DISTRIBUTION, SIZE, AND ABUNDANCE OF MICROCOPEPODS IN THE CALIFORNIA CURRENT SYSTEM AND THEIR POSSIBLE INFLUENCE ON SURVIVAL OF MARINE TELEOST LARVAE[1]

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ABSTRACT

The California Current system can be divided into onshore and offshore faunal zones by a copepod indicator species, *Mecynocera clausii*. Near the outer edge of the onshore zone copepod nauplii densities were higher than usual. There were about 3 times as many microcopepodids and 12 times as many nauplii on the average throughout the onshore as in the offshore zone. Feeding habits of larvae of sardines, anchovies, and jack mackerel may be adapted to the usual naupliar and copepodid concentrations of the zone in which they were spawned. The usual concentration of 56-μm and wider nauplii in the onshore zone was about 3/liter with 17/liter the highest observed which indicates that for nauplii of all sizes there were usually about 36/liter and with the highest density of 195/liter. These concentrations are lower than has usually been reported to be required for rearing larval fish in laboratories. Numbers of nauplii decreased exponentially with increasing size but a naupliar biomass maximum was found to occur at about the 70 μm width. Nauplii of this size are ingested at first feeding by Pacific sardine, northern anchovy, and jack mackerel larvae. It is suggested that larval feeding habits of these fish have evolved to utilize this important food resource at their first feeding.

Copepods form the bulk of most zooplankton hauls from the sea and are important because they are the main convertors of phytoplankton into food suitable for higher organisms (Marshall 1973). Copepods are especially important as food for planktonic larvae of pelagic marine teleosts. Food of the larvae of commercially important marine fishes has been widely reported as being primarily eggs, nauplii, and copepodid stages of small copepods. Yokota et al. (1961) found that food occurring in the feeding larvae of all the 57 species taken in their primarily coastal samples was almost entirely small copepods, especially nauplii. Duka and Gordina (1973) investigated the food of larvae of 26 species of teleosts from the Mediterranean and adjacent areas of the Atlantic and reported that copepod nauplii composed 90% of all items eaten by small larvae (2.3 to 5.0 mm). Stomach content analyses of fish larvae are also corroborated by population dynamic studies of plankton organisms. Fish (1936) noted that in the Gulf of Maine a small copepod, genus *Pseudocalanus*, suffers a much higher predation rate during the naupliar stages than does *Calanus finmarchicus* whose eggs (140 μm wide) and nauplii are too large to be ingested by many fish larvae.

When it became apparent that the population of Pacific sardine, *Sardinops sagax*, was in serious decline, a research program [later to become known as CalCOFI (California Cooperative Oceanic Fisheries Investigations)] was initiated in 1949 to investigate the ecology of this important fish. One part of this investigation was a study of the food and food resources of sardine larvae and consisted of two main objectives: 1) determine what the larvae eat, and 2) to study the abundance and distribution of these food items. The ultimate purpose was to determine if feeding conditions, especially for the first feeding larvae, could be a contributing factor to the sardine's decline, as was proposed by Hjort (1914) to explain poor year class survival of fishes in general.

The identifiable food of first feeding sardine larvae was primarily copepod nauplii ranging from 25 to 80 μm but mostly about 70 μm wide (Arthur 1976). Nauplii of this size are produced only by small species of copepods, roughly less than 1.5 mm long. The assemblage of these small copepods is composed of many species. Several genera have often been recorded as being abun-

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dant in the plankton as well as in the intestinal contents of larval fishes. Among these are the cyclopoid genus *Oithona,* (especially *O. similis*), and the calanoid genera *Pseudocalanus* and *Paracalanus. Oithona similis,* whose first stage nauplius is 70 μm wide (Oberg 1906) and can, therefore, be ingested by sardine larvae, composed over 50% of the cyclopoid fauna in 37 of the 42 samples off Oregon through Baja California examined by Olson (1949). Because of the large number of species, many of whose developmental stages had not been described, no attempt was made in this study to identify eggs, nauplii, and copepodid stages to species.

This report deals with size, abundance, and distribution of naupliar and copepodid stages of copepods captured with relatively fine meshed plankton samplers in and near the California Current. These small species of copepods will be referred to as microcopepods, and all postnaupliar stages, including adults, as copepodids. The term nauplii will include true nauplii and metanauplii.

SAMPLING METHODS

The need for a study of the small crustacean plankton was anticipated early in the CalCOFI program. The 1-m net with its relatively coarse mesh (505 μm) was considered adequate for sampling sardine eggs and large copepods and euphausiids, but most small copepods and nauplii pass through this size mesh. Starting in May 1949, a Clarke–Bumpus sampler (Clarke and Bumpus 1940) equipped with a #8 mesh bolting silk net, (203 μm in unused condition) was used routinely at stations in the central and upper southern California areas. It was towed obliquely from a depth of 70 m, filtering about 5 m^3 of water.

