CHANGES IN THE DISTRIBUTION OF EUPHAUSIID CRUSTACEANS IN THE REGION OF THE CALIFORNIA CURRENT[1]

EDWARD BRINTON

Euphausiids are large zooplankton organisms of shrimp-like appearance that make up a high crustacean Order, the Euphausiacea. All species are marine and pelagic; most are oceanic in distribution and appear to have little dependence upon coastal regions. Some euphausiids, for example *Nyctiphanes* and *Meganyctiphanes*, are frequently most abundant in coastal regions, but it is not yet known whether it is essential for any species or assemblage of species to have access to neritic or coastal waters during its life history,—except as such coastal conditions as upwelling may influence the temperature and fertility of the local pelagic environment.

There are approximately 85 euphausiid species distributed over the oceans. Some Pacific species have very wide ranges: fifteen have cosmopolitan ranges from 40°N to 40°S, and six equatorial and twelve antitropical species occupy east-west oceanwide belts in the tropics and mid-latitudes respectively. Twenty-five of these species are numerically important in the California Cooperative Oceanic Fishery Investigation survey area, and an additional eight are occasional indicators of intruding environments. Eight deep-living cosmopolitan species are sometimes sampled by tows reaching deeper than the standard oblique tow from 0-140 meters.

To use a word that is commonly applied to parameters that are the antithesis of biological activity, the euphausiids might be called *conservative* organisms. They are long lived compared to the majority of plankton forms. It is believed that many species live on the order of a year. Some, notably *Euphausia superba* and *Thysanopoda acutifrons* live two to three years (Bargmann, 1945; Einarsson, 1955), but a year may be a reasonable approximation for the euphausiid life span in temperate waters. Species that live in extreme northern or southern regions, where the seasonal effect upon the waters is conspicuous, may be analyzed in respect to their growth rates and life spans. Warm water species, the populations of which may include breeding individuals and larvae at all times, are more difficult to study from the standpoint of the ages of populations sampled by plankton collections.

Euphausiids are deep-living animals relative to the other major components of the zooplankton in the upper layers of the ocean. Many species perform extraordinary diurnal vertical migrations, rising near the surface of the sea at night and descending to depths of 500 to 700 meters during daylight hours. Thus within a 24 hour period, a migrating population may pass through a range of temperature of as much as 16°C.

If one looks at the distributions of euphausiids on a wide geographical scale, it is evident that many species' boundaries can be compared with environmental factors measured by standard oceanographic sampling techniques. Correlations, particularly with temperature and oxygen, appear to be part of the ecological definition of some of the species distributions (Reid, Roden, and Wyllie, 1958). An environmental factor may act at a particular depth to govern or limit the distribution of a vertically migrating species. A temperature-depth value may limit an essential metabolic activity, such as digestion of food at depth or ability to feed at the surface at night as Moore (1952) has suggested. Enough is not yet known about euphausiid distribution to specify limiting factors.

A summary of the typical patterns of distribution found in the Pacific can provide a framework in which to consider the incursion or the occurrence of euphausiids in more local areas such as the CCOFI survey area. These have been derived from collections made during oceanic expeditions carried out by the Scripps Institution, 1949-56 and are described by Brinton (1957). They are essential to a consideration of the California Current as a region of faunal convergence. Northern (subarctic) species are not consistently carried far to the south in the cool current, but appear sporadically along the coasts of California and Baja California. Offshore (central) forms sometimes are found near shore. *Nyctiphanes simplex* and *Thysanoessa spinifera* are adapted to the shoreward part of the California Current, extending variable distances to the north and south, and may be carried to the west in tongues of distribution. (*Nyctiphanes* is the shallowest living local euphausiid, living above 100 meters at night but descending to near that depth in the daytime). Species adapted to an oceanographic transition zone (Sverdrup, Johnson and Fleming, 1942) are the dominant euphausiids in the California Current, while equatorial species are present off Baja California.

Oceanic species distributions have areas of occurrence that approximate the positions of major temperature-salinity water masses. Certain of the factors that operate to maintain species in an area (current systems, intensity of incident radiation) are the same influences that give integrity to large masses of water.

SUBARCTIC DISTRIBUTIONS

Thysanoessa longipipes and *Tessarabrachion oculatus* occur north of about 42°N in the mid-Pacific and sometimes penetrate southward to the latitude of San Francisco (37-38°N) in the California Current. *Euphausia pacifica* has a distribution in the mid-oceanic area which extends south of the two previous species,

[1] Contribution from Scripps Institution of Oceanography.

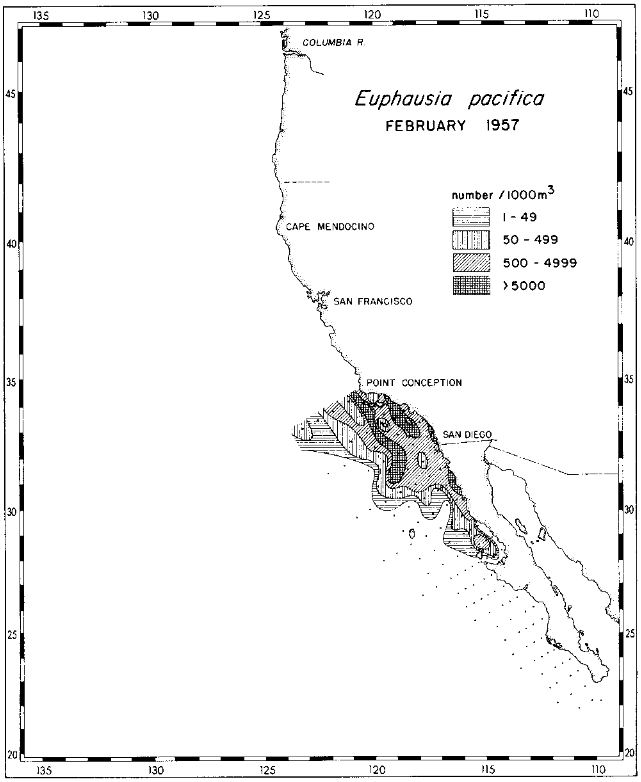

FIGURE 124. Distribution and abundance of the euphausiid *Euphausia pacifica* during February 6 to 20, 1957 (CCOFI Cruise 5702).

