

THE DISTRIBUTION OF PACIFIC EUPHAUSIIDS

BY
EDWARD BRINTON

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SUMMARY

A STUDY has been made of the distribution of 59 euphausiid species in the Pacific Ocean, based upon oceanic surveys carried out from 1949 to 1961 by the Scripps Institution of Oceanography, California Cooperative Oceanic Fisheries Investigations (CalCOFI), and Pacific Oceanic Fisheries Investigations (POFI). Quantitative aspects of the vertical and horizontal distributions are presented.

The species belonging to the genera *Bentheuphausia* and *Thysanopoda* are typically deep-living. *Bentheuphausia ambloyops*, *Thysanopoda cornuta*, and *T. egregia* are widely ranging bathypelagic species, the adults of which inhabit depths greater than 1,500 meters.

Of the ten genera, six (*Thysanopoda*, *Euphausia*, *Thysanoessa*, *Nematoscelis*, *Nematobranchion*, and *Stylocheiron*) contain some species that inhabit a mesopelagic zone between depths of about 500 and 1,500 meters and other species that are characteristically epipelagic, living mainly above 500–700 meters.

The epipelagic species are designated in accord with the analogous water masses inhabited. The Pacific water masses are (1) subarctic, situated to the north of the North Pacific Drift, including only the northern part of the California Current (typical species: *Thysanoessa longipes*, *Tessarabrachion oculatus*); (2) transition-zone, including the cooler part of the California Current south of 40°–45° N. and a belt extending westward to Japan in the region of the North Pacific Drift (typical species: *Thysanoessa gregaria*, *Nematoscelis difficilis*); (3) central, occupying the oceanic gyres of mid-latitudes 15°–40° in both hemispheres (typical species: *Nematoscelis atlantica*, *Euphausia brevis*); and (4) equatorial, occupying a broad tropical belt in the eastern Pacific and a narrower belt to the west (typical species: *Euphausia diomediae*, *E. distinguenda*). Equatorial species occupy equatorial water masses in the Pacific and Indian oceans.

A zone occupied by the transition-zone species *Thysanoessa gregaria* and *Nematoscelis megalops* (corresponding to *N. difficilis* of the Northern Hemisphere) occurs near 35°–45° S. Subantarctic and antarctic species are found south of the Subantarctic Convergence.

The composite range of a tropical western Pacific group of species (e.g., *Euphausia pseudogibba*, *E. fallax*, *E. sibogae*) extends eastward across the Pacific in a zone 10°–20° S., while an eastern tropical group (e.g., *Euphausia distinguenda*, *E. eximia*) extends westward in a tongue having an axis near 10° N.

Ekman's zones of the Pacific littoral fauna each have a counterpart species in the coastal or boundary euphausiid fauna.

Seasonal changes in euphausiid distribution are discussed with respect to five regions: (1) the Kuroshio and East China Sea, (2) the North Pacific Drift Current, (3) the California Current, (4) the Peru Current, and (5) the equatorial mid-Pacific.

Day and night vertical distributions, derived as average densities for broad areas of the range of the species, indicate that nearly all Pacific euphausiids are concentrated at shallower depths during the day than at night. Exceptions include the large bathypelagic species (*Bentheuphausia*, *Thysanopoda cornuta*, *T. egregia*) and the “*Stylocheiron longicorne* group.”

Two of the six species of the “*Stylocheiron longicorne* group,” *Stylocheiron affine* and *S. longicorne*, show morphological variability across their wide geographical ranges, ca. 40° N.–40° S. Five Pacific forms of *S. affine* and two of *S. longicorne* are distinguished on the basis of proportional measurements made of the bilobate eye and the sixth abdominal segment. Forms of *S. affine* are assigned non-Latinized geographical names according to the geographical habitat: “California Current Form,” “Eastern Equatorial Form,” “Western Equatorial Form,” “Central Form,” and “Indo-Australian Form.” Morphological intermediates were found between (1) the “California Current” and “Eastern Equatorial” forms, (2) the “Eastern Equatorial” and “Western Equatorial” forms, and (3) the “Western Equatorial” and “Central” forms. Intermediates were not found between the “Central” and “California Current” forms, even though the region of overlap of those ranges lay in the most thoroughly sampled water.

It is postulated that variability in *S. affine* is ecotypic in basis, related to the different water-mass habitats occupied, and has arisen within a “California Current” → “Central” sequence of environments as a consequence of a tendency to colonize “downstream” waters. Changes in the genetic constitution of the species would be expected to accompany natural selection, favoring the capacity of the species to extend its range. “Upstream” gene flow is expected to be less than “downstream,” and reproductive isolation of the geographical forms may take place when changing ocean climate establishes even short-term barriers to bidirectional transport of populations.

Biantitropical (bipolar) euphausiid species found in the Atlantic, Pacific, and Indian oceans include transition-zone species and central species, but not species occupying higher latitudes. The sibling transition-zone pair *Nematosoelis difficilis* (North Pacific) and *N. megalops* (Atlantic and southern oceans) are interpreted as having undergone relatively recent morphological differentiation.

Biantitropical panoceanic distributions may be a consequence of postulated latitudinal oscillations in Pleistocene oceanic isotherms (2° to 3° C. change at a depth of 200 m.), allowing transition-zone and central species to pass around southern limits of continents during warm epochs. It is suggested that transition-zone distributions may coalesce at the equator in the eastern parts of oceans during cool epochs and central distributions in the western parts of oceans during warm epochs.

The Pacific—Indian Ocean equatorial species have not colonized the Atlantic and may have arisen (1) when tropical distributions became disjunct along east-west axes (e.g., the present distribution of *Euphausia distinguenda*), or (2) as elements of characteristic groups-of-four species (found in each major epipelagic euphausiid genus) arising from the partitioning of a parent population into four oceans, the Atlantic, North Pacific, South Pacific and Indian oceans. In the *Euphausia mutica–recurva–brevis–diomediae* group, *diomediae* is equatorial. *Mutica*, *recurva*, and *brevis* are central species.

Subarctic and subantarctic species are endemic to a single hemisphere and may have become differentiated during cold epochs when the parent populations occupied somewhat lower latitudes than today, being then split up by the north-south continental barriers.

Partition of populations into the tropical-subtropical oceans as a consequence of climatic revolutions, together with extreme antitropicality established at the end of warm epochs, may have provided repeated instances of geographical isolation leading to the evolution of known euphausiid species.

INTRODUCTION

The pelagic environments of the Pacific Ocean encompass a broad complex of zoöplankton populations, which have only recently been sampled in a systematic manner. Surveys carried out since 1949 make possible this analysis and interpretation of Pacific zoögeography from the standpoint of one widespread pelagic animal group, the crustaceans of the Order Euphausiacea.

This study is mainly concerned with the distribution of the 59 Pacific euphausiid species on an oceanwide basis. The qualitative and quantitative aspects of distribution are presented in as much detail as the records seem to warrant. Oceanographic and ecological significance of the local occurrence of particular euphausiids is interpreted in the light of the total distributional ranges of the species—the centers of distribution and the areas of reproduction and dispersal.

The species of the California Current are given special consideration. Waters off western North America are the object of study by the California Cooperative Oceanic Fisheries Investigations, a program sponsored by the Marine Research Committee of California, emanating from the Scripps Institution of Oceanography, the Bureau of Commercial Fisheries, the California Department of Fish and Game, the Hopkins Marine Laboratory of Stanford University, and the California Academy of Sciences.

Waters off California and Baja California provide an appropriate point from which to gain a perspective of the nature of zoögeographic boundaries in the ocean. In the sluggish and often poorly defined current that flows predominantly southward between the latitudes of the Columbia River of Oregon (46° N.) and Cape San Lucas at the tip of Baja California (23° N.) are found the four principal assemblages of species: subarctic, transitional, central, and equatorial. These assemblages appear in latitudinal sequence in any north-south transection of the North and equatorial Pacific.

All known Pacific euphausiid species are included. In addition, consideration has been given to morphological relationships, so as to provide a basis on which to consider evolutionary pathways used by zoöplankton organisms that have become differentiated within the Pacific Ocean, or between the Pacific and other oceans.

ACKNOWLEDGMENTS

I wish particularly to thank Professor M. W. Johnson for his guidance, generously supplied during this investigation. It was he who initiated the study of the euphausiids at the Scripps Institution. The study of California Current species, carried forward by Brian P. Boden, also provided helpful orientation for the

continuing program. Professor C. L. Hubbs's valuable criticism of the original manuscript included many useful suggestions. The expedition leadership of W. S. Wooster contributed much to the broad oceanographic and zoögeographic coverage of the Pacific by the "Northern Holiday," "Shellback," "Transpacific," and "Troll" expeditions. While collecting plankton on the "Transpacific," "Pelagic Area," "Downwind," and "Naga" expeditions, the author received the help and coöperation of the marine technicians and the personnel of the Scripps vessels, here gratefully acknowledged.

I am indebted to Margaret Knight for much help in assembling various sections of this report, and to Grace Barsam, Dorothy Tyler, and Eva Ewing for assistance in various phases of the preparation. Desiree Brinton has helped in many ways during this investigation, and her support has greatly facilitated my work.

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PREVIOUS STUDIES

The cruise of the *Challenger* (1873–1876) provided the first extensive collection of euphausiids, an exclusively marine zoöplanktonic group. Sars's (1885) treatise on the "Challenger" Schizopoda revealed the global distribution of several euphausiid species and presented illustrations of 27 species, there described for the first time (six of which have since been transferred to synonymy or found to have been based on immature specimens).

Hansen's reports (1910, 1912) on collections made by the Dutch *Siboga* in the Indo-Australian Archipelago and by the U. S. Fisheries Commission steamer *Albatross* in the eastern equatorial Pacific in 1904–1905 underlie the systematics of Pacific euphausiids. The plankton program of the 1904–1905 "Albatross" survey was unique in its day: the net tows were taken in a uniform manner, with surface tows at night, and 0–300-fathom tows in the daytime. For this reason the station locations for this survey are plotted on the distribution maps included in this report. Hansen's records and descriptions of species from the temperate North Pacific (1915) and the Philippine Islands (1916) are other basic systematic reports.

More recent work by Banner (1949) on collections made by the International Fisheries Commission, 1928–1941, provided taxonomic and distributional information on the euphausiids of the Gulf of Alaska and the coastal waters off British Columbia and Washington (fig. 1a). Ponomareva (1955) reported on euphausiids from the region of the Kurile-Kamchatka Trench and the northeastern Pacific (1957), and Nemoto (1959) discussed the distribution of North Pacific euphausiids that are important to krill-eating whales.

Descriptions of North Pacific euphausiids were assembled by Boden, Johnson, and Brinton (1955). The ranges of the species were given on the basis of records compiled up to 1954. The present report is an extension of that study.

Available material on South Pacific euphausiids is broad in geographical scope,

though not so extensive as that upon which the North Pacific distributional ranges are based. The equatorial region, to 20° S., was traversed by the Scripps “Capricorn” expedition and by vessels of the Pacific Oceanic Fisheries Investigations, based in Hawaii. The *Albatross* sampled to 25° S. in the eastern Pacific, and the Scripps “Downwind” expedition to 47° S. in mid-ocean and to 32° S. in the

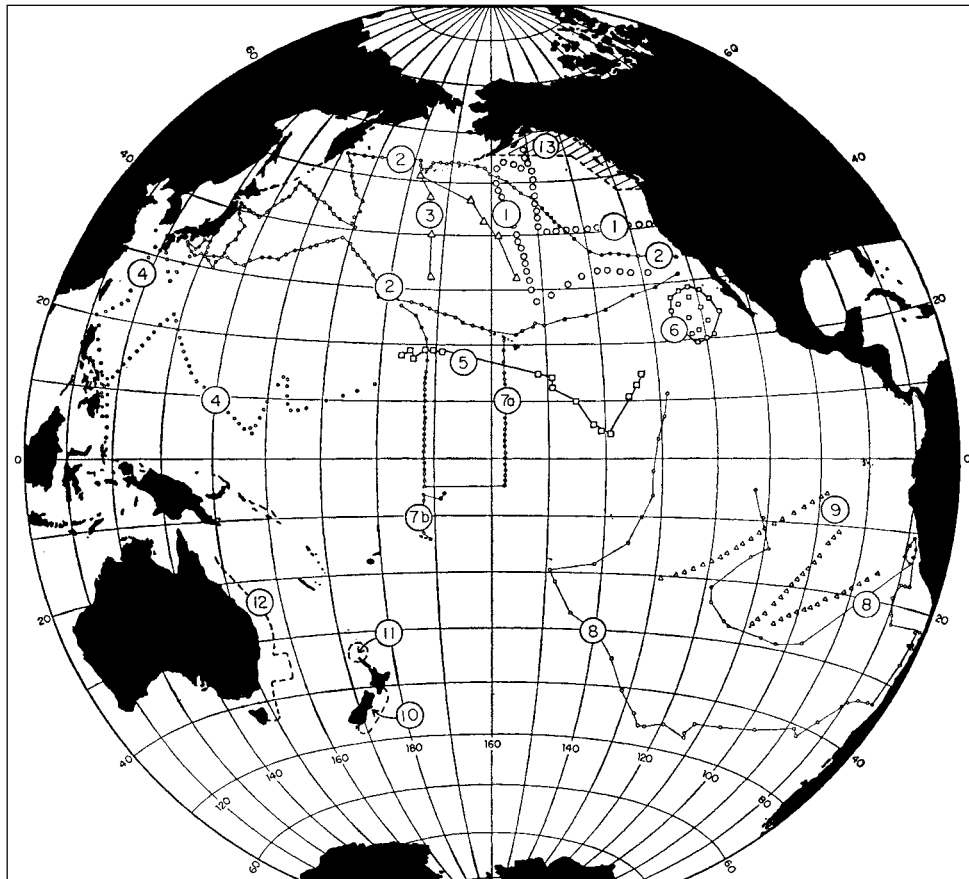


Fig. 1a. Regions of surveys and position of plankton stations from which euphausiid data have been taken. (1) “Northern Holiday” expedition, (2) “Transpacific,” (3) “Chinook,” (4) “Troll,” (5) “Midpacific,” (6) “Pelagic Area,” (7a) POFI Cruise 5, (7b) Part of POFI Cruise 8, (8) “Downwind,” (9) Cruise of *Albatross*, 1904–1905 (Hansen, 1912), (10) New Zealand survey (Bary, 1956), (11) British Antarctic “Terra Nova” Expedition records (Tattersall, 1924), (12) “Warreen” records (Sheard, 1953), (13) International Fisheries Commission records, 1929–1934 (Banner, 1949). Dates of surveys and the sampling methods used are listed in table 1.

Peru Current. In 1960–1961 the “Monsoon” expedition sampled to 64° S. in the western Pacific and Antarctic oceans (figs. 1a, 1b).

The author has recently had an opportunity to examine the euphausiids collected by the R.R.S. *William Scoresby* of the “Discovery” Committee in the Peru Coastal Current, between 5° and 50° S. A separate report on this material is in preparation. The approximate southern limits given here for the ranges of *Nyctiphanes simplex* and *Euphausia mucronata* are based on the *Scoresby* Collections.

Sheard (1953) studied euphausiids taken by the *Warreen* and *Discovery II* from eastern Australian coastal waters, and Tattersall listed species caught by the *Terra Nova* off northern New Zealand (1924) and at the Great Barrier Reef (1936). Bary (1956) reported on species from the coast of eastern New Zealand. These records, though not quantitative, are noted on the maps of this report.

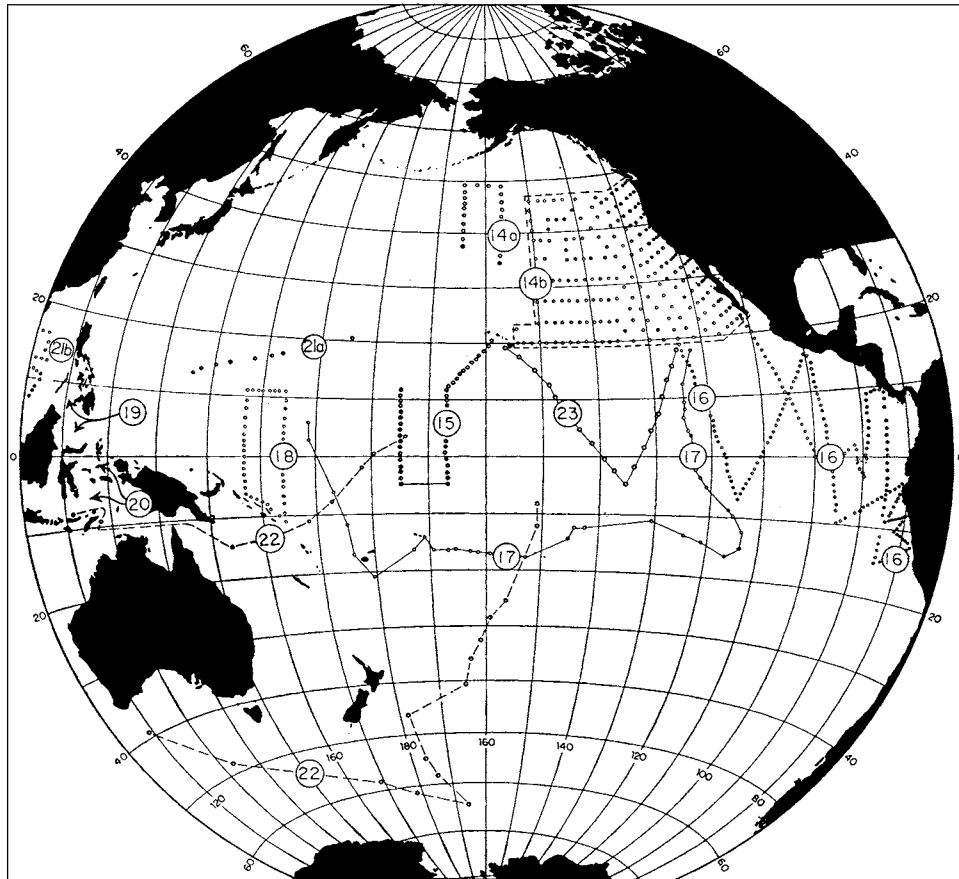


Fig. 1b. Survey areas, continuation of fig. 1a. (14a) "Norpac" CalCOFI, (14b) part of "Norpac" POFI, (15) "Equapac," R.V. *Stranger*, (16) "Shellback," (17) "Capricorn," (18) "Equapac," R.V. *Horizon*, (19) *Albatross*, 1907–1910 (Hansen, 1916), (20) *Siboga*, 1899–1900 (Hansen, 1910), (21a) "Naga," mid-Pacific stations, (21b) part of "Naga" March, 1960, survey, (22) "Monsoon" expedition, (23) "Tethys" expedition, mid-water trawl stations 5–23 only.

Owing to their importance as whale food, the Antarctic species of *Euphausia* have been responsible for much of the understanding of the biology of this Order. Papers by Rustad (1930) and Ruud (1932) dealt with the biogeography and development of Antarctic euphausiids. Fraser (1936), studying the development of the large and abundant *Euphausia superba*, suggested the possible role of subsurface currents—in this instance the warm, southward-flowing deep water—in the return of maturing euphausiids to the spawning zone near the edge of the pack ice. Bargmann (1945) extended Fraser's work on the development of *E. superba*, and amplified Ruud's conclusion that this species has a two-year life cycle.

John (1936) contributed a report on collections of *Euphausia* made by the *Discovery II* in 1931–1932. Stations were occupied around the Antarctic continent in the zone of 34°–70° S. John's conjecture that the Antarctic Convergence and, to a less marked degree, the Subtropical Convergence correspond significantly to the limits of distribution of some southern species is well founded in view of the broad extent of the *Discovery II* sampling. The zoögeography of the eight Antarctic species of *Euphausia* is essentially concentric or longitudinal, rather than latitudinal. This follows from the circumpolar pattern of the surface currents in the Antarctic Ocean. Baker (1959) published a comprehensive report on the circumpolar species *Euphausia triacantha*, showing that this species is most abundant at the Antarctic Convergence and its range is largely exclusive of that of *E. superba*.

Because of their close morphological relationship with *Euphausia pacifica* of the North Pacific, certain of the Antarctic species are of particular interest to the zoögeographer of the Northern Hemisphere. *E. pacifica* occupies a 40°–60° N. zone of the North Pacific which corresponds to that in which *Euphausia lucens* lives in the subantarctic region.

Einarsson's (1945) thorough work on the Euphausiacea of the North Atlantic dealt with the biology, development, and distribution of six important Arcticboreal species, three of which, *Thysanopoda acutifrons*, *Thysanoessa inermis*, and *Thysanoessa raschii*, are now known to be common to the North Atlantic and the North Pacific.

Moore (1952) correlated the North Atlantic and the Mediterranean distributions of ten euphausiids, representing four genera, with the relationship of temperature to water transparency. The success of any species in a specific geographic locality was plotted as the percentage of the total euphausiid catch made up by that species. This definition was accepted by Allee and others (1949), but it is now modified for plankton populations by taking the absolute density into account. Such numbers should be used until it becomes possible to determine with some precision the extent to which there may be overlapping in the critical parts, still unknown, of the vertical ranges of the several species occurring at a given locality or in the same geographical area. The present state of knowledge of the diurnal migrations of euphausiids presents a complex and varied picture in which species and size groups differ in their behavior. Moore's premise—that many species at a given locality migrate with the body of the deep scattering layer and hence compete for the same niche—may be, as its author suggests, an oversimplification. However, there is now little doubt that the adults of many euphausiid species migrate with the layer.

THE VERTICAL RANGES

Murray (1885) observed on the *Challenger* that “the great majority of plankton organisms live at various depths down to and even deeper than 100 fathoms during the day . . . and only come to the surface at night.” It was recognized at an early date that the nocturnal visitations to surface waters by euphausiids were among the most extensive migrations undertaken by plankton.

The first numerical data to demonstrate the diurnal vertical migrations of “deep-living schizopods” were derived from collections from the Bay of Biscay (Holt

and Tattersall, 1905; Fowler, 1905). *Euphausia krohnii*, *Meganyctiphanes norvegica*, *Nematoscelis megalops*, and *Stylocheiron suhmii* were found at greater depths in the daytime than at night. The extent of the migration was greatest for *E. krohnii* and least for *S. suhmii*. It may be noted that the members of this Biscayan assemblage are related to the species of a characteristic assemblage of the Baja California coast: *Euphausia eximia*, *Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Stylocheiron affine*.

Vertical migrations have subsequently been recorded for a number of euphausiid species in the Atlantic, notably by Tattersall (1924), Hickling (1925), Macdonald (1927), Watermann *et al.* (1939), Moore (1949), and Lewis (1954). Lewis adduced evidence of diurnal migrations in the adults of twelve species living in the Florida Current, and in the furcilia larvae of three species. No evidence was noted of diurnal migrations by calytopis larvae or by the species *Stylocheiron elongatum*, *S. longicorne*, and *S. suhmii*. Hardy and Gunther (1935) observed that *Euphausia frigida* and *E. triacantha* migrated diurnally at least 200 meters in the South Georgia whaling grounds. Fraser (1936) found eggs and nauplii of *E. superba* in deep water only. He recorded pronounced migrations of furcilia and even calytopis stages.

The extensive vertical migrations of many euphausiid species has led to the belief that these relatively large zoöplankton forms are important constituents of a sound-scattering layer or "deep scattering layer," found in the daytime at a depth of 200–600 meters on echo-sounding recorders. A biological cause for the scattering of sound signals at mid-depths was suggested in 1945 by Johnson (1948), who first demonstrated the vertical migrations of the layer in June, 1945 (Anonymous, 1946).

Observations by Hersey and Moore (1948) in the Atlantic emphasized the possible role of the stratification of euphausiids in the development of the scattering layer. The migrations of euphausiids at sunrise and sunset were thought to be due to their tendency to remain in a relatively constant light intensity.

Boden (1950) showed that the four dominant species of the San Diego region, *Euphausia pacifica*, *Nyctiphanes simplex*, *Thysanoessa gregaria*, and *Nematoscelis difficilis*, occur in maximum concentration at depths coincident with the deep scattering layer and were undoubtedly associated with it. Barham (1957) found that *Euphausia pacifica* and the decapod *Sergestes* were associated with the layer in the Monterey, California, region.

Published studies dealing with the relationship of the distributions of pelagic species to faunistics and water masses will be discussed in the section dealing with the associations of euphausiid species.

METHODS OF COLLECTION AND ANALYSIS

The plankton here considered was collected during sixteen cruises in the Pacific (figs. 1a, 1b). The samples were usually taken in conjunction with hydrographic observations. Although the surveys were carried out over a 10-year period, nearly all of the North Pacific samples were collected between the months of April and October. A joint Japanese, Canadian, and American study, "Norpac," provided almost synoptic coverage of the Pacific north of 20° N. in August–September, 1955.

However, only those "Norpac" collections from the eastern part of the Pacific sampled using the standard 1-meter net by CalCOFI and POFI were counted for euphausiids. These records, tabulated in a Norpac data volume (Norpac Committee, 1960), were used for the distribution maps included here. Records from other CalCOFI cruises supplement the "Norpac" data in the region of the California Current.

The "Capricorn," "Downwind," and "Monsoon" expeditions to the South Pacific were made during the southern summer, November–February. Surveys of the most westerly part of the equatorial region were carried out in February–April. These included the "Troll" expedition and certain "Naga" expedition stations in the South China Sea. The "Equapac," "Midpacific," "Tethys," and "Shellback" expeditions to other parts of the equatorial region were carried out in spring and summer months, May–September. "Equapac" euphausiid data are tabulated in an Equapac data volume (Equapac Committee, in press).

It became evident during the plotting of the distributions that the principal faunistic boundaries for euphausiids (an essentially subsurface dwelling group of animals) did not appear to be greatly modified by seasonal changes in the superficial layers of subtropical and tropical oceans. This conclusion was based on study of the year-round CalCOFI material, "Transpacific" expedition records (summer and winter data compared), and other material from the several literature sources, to be discussed under the heading Seasonal Changes in Distributions.

The cruises and the collecting gear are listed in table 1. The plankton net routinely used has been described by Ahlstrom (1948). It is conical, 5 meters in length, and 1 meter in diameter at the mouth. Nets made with No. 30 heavy-duty grit gauze, 0.65 mm. between threads, were usually used. King and Demond (1953) described a net of this type used by POFI.

The net-towing procedure for the Scripps oceanic expeditions scarcely differed from that followed by CalCOFI. The tows were oblique. The net was lowered at a speed of 50 meters per minute to the desired depth while the vessel moved at a speed of 1.5–2.0 knots. The ship's speed was regulated so that the angle of the towing wire was maintained as nearly as possible at 45 degrees. The net was retrieved at 20 meters per minute. The hauling time varied between 20 and 40 minutes, so that each sample contained elements of plankton populations integrated across horizontal distances of 0.5–1.0 miles. A 100-lb. weight was suspended from the wire below the point of attachment of the net bridle. The maximum depth attained by the net was estimated from the angle of the wire, assuming a straight wire to the net. With 100 meters of wire out, the depth-of-tow calculated by this method was shown to differ by no more than about 2 meters from the true depth recorded on a film trace made by a pressure bellows (Ahlstrom, 1948).

An Atlas flowmeter was mounted in the mouth of the net to provide an estimate of the volume of water filtered. Such meters were calibrated for the relationship between the number of revolutions of the propeller and the distance towed. The volume of water strained by the net was assumed to be approximately equal to that of a column of water having a cross-section equal to the area of the mouth of the net (0.785 sq. m.). Counts of euphausiids were standardized on the basis of 1,000 cubic meters of water strained.

TABLE 1
CRUISES FROM WHICH EUPHAUSIID MATERIAL IS DERIVED

Cruise(s)	Area sampled	Date	Net used	Depths sampled (m.)
CalCOFI ¹ 4903-5804	Region of California Current	1949-1958	1-m. open No. 30 XXX gauze (0.65 mm. between threads)	0-70 0-140
POFI ² 5, 8	Mid-equatorial Pacific	1950-1951	As above	0-200
Mid-Pacific	San Diego-Hawaii (equatorial eastern Pacific)	1950	40-cm. open 6-ft. Mid-water trawl 1 m. open No. 30 XXX gauze	Various, 0-1,000 (some vertical hauls, especially "scattering layer")
Northern Holiday	Gulf of Alaska eastern Central North Pacific	1951	1-m. open No. 30 XXX gauze	0-140
Shellback	Pacific eastern equatorial	1952	As above	0-300
Capricorn	Equatorial South Pacific (some stations north of equator near 170° E. and 125° W.)	Nov., 1952- Feb., 1953	As above	0-140 0-400 0-1000
Trans- pacific	North Pacific	1953	As above (and opening- closing)	0-150 150-300 300-450 450-600 0-700
Troll	Western equatorial Pacific, north of equator	March-April, 1955	1-m. open No. 30 XXX gauze	0-300
Norpac (CalCOFI 5508)	North Pacific, east of 150° W., 48° N. to 20° N.	Aug.-Sept., 1955	As above (and opening-closing)	0-140 140-280 0-700
Chinook	Central North Pacific, Hawaii - Adak	July-Aug., 1956	As above	0-140
Equapac	Equatorial Pacific, 155° E. to Hawaii	Aug.-Sept., 1956	As above	0-140 140-280 0-280
Downwind	Eastern South Pacific	Oct., 1957- Feb., 1958	As above (and opening-closing)	0-140 140-280 0-280 0-560 0-700
Naga	Stations between Hawaii and Philippines Certain stations in South China Sea	July-Aug., 1959 March, 1960	1-m. open, 2-m. open 1-m. open	0-140 0-300 0-140
Monsoon	Western tropical Pacific, Indian Ocean, western South Pacific	Oct., 1960- March, 1961	1-m. open No. 30 XXX gauze	0-300 Greater depths sampled by Isaacs-Kidd Mid-water trawl
Tethys	Eastern tropical Pacific	June-Aug., 1960	Only Isaacs-Kidd Mid-water trawl records, Stas. 5-23, included here.	0-ca. 2,000 (1 Sta. to 3,500; 1 Sta. to 845)

¹ CalCOFI = California Cooperative Oceanic Fisheries Investigations.

² POFI = Pacific Oceanic Fisheries Investigations.

The Isaacs-Kidd mid-water trawl (Isaacs and Kidd, 1953), equipped with a standard 1-meter plankton net for its aftermost part, effectively collects deep-sea Crustacea, including euphausiids, as well as deep-sea fishes. This net has been used in areas of particular interest or at widely spaced stations during most of the cruises. The euphausiid material obtained was valuable in establishing qualitative distribution records for deep-living species. From studies of the Scripps collections it became evident that the absence of a particular species from a mid-water trawl sample, filtered from a great volume of water by several mesh sizes, indicates the probable absence of that species from the sampling region.

The bathymetric distributions and generalized diurnal vertical ranges of the euphausiid species are discussed. Opening-closing nets were used on "E. W. Scripps" Cruise VIII (1939), "Transpacific" expedition (1953), a "Pelagic Area" Cruise (1954), and the "Norpac" Cruise (1955). During these surveys, samples were collected in subsurface layers. Tripping mechanisms (Leavitt, 1938) were employed to operate the opening and closing lines of the 1-meter nets. During the "Transpacific" expedition, nets were attached so as to sample four layers: 0–140 meters, 140–280 meters, 280–700 meters, and 700–1,000 meters. The net sampling to 1,000 meters was open at all times. Concentrations for the 700–1,000-meter layers were determined by subtracting the actual number of euphausiids caught by the upper nets (those above 700 m.) from the total caught by the 0–1,000-meter net. It was assumed that the amount of water filtered in the 700–1,000-meter layer was nearly equal to the sum of the amounts filtered by the upper nets subtracted from the amount filtered by the net sampling the entire 0–1,000-meter stratum.

In the laboratory treatment of the plankton samples it was often necessary to use aliquots, while retaining as far as possible the quantitative and qualitative worth of the large samples. The procedure included (1) counting and measuring all specimens in an aliquot of the sample, and (2) scanning the remainder of the sample under the microscope for species that appeared not to have been representatively aliquoted, or that were entirely lacking in the aliquot. In general, the fraction served for counts of the dominant species, and for the rarer species all individuals were counted.

When the sample was seen to contain few euphausiids, an aliquot of one-fourth or one-fifth of the sample was taken. One-tenth of the sample was usually counted when the sample was rich, that is, when it appeared to the naked eye to contain 1,000 or more euphausiids. The method used for aliquoting required that the sample first be agitated. When the plankton was in suspension it was poured into a 500-ml. graduated cylinder. The combined volume of plankton and fluid, usually adjusted to about 400 ml., was measured and all but the intended aliquot (approximately the lower one-tenth or one-fifth) was quickly poured back into the original container. Since the larger euphausiids would otherwise have settled to the bottom of the cylinder in 20–40 seconds, the material was kept in a state of agitation during the fractionating, except when the volumetric reading was made. Most of the euphausiid specimens in the Scripps samples were larvae or immature individuals. These remained longer in suspension than the adults.

The reliability of the aliquoting and counting procedure and such variable factors as depth-of-tow and time-of-day-of-sampling were examined (Brinton, 1962*a*).

Replicate counts indicated that aliquots obtained by the above method were random fractions of the samples.

The importance of scanning the entire sample for the rarer species was indicated by the fact that in random aliquots, a species with a mean density of 1 individual per aliquot would be absent in about 37 per cent of all the aliquots, and a species with a mean concentration of 0.5 individuals per aliquot would be absent in about 61 per cent of all the aliquots.

HYDROGRAPHY

With four exceptions, euphausiid species live above a depth of 1,500 meters. The 0–1,500-meter layer includes the epipelagic and mesopelagic zones, according to a recent synthesis of classifications of marine environments (Hedgpeth, 1957). Currents in this layer flow more rapidly than at great depths, with the consequence that vertical and horizontal temperature gradients are relatively sharper in the upper strata. Furthermore, waters between about 150 and 1,500 meters of depth are distinguished as the *upper water masses*, according to characteristic relationships of temperature to salinity (Sverdrup, Johnson, and Fleming, 1942). It therefore seems appropriate to discuss the zoögeography of euphausiids in relation to these conspicuous features of the physical environment. Analogies will frequently be drawn between the zoögeographical provinces of the high seas and the water masses. Both derive integrity from the partly closed patterns of the current systems and from the different zonal influences of climate.

The principal upper water masses of the Pacific (fig. 2) were designated Subarctic, North Pacific Central, Equatorial Pacific, South Pacific Central, and Subantarctic by Sverdrup, Johnson, and Fleming. Eastern and Western Central water, distinguished in the Central Water Mass of each hemisphere, were related to separate eastern and western regions of origin of Central Water.

The regions of the eastern boundary currents of mid-latitudes were called *transition regions*. The California Current consists of merging Subarctic, Central, and Equatorial water, and the Peru Current is made up mainly of mixed Subantarctic and Equatorial water. Coastal upwelling is a second characteristic feature of both currents. The ecological significance of the transition regions and the water masses proper will be considered more fully in the discussion of the geographical groupings of the species.

The currents of the Subarctic Water Mass (fig. 3) are the southward-flowing Oyashio at the western boundary of the ocean and the easterly Aleutian Current in mid-ocean. The Aleutian Current contributes to the cyclonic gyral of the Gulf of Alaska and to the headwaters of the California Current. The California Current also receives a component of the North Pacific Drift which flows eastward along the band of transition between Subarctic and Central waters.

The transition region of the California Current is characterized by southward flow above 200 meters of depth and by deeper northward flow of more southern water (Reid, Roden, and Wyllie, 1958; Reid, 1962*a*). Central Water, moving southward at a sluggish rate, impinges on the western part of this current. Inshore, the northward-flowing Davidson Countercurrent is an element of the winter circulation along the California and Baja California coasts, but may develop whenever the upwelling regime collapses.

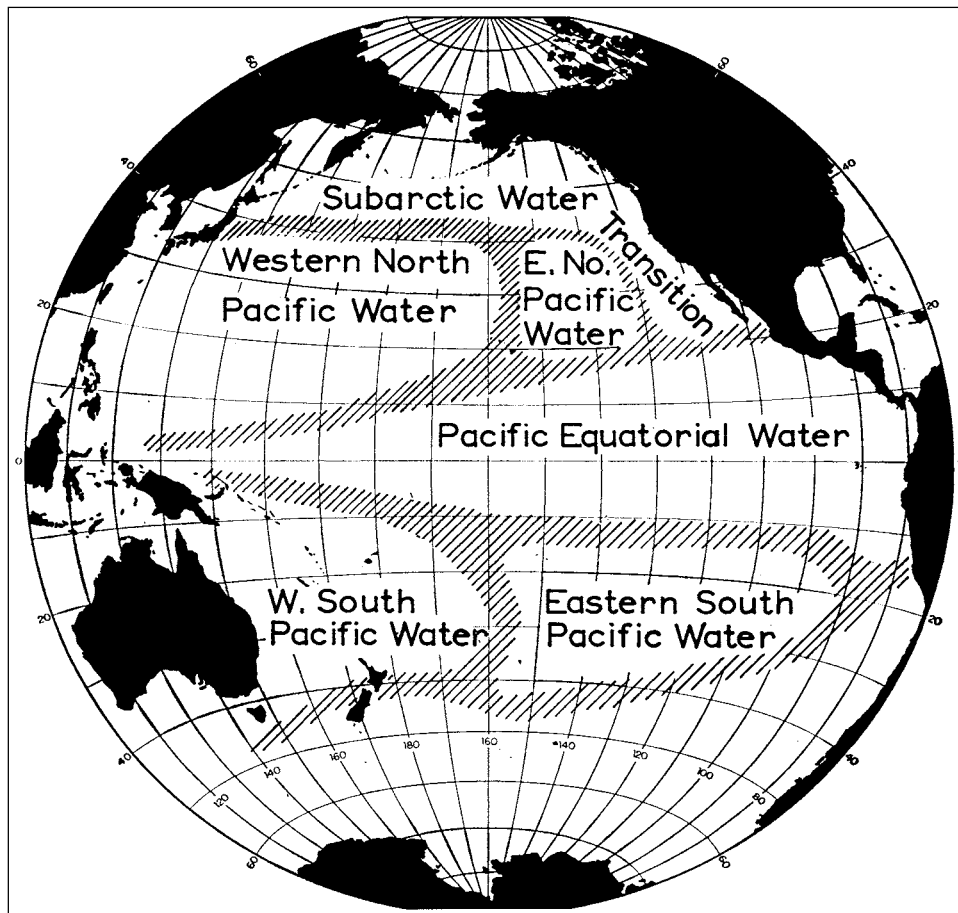


Fig. 2. The principal water masses of the Pacific, after Sverdrup, Johnson, and Fleming (1942). Temperature-salinity characteristics of the water masses are given in a later section, "Horizontal Zonation."

Like the California Current, the Peru Current flows toward low latitudes above approximately 150 meters and toward higher latitudes at variable depths, between 100 and several hundred meters (Wooster and Gilmartin, 1962). Warming of the superficial waters off Peru ("El Niño") is related to either southward-flowing tongues of the Equatorial Countercurrent or to the intrusion of offshore Equatorial Water accompanying the breakdown of coastal upwelling (Gunther, 1936). Cool waters of the Peru Current system are found as far north as the equator, while those of the California Current are not found south of 20° N.

The east-west axis of the Equatorial Water Mass thus falls north of the equator, near 5°–8° N., the axis of the Equatorial Countercurrent. The Countercurrent flows eastward in the zone of 2°–10° N. and contributes water to the warm eastern equatorial basin off Central America. Flowing from east to west on either side of the Countercurrent are the South Equatorial Current, having an axis along the equator, and the North Equatorial Current, with an axis between 10° N. and 18° N.

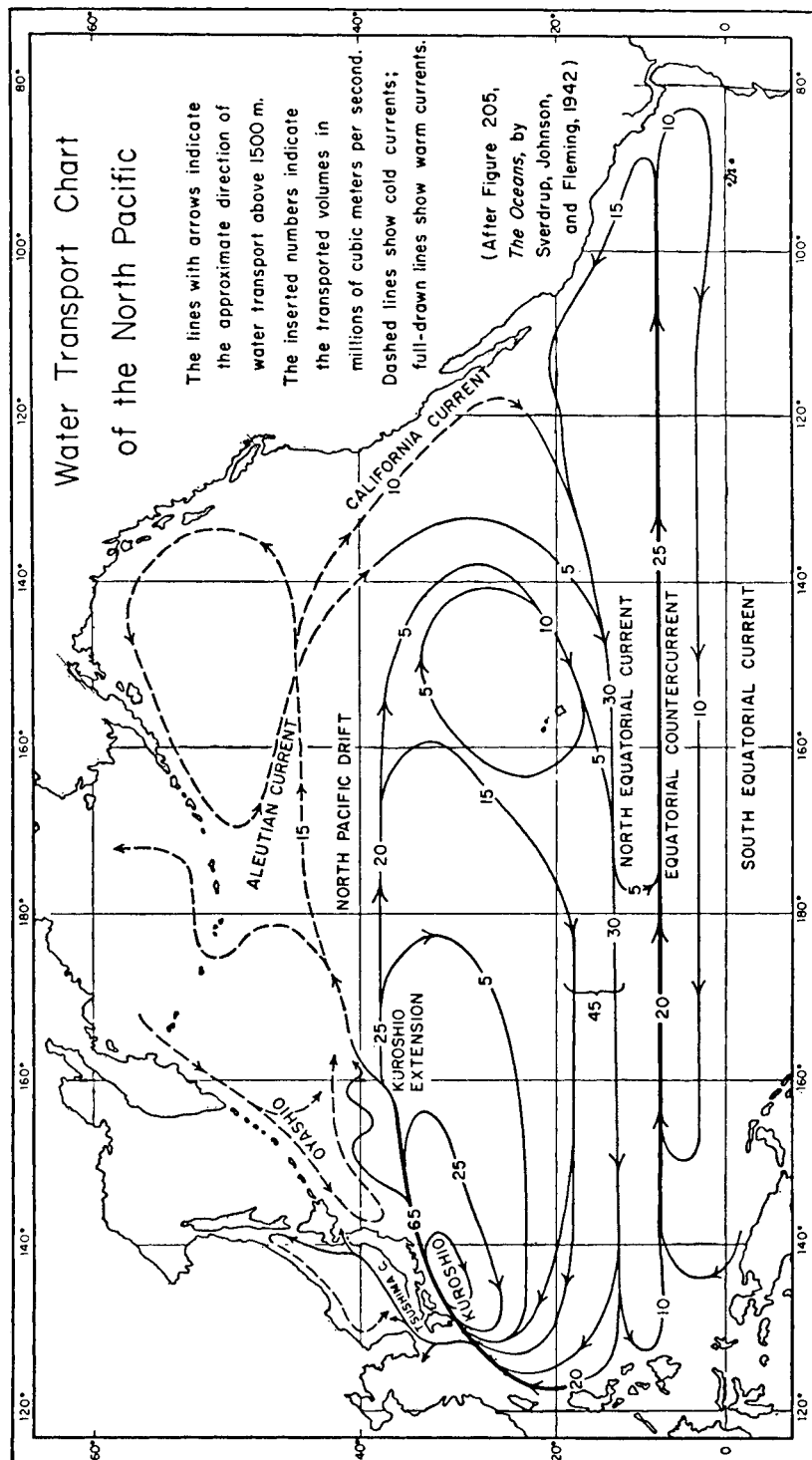


Fig. 3. Water transport and current of the North and equatorial Pacific (from Sverdrup, Johnson, and Fleming [1942]).

These currents, together with the meridional divergence of isotherms at the equator, maintain the Equatorial Water Mass. The Cromwell Undercurrent, moving eastward at depths of 50–400 meters beneath the South Equatorial Current, carries water of western origin as far east as the Galápagos at 92° W. (Knauss, 1959).

Reid (1962*b*) has recently published a description of the currents, PO₄-P distribution, and zoöplankton volumes in the upper layers of the Pacific. Both PO₄-P and zoöplankton were lowest in the anticyclonic central gyral.

Waters having subarctic and subantarctic affinities move toward the equator on the eastern side of the ocean in the California and Peru currents. These currents, together with the upwelling along the coasts of California, Baja California, and Peru, afford environments in mid-latitudes for cold-water species. The warm North Pacific and South Pacific central water masses, on the other hand, are widely separated in the eastern Pacific, but nearly merge in the most western part of the ocean near the Indo-Australian Archipelago. There, from 15° N. to 15° S., the water is of mixed origin, having Central, Equatorial, and Indo-Australian components. It will be seen that euphausiids of those three faunal regions are also present there. The northward-flowing Kuroshio, arising off the Philippines, has the same mixed origin and fauna.

The distributions of temperature, salinity, and dissolved oxygen along a north-south track in mid-ocean illustrate the structure of the upper Pacific water masses (fig. 4a). The profiles are based on measurements made during the "Northern Holiday," "Equapac," and "Downwind" expeditions (fig. 4b). The upper 500 meters of the subarctic region are distinguished by low values for temperature and salinity and by high concentrations of oxygen. In the zone of transition, subarctic isohaline and isothermal surfaces submerge toward the south, there giving rise to water having the relationship of temperature to salinity characteristic of the Eastern North Pacific Central Water Mass. (The T-S properties of the water masses are discussed in a later section dealing with faunas and water masses.) In the Southern Hemisphere, sinking occurs at the convergence of Subantarctic and Central waters, 37°–42° S., along the northern edge of the West Wind Drift where South Pacific Central Water is formed. *Thysanoessa gregaria* and the species pair *Nematoscelis difficilis*–*N. megalops* will be seen to be characteristic of the antitropical transition zones.

The provinces of the North Pacific Central and South Pacific Central water masses lie, in mid-ocean, between the 15° and 40° parallels. These are warm-water zones where temperatures up to 10° C. are found at 400 meters of depth. Salinity is also higher than elsewhere in the ocean—surface values may exceed 36‰.

Whereas the central regions are *gyrals* of circulation, the equatorial province is maintained by the *zonal* flow of the equatorial currents and countercurrents. According to Wooster and Cromwell (1958), the South Equatorial Current flows along the zone where the thermocline slopes upward toward the equator in low latitudes, the Equatorial Countercurrent flows where the thermocline slopes upward toward the north somewhere between 3° N. and 10° N., and the North Equatorial Current is indicated by downward slope of the thermocline northward from the Countercurrent. A second conspicuous feature of the equatorial region is a subsurface core of water low in oxygen content, extending from east to west across the breadth of the ocean. In the mid-oceanic section (fig. 4a) the values are 1–2 ml. per liter at 200 meters of depth.

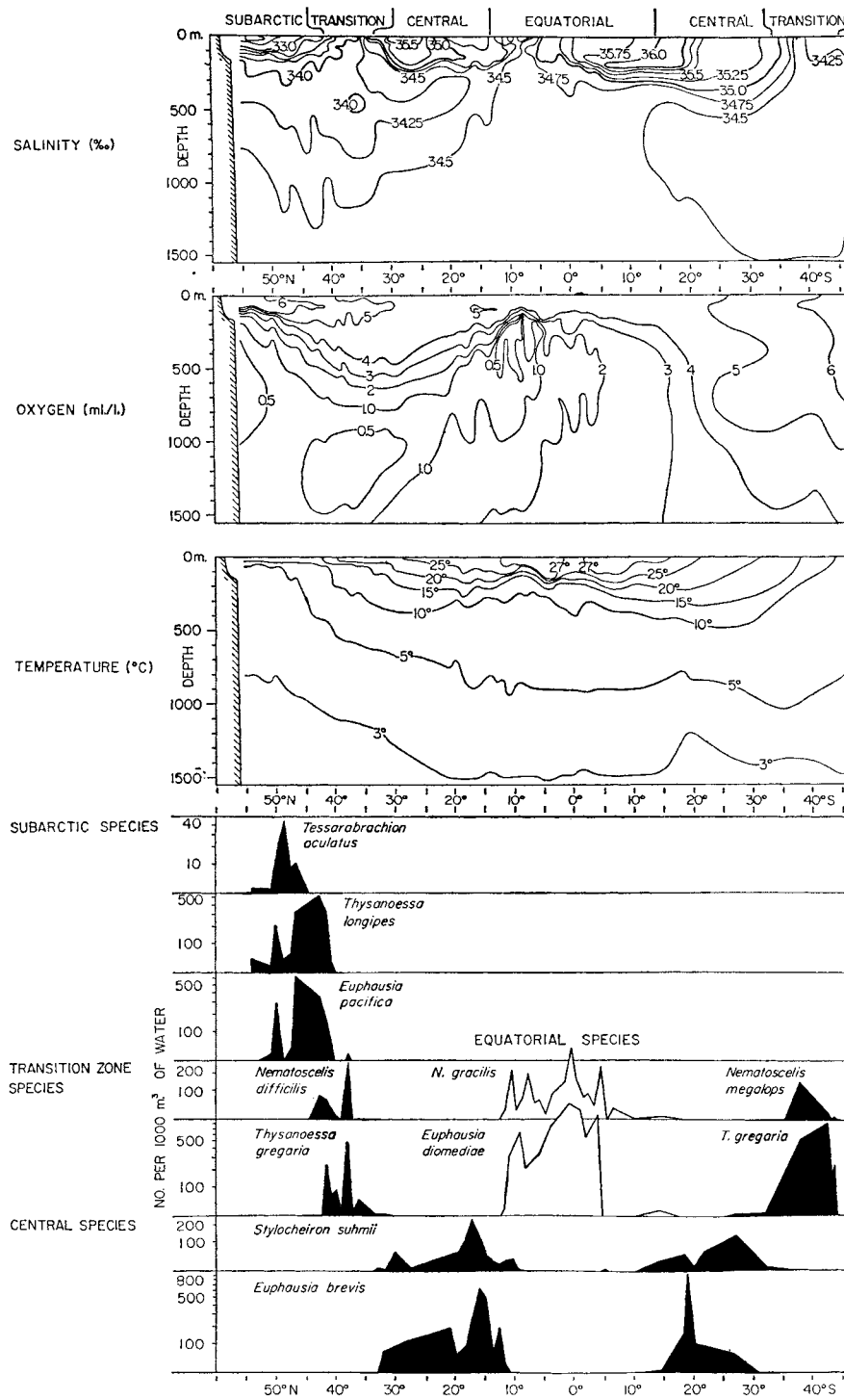


Fig. 4a. North-south abundance of euphausiid species representing four Pacific faunal groups, compared with salinity, oxygen, and temperature profiles based on the same stations at which the plankton was sampled. From the mid-Pacific track (a) shown in fig. 4b.