The Clarke–Bumpus sampler was abandoned after March 1950 in favor of the "high-speed sampler" (California Academy of Sciences et al. 1950) which was modified by having a mouth diameter of 7.6 cm, the same as the main fuselage of this device, rather than being tapered to a narrower opening as in the original high-speed sampler. It was equipped with a 143-μm wire filter and was towed on the same wire as the meter net and was used because the record it made of depth versus volume of water filtered could be used to analyze the meter net track as well as its own. This modified version was called the "microplankton sampler." It was towed obliquely from a depth of 70 m during March 1950–September 1950 and from 130 m on cruises from November 1950 to July 1952.

After a study had been made of the food ingested by ocean-caught sardine larvae, it became obvious that very small copepod nauplii are critical in the ecology of these larvae. Therefore, after August 1951 a plankton sampler of much finer mesh was used. This sampler was essentially a medium Epstein net (Sverdrup et al. 1942:379) with a mouth opening 17.5 cm in diameter, connected by a canvas collar to a filtering cone constructed of #20 bolting silk (76 μm in unused condition). This sampler was hauled vertically from a depth of 50 m and was called the "truncated net."

These three plankton samplers were used between May 1949 and September 1954. Pertinent statistics are compared as follows:

Sampler	*Mouth diameter (cm)*	*Mesh aperture size (μm) New*	*Used*	*No. of samples*
Clarke–Bumpus	12.5	203	120	185
Microplankton	7.6	143	143	612
Truncated net	17.5	76	56	239
				1,036

Because of expansion when wet, and the unraveling of threads when used, the aperture size of used wet silk nets is considerably smaller than new dry ones. The above "used" values were obtained by measuring aperture sizes, when submerged in water in the laboratory, of nets being used in the collections. Even with the smallest aperture size used (56 μm) many nauplii and copepodids must have escaped. Beers and Stewart (1967) reported that a significant quantity of copepods pass through a 35-μm mesh. Most food particles of sardine, anchovy, and jack mackerel larvae, however, are wider than 56 μm (Arthur 1976.)

COUNTING METHOD

The plankton samples were examined in a plastic chamber measuring 60 mm by 70 mm, the floor of which was lined every 5 mm to form a grid. Its total fluid capacity is approximately 50 ml with a water depth of about 12 mm. In practice, the fluid volume in the chamber measured less than half of this. If the amount of material in the sample was not too great, the entire sample was counted. Most samples taken with the Clarke–Bumpus and truncated nets contained so much material that subsampling was necessary. This

was accomplished by first measuring the total fluid volume of the sample, then stirring it vigorously to disperse the material, then drawing off a convenient amount for examination, and finally measuring the remainder in order to determine what percentage the subsample was of the original sample.

FAUNAL AREAS IN THE CALCOFI SECTOR

Although the primary purpose of the microplankton program was a quantitative appraisal of the microcopepod fauna, a few prominent copepod species were routinely recorded. One of these, *Mecynocera clausii,* proved useful as an indicator organism allowing the CalCOFI sector to be roughly divided into two plankton faunal areas, onshore and offshore.

Mecynocera is a monotypic genus. It can readily be distinguished from other copepods by its exceptionally long first antennae (Mori 1964). Its small size (about 1 mm) places it within the microcopepod range. These attributes make it convenient and useful as an indicator of conditions affecting the microcopepod fauna. *Mecynocera clausii* has been reported near the surface throughout tropical areas of the oceans, as well as in temperate areas such as the Mediterranean. In the CalCOFI area its presence may be considered as indicating the more tropical offshore and southern waters.

A typical distribution of *M. clausii* off southern California and off northern and central Baja California is illustrated by data for February 1951 (Figure 1). *Mecynocera* is characteristic of offshore water whereas the occurrence of plutei of benthic echinoderms may indicate coastal water. The two boundaries tend to interdigitate, which must imply alternating tongues of warm offshore water penetrating toward the coast and jets of cold onshore water moving out to sea. The 15°C isotherm supports this interpretation.

Submergence of the water of the California Current under the offshore subtropical water may be indicated at stations where *Mecynocera* and plutei were taken together. This would result if the net in its 130-m deep track caught *Mecynocera* near the surface and plutei at some depth where the submerging water had carried them.

The shoreward boundary of *Mecynocera,* as determined by the various cruises, is presented in Figure 2. In general, the average boundary is

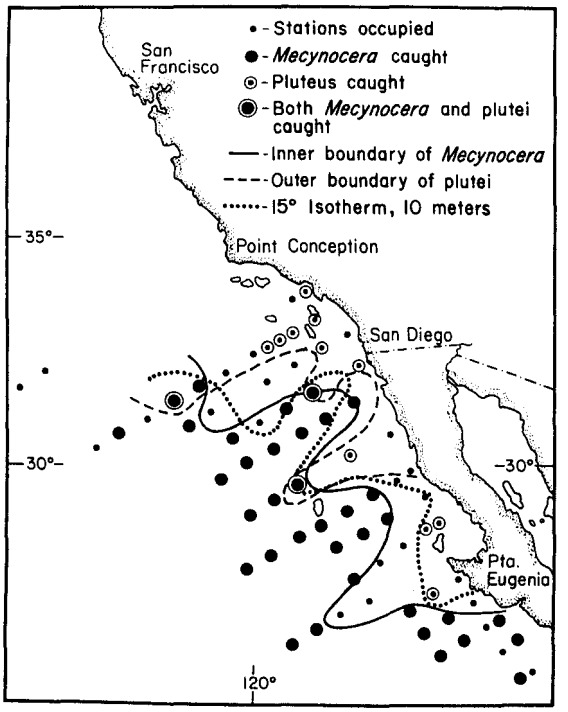

FIGURE 1.—Distribution of *Mecynocera clausii* and pluteus larvae during CalCOFI cruise for February 1951 off California and Baja California.

found about 400 km offshore in the San Francisco area and inclines toward the coast farther south. In the northern Baja California area it may impinge upon the shoreline, but it becomes erratic in the turbulent Punta Eugenia area.

