south by cooler and presumably more fertile areas in which both 11-12 mm and larval modes were again conspicuous.

At this time (October 1955) the range of *E. pacifica* terminated near Punta Eugenia, but it can extend to lat. 23°S (Brinton 1967b). These far downstream parts of the population appear reproductive, but to the south of southern California they are impermanent (Brinton 1967b, 1973). Mature or maturing individuals are expected to be intermittently injected from the north, particularly during the March-June period when southerly flow is intensified. These individuals may find local places of refuge in cool, slowly moving, productive coastal waters from Point Conception southward in association with upwelling centers. The southern California eddy is the largest such refuge, serving also as a major population center which has both coastal and oceanic dimensions.

Spawning and Recruitment

Spawning intensity was estimated indirectly since free-floating eggs were not sampled. Females bearing ripe eggs provided a means of estimating incipient spawning. All females having an attached spermatophore also carried ripe eggs in the ovary. From the several thousands of these counted, 373 of different body lengths were examined with respect to number of ripe eggs carried. The relationship between body length and mean number of ripe eggs was linear between 11 and 20 mm length (means were encompassed by 95% confidence limits of regression line), with the mean number of eggs extending from 20 to 212 across this range (Figure 3). Disproportionately small numbers of eggs were observed in the largest (>20 mm) females. Mean values for each body length were applied to the numbers of each length of ripe female counted in the plankton samples to estimate the spawning potential for each sampling period. These are underestimates since, for 60% of the surveys, the predicted values are not high enough to have produced the density of larvae found at the time of the next survey—even presuming only 50% mortality between surveys (Figure 4c). Evidently some eggs

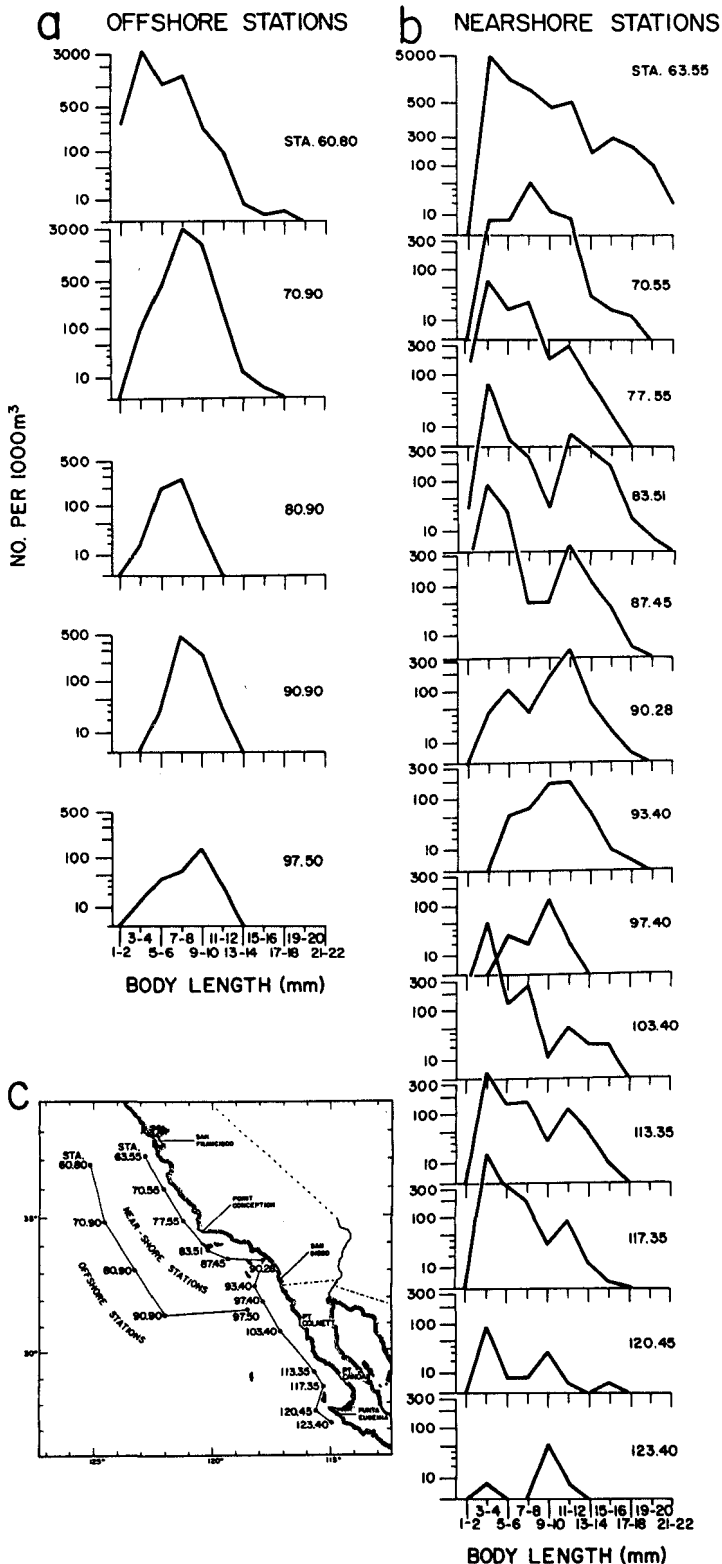


FIGURE 2.—Length-frequency distribution of *Euphausia pacifica* along north-south axes of California Current (cruise 5510). a, Approximately 250 km offshore; b, <100 km offshore; c, positions of stations.

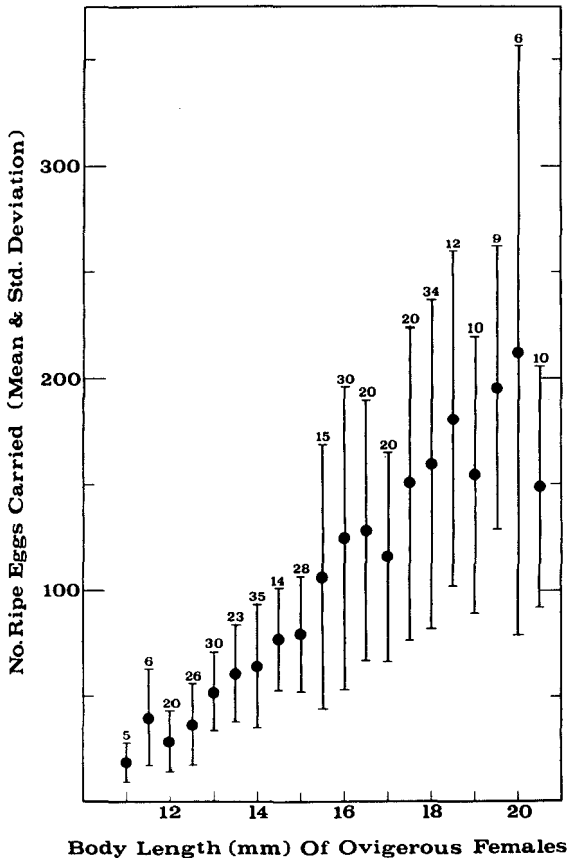


FIGURE 3.—Number of mature eggs in ripe spermatophore-bearing *Euphausia pacifica* in relation to body length. Numbers of individuals examined are indicated.

found to be immature at time of counting, either in ripe or other females, mature in time to contribute to the monthly spawn. The egg estimates are therefore regarded as only relative, month to month.

The production of eggs and larvae in each year (Figure 4c) was considered in relation to four parameters: 1) annual upwelling cycle in the southern California area inferred from atmospheric parameters (Figure 4a) and from minimum water temperatures (Figure 4b), 2) size structure of the spawning stock (Figure 4d), 3) zooplankton biomass (Figure 5a), and 4) *E. pacifica* biomass (Figure 5b).

1953

Upwelling began early (February, cruise 5302) with above-average intensity, accompanied by spawning in February and April. The February

spawn, mainly by females of medium length (12.6-16.5 mm), led to discernable recruitment of larvae in March. The April spawn, mainly by large females (16.6-21.5 mm) led to the year's maximum recruitment in May-June. Upwelling peaked in June, and diminished to an unseasonably low intensity thereafter (Figure 4a), accompanied by local variability in water temperature through October (Figure 4b).

Substantial egg production during June-August, by medium-sized and small (10.6-12.5 mm) spawners, led to less recruitment than in April when spawning was of similar intensity. April was the start of the general spring zooplankton bloom (Figure 5a), presumably a response to the greater availability of phytoplankton food in the spring. Spawning diminished after August although larvae were evident in September and November. Small females became predominant after September when they became important contributors to the production of eggs.

These estimates of relative spawning are supported by a consistent relationship of egg peaks to larva peaks. Three of the four egg peaks in 1953 were followed by larva peaks a month later. Under conditions of laboratory hatching and rearing, euphausiids live as larvae for about 29 days (Gopalakrishnan 1973).

1954

Upwelling commenced in March (Figure 4a), a month later than in 1953. Local temperature minima, however, showed that this process was not obvious until April (Figure 4b). By both criteria, spring upwelling in 1954 was the least intense to be observed during 1953-56. (According to Bakun (1973), it was the least observed during 1953-71, though substantially greater than during 1947-52.) Production of eggs was initiated in March, evidently by a stock of large females derived from the September 1953 recruitment (see sections on growth and survival below, and Figure 9). Recruitment became intense only during June-July, associated with the one peak in spawning observed during 1954.

1955

As in 1954, upwelling started in March (following Bakun 1973, Figure 4a) or in April (using temperature minima, Figure 4b). There was a gradual increase in egg production begin-