The boundaries of water masses are, in general, zones of convergence. It will be seen that certain of these zones are sufficiently broad and uniform to maintain endemic species. Others are narrow, being places where currents that differ extremely with respect to certain properties abut sharply on each other. Two such places are the convergence of the Oyashio and the Kuroshio, near 40° N., east of

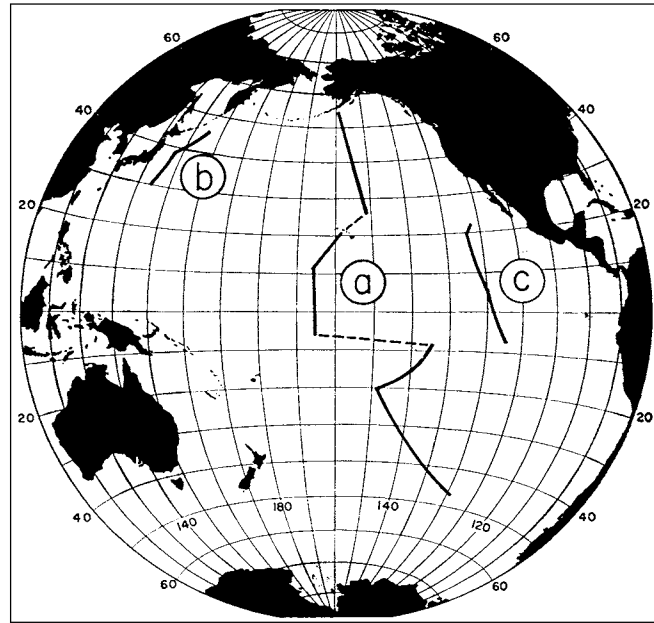


Fig. 4b. Position of hydrographic profiles and euphausiid distributions shown in fig. 4a, from “Northern Holiday” exped., Sept., 1951 (26°–54° N.); “Equapac” exped., Sept.–Oct., 1956 (20° N.–7° S.); and “Downwind” exped., Nov.–Dec., 1957 (8°–47° S.). b. “Transpacific” exped. profiles and distributions shown in fig 5 c. “Shellback” exped. profiles and distributions shown in fig. 6.

Japan (fig. 5), and the frontal region between Central and Equatorial waters, 18° N., west of Baja California, at the end of the westward-bending California Current (fig. 6).

The convergence of the Oyashio and Kuroshio systems was crossed at 35°–40° N., east of Japan, by the “Transpacific” expedition (fig. 4b). From 38° N. to 36.5° N. the temperature at a depth of 100 meters increased from 3.5° C. to 20.6° C. (fig. 5). Isohaline and isothermal surfaces sloped sharply downward toward the south, from near the surface to a depth of about 900 meters. The concentration of dissolved oxygen in the 0–200-meter layer was 5–7 ml. per liter north of the convergence, and 4–5 ml. per liter south of the convergence. The zoögeographical effect was that the subarctic fauna was replaced across a distance of about 70 miles by warm-water assemblages including equatorial species (e.g., *Euphausia diomediae* and *Pseudeuphausia latifrons*). The transition zone is narrow in the region of the convergence; from the standpoint of euphausiid faunistics, it was recognized only at Stations 69 (40° 55' N., 149° 26' E.) and 70 (39° 44' N., 148° 24' E.) where *Nematoscelis difficilis* was found.

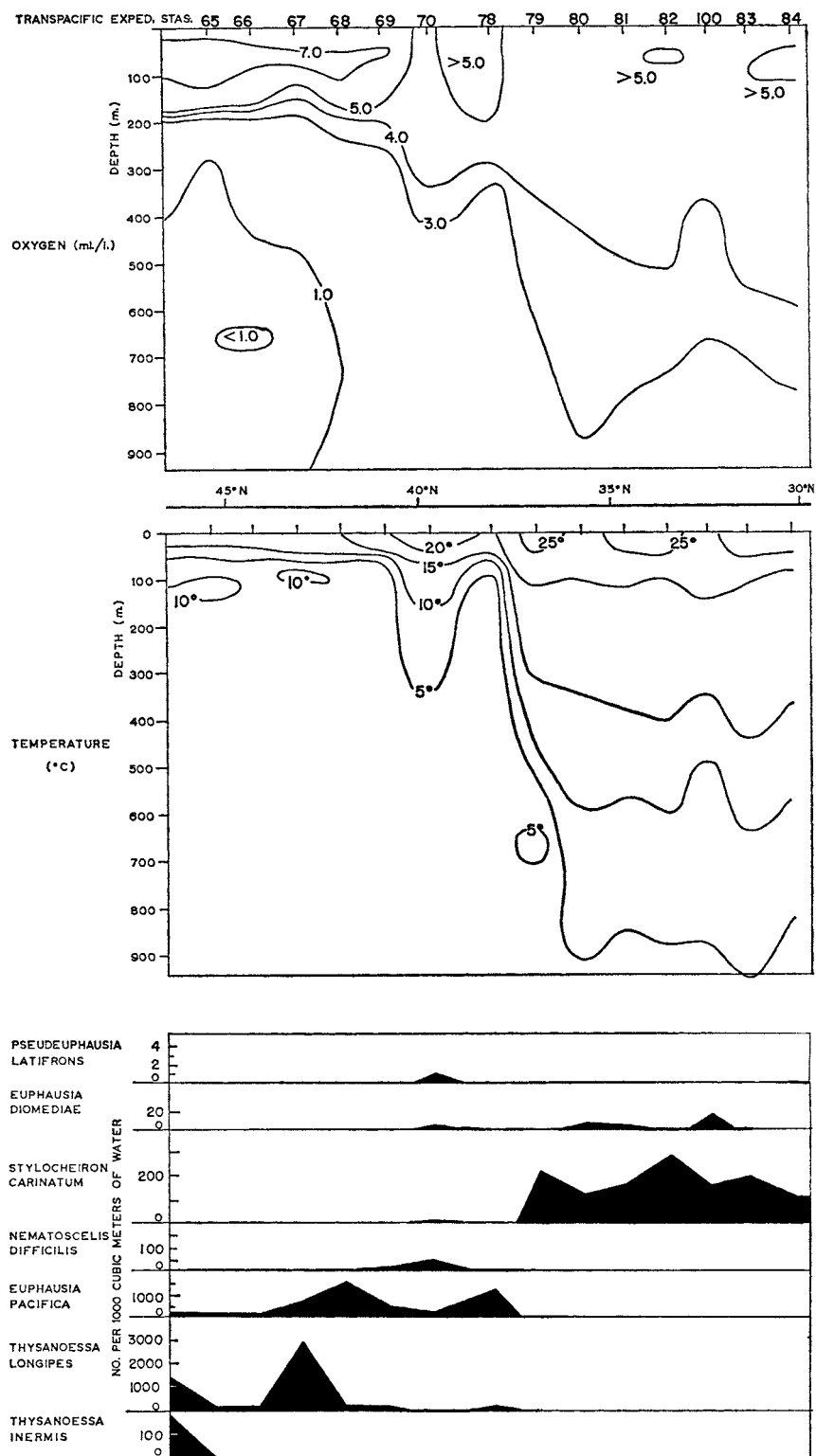


Fig. 5. Profiles of the distribution of dissolved oxygen and temperature in the eastern waters of Japan, compared with euphausiid distributions. From "Transpacific" exped. shown in fig. 4b

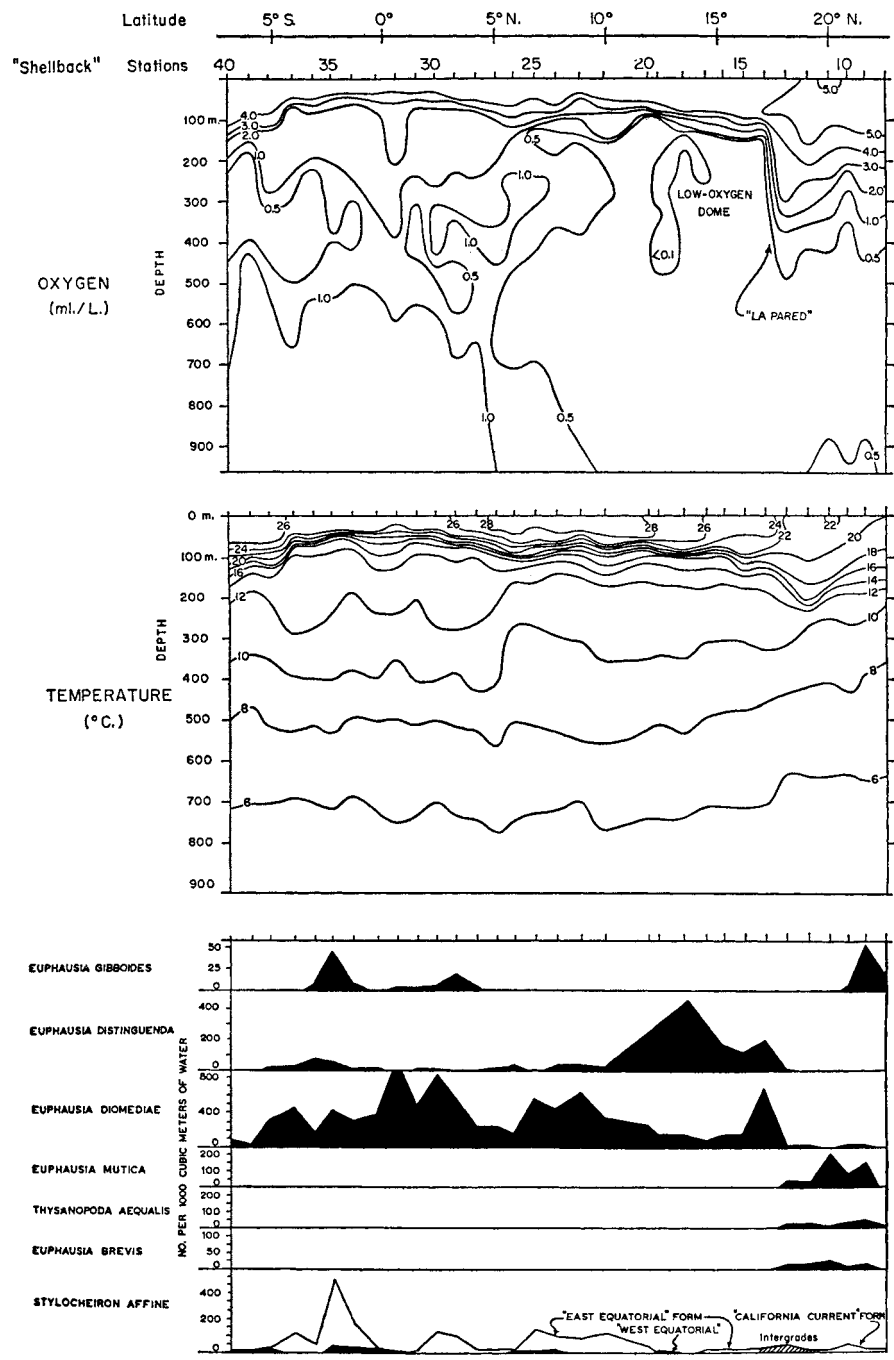


Fig. 6. Profiles of the distribution of dissolved oxygen and temperature in the eastern equatorial Pacific, compared with euphausiid distributions. From "Shellback" exped. track shown in fig. 4b.

The main branch of the Kuroshio bends eastward near 35° N., off southern Japan. Between 35° N. and 40° N. smaller branches and eddies of the warm current swirl irregularly. Uda (1959) discussed the meandering character of this frontal region, and Beklemishev and Semina (1956) discussed the structure of the biogeographical boundary in this region. Evidently a branch of the Kuroshio was intercepted at "Transpacific" Station 70, 39° 44' N., while stations between 37° N. and 39° N. were in Subarctic Water.

These oceanographic and zoögeographic features result from the collision of warm and cold currents moving in opposite directions. There is little mixing in the upper layers of the two dissimilar water masses. A component of the Oyashio submerges beneath the Kuroshio and may flow southward. Subarctic euphausiids, however, were not caught in deep tows taken off Honshu Island and it is to be inferred that the subarctic community was dissipated at the front. The distributions of species of chaetognaths (Bieri, 1959) and foraminifera (Bradshaw, 1959) are sharply bounded by this front, and Ponomareva (1957) found that warm-water and cold-water groups of euphausiids were limited by it. Bogorov and Vinogradov (1955) showed that there were sharp discontinuities in both the biomass and the plankton faunas at the boundary.

Farther east (150°–170° E.) the convergence of Subarctic Water and the Kuroshio Extension gives rise to Western North Pacific Central Water. There, the frontal region is broader than it is near Japan, and the subarctic species *Thysanoessa longipes* and *Euphausia pacifica* were found in cool patches within the northern part of the central province.

A second type of oceanographic boundary having conspicuous zoögeographic significance is found in low latitudes where water masses differing little in temperature converge. Near its southwestern limit the westward-bending California Current is warmed by solar radiation and by admixture of central water. Near 120° W., 17°–18° N. this current was observed to converge sharply with Equatorial Water. In the 100–500-meter layer, the Equatorial Water differed sharply from the California Current water with respect to the concentration of dissolved oxygen (fig. 6) (Wooster and Cromwell, 1958). The zone of strong gradients in temperature and oxygen content of the water was called *La Pared* by the "Shell-back" expedition discoverers. This "wall" delimited the ranges of central and equatorial euphausiids and, as Bieri pointed out, of several chaetognath species.

At both 10° N. and the equator, divergences, indicated by upward sloping isotherms, maintain the cool-water property of the Equatorial Water Mass. Whereas in the central regions the lowest temperatures in the epipelagic area usually lie along the water mass boundaries (where, it will be seen, certain central species are most concentrated), the Equatorial Water Mass is coolest, and most fertile, along its east-west axis. Figure 6 shows that *Euphausia diomediae* is numerous in the regions of divergence. *E. distinguenda*, on the other hand, is concentrated in the region of the low-oxygen dome.

Maps of the distribution of temperature at 0, 100, 200, and 400 meters of depth (figs. 7a, 7b, 7c, 7d) were plotted from measurements made by eight expeditions: "Northern Holiday," "Shellback," "Transpacific," "Troll," "Norpac" (CalCOFI part), "Equapac" (data from R.V.'s *Stranger* and *Horizon*), "Chinook," and

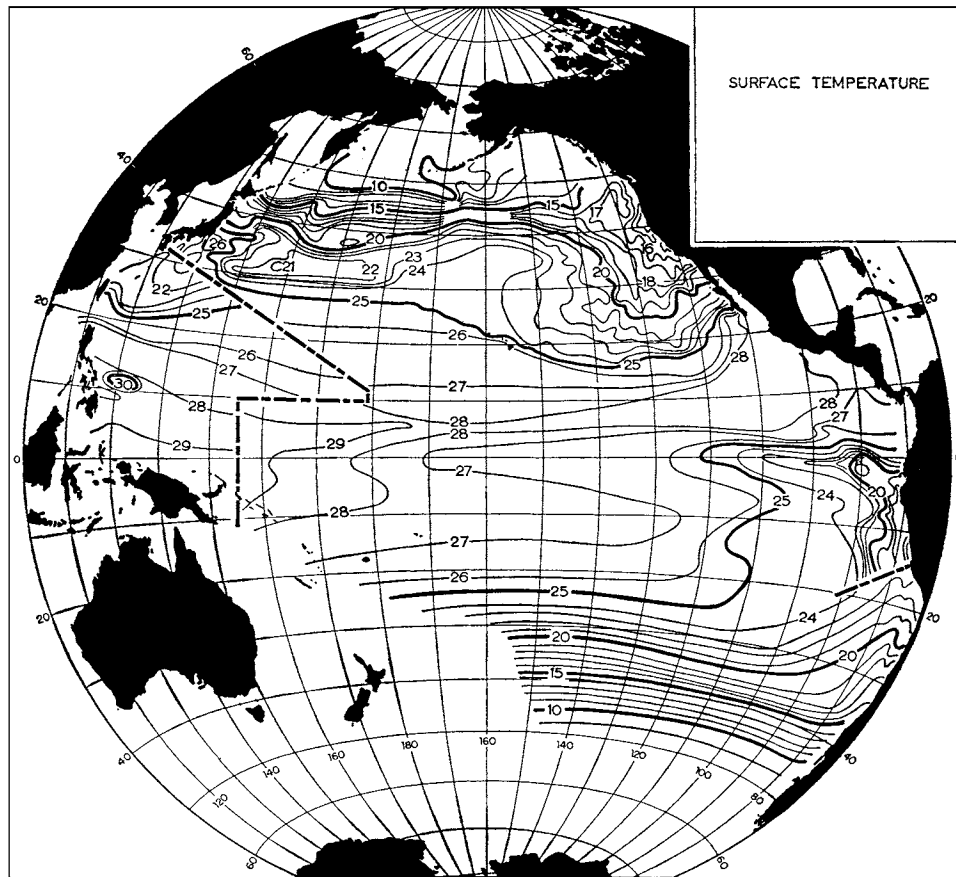


Fig. 7a. (see also figs. 7b, 7c, 7d). Distribution of surface temperature ($^{\circ}$ C.) in the Pacific Ocean, based on the stations at which euphausiid material was collected. The dashed line in the western Pacific separates spring (“Troll” exped.) data from the data of other surveys (“Transpacific” and “Equapac” expeds.) during the summer months. The dashed line off Peru separates summer (“Downwind” exped.) data from autumn (“Shellback” exped.) data. From the data collected by the following surveys: “Northern Holiday,” “Shellback,” “Transpacific,” “Troll,” “Chinook,” CalCOFI sector of “Norpac,” “Equapac” stations occupied by the R. V.’s *Stranger* and *Horizon*, and “Downwind.”

“Downwind.” Thus the temperatures to be discussed in relation to the species distributions were synoptic with the plankton samples examined. Temperatures were not plotted for the Antarctic Ocean south of 47° S. (the southern limit of “Downwind” expedition) or for the western South Pacific.

Five features of temperature distribution have particular significance in euphausiid distribution:

1. The intrusions of cold waters into mid-latitudes along the eastern sides of the ocean are evident at all depths plotted.
2. The Central American warm-water barrier between northern and southern cool-water populations is most evident above a depth of 200 meters; at 2° – 20° N. in surface water, and at 12° – 20° N. and 4° – 6° N. at 100 meters of depth.

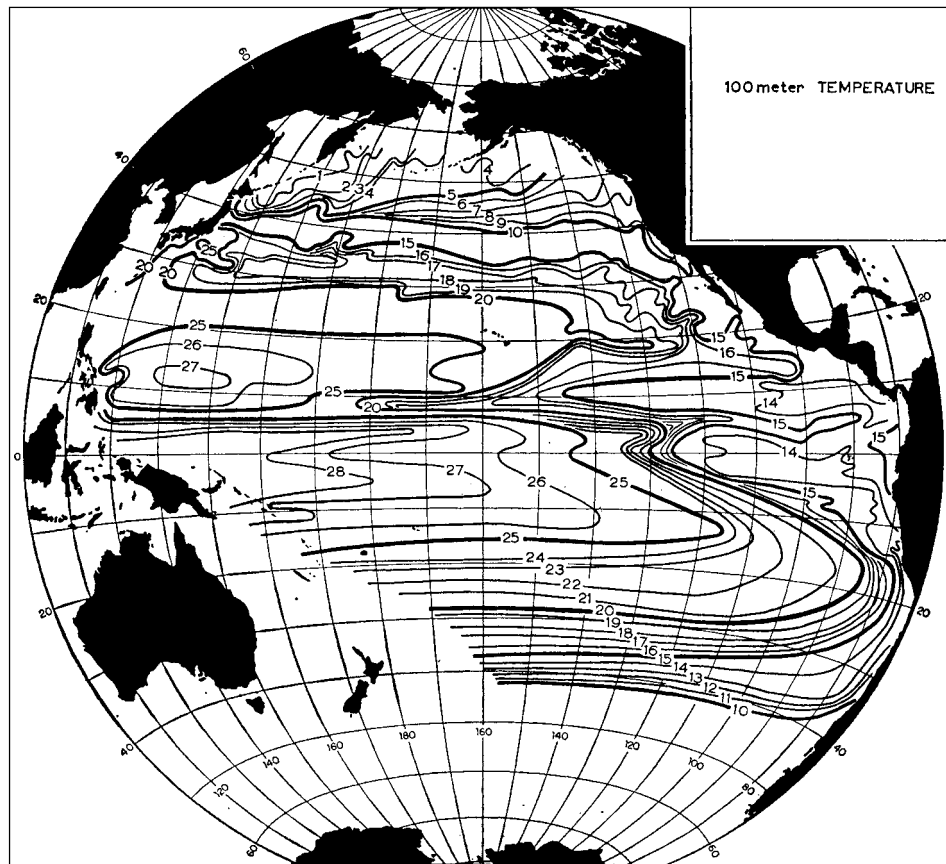


Fig. 7b. 100-meter temperatures ($^{\circ}$ C.) of the Pacific Ocean.

3. The cool-water property of the Equatorial Water Mass is most conspicuous in the eastern Pacific but is also evident at mid-ocean and in the western Pacific. At a depth of 100 meters the westward-reaching cold-water tongue was at 10° N. in mid-ocean. At 200 meters it was in the zone of 0° – 10° N. in the western Pacific and at 400 meters it was in the zone of 10° S.– 15° N. The 27° C. surface isotherm followed the South Equatorial Current westward along the equator to 170° W. However, the warmest surface waters in the Pacific Ocean were found to lie between 12° N. and 12° S. in the far-western Pacific.
4. The deep warm pools of the Central Water Masses are to be noted at depths of 100, 200, and 400 meters. The North Pacific and South Pacific gyral are separated to a greater or lesser degree by the cool equatorial belt. The separation is wider in the deeper layers. Northward flow of the warm Kuroshio is clearly seen at 0, 100, and 200 meters of depth.
5. The bunching of isotherms near 40° – 45° N. and 30° – 40° S. agrees with the positions of east-west boundary zones (the transition zones) between temperate and subtropical zoogeographic provinces.

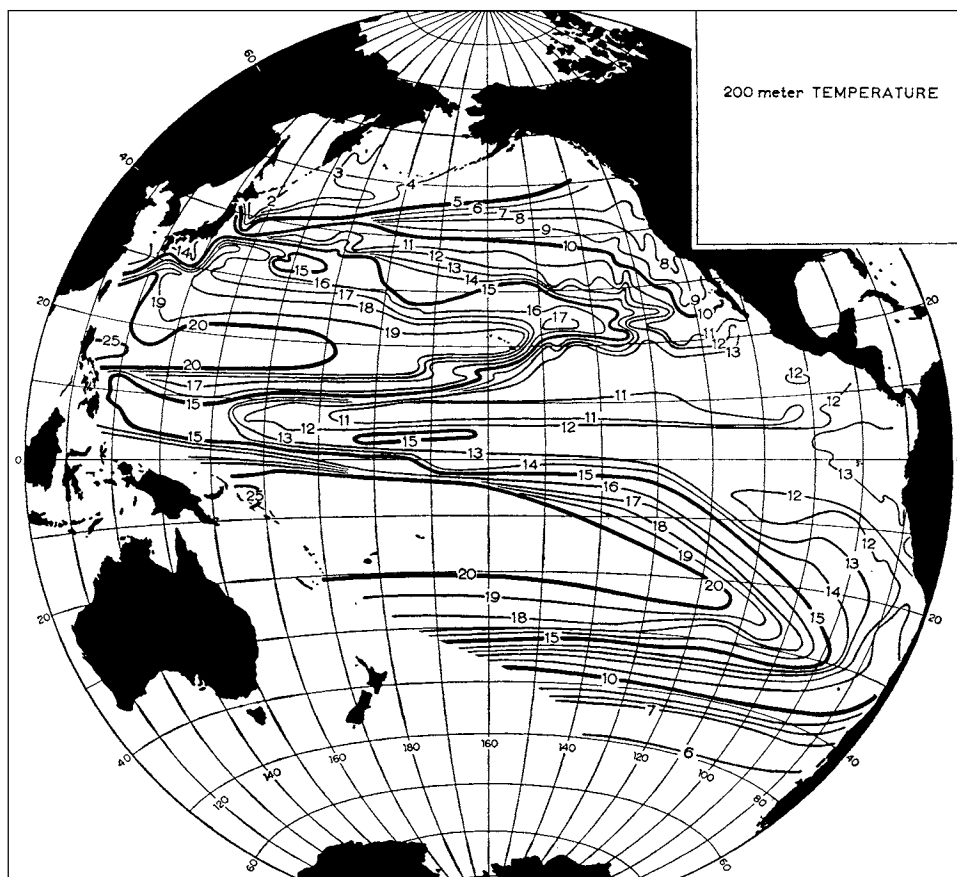


Fig. 7c. 200-meter temperatures ($^{\circ}$ C.) of the Pacific Ocean.

EXPLANATION OF FIGURES

The localities of the quantitative collections are indicated on the distribution maps as circles. Solid black circles indicate positive records and clear circles are negative records. Sampling carried out by the "Midpacific" expedition was not standardized with respect to depth of tow, and two kinds of nets were used. A rough estimate of the amount of water strained was obtained from the timing and depth of the hauls.

In mapping the distributions, the same contour levels for concentration were used throughout. Comparisons could then readily be made between the quantitative aspects of the distributions of different species. Concentration intervals were based on the sequence 1–49, 50–499, 500–4,999, and > 5,000 specimens per 1,000 cubic meters of water strained.

The level of the concentration of a species is consistent for all stations plotted within indicated contour levels. Lines drawn to limit a distributional range indicate that occurrence of the species has not been recorded outside of the indicated limit.

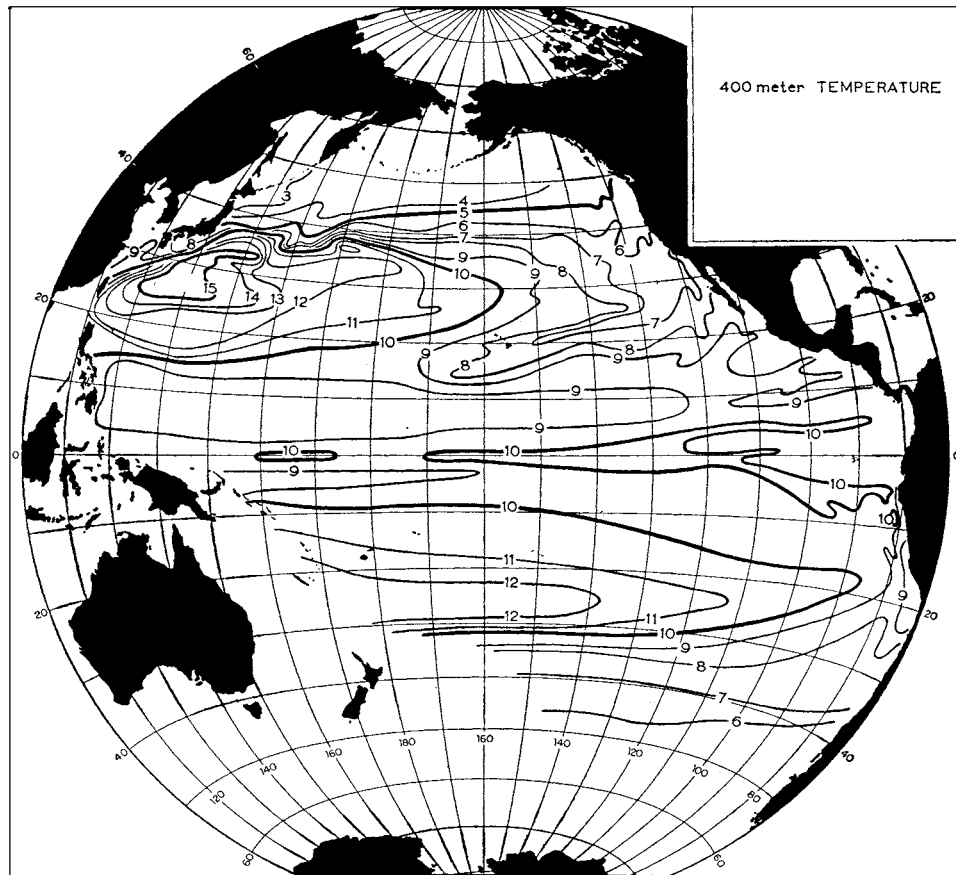


Fig. 7d. 400-meter temperatures ($^{\circ}$ C.) of the Pacific Ocean.

The centers of abundance of mesopelagic and bathypelagic species were too deep to be quantitatively sampled by the standard tows. The positive records for such species are indicated by black symbols (e.g., fig. 8), and the ranges are circumscribed when not cosmopolitan. Records from sources in the literature are usually indicated on the maps as crosses. The Gulf of Alaska localities reported by Banner (1949) are indicated by cross-hatching, or by crosses if the specimens were infrequent. The "Albatross" records from the eastern tropical Pacific (Hansen, 1912) are shown as triangles on the distribution maps of the epipelagic species (these triangles are not to be confused with those on the maps of the deep-living species which are symbols indicating a depth of sampling).

The histograms of vertical distribution included here are based upon average numbers at each depth. Furcilia larvae are indicated by clear bars, immatures, by cross-hatched bars, and adults by solid bars. A logarithmic scale was used so that both low and high concentrations could be shown on the same graph. All collections from the known geographical range of a species were used in deriving each average.

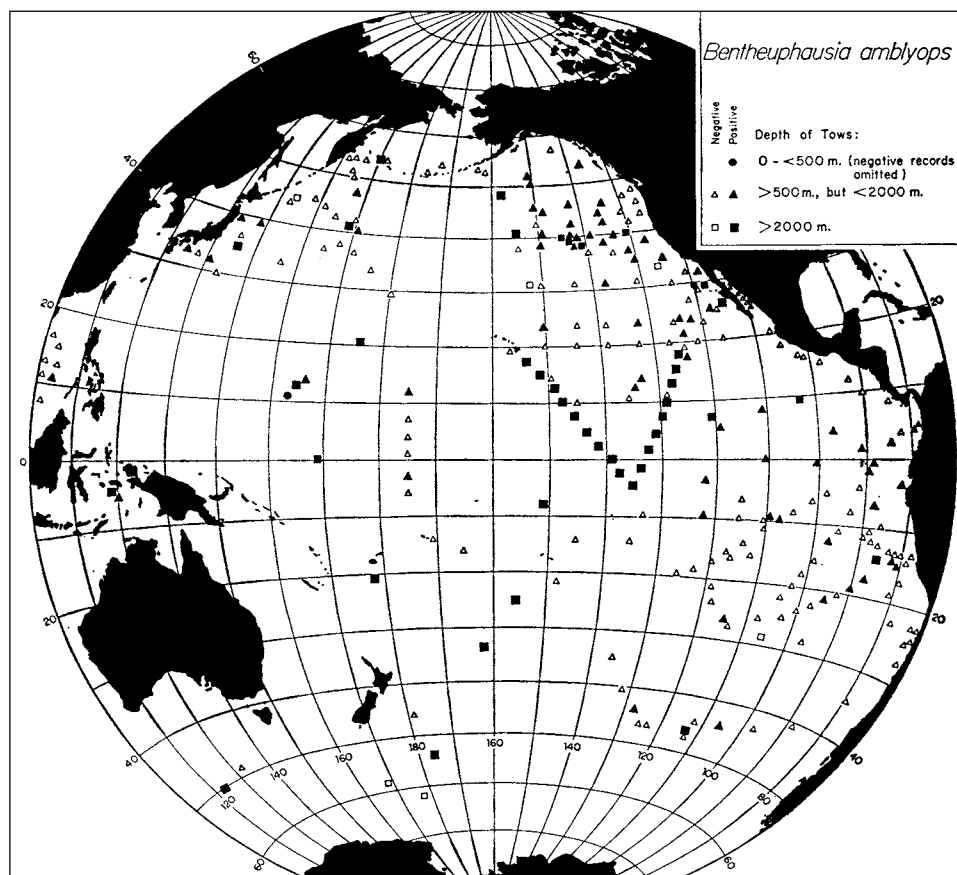


Fig. 8. Geographical distribution of *Bentheuphausia amblyops*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow. On this and the following maps of the distribution of species, blackened symbols represent positive records, clear symbols represent negative records, and crosses represent the localities for published records—unless otherwise indicated.

DISTRIBUTIONS OF THE EUPHAUSIID SPECIES

THE GENUS BENTHEUPHAUSIA G. O. Sars

Bentheuphausia amblyops G. O. Sars

(Fig. 8)

Horizontal distribution.—*Bentheuphausia amblyops* is one of the three most widely distributed euphausiids (cf. *Thysanopoda cornuta* and *Stylocheiron maximum*). A cosmopolitan species living in deep water, it has been captured in all regions of the Pacific where the depth of the ocean is greater than 1,000 meters.

Banner's (1949) material from the Gulf of Alaska yielded one young specimen, caught near 53° N. off British Columbia. The most northerly record in the Scripps collections is an immature individual from east of the Komandorski Islands, where the Bering Sea joins the Pacific. The *Vitjaz* found this species below 1,000 meters in the Kurile-Kamchatka Trench (Ponomareva, 1955).

B. amblyops occurs at 1,000–2,000 meters in the deep basins and troughs of the Continental Borderland off southern California. The deepest sills over which these basins communicate with the open ocean are at a depth of about 1,000 meters. It is evident that the sills are not barriers to *Bentheuphausia*. On the other hand, this species was not listed by Ruud (1936) in the extensive “Dana” records for euphausiids from the Mediterranean Sea, suggesting that the sill depth of 320 meters at the Strait of Gibraltar has kept *B. amblyops* from the deep Mediterranean. A reduced thermal stratification may also have inhibited colonization of the Mediterranean by certain bathypelagic species. There, a temperature of 13° C. is found at 3,000 meters.

B. amblyops has seldom been taken in the central regions of the North and South Pacific where the warm water strata are thicker than elsewhere in the Pacific. There are few deep samples from these areas.

This species was most consistently caught in the eastern North Pacific, 38°–45° N., and the eastern equatorial Pacific, 0°–10° N. These temperate and tropical regions are strongly influenced by cold currents, and emergence of deep-living species is evidently associated here with a shallow upper limit to the unlighted bathypelagic zone, and with upward bending of deep subtropical isotherms. Four samples collected in the two areas yielded the following numbers of specimens:

“Northern Holiday” expedition		
26 specimens (12–25 mm.)	39° 51.8' N., 134° 10.8' W.	450–750 m.
32 specimens (15–30 mm.)	40° 23' N., 139° 23' W.	400–650 m.
49 specimens (15–42 mm.)	40° 37' N., 143° 25' W.	0–4,000 m.
“Shellback” expedition		
49 specimens (7–15 mm.)	0° 17.7' N., 110° 26' W.	0–1,400 m.

In three of the above instances, small individuals were caught in quantity at depths not exceeding 1,400 meters.

B. amblyops was caught at 54° 22' S. by the “Monsoon” expedition but was not taken in two mid-water trawls sampling south of the Antarctic Convergence, near 57° S., where the temperature at depths below 400 meters is less than 3° C. It has been recorded from hauls deeper than 1,000 meters in the Indian and Atlantic oceans, the most northerly Atlantic record being 46° 16' N. and the most southerly near 37° S.

Vertical distribution.—*Bentheuphausia* was present in 28 of the 84 hauls reaching to 700 meters (table 2). It was not consistently caught until the depth-of-tow exceeded 1,000 meters: 14 out of 20 hauls that reached to about 1,500 meters contained this species. Only 5 adults were caught in hauls reaching to less than 1,000 meters. Nevertheless, *Bentheuphausia* appears to be sparsely distributed even in its more usual, deeper habitat: of the 108 records in the Scripps collections, 41 are based on single specimens.

Specimens of *Bentheuphausia* smaller than 7 mm. in length are not known. Most euphausiids 3–5 mm. in length appear to be representatively sampled by the standard 1-meter plankton net (Brinton, 1962*a*). It must be presumed that the young of *B. amblyops* live in very deep water.

No day-night difference is evident in the vertical distribution of this species, although the only two young caught above 280 meters were taken at night.

The horizontal and vertical ranges of *B. amblyops* are associated with a temperature range of 3°–9° C. The apparent absence of the species from superficial layers in high latitudes indicates that it may be physiologically adapted to the bathypelagic zone. The eyes of *Bentheuphausia* are atrophied and probably not stimulated by the solar illumination believed to initiate vertical migration in other species. It could be concurrently proposed that, if matings are facilitated through the recognition of patterns of bioluminescence characteristic of species or stage of sexual maturity, as Marshall (1954) suggested, atrophied eyes and absence of bioluminescent organs would be logically associated. *Bentheuphausia* has no bioluminescent organs.

TABLE 2
VERTICAL DISTRIBUTION OF BENTHEUPHAUSIA AMBLYOPS

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined	No. samples in which species was present	Adults (> 25 mm.)	Immatures (15–25 mm.)	Very young (< 15 mm.)	No. samples examined	No. samples in which species was present	Adults (> 25 mm.)	Immatures (15–25 mm.)	Very young (< 15 mm.)
70.....	727	0				704	0			
140.....	834	0				808	0			
280.....	385	0				376	3			1
500.....	70	5	5	53	4	65	3		11	1
700.....	45	19		20	14	39	9		11	13
1,000.....	20	9	1	9	6	17	5	2	8	6
1,500.....	11	9	4	101	24	9	5	4	10	1
2,000.....	16	16	46	103	2	20	20	77	128	1
3,000.....	4	1	8	2		3	2	3	7	3
4,000.....	0					5	2	8	44	

THE GENUS THYSANOPODA Milne-Edwards

Thysanopoda cornuta Illig; *Thysanopoda egregia* Hansen;

T. spinicaudata Brinton

The widely ranging bathypelagic euphausiids *Thysanopoda cornuta* and *T. egregia* are large, measuring 60–70 mm. at the onset of maturity. Adults of *T. cornuta* and *T. spinicaudata* may exceed 100 mm. in length. Full-grown individuals of other large species, *Bentheuphausia amblyops* (40–50 mm.), *Thysanopoda cristata* (40–55 mm.), *Thysanopoda acutifrons* (40–50 mm.), the North Atlantic species *Meganctiphanes norvegica* (40 mm.), and the Antarctic species *Euphausia superba* (50–60 mm.), scarcely approach the size of the large bathypelagic species.

Illig (1905), Tattersall (1913), and Hansen (1915) recorded the first large specimens of *T. cornuta*. Illig's and Tattersall's records were from the southeastern

Atlantic and Hansen's from the northwestern Pacific. Each of the three specimens was 79 mm. long! Hansen (1916) then listed an 81.5-mm. specimen from off Japan. The first adult male, a 95-mm. individual from the southern part of the Gulf of Alaska, was reported by Boden, Johnson, and Brinton (1955), who described the male copulatory organ.

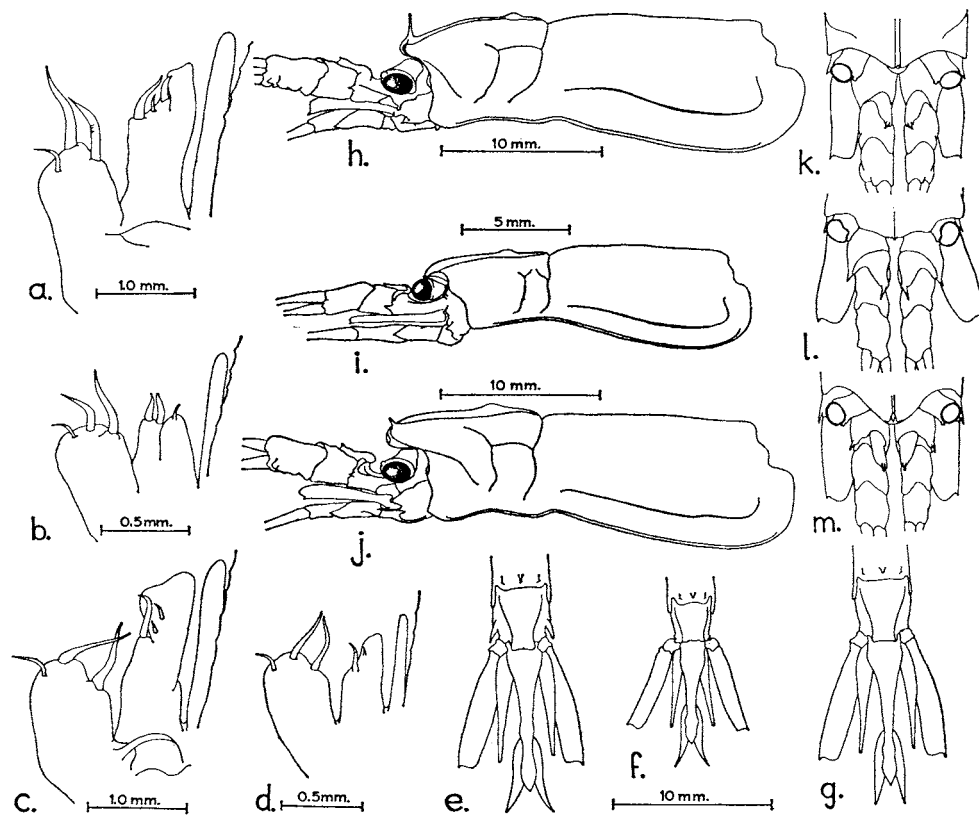


Fig. 9. The bathypelagic giant euphausiids. Male copulatory organs of (a) *Thysanopoda spinicaudata*, 104 mm. in length; (b) *Thysanopoda egregia*, 43 mm. in length; (c) *Thysanopoda cornuta*, 95 mm. in length; (d) *T. cornuta*, 50 mm. in length. Telson and uropods, in dorsal view, of the largest male specimens of (e) *T. spinicaudata*, (f) *T. egregia*, (g) *T. cornuta*. Lateral view of antennal peduncles and carapace of the same large specimens of (h) *T. spinicaudata*, (i) *T. egregia*, (j) *T. cornuta*. Dorsal view of frontal plate and antennal peduncles of the same specimens of (k) *T. spinicaudata*, (l) *T. egregia*, (m) *T. cornuta*.

Ponomareva (1955) found a 98-mm. *T. cornuta* in collections from the Kurile-Kamchatka Trench, and A. de C. Baker of the National Institute of Oceanography, England, showed me a 105-mm. specimen of *T. cornuta* caught in 1958 by the *Discovery II* near the Azores. In June, 1960, the R.V. *Spencer F. Baird*, trawling in mid-water at 2,500 meters off Baja California, 24° 13' N., 121° 35' W., captured a 115-mm. specimen.

Thysanopoda egregia is less well known. The description (Hansen, 1905) is based on immature specimens caught by the Prince of Monaco in the northeastern Atlantic. The copulatory organ of the largest known male, an immature specimen

43 mm. long, was sketched by Boden, Johnson, and Brinton. A 62-mm. female caught at 0° 18' N., 110° 26' W. in the eastern Pacific by the R.V. *Horizon* is the largest known specimen of this species.

Thysanopoda spinicaudata is known only from three adults and three juveniles, 25, 40, and 50 mm. It was described (Brinton, 1953) on the basis of a female 95 mm. long, caught off Baja California. A second specimen was trawled by the R.V. *Spencer F. Baird* off Guadalupe Island, Baja California, in February, 1960. This is a male, 104 mm. long. It agrees completely with the first specimen. The characters that distinguish it from *T. cornuta* include (1) frontal plate not reaching to the mid-point of the eyes; (2) heavy spines directed posteriorly from each side of the sixth abdominal somite; (3) endopodite of the second maxilla elongate, length exceeding three times its width; (4) lower margin of the pre-anal spine, viewed laterally, a continuous unbroken curve; (5) a straight anterior margin of the scale of the second antenna; (6) setose, raised dorsal area of the first article of the peduncle of the first antenna bearing an acute tooth directed upward and *anterolaterally*. A long slender vertical spine on the frontal plate, present on the female, is evidently torn away—judging by a scar—from the male specimen.

A 150-mm. female specimen of *T. spinicaudata* was caught by the R. V. *Horizon* at 33° 38' N., 131° 54' W., in March, 1962. This largest-known euphausiid was collected by a mid-water trawl, sampling 0–2,000 meters.

A 25-mm. specimen, having the large lateral spines on the sixth abdominal segment and a slender vertical spine on the frontal plate was caught by the “Monsoon” expedition at 25° 52' S., 155° 44' W., trawling in midwater at 2,250 meters. A 40-mm. specimen was caught by the “Tethys” expedition at 12° 07' N., 148° 35' W. by a trawl sampling to 2,100 meters. A 50-mm. specimen was caught by the R. V. *Horizon* at 29° 55' N., 120° 12' W., trawling 0–2,000 meters.

The terminal and lateral processes of the male copulatory organ of *T. spinicaudata* (fig. 9, *a*) are bent forward and inward. A large curved additional process is attached near the base of a fold in the distal part of the median lobe. One smaller additional process is situated between the large lateral and additional processes on the left copulatory organ, and two are present at the same place on the right copulatory organ.

The processes of the copulatory organ of the adult of *T. spinicaudata* bear a greater resemblance to those of the immature specimen of *T. egregia* than to those of *T. cornuta* (fig. 9, *d-e*). The terminal and lateral processes are slender in *T. cornuta* and the additional processes are both small. In both *T. egregia* and *T. spinicaudata* the processes are stronger. There is agreement between the two last-named species in the direction in which the terminal, proximal, and lateral processes curve.

The pseudoexopod of the first maxilla is thickened along its outer margin in *T. spinicaudata*, agreeing with *T. egregia*, but not with *T. cornuta* (Brinton, 1953, figs. 9–13).

A further point of interest has to do with identification of the larvae of these giant species. Only two types have been described. Before reaching the length of 14 mm., Tattersall's (1939) “Species A” is characterized by (1) ripplelike markings on the posterolateral parts of the carapace, (2) a broad rostral plate, the anterior margin of which is almost transverse, and (3) a long spiniform process from

TABLE 3
LARVAL STAGES OF THYSANOPODA EGREGIA AND TATTERSALL'S "SPECIES B"
(*T. CORNUTA*-*T. SPINICAUDATA*)

Stage	Length range (mm.)	No. of specimens	Pleopod development ¹	Terminal telson spines ²
<i>Thysanopoda egregia</i>				
Furcilia I.....	4.6-5.4	13	3"	8
Furcilia II.....	4.9-6.1	13	3" + 1'	8
Furcilia III.....	5.7-7.2	5	4" + 1'	2: Specs. 4- <u>1</u> -3 2: Specs. 3- <u>1</u> -3 1: Specs. damaged
Furcilia IV.....	7.3-8.0 (2d antenna flagellum short, slender)	6	5"	2: Specs. 3- <u>1</u> -3 2: Specs. 4- <u>1</u> -3 1: Specs. 3- <u>1</u> -4 1: Specs. damaged
Furcilia V.....	9.0-10.6 (2d antenna flagellum long, bulbous)	4	5"	3: Specs. 3- <u>1</u> -3 1: Specs. 3- <u>1</u> -4 1: Specs. damaged
Furcilia VI.....	10.7-13.0 (2d antenna flagellum segmented)	10	5"	5: Specs. 3- <u>1</u> -3 2: Specs. 2- <u>1</u> -2 1: Specs. 3- <u>1</u> -2 2: Specs. damaged
Cyrtopia I.....	13.0-14.2	2	5"	1
Cyrtopia II.....	13.2-16.0	4	5"	1
Post-larva.....	18.0	1	5"	1
<i>Thysanopoda cornuta</i>				
Calyptopis.....	4.6-5.2	3	0	7
Furcilia I ³			(4' ?)	
Furcilia II.....	8.4-9.0	6	4"	7
Furcilia III.....	10.0	1	5"	7
Cyrtopia I.....	12.0-16.5	3	5"	1
Cyrtopia II.....	16.0-17.0	4	5"	1

¹ The symbol ' designates a simple pleopod, " a setose pleopod (after Einarsson, 1945, and others).

² The larger or dominating spines are underlined.

³ Einarsson (1945) refers to *T. cornuta* development as occurring 4', 4'+1', 5". He does not describe these larvae; it cannot be determined whether they actually are *T. cornuta*.

the dorsolateral margin of the sixth abdominal segment. Belonging to "Species A" are larvae called "*T. cornuta*," described by Hansen (1912) and Zimmer (1914), and two of the three larvae described by Illig (1930). A series of developmental stages of this species, showing it to be *T. egregia*, not *T. cornuta*, is present in the Scripps collections. This series, including six furcilia and two cyrtopia stages, is listed in table 3. The developmental stages of these species will be treated more fully elsewhere.

Tattersall's "Species B" bears no ripple markings on the carapace and no spini form process on the dorsolateral margin of the sixth abdominal segment. It has a

narrow rostral plate with convergent lateral margins, middorsally produced into a conspicuous rostral spine. "Species B" includes larvae described by Hansen (1915), Tattersall (1926, 1939), Illig (1930; one specimen), and Banner (1949). Tattersall suggested that these belonged to *T. egregia* because Hansen and Illig believed "Species A" to be *T. cornuta*. A developmental series shows that, on the contrary, "Species B" certainly

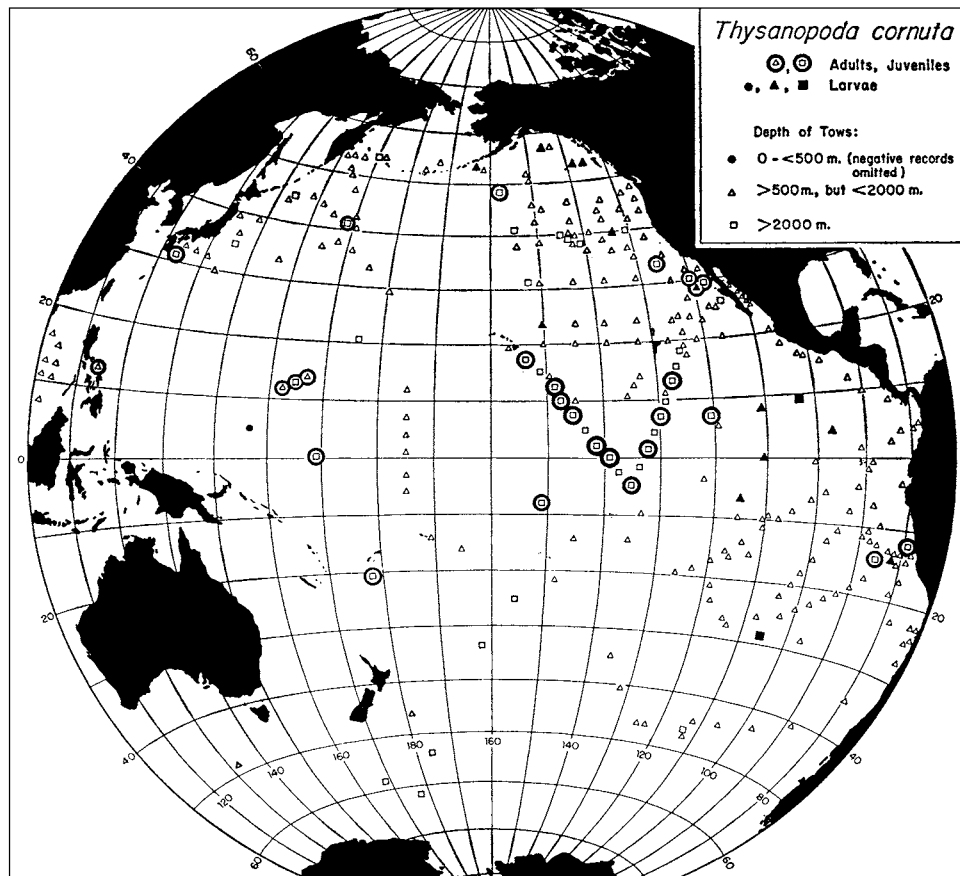


Fig. 10. Geographical distribution of *Thysanopoda cornuta*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow. Records for larvae are based on Tattersall's (1939) "Species B," which may include larvae of both *T. cornuta* and *T. spinicaudata*.

includes *T. cornuta*, and may also include larvae of *T. spinicaudata*. The immature specimen of *T. spinicaudata* more closely resembles *T. cornuta* than it does *T. egregia*. One stage of calyptopis, three of furcilia, and two of cyrtopia have been found of "Species B" (table 3).