ZONE OF COPEPOD NAUPLII MAXIMUM

For a given cruise, if each line is examined and the station which contained the greatest concentration of nauplii is circled and the circled stations for the various lines are connected, one obtains a line of maximum copepod nauplii concentrations. Figure 3 presents a typical distribution of copepod nauplii and their maximum zone in the Channel Island area. Two stations have been circled for the line extending offshore from San Diego. It is common to find a high local concentration at stations near the coast and a second high offshore particularly in the area north of Point Conception. Had the station pattern extended closer to the beach, higher concentrations of nauplii probably would have been encountered there. During a 5-mo

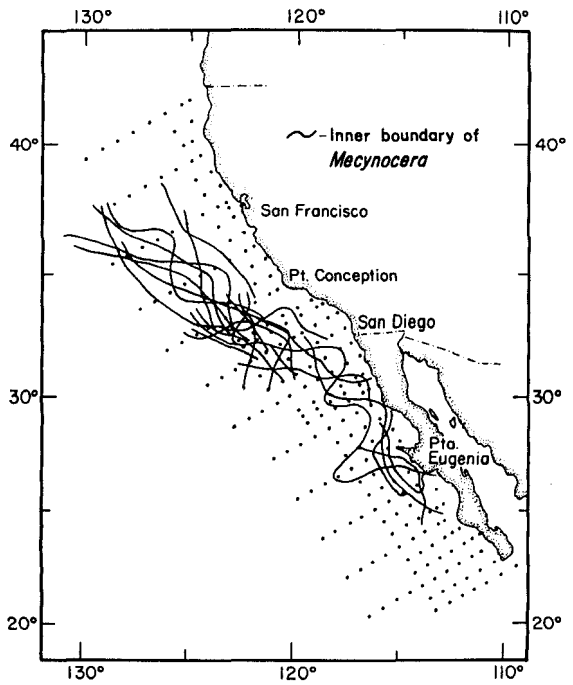

FIGURE 2.—Inner boundary of *Mecynocera* for individual CalCOFI cruises from June 1949 to July 1951 off California and Baja California.

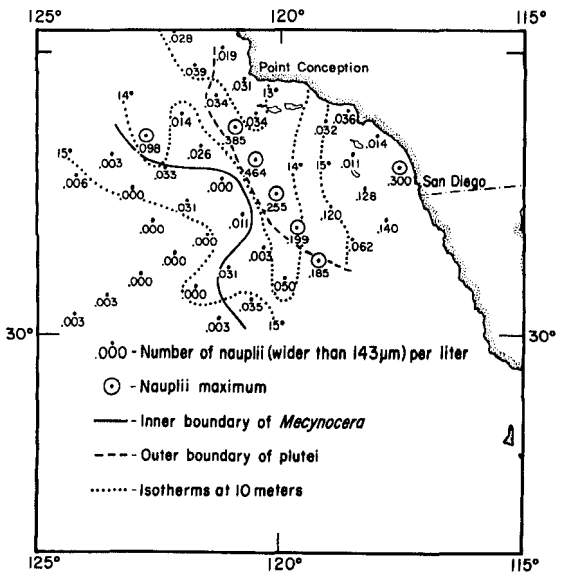

FIGURE 3.—Distribution of copepod nauplii (wider than 143 μm) and their relation to some other biological and physical variables during June 1950.

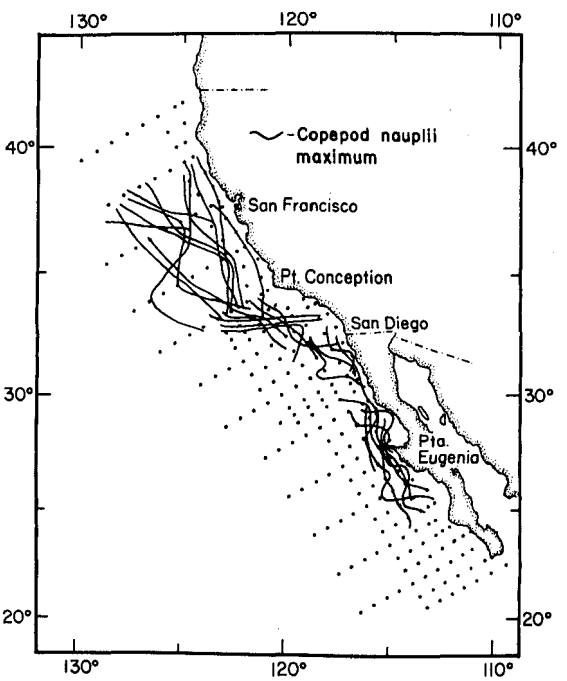

FIGURE 4.—Copepod nauplii maxima for individual CalCOFI cruises from June 1949 to July 1951.

study of plankton off La Jolla, Beers and Stewart (1970), using 35-μm mesh nets, found that for the three stations located 1.4, 4.6, and 12.1 km from shore, naupliar densities averaged 63/liter, 33/liter, and 26/liter, respectively.