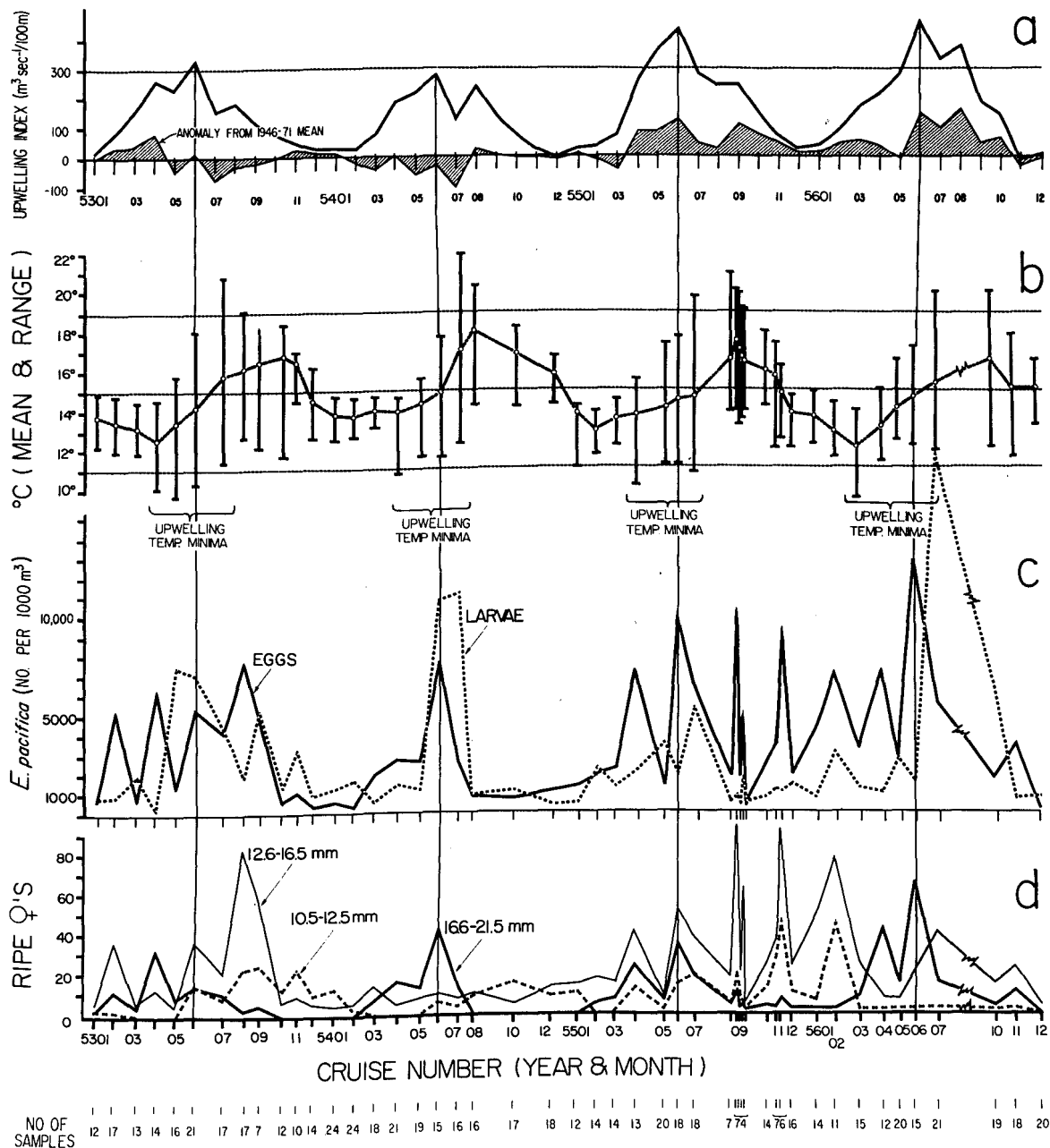


FIGURE 4.—a, Inferred monthly index of upwelling intensity per 100 m of southern California coastline, 1953-56 (from Bakun 1973). b, Temperature range and mean, by cruise, in study area. c, Estimated densities of ripe eggs and <4.5 mm larvae of *Euphausia pacifica* in area. d, Densities of ripe females, three body-length groups. Number of samples examined are indicated by cruise.

ning in December 1954, and the first significant recruitment was in February (cruise 5502). This increase in spawning continued through March, but recruitment did not increase markedly until May, following an April egg maximum. Thereafter

egg production peaked in alternate months, June (the annual upwelling maximum), September, and November—but recruitment was generally low (<2,500 larvae/1,000 m³ in the area) except during May and July. July yielded the year's peak in

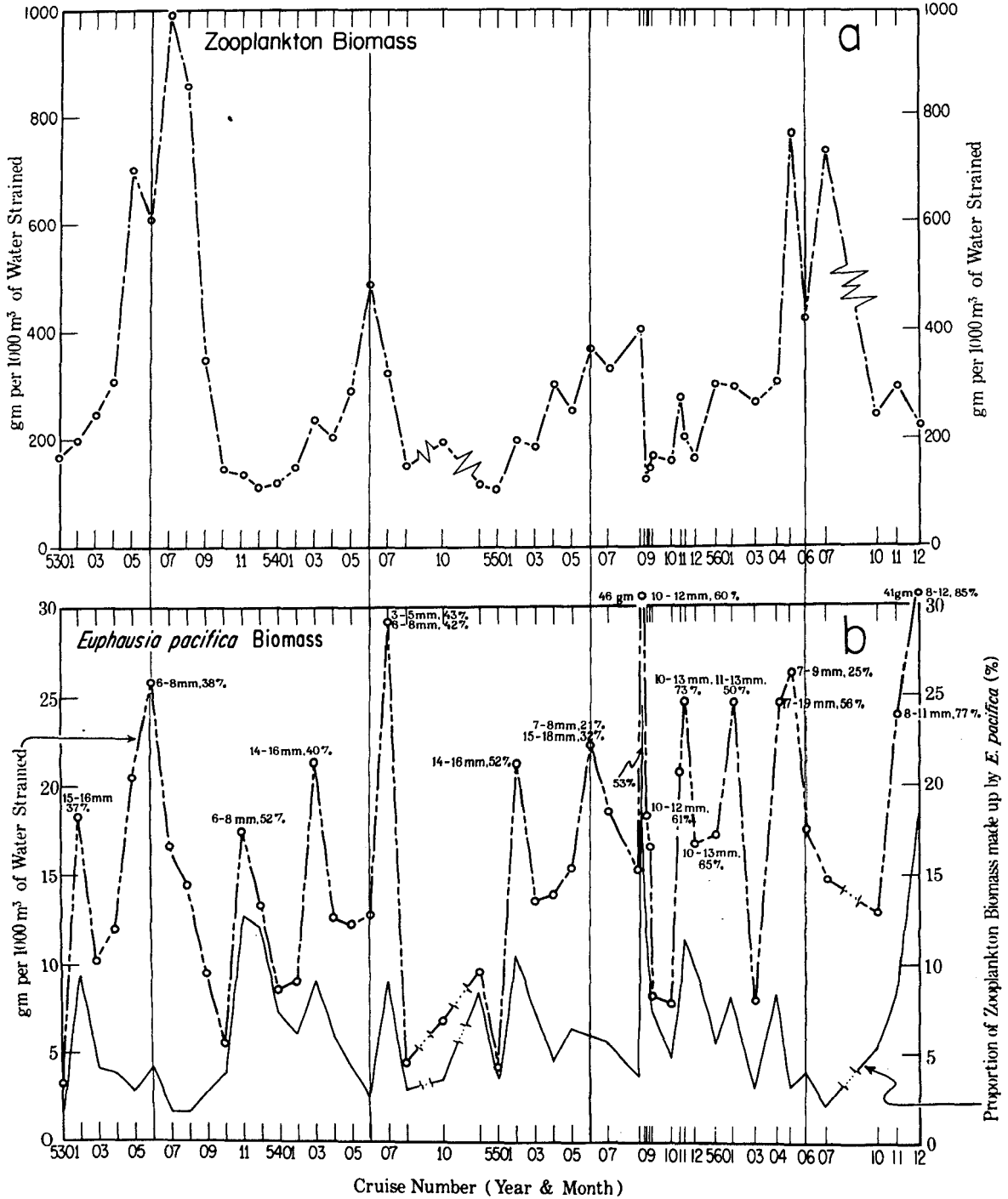


FIGURE 5.—Mean biomass, by cruise, of a, zooplankton in southern California area, based on same samples examined for euphausiids; and b, biomass of *Euphausia pacifica* and its proportion of zooplankton biomass, with dominant body lengths indicated.

larvae. Large and medium-sized spawners were substantial contributors to this recruitment. The latter were predominant and continued to be throughout 1955. This differed from 1953, 1954, and 1956 when small or large spawners were predominant during at least part of the year.

In September a brief increase in larvae closely followed the year's peak in potential egg production, as observed during four September cruises closely spaced in time. This was at the time of maximum water temperatures (Figure 4b). The November peak in eggs, to which small spawning females contributed importantly for the only time in 1955, led to a slight increase in recruitment in December. This November activity was associated with residual upwelling that was significantly more intense than the 20-yr November mean.

1956

Upwelling began early in February as in 1953. February spawning was also high, as in 1953 and differing from 1954-55. Spawners were small and medium-sized females (Figure 4d). Larvae peaked during the same month. Following a March decline in eggs and larvae, April spawning returned to the February level associated with the usual spring appearance of large spawners. This egg maximum was followed in May by a small peak in larvae. In June, egg production reached a peak for the 4-yr period (13,000 eggs/1,000 m³) at the same time as a 4-yr peak in the upwelling index which, however, was not confirmed by the observed temperature minima (Figure 4a, b). In July 1956, larvae showed strong survival from the June spawn with a density of 17,000/1,000 m³. While the upwelling index continued to be well above average through August, CalCOFI sampling did not resume until October. Therefore, August-September recruitment was not recorded. High numbers of larvae observed from 28 September to 5 October (5,000/1,000 m³) together with record numbers of 8-11 mm juveniles appearing in November-December (Figure 10) indicated that August-September spawning was heavy and greater than the substantial August-September spawn of 1953.

An increase in egg production in November 1956 resulted in little recruitment in December, after upwelling had stopped. An explanation may be inferred from the fact that, though zooplankton biomass had peaked earlier (May-July, 5505-07), the euphausiid part of the biomass became extremely high (24-41 g/1,000 m³) only in

November-December, consisting largely of 8-12 mm juveniles and young adults (Figure 5b). *Euphausia pacifica* then made up a larger proportion than ever before of the total biomass (15-20%), indicating a diminished amount of organisms of other taxa, such as salps and copepods. These, like larval euphausiids, depend heavily upon primary production for food. Their reduced numbers suggest diminished phytoplankton food (unless their mortality was not food related), hence the poor December survival of *E. pacifica* larvae emerging from the November spawn. Additional evidence of diminished food in November-December will be seen in the negligible rate of growth during November-December of the massive population of 8-12 mm *E. pacifica*. Alternatively, this population may have consumed the November larvae as well as their food, but this presumption is not supported by its low growth rate.

Recruitment Efficiency and Spatial Aggregation of Eggs

The relationship of spawning potential (density of ripe eggs) to larvae subsequently recruited is irregular, although a trend (Figure 6) indicated that efficiency of recruitment from available eggs was better during spring and summer (March-September) than during fall and winter (October-February). In 1953 the spring-summer peaks in

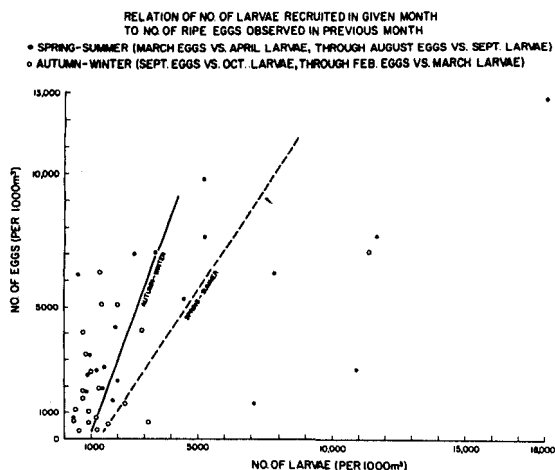


FIGURE 6.—Density of <4.5 mm *Euphausia pacifica* larvae in given month in relation to ripe unspawned eggs observed previous month, 1953-56 data. Regressions (Bartlett's test) for spring-summer (March-September) and autumn-winter (October-February) data are not significantly different.

egg production were followed by proportionately high peaks in larvae, relative to 1955 and early 1956 (January-April) (Figure 4c). Both the one peak in eggs in 1954 (June) and the highest peak in 1956 (June) led to particularly heavy recruitment.

Incipient spawners and larvae were both unevenly distributed in the study area, the larvae usually more patchy than the spawners (Brinton and Wyllie in press). A possible effect of relative aggregation of spawners on recruitment was considered. A monthly index of survival of newly hatched larvae was determined as the ratio of the mean density of larvae observed on a given cruise to the density of ripe eggs calculated for the previous month—usually one cruise earlier. (As noted above, this ratio is >1.0 in about one-third of the instances, indicating that spawning is underestimated. The indices are, therefore, regarded only as relative to each other.) Cruise-to-cruise differences in patchiness of spawners were estimated by comparing, among cruises, variances of number of ripe eggs carried by incipient spawners. Each variance was derived by use of numbers from all stations of a cruise. The regression of patchiness in relation to survival of calyptopis larvae showed a slope not significantly different from zero (Figure 7). Evidently, differences in the degree of aggregation of spawners on the scale observed (32-64 km between stations) did not affect survival of newly hatched larvae.