Horizontal distribution (figs. 10, 11).—Two specimens of *T. egregia* have been previously recorded from the Pacific, and 7 from the Atlantic and Indian oceans; 95 specimens, including 61 larvae, have been found in the Scripps collections from the Pacific. Twenty-five specimens of *T. cornuta*, 11 of which were "Species B" larvae, have been previously reported; 9 were from the Pacific. The Scripps material

TABLE 4
VERTICAL DISTRIBUTION OF BATHYPELAGIC GIANT EUPHAUSIIDS

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined	No. samples in which species was present	Adults (> 53 mm.)	Immatures (16-52 mm.)	Larvae (< 16 mm.)	No. samples examined	No. samples in which species was present	Adults (> 53 mm.)	Immatures (16-52 mm.)	Larvae (< 16 mm.)
<i>Thysanopoda egregia</i>										
70.....	727	5			5	704	1			1
140.....	834	9			9	808	1			1
280.....	385	13			14	376	9			9
500.....	70	19		3	14	65	2			2
700.....	45	4		3	2	39	0			
1,000.....	20	2		1	3	17	1			1
1,500.....	11	3	2	3		9	2		3	1
2,000.....	13	1		4	1	18	8	1	17	
3,000.....	4	1		2		4	0			
4,000.....	0					5	1		1	
<i>Thysanopoda cornuta</i> and "Species B" larvae										
70.....	727	0				704	0			
140.....	834	0				808	0			
280.....	385	1				376	0			
500.....	70	1			1	65	0			
700.....	45	0				39	3			3
1,000.....	20	2	2		3	17	4	1	5	2
1,500.....	11	2			3	9	3		1	4
2,000.....	13	4	3	5		18	12	7	12	4
3,000.....	4	1		1		4	4	5	2	1
4,000.....	0					5	2	2		
<i>Thysanopoda spinicaudata</i> (only six specimens known)										
2,000.....		2	1	1			4	2	2	

contains 51 more specimens, 19 of which are "Species B" larvae. All but one of the postlarval specimens of these species in the Scripps collections have been caught by the Isaacs-Kidd mid-water trawl; the male of *T. spinicaudata* was taken in a 30-ft. otter trawl.

Vertical distribution.—The vertical distributions of *T. egregia*, *T. cornuta*, and "Species B" larvae are given in table 4. Larvae of *T. egregia* have been caught above a depth of 70 meters in only six tows, all off California. Occurrence-per-tow of larvae was greatest when a depth of 500 meters was attained by the net: 16 records in 135 tows. Immature specimens were taken only in tows reaching to at

least 500 meters; the maximum number-per-tow was found near 1,500–2,000 meters. Specimens 45–62 mm. long have been taken only in hauls reaching to 1,500–2,000 meters.

Three and one-half times more larvae were taken above 700 meters in day hauls than in night hauls. This suggests that the young of *T. egregia* perform a reverse vertical migration, being nearest to the surface during

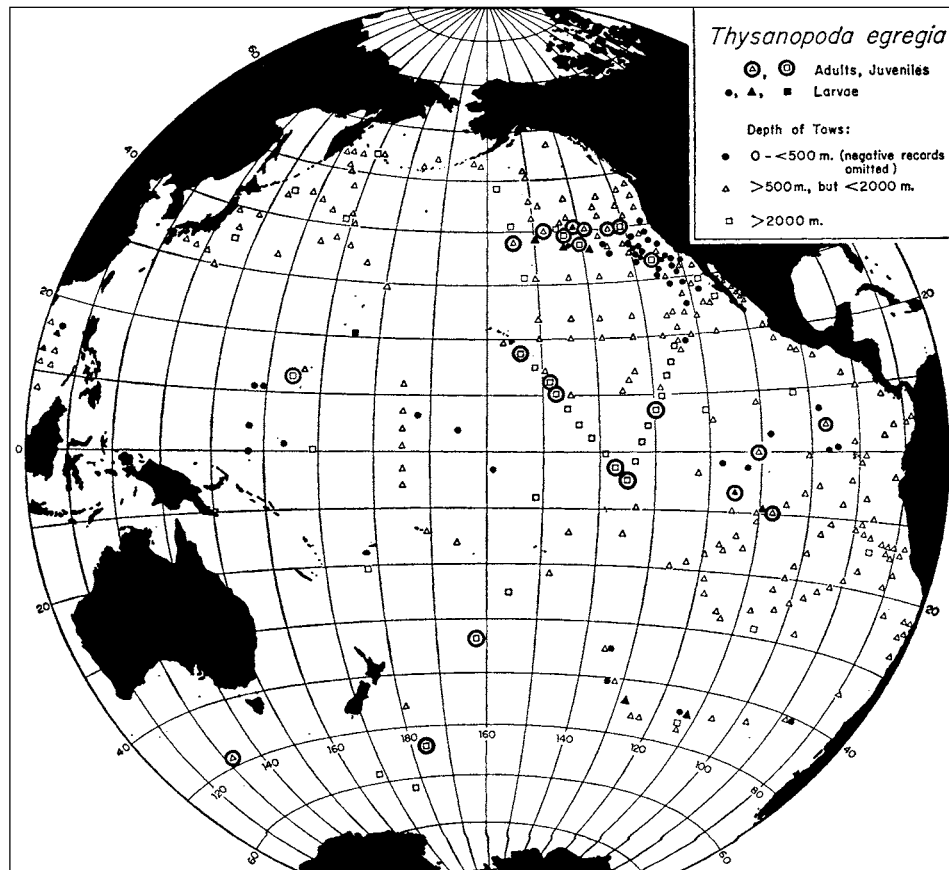


Fig. 11. Geographical distribution of *Thysanopoda egregia*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

the day. The number of samples obtained below 700 meters with fine-mesh nets is insufficient to demonstrate a possible nighttime maximum below that depth.

Immature stages of *T. cornuta* and “Species B” larvae occur at greater depths than analogous stages of *T. egregia*. Only four specimens, all “Species B” furcilia, have been found above 700 meters. Larvae were taken most consistently between 700 and 2,000 meters, immatures of *T. cornuta* near 1,000 meters or deeper, and adults below 2,000 meters. Calyptopis stages were taken in tows that reached to 1,300–1,700 meters. Some of the Furcilia I larvae of *T. egregia*, the youngest known of that species, were taken in tows that reached only to 70 meters.

The horizontal distribution of these two species is interpreted from consideration of the vertical distribution of the young stages.

T. egregia occurs south of 41° N. in the eastern Pacific. The many records of its occurrence in the region of the California Current are certainly a consequence of the intensity of sampling there. This species was not caught between 19° N. and 10° N. in the eastern equatorial region, but was present at a number of stations south of 10° N., outside of the region of the Peru Current. In the mid-equatorial Pacific, *T. egregia* has been found between 18° N. and 5° S. In the western Pacific it has only been caught near 160° E., 0°–10° N. The most southerly records, 44°–45° S., are from the “Downwind” and “Monsoon” expeditions.

If, as is supposed, the larvae of *T. egregia* inhabit depths of 200–500 meters, they live in the region characterized by temperatures of 5°–10° C. at 400 meters and 5°–15° C. at 200 meters. Such limiting isotherms could explain the apparent absence of *T. egregia* from an area east of Japan, from waters north of 41° N., and from the Antarctic Ocean south of 55° S. Deep sampling in the subtropical western Pacific is, as yet, inadequate to indicate absence of *T. egregia* there.

T. cornuta occurs more widely in the North Pacific and the Peru Current region than does *T. egregia*. Larvae of “Species B” live in colder water and at greater depths than larvae of *T. egregia*, and are found as far north as the Gulf of Alaska. Adults have been taken at 49° N., and in all parts of the Pacific except the subtropical South Pacific, from which there is a single record for one “Species B” larva. Like *Bentheuphausia amblyops*, the early larvae of which are not known and probably do not occur above 500 meters, *T. cornuta* appears to be a cosmopolitan species in the bathypelagic zone.

Less stenobathic during the course of its development, *T. egregia* is more restricted in horizontal range than *T. cornuta*. Its adult may inhabit greater depths than those inhabited by the adult of *T. cornuta*; hence, the apparent scarcity of *T. egregia* in the warm subtropical western Pacific where postlarval specimens were caught only in tows reaching deeper than 2,000 meters.

Figures 10 and 11 show that the large bathypelagic species were most often caught in regions where sampling was most intense. However, where cold waters are brought near to the surface of tropical and subtropical seas, the emergence of bathypelagic species (suggested above for *Bentheuphausia amblyops*) would be expected. Conditions characterized by cooled water and enrichment prevail in most of the regions where the giant euphausiids have been found: (1) the northeastern Pacific near 40° N. and the outer margins of the California and Peru currents where warm water masses impinge upon colder currents, and (2) near the equator or at the margins of the Equatorial Countercurrent—places where upwelling and thermal anticlines are found in the open ocean (Cromwell, 1953).

The occurrence of *T. cornuta* and postlarval *T. egregia* may also be correlated with proximity to seamounts, islands, and continental slopes, seaward of the 3,000 meter bathymetric contour. Two of the four records of “Species B” larvae in the Gulf of Alaska are from above the slopes of seamounts, and one is from the north slope of the Aleutian Trench. *T. egregia* was found to be common above the Mendocino Escarpment, 40° N., off northern California. Such a submarine mountain range would be expected to abut upon deep currents and internal waves, causing

deep turbulence and vertical displacement of bathypelagic species. Records of *T. cornuta* from California and Baja California waters are from above the slopes of Erben Bank, Guadalupe Island, an unnamed seamount south of Guadalupe Island, and Rosa Bank. Other records for the adult of *T. cornuta* are from the continental and insular slopes of Peru, the Philippines, Bikini, Japan, and the Kurile Islands. The Pacific records not accounted for above are from waters above relatively undifferentiated bottom topography. In each of these records a depth in excess of 2,000 meters was reached by the net.

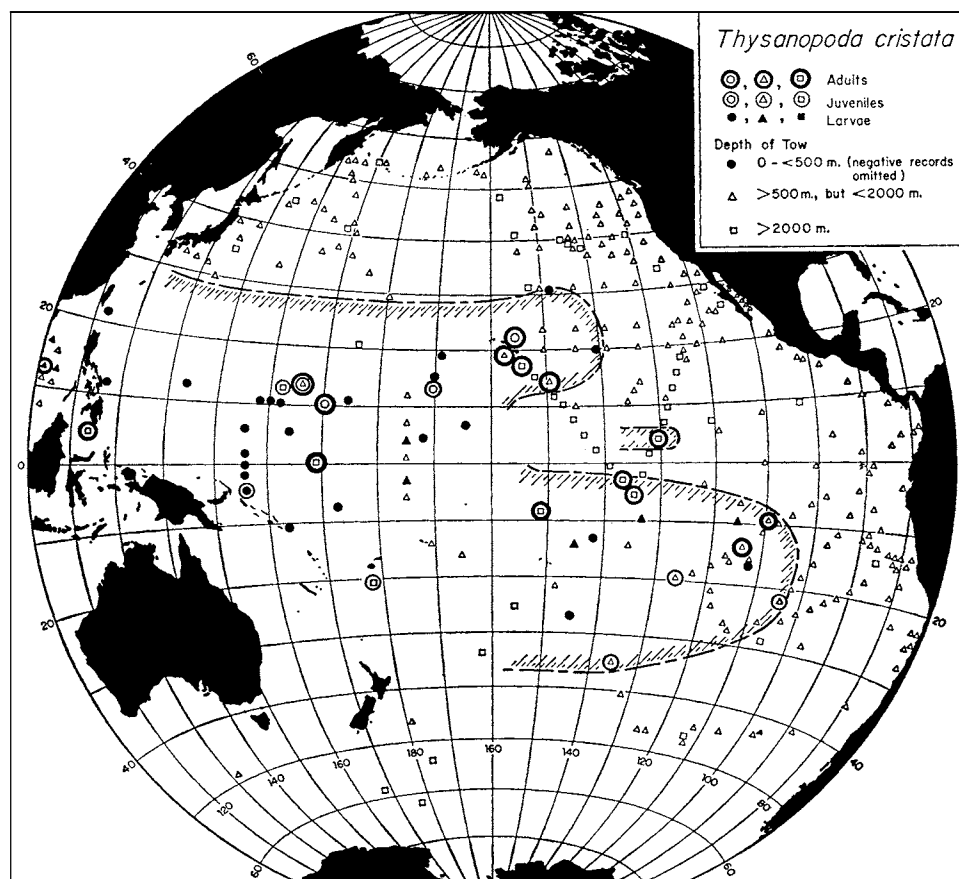


Fig. 12. Geographical distribution of *Thysanopoda cristata*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

Thysanopoda cristata G. O. Sars

(Fig. 12)

Four individuals of this species have been previously recorded from the Pacific. A single young specimen was found in the Atlantic, in the Sargasso Sea (Ortmann, 1893). *T. cristata* has not been previously recorded from the Indian Ocean, but a large female was caught at 10° S., 115° E. by the "Monsoon" expedition. It is possible,

on the basis of 68 specimens in the Scripps material, to describe the approximate range of this species in the Pacific.

Vertical distribution.—Hansen (1912) concluded that adult specimens “live in very considerable depths,” although his three specimens, one of which was adult, all came from above 500 meters.

TABLE 5
VERTICAL DISTRIBUTION OF *THYSANOPODA CRISTATA*

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined (within range of species)	No. samples in which species was present	Adults (> 37 mm.)	Immatures (16-25 mm.)	Larvae (< 15 mm.)	No. samples examined (within range of species)	No. samples in which species was present	Adults (> 37 mm.)	Immatures (16-25 mm.)	Larvae (< 15 mm.)
140.....	59	2			2	32	1			1
280.....	131	16	1	4	16	121	8	2	1	8
500.....	15	5	1	2	3	5				
700.....	6	2	1		2	9	1	1		1
1,000.....	0					1	1	1	3	
1,500.....	0					0				
2,000.....	5	3	2	1		6	5	9	1	
3,000.....	1	1	3	1		0				
4,000.....	0					1	1	1		

Four of the 22 adults from the Pacific were caught at above 500 meters (table 5). However, the occurrence-per-tow, within the known range of the species, was 77 per cent when a depth of at least 1,000 meters was attained by the net. It is therefore supposed that *T. cristata* has an extensive vertical range. However, no evidence for diurnal vertical migration was found.

Occurrence-per-tow of larvae was greatest near 500 and 700 meters, but 27 specimens were caught above 280 meters, 3 of them above 140 meters.

Horizontal distribution.—*T. cristata* has been found in the mid-Pacific, 30° N.–35° S. The range agrees with the positions of the warmest parts of the Central Water Masses. It transgresses Equatorial Water in the west where this water is pinched into a narrow east-west belt (cf. *Nematobranchion sexspinosus* and *Stylocheiron robustum*).

Thysanopoda tricuspidata Milne-Edwards

(Fig. 13)

Thysanopoda tricuspidata, caught at the surface of the eastern Atlantic, was the first euphausiid described. It was placed by Milne-Edwards (1837) in the spurious crustacean order Stomapodes, together with *Mysis*, *Lucifer*, *Phyllosoma*, and *Squilla*.

The larvae, first described by Dana (1852) as *Cyrtopia rostrata*, are readily recognized owing to the characteristic structure of the eye. Before the true cornea

develops, the sensory portion consists of about seven greatly enlarged facets. The eye, the small, slender form of the larvae, and frequent occurrence at the sea surface are peculiar to this species in the genus *Thysanopoda*, which is, however, typically deep-living.

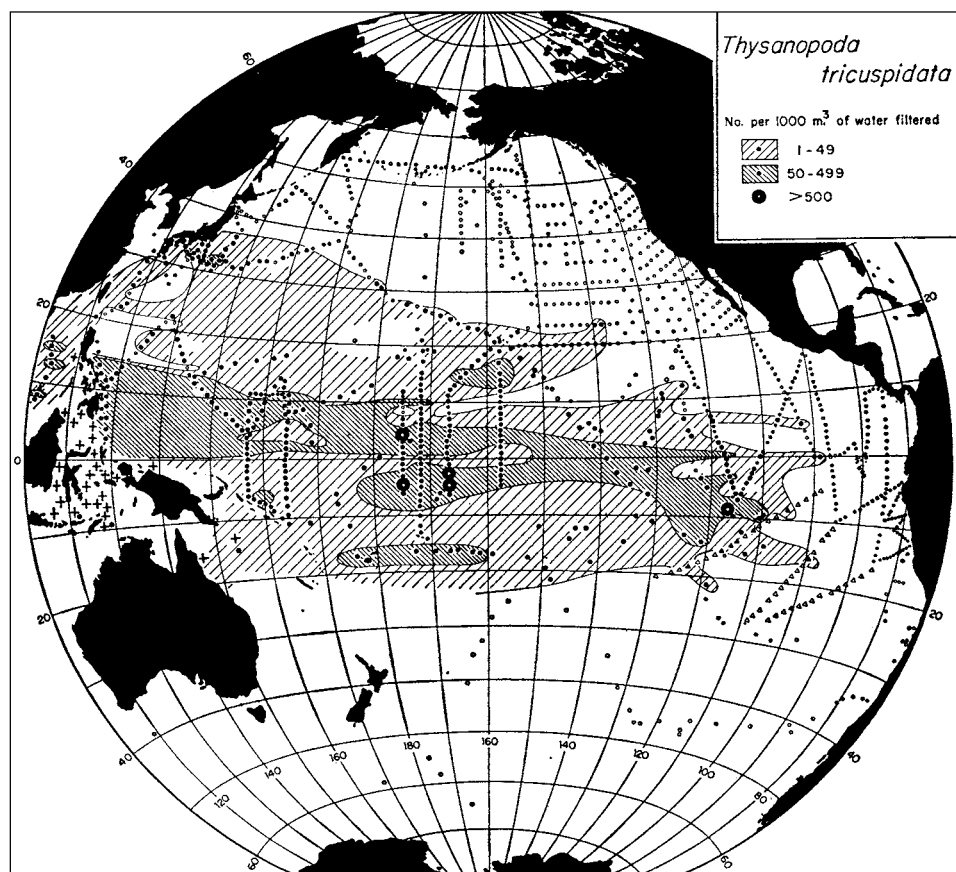


Fig. 13. Geographical distribution of *Thysanopoda tricuspidata*. The triangles are records from Hansen (1912).

T. tricuspidata ranges from 36° N. to at least 21° S. in the western Pacific. It is missing from most of the eastern equatorial basin. The majority of the records on which the distribution is based are of larvae or immature specimens.

The distribution of the adult is incompletely known. Although the species has been found at 268 Scripps and POFI stations, the adult has been caught at only 60 of them. North of 20° N., adults were caught at only four stations, all in the region of the Kuroshio Extension. The four tows were made at night, from 0–140 meters. Records east of 162° E. in the central North Pacific, and in the tongue of distribution extending eastward from Hawaii are based entirely upon larvae and immature specimens.

“Numerous” and “enormous numbers” of specimens were caught near the Philippines by the *Albatross* (Hansen, 1916). This region of high concentration extends

eastward. The number of specimens is small north of 10° N., the northern boundary of the Equatorial Countercurrent in mid-ocean. *T. tricuspida* was lacking at four "Equapac" stations, 8°–10° N., at the northern boundary of the Countercurrent. It was not found in "Midpacific" expedition samples taken north of 9° N. and east of 150° W.

TABLE 6
VERTICAL DISTRIBUTION OF THYSANOPODA TRICUSPIDATA
(In Numbers per 1,000 cu.m. [average per station])

Depths sampled (m.)	Day				Night			
	No. samples (includes only stations where species was found, at some depth)	Adults (15-25 mm.)	Immatures (6-14 mm.)	Larvae (2-5 mm.)	No. samples (includes only stations where species was found, at some depth)	Adults (15-25 mm.)	Immatures (6-14 mm.)	Larvae (2-5 mm.)
I. Kuroshio Region, east of Japan								
0-140.....	14	0	5	9.5	15	1.2	14	8.2
140-280.....	6	0	0	0	9	0	0.3	0.5
280-600.....	1	0	0	0	3	0	0	0
II. North Central Pacific, northwest and east of Hawaii								
0-140.....	9	0	3.6	0.8	10	0	5.3	2.2
140-280.....	5	0	0	0	7	0	0.4	0.1
0-700.....	2	0	2.5	0	2	0	0	0
III. Mid-equatorial Pacific, south and southwest of Hawaii								
0-140.....	29	0.8	63	111	11	0	55	96
0-300.....	28	0.3	11	37	18	2.8	19	49
0-700.....	2	0	2	12	4	0	0.8	0.8

High concentrations were found between the equator and 20° S. in the midequatorial Pacific, and near the eastern limit of the range of the species, 114°–122° W.

T. tricuspida extended east of 110° W. in three places: (1) near 7° N., within the Equatorial Countercurrent, (2) at the equator, and (3) along the northern margin of the South Pacific Central Water Mass. The last-named distribution was plotted from *Albatross* records and is the only one of the three eastward intrusions based on records of adults.

Vertical distribution.—Near Japan, larvae and immature individuals were almost entirely restricted to the upper 140 meters (table 6). Adults were caught above 140 meters at night. Numbers of larvae in the upper layers during the day were approximately equal to numbers found at night; immature specimens were more numerous in the samples taken at night.

East of Hawaii, larvae and immature specimens were most numerous in the 0–140-meter layer at night; in a third area, southwest of Hawaii, day concentrations of larvae and immature specimens at 0–140 meters were nearly equal to night concentrations. With a depth-of-tow of 0–300 meters in the region southwest of Hawaii, concentrations were greatest at night; when the depth was increased to 700 meters, no difference in concentration was noted between day and night hauls. Adults, if present in this area, were not reached by the net.

Hansen's (1911, 1912, 1916) records provide evidence that the larvae of *T. tricuspidata* occur at or near the surface. Larvae were caught in 10 surface tows at the Philippines, in 23 tows at the East Indian Archipelago, and in 2 tows in the eastern equatorial region. Sars's (1885) 8 Pacific localities for this species, which included 2 records for adults, were all based upon surface tows. The Scripps collections do not include surface samples from within the range of the species.

Adult *T. tricuspidata* was caught in East Indian waters in 4 tows, all reaching to at least 1,000 meters. Near the Philippines, adults were caught at the surface on four occasions; on three they were very numerous. The surface catches were made at dusk. Adults caught by the *Albatross* in the eastern equatorial region were in night hauls, from 0–600 meters.

Of the 44 Scripps hauls (all 0–300 meters, or less) in which adults were caught, 36 were made at night. Adults were caught in 6 additional hauls that attained a depth exceeding 1,000 meters. They were found in all mid-water trawl collections (all reached a depth of at least 1,000 meters) made within the known range of the species.

Evidently the adult is to be found above 300 meters only at night. Its daytime habitat is deeper, probably 500–1,000 meters. Lewis (1954) found the daytime maximum of *T. tricuspidata* in the Florida Current to be near 550 meters. The largest Scripps specimens, 30 mm. in length, have been caught only in tows that reached to at least 1,000 meters.

Thysanopoda acutifrons Holt and Tattersall

(Fig. 14, table 7)

Four *Thysanopoda* species comprise a group of closely related species. *T. orientalis* and *T. microphthalma* inhabit deep waters of the temperate and tropical seas. *T. acutifrons* and *T. johnstoni* live north of 40° N. and south of 40° S.

T. acutifrons is undoubtedly the species from the Gulf of Alaska designated *Thysanopoda dubia* by Banner (1949), on the basis of immature specimens. It has been found in the northern and southern parts of the Pacific and Atlantic oceans. *T. orientalis* occurs between 40° N. and 40° S. in the Pacific, Atlantic, and Indian oceans (Hansen, 1912, 1915; Zimmer, 1914; Illig, 1930; Tattersall, 1939). *T. microphthalma* is known from the subtropical North Atlantic (Sars, 1885; Hansen, 1905; Holt and Tattersall, 1906; Tattersall, 1926). *T. johnstoni* was described from southeastern Australian waters (Sheard, 1942), but Einarsson (1945) reported *T. acutifrons* from "Dana" collections made east of New Zealand, and "Monsoon" expedition collections from the southwestern Pacific include only *T. acutifrons*. The latter species was found by the "Downwind" expedition in the mid-South Pacific. *T. johnstoni*, based upon specimens from tuna stomachs, may be the same

as *T. acutifrons*. It was distinguished by the absence of a spine-shaped process on the male copulatory organ.

Einarsson (1942) considered *T. microphthalmalma* to be a “smaller and more southern variety of *T. acutifrons*,” whereas “*T. orientalis* is intermediate, both as to size and shape of the antennular lobe.” But Einarsson showed that the spermathecae differed among the three species. Hansen (1910) had shown that the copulatory organs

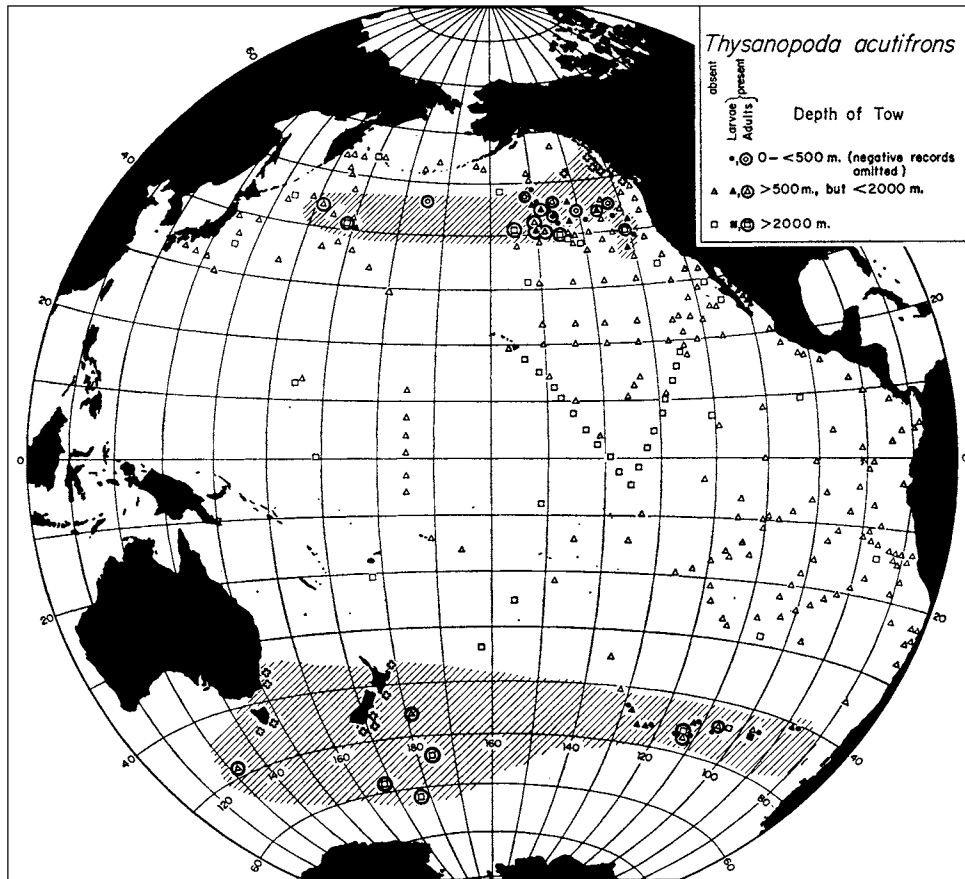


Fig. 14. Geographical distribution of *Thysanopoda acutifrons*.

of the males of the three species differed in significant details.

Larval specimens of *T. acutifrons* and *T. orientalis* are similar. They can be separated most readily on the basis of the larger size of *T. acutifrons* at analogous stages of development.

Horizontal distribution.—Samples collected by the International Fisheries Commission, 1929—1934, which were analyzed for euphausiids by Banner (1949), indicated that *T. acutifrons* was not present in the Gulf of Alaska except in the southeastern part where a total of 19 immature individuals (*T. dubia*) was caught off the Queen Charlotte Islands and Vancouver Island. The Scripps collections extend

the distribution westward across the ocean as far as 161° 39' E. This species was not found by the *Vitjaz* in her survey of the region of the Kurile-Kamchatka Trench, nor is it known from the Bering Sea.

Most records consist of fewer than 10 specimens. The three localities for adults west of 160° W. were based upon single individuals. The most southerly record in the western North Pacific, near 170° E., was of 3 postlarval specimens. Compared to 1 immature individual collected by the Isaacs-Kidd mid-water trawl, trawling to a depth of 0–2,500 meters, near 41° N. in the western Pacific, two trawl samples from the eastern Pacific, sampling to depths of 175 and 850 meters at 43° 08' N., 150° 00' W., and 41° 42' N., 150° 00' W., respectively, collected 184 adult and immature specimens.

TABLE 7
VERTICAL DISTRIBUTION OF THYSANOPODA ACUTIFRONS IN THE NORTH PACIFIC

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (29-50 mm.)	Immatures (13-28 mm.)	Larvae (3-12 mm.)	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (29-50 mm.)	Immatures (13-28 mm.)	Larvae (3-12 mm.)
140.....	28	3	1		9	18	5	136	2	
280.....	18	7			11	8	5	7	3	8
500.....	4	1		1		0				
700.....	6	3			6	2	1	1	1	1
1,000.....	3	3	27	26	5	1	1	1		
2,000.....	1	1	1			1	1	18		
3,000.....	1	1		1		0				
4,000.....	0					1	1		2	

Thus, *T. acutifrons* occupies a latitudinal belt north of 41° N. It is missing north of 45° N. in the western Pacific, a region fed by the Oyashio and Aleutian currents which arise to the north. The main range of this species is within the cooler part of the North Pacific Drift. Banner found peak numbers off Canada during January to March.

There is no obvious system of currents by which the species may be maintained in its postulated North Pacific range. Flow is predominantly toward the east. *T. acutifrons* may make the circuit of the cyclonic gyral in the Gulf of Alaska, or be carried westward by intermittent countercurrents and eddies.

The distribution in the South Pacific occupies a broader zonal belt, 36°–60° S., than in the North Pacific. A single specimen was found in a large mid-water trawl sample from 63° S. ("Monsoon" expedition), suggesting that this is near the southern limit of the range. This species is most concentrated in the subantarctic region, 40°–50° S. Its limits of range are associated with 4° C. and 10° C. isotherms at a depth of 100 meters.

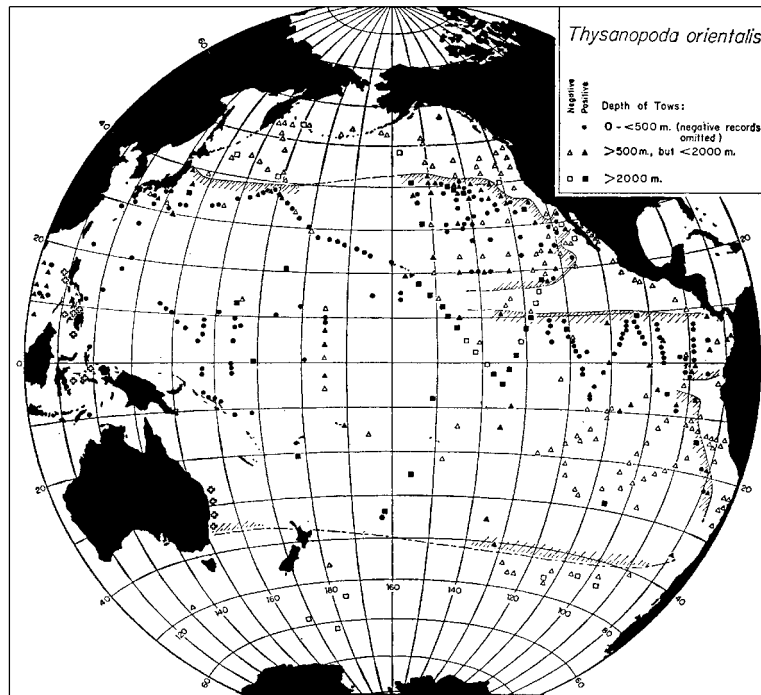


Fig. 15. Geographical distribution of *Thysanopoda orientalis*.

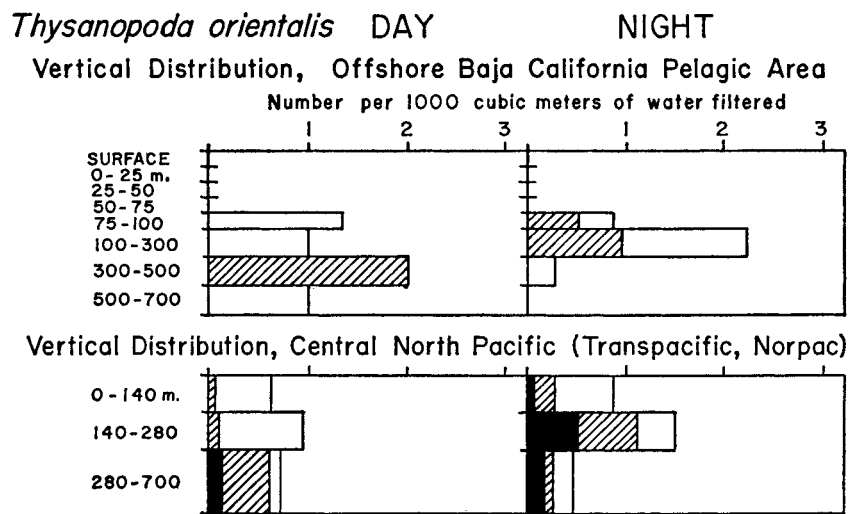


Fig. 16. Vertical distribution of *Thysanopoda orientalis* in the Baja California "Pelagic Area" (fig. 1a) and in the part of its range traversed by "Transpacific" and "Norpac" expeditions. In this and in the following diagrams of vertical distribution, adults are indicated by the solid black bars, immature specimens by the cross-hatched bars, and furcilia larvae by the open bars. The number of specimens at each depth is the average collected at stations within the geographical range of the species.

Thysanopoda orientalis Hansen

(Fig. 15)

Horizontal distribution.—The distribution of *Thysanopoda orientalis* is bounded on the north and south by that of closely related *T. acutifrons*. Both species were found in three mid-water trawl collections from near 41° N., 145°–160° W. Samples taken to the north of this latitude contained, of the two species, only *T. acutifrons*, while those to the south of 41° N., only *T. orientalis*.

TABLE 8
VERTICAL DISTRIBUTION OF THYSANOPODA ORIENTALIS

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (25–39 mm.)	Immatures (10–24 mm.)	Larvae (2–9 mm.)	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (25–39 mm.)	Immatures (10–24 mm.)	Larvae (2–9 mm.)
70.....	303	3			4	238	7		1	9
140.....	371	38		1	53	271	26	2	8	28
280.....	368	90		7	144	286	91	27	46	69
500.....	23	10	128	42	5	26	13	78	170	10
700.....	26	18	5	20	13	28	11	42	49	18
1,000.....	6	6	5	13	4	8	5	10	25	2
1,500.....	6	6	9	13	2	8	8	30	10	3
2,000.....	10	7	37	6		20	16	91	11	1
3,000.....	1	1	4	1		3	3	4		1
4,000.....	1	1	2			4	3	53	29	

An east-west boundary between the two is also drawn in the Southern Hemisphere off southeastern Australia, based upon Sheard's 1953 records, and in midocean, based on "Downwind" expedition material.

Three *Thysanopoda* species, *T. orientalis*, *T. pectinata*, and *T. monacantha*, attain the same size, 30–40 mm., and have nearly the same distributional ranges. These three sympatric mesopelagic species are not closely related to each other, whereas *T. orientalis* and *T. acutifrons*, the ranges of which scarcely overlap, are so similar as to have been considered varieties of the same species (Einarsson, 1942).

T. orientalis occurred at scattered stations in southern and offshore parts of the California Current. Larvae were sometimes found in the 0–70-meter and 0–140-meter CalCOFI collections. Adults have been caught by mid-water trawl in the San Diego Trough off southern California, and west of Cedros Island off central Baja California. Here, the distribution reaches nearest to shore.

This species was missing from an area off Mexico south of Vizcaino Bay, extending southward to 10° N., and westward to at least 125° W. (cf. *T. pectinata* and *T. monacantha*). This area is characterized by a surface temperature of 27°–28°

C., and by a low concentration of subsurface dissolved oxygen, discussed above (pp. 65–70).

T. orientalis was found in offshore waters of the Peru Current, and at 40° S. It is widely distributed in central and equatorial waters of the North and South Pacific, bounded at its northern and southern extremes by the 10° C. isotherm at 100 meters and by the 9° C. isotherm at 200 meters.

Vertical distribution (fig. 16 and table 8).—*Thysanopoda orientalis* occurred throughout the area off Baja California studied during an April-May, 1954, “Pelagic Area” cruise. Sampling was carried out at several depths. Figure 16 shows concentrations of this species, based upon averages for each depth, at all day stations and all night stations within the part of the “Pelagic Area” known to be inhabited by the species. Larvae were found below 75 meters, during both day and night, and immature individuals were at 300–500 meters during the day and at 75–300 meters at night. Adults, if present in the area at all, were beyond the 700-meter limit of sampling.

Figure 16 includes the average vertical distribution of *T. orientalis* for the North Pacific, calculated from data recorded at those stations, within the distributional range, at which sampling was carried out at more than one depth. Larvae occurred at each of the three depths and showed no day-night difference in level. Immature specimens were more numerous above 280 meters at night than during the day. Adults, not found above 280 meters during the day, peaked at 140–280 meters at night.

Table 8 provides evidence that *T. orientalis* was not consistently caught until depth-of-tow approached 500 meters. It was caught in most tows that reached 1,000 meters.

Thysanopoda monacantha Ortmann

(Fig. 17)

Horizontal distribution.—*Thysanopoda monacantha* was found south of 35°–36° N. in the North Pacific. Absent from cool coastal water of the California Current, this species is typically present in small numbers at stations 150–300 miles off southern California.

T. monacantha is not known to occur in Central American waters north of 10° N. but was consistently found near the equator, from the Philippines to the Gulf of Panama. It was lacking in the Peru Current, according to records from “Shellback” expedition, except at four stations off Peru. There, larvae were found, having apparently intruded from a source north of the equator. The most southerly of these localities was 6° 21.5' S., 82° 23' W. A single specimen captured by the *William Scoresby* was from within this narrow southward-ranging tongue.

Sheard (1953) reported *T. monacantha* from southeastern Australia, and indicated that the southern limit may be near 37°–38° S. In mid-ocean this species was caught at 34° S., but the most southerly record in the eastern Pacific was 23° S., from the “Downwind” expedition. The apparent absence of *T. monacantha* from much of the eastern part of the South Pacific differs from the distribution of other mesopelagic species, *T. orientalis* and *T. pectinata*.

The known range of this species is based largely on records for larval and immature

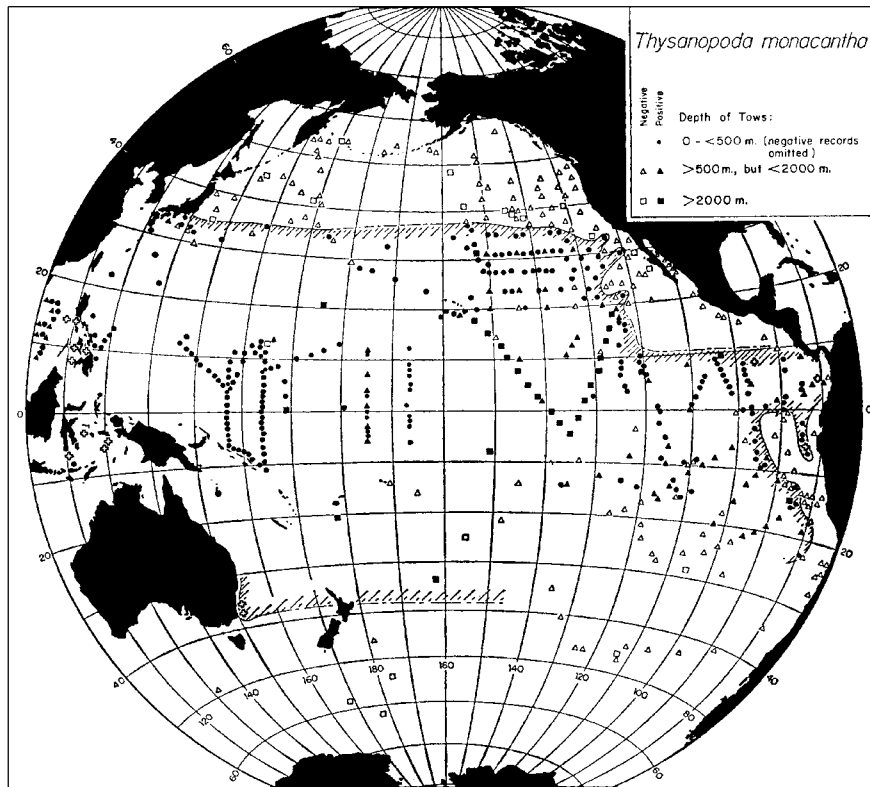


Fig. 17. Geographical distribution of *Thysanopoda monacantha*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

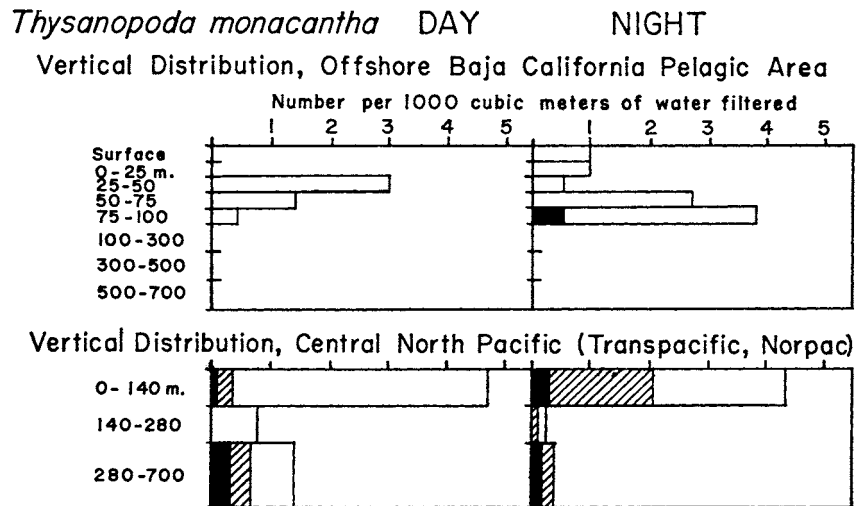


Fig. 18. Vertical distribution of *Thysanopoda monacantha*.

individuals. The frequency of these was highest in the eastern central North Pacific ("Norpac" cruise) and near the equator. They were found less consistently in the warm upper layers of the western central North Pacific, 12°–34° N. *T. monacantha* was scarce in the collections made by the "Capricorn" expedition, south of 10° S., west of 140° W.

TABLE 9
VERTICAL DISTRIBUTION OF THYSANOPODA MONACANTHA

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined (within known geo- graphic range of species)	No. samples in which species was present	Adults (25-35 mm.)	Immatures (10-24 mm.)	Larvae (2-9 mm.)	No. samples examined (within known geo- graphic range of species)	No. samples in which species was present	Adults (25-35 mm.)	Immatures (10-24 mm.)	Larvae (2-9 mm.)
70.....	98	43		2	99	61	25		6	66
140.....	128	78	2	33	348	74	8	18		105
280.....	259	133	7	33	518	207	25	71		353
500.....	16	3	28	16	3	8	2	3	11	1
700.....	13	13	3	5	70	16	7	1	3	11
1,000.....	2	2	6	1	2	7	7	15	2	1
1,500.....	6	6	21	3		5	5	22	1	
2,000.....	8	7	57	29	1	17	15	126	36	
3,000.....	1	1	11	2		1	1	7		
4,000.....	0					1	1	2		

Vertical distribution (fig. 18 and table 9).—Larvae of *T. monacantha* were found at 25–100 meters during the day, and at 0–100 meters at night off Baja California. The only adults caught there were from 75–100 meters, at night. Table 9 shows that this species was consistently caught below about 700 meters during the day and below 140 meters at night. Most individuals caught in the upper part of the vertical range were larvae.

North Pacific data (fig. 18) provide evidence of diurnal vertical migration of the immature and adult of *T. monacantha*. These size groups were most common below 280 meters during the day and above 140 meters at night.

Thysanopoda pectinata Ortmann

(Fig. 19)

Horizontal distribution.—*Thysanopoda pectinata* was found somewhat deeper than *T. monacantha* and *T. orientalis*, and is less tolerant of northern waters and the eastern boundary currents of the Pacific than are the last two species. It was found south of 34° N. in the eastern central Pacific. In the western central Pacific there is a single record for a larva off southern Japan, from a tow that reached to a depth of 1,000 meters. The position of the 13° C. isotherm at 200 meters agrees with the limits of the distribution.

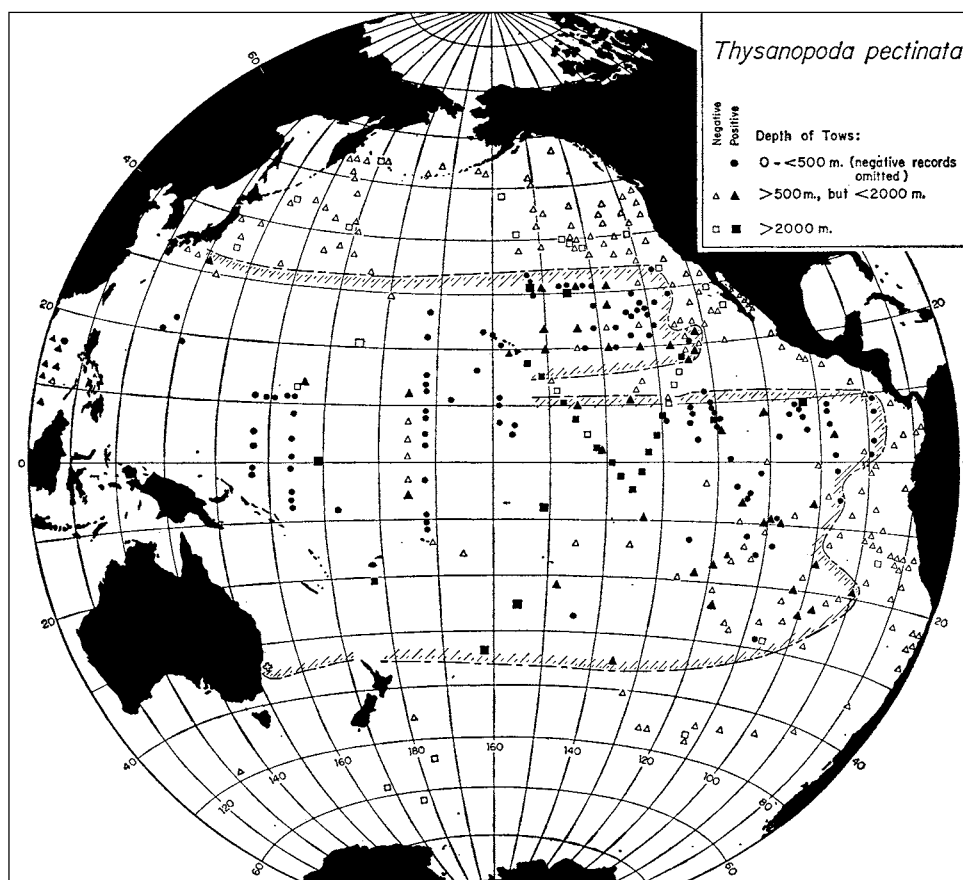


Fig. 19. Geographical distribution of *Thysanopoda pectinata*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

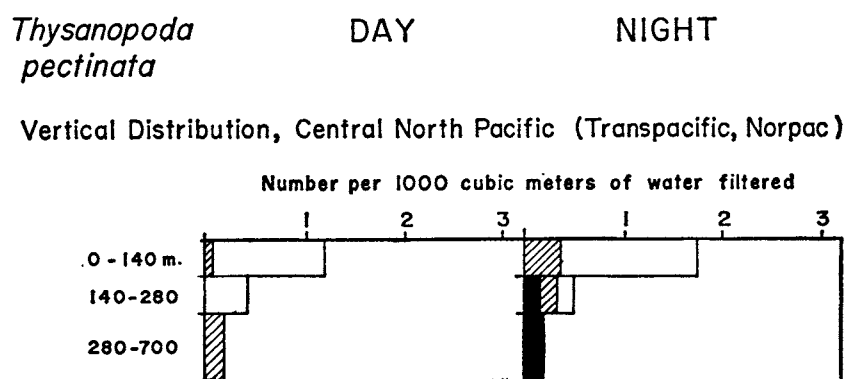


Fig. 20. Vertical distribution of *Thysanopoda pectinata*.

Vertical distribution (fig. 20 and table 10).—In the central North Pacific the adult of *T. pectinata* was not present above 700 meters during the day, while larvae occurred above 280 meters. At night, adults were taken from 140 to 700 meters, immature individuals above 280 meters, and larvae mainly in the upper 140 meters.

TABLE 10
VERTICAL DISTRIBUTION OF THYSANOPODA PECTINATA

Maximum depth attained by net (m.)	Day					Night				
	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (25-38 mm.)	Immatures (10-24 mm.)	Larvae (2-9 mm.)	No. samples examined (within known geographic range of species)	No. samples in which species was present	Adults (25-38 mm.)	Immatures (10-24 mm.)	Larvae (2-9 mm.)
70.....	9	2			3	8	4		1	4
140.....	84	24		7	56	53	16		5	13
280.....	193	105	1	30	41	168	48	12	21	55
500.....	14	7	16	9	4	11	3	2	3	7
700.....	11	3		10		15	6	3	3	2
1,000.....	1	1	1	1		5	3	4	1	
1,500.....	2	2	2			1	1	3	1	
2,000.....	8	6	32	21		15	14	107	27	
3,000.....	2	2	11	2		2	1	2		
4,000.....	0					0				

Table 10 shows that *T. pectinata* was caught in nearly all tows that reached a depth of at least 1,000 meters. On one occasion adults were found above 1,000 meters during the day. At night they were caught at 140–700 meters.

Thysanopoda obtusifrons G. O. Sars

(Fig. 21)

Horizontal distribution.—*Thysanopoda obtusifrons* occurs south of 34° N. in the western central North Pacific. Like *T. orientalis*, *T. monacantha*, and *T. pectinata*, it is consistently present in small numbers—one to five per sample. However, the adult of *T. obtusifrons* is more frequently found near the surface than that of the above three species.

This euphausiid occurred at three stations east of Japan in the region of the Kuroshio extension. It was not found at other stations in the western Pacific, north of 30° N. *T. obtusifrons* was usually found north of 5° N. in the western equatorial Pacific, but was entirely lacking from the eastern equatorial region. It was found at 7°–9° N. in the mid-Pacific, in the Equatorial Countercurrent (cf. *Euphausia mutica*.)

Sampling carried out in the western equatorial region indicated that there, at least, the North Pacific and South Pacific distributions are disjunct. This species was not caught near the Philippines by the *Albatross*, nor in the East Indian Archipelago by the *Siboga* (Hansen 1916, 1910).