The zone of maximum nauplii seems to be associated with the *Mecynocera* boundary, which is also indicated in Figure 3. The station of maximum nauplii for a line usually occurs one to three stations onshore of this boundary.

As may be seen in Figure 3, there appears to be an association between the zone of maximum nauplii and the tongue of relatively cold water (13° and 14° isotherms) extending south of Point Conception. This cold tongue probably is nutrient rich water upwelled north of Point Conception. Shoreward from this zone lies the counterclockwise gyre of the Southern California Bight, extending from Point Conception to northern Baja California. Allen (1939) stated that his most offshore station, located 120 km from the coast, which is in the general vicinity of the nauplii maximum, was consistently the richest station for microcrustacea. Berner (1959) noted that stations where he found anchovy larvae to be feeding were in the area of the copepod nauplii maximum as described by Arthur (1956).

In the San Francisco area, where two maxima are commonly found, the outer one is usually about 115 to 400 km offshore (Figure 4). The maximum zone is consistently found seaward from the Channel Islands, about 100 to 320 km off the mainland shore. Occasionally nauplii-rich stations are found inside the islands. The average nauplii maximum approaches the coast south of San Diego, and is adjacent to the shoreline in northern Baja California, probably a result of upwelling along the coast. From Punta Eugenia south, this zone becomes irregular, as does the *Mecynocera* boundary.

QUANTITATIVE DISTRIBUTION OF MICROCOPEPODIDS AND NAUPLII IN THE CALCOFI AREA

On examining the values obtained in this program, it is apparent that there are very wide ranges in densities. Values for microcopepodids range from 0.003 to 7.886/liter. Nauplii were sampled in numbers ranging from 0 to 17.280/liter. Frequency distributions are highly skewed toward the lower densities. To overcome this problem, the data are presented as logarithms to normalize the frequency distributions.

The method used for comparing data is the ogive, or cumulative frequency curve. The ogive is useful to depict what percentage of the samples from an area contains any particular concentration of copepodids or their nauplii. Furthermore, in considering concentrations of any two areas, the value of the 50 percentile concentrations can be quickly read off and compared. The 50 percentile value in this particular type of distribution lies very near the mode and so may be considered to closely represent the most common value of concentration for a given area.

Ogives for nauplii and microcopepodids as sampled by all Clarke–Bumpus and all microplankton samples in both the onshore zone and offshore zone are presented in Figure 5. Because of the large mesh size of the nets used, most nauplii escaped which resulted in more copepodids than nauplii being caught. The truncated net (56-μm mesh) caught more nauplii than copepodids. Very few samples were taken in the offshore zone with the truncated net and so it cannot be compared with the other two samplers in this manner. Differences in the ratios of onshore zone to offshore zone for the 50 percentile values are as follows:

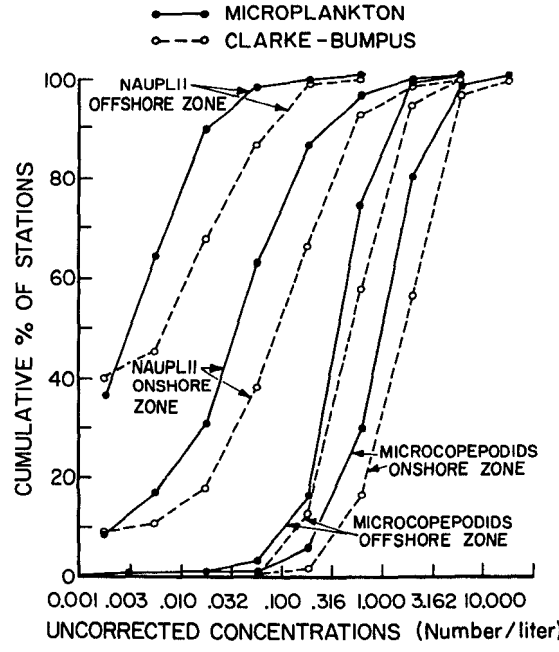

FIGURE 5.—Ogives for abundance of nauplii and microcopepodids in offshore and onshore zones as sampled with the Clarke–Bumpus (120-μm mesh) and microplankton samplers (143-μm mesh).

Sampler	*Microcopepodids*	*Nauplii*
Clarke–Bumpus	3.17:1	12.58:1
Microplankton	2.57:1	11.22:1

There are about two and one-half to three times as many copepodids in the onshore zone as there are in the offshore zone. There are, however, about 12 times as many nauplii in the former as in the latter. There are about four times as many nauplii per copepodid in the onshore zone as in the offshore zone. This is probably a result of the increased fecundity of copepods living in the richer phytoplankton owing to upwelling in the onshore zone.