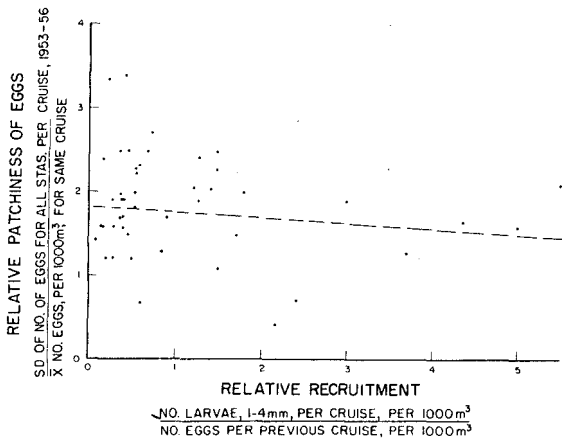


FIGURE 7.—Index of patchiness of ripe unspawned eggs of *Euphausia pacifica* in relation to index of recruitment during succeeding month. Slope of regression not significantly different from 0 ($P > 0.05$, t -test). Standard deviation is used as a measure of dispersion and in no way assumes normality of the data.

Temperature Relationships of Spawners and Larvae

Abundances of spawners and recently hatched larvae (calyptopes of <2.5 mm) were plotted in relation to ambient temperature at 10 m depth (Figure 8). A relationship of spring-summer upwelling to maxima in reproduction, however indirect, was evident in foregoing observations. Therefore, data for the months of strong upwelling (April-July) are separated from those of the other months.

Both spawners and larvae occurred across a range 10°-21.6°C, virtually the available range. When lumped by 0.5°C increments, close to 40% of the stations yielded some calyptopis larvae and 40% yielded incipient spawners. During August-March (Figure 10a) larvae were most concentrated within the range of 12°-16.5°C, the same as the spawners. There, mean densities of larvae were 50-200/1,000 m³. During April-July (Figure 8b), maximum densities of larvae, 200-7,000/1,000 m³,

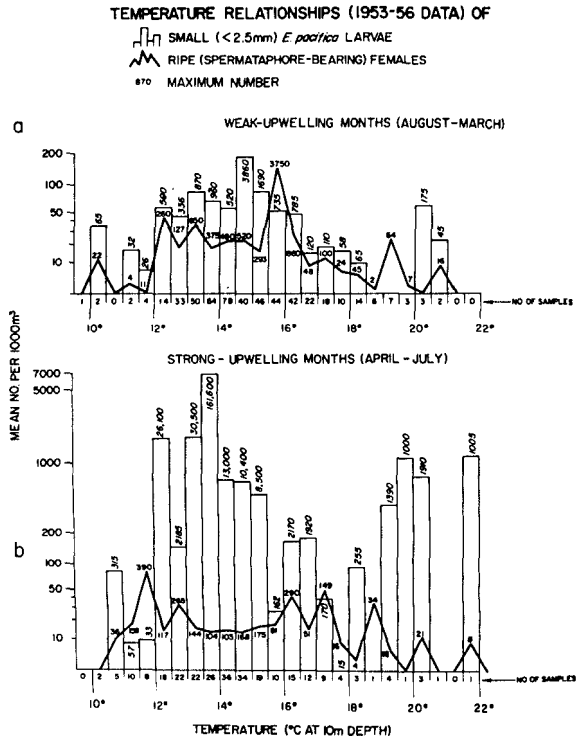


FIGURE 8.—Densities of *Euphausia pacifica* larvae <2.5 mm length and ripe females in relation to water temperature at 10 m depth. a, August-March; b, April-July.

were within a somewhat narrow range of temperature, 12°-15.5°C, as compared with the weak-upwelling period, and most spawners were within a broader range, 11.5°-17.5°C.

By years, during 1953, 1955, and 1956 the mean maxima of larvae were at 14°-15°C. In 1954 there were maxima at both 13°-14°C and 14.5°-16°C. Occurrences of larvae and spawners at temperatures >18.5°C during January-March and August-December were only during 1955, the year in which spawning extended on into September and November. Occurrences of April-July larvae at temperatures >18°C were all during 1954, the year of weakest upwelling, except for a single record in 1953.

Overall frequency of spawners did not differ between the periods of strong and weak upwelling, in contrast to large differences in the frequency of recruits. This implies that factors other than temperature are important to recruitment—probably the production of food associated with the upwelling period. Patchy local increases in surface nutrients associated with the upwelling season of 1969 are described in the Discussion.

It is also noteworthy that during periods of both strong and weak upwelling, mean maxima of spawners occurred at or just outside the limits of the optimal temperature range for recruits: during weak upwelling months, at 12°-12.5°C and 15.5°-16°C; and during strong upwelling months, at 11.5°-12°C and 17°-17.5°C. This implies that stations showing maximum densities of larvae and those showing maxima of spawners were mutually exclusive—an impression gained earlier during counting. Removal of adults from the region where they might fortuitously feed upon their young could be brought about by the vertical migration of the adults and their consequent differential transport at greater daytime depths, in accordance with the hypothesis of Hardy (1956).

Growth

Monthly L-F polygons for *E. pacifica* consistently peak at larvae 3-4 mm in length (Figures 9, 10). In the stream of continuous recruitment, a month-class is first distinguishable as high numbers of larvae relative to those produced in the months before and after. Subsequent growth can be traced through successive months as an L-F mode, either in the form of a crest, irregularity in slope, or change in height relative to the month

before. Observations of growth and survival appear most reliable when cohorts are traced that begin as densities in excess of 2,000 larvae per 1 mm length increment per 1,000 m³.

A cohort is designated by the year-month (e.g., 5303) in which its larva maximum is observed. Presumed relationships of egg maxima (Figure 4c) to subsequent recruitment are indicated in Figure 12.

When presented in terms of biomass (Figures 9, 10), population composition differs from that indicated by length frequency. For example, biomass modes may increase in height with time owing to growth, while corresponding L-F modes decrease in height because of mortality. As a consequence, cohorts are often more conspicuous when plotted as biomass. Biomass is plotted on a linear scale while abundances (length frequency) were plotted on a logarithmic scale to accommodate fluctuations in the many larvae and the few large adults. The biomass of larvae was generally low but periods of heavy recruitment are conspicuous.

1953 Cohorts

A small February 1953 cohort (Figures 9, 12) was tentatively traced through April as 10-11 mm adolescents. More substantial recruitment occurred in March from the February egg maximum, followed by little recruitment in April; growth appears to have been to 7-8 mm in April, 10 mm in May, 13 mm in June, 15-17 mm in July, 18 mm in August, and 18-19 mm in September.

Production of larvae first became intense during May-July 1953 (cruises 5305-5307), resulting in a broad mode recognizable as 3-7 mm in June (enclosed by a pair of dashed lines in Figure 11, one originating at 3 mm in May and the other at 3 mm in June). July larvae appeared to show poor survival, as shown in the reduced 5-7 mm component of the population in August. This is interpreted as leading to graphic separation of the May-June cohort as a conspicuous L-F mode, first observed in August (5308) as 8-13 mm juveniles and young adults (Figures 9, 11a), persisting into September at 12-15 mm, and perhaps surviving without growth into October, though decimated. Development of this cohort is even more conspicuous through the sequence of biomass modes.

An increase in recruitment in September (5309) over August, followed by low production in October, yielded a particularly conspicuous cohort

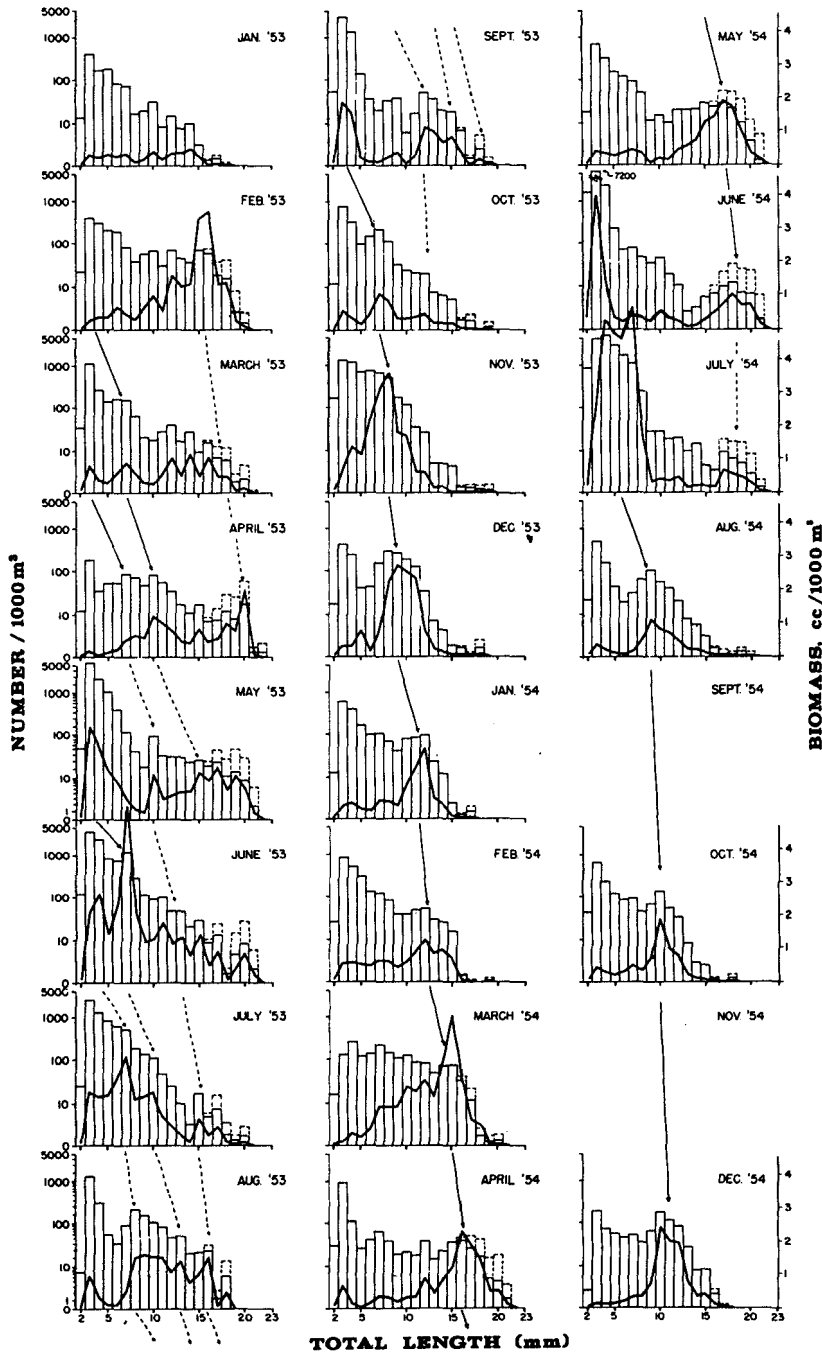


FIGURE 9.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1953-54 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