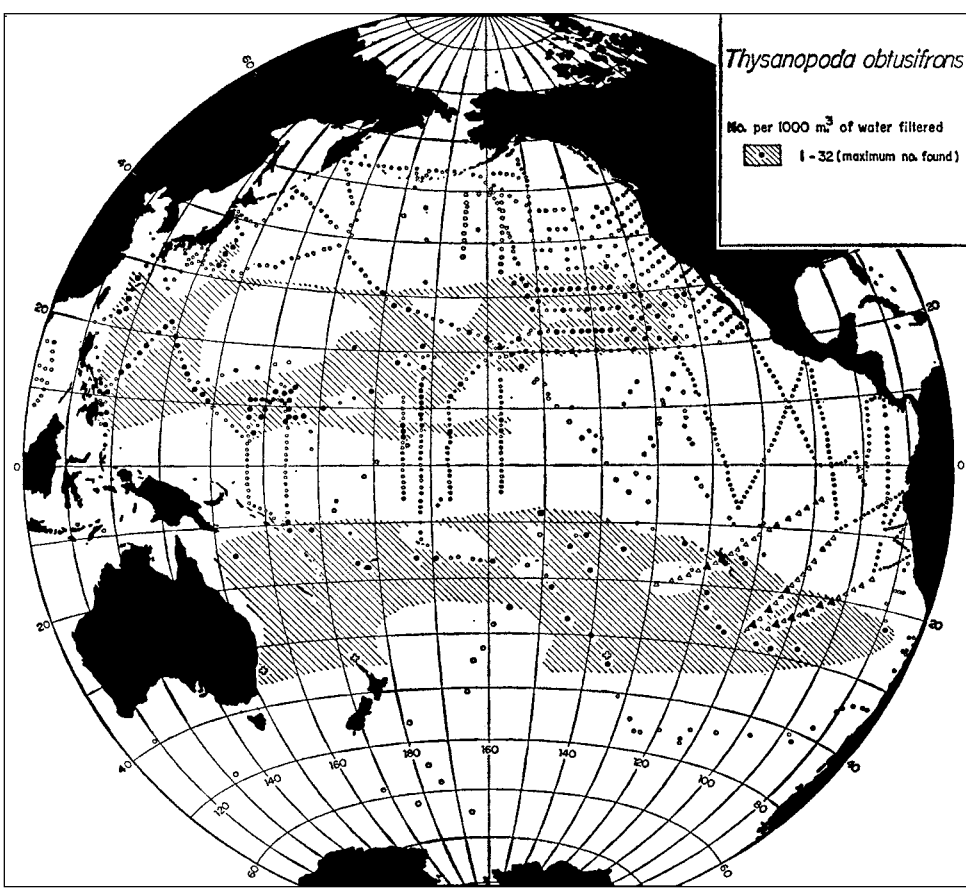


Fig. 21. Geographical distribution of *Thysanopoda obtusifrons*.

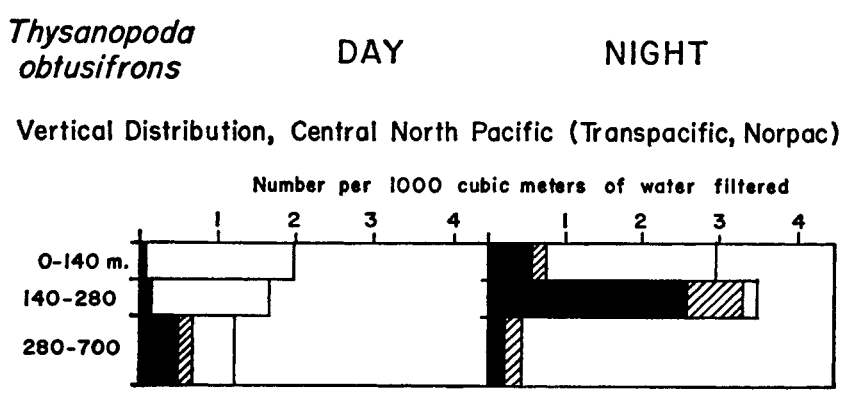


Fig. 22. Vertical distribution of *Thysanopoda obtusifrons*.

T. obtusifrons occurred at 9° 30' S., east of the Solomon Islands, together with other central South Pacific species (cf. *Euphausia brevis*). The "Capricorn" expedition skirted the northern limit of its range, near 15° S., from 175° E. to 113° W. Records from the "Challenger" (Sars, 1885), the "Terra Nova" (Tattersall, 1924), Sheard (1953), and "Downwind" expeditions indicate that the southern limit of occurrence is near 35° S.

Vertical distribution (fig. 22).—Larvae of *T. obtusifrons* were most numerous above 280 meters in the daytime and above 140 meters at night. Most immature individuals and adults were below 280 meters during the day, but both size groups were present above 280 meters at night, with a maximum at 140–280 meters.

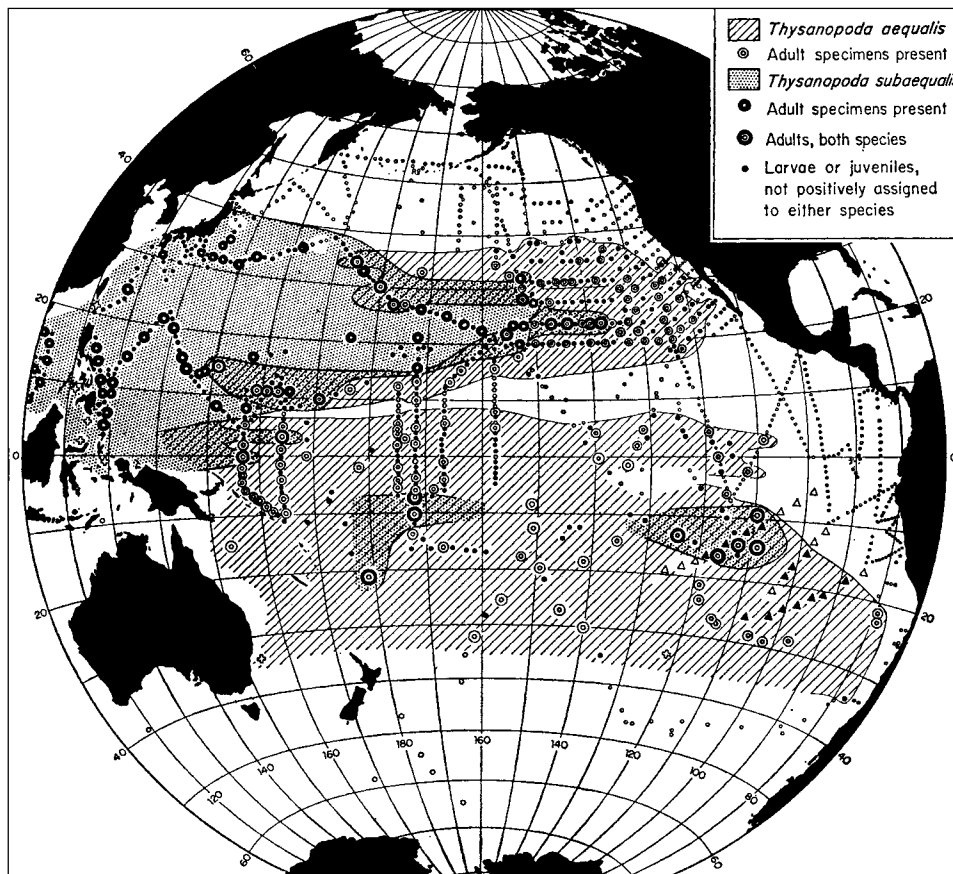


Fig. 23. Geographical distributions of *Thysanopoda aequalis* and *T. subaequalis*.

Thysanopoda aequalis Hansen; *Thysanopoda subaequalis* Boden

(Fig. 23)

These species were distinguished by Boden and Brinton (1957). The propodus of the third thoracic leg of the adult male of *T. subaequalis* is reduced and the dactylus modified as an elongate spine. In *T. aequalis* the third leg is not modified. If

this diagnostic character was of genotypic basis, a hybrid between *T. subaequalis* and *T. aequalis* might be indistinguishable as such; that is, the euphausiid might either have the spine or not. No adult individuals with a rudimentary spine have been found.

There is overlap in the geographical ranges of the two species. However, there is no evidence regarding reproductive isolation. The possibility of a subspecific relationship was assumed by Boden (1954) in the name *T. subaequalis*. Boden and Brinton considered that the two must be retained, for the present, as distinct species.

It has not been possible to distinguish between larval specimens of the two species. Only in the eastern North Pacific or western North Pacific where the adults of one species or the other are in pure population can the larvae be assigned with reasonable certainty to *T. aequalis* or *T. subaequalis* respectively.

Immature individuals cannot often be accurately separated. In *T. subaequalis* the dactylus of the third thoracic leg of the male is not modified until the onset of maturity, at a length of about 12.5 mm. Specimens of this length carry the modified dactylus in addition to a number of normal setae on the reduced propodus. Specimens longer than 13 mm. bear only the naked terminal spine.

Horizontal distribution.—The composite range of *T. aequalis* and *T. subaequalis* extends from 40° N. to 35° S. or 40° S. in the South Pacific. Both species are missing from the eastern equatorial basin and from a tongue-like westward extension of equatorial waters reaching to at least 175° W., with an east-west axis at 9°–10° N. These species were absent from one station, 8° N., on a north-south line of stations at 164° E. occupied during the “Equapac” cruise, 1956. On the basis of this negative record, the area from which they are apparently excluded extended westward to 164° E. Cool subsurface water at the northern margin of the Equatorial Countercurrent, and very low concentrations of oxygen at 150–450 meters are associated with the entire east-west extent of this tongue of exclusion.

The distribution of *T. subaequalis* is based upon the identification of 353 adults in 64 collections, and that of *T. aequalis* upon 614 adults in 137 collections.

In the North Pacific the center of distribution of *T. aequalis* is in the east. *T. subaequalis*, which centers in the west, was not found by repeated CalCOFI surveys of the region of the California Current, 1949–1959. *T. aequalis* was present in offshore waters of California and Baja California during all seasons.

The “Norpac” plankton provided evidence that the range of *T. subaequalis* penetrates a warm core, northeast of Hawaii, of the Eastern North Pacific Central Water Mass. There, the temperature is 16°–17° C. at 200 meters and 8°–9° C. at 400 meters (figs. 7c, 7d). In the North Pacific, *T. aequalis* is associated with the Eastern Central Water Mass, distinguished by Sverdrup, Johnson, and Fleming (1942), whereas *T. subaequalis* inhabits the Western North Pacific Central Water Mass and *T. aequalis* is found at its cool northern and southern margins.

The distribution in the Southern Hemisphere is different. *T. aequalis* occupies both eastern and western regions of the South Pacific Central Water Mass, from offshore waters of Chile (79° W.) to Fiji (178° E.), the westernmost Scripps record south of 20° S. *T. subaequalis* has been found only between 9° S. and 17° S. in the eastern part of the South Pacific and from 7° S. to 21° S. in the western part.

It occurred together with *T. aequalis* at its eight localities in the South Pacific. There, no geographical segregation of the two species was found.

The limited range of *T. subaequalis* in the eastern South Pacific agrees with that of one other euphausiid, *Euphausia pseudogibba*, also, typically, a western Pacific species. Both species were found by "Capricorn" and

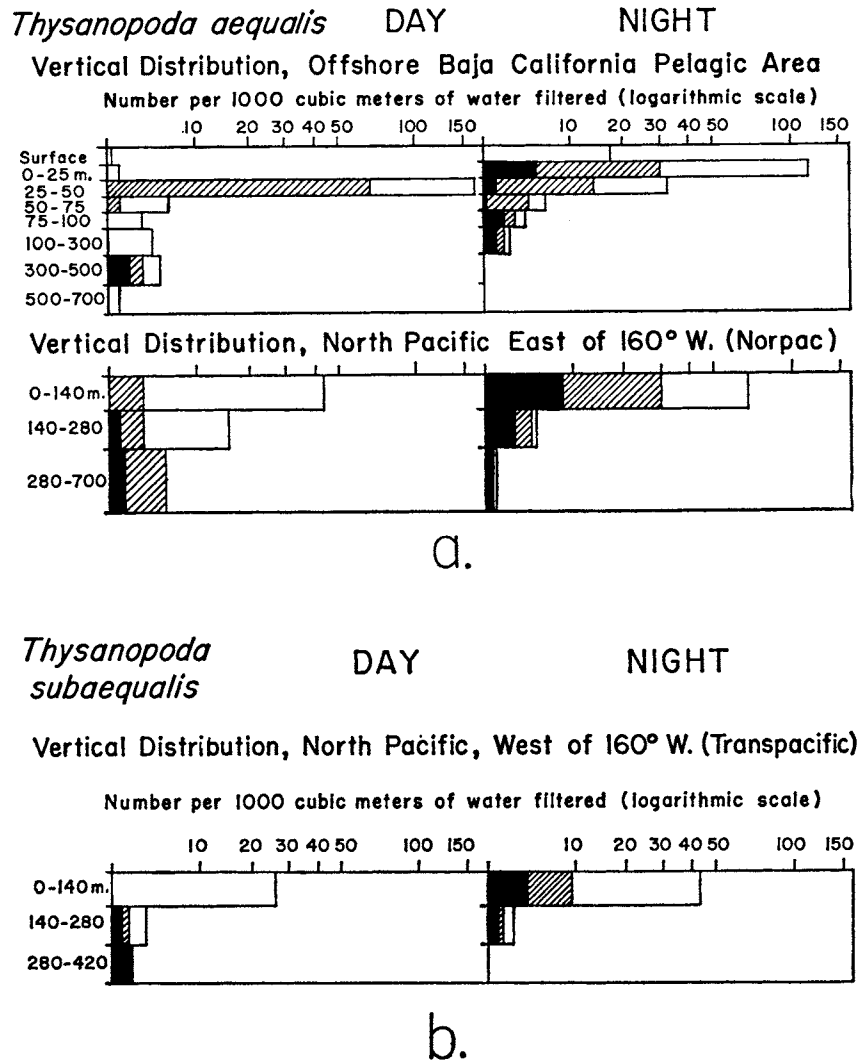


Fig. 24. Vertical distributions. a. *Thysanopoda aequalis*. b. *T. subaequalis*.

"Downwind" expeditions in a narrow east-west zone (108°-125° W.) where water from the South Equatorial Current system mixes with that derived from the South Pacific central region. Stability of this eastern pocket of distribution is indicated by the catch of *E. pseudogibba* by the *Albatross* in 1904-1905 at two stations: 13° 47.5' S., 114° 22' W.; 16° 32.5' S., 119° 59' W. (Hansen, 1912). These were the only individuals of *E. pseudogibba* recorded from samples of the extensive "Albatross" survey. Hansen

did not distinguish between *T. aequalis* and *T. subaequalis*, or did not recognize any of the latter in his collections.

In the North Pacific, *T. aequalis* was found in the cooler part (11° – 16° C. at 200 meters) of the composite range of the two species. *T. subaequalis* predominated in a warmer western zone where the 200-meter temperature was higher than 16° C. *T. aequalis* was found throughout the composite range in the South Pacific, whereas *T. subaequalis* appeared to be limited to the warmer water, approximately prescribed by the 21° C. isotherm at a depth of 200 meters.

Vertical distribution (fig. 24, a, b).—The vertical ranges of these two species in the North Pacific appear to be the same. Furcilia larvae were found above 280 meters at all times. Adults were present below 140 meters during the day and moved into the 0–280 meter layer at night. Most immature individuals were present above 140 meters at night.

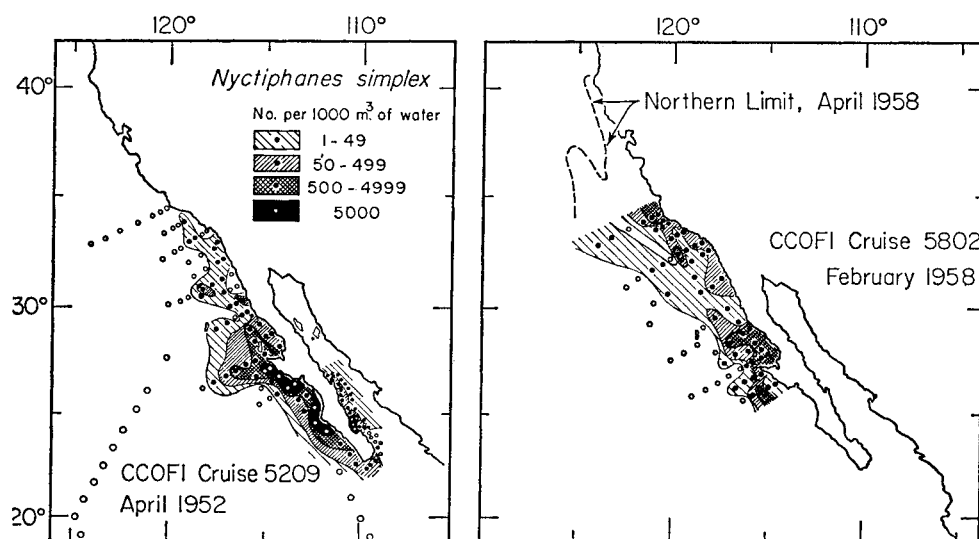


Fig. 25a. Geographical distribution of *Nyctiphanes simplex* in the California Current region.

THE GENUS NYCTIPHANES Hansen

Nyctiphanes simplex Hansen

(Figs. 25a, 25b)

Nyctiphanes is associated with near-shore waters in regions of transition between warm and cold currents. It is a conspicuous element of the plankton where coastal upwelling is a characteristic feature. *Nyctiphanes australis* is found off Australia (Sheard, 1953) and New Zealand (Bary, 1956), *N. capensis* is limited to near-shore South Africa (Boden, 1955), and *N. couchii* is found along the Atlantic and Mediterranean coasts of Europe (Ruud, 1936; Glover, 1952).

Horizontal distribution.—CalCOFI cruises to California and Baja California waters have established that *N. simplex* is coastal, although not exclusively neritic. Spawning occurs near shore where countercurrents are probably instrumental in

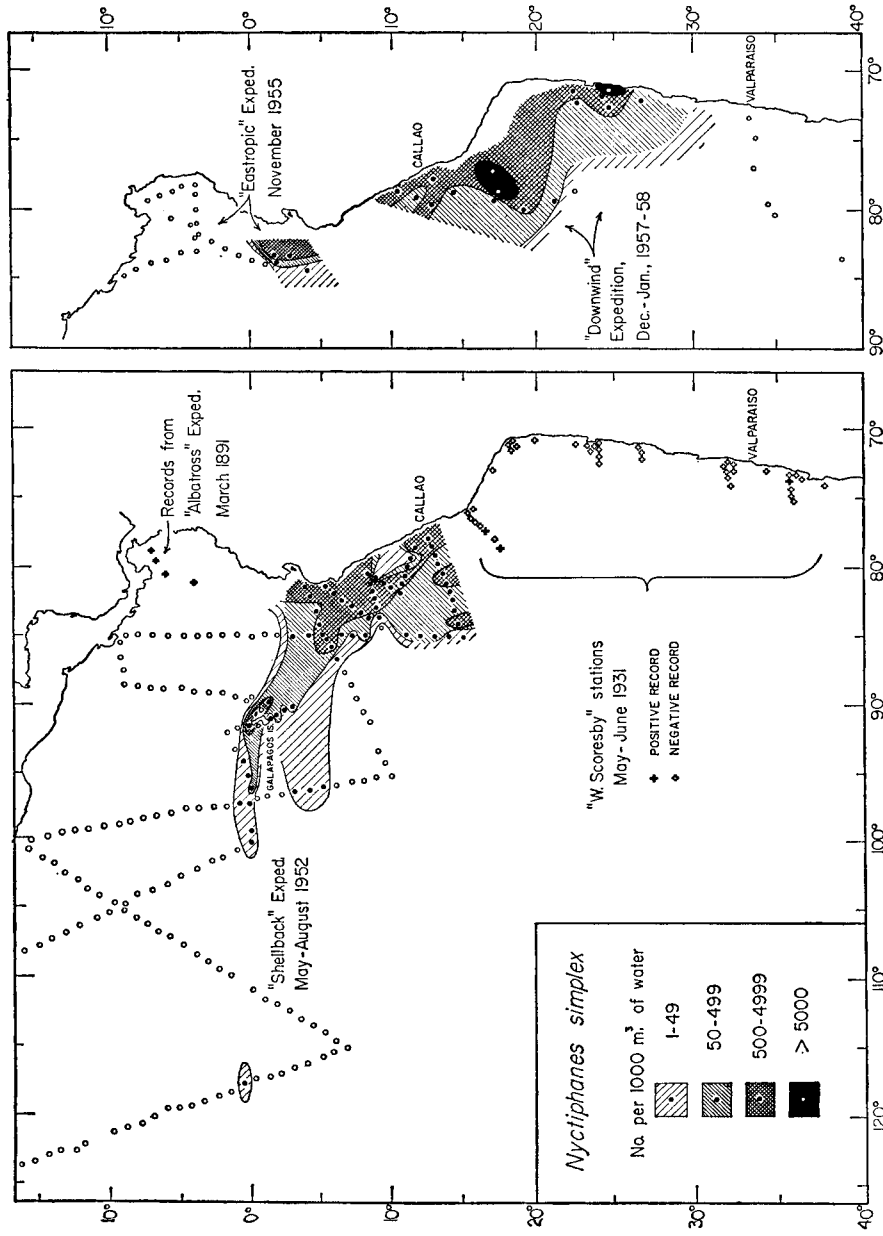


Fig. 25b. Geographical distribution of *Nyctiphanes simplex* in the Peru Current region.

maintaining the geographical range of the species; the predominant direction of flow of the California Current is southward.

The range extended as far north as Cape Mendocino (40° N.) in April, 1958. *N. simplex* was regularly found off central California during the “warm years” 1957–1959 (Brinton, 1960), but during a cooler period, 1949–1956, was rarely carried north of Point Conception ($34^{\circ} 30'$ N.).

The distribution is based upon samples obtained during two cruises off southern California and Baja California, and one to the Gulf of California (fig. 25a). During September, 1952 (CalCOFI Cruise 5209), the Gulf population was separated from that on the outside by a belt of water 40 miles wide, near the mouth of the Gulf. Steinbeck and Ricketts (1941) found the Gulf water to be “soupy” with *N. simplex* at Point Marcial.

N. simplex has a wider range in the Peru Current and in its extension into waters near the Galápagos Islands (fig. 25b) than in the California Current. “Shellback” expedition material showed that this species may be carried to 117° W. by the South Equatorial Current. It was found in the region of the Gulf of Panama during the 1891 cruise of the *Albatross* (Hansen, 1915; based on Ortmann’s 1894 specimens), but not during the “Eastropic” expedition, November, 1955. The northern boundary of the southern population of *N. simplex* was placed at 1° – 3° S. on the basis of the “Shellback” material collected in July, 1952. The position of this boundary agreed closely with that found in “Eastropic” expedition.

The southern limit of range was found to be near 30° S. by “Downwind” expedition, sampling in January, 1958. Temperatures of 11° – 12° C. at 100 meters and 16° – 17° C. at the surface were associated with the boundaries at 35° N. (California Current) and 30° S. (Peru Current).

N. simplex was scarce in the near-shore part of the Peru Current, south of 15° S., surveyed by the *William Scoresby*, May–June, 1931. One specimen was caught near $35^{\circ} 50'$ S., in a closing net sampling between 90 and 240 meters. In contrast, the surface water was teeming with *Nyctiphanes* at 17° S., 200 miles off southern Peru, in January, 1949 (“Downwind” expedition).

There is no evidence from the material collected during two cruises of the *Albatross*, the “Shellback” expedition, and the “Eastropic” expedition that there is even intermittent exchange between the California Current and Peru Current populations, across the warm (26° – 28° C.) surface waters off Central America. The separation must be considered Recent in the evolutionary sense. Differentiation is well advanced among the clearly isolated Australian, American, African, and European distributions of the *Nyctiphanes* species.

Vertical distribution (fig. 26, a,b).—During “E. W. Scripps” Cruise VIII, *N. simplex* was mainly above 100 meters in the daytime, although the few adults caught were at 100–150 meters. Most of the population was above 50 meters at night. Sampling carried out on the “Norpac” cruise reemphasized that *N. simplex* is associated with the layer between the surface and 140 meters. At a near-shore station off San Pedro, California, the bulk of this species was above 10 meters, during both night and day (fig. 26, b).

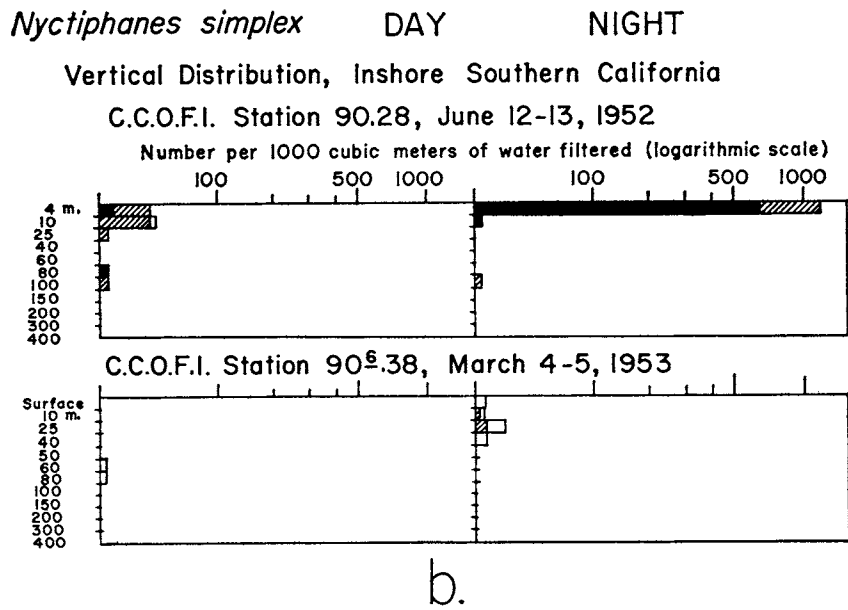
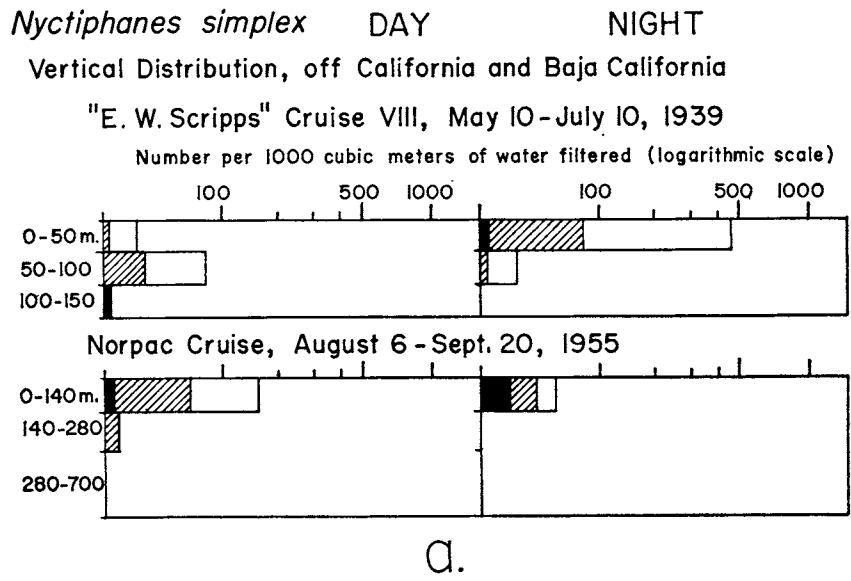


Fig. 26. Vertical distribution of *Nyctiphanes simplex*. a. "Norpac" expedition and "E. W. Scripps" Cruise VIII data. b. Inshore southern California CalCOFI data.

THE GENUS PSEUDEUPHAUSIA Hansen

Pseudeuphausia latifrons (G. O. Sars) Hansen

(Fig. 27)

Horizontal distribution.—*Pseudeuphausia latifrons* lives in the tropical western Pacific in the near-shore habitat occupied by *Nyctiphanes simplex* along the upwelling coasts of the temperate-tropical eastern Pacific.

Large numbers of this species were dip-netted in Eniwetok and Bikini lagoons during the “Capricorn” and “Midpacific” expeditions. *P. latifrons* was caught consistently by the *Siboga* in the East Indian Archipelago

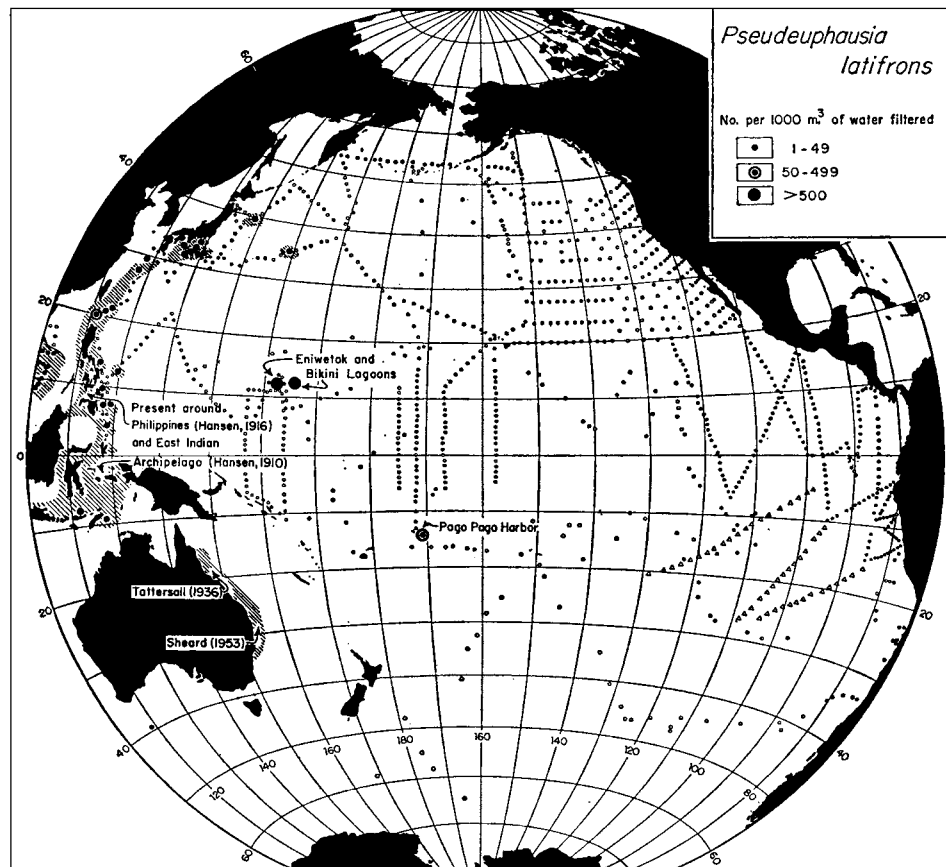


Fig. 27. Geographical distribution of *Pseudeuphausia latifrons*.

(Hansen, 1910), and in waters of the Philippine Archipelago by the *Albatross* (Hansen, 1916). It was found by the “Naga” expedition to be the characteristic species of the coastal waters of the South China Sea. A few individuals were caught at six stations east of the Philippines during the “Troll” cruise.

P. latifrons was found between the Philippines and Japan by the “Troll” cruise and was present, though scarce, at nine “Transpacific” expedition stations east of Japan in the region of the Kuroshio. It was an important food of whales caught in

the Yellow Sea (Nemoto, 1959), and lives in the East China Sea, over the broad continental shelf.

This is the only euphausiid that permanently inhabits the lagoon of the Great Barrier Reef of Australia (Tattersall, 1936). Sars (1885) reported it from the southeastern coast of Australia, where Sheard (1953) also found it to be abundant.

P. latifrons was dip-netted at night in Pago Pago Harbor during the "Capricorn" expedition. It was not caught in waters of the Fiji Islands, either by the *Albatross* in 1897 or by the "Capricorn" expedition, nor was it found along the Solomon Island chain by the "Equapac" expedition. The infrequent occurrence of *P. latifrons* in the oceanic western equatorial Pacific suggests that this species is neritic in habitat, and that the atoll populations are isolated from each other.

Vertical distribution.—In its areas of greatest numbers, *P. latifrons* was caught near the surface. Thirty of the 34 *Siboga* records and 26 of 29 *Albatross* records were from tows reaching to less than 40 meters; most were from surface collections.

Tattersall found a daytime maximum at a depth of 12 meters, at two stations inside the Great Barrier Reef.

Of the "Transpacific" expedition records from the Kuroshio, eight were from night samples and one was from a daytime sample. Six of the night records were from 0–140 meters, and two night records and the one daytime record were from tows sampling the 140–280 meter layer.

THE GENUS EUPHAUSIA Dana

Euphausia pacifica Hansen

(Fig. 28)

Horizontal distribution.—*Euphausia pacifica* lives in the subarctic and transition zones of the North Pacific and is the only northern *Euphausia* species. It occurs from the Sea of Japan eastward to the Gulf of Alaska and the California Current, and is present in the southern parts of the Sea of Okhotsk and the Bering Sea. It has not been found in the Arctic Ocean (Schmitt, 1919; Johnson, 1956). The southern limit of range is associated with the 9.5° C. isotherm at a depth of 200 meters.

Larvae were found throughout the range, except in the northwestern corner of the Pacific (west of 170° E. and north of 47° N.; "Transpacific" stations 41–49). There, off Kamchatka and the Kurile Islands, only adults were found, except at Station 47–49° 50' N., 165° 49' E.—where one-fifth of the population was made up of half-grown individuals.

Heaviest concentrations of *E. pacifica* were along the east-west axis of the distributional range, in the North Pacific Drift and the Aleutian Current. These currents give rise to the California Current, where there is also a center of abundance of *E. pacifica*. Banner found it in greatest numbers along the northern and eastern margins of the Gulf of Alaska.

E. pacifica is known in the Sea of Japan (Nemoto, 1959). Specimens collected by the *Vitjaz* at 38° N., 135° E. were generously provided by Larissa A. Ponomareva of the Institute of Oceanology, Moscow.

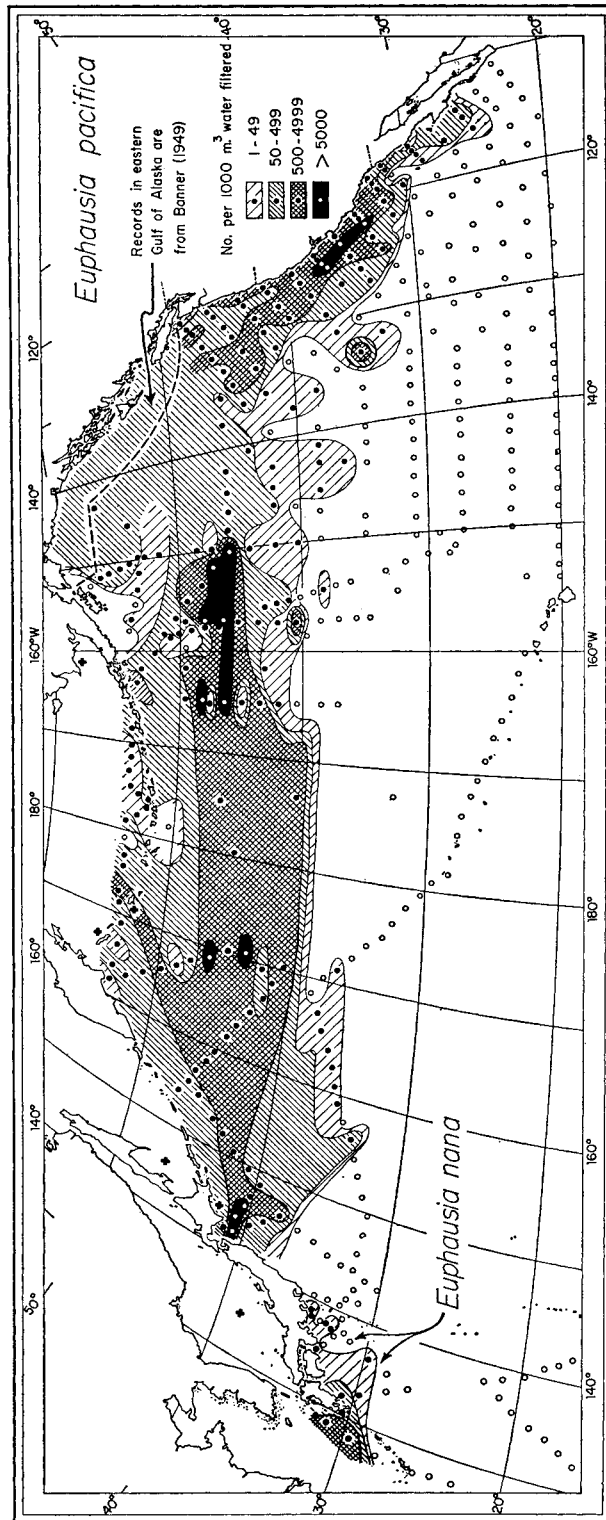
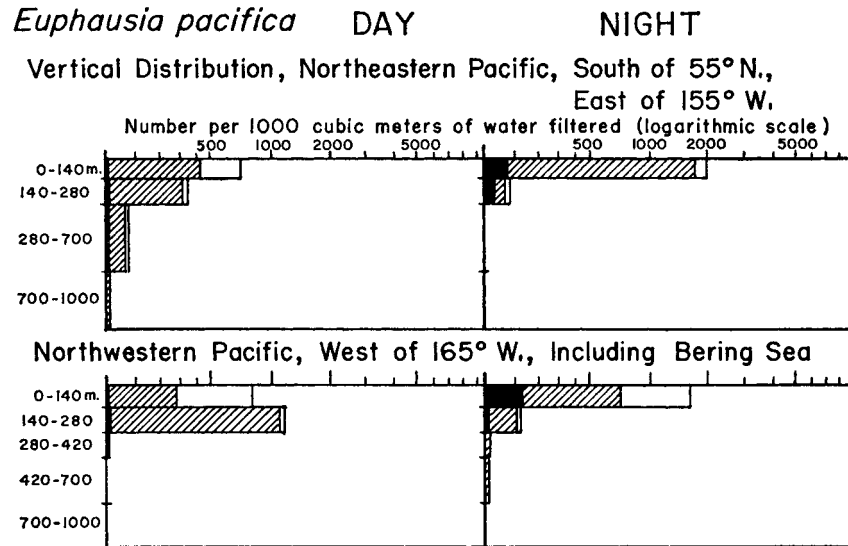


Fig. 28. Geographical distributions of *Euphausia pacifica* and *E. nana*.

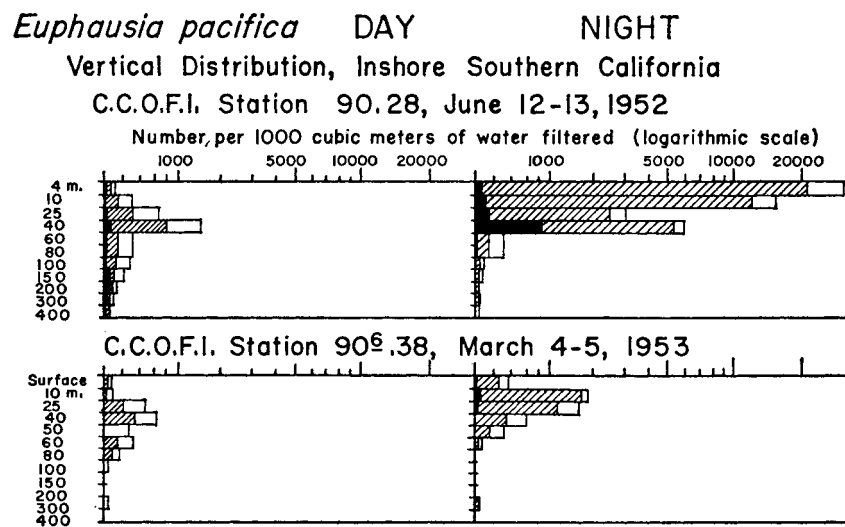
TABLE 11
 VERTICAL DISTRIBUTION OF EUPHAUSIA PACIFICA, FROM A LINE OF "TRANSPACIFIC" EXPEDITION
 STATIONS WHICH EXTENDS WESTWARD ACROSS THE CALIFORNIA CURRENT, THEN
 NORTHWESTWARD ACROSS THE NORTH PACIFIC DRIFT

Station	Position	Time	No. per 1,000 m. ³ at different depths sampled (m.)				
			0-140	140-280	280-420	420-700	700-1,000
1.....	33° 57' N., 122° 28' W.	2036-2135 (dark)	7,656 (1,221)	<u>70</u> 640	—	—	—
3.....	35° 05' N., 127° 38' W.	2159-2255 (moonlight)	106 (4)	0	—	—	—
4.....	35° 47' N., 130° 02' W.	1640-1800 (part o'cast)	0	0	144	0	0
5.....	35° 54' N., 131° 44' W.	0450-0540 (sunrise)	0	1	—	—	—
6.....	36° 09' N., 133° 20' W.	1644-1732 (part o'cast)	0	0	—	—	—
7.....	36° 22' N., 134° 53' W.	1655-1808 (overcast)	0	0	0	11	4
8.....	36° 44' N., 137° 24' W.	0817-0910 (clear)	0	0	—	—	—
9.....	37° 00' N., 140° 01' W.	2159-2227 (dark)	0	0	0	0	0
10.....	38° 22' N., 141° 23' W.	0242-0338 (dark)	138	0	—	—	—
11.....	39° 36' N., 142° 23' W.	0110-0153 (dark)	31	1	0	4	0
12.....	40° 27' N., 143° 32' W.	1600-1733 (overcast)	2	0	339	37	1
13.....	41° 54' N., 145° 13' W.	0432-0522 (dawn, o'cast)	(12)	109	—	—	—
14.....	42° 57' N., 146° 15' W.	1950-2052 (dark)	136 (15)	2	—	—	—
15.....	44° 02' N., 147° 29' W.	0500-0603 (overcast)	1,673 (51)	843	—	—	—
16.....	44° 59' N., 148° 46' W.	1617-1733 (clear)	25 (191)	299	<u>1</u> 37	0	0
17.....	46° 00' N., 149° 54' W.	0530-0624 (overcast)	2,676 (4,300)	292	—	—	—
18.....	47° 14' N., 151° 43' W.	2215-2305 (dark)	<u>56</u> 2,844 (3,386)	0	—	—	—

NOTES: Dashes indicate no sample collected. Underlined numbers are for adult *E. pacifica*; plain numbers, juveniles; numbers in parentheses, larvae.



a.



b.

Fig. 29. Vertical distribution of *Euphausia pacifica* in the North Pacific a. Oceanic. b. Inshore southern California.

This species is the cold-water euphausiid of the California Current. Swarms were observed north of Point Conception (34.5° N.) in April, 1956 (D. Miller, California Division of Fish and Game, personal communication). CalCOFI plankton samples from the area indicated that the shoals consisted of spawning and spawned-out specimens of *E. pacifica*.

Near-shore spawning is undoubtedly important in the maintenance of the coastal species of California (cf. *Nyctiphanes simplex*). The Davidson Countercurrent, which flows northward very close to shore in the winter, returns eggs and young toward the headwaters of the current system. Adults, often found well offshore, are able to migrate to depth in the daytime, there taking advantage of subsurface northerly countercurrents.

E. pacifica lives off central California, 34°–40° N., during all seasons. Its occurrence in coastal waters of southern California and Baja California is discussed in a later section on seasonal change in distribution.

Vertical distribution.—The vertical distribution of this species, determined from sampling carried out on the first leg of the “Transpacific” expedition, is shown in table 11. This line of stations crossed the California Current, extended westward toward central waters where *E. pacifica* was missing at Stations 8 and 9. The line then extended northwestward into the regions of high density of *E. pacifica*, shown by sampling at Station 17, near the northern boundary of the North Pacific Drift. Adults were not found near the margins of the range of the species; there, the populations were of immature individuals. The data gave no evidence for submergence of *E. pacifica* near the limits of its range. Rather, numbers were reduced in the surface layers at localities nearest to modified Central Water (Sta. 9).

Figure 29 shows that *E. pacifica* belongs mainly to the upper 280 meters, although the daytime adult population, not all accounted for in the “Transpacific” and “Norpac” sampling, may live deeper. An upward nighttime migration of adults, into the 0–140 meter layer, is apparent. The average vertical ranges calculated for the eastern and western Pacific differ only slightly, if at all. The daytime habitat may be more variable in depth in the eastern Pacific.

Stratified sampling was carried out at two stations near southern California where *E. pacifica*, was numerous. Most immature individuals and larvae were near 40 meters in the daytime. Adults ranged between the surface and 400 meters at Station 90.28, but were not found at Station 90⁰⁶-.38. Most of the population was above 80 meters at night at both stations.

Euphausia nana Brinton

(Figs. 28, 30)

Euphausia nana was distinguished (Brinton, 1962*b*) from the allied species *Euphausia pacifica* Hansen on the basis of the following:

1. The terminal process (t.p. in fig. 30) and the proximal process (p.p.) of the male copulatory organ are shorter and more robust in *E. nana* than in *E. pacifica*. The terminal blade of the proximal process of *E. nana* distally broadened, nonserrate, and bears a small median tooth. In *E. pacifica* the distal part of this blade is almost rounded and sometimes serrated.

2. *E. nana* is distinctly smaller than *E. pacifica* and is consistent in form and size. Adult specimens of *E. nana* caught in the region of the East China Sea and the Kuroshio during October, 1953, by the “Transpacific” expedition and in April, 1955, by the “Troll” expedition were in the size range 7.3–8.5 mm. This is half the length of mature *E. pacifica* from northern Japan eastward, including the California Current, where maturity occurs after attainment of a length of at least 13.0 mm. (Two length groups of spawning populations of *E. pacifica* are to be found off California. The first includes males of 13–14 mm. and females of 13–16 mm., and the second includes males of 17–19 mm. and females of 18–24 mm. Inasmuch as there has been found to be a major, April–June spawning period for *E. pacifica* off central California, it seems likely that this species lives two years, spawning twice.) Gravid females of *E. nana* contained 10–12 eggs, compared with 50–100 eggs for the 13–16-mm. females of *E. pacifica*, and 50–200 for the 18–24-mm. specimens.
3. *Horizontal distribution.* *Euphausia nana* has been found only off southern Japan. On the basis of the “Troll” samples, the distributional range centered in the East China Sea. There, the northwardflowing Tusima Current develops along the broad continental shelf of China as the Kuroshio is mixed with coastal water and with water upwelled from a depth of 50–200 meters to form what Uda (1959) has called the Tusima Water Mass. Southwest of Kyushu, the Tusima Current branches to the northwest, away from the Kuroshio, and diverges into the Yellow Sea and the Sea of Japan.

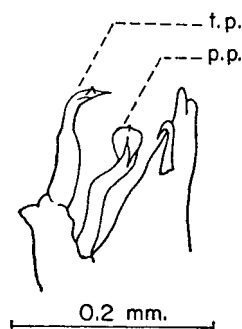


Fig. 30. *Euphausia nana*, male copulatory organ (p.p. [proximal process], t.p. [terminal process]).

Free north-south population exchange between northern *E. pacifica* and southern *E. nana* probably does not take place. The warm Tusima Current containing *E. nana* flows at a depth of 20–200 meters until it is mixed with colder Japan Sea water at the Tusima Strait. There, where the environment in which *E. nana* lives is altered, the sill is no deeper than 150 meters, and for the most part shallower than 100 meters. The sill also prevents the cool northern water inhabited by *E. pacifica* from flowing southward at depths below 100–150 meters.

During the time of the “Transpacific” expedition sampling in the Kuroshio region, the ranges of the two species did not overlap. *E. nana* was found southeast of Japan where upwelling was developed in a divergent eddy within the Kuroshio system. According to Ichiye (1955), this is a semipermanent cyclonic vortex, bounded on its eastern side by the Kuroshio. *E. pacifica* was then concentrated north of the Kuroshio-Oyashio front, north of 38°–40° N.

E. pacifica reported from Wakayama waters off southern Honshu (Nemoto, 1959) was, in fact, the large form, 15–20 mm. in length (Nemoto, personal communication); specimens reported as *E. pacifica* from the stomachs of whales caught in the East China Sea, however, were 10 mm. or less in length, and were probably *E. nana*.

Larvae of *E. nana* were most numerous in the “Troll” samples from the East China Sea. Adults and immature individuals, but few larvae, were found off southeastern Japan.

Vertical distribution.—The eight “Troll” records, April 1955, were from samples taken at 0–300 meters. Adult specimens of *E. nana* were taken at two of the three night stations occupied within the range of the species, and at one of five day stations, this one being in the coolest water surveyed in the East China Sea. Immature specimens and larvae were found at all of the eight stations.

During the “Transpacific” expedition, October, 1953, adults were caught above 110 meters at three night stations off southern Honshu, and at 120–260 meters at a fourth, where they were missing from the 0–120 meter layer. *E. nana* was not present there in day hauls.

Thus, adults were usually present above 140 meters at night, and below 300 meters during the day. Other size groups are above 300 meters at all times.

Euphausia similis G. O. Sars

(Fig. 31)

Horizontal distribution.—The North Pacific distribution of *Euphausia similis* was found by the “Troll” and “Transpacific” expeditions to be restricted to approximately

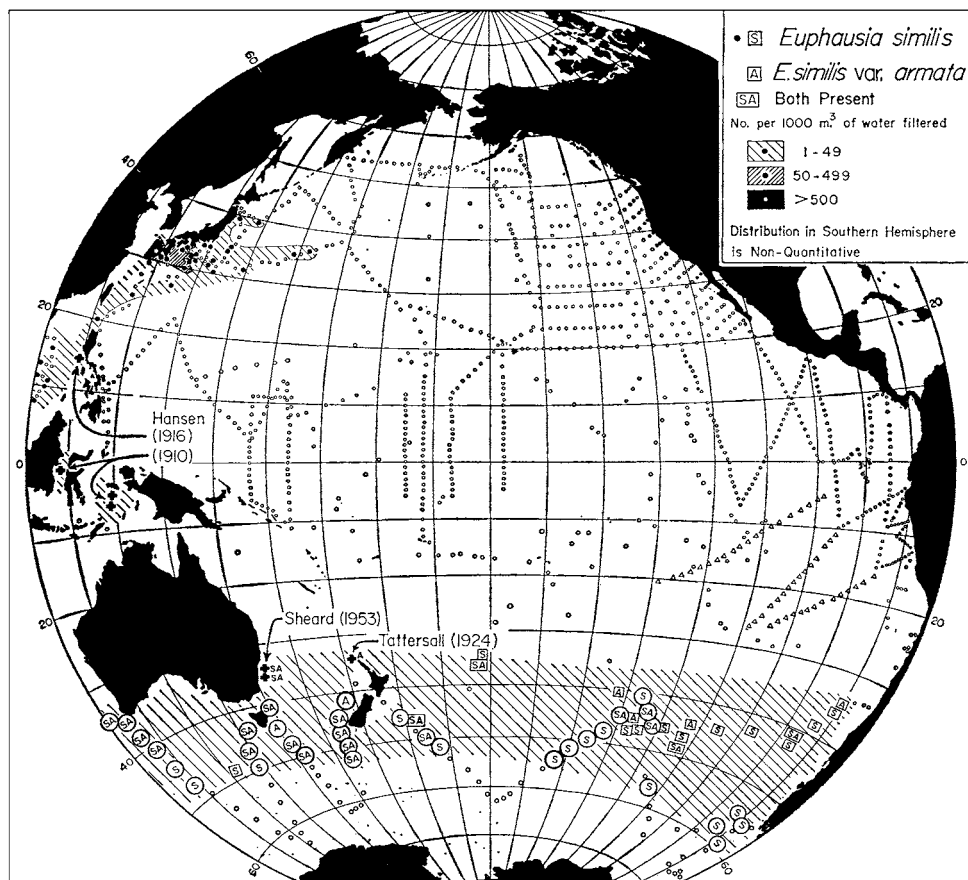


Fig. 31. Geographical distribution of *Euphausia similis*. Subantarctic distribution is from John (1936), except for the “Downwind” and “Monsoon” expedition records shown as squares.

the same area as that of *E. nana* (fig. 28). “Troll” samples indicated that larvae and post-larvae of *E. similis* were numerous during April, 1955, in the East China Sea and along the Ryukyu Island chain. Juvenile specimens and adults were found off southeastern Japan.