CORRECTING FOR CALIBRATION ERRORS AND ESCAPEMENT

The ogive was useful to correct errors of the various samplers used in this survey. Figure 6 presents the ogives obtained for microcopepodids by all samples taken in the onshore zone with the three different samplers. Of the three samplers, the Clarke–Bumpus was the most accurately calibrated for volume and so the other two samplers were corrected to it. Such a correction can be made

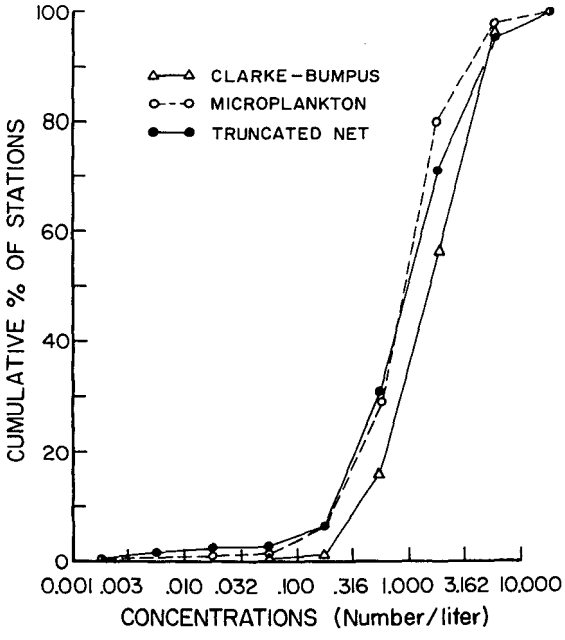

FIGURE 6.—Ogives for abundance of microcopepodids in the onshore zone as sampled by the three samplers.

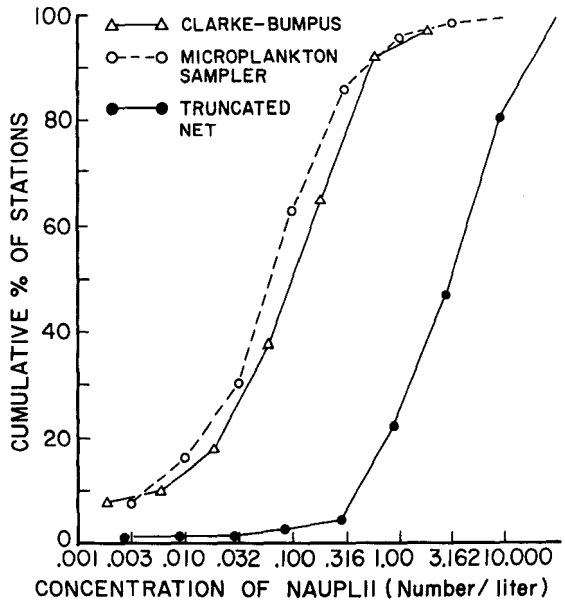

FIGURE 7.—Ogives for nauplii of all sizes retained by each of the three samplers in the onshore zone corrected for volume filtered.

by measuring their 50 percentile differences and adding this value to all the points along their respective curves. This correction assumes that all net meshes used retained copepodids in equal percentages. This is not entirely correct as Beers and Stewart (1967) reported that some copepodids can escape even a 35-μm mesh.

Having corrected the volume errors of the three devices (or, at least, made them comparable in value), we can now roughly correct for the amount of escapement by nauplii through the three different mesh sizes. Figure 7 presents ogives for nauplii in the onshore zone as sampled by the three devices, the numbers of which have been corrected for volume strained by values obtained by the 50 percentile differences in Figure 6. These ogives are based upon the same amount of water filtered, thus their differences are due to differential escapement of nauplii. By comparing the 50 percentile values in Figure 7, the following approximation of the size distribution of the naupliar population in the onshore zone is obtained:

Sampler	*Mesh opening (μm)*	*Usual number retained/liter*
Truncated net	56	2.884
Clarke–Bumpus	120	0.095
Microplankton	143	0.058

A plankton net hauled from some depth to the surface may pass through a wide range of plankton concentrations but its catch will represent only the average of these conditions and will not reveal rich but thin strata that might exist. The above concentrations, therefore, probably underestimate somewhat the highest concentrations found in the usual water column.

When the ogives for the three samplers are corrected to the Clarke–Bumpus for volume and to the truncated net for escapement, by their 50 percentile differences (Figure 8), they are similar over the mid-60% of their ranges. It is interesting that the three curves for nauplii are so similar when it is considered that two of them represent, primarily, the small percentage contributed by larger nauplii. This implies that the various sizes of nauplii have essentially the same type of distribution and with the same degree of patchiness.

The slope of an ogive is determined by the degree of dispersion within the samples. If the distribution of an organism is so homogeneous that all the observations should fall in one interval, then the resultant ogive would be a vertical line. With wider ranges of densities the ogive will slope less abruptly. By comparing slopes of the two sets of ogives in Figure 8, it can be seen that the copepodid stages are more uniformly distributed than are nauplii.