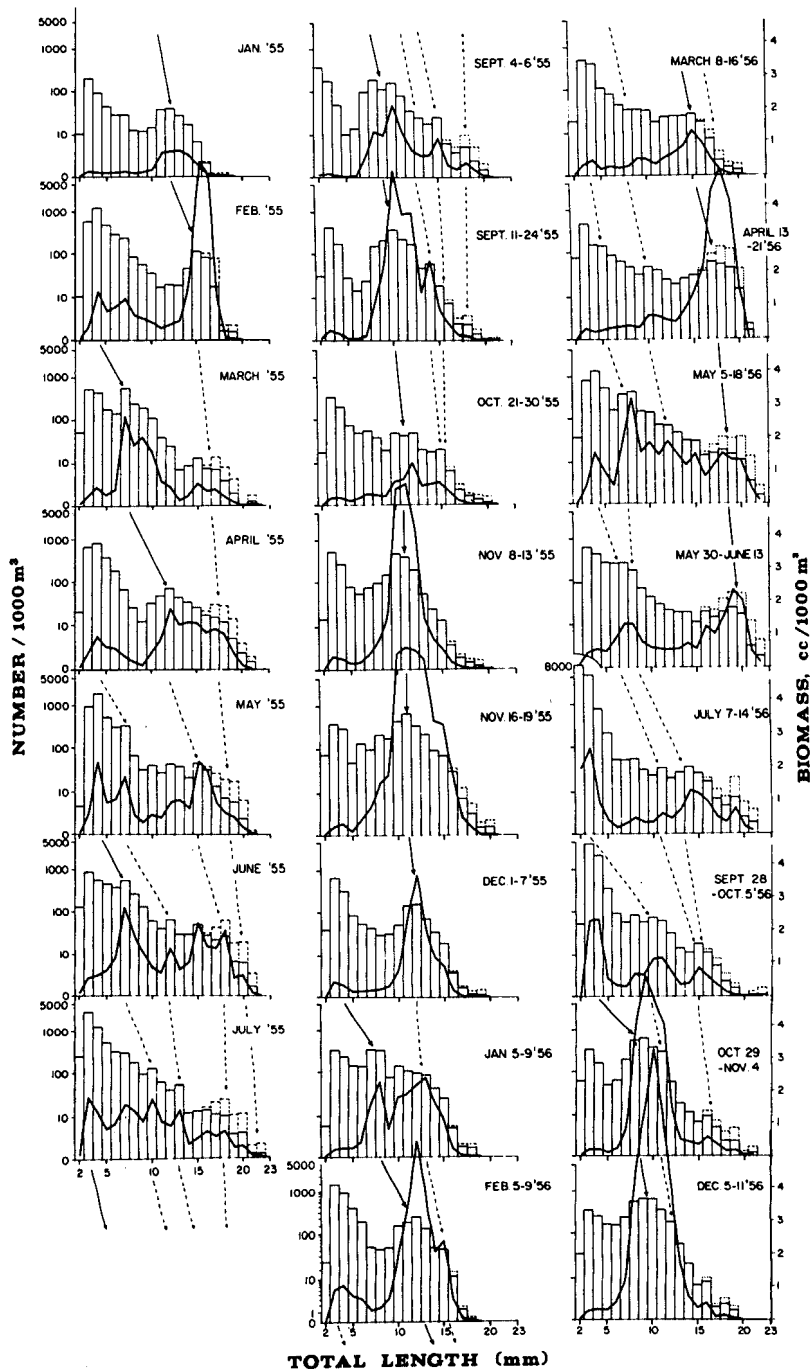


FIGURE 10.—Length-frequency (histograms) and biomass (line graphs) distributions, of *Euphausia pacifica*, 1955-56 cruises. Dotted boxes appended to histograms for body lengths 16-21 mm are corrections for net avoidance using Isaacs' (1965) factors derived for anchovy larvae of those sizes. Corrections are not applied to biomass. Arrows trace development of cohorts. Solid arrows trace sequences considered clear, dashed arrows trace those less clear.

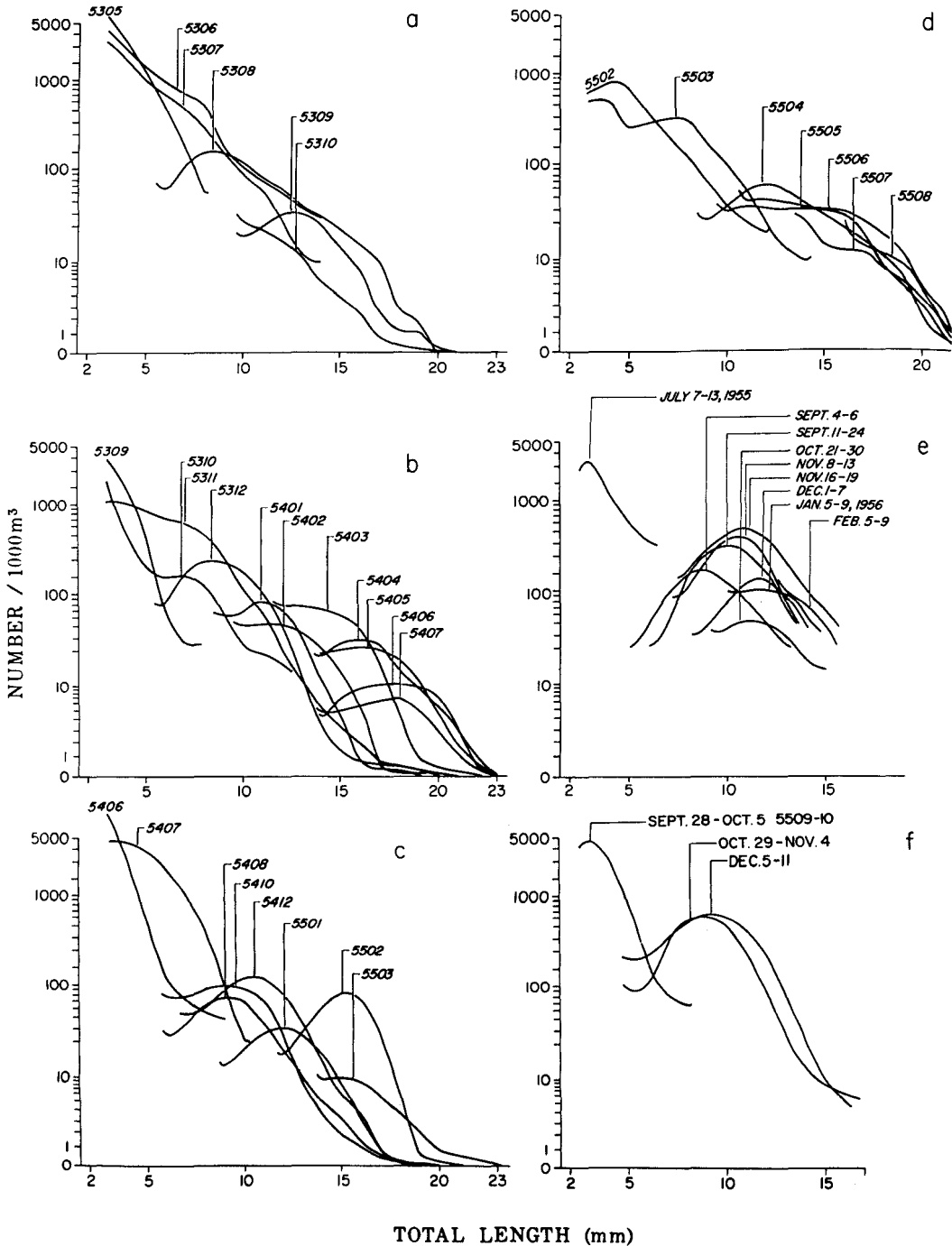


FIGURE 11.—Cohort development of *Euphausia pacifica*, shown as progressions of length-frequency modes. Curves are three-point running averages of portions of histograms in Figures 9 and 10. Cohort is identified by date (cruise) at appearance of conspicuous mode of 2-3 mm larvae. a, 5305; b, 5309; c, 5406; d, 5502; e, 5505; f, 5509-10.

traceable for 10 mo through July 1954 (5407) when it had achieved large-adult size, 17-20 mm (Figures 9, 11b, 12). Separate L-F curves for males and females (Figure 13), commencing at the onset of maturity ca. 11 mm, show that the modes for the 5309 cohort illustrated in Figures 9 and 11b actually are made up of paired overlapping peaks, for females regularly at a larger body-length increment by about 1 mm and for males where the difference in absolute frequency between males and females is greatest.

It is not likely that females, upon maturity, have undergone sudden, relatively rapid growth so as to exceed males in size. The curves (Figure 13) show larger females to be at a relatively greater frequency than males and the converse would be expected with increased female growth-rate. (Average male/female ratio is probably 1:1 at onset of adulthood, discussed under Sex Ratio.) Rather, the most mature females—those at the leading edge of the mode-cohort at the onset of February-March breeding—are growing slower than before, thereby appearing more numerous. At the same time, decreasing relative male survivorship could contribute to the increasing inequality in sex ratio. At body lengths >16 mm, females tend to dominate by 2:1 or more, indicating that they then spend twice as long as males at given sizes, at least while breeding, or that their survivorship is then greater, or that males remain below sampling depths at night. These alternatives are considered in the discussion of Sex Ratio, below.

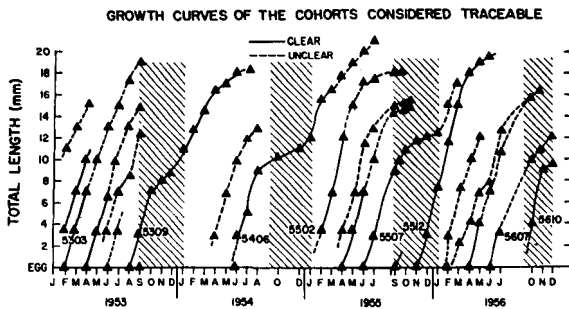


FIGURE 12.—Growth curves of *Euphausia pacifica* inferred from length-frequency modes. Clear (solid lines) and unclear (dashed lines) sequences as in Figures 9 and 10. Times of egg production are extrapolated, see Figure 4c. Fall-winter period of slowed growth is crosshatched.

1954 Cohorts

The single intense spawn of 1954 (June) led to strong June-July recruitment, establishing a

cohort (5406) that was followed through a 10-mo period to 17-19 mm in April 1955 and, with less certainty, to 20 mm in June (Figures 9, 10, 11c, 13).

1955 Cohorts

Conspicuous 1955 cohorts arose in February (5502) and July (5507). The former appeared to attain 18 mm after 7 mo (September) and the latter reached 17-18 mm after 8 mo, following slowed growth during October-January (Figures 11d-e, 12). This cohort appeared at too-low density in October (5510) relative to a month later. This may be due either to sampling variability or to "piling up" at the 11-12 mm increment in November owing to growth being faster into the newly adult phase than out of it, energy then being diverted to gonad development. Nevertheless, it is noteworthy that the 5502 and 5507 cohorts appeared to be distinguishable in October (5510) as modes of 10-12 mm and 15-16 mm, Figure 1e, discussed earlier when the southern California area was compared with the California Current as a whole.

The December 1955 cohort was the only distinct year-end cohort observed during 1953-56 (Figures 10, 12, 13). It grew rapidly at 4 to 5 mm/mo during December-February and 3 to 4 mm/mo during February-April, apparently attaining 18 to 20 mm length by June 1956.

1956 Cohorts

These were scarcely traceable except for that appearing as 8-11 mm individuals in early November and as 8-12 mm in December. This mode doubtless derives from extremely dense larvae sampled during 5507 and 5509-10, its crest appearing to relate mainly to the latter. The small biomass peak at 10-11 mm during 29 September-5 October is clearly derived from the very heavy July recruitment. It subsequently becomes indistinguishable during November and December from the biomass of 8-12 mm juvenile-adults considered to have grown from 5509-10 larvae. The 29 October-4 November peak appears most likely to have derived from the 5509-10 larvae.