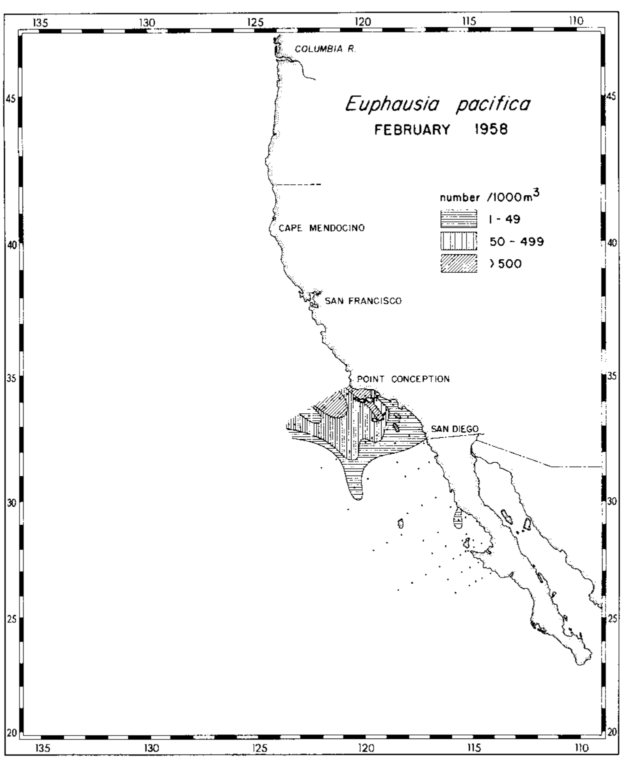

FIGURE 125. Distribution and abundance of *Euphausia pacifica* during February 6 to 24, 1958 (CCOFI Cruise 5802).

to near 40°N. It ranges southward in the California Current, terminating off Southern California or Baja California (Figs. 124, 125, 126). *E. pacifica* is frequently abundant, and its distribution may be used as a measure of the southward extension of the cold-water fauna.

TRANSITION ZONE DISTRIBUTIONS

Nematoscelis difficilis and *Thysanoessa gregaria* are present along the boundary between the subarctic and central regions, overlapping both. In the California Current region their distributions bend southward toward equatorial waters. They are dominent off Central California. If plankton sampling were limited to the CCOFI area, these species would be present at nearly all stations, suggesting a wide range. Actually they are present in a narrow (35-44°N) east-west oceanic belt with a southward extension in that part of the California Current which contains semi-permament eddies of Southern California and mid-Baja California.

CENTRAL DISTRIBUTIONS

Euphausia brevis and *E. hemigibba* represent an assemblage that is dominant south of 40°N and north of about 20°S. extending eastward to the offshore waters of central and southern California and Baja California. In these latter waters their presence is regarded as an indication of encroachment of the offshore "central" environment upon the coastal waters (Figs. 127, 128, 129). In order to consider assemblages one must lump together those species that have similar zoogeographical affinities, even though no two species have exactly the same range.

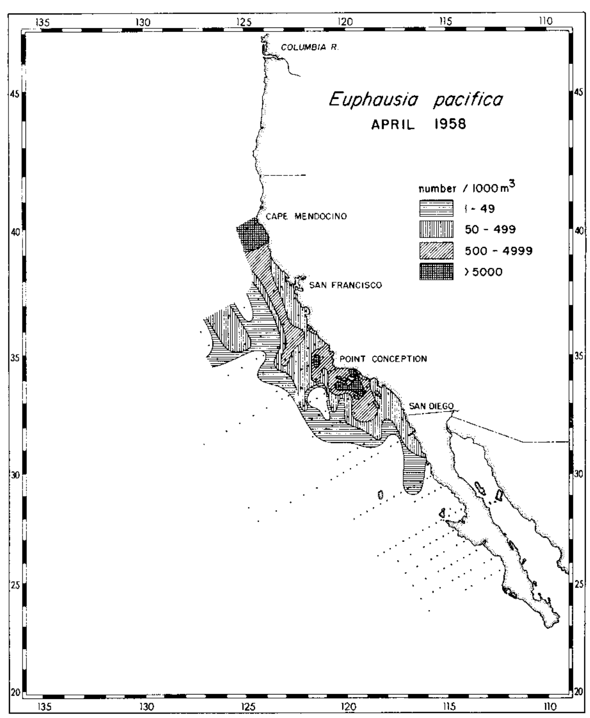

FIGURE 126. Distribution and abundance of *Euphausia pacifica* during March 30 to April 27, 1958 (CCOFI Cruise 5804).

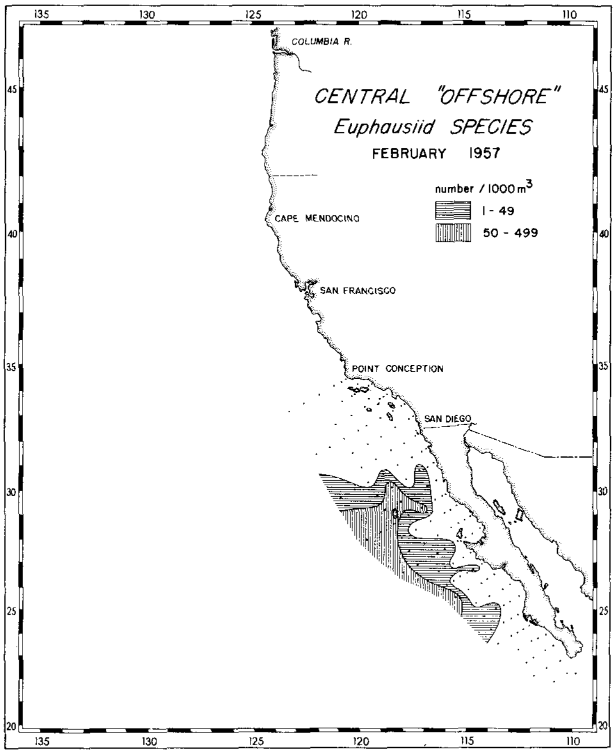

FIGURE 127. Distribution and abundance of central offshore euphausiid species during February 6 to 20, 1957 (CCOFI Cruise 5702).