Nemoto (1959) regarded *E. similis* as oceanic in Japanese waters, and *E. Pacifica* (which included *E. nana*) as coastal. He found *E. similis* to be an important food of whales off southeastern Japan and at the Bonin Islands, 27° N., 142° E. Honjo (1957) considered *E. similis* to be distributed in offshore waters off southern Japan, usually 20 miles from land.

“Transpacific” expedition records extended the known range of *E. similis* to 40° N. off northern Honshu and to 162° E. in the Kuroshio Extension. Larvae were not found in the samples taken west of Japan.

E. similis is circumpolar in the Antarctic Ocean, occurring mainly in the belt between the Antarctic and Subtropical convergences (John, 1936). Its distribution in temperate and tropical waters is therefore anomalous. Several expeditions have recorded *E. similis* in the Atlantic, but none from north of 33° S. It has not been found in the subtropical South Pacific. Sheard’s (1953) most northerly record from southeastern Australia is 34° S., and Scripps’s “Downwind” expeditions found it only south of 34° S. in the Peru Current.

The “John Murray” and “Valdivia” expeditions (Tattersall, 1939; Illig, 1930) listed *E. similis* at a total of seven localities north of 5° S. in the Indian Ocean. It has not yet been caught in an east-west belt, 5°–26° S., where temperatures at 200 and 400 meters are the warmest in the Indian Ocean, except in the Gulf of Arabia where *E. similis* is also unknown. The “Valdivia” records include five localities south of 26° S. in mid-ocean.

To the north and south of the warm belt that lacks *E. similis*, the 200-meter temperature is 13°–15° C. The temperature range at 200 meters is 6°–15° C. in the subantarctic zone of distribution and 12°–18° C. off Southern Japan.

There are, as yet, insufficient data to clarify whether the occurrence of this species in deep waters of the Indo-Australian Archipelago (Hansen, 1910) is related to the distributions of *E. similis* in the northern part of the Indian Ocean. Scattered records for both larvae and adults from subsurface waters of the South China Sea (“Naga” expedition) link the Indo-Australian records with the East China Sea habitat.

E. similis variety *armata* Hansen (1911) was found together with *E. similis* in the subantarctic belt, according to John. The variety *armata* has not been found in the equatorial region or the North Pacific. Hansen (1910) established a second named variety, *E. similis crassirostris*, on the basis of three specimens having deformed rostra, collected in the Banda and Java seas of the East Indies. John reported a low incidence of such specimens from the Antarctic, and the Scripps material records only a single individual at each of two stations, 27° N., 135° E. and 31° 17' N., 137° 27' E. Variety *crassirostris* cannot, therefore, be regarded as having taxonomic significance.

The distribution shown by *E. similis* is unique among the euphausiids. Other biantitropical (bipolar) species or species pairs that occur in the Atlantic and in the Pacific oceans (e.g., *Euphausia gibboides*, *E. recurva*, *Thysanoessa gregaria*,

Nematoscelis difficilis–*N. megalops*) are broadly distributed in the Northern as well as the Southern Hemisphere.

At the northern and southern extremes of its range, *E. similis* is associated with cooler waters than are the five species listed above. A zone in the North Pacific similar in latitude and temperature to the subantarctic habitat of *E. similis* is that occupied by *E. pacifica*. Apparently neither *E. pacifica* nor *E. nana* has transgressed the tropics in recent times.

In the East China Sea off southeastern Japan, intermediate water believed to be of subarctic origin is influenced by the warm Kuroshio. In the subantarctic region, subtropical water mixes with antarctic water (Deacon, 1937). Both regions of mixed water support *E. similis*.

The larvae of *E. similis* and *E. nana* have been found in abundance only in Uda's Tusima Water Mass, along the western slope of the Kuroshio. This indicates that coastal waters of the China Seas may be critical and specific to the zoögeography of both.

Vertical distribution.—*E. similis* has been caught at 0–300 meters only in the most northern and the most southern parts of its range, off Japan and in the subantarctic region, respectively. In Japanese waters, immature individuals and larvae were caught in the 0–300-meter layer during both day and night. Adults were found at 0–300 meters only at night.

In the antarctic region, both *E. similis* and *E. similis* variety *armata* were caught almost as often in the 0–100-meter layer as in the 100–250-meter layer (John, 1936). Variety *armata* was caught somewhat more often at 0–100 meters, and *E. similis* was more frequently present in the deeper tows.

In waters of the Indo-Australian Archipelago, none of these forms has been caught in hauls reaching to less than 500 meters, and rarely in hauls reaching to less than 750 meters. There is no evidence that *E. similis* reproduces there, or in the tropical Indian Ocean; however, some larvae and juveniles were found in the South China Sea by the "Naga" expedition.

Euphausia gibboides Ortmann; *Euphausia fallax* Hansen

(Fig. 32)

Three species belonging to a "*Euphausia gibboides* group" have been described. They are distinguishable by small differences in the male copulatory organ, as follows:

E. gibboides Ortmann, 1893. The distal part of the terminal process is simple. The median lobe bears a single triangular tubercle near the base of the lateral process.

E. fallax Hansen, 1916. The distal part of the terminal process is trifid. The median lobe bears no tubercles.

E. sanzoi Torelli, 1934. The distal part of the terminal lobe is bifid. The median lobe bears two triangular tubercles.

The close relationship of these species is clear. Tattersall (1939) questioned the validity of *E. sanzoi*, noting that "the differences between it and *E. gibboides* are almost all confined to the copulatory organs on the first pleopod of the male." Tattersall (1925) assigned a specimen (from the coast of Natal) bearing a bifid

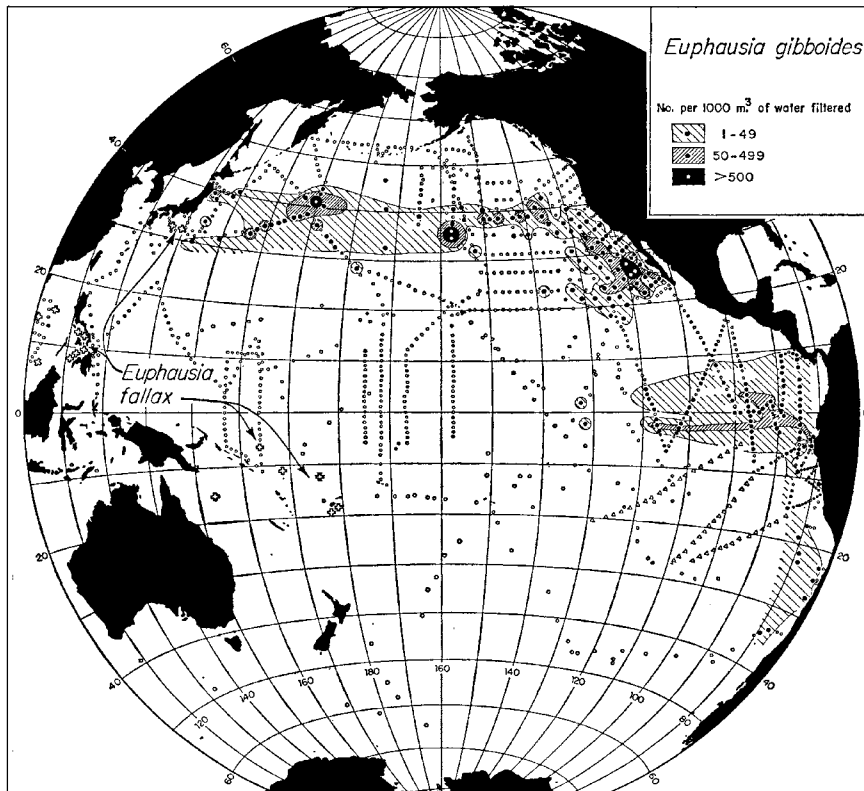


Fig. 32. Geographical distribution of *Euphausia gibboides* and the allied species *Euphausia fallax* (positive records indicated as crosses).

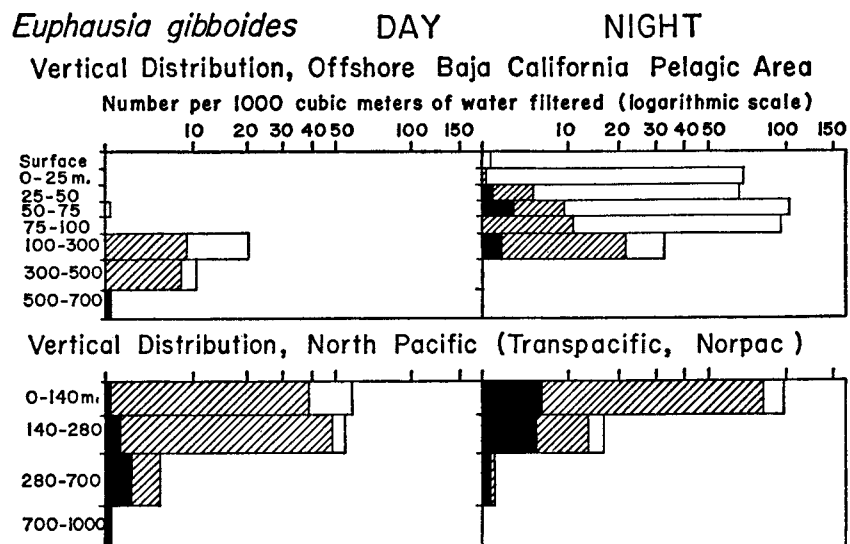


Fig. 33. Vertical distribution of *Euphausia gibboides*.

terminal process to *E. gibboides*. Subsequently, Torelli (1934) described the “bifid form,” *E. sanzoi*, from the Red Sea. Tattersall (1939) referred female specimens, collected in the Red Sea by the John Murray Expedition, to *E. gibboides*.

The validity of *E. fallax*, based on characteristics no more extreme than those of *E. sanzoi*, cannot be questioned. Adult males of *E. fallax* were caught during the 1907–1910 cruise of the *Albatross* and I have seen specimens in the “Naga” expedition collections from the South China Sea. Sheard (1953) suggested that *E. consuelae* Boone, not adequately described, may belong to *E. fallax*. The locality for *E. consuelae*, the Arafura Sea, is near the known localities for *E. fallax*.

Immature specimens collected during Scripps cruises at four stations in the western tropical Pacific, and at two off southern Japan, resemble *E. gibboides*. However, the eyes of these specimens are more heavily pigmented and contain more facets than those of *E. gibboides* at the same stage of development. Also, a higher lappet is present on the first segment of the antennal peduncle. These specimens are referred to *E. fallax*. They were found in the western tropical part of the ocean in which *E. fallax* is known to occur.

Horizontal distribution.—Distributional evidence supports the separation of the three species of the “*E. gibboides* group.” In the North Atlantic *E. gibboides* occupies the same range of latitude as that in which it is found in the North Pacific: a belt between 30° N. and 40°–45° N., swinging southward with the California Current in the North Pacific, and with the Canaries Current in the North Atlantic.

E. gibboides is concentrated near 40° N. in the oceanic part of its range. It is also numerous where the California Current bends westward near mid-Baja California, 25° N.

This species is found again near the equator in the eastern equatorial basin of the Pacific. As in the Northern Hemisphere, it is concentrated where a cold current is dissipated into warmer waters.

E. gibboides appears not to have a transoceanic distribution in the southern hemisphere. It was caught at eleven “Downwind” stations in the Peru Current, but not along the north-south transect near 130° W., nor in waters of Australia and New Zealand.

In the western North Atlantic *E. gibboides* was present from the Florida Current, at the south (Lewis, 1954), to 37° 40' N., 70° 37' W. at the north (Hansen, 1915). In the eastern North Atlantic it occurred from Cadiz Bay (Ruud, 1936) to 24° 15' N., 17° W. Inasmuch as *E. gibboides* has not been reported from between 30° W. and 66° W., it is not known whether or not there is an east-west belt of distribution in the North Atlantic.

There are 27 records from the eastern Atlantic, between 18° N. and 10° S., and between 30° W. and 2° W. (Ortmann, 1893; Zimmer, 1914; Illig, 1930). This tropical part of the distribution is similar to that found in the Pacific, 10° N.–10° S. *E. gibboides* has not been found in the western South Atlantic but has been caught at four stations west of the Cape of Good Hope, the most easterly being at the Cape (Zimmer, 1914) and the most westerly, 5° 54' E., 26° 49' S. (Illig, 1930).

It is likely that *E. gibboides* is replaced by *E. sanzoi* in the Indian Ocean. *E. sanzoi* was found in the Red Sea and off Natal, 27° S. As mentioned above, Tattersall's

E. gibboides from Natal is probably *E. sanzoi*. The specimens from the Red Sea were females; hence indeterminable.

Illig (1930) lists three records for *E. gibboides* from the Indian Ocean, off Africa. Adult males were not reported. Thus, the occurrence of *E. gibboides* in the Indian Ocean cannot be confirmed on the basis of these three records.

E. fallax was caught by the *Albatross* at five stations inside the Philippine Archipelago. Curiously, it was not found in "Troll" samples from the eastern coast of the Philippines.

Two records for *E. gibboides* from the Fiji Islands and one from the South China Sea (Hansen, 1912) may not have been based upon adult males. The records were published by Hansen before he had established *E. fallax*. Judging from the localities, it is likely that the specimens are *E. fallax*, which lives in warmer waters than *E. gibboides*.

Vertical distribution (fig. 33).—*E. gibboides* was caught mainly above 280 meters at night. Adults were most frequently at 280–700 meters in the daytime. Immature individuals and larvae were almost entirely above a depth of 280 meters at all times.

The vertical distribution off Baja California shows that this species, excepting small numbers of its larvae, does not occur at the surface. Adults and immature individuals were found between 25 and 300 meters at night, and below 100 meters in the daytime.

The Scripps records for *E. fallax* are from tows that reached to at least 140 meters. Adults were occasionally caught in the 0–140-meter layer at night in the South China Sea.

At the Philippines the *Albatross* found *E. fallax* at the surface on three occasions. The numbers caught suggest that swarming was taking place. The tows were made at dusk. Surface temperatures were 28°–29° C. In the most southerly part of the range of *E. gibboides* in the California Current, surface temperatures were as high as 22° C., but reached 27°–28° C. between the Galápagos Islands and Costa Rica where *E. gibboides* was also found. The thermocline was shallow in this latter region. Judging from the vertical distribution of *E. gibboides* off California, this species was probably present in the cooler layers in the zone 0°–10° N. Temperatures at 100 meters were 12°–15° C., the same range that is associated with the North Pacific distribution.

Euphausia recurva Hansen; *Euphausia mutica* Hansen

(Figs. 34, 35)

Horizontal distribution.—The North Pacific distributions of *E. recurva* and *E. mutica* are similar. Both species are found in the offshore part of the California Current and across the breadth of the Pacific, south of 40°–43° N. Furcilia larvae of the two have not been reliably separated. For this reason they will be discussed together.

E. recurva is biantitropical in the Pacific, extending southward to 20° N. in the California Current. It was numerous along the northern and eastern margins of its range and scarce in the central part of the eastern North Pacific. The distribution extends as far south as Hawaii in the mid-Pacific, and to 15° N., east of the

Philippines. It was caught at one “Troll” station southeast of Mindanao, 7° N.

E. recurva was not reported from the Philippines or the East Indian Archipelago by Hansen (1916, 1910). It was listed from the South Pacific by Hansen (1915), Tattersall (1924), and Sheard (1953). The “Downwind” expedition recorded five localities in offshore waters of Chile. Although *E. recurva* was not caught along the

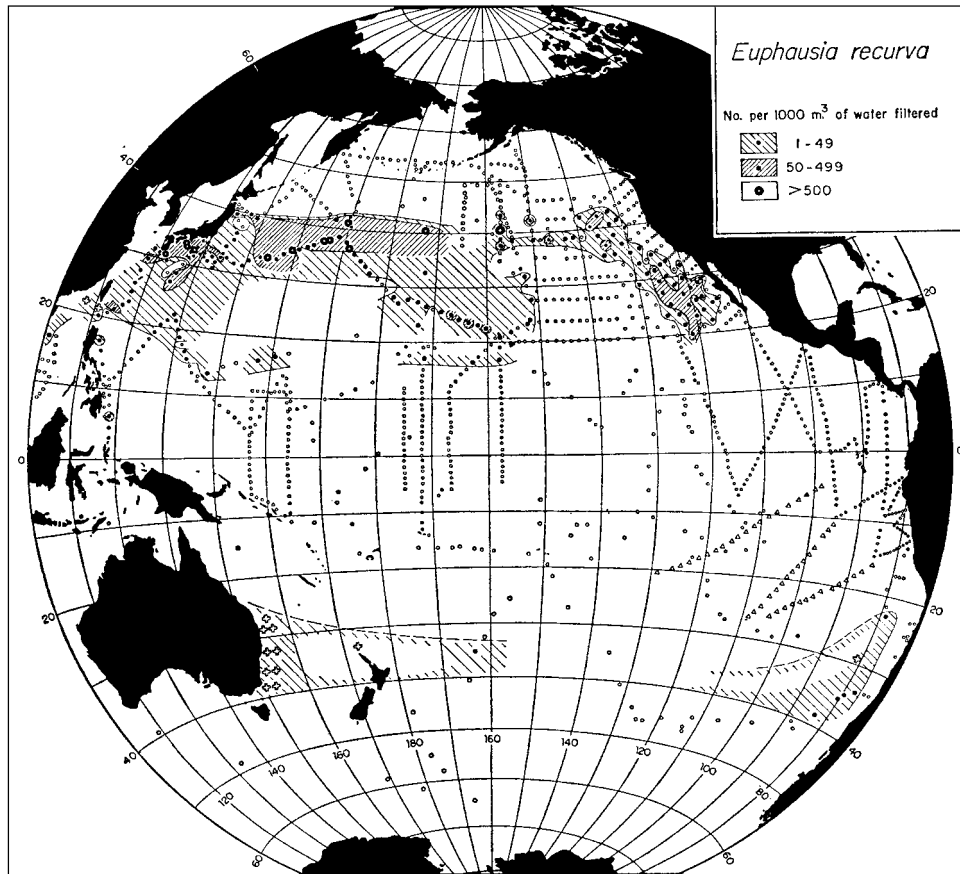


Fig. 34. Geographical distribution of *Euphausia recurva*.

meridional transect near 140° W., in mid-ocean, it was taken at 36° 29' S., 163° 09' W. by the “Monsoon” expedition, suggesting that the eastern and western South Pacific ranges are in communication with each other.

E. recurva is known in the Indian Ocean from near the Cape of Good Hope, 34° 31' S., 93° 44' E., almost to Australia, 34° 14' S., 26° E. (Illig, 1930). It was not found in the northwestern part of the Indian Ocean by the John Murray Expedition, but Illig reported three localities in the northeastern part: 7° 58' N., 91° 47' E.; 4° 56' N., 78° 15' E.; 6° 19' W., 73° 19' E. This species appears to be missing from 7° S. to 25° S. in the Indian Ocean. Hansen (1912) reported it at 25° 40' S.

E. recurva has been recorded from the eastern South Atlantic, from 11° 19' S., 18° 34' W. (Zimmer, 1914) to 37° 31' S., 17° 02' E. (Illig, 1930). There is one

record from the North Atlantic. Illig (1930) reported *E. recurva* from a station near the coast of Africa, 24° 13' N., 17° 01' W., but did not find it between 24° N. and 26° S. along the track of the *Valdivia*.

Like *E. recurva*, *E. mutica* was not found in the middle area of the eastern central zone of the North Pacific. However, *E. mutica* was numerous along the southern

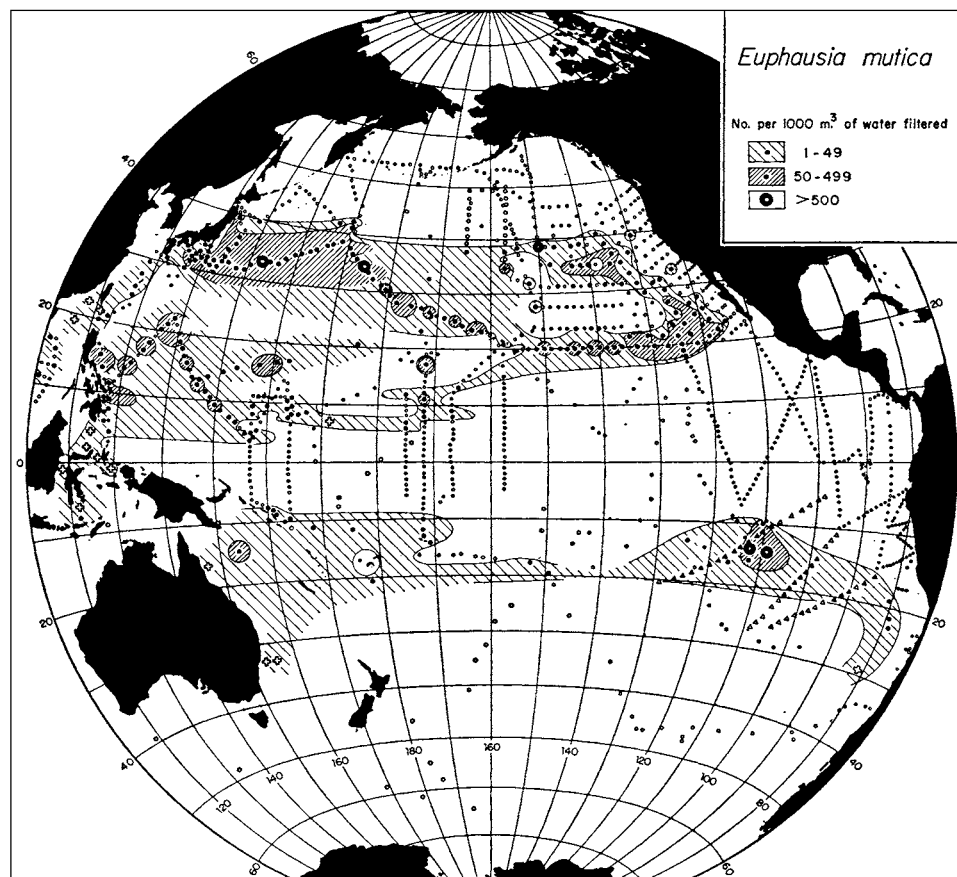


Fig. 35. Geographical distribution of *Euphausia mutica*.

margin of the central zone. In the western South Pacific it was found as far north as 8° S. by the “Equapac” expedition. In the eastern South Pacific surveyed by the “Downwind” expedition, *E. mutica* was found south of 10° S. *E. recurva* was lacking from the equatorial region 8°–21° S. where *E. mutica* occurred.

It is not known whether the North Pacific and South Pacific ranges of *E. mutica* merge in the extreme western part of the ocean. This species was found only to the north of 9° N. in the South China Sea (“Naga” expedition). It was present, although scarce, in the *Siboga* material from the East Indian Archipelago (Hansen, 1910), and was reported from the Great Barrier Reef (Tattersall, 1936).

The distribution extends eastward from the Philippines to 165° W., between 4° N. and 13° N. The Equatorial Countercurrent and a thermal anticline (Cromwell, 1953) associated with its northern edge (17°–20° C. at 100 meters) appear to have

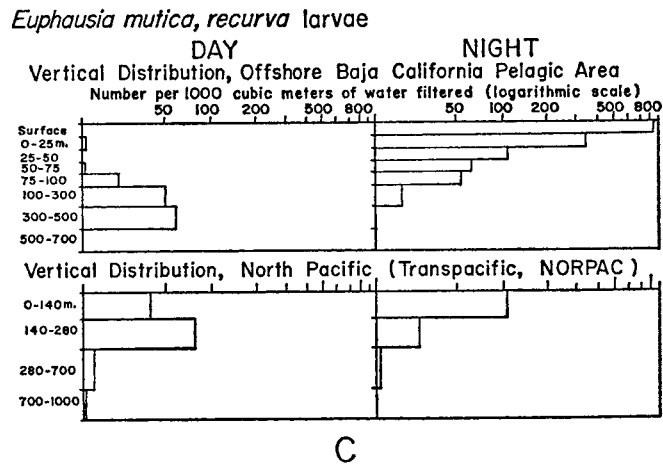
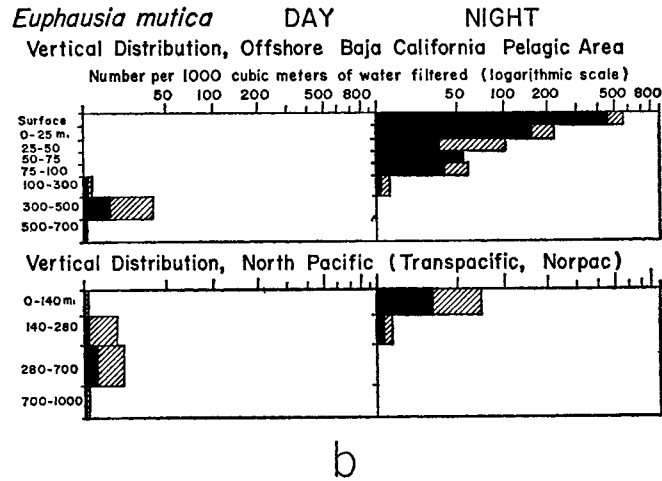
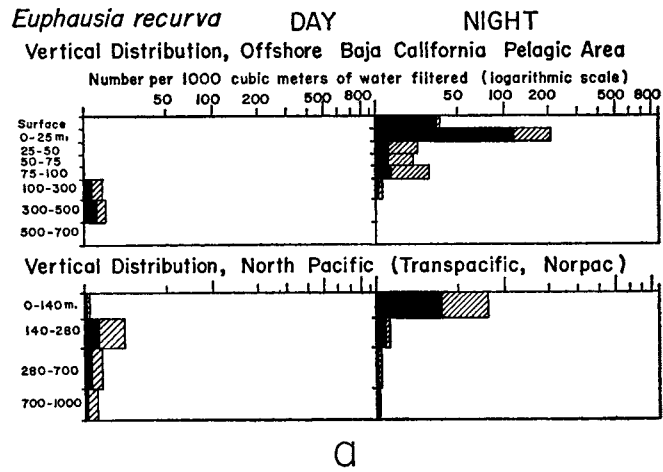


Fig. 36. Vertical distributions. a. Adults and juveniles of *Euphausia recurva*. b. Adults and juveniles of *Euphausia mutica*. c. Furcilia larvae of the two species, not separated.

established an environment for this species in mid-ocean, within the equatorial zone. The distribution in the North Pacific was associated with the temperature range of 16°–25° C. at 100 meters. In the South Pacific *E. mutica* was excluded from the South Equatorial Current and the West Wind Drift—regions within the above temperature range.

E. mutica is known from the Atlantic, 42° N. to 38° S. (Hansen, 1905). As in the Pacific, it has not been found in the eastern part of the ocean, north of about 28° N. Illig recorded it from along the west coast of Africa, within the equatorial region. This is in contrast to the absence of *E. mutica* from the eastern equatorial basin of the Pacific. Ruud (1936) found neither *E. recurva* nor *E. mutica* in the Mediterranean.

Hansen (1905) listed *E. mutica* from the Red Sea, and the *Valdivia* (Illig, 1930) found it to be widespread in the Indian Ocean, from 30° S. in mid-ocean to (1) 8° N. in the Bay of Bengal, (2) 9° N. in the Arabian Sea, and (3) 13° N. in the Gulf of Oman. The John Murray Expedition, September, 1933-May, 1934, did not find this species in the northwestern Indian Ocean, north of 10° S., previously surveyed by the *Valdivia*, March-April, 1898.

Vertical distribution (fig. 36, a-c).—The differences between the geographical distributions of *E. recurva* and *E. mutica*, particularly in the region of the California Current, suggest that these two species have different ranges with respect to depth. However, the strata sampled were not thin enough to show any difference if it does exist.

Both *E. mutica* and *E. recurva* were almost entirely above 100 meters at night and between 140 and 700 meters during the day. The aggregate of the furcilia larvae (both species) showed a daytime maximum below 140 meters, although substantial numbers were present above that depth. Off Baja California, near the southern limits of the distributions, the daytime level for furcilia was somewhat deeper than the average based on oceanwide sampling. The night maximum was at the surface.

Euphausia brevis Hansen

(Fig-37)

Horizontal distribution.—*Euphausia brevis* was found in the central water masses of the North and South Pacific. Like *E. recurva* and *E. mutica*, this species is antitropical. In each hemisphere, the distribution of *E. brevis* is centered in the circulation gyral. In contrast, *E. recurva* and *E. mutica* are most concentrated near the borders of their ranges.

E. brevis was not found east of Japan in the region of mixed Oyashio, Kuroshio, and Central water (cf. *Euphausia hemigibba*), nor was it found in the South China Sea by the “Naga” expedition. During CalCOFI surveys, 1949–1959, it occurred only in the warm offshore part of the California Current.

The boundary of distribution south of Hawaii was at 11°–14° N. during the summer (POFI Cruise 5, 1950; “Equapac” expedition, 1956), and at 7°–9° N. during January–March, 1951 (POFI Cruise 8). There, surface temperature of the North Equatorial Current was 1°–2° C. cooler in the winter than in the summer. At the 100-meter and 200-meter levels, little or no temperature change was associated with

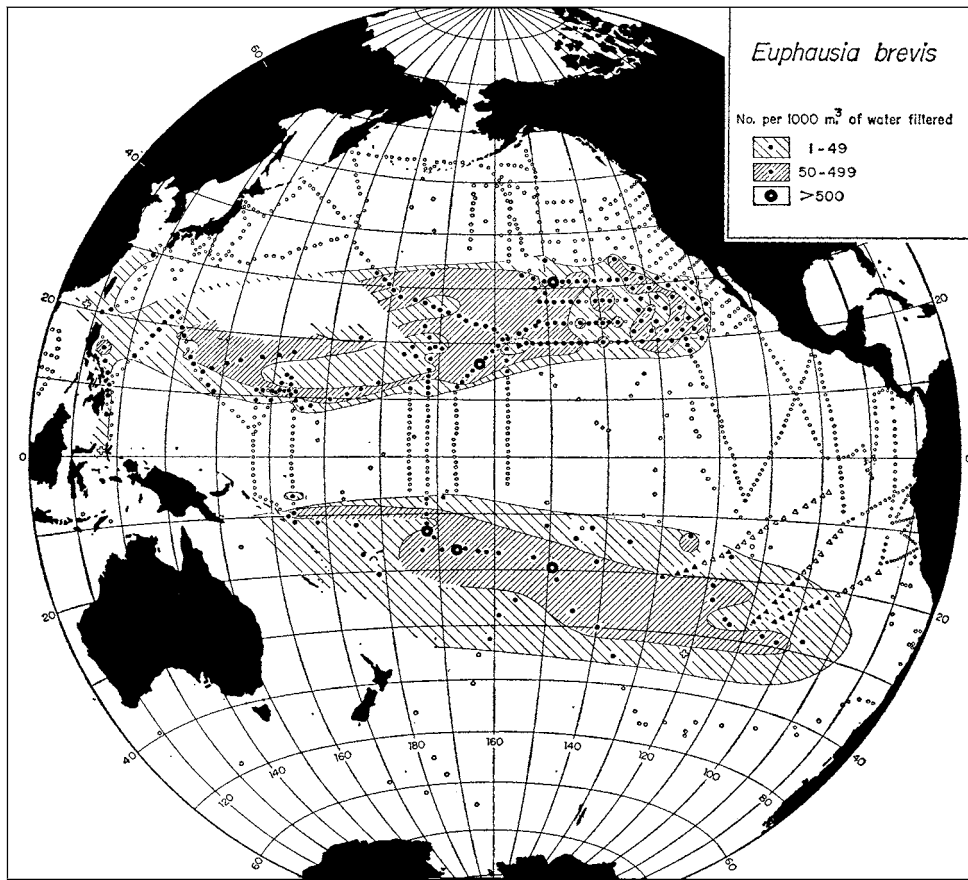


Fig. 37. Geographical distribution of *Euphausia brevis*.

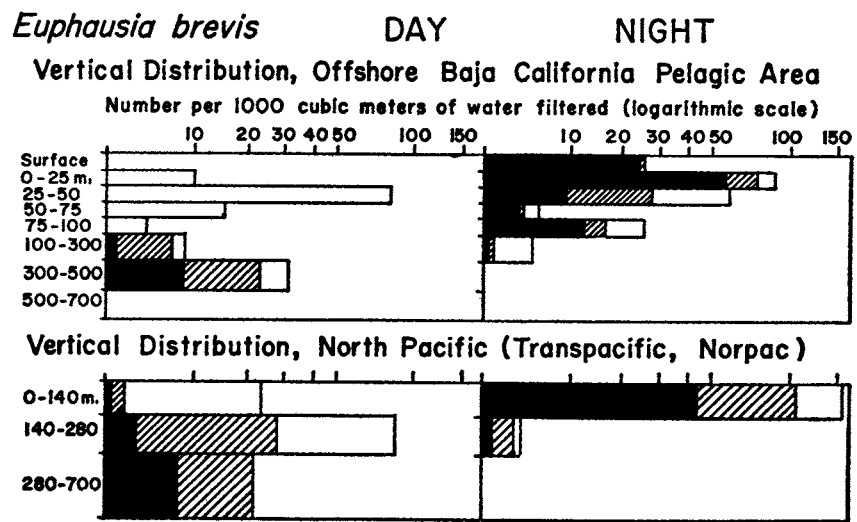


Fig. 38. Vertical distribution of *Euphausia brevis*.

change of season. In the belt 7°–14° N., some winter isotherms were deeper than the same summer isotherms.

The distribution in the Southern Hemisphere is a mirror image of that in the North Pacific. *E. brevis* ranged to 35° S. and 35° N. in mid-latitudes, and to the margins of the Equatorial Water Mass in low latitudes. This species is widespread in the North and the South Atlantic, occurring from 41° N., 40°–41° W. (Hansen, 1912) to 33° 23' S., 16° 19' E. (Illig, 1930). Moore (1952) indicated records from 5°–10° N. off South America, and from 50°–55° N. off Ireland. *E. brevis* has been found infrequently near the northwest coast of Europe (Hansen, 1912; Moore, 1952), but it occurs widely in the Mediterranean (Ruud, 1936). As in the Pacific, *E. brevis* is rare or absent in the eastern half of the Atlantic, 20° N. (Moore, 1952) to 11° S. (Zimmer, 1914). There is one record at 2° N. near the coast of Africa (Illig, 1930).

This euphausiid has been reported from the Indian Ocean, the most southerly record being 34° 14' S., 80° 31' E., and the most northerly 9° 06' N., 53° 41' E. (Illig, 1930). Tattersall (1939) found it only at 1° 39' S., 61° 14' E., in the northwestern part of the ocean traversed by the John Murray Expedition.

Vertical distribution (fig. 38).—Adults of *E. brevis* showed a daytime maximum at 300–500 meters off Baja California. This agreed with the depth of the density maximum in the average North Pacific vertical distribution. Immature specimens were somewhat more numerous than adults above 280 meters. Furcilia larvae were concentrated above 75 meters in the Baja California samples; however, the North Pacific average indicated that furcilia were as numerous at 140–280 meters as at 0–140 meters.

Each of the three size groups occurred mainly above 100 meters at night, although only adults and immature specimens were found at the surface.

Euphausia hemigibba Hansen; *E. paragibba* Hansen; *E. pseudogibba* Ortmann;

E. gibba G. O. Sars (Figs. 39, 40)

The four species of the “*Euphausia gibba* group” (Hansen, 1910) can be distinguished with certainty by the structure of the male copulatory organ. Immature individuals and females are not easily separated. Conveniently, the four distributional ranges in the Pacific overlap only at their margins.

The similarity of the four species and the separateness of their Pacific ranges suggest that they are closely related. However, John (1936) stated that only *E. hemigibba*, *E. paragibba*, and *E. pseudogibba* are a natural group. He pointed out, as did Hansen (1912), that the male copulatory organ of *E. gibba* differs greatly from that of the other three species.

It has been possible to examine specimens of *E. gibba* collected by the “Capricorn,” “Downwind,” and “Monsoon” expeditions. The main trunk of the median lobe of the male copulatory organ is shorter than in other euphausiid species, but bears a curved “thin-skinned finger” (Hansen, 1911), originating at the outer distal angle (fig. 39). The terminal process is short, compared with that of other species, and the proximal and lateral processes are long.

Unlike the terminal, proximal, and lateral processes, the “finger” does not articulate

with a lobe of the organ. It appears to be an extension of the median lobe proper. *E. pseudogibba* and *E. paragibba* are the only other euphausiid species in which the distal part of the median lobe is narrowed to less than one-half the width of the proximal part. In *E. hemigibba* it is somewhat narrowed.

It is possible that in *E. gibba* the distal part of the median lobe became fragile as a consequence of overspecialization. At the same time, the lateral process, attached to the trunk of the median lobe, may have enlarged to compensate for reduction of the distal part of the lobe. This was accompanied by extreme

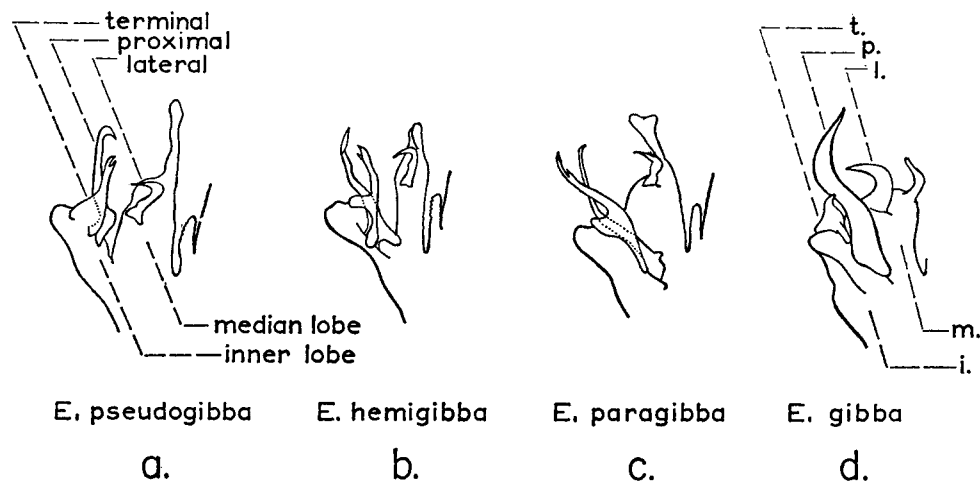


Fig. 39. Male copulatory organs of the “*Euphausia gibba* group.” a. *E. pseudogibba*. b. *E. hemigibba*. c. *E. paragibba*. d. *E. gibba*. Processes and lobes are designated.

modification of the terminal and proximal processes. The latter, much lengthened, is juxtaposed to the enlarged lateral process.

The bizarre differentiation of the processes of the copulatory organ in *E. gibba* may therefore be viewed as a structural compensation for the extreme modification of the median lobe. Narrowing of the median lobe is characteristic of the “*gibba* group.” For this reason, *E. gibba* should probably be retained in it.

Horizontal distribution.—*E. hemigibba* was found in the central North Pacific, ca. 18°–42° N. The regions of high concentration, like those of *E. brevis* (fig. 37), are in general away from the margins of the range. *E. hemigibba* is an offshore species in the California Current.

E. hemigibba occurred east of Japan (*E. brevis* was missing from the region of mixed Oyashio and Kuroshio water). It has not been caught in the equatorial region, including the Philippine and East Indian archipelagos, except at one station, 0° 17.6' S., 129° 15.4' E. There, *E. pseudogibba* and *E. paragibba* also were found. *E. hemigibba* is not known to occur in the South Pacific.

This species was reported by Illig from three places in the Indian Ocean: 29° 06' S., 89° 39' E.; 26° 04' S., 93° 44' E.; and 9° 06' N., 53° 41' E.; but it was not found in the Arabian Sea by the John Murray Expedition.

E. hemigibba is widely distributed in the central parts of the North and South Atlantic. Moore (1952) showed it to occur north of 45° N., 25°–30° W., where the North Atlantic Current bends northward. *E. hemigibba* appeared to be missing

from the eastern equatorial belt, 8° S.–15° N. Zimmer (1914) reported it from 8° to 35° S. in the eastern Atlantic, and Ruud (1936) from the Mediterranean, where it was the only species of the “*gibba* group” found. Of these species, Tattersall found only *E. hemigibba* in the western Atlantic near 30° W., at 18°–21° S. and at 23°–29° N.

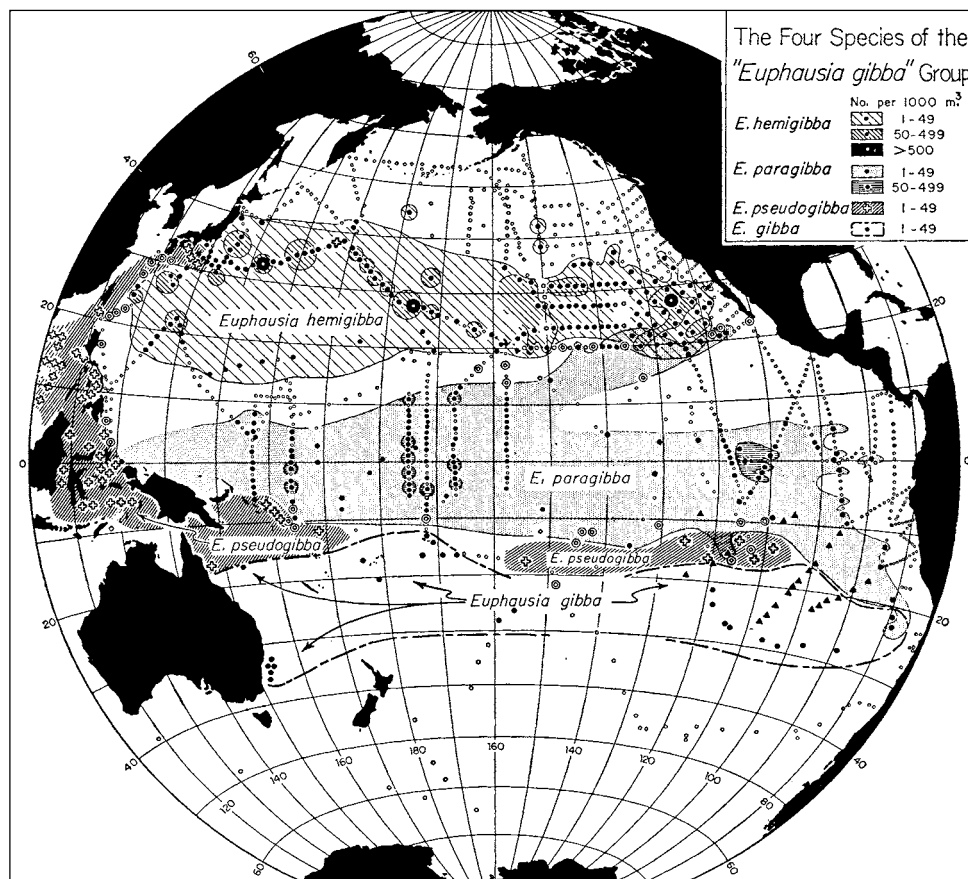


Fig. 40. Geographical distribution of the four species of the “*Euphausia gibba* group.”

In the Pacific *E. paragibba* was most concentrated near the equator, 160° E. to 110° W. The range extends eastward to the Galápagos Islands, and to offshore waters of the Peru Current, 10°–23° S. This species has not been found in the eastern equatorial region, 7°–20° N., but was caught near 20° N., between Hawaii and Baja California, by three cruises: “Shellback” expedition, the 1953 “Pelagic Area” cruise, and “Norpac” cruise.

According to Tattersall, *E. paragibba* lives in the western half of the Arabian Sea, whereas *E. pseudogibba* was found in the eastern half. Illig reported *E. paragibba* at 33° 23' S., 16° 19' E., near the Cape of Good Hope, but it has not been found elsewhere in the Atlantic. If this latter record is correct, *E. paragibba* was carried from the tropical Indian Ocean to South Africa by the warm Agulhas Current. Other *Valdivia* records included 13° N., 47° E., in the Gulf of Oman, a

series of stations extending from 8° N., 89° E. to 4° S., west of the Seychelles, and a more southerly record, 27° 58' S., 91° 40' E.

E. gibba is endemic to the central South Pacific. The Scripps records are from 15° S. to 30° S. in the eastern Pacific and from 13° S. to 28° S. in the western Pacific. Localities off Australia are from Sheard (1953). Esterly's (1914) record from the San Diego region appears to have been based on *E. hemigibba*.

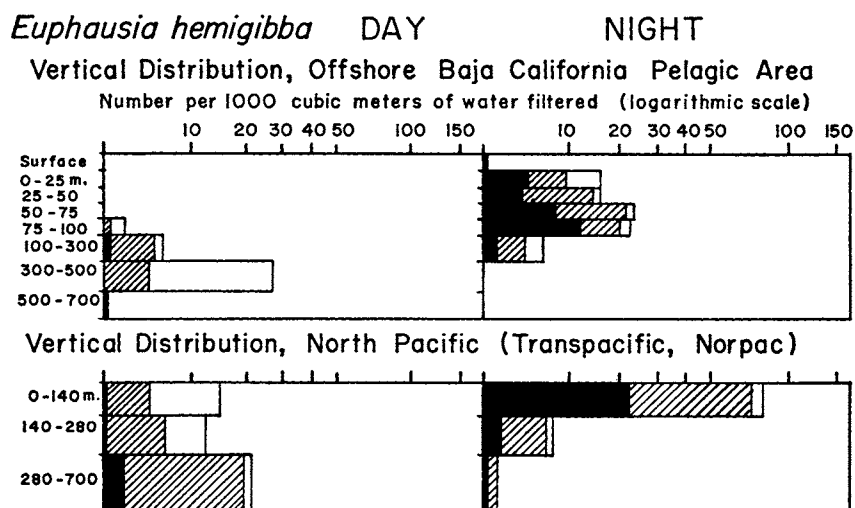


Fig. 41. Vertical distribution of *Euphausia hemigibba*.

E. pseudogibba has been found in the South China Sea, the East Indian Archipelago, including the Solomon Islands, and south and west of Japan in the Kuroshio and the Kuroshio Extension. It was reported from the Great Barrier Reef (Tattersall, 1936). The most eastern segment of the range is based upon records from 12° S. to 18° S. in mid-ocean (108°–155° W.) (cf. *Thysanopoda subaequalis*, fig. 23). The *Albatross* caught *E. pseudogibba* at two stations in this region, as did the “Capricorn” expedition. The “Downwind” expedition added three records.

E. pseudogibba was present at 4° 55' S., 73° 16' E., in the northwestern part of the Indian Ocean surveyed by the John Murray Expedition. Illig reported it from 34° 14' S., 80° 31' E., northward to 8° N. in the Bay of Bengal, and at 4° 45' S., 48° 59' E., near the Seychelles. In the eastern Atlantic it lives from 32° N. to 37° S., according to Illig, but Zimmer found it only between 17° N. and 8° S. in the mid-Atlantic. Leavitt (1938) listed *E. pseudogibba* from 35° N. to 40° N. in the northwestern Atlantic.

Vertical distribution.—*E. hemigibba* was found at night mainly above 140 meters by the “Transpacific” and “Norpac” expeditions (fig. 41); it was above 100 meters at night off Baja California, but few adult specimens were at the surface. Adults were uncommon above 280 meters during the day, but individuals belonging to each of the three size groups were at both 0–140 meters and 140–280 meters. Furcilia larvae were most common in the 0–280-meter layer, according to the average for the North Pacific traverses, but were concentrated at 300–500 meters off Baja California.

E. paragibba was found almost entirely above 140 meters at night in the southern part of the region surveyed by the "Norpac" cruise, near 20° N. At the two day stations within the range of this species, larvae were caught at 0–280 meters; adults, at 280–700 meters.

E. pseudogibba was found at two night stations off Japan. Immature and adult specimens were caught above 140 meters at both stations, and adults were also present at 280–520 meters at one of the two. At the single daytime locality, immature individuals and larvae were found at 140–280 meters. Of Hansen's twelve records from the Indo-Australian Archipelago, nine were based on tows reaching to 900 meters and three were from surface tows. Of the sixteen *Albatross* records from the Philippines, eight were from surface tows. Three of these contained large numbers of *E. pseudogibba*.

The vertical distribution of *E. gibba* in the South Pacific appears to be similar to that of the three other species of the "gibba group." Adults were caught at three "Capricorn" expedition stations, all occupied at night to depths of 140 meters, 600 meters, and 2,000 meters. The "Downwind" expedition records were from two day samples, 0–550 meters and 0–1,830 meters, and twelve night samples (two were 0–150 m., the others deeper).

E. gibba was caught by the *Albatross* at thirteen stations in the eastern South Pacific: seven were daytime hauls to 600 meters; six were surface hauls made at night.

Euphausia diomediae Ortmann

(Fig. 42)

Horizontal distribution.—*Euphausia diomediae* is a characteristic, sometimes dominant species of the Pacific equatorial group. In the eastern Pacific it ranges from the tip of Baja California, 22° N., to near 18° S. in the warm offshore part of the Peru Current. It was not found by the "Shellback" and "Downwind" expeditions in coastal waters of Peru, or immediately south of the Galápagos Islands.

E. diomediae is common in the region of the Indo-Australian Archipelago and in the Philippines (Hansen, 1910, 1916). It occurred in the South China Sea, and northward to Japan and east of Japan in the Kuroshio Extension. It has not been found elsewhere in the western North Pacific.

Hansen (1912) reported three specimens from 30° 35' N., 117° 15' W., caught in October, 1904, off northern Baja California. The euphausiids from that station, other than *E. diomediae*, were not equatorial types. CalCOFI cruises in this area have not caught *E. diomediae* north of 23° N. during 1949–1958.

This distribution is closely associated with the Pacific Equatorial Water Mass (cf. *Nematoscelis gracilis*, *Stylocheiron micropthalma*). Within the geographical range of *E. diomediae*, surface temperatures along the axis of the distribution are cooler than in central waters (e.g., 11°–15° C. at 200 meters).

E. diomediae is not known from the Atlantic, but is widely distributed in the northwestern part of the Indian Ocean (Tattersall, 1939). *Valdivia* collections (Illig, 1930) indicated that this species, like *E. paragibba*, was carried southwestward, near to the Cape of Good Hope. It was present in the eastern part of the Indian Ocean, 10° S.–8° N., in the Bay of Bengal.

Vertical distribution.—Adults were caught at night in the 0–140-meter layer at

four "Norpac" stations along 20° N. in the eastern Pacific. *E. diomediae* was not found in daytime hauls along this line of stations, located at the northern limit of the range of the species.