Survivorship

The average L-F distribution for all samples (Figure 14) shows that decline in density with body length is roughly exponential. The decline is

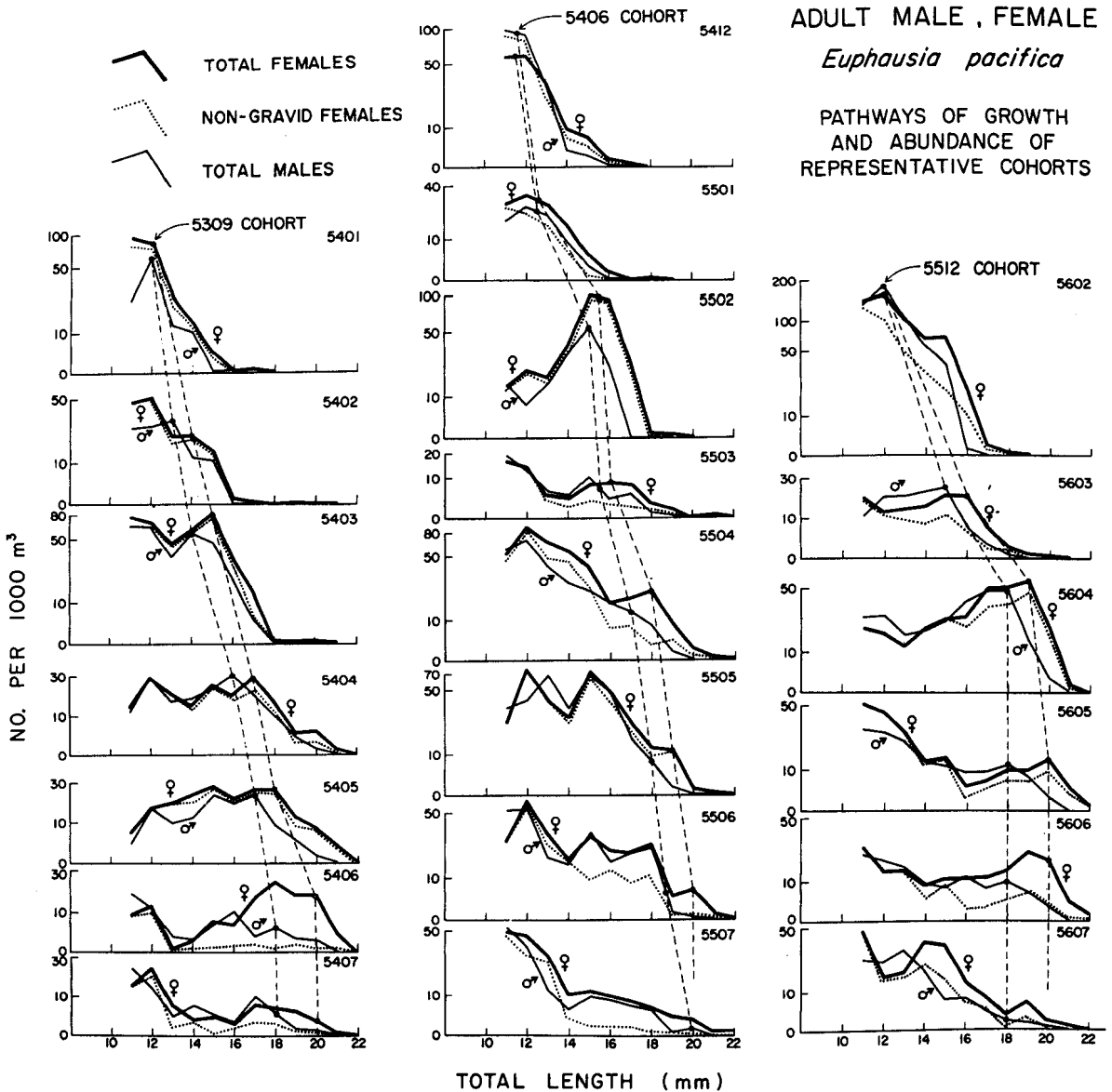


FIGURE 13.—Length-frequencies of adult males and females of *Euphausia pacifica*. Dashed lines trace development in males and females. Frequencies of females without ripe eggs are indicated (pertinent to discussion of Sex Ratio).

rapid during the larval phase and slower thereafter until large adulthood, 18-19 mm. Positive perturbations appear at 6-7 mm, 9-10 mm, and 14-15 mm. Average survivorship is 16% during the 1 mo furcilia larva phase, as seen in the decline in mean population density from 1,850 to 300/1,000 m³ (Figure 14) between 3 mm and about 6 mm in body length which Boden (1950) has shown to be

larval phase. For juveniles, 6 mm through 9 mm, survivorship is near 67%/mo over about 2 mo.

For adolescents and young adults of 9-14 mm, average survivorship remains nearly the same, 64%/mo, then decreasing to 60%/mo through 18 mm. After that, population decline appears rapid, possibly because sampling of such large individuals is not representative. Apparent

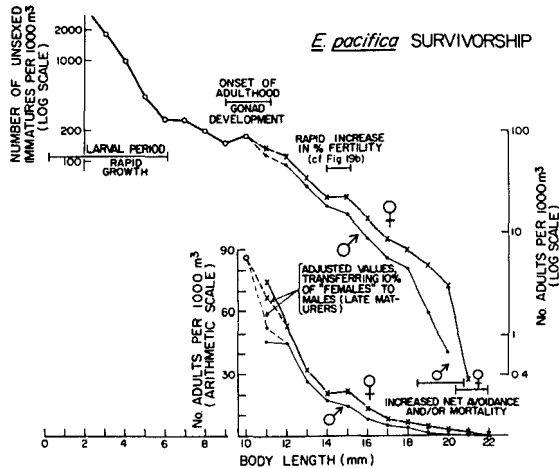


FIGURE 14.—Catch curves for all *Euphausia pacifica* sampled, densities shown on logarithmic and linear (adults only) scales. Periods of changing slope (changing survivorship, net avoidance and/or growth rates) indicated as related to life phases. Scale used for density of sexed adults (right) is doubled for lumped immatures (left).

differences in survivorship between males and females (Figure 14) are discussed below under Sex Ratio.

Survival rates for individual cohorts were approximated from relative amplitudes of month-to-month modes in the sequences used to trace growth (e.g., Figure 11). Percent survivorship plotted against estimated age shows cohort curves to be similar (Figure 15a). A positive change in slope consistently occurs within the range of 8-12 mm body length encompassing adolescence. However, regressions of \log_{10} density on age take two forms:

1) Mean life-span survival rate calculated as a single linear regression for individual cohorts is highest among those recruited during June-December (06-12). For example, it is 51%/mo for the 5512 cohort, 58% for 5610, and 59% for 5309. In such late-year cohorts most of the juvenile-adult phase is during August-March, the period of reduced food and slowed growth. For example, the cohort 5507 attained adolescence (9-10 mm) in September and large adulthood (17 mm) in March (Figure 15b), having an estimated life span of 10 mo. (Egg stage to 3 or 4 mm length is considered the first month.) The cohort 5406 (Figure 15c) attained adolescence at 9 mm in August, appeared to show strong survival through 15-16 mm in February, and was distinguishable at 20 mm size in June—a life span of 13 mo. Thus those cohorts which attained 15-16 mm with densities $>50/1,000$

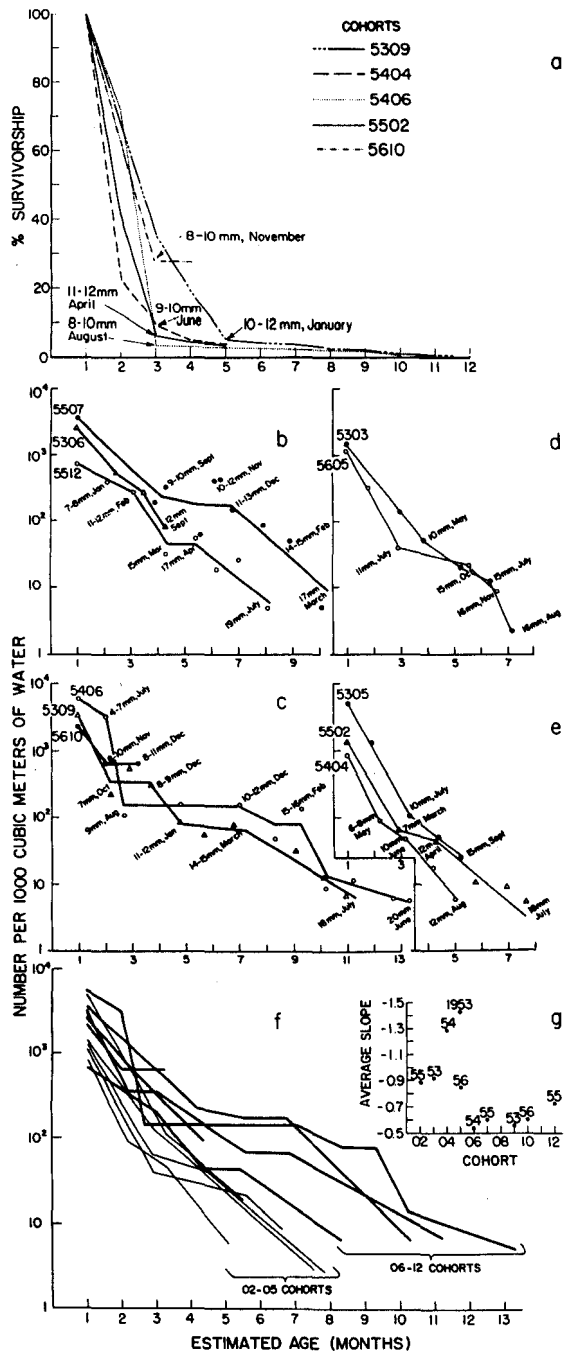


FIGURE 15.—Survivorship of cohorts of *Euphausia pacifica*, from amplitudes of length-frequency modes. a, Percent survivorship showing rapid decline until adolescence, ca. 9-11 mm. b, c, Age-frequency distributions of 06-12 cohorts smoothed for apparent piling up at times of slowed growth. d, e, Age-frequency distributions of 02-05 cohorts. f, Curves seen in b-e, clustered. g, Average slopes (from straight line regressions) for 02-05 cohorts seen as steeper than for 06-12 cohorts.

m³ by February-March continued to be evident on into the spring bloom.

Two exceptionally large cohorts, 5406 and 5507, were initiated during late June-July. At first, these survived poorly, 8-10%/mo for 5406 through August-September and 40%/mo for 5507 through October (Figures 11c, f; 15b, c). Growth apparently then stopped after 9-11 mm body length, and the density had declined to 100/1,000 m³. This took place when the onset of maturity was in September-October. This is presumably the start of the fall-winter period during which food supply is inadequate to permit both gonad development and size increase. During October-December, the 10-12 mm sizes increased in frequency, indicating continuing growth into that range by younger elements of the overall population and much reduced growth out of it. Therefore survivorship of the 5406 and 5507 cohorts during September-December could not be determined, but it appears to have been high. By January, body-length growth of these cohorts, now numerically enhanced, resumed. Survivorship of "5406" prevailed at about 47%/mo through June 1955 (21 mm), and for "5507" at 40%/mo as before September.

The large 5607 and 5610 cohorts appear to have undergone similar development (Figure 10), appearing to coalesce at 9-12 mm during November-December, with much increased frequencies at those body lengths.

2) Survival rate is poorer, 26-45%/mo, for recruits produced earlier in the year, February-June. Mean life-span survival was 43%/mo for the 5303 cohort, 26% for 5305, 37% for 5306, 30% for 5404, 44% for 5502, and 45% for 5605. Nonlinear details of survivorship in these cohorts are depicted in Figure 15d, e, while differences between early-year and late-year cohorts in mean slope of survivorship regressions are seen in Figure 15g. Coincidence of the juvenile-adult phases of early-year cohorts with the productive period May-September evidently accounts for the observed rapid growth during this period, hence the poor survival rate. These cohorts were traced to body lengths of 16-18 mm after 7.5-8 mo (5502, 5303, 5605) or to 13-15 mm after 4-5 mo (5404, 5305). Having declined to densities <10/1,000 m³ during summer-fall, they were no longer recognizable in winter sampling.