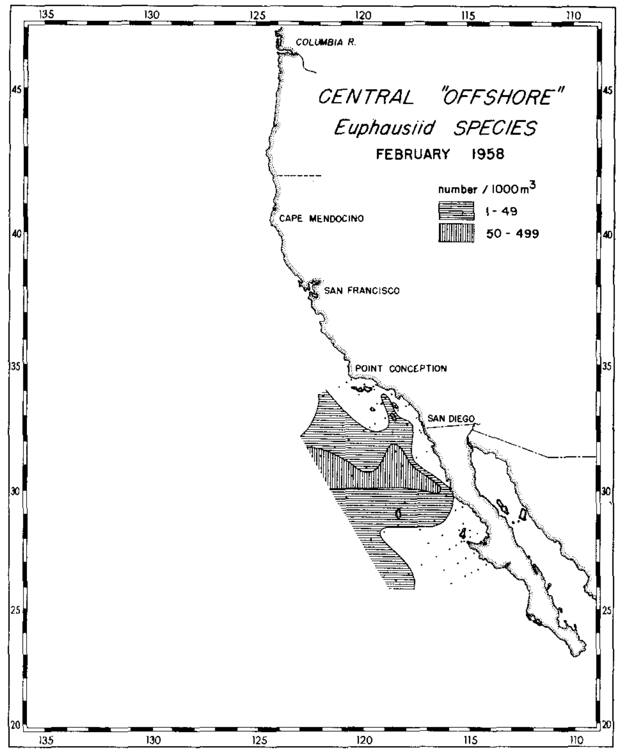

FIGURE 128. Distribution and abundance of central offshore euphausiid species during February 6 to 24, 1958 (CCOFI Cruise 5802).

EQUATORIAL DISTRIBUTIONS

Euphausia eximia (Figs. 130, 131) is a species which is confined to the Eastern Equatorial Pacific. It has a more restricted type of equatorial distribution than *E. diomediae,* which extends all the way across the Pacific between approximately 20°N and 20°S. *E. eximia* is most numerous in two regions: 1) where California Current waters merge with the equatorial current system, and 2) where the Peru Current contributes to the fertility of an environment near the beginning of the South Equatorial Current. The distribution boundaries of equatorial species undergo changes in their terminal region off Southern California and Baja California. The equatorial assemblage is dominant south of 20-23°N.

We have reason to think that *E. eximia* is deeper than, for example, *Euphausia pacifica* and *Nyctiphanes. E. eximia's* vertical distribution indicates that it migrates to a depth of about 300-700 meters in the daytime; adults approach the surface at night, but have not been found at the surface. Off Southern California *Nyctiphanes* migrates within the 0-150 meter layer.

Compared to *E. eximia, E. distinguenda* is an eastern equatorial species that is consistently present only south of the latitude of Cape San Lucas (23°N). When it occurs in the California Current off Baja California it is rarely numerous but may indicate northward transport of water. However, in late 1957 *E. distinguenda* was more numerous off Baja California south of Pta. Eugenia than at any previous

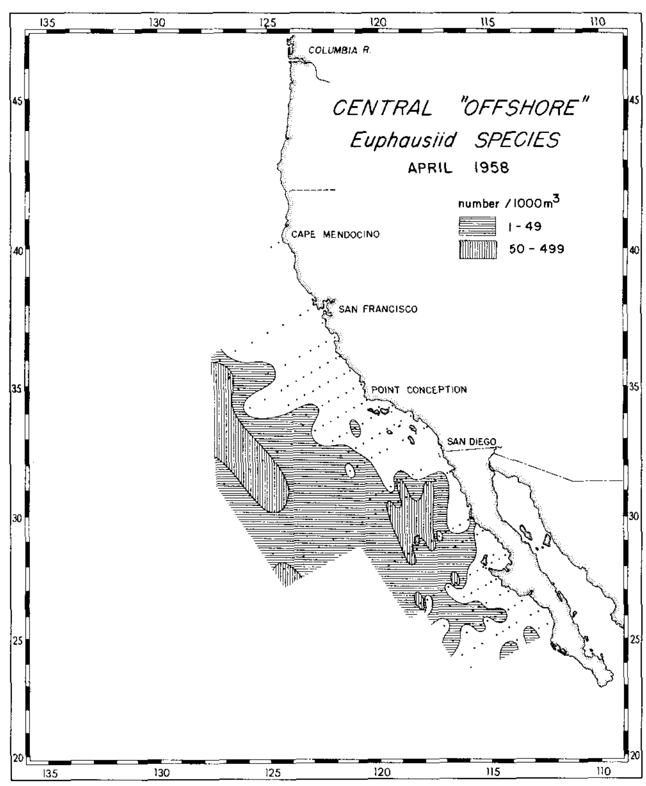

FIGURE 129. Distribution and abundance of central offshore euphausiid species during March 30 to April 27, 1958 (CCOFI Cruise 5804).

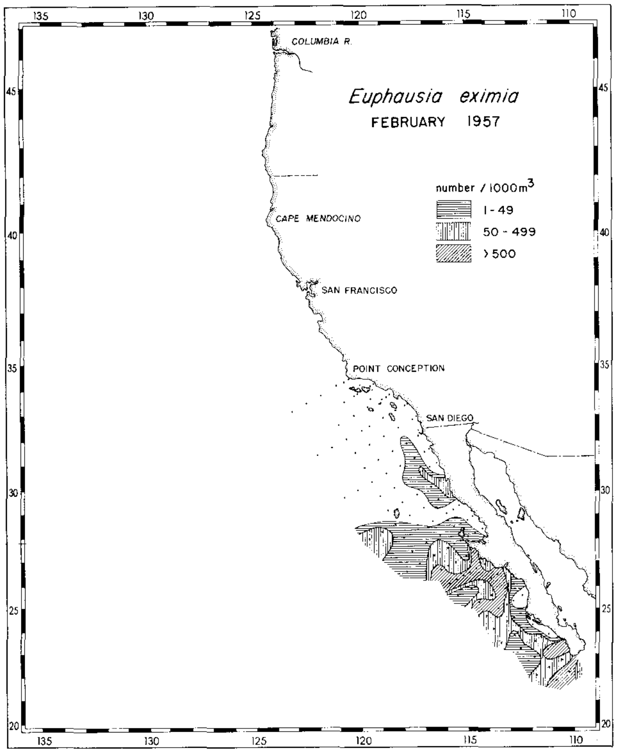

FIGURE 130. Distribution and abundance of the euphausiid *Euphausia eximia* during February 6 to 20, 1957 (CCOFI Cruise 5702).