In the region east of Japan, night records based upon 13 collections ("Transpacific" expedition) averaged 8.5 adults and 8.5 immature individuals per 1,000 cubic meters in the 0–140-meter layer. Averages for the

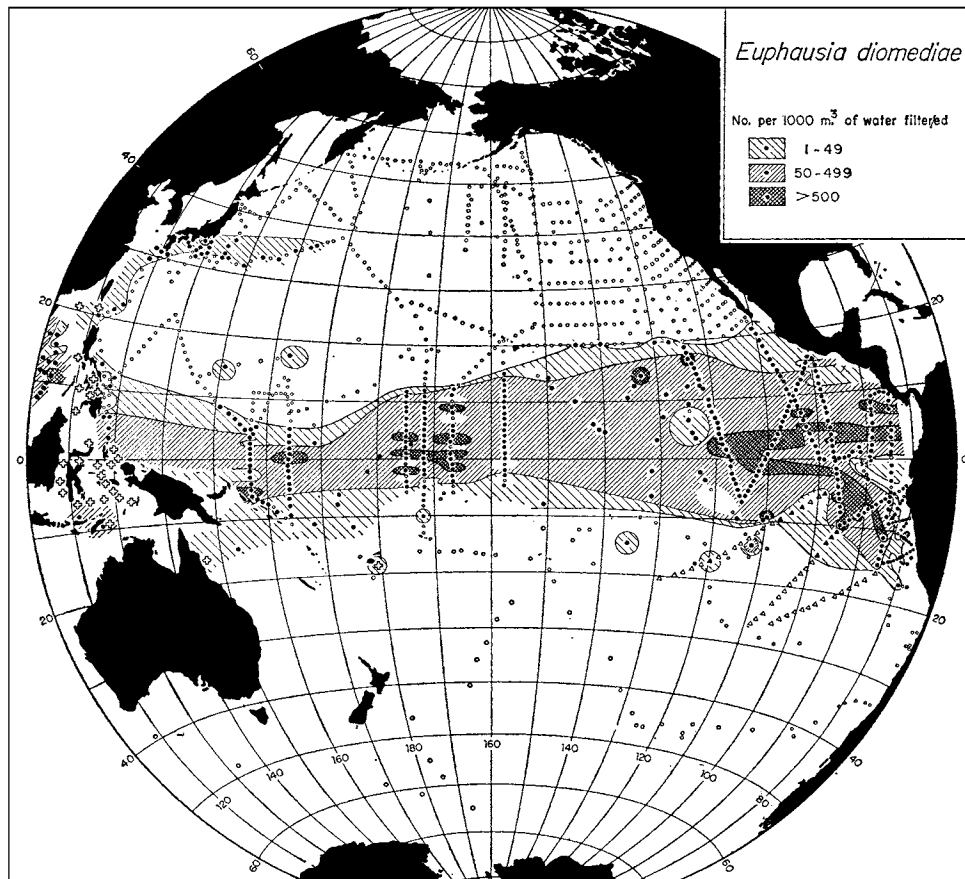


Fig. 42. Geographical distribution of *Euphausia diomediae*.

140–280-meter nighttime layer were 0.6 of an adult and 0.1 of a juvenile, based upon 10 collections. *E. diomediae* was lacking in 5 daytime hauls, 0–140 meters, in this same region; averages of 1.8 adults and 13.2 immature individuals per 1,000 cubic meters were found in the 140–280-meter layer.

Hansen (1910, 1912, 1916) listed a number of surface records for *E. diomediae* all based on night collections, from both the eastern and western equatorial regions.

Euphausia tenera Hansen

(Fig. 43)

Horizontal distribution.—*Euphausia tenera* occupies a wide geographical range in tropical and subtropical waters of the Atlantic, Pacific, and Indian oceans. It has

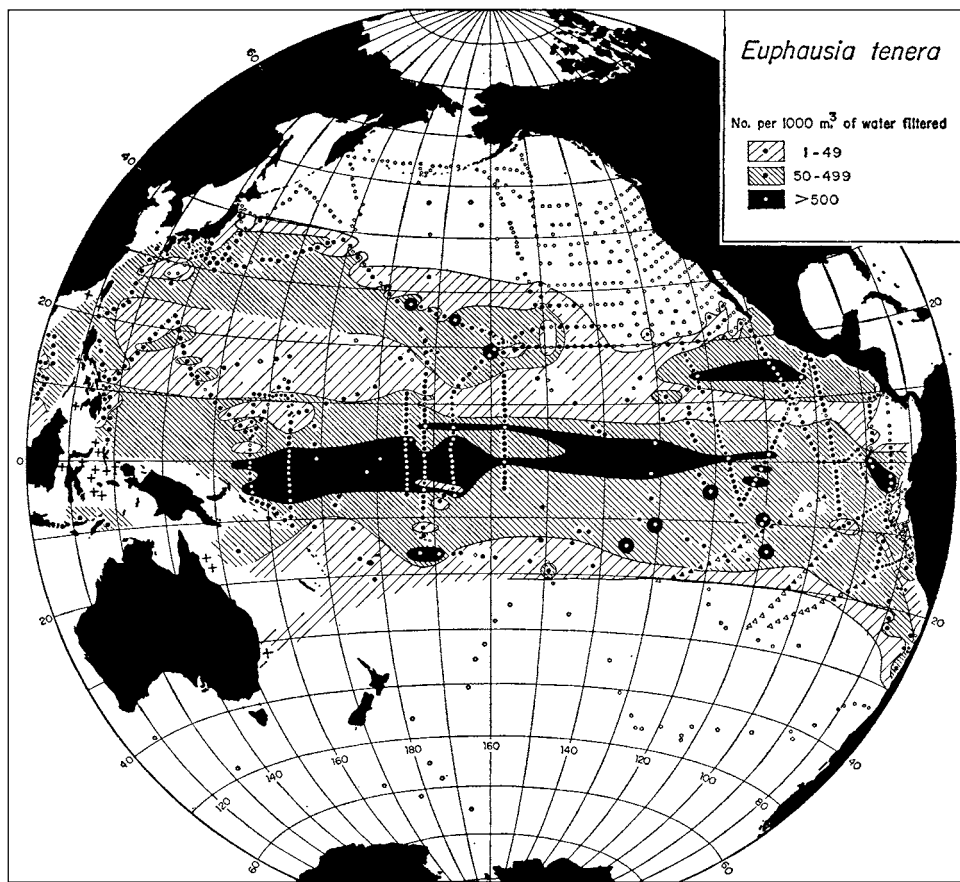


Fig. 43. Geographical distribution of *Euphausia tenera*.

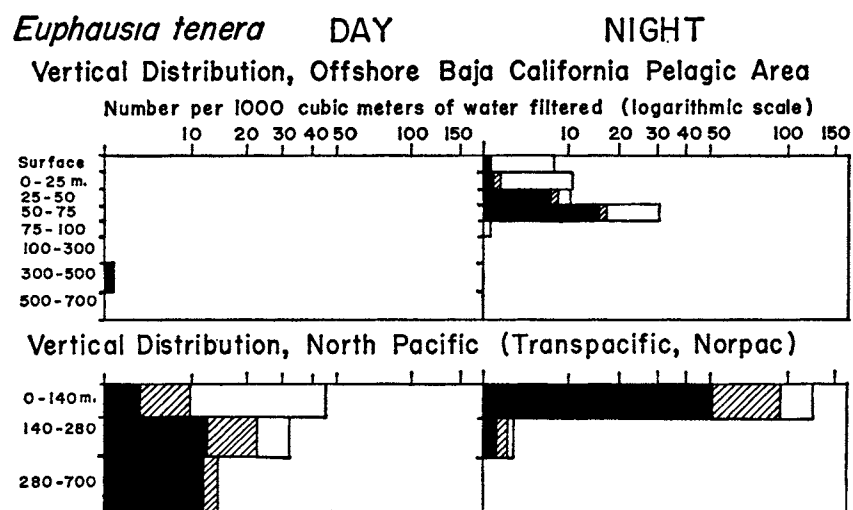


Fig. 44. Vertical distribution of *Euphausia tenera*.

been found from 40° N. to 35° S. in the western Pacific, and from 23° N. to 28° S. in the eastern Pacific, including the Gulf of California. It is missing from all but the most southerly part of the California Current.

During the "Shellback" expedition, June, 1952, *E. tenera* was not found at ten stations in cool coastal waters (16°–18° C. at the surface) of Ecuador and Peru; it was numerous in the warmer offshore region. The northern and southern limits of the range are in rough agreement with the position of the 23° C. surface isotherm.

Numbers of *E. tenera* in excess of 500 per 1,000 cubic meters were most consistently found near the equator in mid-ocean. A belt of low concentration extended from east to west in the region of the North Equatorial Current.

The distribution in the Atlantic is like that in the Pacific: *E. tenera* ranges to 40°–45° N. in the Gulf Stream (Moore, 1952), but is not known from the subtropical eastern part of the ocean. Zimmer (1914) records it from 35° 10' S., 2° 33' E. in the southeastern Atlantic. According to Tattersall (1939) and Illig (1930), *E. tenera* is widely distributed in the Indian Ocean.

Vertical distribution (fig. 44).—*E. tenera* occurred at two daytime stations, at 300–500 meters, near the northern limit of its range off Baja California. It was caught at three night stations in the same area during the "Pelagic Area" survey, 1954; adults were most numerous at 25–75 meters. Larvae occurred from the surface to 100 meters.

The "Norpac" and "Transpacific" expedition sampling showed that east of Japan the depth of the daytime habitat of *E. tenera* is variable; most specimens were found above 280 meters during the daytime, and above 140 meters at night at those stations where stratified sampling was carried out.

Euphausia eximia Hansen

(Fig. 45)

Horizontal distribution.—*Euphausia eximia* is endemic to the eastern equatorial Pacific. It has been found to be most numerous in five areas: (1) oceanic waters west of Baja California, (2) the southern part of the Gulf of California, (3) the region of a thermal anticline off Costa Rica; (4) the South Equatorial Current, from the Galápagos Islands to 110° W., and (5) the Peru Current off southern Peru, 15° S.

E. eximia was found as far west as 145° W. in the North Equatorial Current ("Midpacific" expedition), and at 118° W. in the South Equatorial Current ("Shellback" expedition). It was lacking in the Equatorial Countercurrent, 2°–10° N., and in coastal waters of Colombia and Ecuador, 5° S.–5° N.

The northern limit of the distribution was off southern California, 32°–34° N., during the 1949–1957 CalCOFI surveys. During the "warm year" 1958, *E. eximia* appeared off central California to 36° N.

As off Peru and Chile, a countercurrent is found at 200–400 meters in the California Current region (Sverdrup and Fleming, 1941; Reid, Roden, and Wyllie, 1958). These countercurrents must be instrumental in maintaining the range of *E. eximia*, which undergoes an extensive diurnal vertical migration. The limits of range of this species are closely associated with the positions of the 10° C. and 15°

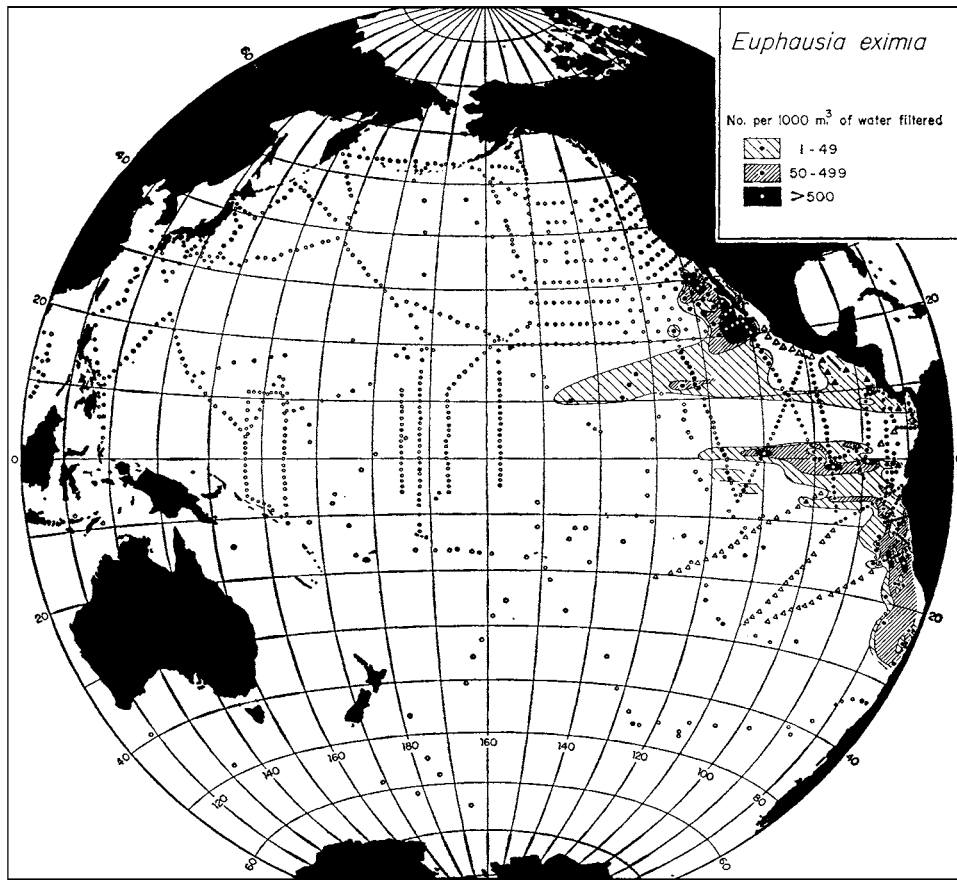


Fig. 45. Geographical distribution of *Euphausia eximia*.

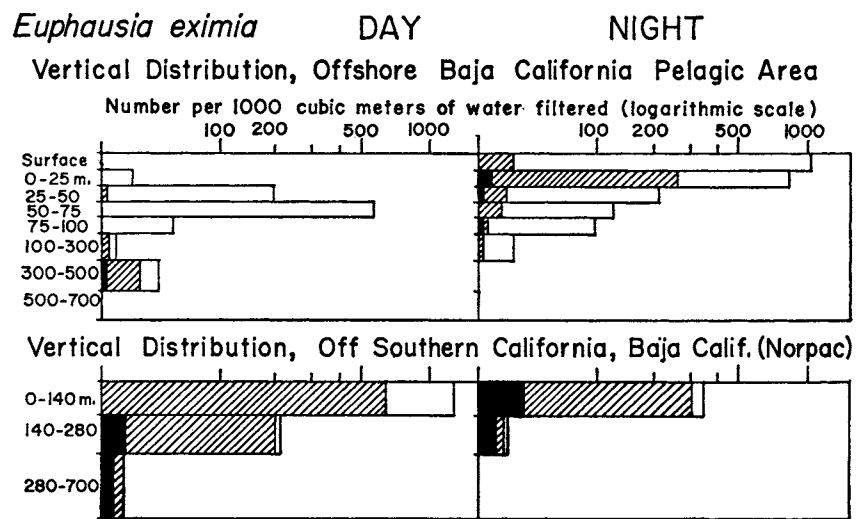


Fig. 46. Vertical distribution of *Euphausia eximia*.

C. isotherms at 100 meters. Temperatures were high (15°–20° C. at 100 meters) in a region off southern Mexico from which *E. eximia* was apparently excluded during the “Shellback” expedition and during sampling by the *Albatross* in October, 1904.

E. eximia and *E. gibboides* (fig. 32) are similar in size, 25–30 mm., being larger than the other temperate-tropical *Euphausia* species. Although not closely related, these species have similar vertical and horizontal ranges. *E. gibboides* is able to live in the cool superficial layers of the North Pacific Drift, and ranges westward to Japan in water that is 15°–20° C. at the surface and 10°–15° C. at 100 meters. This is the same range of temperature at a depth of 100 meters as that associated with the eastern equatorial distributions of both species. However, *E. eximia* is rarely found where surface waters are cooler than 18°–19° C., and does not range northward into the North Pacific Drift.

Vertical distribution (fig. 46).—Adults of *E. eximia* were present in the 140–280-meter and 280–700-meter layers during daylight, but were almost entirely above 140 meters at night. The “Pelagic Area” sampling showed furcilia to be most numerous at the surface at night, but present at all depths above 300 meters (as are the furcilia of *E. gibboides*). Furcilia of *E. eximia* were found during the day in all layers sampled above 500 meters, but not at the surface.

Euphausia distinguenda Hansen; *E. lamelligera* Hansen; *E. sibogae* Hansen

(Figs. 47, 48)

Horizontal distribution.—These related species have limited geographical ranges in the equatorial Pacific. Of the three, *E. distinguenda* of the eastern Pacific and *E. sibogae* of the East Indian Archipelago are most similar in morphology, but their ranges do not overlap. *E. lamelligera* lives in the eastern part of the region occupied by *E. distinguenda*.

The distribution of *E. distinguenda* is similar to that of *E. eximia*, but differs in three respects:

1. *E. distinguenda* is carried to mid-ocean in the region of the North Equatorial Current and the thermal anticline lying along the northern edge of the Equatorial Countercurrent. It was found at 158° W. in July–August, 1950 (POFI Cruise 5), and again in January–March, 1951 (POFI Cruise 8); “Equapac” expedition found it at 175° W. in August–September, 1956.
2. *E. eximia* was not found in the Equatorial Countercurrent, 3°–9° N.; *E. distinguenda* was scarce in the Countercurrent west of 118° W., but was found at all stations east of that meridian.
3. *E. distinguenda* has been infrequently caught north of 25° N. in the California Current, and south of 20° S. in the Peru Current. In contrast, *E. eximia* has centers of abundance off Baja California, 20°–30° N., and off southern Peru, 10°–25° S.

Whereas *E. eximia* inhabits cool upstream waters of the eastern boundary current systems, *E. distinguenda* is concentrated in the equatorial part of the eastern Pacific basin. The 17°–19° C. isotherms at 100 meters are more closely associated with the limits of range of *E. distinguenda* than with those of *E. eximia*.

Like *E. tenera* and *E. eximia*, *E. distinguenda* occurs in the Gulf of California

and was lacking at coastal stations occupied off Ecuador in June, 1952 (“Shellback” expedition).

E. lamelligera and *E. sibogae* are not known from the Atlantic or Indian oceans. *E. distinguenda* has been reported from the Indian Ocean; according to Tattersall, it was the most numerous euphausiid sampled in the Arabian Sea by the John Murray Expedition. It was not found by Illig (1930) in the southern and eastern parts

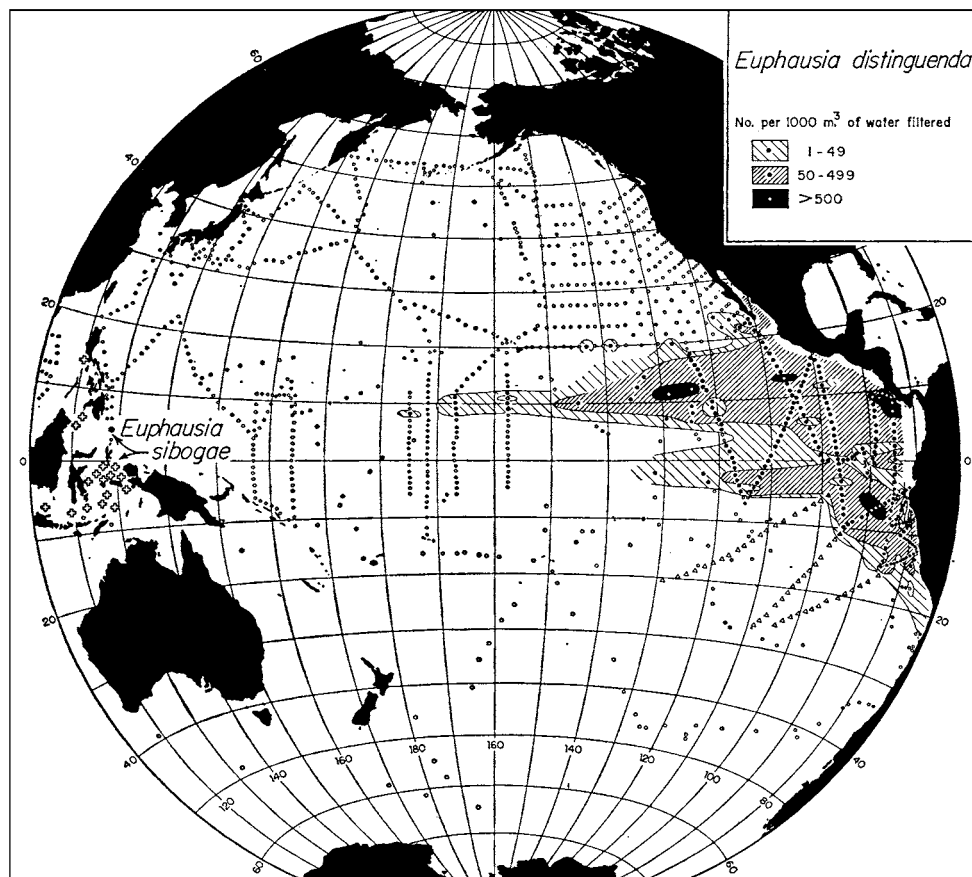


Fig. 47. Geographical distributions of *Euphausia sibogae* (crosses are “Siboga” exped. records and blackened circle is single “Troll” exped. record) and *Euphausia distinguenda*.

of the Indian Ocean.

E. lamelligera is more limited to coastal waters than is *E. distinguenda*. Like *E. distinguenda*, it has centers of abundance in the Gulf of California, a region off Costa Rica having a shallow thermocline, and the northern part of the Peru Current system. Like *E. eximia*, it is scarce in the Equatorial Countercurrent (“Shellback” and “Eastropic” expeditions).

E. lamelligera occupies regions that differ greatly from each other with respect to surface temperature: Peruvian waters, 18°–22° C., and Central American waters, 26°–28° C. It was numerous off Peru in January, 1958 (“Downwind” expedition),

where abnormally warm water, "El Niño," was present; it was scarce in the same coastal waters in June, 1952 ("Shellback" expedition).

E. sibogae (fig. 47) has been found only in the East Indian Archipelago and near the western coast of the

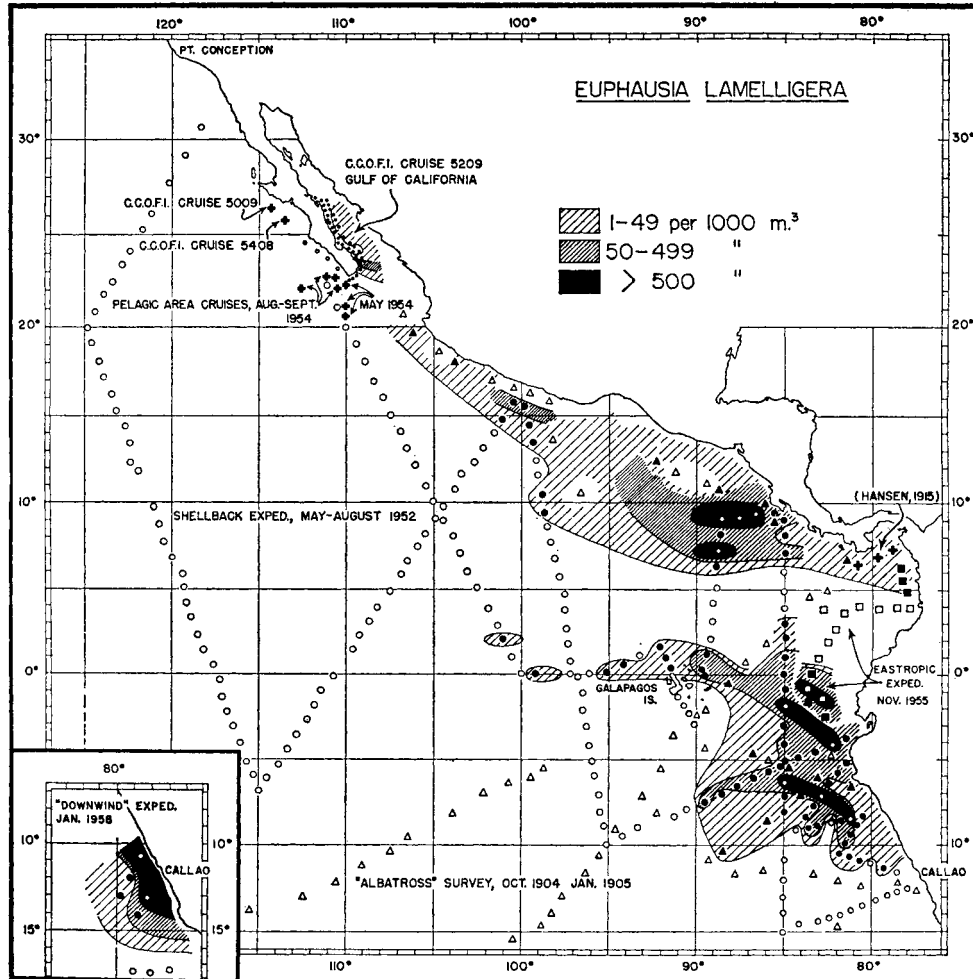


Fig. 48. Geographical distribution of *Euphausia lamelligera*.

Philippines (Hansen, 1910, 1916). It was not found in the South China Sea by the "Naga" expedition. The "Troll" cruise caught six adults in a 0–300 meter night haul at 3° N., 128.5° E.

Vertical distribution.—Nine of the sixteen *Sibogae* records for *E. sibogae* and one of the two *Albatross* records from the Philippines were based on surface collections. Nine of the "Norpac" records for *E. distinguenda* were from stations where two layers were sampled by opening-closing nets. Immature individuals were found at 0–140 meters in three of the four day samples collected within the range of the species, and at 140–280 meters in two of the four daytime samples. Adults were present in a single day haul, sampling 140–280 meters.

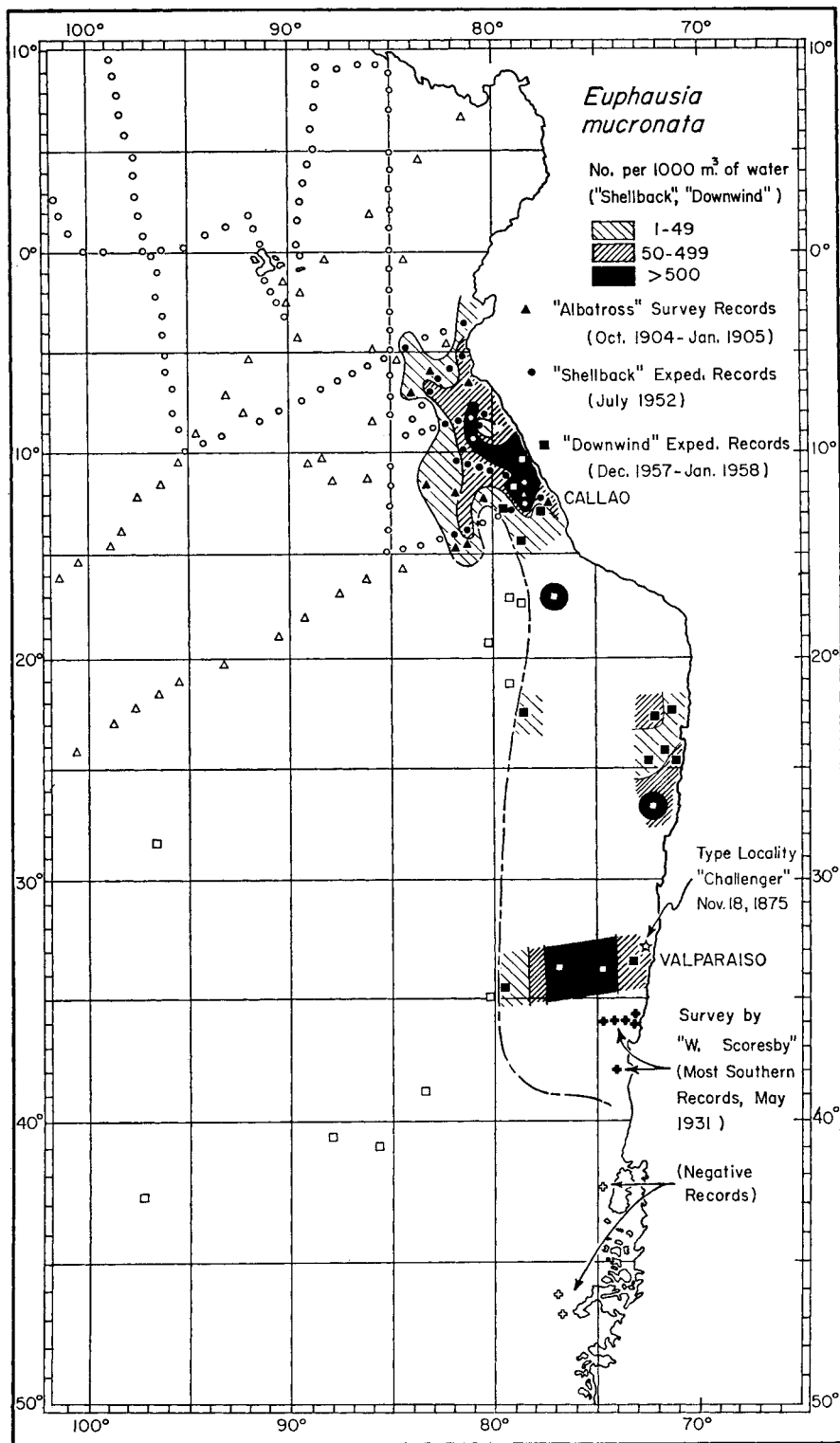


Fig. 49. Geographical distributions of *Euphausia mucronata*.

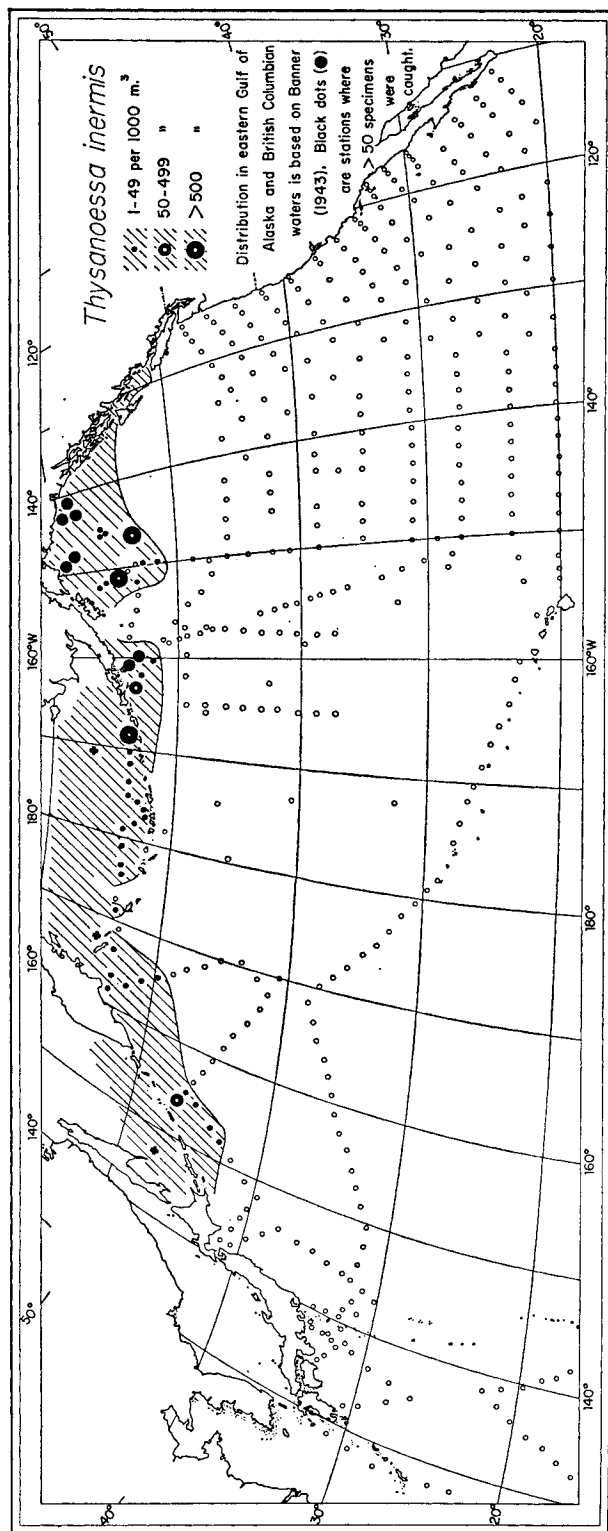


Fig. 50. Geographical distribution of *Thysanoessa inermis*.

Six night collections, from 0–140 meters, contained adults and larvae of *E. distinguenda*. This species was not found deeper than 140 meters at night.

E. lamelligera was taken at only two “Norpac” stations, both occupied during the day. It occurred at 0–140 meters at both localities, and was lacking in both samples taken at 140–280 meters. Most of the *Albatross* records (Hansen, 1912) were from surface tows made at night. Few adults were caught in the daytime, suggesting that they then live deeper than 300 meters.

Euphausia mucronata G. O. Sars

(Fig. 49)

Horizontal distribution.—*Euphausia mucronata* occurs in the Peru Current. The most northerly locality is at the mouth of the Gulf of Guayaquil, 3.5° S. (“Shellback” expedition), and the most southerly 37.5° S., near the Chilean coast (survey of the *W. Scoresby*, May, 1931).

This euphausiid has not been found in the subantarctic region, but was numerous at scattered “Downwind” and “Shellback” expedition stations from 34° S. to the upwelling center off Peru, 9°–12° S., discussed by Gunther (1936). It is of interest to note that *E. mucronata* was heavily concentrated off Peru during all of the three cruises to the region (“Albatross,” “Shellback,” and “Downwind”), plotted in figure 49.

The environment of this species does not extend westward toward the Galápagos Islands—in contrast with the range of the habitats of *Nyctiphanes simplex* and *Euphausia lamelligera*.

Vertical distribution.—Adults were caught at the surface by the *Challenger* near Valparaiso. Three of the *Albatross* records are from night hauls, made at the surface. Adults were caught by the “Shellback” expedition in seven day hauls and four night hauls, all 0–300 meters. It is presumed that *E. mucronata* performs a diurnal vertical migration within the 0–300 meter layer, coming to the surface at night in the cooler parts of its range.

THE GENUS THYSANOESSA Brandt

Thysanoessa inermis (Krøyer) Hansen

(Fig. 50)

Horizontal distribution.—*Thysanoessa inermis* is an arctic-boreal species found north of 50° N. in the Pacific (cf. distribution of the “Spined Form” of *T. longipes*). It was caught in numbers exceeding 50 per 1,000 cubic meters of water at only five stations during the “Transpacific” and “Northern Holiday” expeditions, but Banner records this species as the main item of diet of finback, humpback, and blue whales caught in the Bering Sea. *T. spinifera* and *T. longipes* were other euphausiids found in whale stomachs from the Bering Sea.

In discussing the distribution of two types of *T. inermis*, Nemoto (1959) pointed out that a form having spines on the fifth and sixth abdominal segments was widely distributed in the Bering Sea and the Oyashio. The second form, which has a spine only on the sixth segment, occurs in the Atlantic; in the Pacific it appears to be limited to the Okhotsk Sea and the Sea of Japan.

Nemoto found *T. inermis* in the stomachs of whales caught along the Aleutian chain. This species occurred northward to 63° N. in the Bering Sea, southward to the north coast of Hokkaido, and to 41° N. in the Japan Sea.

T. inermis is apparently lacking in the North Pacific Drift and the eastern part of the Gulf of Alaska influenced by it. Off the coast of Canada, the distribution extends southward only to about 52° N.

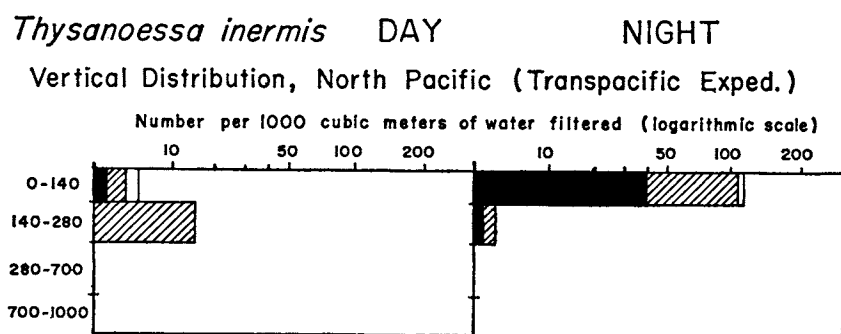


Fig. 51. Vertical distribution of *Thysanoessa inermis*.

The southern limit of the range corresponds to the positions of the 14° C. August surface isotherm and the 4° C. February surface isotherm. Most of the Scripps collections from this northern region were made during August and September.

T. inermis has been found in the Chukchi Sea (Johnson, 1956) and in the Beaufort Sea (Schmitt, 1919), but it is not known whether the Atlantic and Pacific populations are now in communication with each other through the Arctic Ocean.

Einarsson (1945) shows that the Atlantic distribution extends from the English Channel, 48° N., to at least 80° N. in the eastern part of the ocean. *T. inermis* has been found in the western Atlantic, from the Gulf of Maine, 39° N. (Bigelow, 1926), to the Labrador Sea, 72° N. Einarsson concluded that spawning was restricted to coastal regions north of 57° N., including also the Bay of Fundy, 43°–45° N., on the American coast.

Immature and larval specimens caught during the Scripps cruises were nearly all from the Bering Sea.

Vertical distribution (fig. 51).—A majority of the individuals in all size groups were found above 140 meters at night. Aggregate daytime numbers were relatively smaller, but the density of immature specimens was greater at 140–280 meters during the day than at night.

Thysanoessa raschii (M. Sars) Hansen

(Fig. 52)

Horizontal distribution.—The latitudinal range of *Thysanoessa raschii* is nearly the same as that of *T. inermis*. However, *T. raschii* is almost entirely restricted to neritic waters, north of 45° N. The Scripps oceanic collections contain five records from the region of the Oyashio where coastal populations were dispersed seaward.

Banner listed localities from near the Columbia River of Oregon, the inland waterway off British Columbia and Alaska, Kodiak Island, and the Pribilof Islands in the eastern Bering Sea. Nemoto recorded *T. raschii* from whales caught on the

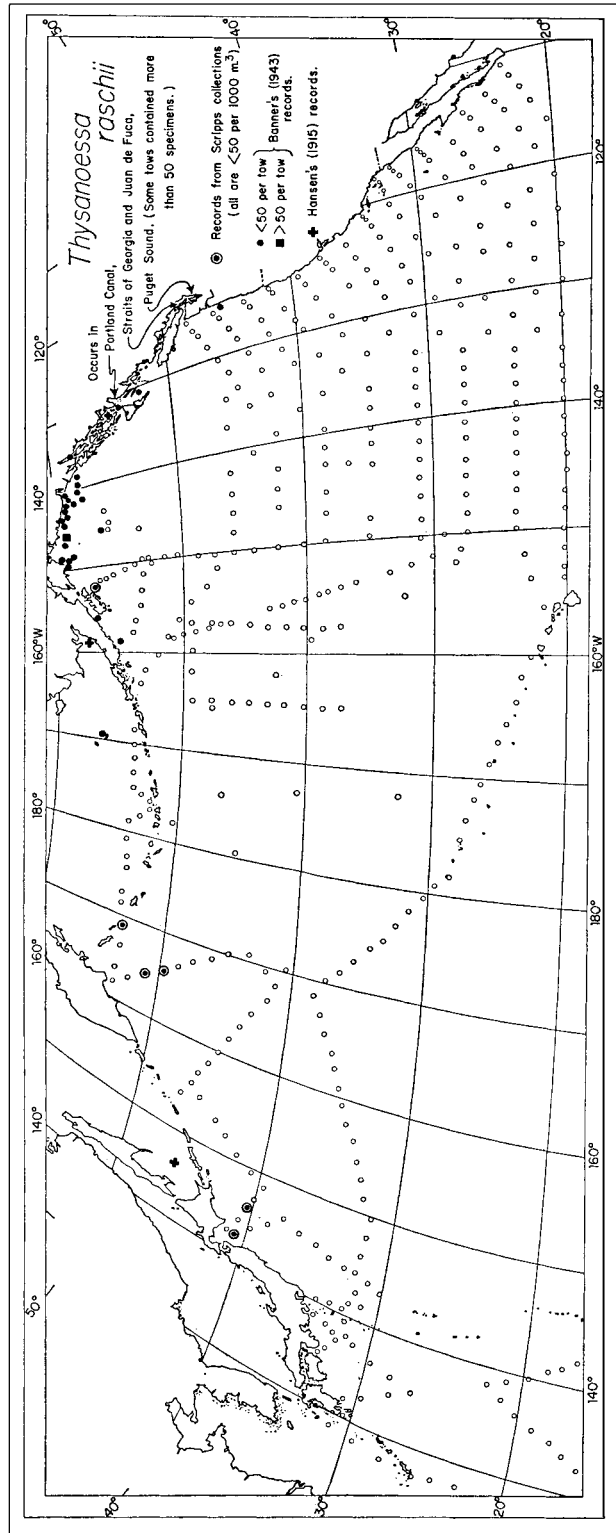


Fig. 52. Geographical distribution of *Thysanoessa raschii*.

north coast of Hokkaido, the Kurile Island chain, and the broad eastern shelf of the Bering Sea.

This species was found in the Sea of Okhotsk (Hansen, 1915), the eastern slope of the Kuriles (Ponomareva, 1955), and the Chukchi and Beaufort seas (Johnson, 1956). As with *T. inermis*, it is not known whether the distribution of *T. raschii* is now continuous between the Atlantic and Pacific oceans through the Arctic Ocean.

According to Einarsson, this euphausiid has more northern affinities in the Atlantic than *T. inermis*. It was found only in the northern waters of the British Isles, whereas *T. inermis* occurred in the English Channel. The ranges of both species extend northward to at least 78° N. Bigelow determined that *T. raschii* was an immigrant to the Gulf of Maine and *T. inermis* was a regular inhabitant of the shelf region.

Vertical distribution.—Each of the five localities from the “Transpacific” expedition is based upon fewer than five specimens. This species was caught twice at night at 0–114 meters, and once at 0–1,000 meters. It was caught twice at 140–280 meters: once at dawn and once at dusk.

Ponomareva found *T. raschii* at 0–200 meters along the eastern shelf of the Kurile Island chain. Einarsson found the greatest number of this species within the 200-meter bathymetric contour in the North Atlantic.

Thysanoessa spinifera Holmes

(Fig. 53)

Horizontal distribution.—*Thysanoessa spinifera*, like *T. raschii*, inhabits a neritic environment. *T. raschii* was found together with *T. spinifera* in near-shore waters of the Gulf of Alaska. Unlike *T. raschii*, *T. spinifera* was caught in the oceanic Gulf of Alaska, though in small numbers.

This species has not been found in the coastal region of the western Pacific or in the Arctic Ocean. Its appearance in whale stomachs (Banner, 1949) suggests that it may be numerous in Bristol Bay and in shallow waters of the southeastern part of the Bering Sea.

The range extends far to the south, along the coasts of California and Baja California, but apparently was not continuous from north to south during the “Norpac” cruise. However, the species was caught along the coasts of Oregon and California by CalCOFI cruises to those waters in 1949.

Regions of high density in the southern part of the distributional range are associated with centers of upwelling at (1) the Channel Islands, south of Point Conception, (2) Guadalupe Island, and (3) the coast immediately south of Punta Eugenia, Baja California.

King salmon collected in the vicinity of San Francisco and the Farallon Islands during March–July, 1955, were found to have fed almost exclusively on *T. spinifera* (Merkel, 1957). This euphausiid has been observed to form extensive nearshore surface shoals along the coast from Tomales Bay, north of San Francisco, to the Channel Islands. Shoaling has been most conspicuous from July to September. Swarms of spent females were washed up on the beach at La Jolla, California, on June 9, 1948.

Vertical distribution (fig. 54).—*T. spinifera* appeared to be restricted almost

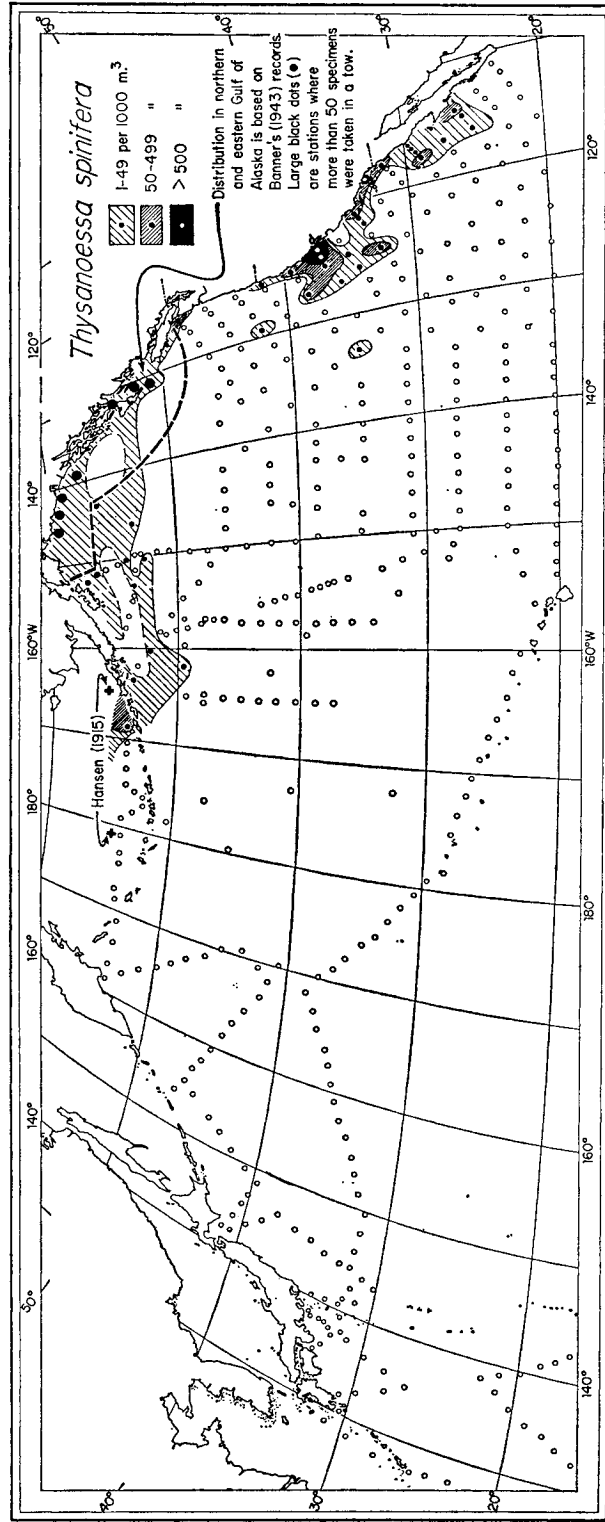


Fig. 53. Geographical distribution of *Thysanoessa spinifera*.

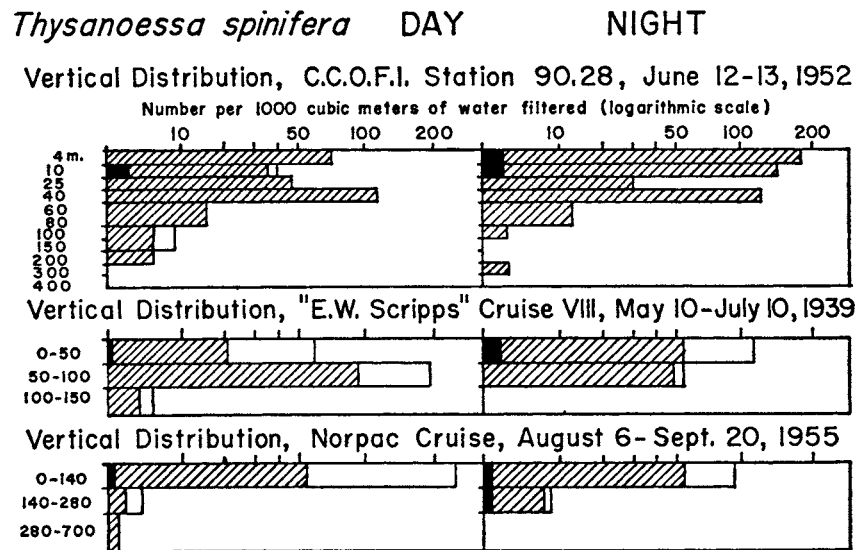


Fig. 54. Vertical distribution of *Thysanoessa spinifera*.

entirely to depths of less than 100 meters. There was no evidence for diurnal vertical migration. At a near-shore station occupied off San Pedro, June 12-13, 1952, the great majority of a population (made up largely of immature individuals, was above 50 meters during both day and night.

Thysanoessa longipes Brandt

(Fig. 55)

Two forms of *Thysanoessa longipes* were distinguished by Banner (1949) on the basis of material collected in the northeastern Pacific. Brandt (1851) and Hansen (1915) based the species on a large form, 22-30 mm. long. This bears conspicuous dorsal spines on the third, fourth, and fifth abdominal segments and is called the "Spined Form." Banner noted that a smaller form, 12-17 mm. long, bore middorsal keels, rather than spines, on the third to fifth abdominal segments. This is called the "Unspined Form." No differences between the male copulatory organs of the two were noted.

Horizontal distribution.—*T. longipes* is limited to the North Pacific and the American sector of the Arctic. Johnson (1956) reported it from the Chukchi Sea. Adults of the two forms were separated from each other near 50° N. in the eastern Pacific and near 45° N. in the western Pacific. The large "Spined Form" occurred north of the east-west boundary. The southern limit of distribution of "Unspined" *T. longipes* was in the North Pacific Drift, 41°-42° N., across most of the ocean. It is frequently carried south of the 40° N. parallel by the California Current. Young and larval individuals of the two forms cannot be separated at the present time. It is not yet known whether the forms are subspecies, geographical races, or separate species.