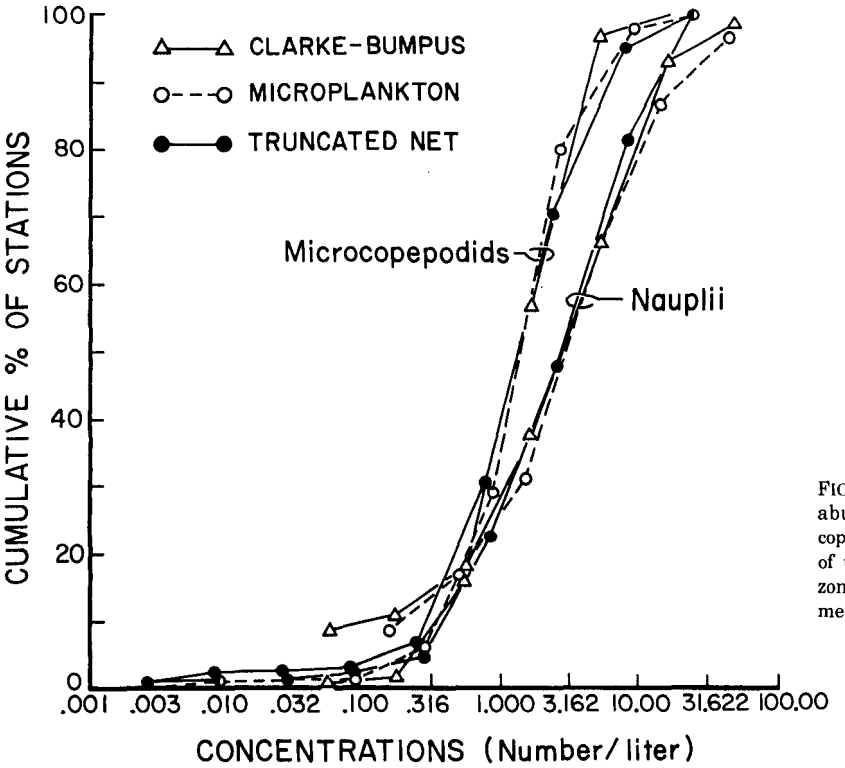

FIGURE 8.—Comparison of ogives for abundance of nauplii and microcopepodids for all sizes retained by each of the three samplers in the onshore zone corrected for volume and escapement.

DISCUSSION

Microcopepod Size and Feeding Habits of Three Larval Fishes

Feeding habits of larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, as reported by Arthur (1976), may have been associated with spawning distribution of the adult fish as well as with the distribution of microcopepods and nauplii during the years of this program. Jack mackerel spawned mainly in the offshore zone, as can be determined by comparing the *Mecynocera* boundary with the distribution of jack mackerel larvae (Anonymous 1953:36). Jack mackerel larvae first start to feed when 3.0 mm long and ingest mostly 60- to 70-μm wide (total range 50 to 200 μm) copepod nauplii. However, when they have grown to 3.5 mm their food is primarily about 125-μm wide copepodid stages of small copepod species and when 9.0 mm long they eat 250- to 450-μm wide copepodids of larger species. The quick change from nauplii to copepodids, which is facilitated by their relatively large mouths, may be related to the low nauplii/copepodid ratio of the offshore zone.

Most anchovy larvae were caught inside the *Mecynocera* boundary (Anonymous 1953:34). The more omnivorous 3.0-mm long first feeding anchovy larvae select food from the 25 to 100 μm range with little preference for any size within this range. Food size increases to 125 μm when larvae are about 4.0 mm after which, though there is some increase, food size does not increase isometrically with the increase in length of larvae. This curious slow increase in food size appears to be common to early larval stages of the genus *Engraulis*, as can be observed in food-size/larval-length graphs for Japanese anchovy, *E. japonica* (Yokota et al. 1961), Argentine anchovy, *E. anchoita* (Ciechomski 1967), Peruvian anchovy, *E. ringens* (Rojas de Mendiola 1974), and can be calculated for northern anchovy, *E. mordax*, from data presented by Berner (1959) and Arthur (1976). This lack of selecting for the largest ingestible food size may be related to the high nauplii/copepodid ratio of the inshore zone and may also account for the importance of copepod eggs in the diets of anchovy larvae as reported by the above authors except Yokota et al. (1961).

Sardines spawn near the *Mecynocera* boundary, inshore of the jack mackerel and mostly offshore of anchovy (Anonymous 1953:22), but, also, more southerly of the other two. Sardine larvae combine some feeding characteristics of jack mackerel and anchovy larvae. Food particle size of sardine larvae increases isometrically with length of larvae as in jack mackerel but is smaller for unit larval length and is composed more of copepod eggs and nauplii as in anchovy larvae.