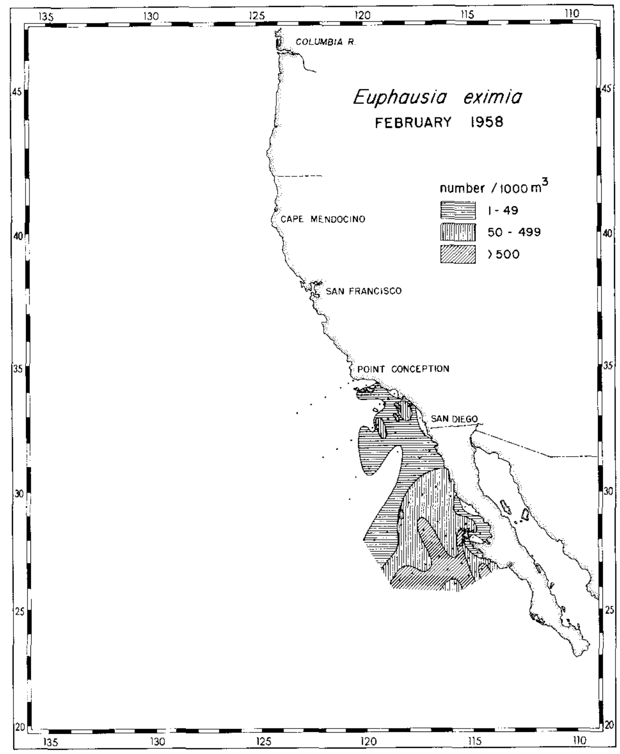

FIGURE 131. *Distribution and abundance of Euphausia eximia during February 6 to 24, 1958 (CCOFI Cruise 5802).*

time, 1949-1956. The population contained many developmental stages, suggesting that an equatorial environment had developed to the north enabling individuals to reproduce there. In addition to being carried north from its eastern equatorial habitat, this species was found to have been carried as far west as 175°W in the latitude of the North Equatorial Current (Equapac Expedition, Sept. 1956). This is one of the dominant species in the Gulf of California; populations live and develop there. But the occurrence of *E. distinguenda* in the waters west of Baja California is exceptional.

The standard oblique plankton tow made in the course of CCOFI sampling is to a depth of 140 meters, using a net one meter in mouth diameter, of 0.6-0.7 mm mesh width. Most euphausiids counted are immature. Tows made below 140 meters indicate that there the adults are dominant, particularly during the daytime. Thus the counts for the CCOFI data are weighted toward small specimens.

If the tows upon which the distributions are based had been made to a depth of 300 meters (as were the tows made by POFI and the Scripps Expedition) some differences in species boundaries would be expected, but differences would be in details. For instance, during the 1953 Transpac Expedition tows were made to at least two different depths at each station. In some cases the 0-700 and 0-1,000 meter strata were sampled. A change in the southern boundary of northern cold-water species was found at only a few stations by deepening the stratum sampled. A good measure of the importance of stratum thickness was derived from sampling done during the Scripps Institution's 1939 cruise off the coast of California, where the series of station lines was similar to the present CCOFI pattern. Changes in apparent distribution brought about by deepening the stratum sampled from 0-70 meters to 0-140 meters or to 0-180 meters were few, qualitatively. The three depths were sampled on the 1939 cruise. If the species was present in—or was absent in—the shoaler tow, the chances that a different record would be shown by the deeper tow were about two or three in fifty. Multiple tows were also made on NORPAC cruise, 1955. The deepest (0-700 meter) tow was not made at every station, but considered on the basis of tows through 0-140 meters and 0-280 meters, species' distribution boundaries were rarely altered by taking the deeper sample into consideration.

Some species (e.g. *Thysanoessa gregaria*) descend to a limited extent as warm waters are approached. There are also warm water mesopelagic species (e.g. *Nematobrachion boopis*), which ascend as their cool-water distribution boundaries are approached. These are local phenomena and do not greatly alter the broad scale distributions derived from 0-140 or 0-280 meter sampling.

Animals that do not have unlimited depth tolerance might be restricted horizontally by superficial isotherms.

Certain isotherm lines nearly coincide with species distribution boundaries indicating that there are physical properties that have the same type of distribution. For example the 12°C. isotherm at 100 meters bounds the southern limit of *Euphausia pacifica*. Certain species relate best to surface or shallow temperatures. Others relate to deeper isotherms, and inasmuch as the vertical ranges of most species are considerable, it is not easy to say how the isotherms could be limiting for each species.

It may be useful, before considering 1957-58 changes, to review the three main zoogeographic features of the coast of California and Baja California—features that may fluctuate from season to season or year to year.

SOUTHWARD EXTENSION OF THE SUBARCTIC AND TRANSITION ZONE DISTRIBUTIONS

Cold water species were consistently present in large numbers off Central California and in small numbers off Punta Eugenia, Baja California, in the years of the CCOFI program 1949-1954. Populations of these species changed quantitatively off Punta Eugenia in 1954-55. *Euphausia pacifica* and *Thysanoessa spinifera* became numerous and widespread in this region in April of 1954, and 1955, related to cooled waters there and an extensive eddy west of mid-Baja California, near the southern limits of the ranges of the species. In April-June of the years 1949-1952 the cold-water populations in this southern region were inconspicuous.

EASTWARD INCURSION OF OFFSHORE "CENTRAL" SPECIES INTO THE COASTAL AREA

This group has a distribution complementary to that shown by the westward tending tongues of cold-water. The central euphausiids may appear close to shore, usually off northern Baja California and Southern California, apparently in relation to the cyclonic circulation there. They are carried eastward as they are caught up in the southern half of this gyre, and sometimes enter the coastal region of Viscaino Bay, overlapping the western boundaries of the cold-water animals.

NORTHWARD EXTENSIONS OF EQUATORIAL DISTRIBUTIONS IN THE COASTAL REGION

Euphausia exima has been consistently abundant off mid-Baja California, 1949-1955. Other species with equatorial affinities *(Euphausia distinguenda, E. tenera, E. diomediae)* sometimes have been present in small numbers south of 27° north; there have been very few records from waters north of Viscaino Bay (28° N).

1957-1958 OBSERVATIONS

February and October, 1957, cruises and February and April, 1958 cruises have been examined for euphausiids. The distribution of *Euphausia pacifica* in February 1957 (Fig. 124) was normal for that month both qualitatively and quantitatively. In contrast, February 1958 (Fig. 125) found this species distribution extremely retracted from the southern part of the coastal area. This is normal for October-December, but not for February. By December *E. pacifica* has usually (1949-55) withdrawn northward to near the latitude of San Diego (33° N).

During April *E. pacifica* was characteristically (1949-55) present in the oceanic area from Guadalupe Island to Pta. Eugenia, sometimes occurring even farther to the south. In contrast, in April 1958 (Fig. 126) this species was sparse in this region and its distribution off Southern California was more inshore than had been previously found for this month of the year. Nevertheless, it must be noted that this cold-water species was *still present* in substantial numbers off Southern California in 1958.