Annual Biomass

Annual biomass by body length shows year-to-

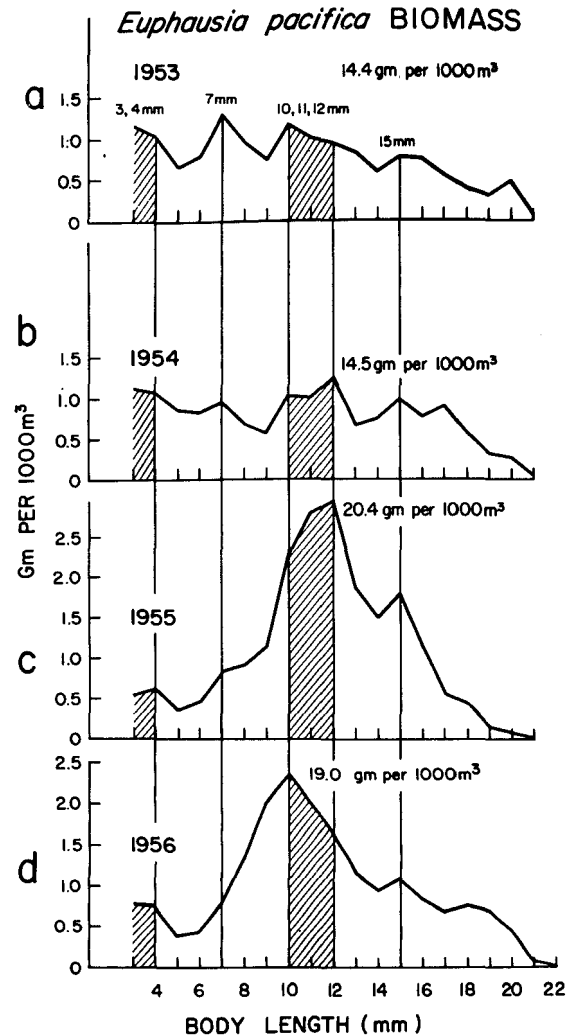


FIGURE 16.—Biomass, annual mean values for *Euphausia pacifica* and distributions per 1 mm body length. a, b, Uniform distributions for 1953, 1954, with modes at 3-4 mm, 7 mm (onset of juvenile phase), 10-12 mm (onset of adulthood) and 15-16 mm (start of maximum egg production, cf. Figure 21b). c, d, Distributions, strongly peaked at adolescence, biased by large 5507 and 5609-10 cohorts respectively.

year similarities (Figure 16). Peaks are at 1) 3-4 mm, owing to consistent abundances of larvae in early furcilia phase; 2) 7 mm (except 1956), the onset of juvenile phase; 3) 10-12 mm (9-11 mm in 1956) the onset of adult phase; and 4) 15 mm, early in the peak reproductive phase. It was noted (Figure 5b) that monthly biomass peaks were usually dominated by one or another of these four body lengths. The larva peak occurs in spite of rapid early growth. The other three peaks are at ages when slowed body-length growth would be

expected: onset of juvenile phase, onset of gonad development, and time of maximum gamete production.

Biomass on body-length distribution was most even during 1953 and 1954 (Figure 16a, b). Recruitment in May and September 1953 led to the 7-mm peak of that year, and the September cohort was the main contributor to the 10-12 mm peak. The 1954 crest at 10-12 mm stemmed mainly from October and December sampling of the June 1954 cohort.

In 1955 and 1956, 3-4 mm larvae were reduced in average biomass compared with 1953 and 1954 while biomass of 9-12 mm adolescents was two times greater. The November 1955 stock of 11-12 mm stages (5507 cohort) was mainly responsible for the 1955 biomass peaks. The November-December 1956 stock of 9-11 mm stages (5609-10 cohort) provided much of the 1956 peak.

Large 18-20 mm adults showed their greatest biomass in 1956 following the strong upwelling year 1955, and lowest in 1955 following least productive year 1954.

Monthly changes in biomass are traced for each of three conspicuous sizes (Figure 17). Small (7 mm) juvenile bulk is greatest within May-July following spring recruitment. Other high values for the 7-mm size are not consistent seasonally, occurring during October-March.

Adolescents (10 mm), considered representative of the 9-12 mm juvenile-adult phase change, tend to be at greatest volume during August-January (when the smallest spawners, 10.6-12.5 mm, were also observed to peak, Figure 4d). Increased survivorship and slowed growth during fall-winter maturation of spring cohorts, discussed above, are considered responsible.

Subsequent February-March peaking of biomass at 15-mm size occurs as egg development accelerates. (This is preliminary to the appearance of the large >16.5 mm spawners during April-June, Figure 4d.)

A close relationship is evident (Figure 17) between biomass of each of the three sizes and their percent of the total *E. pacifica* biomass. This indicates that a given month's increase in biomass of the 7-mm size (or of the 10-mm or 15-mm size) is not accompanied by proportionate increase in the composite biomass of all other sizes. Therefore, the periodic peaks in biomass shown in Figure 5b should be largely due to peaks at these or very similar sizes, which was indeed the case.

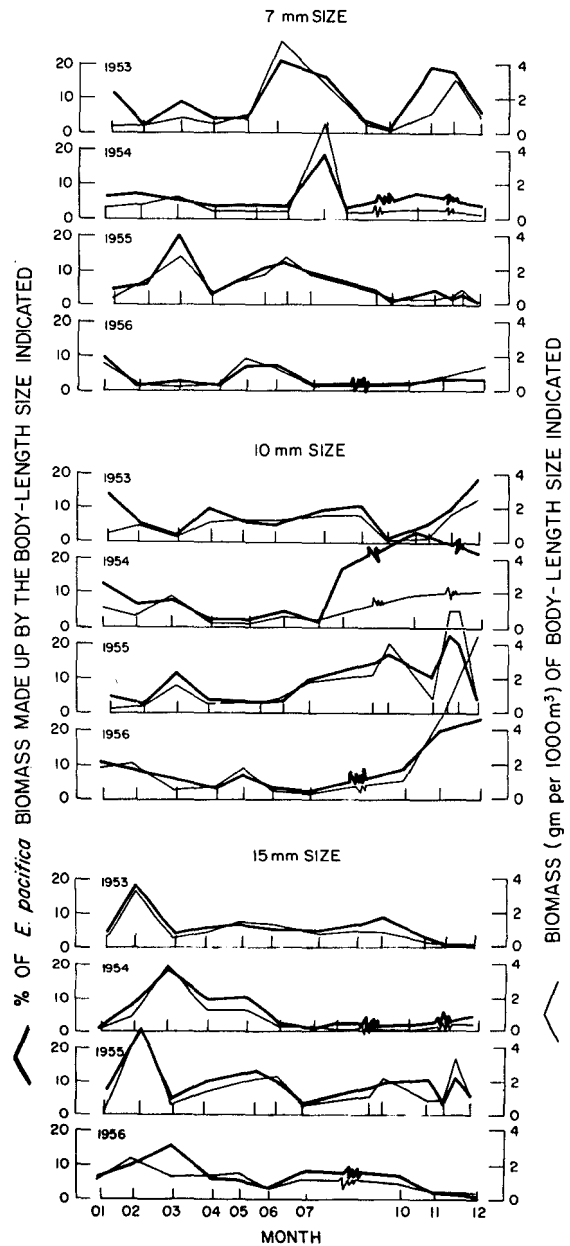


FIGURE 17.—Annual length-biomass modes of *Euphausia pacifica* analyzed by months. The 7-mm size peaks heavily in June-July (May-June in 1956), with other peaks in March and November-January; the 10-mm size peaks September-January; and 15-mm size peaks February or March.

There are variations from this relationship: 1) moderate increase in biomass of 10-mm size during August-December 1954 caused a disproportionately large percent-increase in it—an effect of the single large 1954 cohort (5406-07) developing

unaccompanied by other substantial cohorts (Figure 16b); 2) the converse, when November-December 1955 biomass of 10-mm size (together with 11-12 mm, Figure 16c) increased extremely but the percent increase did not keep pace because of strong survival from extended July-September recruitment, seen as piling up in December across 8-12 mm range.

Rate of growth (body length) was seen, above, to be generally steady (Figure 12). Slowed growth was commonest when adolescence or late adulthood took place during fall-winter. Exceptionally high biomass of 10-12 mm sizes in 1955 and 1956 was attributed to greatly slowed growth of adolescents of large cohorts during November-December of both years.

Regular, less extreme peaking of biomass at the four body lengths just described as prominent may be interpreted in terms of differing survival rates among life phases:

If body-length growth is steady during a given life phase, such as the larval period, biomass growth would proceed as the cube of body length, while population size would be expected to decline exponentially. This inequality leads to a biomass peak at a particular body length which depends on survival rate (Figure 18a). A survival rate of about 24%/mo for the larval phase is found to yield such a peak at 4 mm length in the biomass on body-length distribution, a size at which biomass regularly peaks during *E. pacifica* development.

Other survival rates were extrapolated from a cluster of age-density curves so as to yield biomass peaks which coincide with real average peaks shown in Figure 16: 43%/mo was found to peak at 7 mm, 54%/mo at 10-11 mm, and 66%/mo at 15 mm. A derived age-biomass distribution, linear scale (Figure 18b), is composed of segments based on the above sequence of survival rates. Segments end at 5.8 mm (end of larval phase), 9.3 mm (end of juvenile phase), and 13.2 mm (start of intensive reproduction, after Figure 21b).

The derived distribution is similar in shape to the observed average annual biomass distributions for 1953 and 1954 (Figure 16a, b). (Growth rates of 1953 cohorts were relatively steady, Figure 12. Those of 1954 appeared less steady but were still without the massive November-December pile-ups of adolescents noted in 1955 and 1956.) However, except for the larval period for which the derived and observed mean survival rates (from Figure 14) were both about 23%/mo; other derived rates had to be different from the

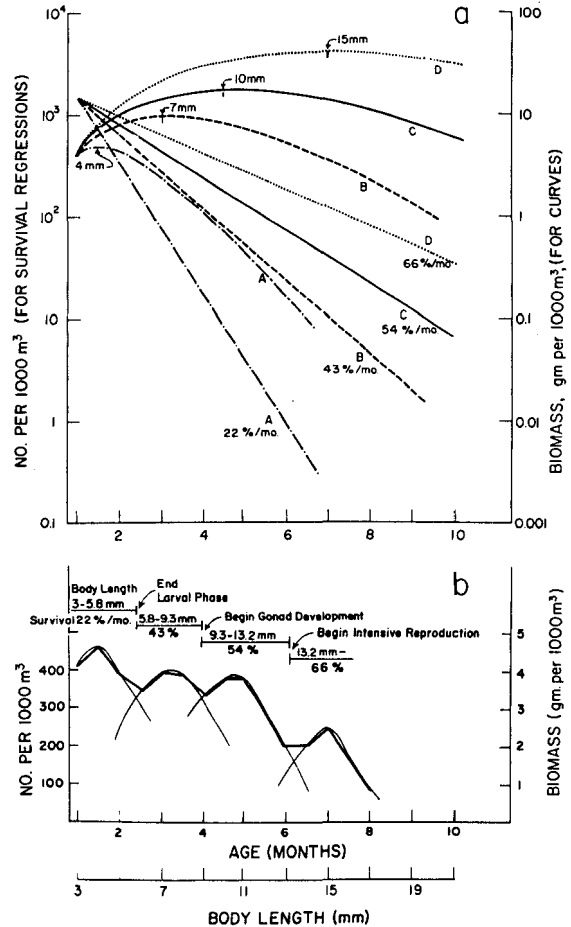


FIGURE 18.—Hypothetical age-frequency and age-biomass distributions of *Euphausia pacifica* assuming uniform body-length growth. a, Constant survivorship at each of four rates, selected to yield biomass peaking at 4, 7, 10, and 15 mm, respectively. b, An approximation of annual length-biomass distributions shown in Figure 17, obtained by changing survivorship at life-phase change.

mean observed rates so as to yield the observed peaks at 7, 10-11, and 15 mm length. These were lower by 24% and 10% for the juvenile and young adult phases respectively, and higher by 6% for the 14-18 mm sizes. This means that after the larval phase observed, mean survivorship decreased phase-to-phase by about 4%/mo, whereas in the derived distribution it increased by 11-12%/mo at phase change. This is attributed to deviations from evenness in real growth rates. However, there is a tendency toward progressively positive inflexion with age in certain of the survivorship curves of individual cohorts (Figure 15b-g).

Sex Ratio

Fifty percent of the estimates of prespawned eggs were two to four times greater than the estimates of larvae in the plankton a month later. The other 50% of egg/larva ratios were even lower than two (Figures 4d, 6). Further evidence that spawning was underestimated is seen in an examination of ratio of the sexes and state of their reproductive products.