Microcopepod Densities Influence Larval Fish Survival

Other investigations in the CalCOFI area, and in similar latitudes in Japanese waters, helped to approximate the biomass spectrum of the naupliar population. Beers and Stewart (1967) estimated numbers of various microzooplankton at five locations across the California Current. Samples were taken by pumping water through several sizes of filters from depths ranging from the surface to 105 m. Their values for copepod nauplii, averaged and integrated, are compared with the values reported herein as follows:

Mesh size	*Nauplii/ liter*	*Logrithm*	*Source*
Total no., all sizes	22.078	1.3440	Beers and Stewart
Retained by 35 μm	3.878	0.5886	Beers and Stewart
Retained by 56 μm	2.884	0.4600	This report
Retained by 103 μm	0.198	−0.7033	Beers and Stewart
Retained by 120 μm	0.095	−1.0223	This report
Retained by 143 μm	0.058	−1.2366	This report

Logarithms of the above, plotted in Figure 9, are highly correlated with mesh size for the two individual sets of data as well as when they are combined. The line in Figure 9 is a least square fit to all data points combined and is expressed as:

$$N = -0.0188w + 1.3370 \quad \text{(intercept at size 0)} \qquad (1)$$

where N is concentration of nauplii (number per liter) and w is mesh aperture size. The correlation coefficient, r, is 0.9931 and the coefficient of determination, r^2, implies that 98.62% of the variation of naupliar concentrations can be explained by mesh size alone.

Least square fits for the two individual sets of data are as follows:

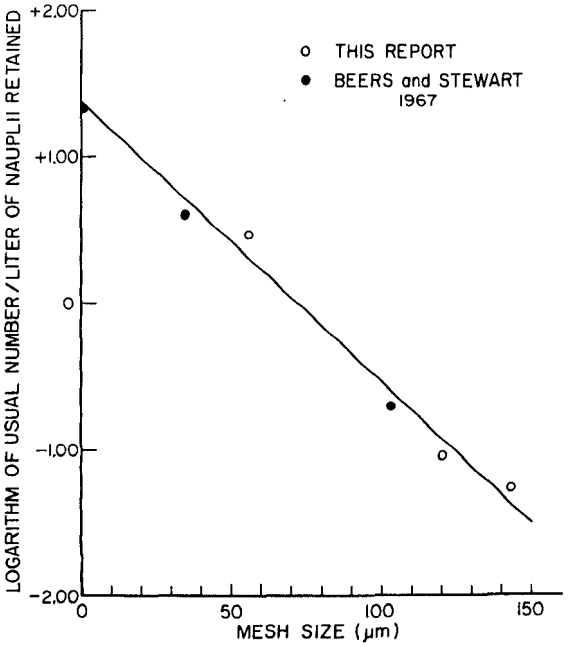

FIGURE 9.—Logarithms of the usual densities of various sizes of nauplii in relation to mesh size. The line is a least square fit to all data points combined from the equation $N = -0.0188w + 1.3370$.

Beers and Stewart

$$N = -0.01976w + 1.31857 \qquad (2)$$
$$r = 0.9994,\ r^2 = 0.9988.$$

This report

$$N = -0.02029w + 1.5577 \qquad (3)$$
$$r = 0.9900,\ r^2 = 0.9801.$$

The microcopepod assemblage in onshore water off the southern California–northern Baja California coast is strikingly similar to that in coastal waters at the same latitudes on the other side of the Pacific. Yokota et al. (1961) measured widths and lengths of 8,839 copepod nauplii and 1,389 copepodids from 666 samples captured in 1-liter containers from an area off the southeast coast of Kyushu over a 2-yr period. Average widths and lengths of nauplii were 67.7 and 156.1 μm, respectively, with a length to width ratio of 2.306. Assuming a cylindrical form, the average Kyushu nauplius has a volume of about 562,000 μm^3 which differs by only about 10% from the 510,000 μm^3 volume of the average La Jolla nauplius (Beers and Stewart 1970). Concentrations ranged from 0 to 524 nauplii/liter (only two samples were greater than 100/liter) with an

average of 13.27/liter. Size distribution as calculated from the data of Yokota et al. (1961) is:

Width of nauplii	*Average number/liter*
All sizes	13.27
>50 μm	3.87
>100 μm	0.53
>150 μm	0.10
>200 μm	0.05

In comparing the Kyushu to the California area it appears that there are fewer very small nauplii but about twice as many larger nauplii. These differences may result from the Kyushu samples being taken at the surface whereas the California samples were collected at varying depths.

Usual densities of total nauplii and copepodids of all sizes calculated from the several investigations discussed herein are as follows:

Nauplii/ liter	*Copepodids/ liter*	*Source*
36.12	1.41	This report, Equation (3)
13.27	2.10	Averaged from Yokota et al. 1961
22.08	36.35	Averaged from Beers and Stewart 1967
34.33	4.17	Averaged from Beers and Stewart 1970

The calculated number of nauplii of all sizes from this report appears to be somewhat high which may result from being derived by extrapolating from Equation (3). The average number of copepodids found by Beers and Stewart (1967) appeared to be much higher than the other investigations and may be a result of sampling an unusually rich but short-lived condition (all samples were taken during a 7-day period). Numbers of nauplii and copepodids of Beers and Stewart (1970) should be somewhat higher than the average for coastal areas because they were taken very close to the beach. In general, the usual densities in onshore areas at these latitudes (30°–35°N) is about 1.5 to 4 copepodids/liter and about 13 to 30 nauplii/liter. These densities are similar to those found by Allen (1939) who, while studying phytoplankton off California by trapping 5-liter samples, found that the combined densities of nauplii and copepodids ranged from 10 to 30/liter. Copepod nauplii average about 20–30/liter in Japanese coastal waters and 10 or less/liter in the warm offshore Kuroshio (Honjo et al.[3,4]).