E. pacifica probably lives somewhat deeper than the next species, *Nyctiphanes simplex*, which in 1949-57 occupied the coastal region, usually south of Point Conception. In February 1957 (Fig. 132) *Nyctiphanes* was present in low concentration south of the Point. This was like previous years. In October 1957 all developmental stages of this species were more numerous than usual at the northern limit of its range in the region of the Southern California Channel Islands. I interpret this as meaning that the environment in the upper water layers off Southern California was modified in late 1957, permitting *N. simplex* to reproduce in a relatively northern area. It has subsequently (Figs. 133, 134) reproduced heavily in the areas immediately south and just north of Point Conception, where it had heretofore been rare or absent in April. The April 1958 cruise (Fig. 134) shows that *Nyctiphanes* occurred all the way to Cape Mendocino (40°N) though in very small numbers; but off San Francisco (38°N) concentrations were greater than 50 per 1,000 cubic meters at two stations. I do not think we can regard this northward distribution as necessarily a manifestation of a persistent countercurrent. Drogue measurements made in March showed that the countercurrent was not present at the surface at that time. The large populations of *Nyctiphanes* that were off Northern California in April 1958 must have been residual there, if continuing transport from the south had not been maintained through the winter. These southern animals have, during this 1957-1958 period of change, extended far north of their "normal" range.

The offshore occurrence of warm water animals of the central type seems to have undergone little change in the critical region off California. This is the region off San Diego and south of Point Conception. The warm water animals are few here, and while their encroachment toward the east is somewhat greater in February and April 1958 (Figs. 128, 129) than in February 1957 (Fig. 127) or February 1949-55, interpretation in terms of water movements must be speculative. This warm water environment has moved northward and toward shore, but the area *dominated* by the central species is still far offshore.

Another species, *Euphausia eximia* (Fig. 130) is an equatorial type, which occurs in the southern part of the CCOFI survey region and was present north of its usual range, close to shore in 1957-58. It was more numerous to the north, off Southern California in February 1958 (Fig. 131) than during 1949-55. This might be regarded as another indication of the northerly extension of the warm-water environment provided by the current system that distributes the animals.

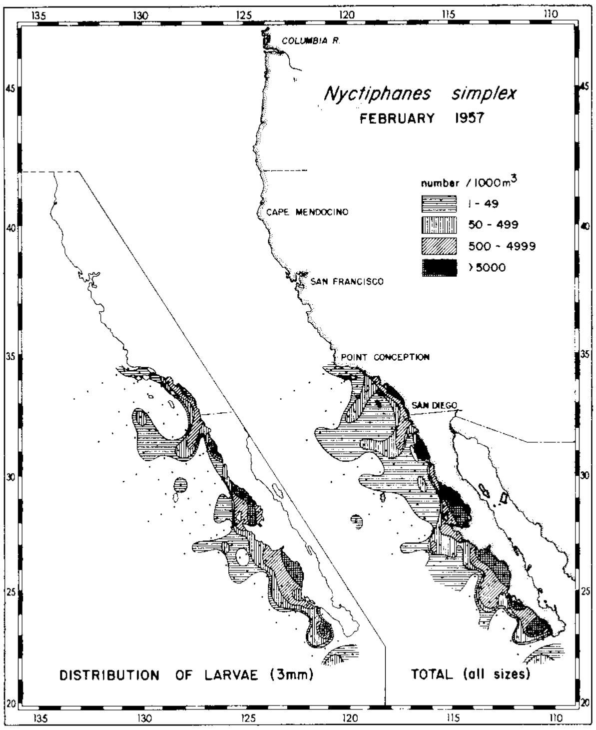

FIGURE 132. Distribution and abundance of the euphausiid *Nyctiphanes simplex* during February 6 to 20, 1957 (CCOFI Cruise 5702).

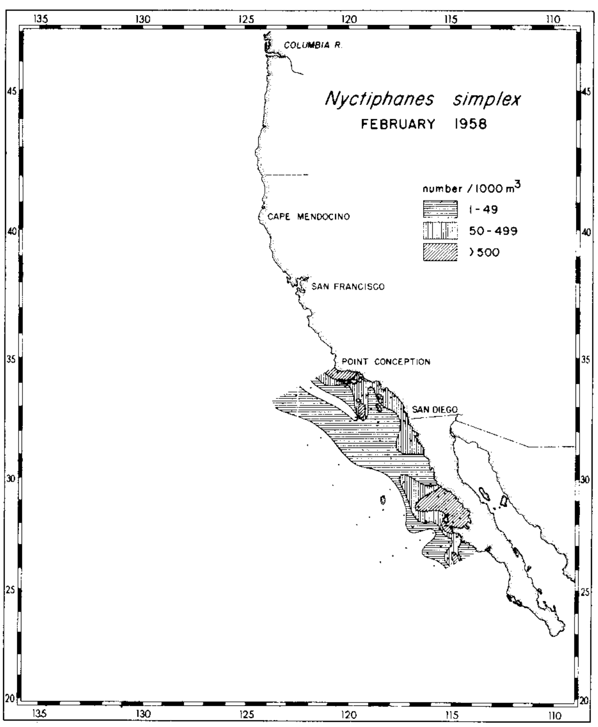

FIGURE 133. Distribution and abundance of *Nyctiphanes simplex* during February 6 to 24, 1958 (CCOFI Cruise 5802).

DISCUSSION

Revelle: Does *E. eximia* occur in the same area where you have *Nyctiphanes simplex?*

Brinton: No, *E. eximia* is in a slightly more offshore region and behaves differently from *Nyctiphanes* because it is a deeper living animal. If there were a very shallow northerly current, you might expect *Nyctiphanes simplex* to be transported farthest, because it would be in the surface layer more continuously than *E. eximia,* which rises into the superficial layers only at night.

Isaacs: Was *E. eximia* found north of Point Conception in April 1958?

Brinton: Yes, it was present at one station off Monterey Bay, and at two other stations north of Point Conception. *E. eximia* had never been previously found north of Point Conception.

Fleming: Practically all your figures show that euphausiids are mostly concentrated near the coast —an example of the Fuglister principle?

Brinton: That is the trouble with our area, I think, rather than with the animals. A feature of our coast is that regions of fertility occur just south of Point Conception, off Punta Eugenia and very close to shore in the intermediate region 28-33°N. All are cool regions as far as the northern species are concerned. The animals might be basically oceanic and still be numerous near-shore because of nutrient renewal expected in the coastal regions.