The ripe male *E. pacifica* stores two spermatophores in a pair of ducts. The fertilized female possesses a single attached spermatophore (Brinton in press). This discrepancy might be attributed to a sex ratio in which females predominate, or to a need for more than one fertilization when spawning is protracted or intermittent across days, intermolt periods or longer. If such multiple fertilizations take place, males transfer one spermatophore to each of two females, probably quickly because single ripe spermatophores were not observed in males. The paired spermatophores in males were observed always to be of equal size, color, and readiness for extrusion. (Ready spermatophores may be easily expelled with gentle external pressure in the laboratory.) A continuing preponderance of ripe males, as shown in Figure 19, would tend to insure fertilization of females whenever they ripen. Mauchline and Fisher (1969) have explained, with reference to *Meganyctiphanes norvegica*, that fully formed spermatophores may be stored in the ejaculatory ducts for some time.

Here, ripe and unripe females outnumber males by about 1.5 times at 15 mm, and 3 times at 20 mm (See Figure 21a). Ponomareva's (1963) data on *E. pacifica* from the Sea of Japan showed females to be 56% of the adult population, and from the Okhotsk Sea 63% in April, 62% in June-July, and 44% in October. Four factors may contribute to the apparently greater number of females:

- 1) In the present data, apparent dominance by females (all body lengths lumped, Figure 20) is partly due to periods in which the population included late-maturing individuals of 10.5-11.5 mm length, some males of which were as yet without petasmas and were therefore categorized as females. (Secondary sexual characters of *E. pacifica* are usually evident at this size.) For example, this apparently happened during counting of material from cruises 5401 and 5402 (Figure 13), and cruises 5610-12 (Figure 20) when

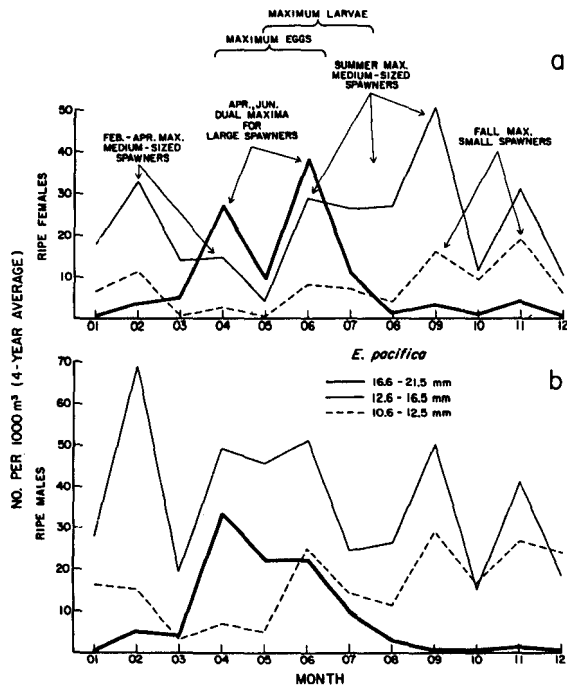


FIGURE 19.—a, Densities of ripe female *Euphausia pacifica* by months, three body-length groups, 1953-56 data combined from Figure 6d. b, Densities of males with ready spermatophores, same body-length groups.

"females" dominated the dense population of 8-12 mm individuals.

- 2) Increasing mortality in males relative to that in females may take place after 12 mm body length. Since the ratio of males to females decreases with body length, multiple fertilizations by males would be increasingly important with increasing size. (Mates are probably of similar size, in view of large spermatophores being attached to large females and small spermatophores to small females.)

- 3) Large males and unripe females may be more underestimated than egg-bearing females if the latter are less able to avoid net capture. For anchovy larvae, Isaacs (1965) hypothesized that avoidance of the 1-m net becomes significant after 15 mm body length. Similar differential avoidance might contribute to the female/male bias here. For 3 of the 4 yr, the average percentage of females that are ripe crested at 15-16 mm (Figure 21b). It remained high, 40-60%, through the larger size groups. The 1954 data differed in that the proportion of ripe/unripe females remained low through 16 mm body length. This is also seen in Figure 4d in which the 12.6-16.5 mm group showed

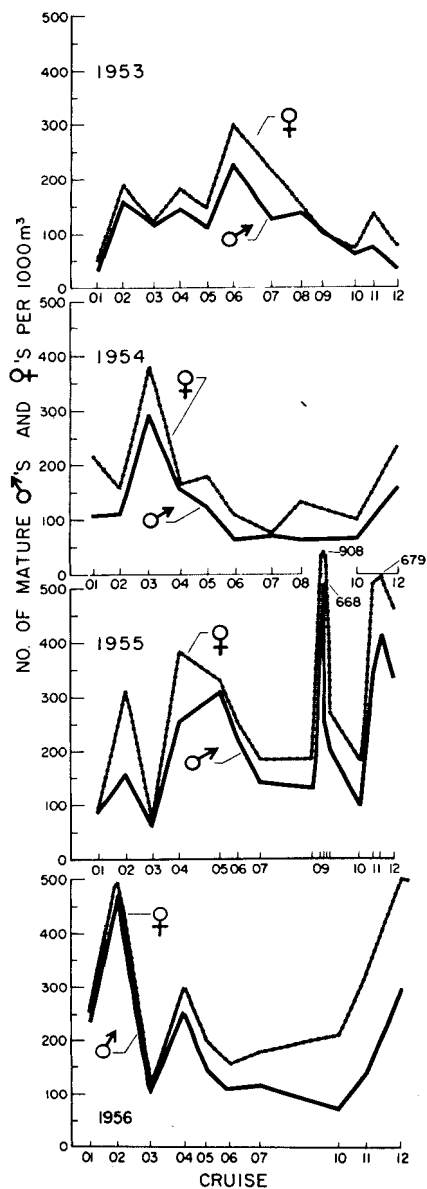


FIGURE 20.—Mean densities of presumed mature (>10.5 mm) male and female *Euphausia pacifica*, by month.

low reproductive activity. Furthermore, in 1954 the sex ratios for 13, 14, and 16 mm body length were 1:1, as compared with other years (Figure 21a). However, no relationship was seen (Figure 13) between numbers of gravid females of a given size and the difference between numbers of males and total females of the same size. Therefore, the observed increase with body length (at least to 15-16 mm) in the ratio of gravid to nongravid females appears natural, attributable either to

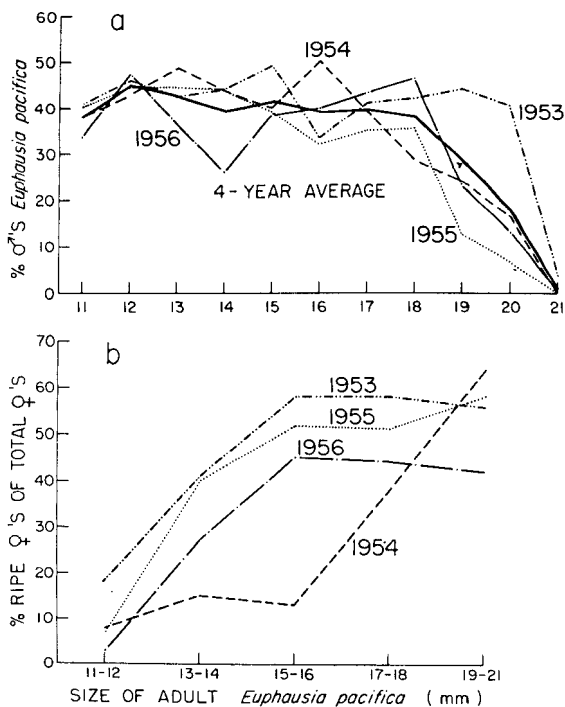


FIGURE 21.—a, Sex ratios for *Euphausia pacifica* by 1 mm body length, all data for each year averaged and 4-yr average. b, Annual gravidity ratios, by body length.

higher frequency or longer duration of egg production with increasing body length.

4) An increase with body length in female/male ratio may be due to their differing growth rates. Both sexes tend to mature at the same size, ca. 11 mm. Thereafter, females grow slower, appearing increasingly numerous relative to males at successive body-length increments (Figures 14, 21a). Nemoto's (1957) data suggested that the adult male of *E. pacifica* tends to be smaller than the female of the same age, and Mauchline (1960) stated this to be the case in *Meganycitiphanes norvegica*. Slower growth rate in females indicates shorter life span for males, probably by 1 or 2 mo, since females grow to 21 mm length off southern California (rarely more) compared with 20 mm for males.

In summary, reasons were sought for a) underestimation of spawning, b) paired spermatozoa in males, and c) apparent imbalance in sex ratio. These explanations were considered: eggs can ripen and females can spawn more often than the frequency of the surveys, applicable to a) and b); the bias in sex ratio favoring females is real and develops either with higher male mortality at

all sizes after maturity, applicable to b) and c), or because females grow slower and live longer, also applicable to b) and c); and the bias is an artifact of reduced net avoidance by ripe females and of observations during seasons when some males mature relatively late, resembling females for a time, applicable to c). Evidence supports each of the above. With regard to the increasing female/male ratio with body size, there are particularly strong indications of relatively slow growth in females, apparently leading to better survival than in males at given sizes and ages.

DISCUSSION

The predominance of *E. pacifica* among zooplankters off southern California appears related to the spring-early summer upwelling regime, which coincides with heaviest spawning. Recruitment consistently crested during May-July following annual surface temperature minima in April or May. Although this species may range southward along California and Mexico because of currents and the cool (10°-18°C) water, sole dependence on temperature effect in the southern California area for reproductivity is not likely because the area as a whole is coolest during December-April and the most substantial recruitment is later.

That the dependence is partly effected by food, as indicated by the seasonal pattern in availability of nutrients (plants), was shown in charts of the California Current region for 1969 for nutrients (Thomas and Seibert 1974) and for chlorophyll *a* (Owen 1974). The assumption is made that timing of the seasons in 1969 agrees enough with 1953-56 so that the April-June buildup in upwelling applies to both periods. Off southern California nutrient concentrations intensified in April and peaked in May in a patchy distribution corresponding to the areas of low surface temperature. For example, PO₄-P (integrated through 0-50 m depth) was in the range of 10-40 mg-at./m² during January-February and August-December but increased to 40-60 mg-at./m² during April-June. Silicate-Si peaked at 400-1,000 mg-at./m² during April-June; during the other months concentrations >400 mg-at./m² were rare.

Correspondingly, during the main upwelling period, April-September, chlorophyll *a* in the surface waters inhabited by newly hatched euphausiid larvae showed the patchy pattern of extreme concentrations shown also by the nu-

trients. Values peaked at 3.0 mg/m³ during April-September compared with 2.0 mg/m³ for January-March and 0.5 mg/m³ for October-December. The possible importance of shallow (12-19.5 m), intense (to 50 µg/liter) chlorophyll maxima—particularly those containing the dinoflagellate *Gymnodinium splendens*—to first feeding of anchovy larvae was put forward by Lasker (1975). These maxima were found during March-April 1974 within 15 km of the southern California coast. Such layering of food particles could have broad significance to feeding and survival of zooplankton larvae.

Most larvae of *E. pacifica* are found in nearshore areas described above as recruitment refuges where upwelling prevails and currents are sluggish. Similarly, off Oregon (Smiles and Pearcy 1971), more larvae were in nearshore upwellings than in offshore water characterized by a summer productivity minimum typical of the region. Also working off Oregon, Peterson and Miller (1975) found no relationship between year-to-year (1969-71) intensity of summer upwelling and abundances of euphausiid eggs and larvae (not identified to species).