East of Japan where the Oyashio submerges beneath the Kuroshio, *T. longipes* "Unspined Form" was found at scattered stations south of 40° N. The most southerly

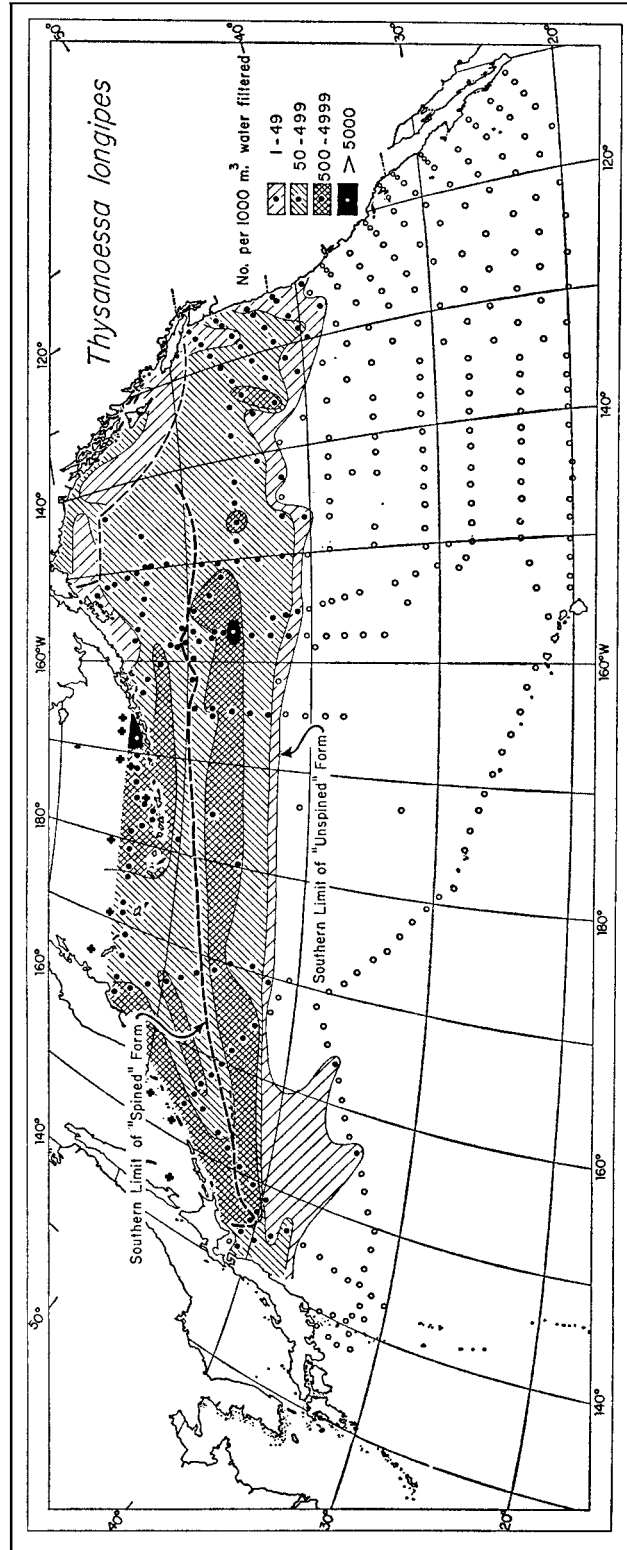


Fig. 55. Geographical distribution of *Thysanoessa longipes*, "Spined" and "Unspined" Forms.

record, 34° 07' N., 156° 11' E., is from a night haul at 240–700 meters, suggesting submergence at the southern margin of the range. The record from 36° 35' N., 163° 46' E. is from a day haul at 0–140 meters.

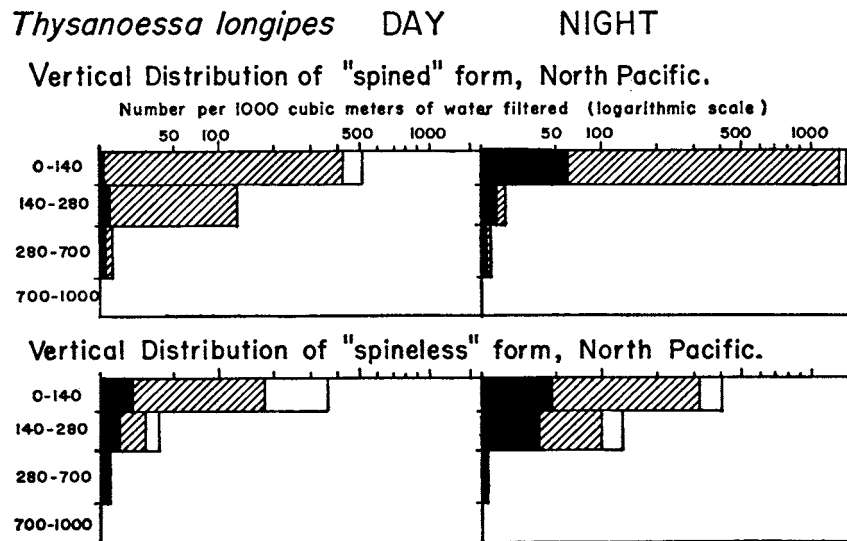


Fig. 56. Vertical distribution of *Thysanoessa longipes*.

Vertical distribution (fig. 56).—*T. longipes* belongs to the upper layers. The vertical distribution of the northern "Spined Form" was nearly the same as that of the "Unspined Form." There appeared to be a movement of immature individuals and adults of the "Spined Form" from the 140–280-meter layer into the 0–140-meter layer at night. There was no evidence for diurnal vertical migration of the smaller, more southern form.

Thysanoessa gregaria G. O. Sars

(Fig. 57)

Horizontal distribution.—*Thysanoessa longipes* "Spined Form," *T. longipes* "Unspined Form," *T. gregaria*, and *T. parva* are a group of closely related euphausiids which intergrade in body size and in depth of habitat from the large northern *T. longipes*, living in the upper layers, to the small, deep-living *T. parva* in the midlatitudes. *Thysanoessa* appears to be more stenothermal than other euphausiid genera.

T. gregaria occupies an ecological position intermediate between those of *T. longipes* and *T. parva* in the North Pacific. It inhabits a zone of oceanographic transition, the axis of which is near 40°–42° N. in the North Pacific Drift, between Subarctic and Central waters. *T. gregaria* is a characteristic species of the region of the California Current and ranges southward to 22°–25° N., off Baja California.

Samples collected by the "Troll" cruise showed that this species is present in the region of a large anticyclonic eddy, located at the eastern edge of the Kuroshio system off southeastern Japan. *T. gregaria* was not found in the warmest parts of the Kuroshio and the Kuroshio Extension.

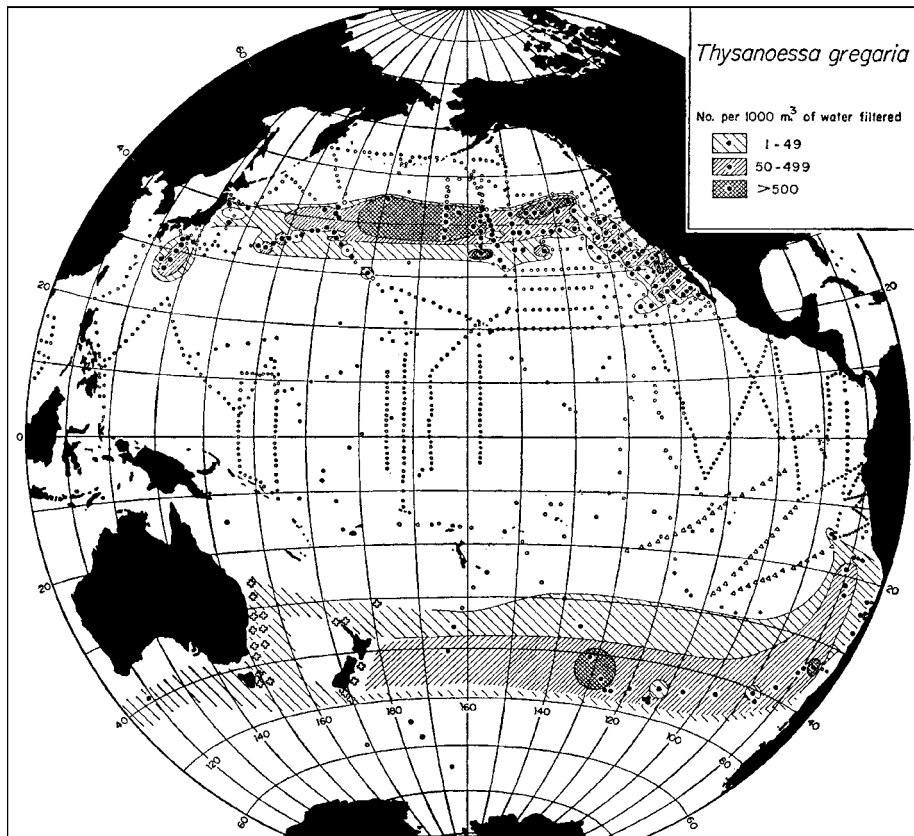


Fig. 57. Geographical distribution of *Thysanoessa gregaria*.

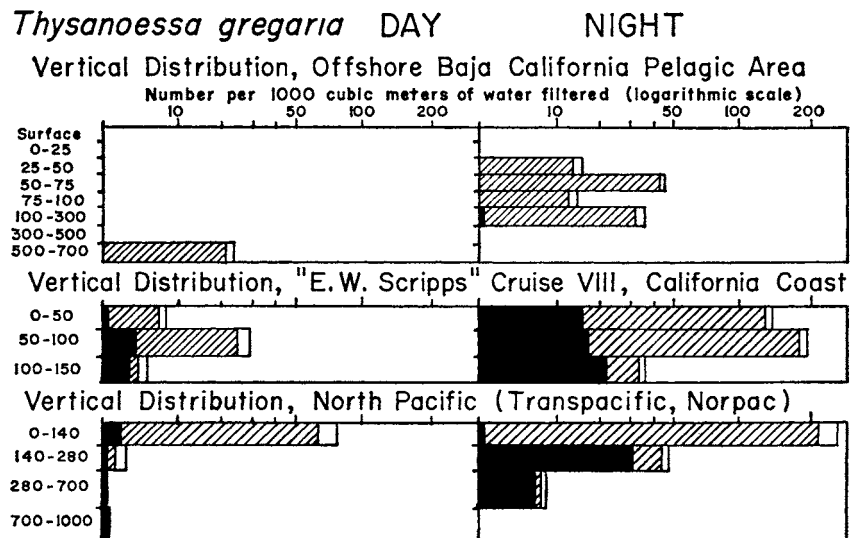


Fig. 58. Vertical distribution of *Thysanoessa gregaria*.

T. longipes is confined to the North Pacific. However, the temperate species *T. gregaria* and *T. parva* are biantitropical and occur also in the Atlantic. *T. gregaria* was present at the most southerly "Shellback" station, 14° 59' S., 85° 03' W., and occupied an east—west belt, 35°–48° S., across the South Pacific.

Moore (1952) showed *T. gregaria* occurring to at least 50° N. west of Ireland, and as far south as 35° N. in the eastern North Atlantic. It was present in the Gulf of Maine during summer months (Bigelow, 1926), this being the northern limit of the range in the western Atlantic. Tattersall (1926) reported it from as far south as 27° 46' N., 78° 46' W., north of the Bahama Bank, in a region corresponding to the gyral east of the Kuroshio where *T. gregaria* was present in a southerly pocket.

Zimmer (1914) found *T. gregaria* from 29° S. to 32° S. in the southeastern Atlantic, 8° W.–12° E. Illig's (1930) two most northerly records from the Indian Ocean, 0° 46' N., 96° 23' E. and 26° 04' S., 93° 44' E., are widely separated, suggesting that this species also has a latitudinally disjunct range in the Indian Ocean.

Vertical distribution (fig. 58).—*T. gregaria* occurred between depths of 25 meters and 300 meters at night in the Baja California "Pelagic Area," located near the southern limit of the range of the species. During the day it was deeper than 500 meters. In a comparable part of the Atlantic, northwest of Bermuda, Leavitt found the maximum numbers of *T. gregaria* at 200 meters, but some individuals occurred as deep as 1,200 meters.

The 1939 "E. W. Scripps" cruise off California showed that *T. gregaria* was evenly distributed throughout the layers sampled, 0–50 meters, 50–100 meters, and 100–150 meters. The average depth distribution for the breadth of the North Pacific indicated that most immature individuals were at 0–140 meters at all times, and most adults were at 140–280 meters at night. Fewer adults were caught during the day than at night. Those caught during the day were evenly distributed through the layers sampled, 0–1,000 meters.

Thysanoessa parva Hansen

(Fig. 59)

Horizontal distribution.—There are nine records for this species from the North Pacific. All are from tows reaching to at least 700 meters. Five of the stations were situated along the southeastern margin of the Kuroshio in the region where this current bends eastward from the coast of southern Japan. Four records are from stations along the western margin of the California Current. Sampling carried out by the "Norpac" cruise indicated that the eastern and western areas of distribution were probably not connected. In each of the two, *T. parva* appears to utilize local eddies and deep countercurrents to maintain its geographical distribution. The pattern of surface flow provides no obvious explanation of the restricted areas of distribution. It is probable that both are regions of oceanographic convergence, where sinking of water takes place along the seaward margins of the Kuroshio and California Current systems, respectively.

T. parva was taken at three localities in the South Pacific by the "Monsoon" expedition:

40° 37' S., 164° 08' W., 0–300 m., one specimen

34° 01' S., 161° 49' W., 0–2,700 m., numerous specimens

25° 52' S., 155° 44' W., 0–2,250 m., several specimens

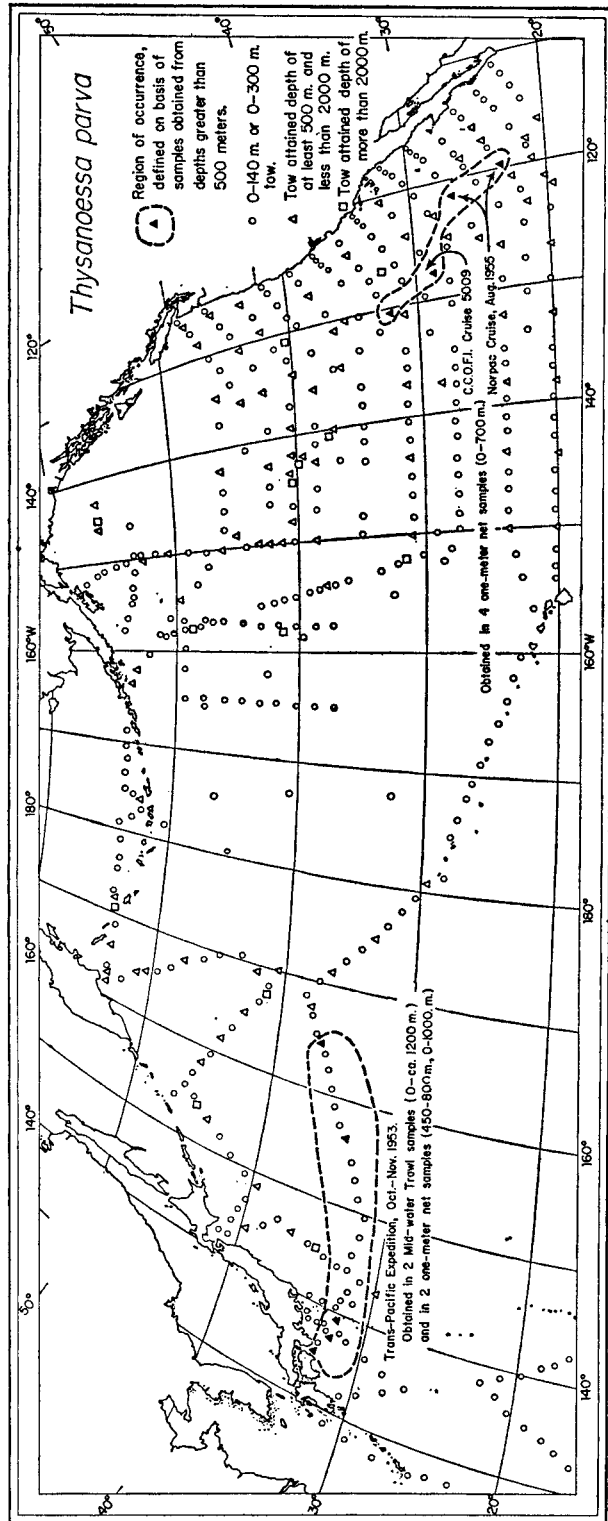


Fig. 59. Geographical distribution of *Thysanoessa parva*. The two known North Pacific regions of occurrence are enclosed in dashed lines.

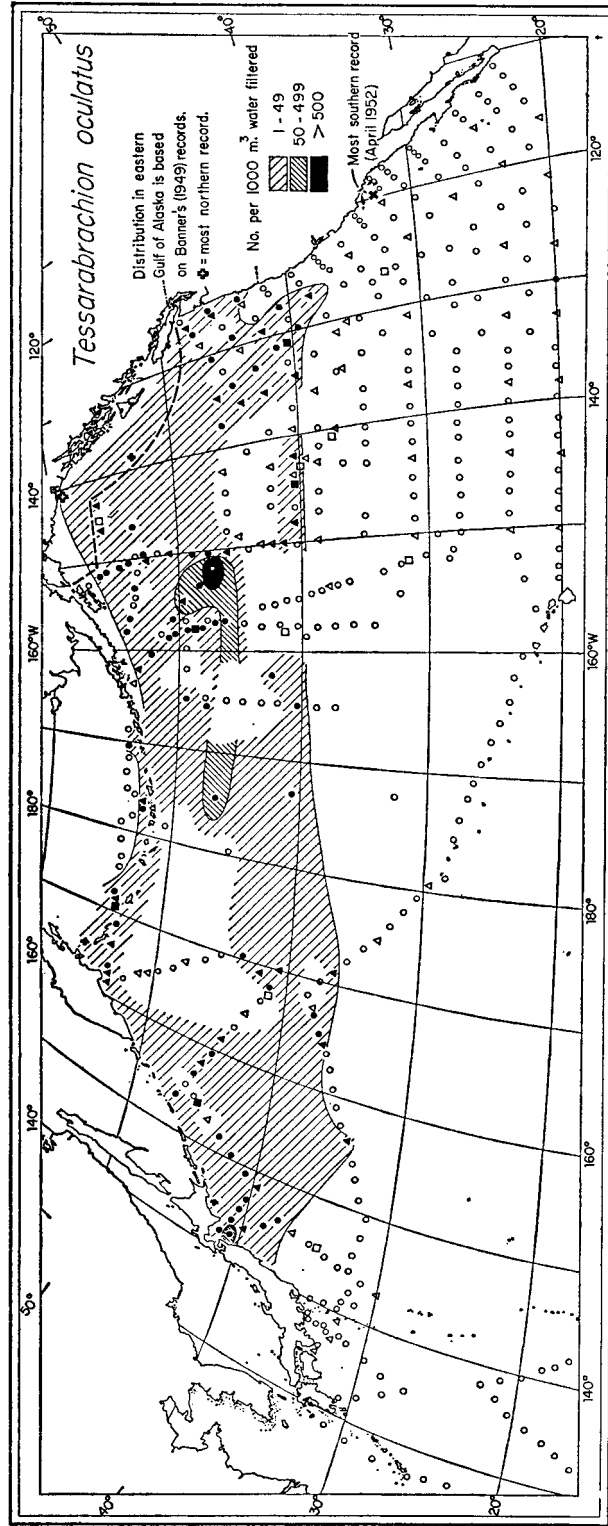


Fig. 60. Geographical distribution of *Tessarabrachion oculatus*.

This part of the southwestern Pacific, bounded on the south (*ca.* 40° S.) by the Subtropical Convergence, is geographically comparable to the North Pacific habitats of this species.

T. parva was first captured by the Prince of Monaco at six stations between the Azores and the Canary Islands in the northeastern Atlantic (Hansen, 1905). Illig (1930) reported it from farther north, 43° 32' N., 14° 27' W., and from five stations between Madeira, 32° N., and the Gulf of Guinea, 2° S. He records it from two stations in the South Atlantic, 26° 49' S., 5° 54' E. and 33° 23' S., 16° 19' E., and from one station in the Indian Ocean, 5° 23' N., 94° 48' E. Leavitt found this species in quantity in deep hauls made northwest of Bermuda.

Vertical distribution.—The Scripps records from the northeastern Pacific were from 0–700-meter hauls. *T. parva* was twice caught at 450–800 meters off Japan, and three times in open nets reaching to about 1,000 meters. In the North Atlantic, Leavitt found this species at all depths between 400 meters and 3,000 meters, with maximum numbers at 800 meters and 1,600 meters.

THE GENUS TESSARABRACHION Hansen

Tessarabrachion oculatus Hansen

(Fig. 60)

Horizontal distribution.—This monotypic genus is confined to the subarctic North Pacific. It has not been recorded from the Okhotsk Sea, and appears to be absent from the Bering Sea, except along the Aleutian Island chain. *T. oculatus* was not found in a broad oceanic area southeast of Kamchatka, 41°–53° N. This is the region in which the Aleutian Current arises and where water flowing southeastward converges with the North Pacific Drift.

Tessarabrachion oculatus

Vertical Distribution, North Pacific (Norpac, Transpacific, Northern Holiday)

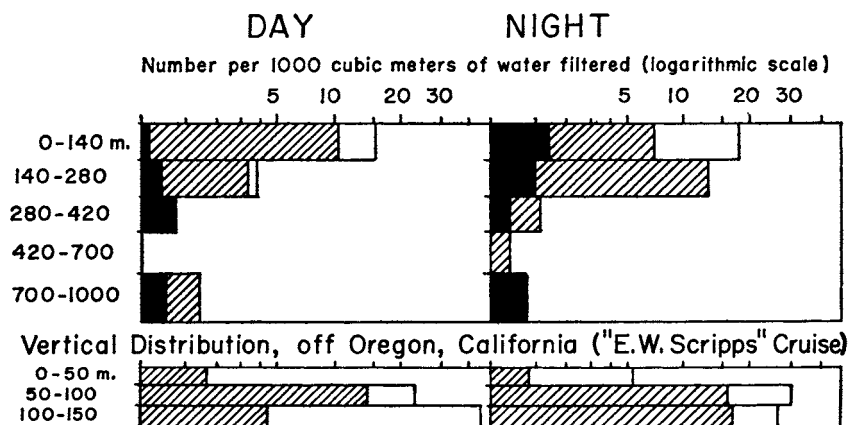


Fig. 61. Vertical distribution of *Tessarabrachion oculatus*.

This species ranged southward to 37° N. in the western Pacific, but it has rarely been caught south of 40° N. in the region of the California Current. Only once during the CalCOFI surveys has *T. oculatus* been found south of 37° N.: two immature specimens were caught at 32° 38' N., 119° 28.5' W., April 2, 1952, in a daytime haul sampling at 0–177 meters.

T. oculatus was found in numbers exceeding 50 per 1,000 cubic meters of water at only five Scripps stations, but the species appeared to be uniformly distributed in low density across the breadth of its distribution. This was the only northern euphausiid not found by Nemoto (1959) to be a food of whales in the North Pacific.

Vertical distribution (fig. 61).—The adult of *T. oculatus* was found at all depths sampled. However, it was not caught in the upper layers, 0–150 meters, near the southern limit of its range.

Nighttime movement of adults and larvae into the 0–140-meter layer was indicated. No vertical migration of immature individuals was shown.

THE GENUS NEMATOSCELIS G. O. Sars

Nematoscelis difficilis Hansen; *Nematoscelis megalops* Hansen

(Fig. 62)

Horizontal distribution.—*Nematoscelis difficilis* and *N. megalops* are a species pair, distinguishable by the morphology of the male copulatory organ. They occupy transoceanic belts at mid-latitudes in the North and South Pacific respectively.

Nematoscelis, comprising five species, is a subtropical-tropical genus. *Thysanoessa*, closely related to it, is arctic-boreal. *N. difficilis*, the most northerly species of *Nematoscelis*, and *N. megalops*, the most southerly species, occupy the same ranges of latitude (ca. 30°–45°) as the most warm-water *Thysanoessa* species, *T. gregaria* and *T. parva*. Thus, the ranges of the two genera overlap only along the east–west zones of oceanographic transition lying between Subarctic and Central waters in the Northern Hemisphere, including the California Current, and between Subantarctic and Central waters in the Southern Hemisphere, including the more southerly part of the Peru Current.

N. difficilis is found in the North Pacific Drift and the California Current. A population living in the Gulf of California is sometimes separated from that of the west coast of Baja California by a body of warm water lying at the mouth of the Gulf, 23° N.

Specimens were found by the “Transpacific” expedition at three localities off southern Japan and at four near 40° N., east of northern Japan.

The range in coastal waters of North America is more extensive than in the western Pacific. Banner found *N. difficilis* to 51° N. off British Columbia. It is rare in cold upwelled water near the coasts of Oregon, Washington, and northern California, but is characteristic of the main part of the California Current.

Nematoscelis megalops was found by the “Downwind” expedition from 33° S. to 48° S. in mid-ocean, and the “Monsoon” expedition caught it as far south as 54° 21' S., southeast of New Zealand. Materials from the coast of New Zealand, tentatively assigned by Bary (1956) to *N. megalops*, contained no adult males. Sheard (1953) did not remark whether *N. difficilis* reported by him from waters off southeastern Australia included the adult males essential for diagnosis.

N. megalops occurs widely in the North Atlantic, 35°–55° N. (Moore, 1952), and is common in the Mediterranean Sea in all but the southeastern part (Ruud, 1936).

Boden (1955) found *N. megalops* in the Benguela Current, 22°–29° S., west of South Africa, and Sheard reported it from 38° 33' S., 109° 22' E., off western Australia.

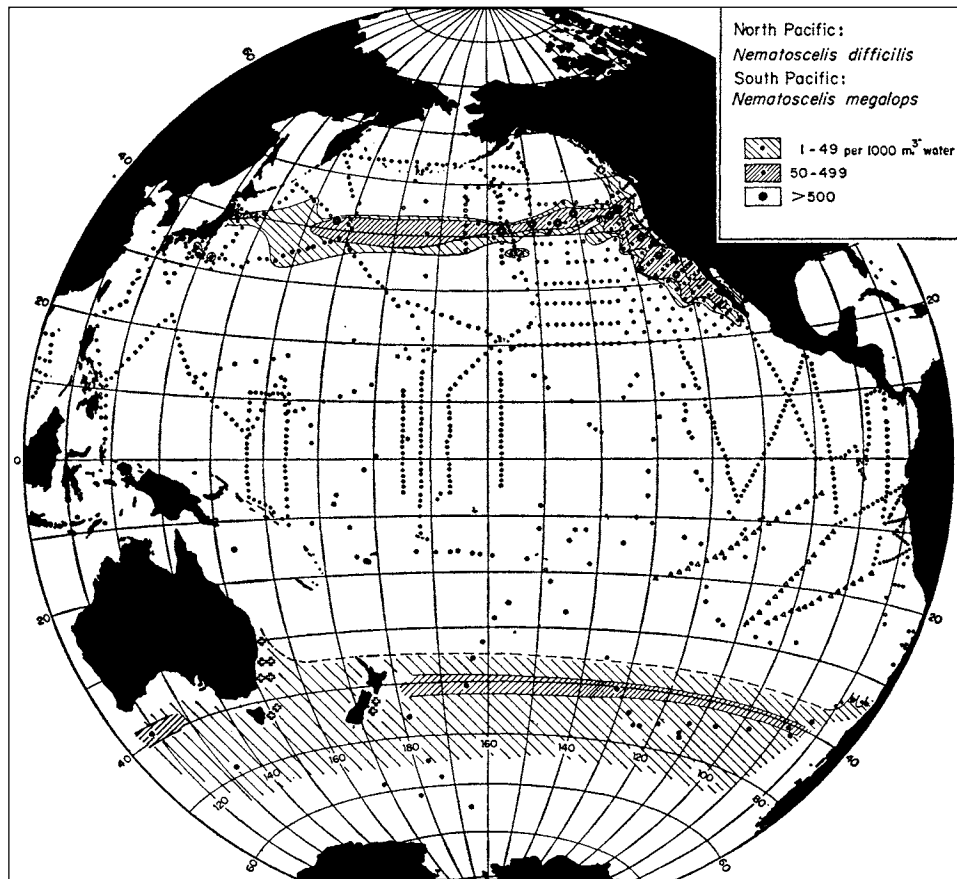


Fig. 62. Geographical distributions of *Nematoscelis difficilis* and *Nematoscelis megalops*.

There is no firm evidence to indicate that the ranges of *N. difficilis* and *N. megalops* merge. Unless Sheard's records from Australia are substantiated, *N. difficilis* is isolated in the North Pacific.

Vertical distribution (fig. 63, a–b).—*N. difficilis* is most common above 140 meters. There is no clear indication of diurnal vertical migration. At each depth sampled, more adults were caught at night than during the day.

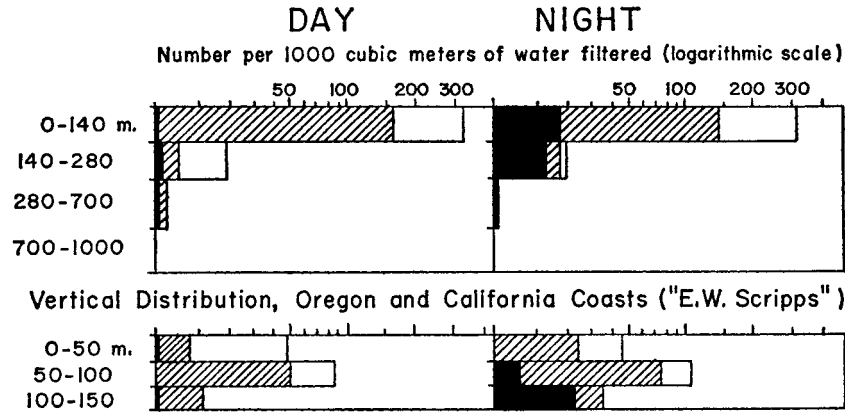
Sampling based on the "E. W. Scripps" Cruise VIII off California and Oregon showed that *N. difficilis* lives in each of the three strata sampled (0–50, 50–100, 100–150 m.), although adults were rarely found above 50 meters.

During the "Downwind" expedition, the adult of *N. megalops* was caught above

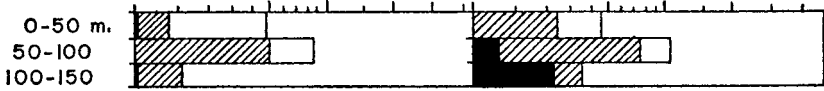
a depth of 300 meters only at night. The single daytime record for adults of this species was from a haul reaching to 600 meters. Juveniles and larvae were regularly found above 300 meters at all times.

Nematoscelis difficilis

Vertical Distribution, North Pacific (Norpac, Transpacific)



Vertical Distribution, Oregon and California Coasts ("E.W. Scripps")

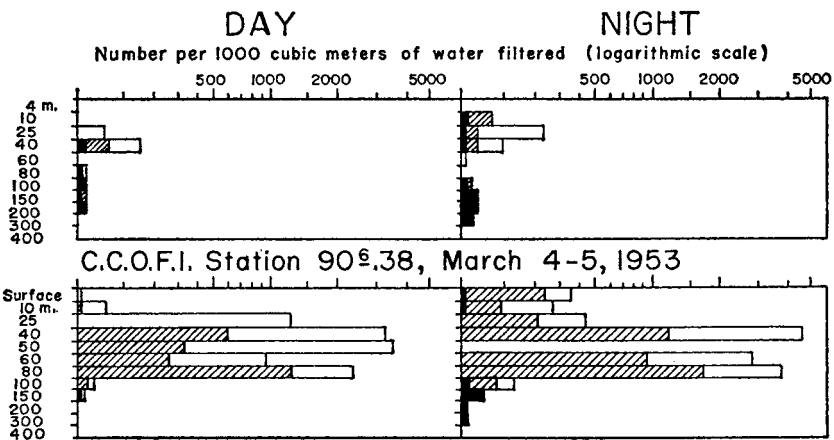


a.

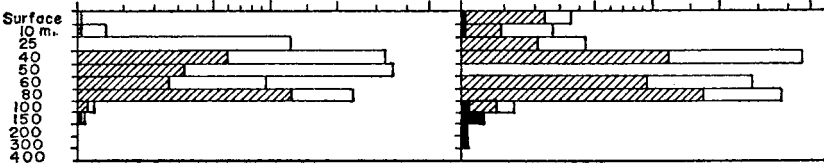
Nematoscelis difficilis

Vertical Distribution, Inshore Southern California

C.C.O.F.I. Station 90.28, June 12-13, 1952



C.C.O.F.I. Station 90^o.38, March 4-5, 1953



b.

Fig. 63. Vertical distributions of *Nematoscelis difficilis*. a. Oceanic North Pacific. b. Inshore southern California.

Nematoscelis tenella G. O. Sars

(Fig. 64)

Horizontal distribution.—*Nematoscelis tenella* was found south of 40° N. in the North Pacific, except in the cooler part of the California Current and its southward extension into the eastern equatorial basin. It occurred south of 10°–12° S., the northern edge of the Equatorial Countercurrent.

In the South Pacific, *N. tenella* was scarce in the region of the Peru Current. The most southerly record is 34° 01' S., 161° 49' W. in the western South Pacific.

Much of the distributional range is based on the occurrence of immature and larval specimens. As with *N. microps*, the depth inhabited by *N. tenella* has not been quantitatively sampled on a routine basis. Many negative records are found within the indicated limits of range.

N. tenella has been found in the Atlantic, from 59° 37' N., 8° 50' W., in the North Atlantic Current off Ireland, to 37° 31' S., 17° 02' E., near the Cape of Good Hope (Illig, 1930). It was reported from the Indian Ocean from 11° N. in the Gulf of Aden (Tattersall, 1939) to 29° 06' S., 89° 39' E. (Illig, 1930).

Vertical distribution (fig. 65).—This species was found at 25–500 meters off Baja California. Most furcilia occurred between 25 meters and 100 meters; maximum numbers were at 25–74 meters. Immature individuals were not caught above 25 meters during the day, but were most numerous at 0–25 meters at night.

Adults were found at 100–300 meters in samples collected during both day and night by the “Pelagic Area” Survey off Baja California. However, the vertical distribution based on “Transpacific” and “Norpac” expeditions indicated a nighttime increase in numbers above 280 meters.

Records for *N. tenella* from the “E. W. Scripps” Cruise VIII off California showed only that greater numbers of this species were caught at night than during the day in each of the three layers sampled—all above 150 meters.

Nematoscelis microps G. O. Sars

(Fig. 66)

Horizontal distribution.—*Nematoscelis microps* has been found from 40° N. to near 40° S. in the western Pacific. It was rarely caught in the region of the California Current, and lives only in the southern part of the eastern North Pacific central region, 20°–30° N.

N. microps appears to be present in the eastern equatorial basin only at stations situated near the equator, 110°–140° W. This is the belt of the eastward-flowing equatorial Cromwell Undercurrent.

This species is not known from the Peru Current or its extension into the South Equatorial Current, but occurs widely in the central South Pacific. The 13° C. isotherm at 200 meters lies along the approximate limit of distribution.

The range of *N. microps* in the Atlantic appears to be similar to that found in the Pacific. Illig's records for this rather difficult genus are probably unreliable. He reported it as far north as 59° 37' N., 8° 50' W. in the eastern Atlantic, but the most northerly record from other sources is 37° N. in Cadiz Bay (Ruud, 1936). Moore showed that *N. microps* occurs in the western Atlantic, from the equator to 40°–45° N. in the region of the Gulf Stream.

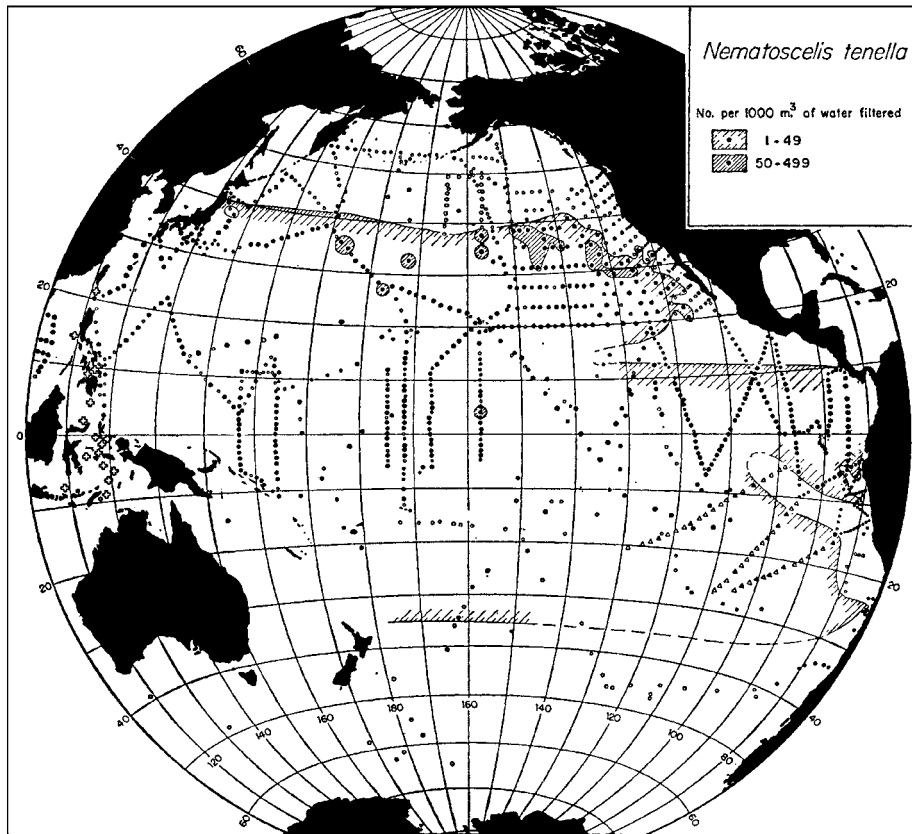


Fig. 64. Geographical distribution of *Nematoscelis tenella*.

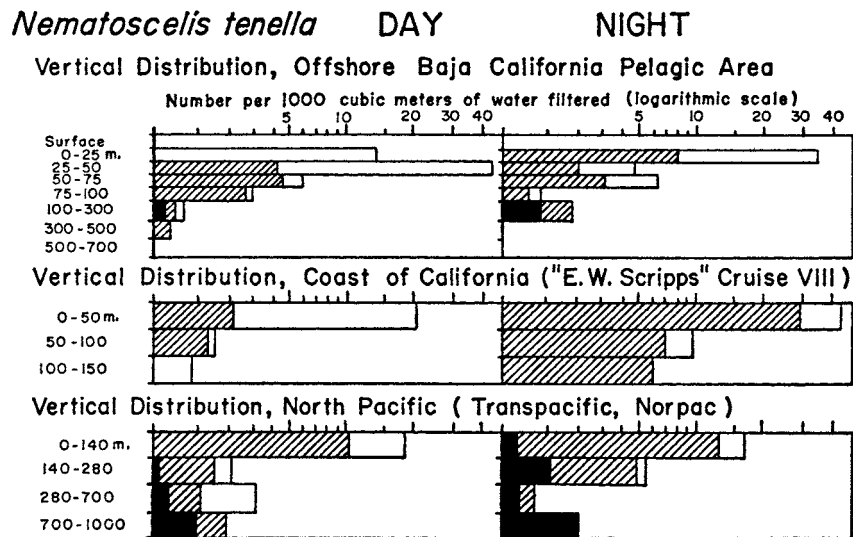


Fig. 65. Vertical distribution of *Nematoscelis tenella*.

The John Murray Expedition caught *N. microps* at a single station, 9° 40' N., 54° 33' E., in the Indian Ocean. Illig found it widely distributed there, from 13° S. to 36° N.

Variability in the length of the rostrum of this species was noted by Hansen (1912). The "Albatross" material from the eastern equatorial Pacific included female specimens that had short frontal plates without rostral processes, as well as females with the long acute rostra found also on the males from that region.

In contrast, the "Siboga" material from the Indo-Australian Archipelago included females having short frontal plates with long acute rostra. Males from these collections had short frontal plates with short, broad, triangular rostra. The "Naga" expedition specimens from the South China Sea agreed with the "Siboga" specimens.

Variability was noted in rostrum-length in the "Shellback" expedition specimens from the eastern Pacific, although the rostrum was acute in all adults.

Hansen (1916) described *Nematoscelis lobata* on the basis of collections made by the *Albatross* at the Philippines. Two specimens were caught at the Gulf of Davao, off southeastern Mindanao, and "an immense number" were taken off Matabat Point, western Luzon. This species was not in the "Siboga" material from the East Indian Archipelago, and was not found in the "Troll" collections made along the eastern coast of the Philippines, nor in "Naga" expedition collections from the South China Sea. *N. lobata*, therefore, appears to be limited to waters of the Philippines.

N. lobata, like *N. atlantica*, is closely related to *N. microps*, but differs in that the terminal process of the male copulatory organ is much shorter than either the proximal or spine-shaped processes. The median lobe is very large and its convex inner margin forms an acute distal angle with the broadly convex outer margin.

The median lobe is relatively narrow in both *N. atlantica* and *N. microps*. The body form of *N. lobata* is slender, as is that of *N. atlantica*. However, the relative proportions of the processes of the copulatory organ place *N. microps* in an intermediate position, from the standpoint of phylogeny, between *N. lobata* and *N. atlantica*.

Vertical distribution (fig. 67).—Furcilia of *N. microps* were found above 300 meters in the "Pelagic Area" off Baja California. Immature individuals were between 25 meters and 200 meters at night, but not above 100 meters during the day. Adults have been caught in only one daytime haul that reached to less than 1,000 meters. They were frequently caught at lesser depths during the night, suggesting that they perform an extensive vertical migration.

Nematoscelis atlantica Hansen

(Fig. 68)

Horizontal distribution.—*N. atlantica* occupies a Central Water Mass habitat in both hemispheres. It was found to live between the 13° and 38° parallels in both the North and the South Pacific.

This species has been reported from 39° 38' N., 71° 19' W. in the North Atlantic (Hansen, 1915), and from 35° 10' S., 2° 33' E. in the South Atlantic (Zimmer, 1914). The German South Polar Expedition records indicate that there is no discontinuity in the north-south distribution of this species in the Atlantic.

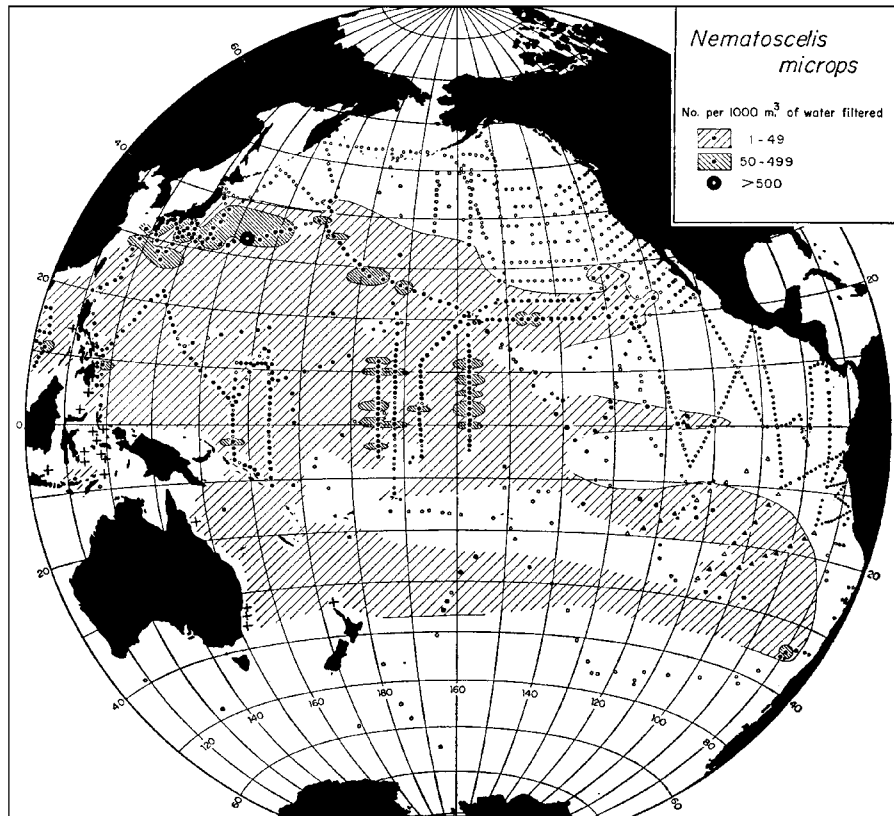


Fig. 66. Geographical distribution of *Nematoscelis microps*.

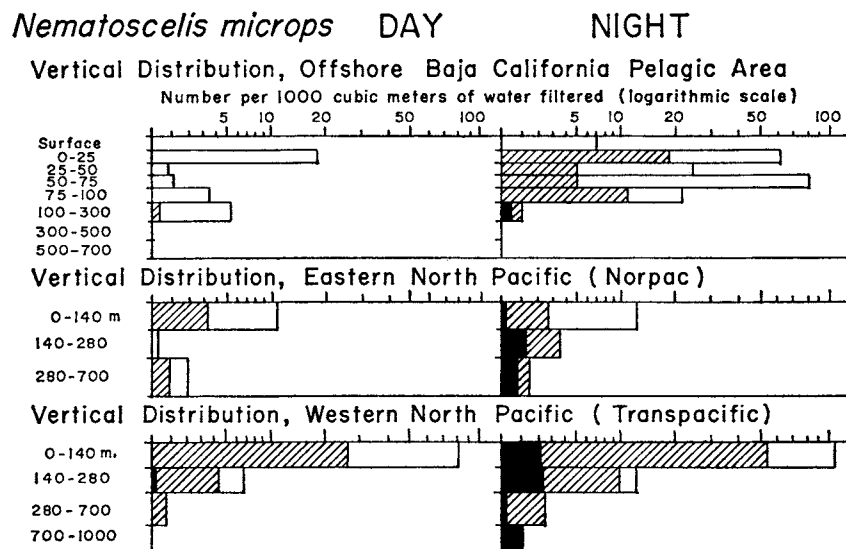


Fig. 67. Vertical distribution of *Nematoscelis microps*.

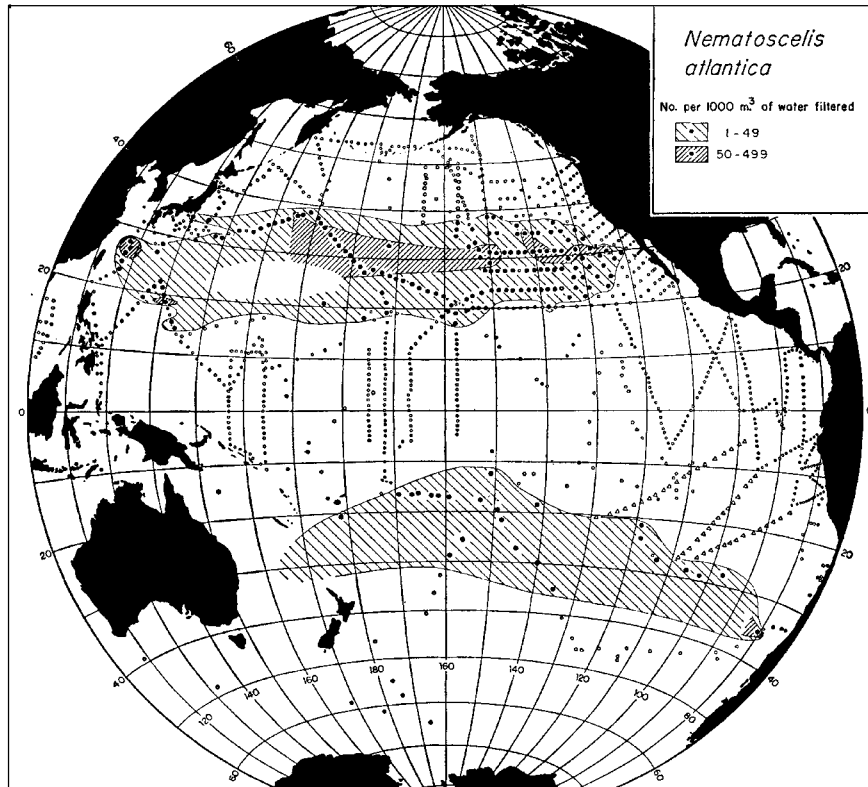


Fig. 68. Geographical distribution of *Nematoscelis atlantica*.

Nematoscelis atlantica

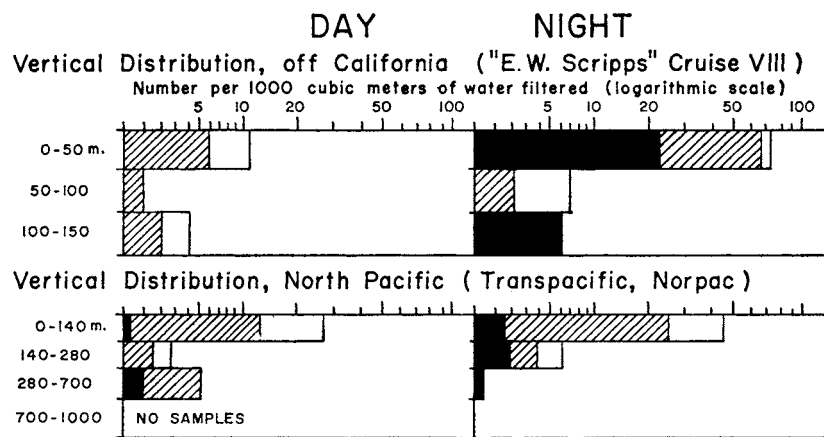


Fig. 69. Vertical distribution of *Nematoscelis atlantica*.

N. atlantica has not been reported from the Indian Ocean. It is the only euphausiid species known to occur in both the Atlantic and the Pacific Oceans that has not been found in the Indian Ocean.

Vertical distribution (fig. 69).—Furcilia and immature specimens were consistently caught above 140 meters, both off California and in mid-ocean. Adults, rarely found above 140 meters during the day, were frequent in this layer at night.

Nematoscelis gracilis Hansen

(Fig. 70)

Horizontal distribution.—*N. gracilis* occurs throughout the equatorial zone in the Pacific and is carried by the Kuroshio system to 40° N., east of Japan, according to samples collected by the “Transpacific” expedition. This is a characteristic species of the northwestern part of the Indian Ocean investigated by the John Murray Expedition, and was reported from 30° S. to 13° N. in the eastern part by Illig (1930).

N. gracilis is apparently not present in the Atlantic. Illig lists it as occurring there, at 2° 37' N., 3° 28' E., but its presence in the Atlantic cannot be based on this one record, in view of the several unsubstantiated finds listed in that “Valdivia” report.

Vertical distribution (fig. 71).—*N. gracilis* was found in quantity in the “Pelagic Area” off Baja California. Furcilia were present from the surface to 100 meters, with maximum numbers above 50 meters. Immature individuals occupied the same vertical range as larvae, whereas adults were found at a depth of 300–500 meters during the day and at 100–300 meters at night. The “Norpac” collections from the same area showed a similar vertical range for larvae (0–140 meters), and provided evidence for the vertical migration of adults from below 280 meters during the day into the 140–280-meter layer at night.

THE GENUS NEMATOBRACHION Calman

Nematobrachion flexipes (Ortmann) Calman

(Fig. 72)

Horizontal distribution.—The three species comprising the genus *Nematobrachion* have broad distributions but are rarely caught in large numbers.

N. flexipes is found south of 40° N. across most of the North Pacific, but Banner includes three records from coastal waters of Alaska and British Columbia (cf. other subtropical species sometimes found there: *Stylocheiron longicorne* and *Nematoscelis difficilis*). This species lives in all but the most coastal part of the California Current. It was not found off Mexico, 12°–20° N., by the “Shellback” expedition, but was consistently caught in the region of the Peru Current and its extension into the South Equatorial Current. Sheard found *N. flexipes* as far south as 37° S. off southeastern Australia, “Downwind” expedition found it at 30° S. in mid-ocean, and it was caught near 36° S. off Chile by the *William Scoresby*.