These animals appear to hug the coast in these regions. I still think they may be regarded as oceanic animals. Euphausiids are primarily phytoplankton-filtering animals that are not found near the surf zone so to speak, but offshore. These small-scale maps are somewhat misleading, particularly where you have heavy concentrations against the shore. Here high euphausiid concentrations are adapted to the cool oceanic waters in coastal regions.

Berner: I think this is true of many species.

Reid: Our region is relatively barren offshore. There are more animals living in the inshore regions which are seasonally rather stable compared to the offshore areas. These animals take advantage of the small seasonal changes in temperature and the cold water masses which are found year round somewhere within the range of 200 miles—a characteristic of this transitional region.

Hubbs: Do you have any collections from the previous warm years, say like 1926, '31 or '41 from Monterey or from anywhere up that way?

Brinton: No. I had intended to make reference to the 1939 cruise. It extended from the Columbia River to south of Punta Eugenia. This is significant from the standpoint of our survey program because the cruise was carried out at a time when many of the subtropical fish were taken off Central California, and when the sardine was spawning there.

Hubbs: What part of 1939?

Brinton: May through July. That is before it got very warm off Southern California. The southern line

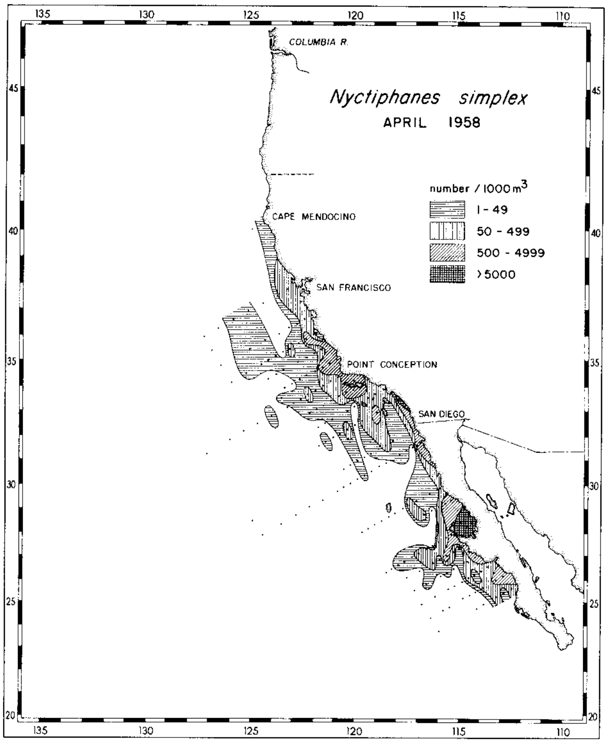

FIGURE 134. Distribution and abundance of *Nyctiphanes simplex* during March 30 to April 27, 1958 (CCOFI Cruise 5804).

of stations, extending westward from Viscaino Bay, was occupied in July.

Hubbs: Then we missed that warm water north of Point Conception that year.

Brinton: Yes. According to the chart of *Nyctiphanes* for 1939, one feature that I think is remarkable, and unique for 1939, is the occurrence of a cool water population off Point Eugenia as late as July, including large numbers of *Nyctiphanes* and *E. pacifica*. Cold eddies in this region in 1954 and 1955 were not observed later than April, I believe. In 1939 they persisted at least until early July. There was a very cold spring that year. The cruise was too late to record what was going on in the winter time, of course. In general the 1939 May through July distributions looked typical, with the exception of this particular area off Point Eugenia.

Sette: As I recall, February was almost a record cool month.

Isaacs: One of the coldest springs on record occurred in 1939, and one of the hottest falls.

Brinton: In February 1957 *Nyctiphanes* (Fig. 132) ranged north of Point Conception where it was present in small numbers near shore. This was not strikingly different from previous Februarys. The countercurrent, which seems to have been conspicuous in April 1958, was already pronounced in the winter of 1957-58 when *Nyctiphanes* was abundant as far north as the survey went (Pt. Conception) and *E. eximia* was well north of its distribution of February 1957 (Fig. 130). Where we have stations to the north of Pt. Conception it is evident that *Nyctiphanes* extended as far north as Cape Mendocino (Fig. 134). The central species had moved nearer than usual to the shore off Southern California in April 1958. This change is not great. Nevertheless we have to look for small changes. Only the northward extension of *Nyctiphanes* was conspicuously different in 1957-58.

Hubbs: The distribution of *Nyctiphanes* in April 1958 (Fig. 134) is the only one that shows numbers offshore at all, north of Pt. Conception.

Brinton: In the waters off Baja California there is an example of a change, which is evident in February 1957, however slight. This change was the northern occurrence of other equatorial species that normally do not occur north of Cape San Lucas except for occasional stragglers. They were not present at all stations, but in February 1957 there were more stations where equatorial animals occurred than is usual off Baja California. Again, these equatorial species were not being swept into the area, but were present in larger numbers at the southern stations in early 1957 than in the first three months of any of the years 1949-55.

Berner: The animals that apparently live in the upper layers show the changes more than those that live throughout deeper layers. Apparently *Nyctiphanes* and *D. denticulatum* are more inclined to the upper layer, and show this northward movement more than the other animals that live at a greater depth.

Brinton: Yes, I would say that of the species I have looked at, the one that shows the strongest northward shift in distribution seems to be restricted to the waters above 100 meters. Some of the deeper ones are slightly farther north than is normal.

Johnson: What are the youngest stages included in your counts?

Brinton: The youngest stages are about 3mm in length, sometimes smaller. Some of the small stages are lost through the net mesh. These larvae are probably two to four weeks old by the time the net retains them.

Johnson: So the count indicates a smaller population than is actually present.

Brinton: Yes, and larvae of *Nyctiphanes* made up some of the population north of Point Conception. The general distribution of larvae is not as extensive as that of adults, as is evident for February 1957 (Fig. 132). Spawning occurs close to shore; the adult population diffuses somewhat seaward. In February 1954 spawning occurred to the northern limit of the adult range. There is always a possibility that only the population of larvae near the surface, may be swept into an area, but, more often, the general population is carried together.

Reid: One thing that seems to stand out is the change in the distribution of the southern types rather than in that of the central types. Is the central type documented well enough to say that it did not move in?

Brinton: It is not documented well enough to be definitive. The central types that I have plotted for California waters in February and April 1958 (Figs.