These densities are considerably lower than those usually reported to be required to support growth of marine teleost larvae in the laboratory as is illustrated by a few examples. O'Connell and Raymond (1970) found poor survival of anchovy larvae in densities of nauplii and copepodids of less than 4,000/liter. Hunter (in press) used 100,000 *Gymnodinum*/liter combined with 8,000 to 115,000 rotifers/liter to grow early anchovy larvae. Houde (1975) found best survival of larval sea bream, *Archosargus rhomboidalis*, was on 50- to 100-μm wide nauplii and copepodids in densities of 1,500–3,000/liter, but 10% survived at 100/liter at low larval stock densities. In coastal and offshore areas even the highest densities of nauplii reported do not equal those used in most laboratory rearing experiments. The highest concentration of larger than 56-μm nauplii I encountered was 17.28/liter which indicates that, calculating from Equation (1), for nauplii of all sizes there were about 195/liter. Highest concentrations reported by others are 524/liter (Yokota et al. 1961), 180/liter (Beers and Stewart 1970), and 134/liter (Allen 1939).

Gallagher and Burdick (1970) calculated that the mean distance $\bar{R}$, between a particle and its nearest neighbor in a random three-dimensional array can be computed from $\bar{R} = 0.553960\rho^{-1/3}$, where ρ is their mean density in space. At concentrations of 25 nauplii/liter the distance from the mouth of a fish larva to the nearest nauplius is on the average about 18.9 mm, whereas at 200 nauplii/liter this distance is 9.5 mm.

Concentrations approaching laboratory requirements are encountered in localized conditions, i.e., Schnack (1974) caught nauplii with a 55-μm net in numbers up to 917/liter in a shallow fjord off the western Baltic. Lasker (1975) found the dinoflagellate, *Gymnodinum splendens*, in the ocean in high enough densities (20,000–40,000/liter) to support life of early laboratory-spawned anchovies. These densities were dependent on stable oceanic conditions which were quickly dispersed by a storm.

The reason for the disparity between the observed naupliar densities in the ocean and the

[3]Honjo, K., T. Kidechi, and H. Suzuki. 1959. On the food distribution and survival of post larval iwashi-I-Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.–Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (Preliminary Report), February 1959, 7 p. Engl. transl. by S. Hayashi.

[4]Honjo, K., T. Kitachi, and M. Kudo. 1957. Food of the post-larvae of iwashi. Reports of the major coastal fish investigations for 1956 (Preliminary Report) November 1957, 5 p. Engl. transl. by S. Hayashi.

densities required for larval survival in the laboratory may be that present microplankton sampling techniques do not detect small but dense aggregations of nauplii which, however, can be found by fish larvae. It, also, may be that present rearing techniques do not approximate oceanic conditions sufficiently to permit assaying of actual prey concentrations required to allow significant larval survival. Blaxter (1965) reported that the condition factor of herring larvae living in the ocean is worse than that of larvae which died presumably of starvation in the laboratory. This may attest to greater ability of larvae to survive poor rations in the usual oceanic environment than in the laboratory.

Maximum of Naupliar Biomass Spectrum

The abundance of copepod nauplii decreases exponentially with increasing size of individuals (Figure 9), whereas the volume of an individual nauplius increases exponentially with increasing size (roughly by the cube of width). When the naupliar size range is divided into 10-μm wide size classes and the average volume per nauplius is multiplied by numbers of individuals per class (calculated from the equation for combined data, Figure 9) it is seen that the naupliar biomass is at a maximum at about the 70 μm width (Figure 10) even though there are many more nauplii of smaller sizes.

Figure 10 includes, also, the food-particle size range at first feeding of larvae of Pacific sardine, northern anchovy, and jack mackerel (Arthur 1976). It is interesting to note that these ranges overlap at the 50- to 80-μm width range which brackets the naupliar biomass spectrum maximum. This suggests that larval feeding habits of these three fishes have evolved to take advantage of this important food resource at first feeding.

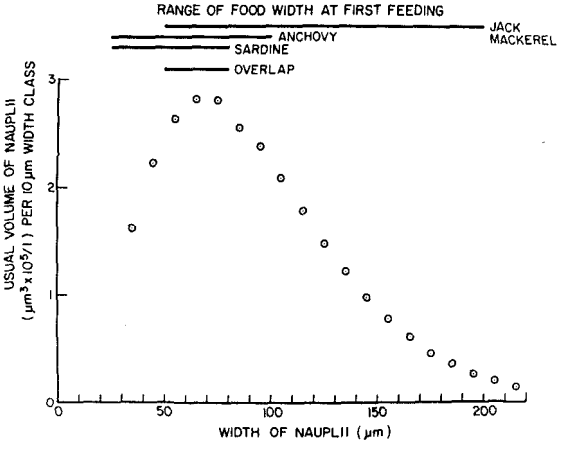

FIGURE 10.—Biomass spectrum of naupliar size range compared with food size at first feeding of the larvae of three fishes in the California Current system.

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