Evidence that larvae occupying southern California waters are produced locally is seen in the time of the upwelling season along the coast. Upwelling peaks off southern Baja California in February-March. Progressing northward, its maximum off Oregon is during August-September. Hence maximum spawning and recruitment, if upwelling induced, should develop along the same northerly track, counter to the direction of main flow in the California Current during this period of relatively consistent northeast winds. This is the case: recruitment off mid-Baja California, lat. 27°-29°N, is mainly February-April (Brinton 1967b, 1973), in Monterey Bay it is both spring and summer (Barham 1957), off southern California it is mainly May-July, and off Oregon, August-December.

Although ripening of ovaries, spawning, and recruitment reach maxima as consequence of upwelling-associated events, the southern California population includes ripe females and newly hatched larvae year-round (Figures 4c, d; 19). Off Oregon, *E. pacifica* also includes some larvae at all times (Smiles and Pearcy 1971); while in the Sea of Japan (lat. 40°-50°N) and south of Kamchatka, Alaska (lat. 50°-55°N), in areas enriched by winter mixing of the water column, *E. pacifica* possesses ripe gonads in May-June, the

presumed breeding period (Ponomareva 1963), though eggs were abundant in August nearby in the Sea of Okhotsk. To the north and south of the eastern Aleutian Islands, Nemoto (1957) found females of *E. pacifica* with attached spermatophores during July.

Dominance of the southern California population by the particular cohorts followed in the analyses of growth tends to obscure the regular contribution of small classes, including those of fall-winter in which densities of larvae are usually 1,000-2,000/1,000 m³.

Such continuous recruitment of variable intensity is seen as an adaptation to midlatitude irregularity in oceanographic conditions, both seasonal and year-to-year, as compared with cycles at high latitudes. Continuous recruitment permits the stock to always include a wide spectrum of sizes and maturity stages, providing a potential for one or another to adapt to periods of poor climate or food availability, of differing duration or amplitude. For example, in 1954, a year of weak upwelling, recruitment was all but limited to June-July; nevertheless, spawning resumed at high intensity during four different periods in 1955.

Periodicity was observed in maxima of spawning and recruitment, and recruitment is appropriately out of phase with the inferred spawning (Figure 4c), implying substantial synchrony among breeders. Spawning apparently pulses at a 2-mo frequency during the period of maximum gamete generation, which also must be the period of maximum food use by breeders and larvae. This is to be compared with the annual (or at most, semiannual) frequency of breeding noted in the subarctic North Pacific. Thus it appears possible that, under optimal feeding conditions off southern California, a female might spawn every 2 mo: first at about 11.5 mm length (20-50 eggs), second at 16 mm (50-200 eggs), and third at 20 mm (100-400 eggs), during which time an individual might be expected to produce a maximum of 650 eggs. This is compatible with an observation of 1,400 oocytes (all stages of development) in ovaries of an *E. pacifica* in the springtime in the northeastern Pacific (Ponomareva 1963) where spawning is concentrated into one season, and with Lasker's observation, reported in Mauchline and Fisher (1969), that an *E. pacifica* from southern California shed 230 eggs after capture.

The long duration of maturity—probably half of this species' life expectancy—further contributes

to population stability and continuity. In conjunction with substantial horizontal transport, the capacity to breed several times enhances genetic integration across the distributional range.

The first observations on growth in *E. pacifica* were from specimens maintained in the laboratory by Lasker (1966) at 10°C with excess food. In small juveniles, growth was steady at 2.5 or 2.9 mm during 2 mo, from about 5 to 8 mm length. In the southern California field populations, growth of juveniles of this size was consistently in the range of 3-3.5 mm/mo. However, the 5309 cohort, having reached 5 mm by the start of the fall period of reduced growth, then grew only 3 mm in 1.5 mo.

Larger *E. pacifica* were observed by Lasker to grow somewhat slower. A 6.5-mm specimen grew 1.5 mm in 70 days, but added only 1.5 mm in 230 more days before dying, not having reached fully adult size. A 7.9-mm specimen grew 1.5 mm in 75 days, an 8.0-mm specimen grew 1.5 mm in 130 days, and an 8.4-mm specimen grew 1.0 mm in 160 days. These rates are smaller than those for the local field populations. They are closer to those supposed for *E. pacifica* in the northeastern Pacific where environmental enrichment is not by intermittent upwelling but by winter mixing followed by spring stability in the water column, hence not a continuing process.

In the analysis of growth, cohorts are considered as normal L-F distributions representing broods continuously hatched during a few days to a month or more. Observation on duration of reproduction is limited by the character of the sampling, here in approximately 1-wk period with a 2-3 wk interval between surveys. Only in a few of the months can a pulse in recruitment be recognized as distinct to that month. In most months, the larvae derive from the beginning, continuation, or end of a period of cohort formation which extends beyond one survey period and into another. Recruitment found less than in past or succeeding months is neither recognizable initially as a cohort nor traceable thereafter.

The area's population, therefore, is constantly polymodal in character, being compounded of individuals belonging to different age-groups and sexes. The possible difference in size between the sexes after about 15 mm length was not taken into consideration in the growth study.

The simplest method of analyzing growth and survival is that of following obvious modes, survey to survey. This is probably the most significant means biologically. Nevertheless, certain im-

precise trends in development of presumed cohorts provide growth rates which corroborate the more obvious trends. Some pathways of development indicated in Figures 9 and 10 may appear imaginary unless the shapes and amplitudes of the related L-F distributions, adjacent in time, are closely compared. When such indistinct modes are followed, precision and accuracy in recognizing rates of development are reduced. Graphical procedures for mathematically defining cohorts composing irregular L-F polygons (e.g., Harding 1949) required some subjectivity in recognizing modes and were employed only in an exploratory way.

There can be important inaccuracies in field estimates of growth rate when reliance is upon time-sequences in L-F modes. Even with steady, uniform recruitment, peaks or troughs would appear in the L-F distribution owing to differing growth rates and survivorship among life phases or between sexes. With unsteady recruitment, such peaks may sometimes lie in phase with the cohort being traced, but the cohort nevertheless becomes compounded by younger individuals when its growth is differentially slowed or by older individuals when accelerated.

It is possible that the individuals composing a mode could be totally replaced in the course of its time progression, although the modal assemblage persists as a size group, presumably feeding and mating as a unit. I have noted above that spring-summer cohorts tend to "pile up" in fall-winter when growth of adolescents appears to be food limited.

In tracing growth, reliance is therefore upon the more substantial cohorts. Although these can be masked, their frequent appearance as modes at sizes not associated with life-phase changes gives credence to the method.

Growth rates of *E. pacifica* off southern California appear similar to those off Oregon (Smiles and Pearcy 1971). Figure 22 shows generalized growth curves for this species from four areas in the North Pacific. The Oregon population showed steady growth after September recruitment. The juvenile and adolescent phases were during the winter and 13 mm was reached by February. About 22 mm was attained after 1 yr. This parallels development of a winter cohort (5512) off southern California which grew to 12 mm in 3 mo and was traced to about 21 mm after 8 mo.

Spring (5406) and summer (5309) cohorts off southern California grew at rates similar to the

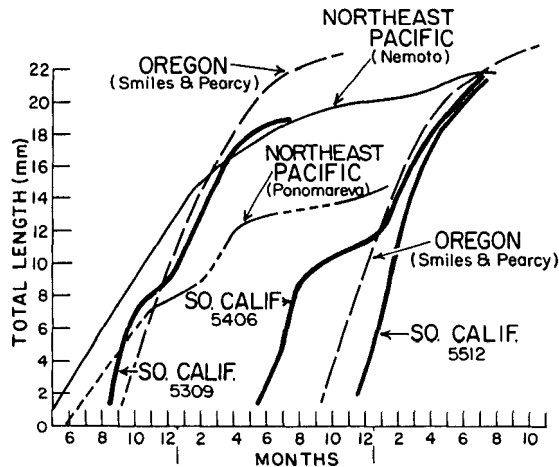


FIGURE 22.—Representative growth curves from southern California area compared with curves previously derived for *Euphausia pacifica* and illustrated by Smiles and Pearcy (1971).

winter cohort, except for slowing during October–December—5406 during adolescence and 5309 during the juvenile phase.

Here, life expectancy appears to be about 8 mo for winter and early-spring cohorts, to sizes of 18–20 mm by August–October. December–January populations never included individuals larger than 19 mm. Life expectancy is up to 12 mo for late-spring and summer cohorts, which grew to 21–22 mm by the following April–July. This agrees with estimates of 12 mo for September cohorts off Oregon.

Growth in other euphausiid species, mostly summarized in Smiles and Pearcy (1971), is similar. Several reach about 22 mm after 1 yr: *E. superba* (Ruud 1932; Bargmann 1945; Marr 1962), *E. triacantha* (Baker 1959), *Thysanoessa raschii* (Mauchline 1966), *Meganctiphanes norvegica* (Ruud 1936; Einarsson 1945; Mauchline 1960; Matthews 1973), and *Thysanopoda acutifrons* (Einarsson 1945). Most of these species have a life expectancy of 2 yr, reproducing in each and growing slowly or not at all in winter.

During winter in the westernmost North Pacific (Sea of Okhotsk), Ponomareva (1963) found *E. pacifica* to be 8 mm (considered to have hatched the previous summer) and 14–15 mm (considered 2 yr old). In the spring it was 12–13 mm (1 yr old) and 19 mm (2 yr old). Both groups bred in June. Off nearby Kamchatka in the summer, Nemoto (1957) found a size range of 12–22 mm, much like that found by Ponomareva, but with most at 14–20 mm. There were no larvae, but females with spermatophores were present in September, as off Oregon.

South of the Aleutian Islands in September, he found a 6-12 mm group interpreted as having hatched in the spring or early summer. Maximum numbers of adult females were 16-19 mm in May, 17-21 mm in June, and 18-22 mm in September.

Thus growth of *E. pacifica* is inferred to be slower and of longer duration in the Subarctic seas than off Oregon and California (Figure 22). Nemoto's (1957) estimate from south of the Aleutians was intermediate between Ponomareva's (1963) from the western Pacific and those from the American coast. Ponomareva's finding that sexual maturity is attained by 15-17 mm, with some mature at only 11-12 mm, agreed with the observations off southern California.

During *E. pacifica*'s main reproductive season there is similarity in surface water temperatures (Sverdrup et al. 1942; Anonymous 1963) among the five North Pacific areas from which information on life history comes; there is less agreement in winter temperatures:

Sea of Okhotsk	10-13°C (Aug.),	0°C (Feb.)
Off Kamchatka	9-11°C (Aug.),	0°- 1°C (Feb.)
South of Aleutians	10-12°C (Aug.),	2°- 4°C (Feb.)
Off Oregon	10-14°C (Sept.),	9°-11°C (Feb.)
Off southern California	10-18°C (June),	12°-15°C (Feb.)

Winter temperatures in the three subarctic areas are near 0°C whereas off Oregon and California they differ little from spring-summer temperatures influenced by upwelling. An overall temperature regime for *E. pacifica* is thereby described in which low temperature does not limit occupancy but in which 9°-16°C is suitable for reproduction, food permitting. In the subarctic region reproduction takes place at 9-13°C, the highest annual temperatures there. To the south of the California Current off mainland Mexico, food seems to be abundant, but other factors (temperatures >20°C, oxygen concentrations <0.1 ml/liter, different current systems) appear there to curtail the species' range.

The serial biomass representations included here clearly show rise and decline of cohorts, but are less exact than length frequency in determining growth and do not serve in estimating survivorship. It is evident that biomass of the species fluctuates month-to-month, with recruitment and growth not balancing mortality in any regular way. However in 34 of the 48 mo, the biomass was within the range of 8-22 g/1,000 m³.

The intense densities of *E. pacifica* at 8-12 mm, also appearing as conspicuous biomass peaks, are the rule rather than the exception. Therefore, such regular concentrating at the adolescence interphase, particularly in fall-winter, may be other than an incidental consequence of reduced food. It appears as a means of increasing size uniformity in the population, hence improved breeding efficiency, by the time of the spring bloom—a condition fulfilled by stricter seasonality in the high-latitude populations of *E. pacifica*.

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