128, 129) suggest that they all move slightly toward shore. But I feel that this change is not as conspicuous as the northward movement of *Nyctiphanes* and *E. eximia*. The presence of unusually warm water in the California Current could lead to intrusion of both assemblages.

Question: The results might show some on-shore encroachment although they do not swim in but are moved in by the water.

Brinton: They probably do not swim in very actively. Encroachment in the course of a month or two months may be helped by random diffusion of the population in mixed areas. The animals swim up and down—spending most of their lives in swimming up and down. They probably move at random laterally, some of the time, and this could be enough to extend their range into an adjacent region that might be tolerable to them.

Johnson: Directive forces drive them up and down, so they swim straight up or straight down, but the thermal gradients to the right or left are less. Perhaps they do respond to smaller gradients than we think.

Murphy: Do all euphausiids come to the surface during a 24 hour period?

Brinton: No, not all species. I have lumped the species into three bathymetric groups. One group of species lives above 700 meters; these migrate near to the surface at night. A second group lives between 500 and 2,000 meters. These never get to the surface. The third group is bathypelagic—only the larvae live in the upper layers while adults live below 1,500 meters.

If you take the depth distribution of a species which lives in the 0-700 meter environment the youngest vertically migrating stages of development are nearest the surface. The adults would be the deepest. Many of the larvae which are one to two months old live within 20-25 meters of the surface.

Question: Do you suppose sampling of plankton should be switched to the night stations because more adults are found then?

Brinton: Night hauls frequently contain more adults than day hauls. Numbers of larvae and immatures may or may not vary in this way. Most of the animals that are immature seem to be well sampled by the relatively shallow 0-140 meter tows. However, the picture would be much more reliable with a standard time of sampling.

Reid: Your pictures are very coherent.

Brinton: Considering this type of difficulty there still seems to be coherence to the distributions.

Wooster: I would like to borrow Dick Fleming's iconoclastic role for a moment, if I may. We have said before this session started that in many ways the animals might be better oceanographers than the oceanographers, and I am beginning to think that, like many a good oceanographer, they are very difficult to understand. It seems to me the use of zoogeography as an indication of oceanographic circulation has to be calibrated with physical or chemical oceanographic parameters. If species distribution agrees with distribution of temperatures, it is good that this all fits together. Actually, you have not learned anything about circulation; you have learned something about the temperature tolerance or affinity of the organisms. If distribution does not agree with the particular physical parameters with which it is compared, then you are sort of perplexed. One of two things happened: either you chose the wrong physical parameter, such as surface temperature (often it must be that, I think), or something else has happened that you do not really understand. It seems to me that looking at this in general, the comparison of distribution of organisms to those of physical and chemical parameters is likely to show more about the beast than about the ocean.

Johnson: It brings out some points where an oceanographer should look for more information than he has.

Wooster: What he is saying is that where distribution of the physical parameters and the distribution of the beast do not agree, then the oceanographers may have the responsibility of explaining this. It may be something in the biology of the beast, or it might be something not being looked at properly in oceanography.

Isaacs: Euphausiids migrate vertically through a range of 10 to 12 degrees Centigrade, and yet for years they had a distribution that turned out to be consistently limited within 0.2°C by a certain 10 meter isotherm and this all in a moving current. Does anyone think that the temperature of this isotherm was restricting this distribution?

Brinton: It is hard to say. So little is known about the actual physiological requirements of the animals. One temperature might be limiting for feeding, another for reproduction, another for a metabolic function. So it is probably an extremely complex business. One isotherm might be limiting in one area and a different isotherm in another.

Johnson: I think probably while we are on the particular question of temperature requirements and also in the matter of deposition of eggs near the surface, I might point out the case of *Thysanoessa spinifera* washed up on the beach at La Jolla in large numbers. They all turned out to be spent females. What actually happened may have been that they had risen unusually close to the surface to spawn and had been caught in inshore currents and washed up on the shore. Surface temperature might be exceedingly important to spawning.

Ewing: There is one feature that perhaps we are missing or have overlooked, that is the biological edge effect, which we all know, does not affect the extent of distribution, but the density of populations. This is very dependent on boundaries between currents or water masses. On land the transition conditions between dissimilar environments very much increase the carrying capacity of the environment, cutting it up into smaller areas so that the animals have a longer boundary environment. There are cases where this seems to be true in the ocean as well, such as at a front. It is not so much the average temperatures of the water mass itself that determines the carrying capacity of the water as it is the amount of boundary. The albacore is quite sensitive to this. It likes to stay in fairly warm water and feed in cool inshore water. It likes to feed in one environment and live in another. One reason why many so-called warm water animals are at times most abundant along the edge of the California Current, or at least along the cold water, is that they can stay within their temperature tolerance and have access to cold waters which are in general more nutritious. They get as close to their food as they can and still stay in their own temperature range. As an example, the boundary off Cape San Lucas is very nutritious and always full of marine life. Very high gradients are found there. So it is very easy for an animal to pick an optimum area. Many animals must choose environments adjacent to boundaries where there are gradients rather than those areas where optimum conditions prevail.

Ahlstrom: These temperature ranges that I believe we are mentioning, none of these concerns both adults and the larvae. The larvae could have quite different and much smaller temperature ranges, and I think for each stage this has to be established. I think it is a mistake to take the range of an adult and apply it to larvae.

Brinton: Yes, I think there is danger in that too. However, the thing that is remarkable to me is that more often than not, you find very many stages of development together. But of course this is sampling through a long vertical column. In this extreme northern extension of *Nyctiphanes* (Fig. 134) occurring off Mendocino all were adults however. At the stations off San Francisco there were some larvae present. Surface temperatures were 12°C. off Cape Mendocino. I am certain that this species could not survive long there.

Isaacs: What are the comparative ranges of temperature of the distributions of *Nyctiphanes simplex* in the two hemispheres?

Brinton: The temperatures circumscribing the distribution of *simplex* in the Peru Current on Shellback Expedition were very similar to the temperatures found in our CCOFI region: the 20°C. isotherm, normally, I think. But in 1958 it was in colder water at Cape Mendocino, 8 degrees cooler than the usual limiting temperature.

Revelle: What interests the biologists, what interests the organism, what interests the physical oceanographer? The physical oceanographer can measure the temperature very easily and is not interested in using organisms as a thermometer. But he cannot always follow the water masses around by temperature alone; he likes to use organisms as drift bottles. In order to use the drift bottle you have to know where you release it and where you pick it up. These animals are very easy to identify as to where they are picked up, but not as to where they were released. The second difficulty is of course that they apparently migrate vertically as well as horizontally and therefore they are drift bottles that can be used in a kind of hazy way for water at different depths. Looking at this from the standpoint of the organism, the biologist or the physical oceanographer, you have three different things you are concerned about—can the organism swim? How fast can he swim? How far does he swim horizontally? Really, they are no good as drift bottles because they can migrate from that deep scattering layer to the surface in half an hour. This is 400 meters which means they can swim roughly a kilometer an hour or about 20 kilometers a day. They could move extensively in a rather short time.

Brinton: There is no question that they could move into an area that is tolerable as to temperature. It would be nice to know the extent to which they do move laterally, but the observations that have been made on their swimming behavior are only on their vertical movements. They are usually in a sort of spiral path.

Question: What would happen in a boundary region where an animal might be expected to extend his range by random swimming?

Brinton: I do not know what would happen. I do not think there is much likelihood that it would purposefully swim in any given direction horizontally.

Revelle: If you invoke random swimming, though, you would not have as sharp a boundary as you actually have. Look at these February distributions of *Euphausia eximia* (Figs. 130 and 131). A great many are in a certain region, then they stop abruptly. That is true in almost all cases. Your distribution has quite definite boundaries.

Isaacs: This is a strong argument against random dispersion—they do not randomly swim as individuals but as swarms.

Revelle: But it will still cause a dispersion.

Murphy: The map says they are not randomly distributed.

Wooster: Why can not these organisms be spreading, diffusing, or swimming horizontally in a random fashion? In fact, they probably are. They are exerting pressure on the limits of their distribution at all times. Due to physical circumstances the population is tending to spread all the time for one reason or another, and when it goes into an environment that is not favorable, it is dying off or somehow being wiped out. When it spreads out and finds a suitable environment, then it prospers and would develop a tongue by diffusion. On the other hand, a distribution might be reduced around the edge by attrition. A group of parameters rather than a single one, limit its distribution.

Sette: I think we are all agreed that the animals are reacting to something essentially other than temperatures. Nonetheless we use temperature as a marker of water masses or circulation systems. An animal or a group of animals may be an indication of many things—just as temperature is, by the way. The observation of events would not be confined to the physical parameters if other things could as easily be measured.

Murphy: I agree with Warren Wooster; you just do not know the life requirements of these animals, so that finding an animal in a particular place does not say very much about the reasons it was there. We need a better history of it. As to temperature, as it was pointed out before, if you want to know the temperature, you might as well go out and measure it. We do get some data on living things without sending an expedition. Fish kills and unusual distributions of fish are reported by fishermen.

Revelle: I am not arguing; I do not object to the collection of animals. I am simply saying that in the process it is also very easy to measure temperature.

Radovich: Regarding the question of whether or not euphausiids can swim purposefully, I recall that during one of our sardine conferences Dan Miller of the Department of Fish and Game mentioned that schools of gravid *E. pacifica* were seen in Monterey Bay from an airplane. These schools were subsequently sampled from a boat—they were moving similarly to fish schools. I also observed what I thought was a school of euphausiids off Anacapa Island several years ago. I tried to observe the way they were moving.

Question: With the current?

Radovich: No, they were swimming. As we came upon them the school would separate and move away from the boat.

Murphy: This means they do have capacity for coherent motion.

Brinton: Their spawning behavior shows a local peculiarity. For example, these schools have never been observed in the open temperate ocean to my knowledge.

Berner: These schools of *Euphausia pacifica* have been observed at one time or another off central California between Point Conception and Cape Mendocino.

Johnson: Where you have shading on the map—it does not mean that every station yielded animals, does it? There would be zero values in a number of cases.

Brinton: Where the relative numbers of animals belonging to the different assemblages are plotted, for example as the "central offshore" species are plotted (Figs. 127, 128, 129) the zero values for the assemblage would be shown as clear places. There is continuity within these species distributions. Within the distribution there might be smaller dense patches. Often whales actively seek out swarms of euphausiids; that is the only way they can get as many as they do. A plotted record is, of course, a reflection of the situation at a moment, perhaps a week before a species did occur at stations outside of its indicated range. A southern group extending northward as a tongue may be really receding, having had earlier a more extensive distribution.

Isaacs: Some areas of apparently low concentration result from day samples when the euphausiids are at deeper levels as compared with night samples when more of them are in the upper layers.

Brinton: Possibly. I have sometimes in the past tried to correct for day-night differences in apparent concentration. Sometimes numbers are consistently higher in night hauls, sometimes not. If you omit all the day stations on the periphery of a range, it sometimes makes a much improved contour—a smoother one. In other instances there seems to be no reason for concentration irregularity. It would be nice to have all night stations, then you would know that the animals are within the sampling limits.

Revelle: Is it possible to interpret these in terms of onshore movements?

Brinton: Not with certainty. It is impossible to say that there is movement of water in any particular direction. However, I have tried to speak in terms of the environment of the animals being extended in one direction or another. This may be due to local changes or it may not, but I do see examples from time to time where I feel that there are movements of the water.

Revelle: I am talking about the change that we are discussing during this Symposium, that is, whether the water moves from the center of the ocean to the edge, or whether it is actually motion in a north or south direction. I wonder if any light can be thrown on this from the various kinds of critters. I gather the impression that, except for small features and except for coastal species found to the north, the distribution may very well be accounted for by the major movement of the warm offshore waters toward shore, plus the ability of these critters to seek out environments that they like.

Sette: The evidence does not clearly settle the question of whether or not the euphausiids were drifted, or whether they moved by their own effort or a combination of both.

LITERATURE CITED

Bargmann, H. E., 1945. The development and life-history of adolescent and adult krill, *Euphausia superba*. *"Discovery" Rep.* Vol. 23 pp. 103-176.

Brinton, E., 1957. Distribution, Faunistics and Evolution of Pacific Euphausiids. Doctral Dissertation, Scripps Inst., Oceanog., U. Calif.

Einarsson, H., 1945. Euphausiacea 1. Northern Atlantic species. *Dana. Rept.* No. 27: 1-185.

Moore, H. B., 1952. Physical factors affecting the distribution of euphausiids in the North Atlantic. *Bull. Marine Sciences Gulf and Carib.*, Vol. 1 (4): 278-395.

Reid, J. L., Jr., G. I. Roden, and J. G. Wyllie, 1958. Studies of the California Current system. *Progress Rep., California Cooperative Oceanic Fisheries Investigations.* pp. 27-56.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming, 1942. *The Oceans.* 1087 pp.