N. flexipes occurs throughout the tropical and subtropical Pacific. Two centers of abundance were noted: (1) the terminal part of the California Current off Baja California, 20°–25° N., (2) a region near the equator, off Peru and Ecuador, where the Peru Current merges with the South Equatorial Current. In both places

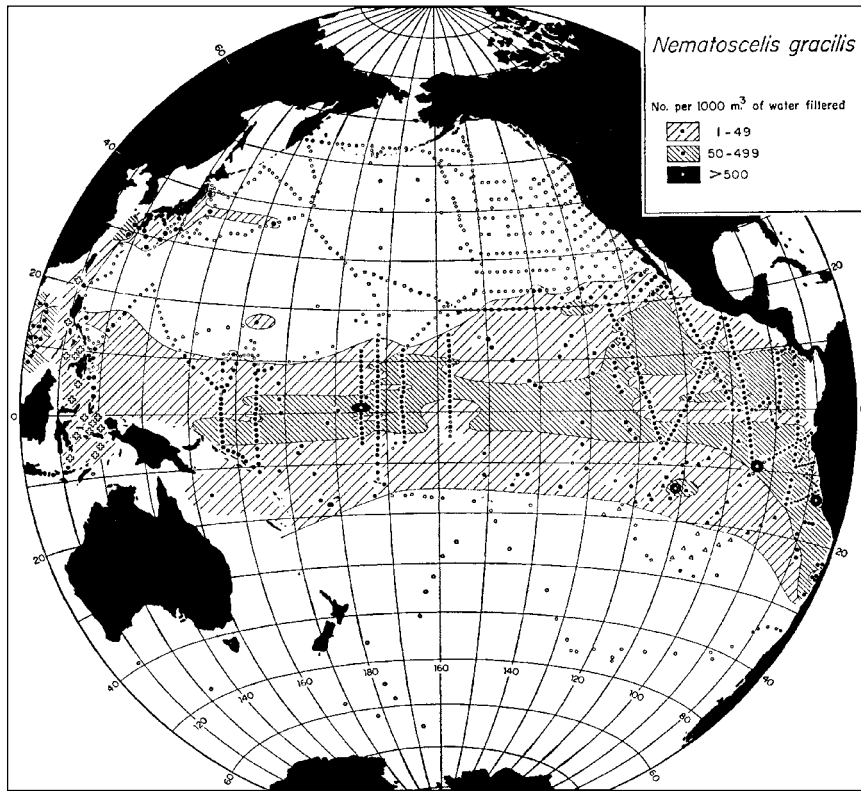


Fig. 70. Geographical distribution of *Nematoscelis gracilis*.

Nematoscelis gracilis

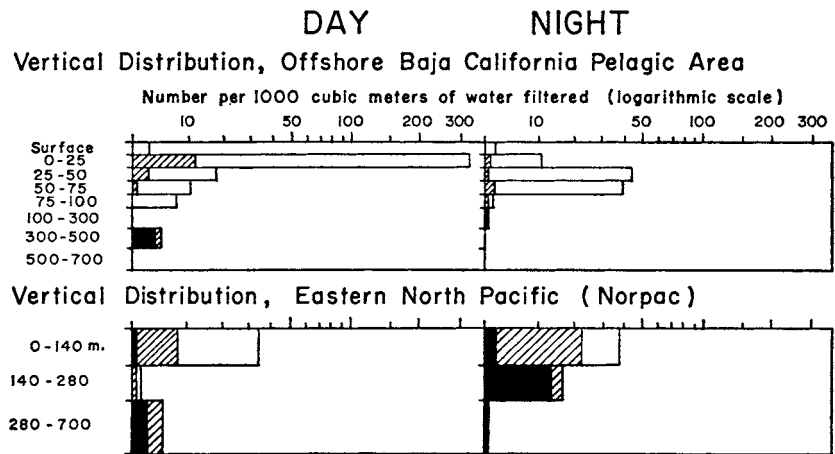


Fig. 71. Vertical distribution of *Nematoscelis gracilis*.

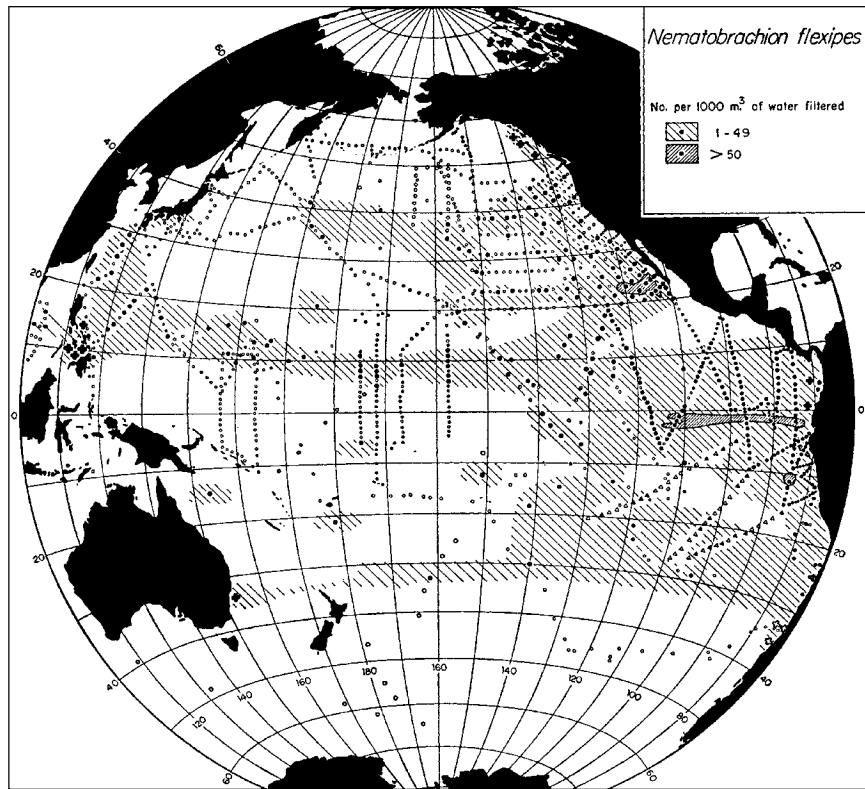


Fig. 72. Geographical distribution of *Nematobranchion flexipes*.

Nematobranchion flexipes

Vertical Distribution, Offshore Baja California Pelagic Area

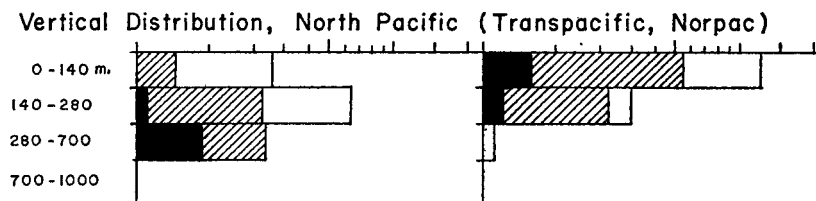
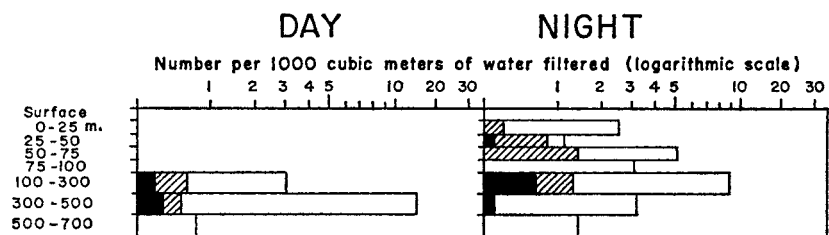


Fig. 73. Vertical distribution of *Nematobranchion flexipes*.

larvae make up most of the numbers found; these appear to be principal reproductive areas.

The distribution of *N. flexipes* extends across the ocean at the northern boundary of the Equatorial Counter-current, 7°–13° N. There, the shallow thermocline allows this cool-water species to live within the 300-meter layer routinely sampled by POFI, "Troll," and "Equapac" cruises. *N. flexipes* was infrequently caught in central waters of the western Pacific.

Vertical distribution (fig. 73).—*N. flexipes* was found below 100 meters during the daytime in the "Pelagic Area" off Baja California. Some immature individuals, larvae, and one adult were caught above 100 meters at night; the bulk of the population remained near 100–300 meters. The oceanwide North Pacific data show that larvae were found in two upper strata, 0–140 and 140–280 meters, sampled during both day and night. Most immature specimens were below 140 meters during the day and above 280 meters at night. Adults were mainly at 280–700 meters in the daytime and above 280 meters at night.

Nematobranchion sexspinosus Hansen

(Fig. 74)

Horizontal distribution.—The known Pacific range of this species lies in those

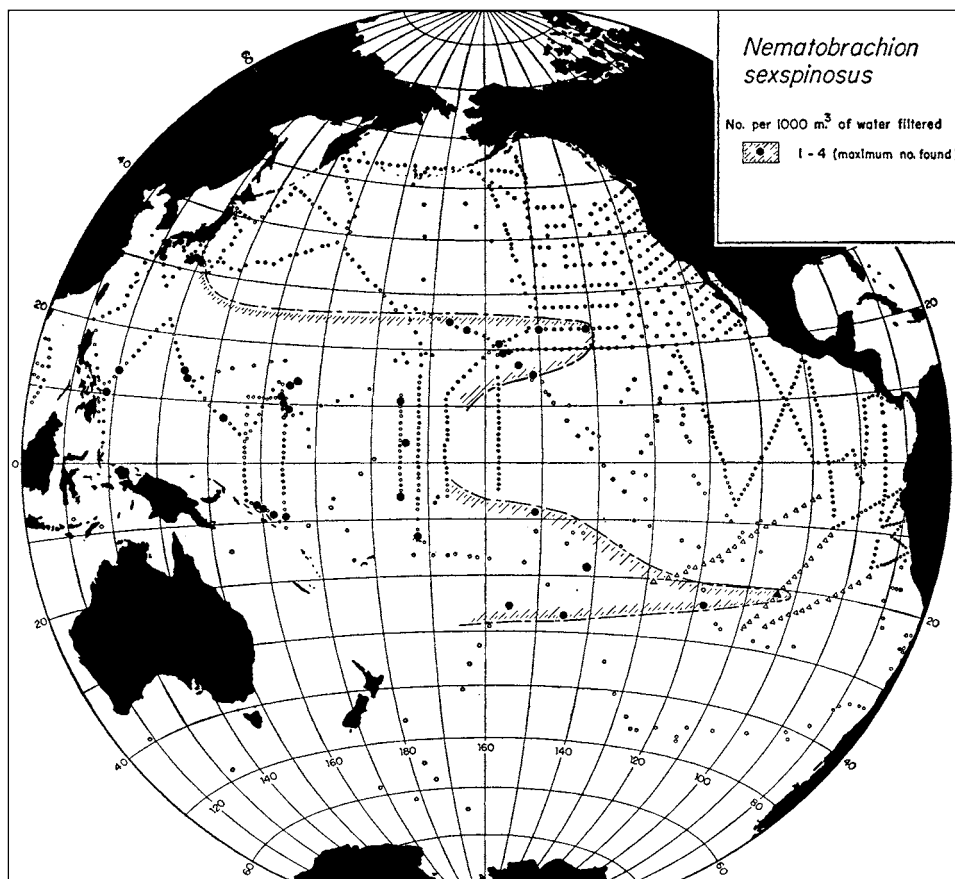


Fig. 74. Geographical distribution of *Nematobranchion sexspinosus*.

central waters of the North and South Pacific having a temperature higher than about 17° C. at a depth of 200 meters.

Of the 37 Scripps records for *N. sexspinosus*, 29 are based on 1 specimen. The Isaacs-Kidd mid-water trawl, sampling near the Marshall Islands, caught only 3 specimens in two tows. The distributional pattern of this species corresponds with those of *Thysanopoda cristata* and *Stylocheiron robustum*, two other rare species which may, with *N. sexspinosus*, have an extensive vertical range.

There is one Pacific record from other than the present collections: 21° 39' S., 104° 30' W. (Hansen, 1912). *N. sexspinosus* has not been reported from the Indian Ocean. Five specimens were caught in the subtropical North Atlantic, at 32° N. in the eastern Atlantic (Hansen, 1911), and at 28°–29° N., in the western Atlantic (Tattersall, 1926; Leavitt, 1938).

Nematobranchion boopis Calman

(Fig. 75)

Like *Nematobranchion flexipes*, *N. boopis* lives south of 40°–42° N. in the North Pacific. The most southerly record in the South Pacific is at 54° 22' S., 177° 17' W. ("Monsoon" expedition). This species has not been found in the eastern equatorial basin except in the region of the Equatorial Countercurrent and the Cromwell Current, where it was found eastward to the Galápagos Islands.

N. boopis is widely distributed in both the North and the South Pacific. However, owing to its deep habitat there are few records from the tropical western Pacific. This species was caught in most tows that attained a depth of at least 500 meters, especially in the northern and eastern parts of the distribution range. This characteristically mid-water euphausiid is found to occur at relatively shallow depths where the limits of its range impinge upon subarctic and subantarctic zones.

The "Valdivia" records indicate that *N. boopis* lives from 43° 32' N., 14° 27' W. to 40° 31' S., 15° 07' E. in the Atlantic. The most southerly record in the Indian Ocean is 34° 14' S., 80° 31' E., and the most northerly is 10° 55' N., 61° 21' E. (Tattersall, 1939).

Vertical distribution (fig. 76).—Adults were not caught above 700 meters during the day in the Baja California Pelagic Area; they were found at 500–700 meters at night. Larvae and immature individuals were below 100 meters during both day and night.

The "Transpacific" and "Norpac" data show that *N. boopis* does not live above about 140 meters. A few adults were caught above 280 meters during the night near the northern limit of the distributional range, but none during the day. Immature specimens and larvae showed no significant diurnal change in depth.

THE GENUS STYLOCHEIRON G. O. Sars

The species of this genus fall into two natural groups, with the exception of *Stylocheiron carinatum*, which is not closely allied with either. The pair *S. maximum* and *S. abbreviatum* with the addition of *S. robustum* (Brinton, 1962b) form one group. The other, the "*Stylocheiron longicorne* group," was recognized by Hansen (1910, 1911); he added three species, *S. affine*, *S. insulare*, and *S. microphthalma*,

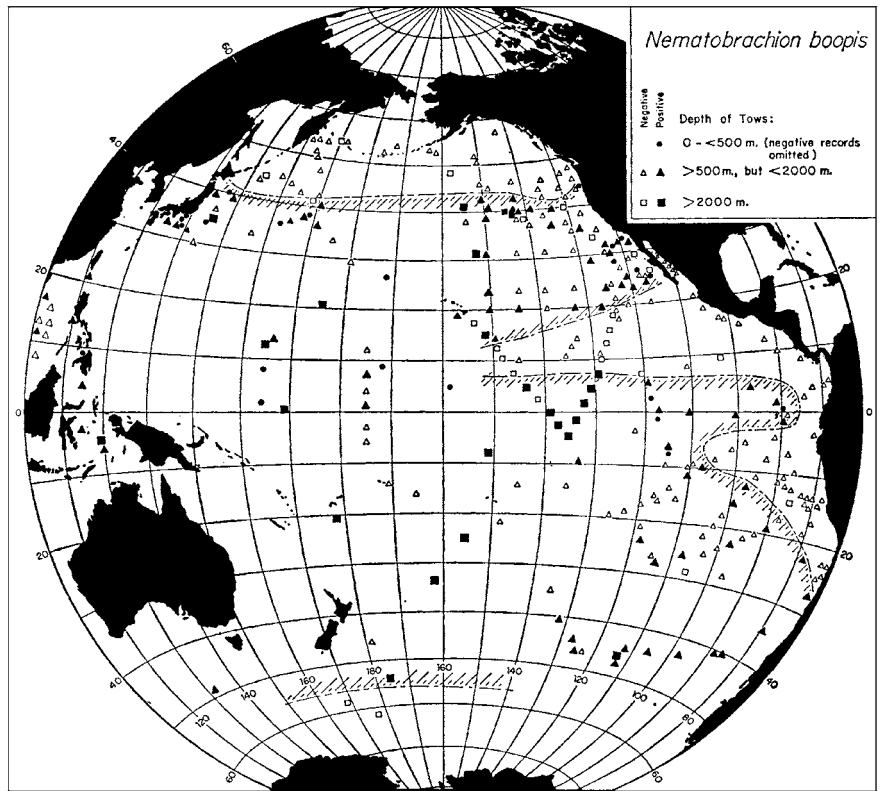


Fig. 75. Geographical distribution of *Nematobranchion boopis*.

Nematobranchion boopis

Vertical Distribution, Offshore Baja California Pelagic Area

DAY NIGHT

Number per 1000 cubic meters of water filtered (logarithmic scale)

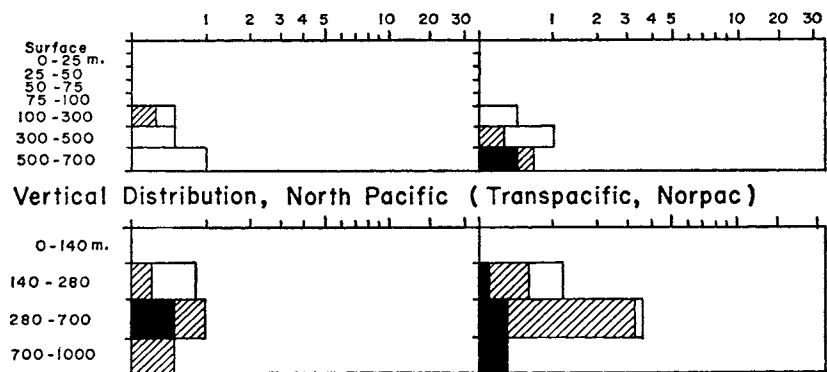


Fig. 76. Vertical distribution of *Nematobranchion boopis*.

to the three described by G. O. Sars (1883) from the *Challenger* collections: *S. longicorne*, *S. suhmii*, and *S. elongatum*.

The “*Stylocheiron longicorne* group” becomes more ramified in the present treatment. Differentiation within each of the species *S. affine* and *S. longicorne* is discussed below in relation to the water-mass habitats of the several forms.

The eye is conspicuously bilobed in *Stylocheiron* and the fourth to the eighth thoracic legs are much reduced or lacking. The third thoracic leg is greatly elongated; strong spiniform bristles on the propodal and terminal segments form a prehensile hand. In the “*S. maximum* group” the hand is a true chela, suggesting that this group contains highly specialized species. (On the other hand, the more specialized adaptation may be uniformity in structure of the thoracic legs, making possible a high level of efficiency in filtering [Isabella Gordon, personal communication.])

Euphausia, the genus having the most uniform thoracic legs, is as highly successful from the standpoint of population size, number of species, and area colonized, as *Stylocheiron* with its prehensile hand or claw. Essentially an epipelagic warm-water genus, *Stylocheiron* has colonized deep waters through the “*S. maximum* group.” *Euphausia* remains epipelagic, but occurs in the Subantarctic, Antarctic, and Subarctic zones, (nine species are endemic to these high latitudes) as well as in tropical and subtropical waters.

Stylocheiron carinatum G. O. Sars

(Fig. 77)

Horizontal distribution.—*Stylocheiron carinatum* has been found throughout the subtropical and tropical regions of the Pacific between the subtropical convergences, 40° N.—40° S. It has been rarely taken in cool coastal waters of the California and Peru currents, but occurs throughout the eastern equatorial basin.

Centers of abundance are associated with eastern central regions of the North and South Pacific, and with mid-equatorial and eastern equatorial waters. Lower numbers were found in the eastern part of the North Equatorial Current, 10°–20° N.

There is a long list of records for this species from the tropical-subtropical Atlantic and Indian oceans (Hansen, 1915; Tattersall, 1926, 1939; Illig, 1930).

Vertical distribution (fig. 78).—The collections from the Baja California “Pelagic Area,” a region not optimal for *S. carinatum* judging from the number found there, indicate that this species migrates from a daytime level of 50–300 meters to a nighttime level of 0–100 meters. (This is in contrast to the apparent nonmigrating behavior of the “*S. longicorne* group” discussed below.)

The “Transpacific” and “Norpac” expedition data on vertical distribution provide further evidence that this species moves into the upper layers at night. Most of the population was above 140 meters at all times; however, many individuals found at 280–700 meters during the day appeared to be above that level at night.

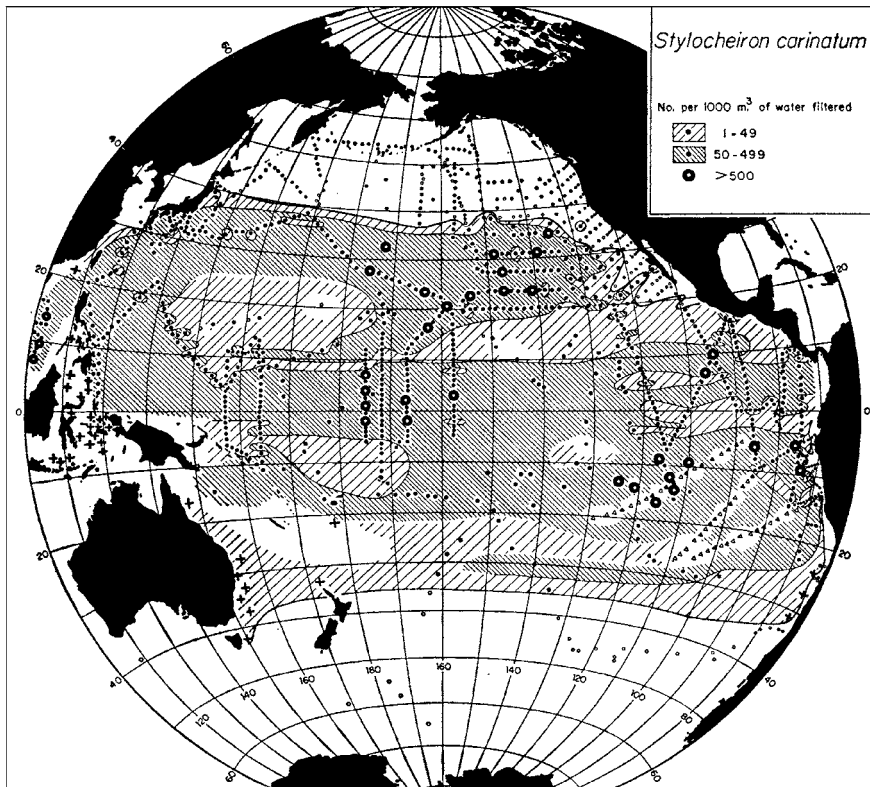
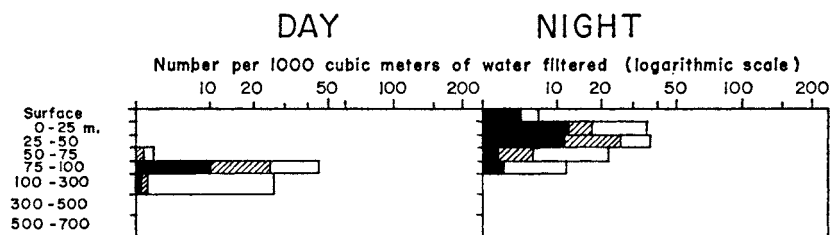


Fig. 77. Geographical distribution of *Stylocheiron carinatum*.

Stylocheiron carinatum

Vertical Distribution, Offshore Baja California Pelagic Area



Vertical Distribution, North Pacific (Transpacific, Norpac)

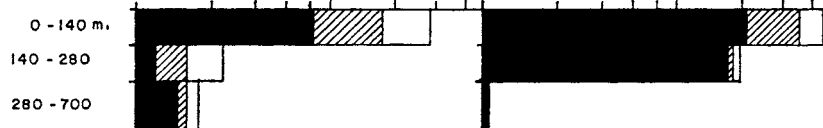


Fig. 78. Vertical distribution of *Stylocheiron carinatum*.

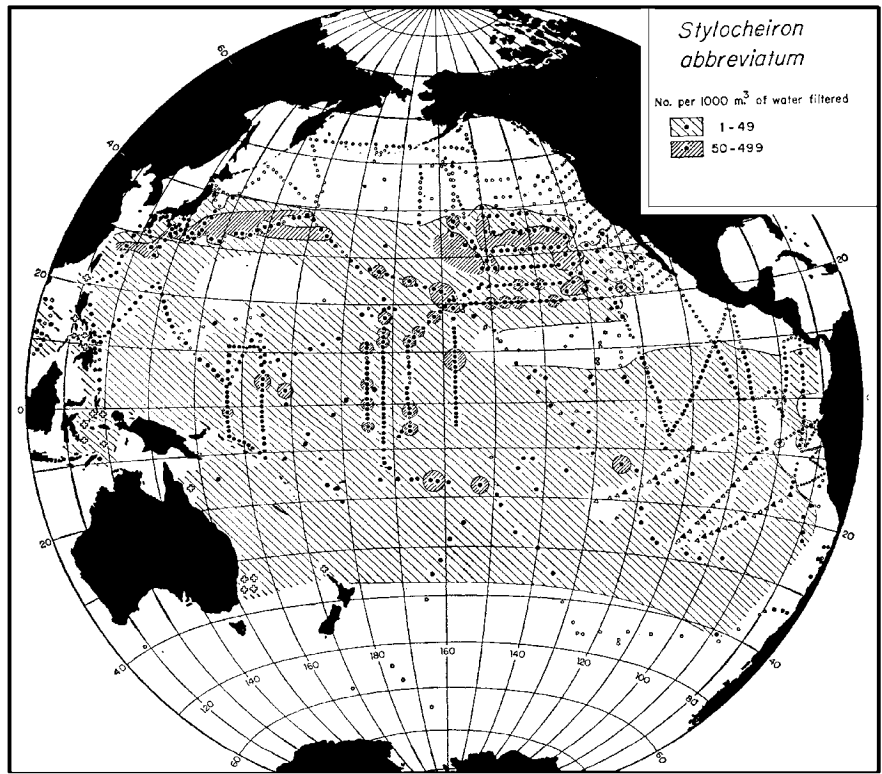
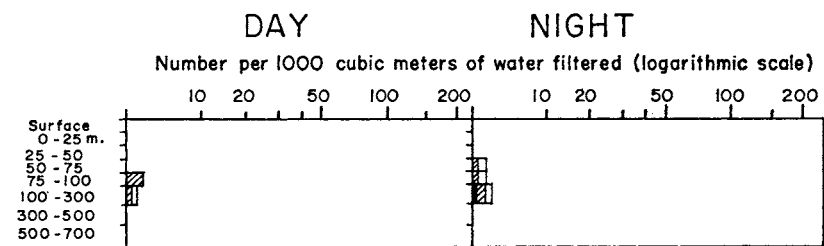


Fig. 79. Geographical distribution of *Stylocheiron abbreviatum*.

Stylocheiron abbreviatum

Vertical Distribution, Offshore Baja California Pelagic Area



Vertical Distribution, North Pacific (Transpacific, Norpac)



Fig. 80. Vertical distribution of *Stylocheiron abbreviatum*.

THE "STYLOCHEIRON MAXIMUM GROUP"

Stylocheiron abbreviatum G. O. Sars

(Fig. 79)

Horizontal distribution.—The range of this species parallels that of *Stylocheiron carinatum*, differing in that *S. abbreviatum* is apparently lacking in the eastern equatorial region, 10°–17° N. Like *S. carinatum*, it is an offshore warm-water species in the regions of the California and Peru currents. The most northerly and most southerly records are from near the 40° parallels.

S. abbreviatum has been reported from temperate waters of the Atlantic and Indian oceans (Hansen, 1912; Tattersall, 1926, 1939; Illig, 1930; Boden, 1954).

Vertical distribution (fig. 80).—The sampling carried out off Baja California showed that *S. abbreviatum* was present at a depth of 75–300 meters during the day and at 50–300 meters at night. The average vertical distribution, based upon "Norpac" and "Transpacific" expedition sampling, indicated no diurnal migration and little vertical stratification of numbers, although most immature individuals and furcilia were caught at 0–140 meters.

Stylocheiron maximum Hansen

(Fig. 81)

Horizontal distribution.—This large mesopelagic species is found as far north as the Gulf of Alaska, but was not caught by the "Transpacific" expedition in the Bering Sea. *Stylocheiron maximum* is present throughout the central and equatorial regions of the Pacific, but not found by the "Shellback" expedition in waters west of Central America, 10°–20° N.—the region characterized by high surface temperatures and low oxygen concentrations at relatively shallow depths.

This species was found at the southern limit of sampling by the "Monsoon" expedition, 63° S. in the South Pacific. It is widespread in the Atlantic and Indian oceans. Hansen (1912) reported that the *Ingolf* caught it at 61° 49' N., 14° 11' W., west of the Faeroe Islands, but Einarsson (1945) did not regard it as a member of the boreal community in the North Atlantic.

Vertical distribution (fig. 82).—The adult of *S. maximum* is rarely found above a depth of 140 meters; it has been caught in large numbers only by mid-water trawl sampling below 500 meters. Larvae and immature specimens were found to be most common at 140–280 meters. There is no evidence that this species performs a diurnal vertical migration, although adults were caught more consistently at night than during the day.

Stylocheiron robustum Brinton

(Figs. 83, 84)

Stylocheiron robustum is a third species of the "*S. maximum* group" (Brinton, 1962*b*). Hansen (1910) recognized that *S. maximum* and *S. abbreviatum* were a

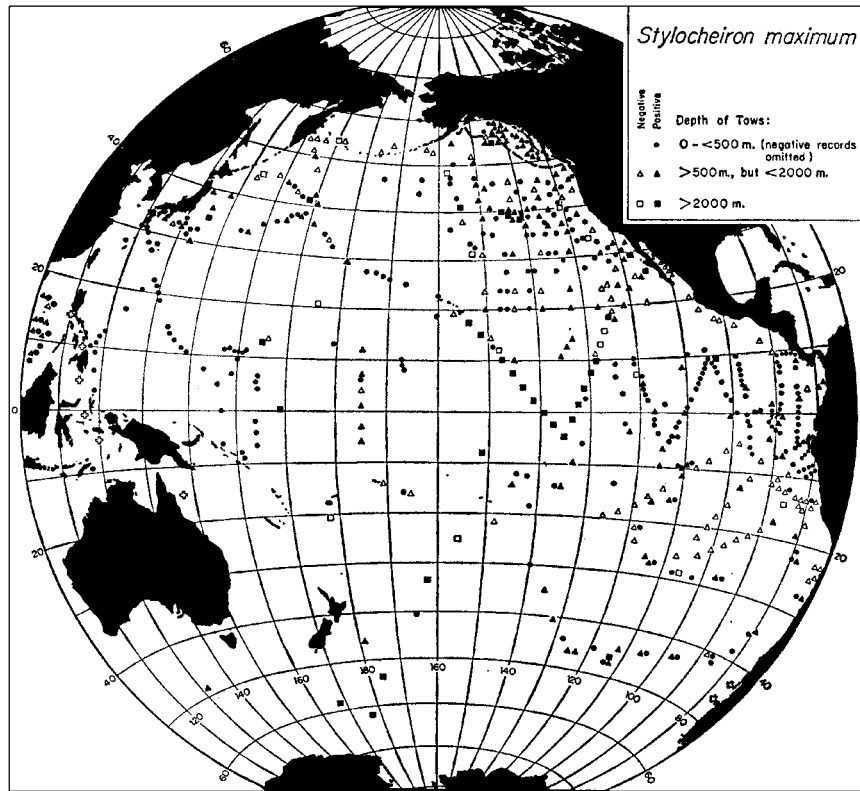


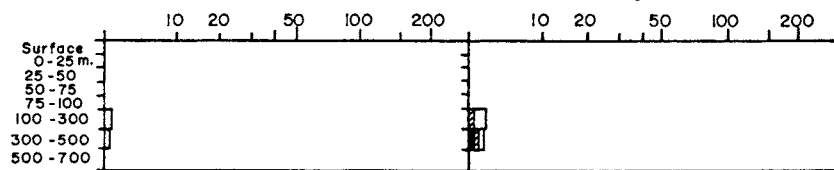
Fig. 81. Geographical distribution of *Stylocheiron maximum*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

Stylocheiron maximum

Vertical Distribution, Offshore Baja California Pelagic Area

DAY NIGHT

Number per 1000 cubic meters of water filtered (logarithmic scale)



Vertical Distribution, North Pacific (Transpacific, Norpac)

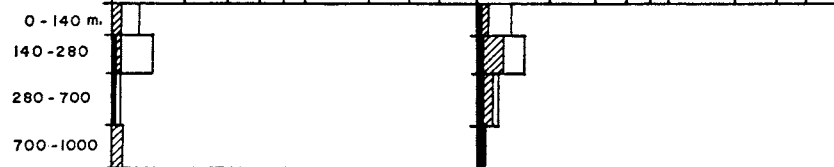


Fig. 82. Vertical distribution of *Stulocheiron maximum*.

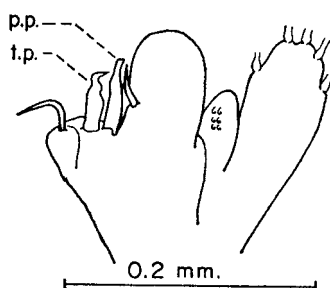


Fig. 83. *Stylocheiron robustum*, male copulatory organ (p.p. [proximal process], t.p. [terminal process]).

natural pair of species, having the elongated third pair of thoracic legs terminating in true chaelae with well-developed immovable fingers from the penultimate joints.

S. robustum is similar to *S. abbreviatum* in size but is stockier in general appearance. The eye is pyriform in both species, but the upper portion is broader in *S. robustum* than in *S. abbreviatum*. The flagella of the first antennae of the male are not flattened, in contrast to *S. abbreviatum*, but are nearly cylindrical as in *S. maximum*. The processes of the copulatory organ differ from those of *S. maximum* and *S. abbreviatum*: in neither of the two last-named species is the terminal process bent sharply outward distally as in *S. robustum* (fig. 83), and only in *S. robustum* is the proximal process longer than the terminal.

Horizontal distribution (fig. 84).—This species has been caught only in the warmest parts of the North and South Pacific central gyres of circulation and in the tropical western Pacific. In the eastern half of the Pacific the northern and southern records are separated from each other by the full breadth of the Equatorial Water Mass, 20° N. to 14° S. The known distribution range can be approximately circumscribed by the 14° C. isotherm at a depth of 200 meters. Surface temperature shows no clear relationship to the pattern of distribution of this species.

S. abbreviatum ranges from 40° N. to the zone of the Subtropical Convergence, near 40° S., in the Pacific, whereas *S. maximum* has been found in all water masses and oceans except the Arctic Ocean. Thus, *S. robustum* is the species of the “*S. maximum* group” most restricted in distribution.

An adult of *S. robustum* was present in a sample of euphausiids from the Atlantic coast of South Africa, 32° 05' S., 17° 31' E., taken in November, 1955. This specimen was in material sent by Mr. C. S. de V. Nepgen of the South African Division of Fisheries, and was, at that time, incorrectly identified by me as *S. abbreviatum*.

Vertical distribution.—The adult of *S. robustum* has not been caught in any haul that reached less than a depth of 280 meters. The only catch with an opening-closing net was at 140–280 meters, east of Hawaii, during the night. The other records were from open-net hauls, three to 300 meters, two to 700 meters, and one to 2,000 meters. Three of the four adults caught above 300 meters were taken at night.

The juveniles and larvae were all caught in open nets: 0–140 meters, four records; 0–300 meters, ten records; 0–400 meters, two records; 0–700 meters, one record. No difference in depth with respect to time-of-day of catch was found.

THE “STYLOCHEIRON LONGICORNE GROUP”

The number of crystalline cones in a transverse row in the upper eye distinguishes *Stylocheiron microphthalmum* (two cones) and *S. suhmii* (three cones) from all other species.

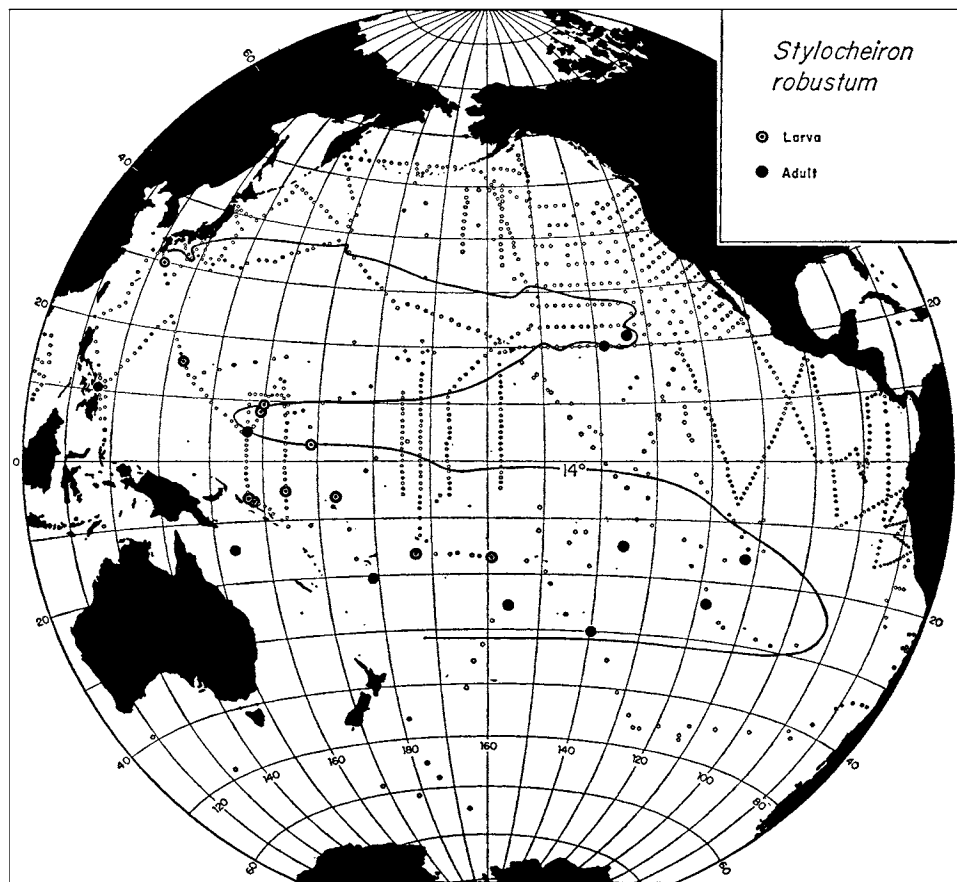


Fig. 84. Geographical distribution of *Stylocheiron robustum*.

Among the specific characteristics of *S. insulare* are (1) uropods that do not reach the tip of the telson; (2) the lower margin of the sixth segment bent sharply upward toward the end; (3) two distal peduncular joints of the male shorter and thicker than in other species of the "*S. longicorne* group," and both flagella 7-jointed; (4) the lower part of the eye more than three times as broad as the upper part at the end.

S. elongatum is a large species having a sixth abdominal segment that is extremely long—four times as long as its depth.

S. affine and *S. longicorne* are more variable than any of the above four species.

Stylocheiron microphthalmum Hansen

(Fig. 85)

Horizontal distribution.—*Stylocheiron microphthalmum* is a small tropical species, more widespread in the western Pacific than in the eastern Pacific. During the "Shellback" expedition the distribution extended into the equatorial basin in the terminal part of the Equatorial Countercurrent and in the adjacent region to the north where the North Equatorial Current arises. *S. microphthalmum* was then

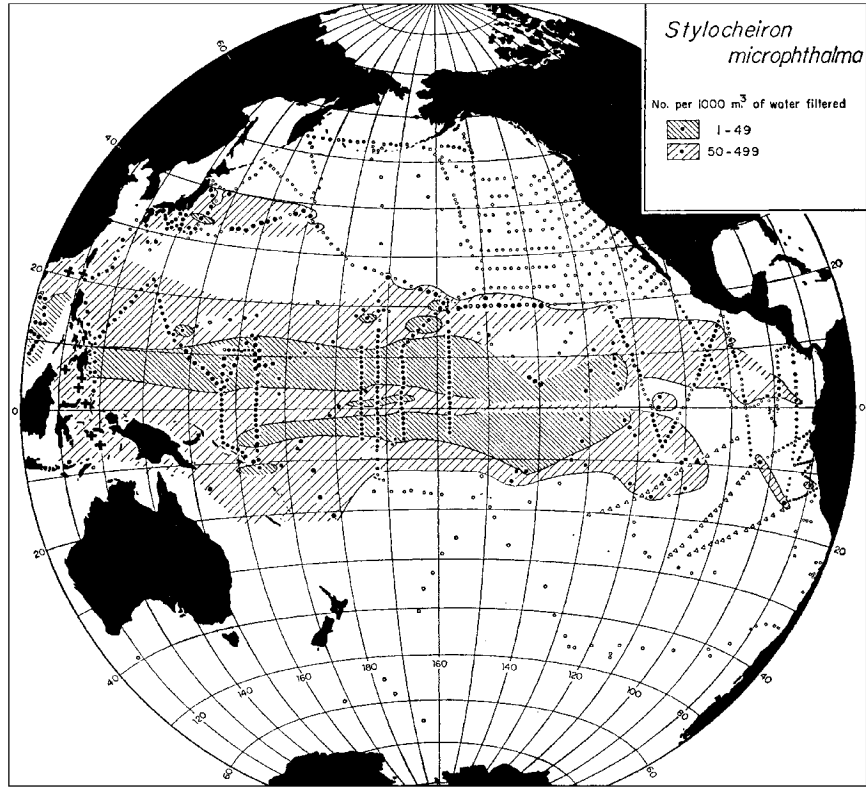


Fig. 85. Geographical distribution of *Stylocheiron microphthalmum*.

Stylocheiron microphthalmum

Vertical Distribution, North Pacific (Transpacific, Norpac)

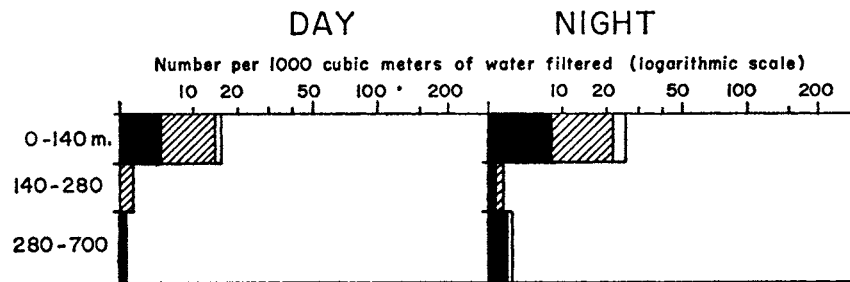


Fig. 86. Vertical distribution of *Stylocheiron microphthalmum*.

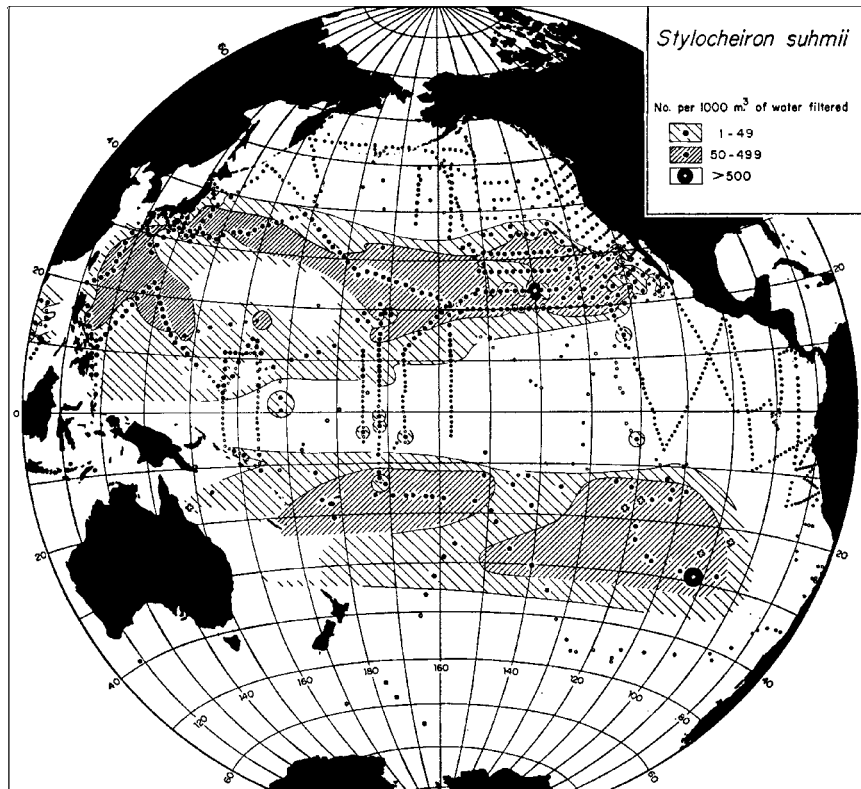
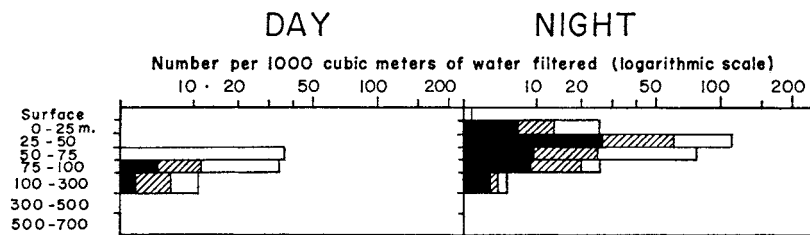


Fig. 87. Geographical distribution of *Stylocheiron suhmii*.

Stylocheiron suhmii

Vertical Distribution, Offshore Baja California Pelagic Area



Vertical Distribution, North Pacific (Transpacific, Norpac)

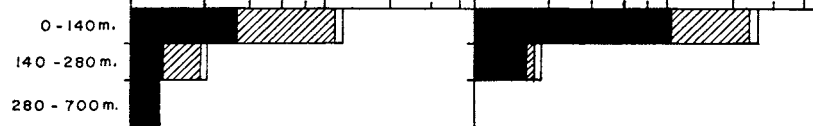


Fig. 88. Vertical distribution of *Stylocheiron suhmii*.

(June, 1952) lacking in the Peru Current where the surface temperatures were 16–19° C.; however, it was found at one station off Callao, Peru, by the “Downwind” expedition (January, 1958) when surface temperatures were warmer than 22° C.

In the western Pacific this species ranges from 40° N., in the Kuroshio system, to at least 21° S., near the Fiji Islands. It was found to be most numerous in waters of the equatorial current system, except at the equator proper.

S. microphthalma has not been reported from the Atlantic, except at one locality, 24° 13' N., 17° 01' W., by Illig. In view of the similarity of post-larvae of *S. suhmii* and *S. microphthalma* (both may have two pairs of crystalline cones in the upper eye), it is likely that Illig's record is based on *S. suhmii*. Illig adds sixteen records for *S. microphthalma* from the warm part of the Indian Ocean, but this species was not found in the northwestern part by the John Murray Expedition. Like *Euphausia diomediae* and *Nematoscelis gracilis*, *S. microphthalma* appears to be confined to tropical waters of the Pacific and Indian oceans.

Vertical distribution (fig. 86).—*S. microphthalma* was found mainly above 140 meters at the few “Norpac” and “Transpacific” expedition stations occupied within its distributional range. It was sometimes present in the 140–280- and 280–700-meter layers, however.

Stylocheiron suhmii G. O. Sars

(Fig. 87)

Horizontal distribution.—This is a central Pacific species, found from 38° or 39° N. in the North Pacific to at least 35° S. in the South Pacific. Northern and southern distributions are separated by the region of the Equatorial Water Mass. *S. suhmii* was not caught by the *Siboga* in waters of the Indo-Australian Archipelago. Like *Euphausia hemigibba* (but unlike *E. brevis*), *S. suhmii* was found in the Kuroshio system, near Japan. These three species are most numerous in the barren central waters, away from the periphery of their ranges.

According to the *Valdivia* records, *S. suhmii* is widely distributed in the subtropical North and South Atlantic and the tropical part of the Indian Ocean; however, the John Murray Expedition did not find it in the northwestern part of the Indian Ocean.

Vertical distribution (fig. 88).—In the “Pelagic Area” off Baja California, *S. suhmii* was found at 50–300 meters during the day and at 0–500 meters at night. The average picture of vertical distribution from the wider North Pacific range indicated that *S. suhmii* was most common above 140 meters during both day and night.

Stylocheiron insulare Hansen

(Fig. 89)

Horizontal distribution.—All of the known localities for this species are from near the equator in the far-western Pacific. Hansen's (1911) seven records from the *Siboga* collections were from the Celebes, Molucca, Ceram, and Banda seas. *S. insulare* was caught north of the Solomon Islands at eighteen “Equapac” expedition stations. Evidently this species lives in the region of the East Indian Archipelago. It was not recorded by Hansen (1916) in the *Albatross* collections from

the Philippine Islands, nor was it found in "Naga" expedition material from the South China Sea.

Vertical distribution.—Six of the *Siboga* records were from hauls reaching to a depth of at least 900 meters. A seventh listed a small specimen caught at 0–278 meters. The Scripps specimens from somewhat farther east are based on 0–300-meter

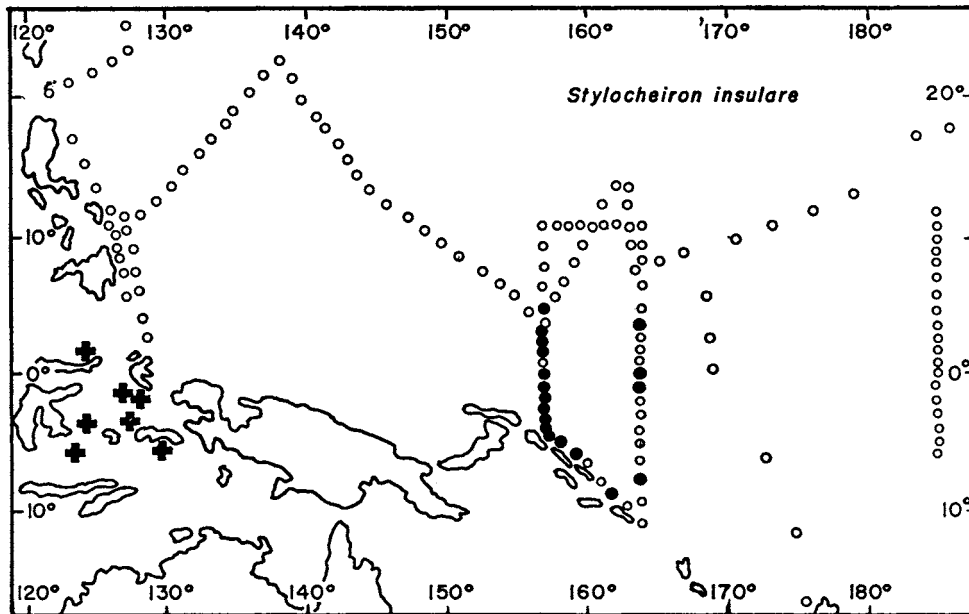


Fig. 89. Geographical distribution of *Stylocheiron insulare*. All known records are shown as crosses ("Siboga" exped.) and blackened circles ("Equapac" exped.).

hauls. All records were of adults or near-adults, but were each based on fewer than four specimens.

Stylocheiron elongatum G. O. Sars

(Fig. 90)

Horizontal distribution.—This species is known from 40° N. to 35° S. in the Pacific. It has not been found in the northern part of the California Current, but lives in Baja California waters, 20°–32° N. The only records for *S. elongatum* in the eastern equatorial basin are from the latitude of the Equatorial Countercurrent, 3°–9° N. The known range extends into the Peru Current only between 20° S. and 33° S., off Chile.

S. elongatum is widespread in the Atlantic and Indian oceans (Hansen, 1905, 1915; Tattersall, 1926, 1939; Illig, 1930).

Vertical distribution (fig. 91).—This is the deepest-living species of the "*Stylocheiron longicorne* group." In the Baja California "Pelagic Area" it was present at 100–500 meters. The "Norpac" and "Transpacific" expeditions found this species in all layers sampled, with a maximum at 140–280 meters. Adults were caught more often at night than in the daytime but the data do not indicate a diurnal vertical migration.

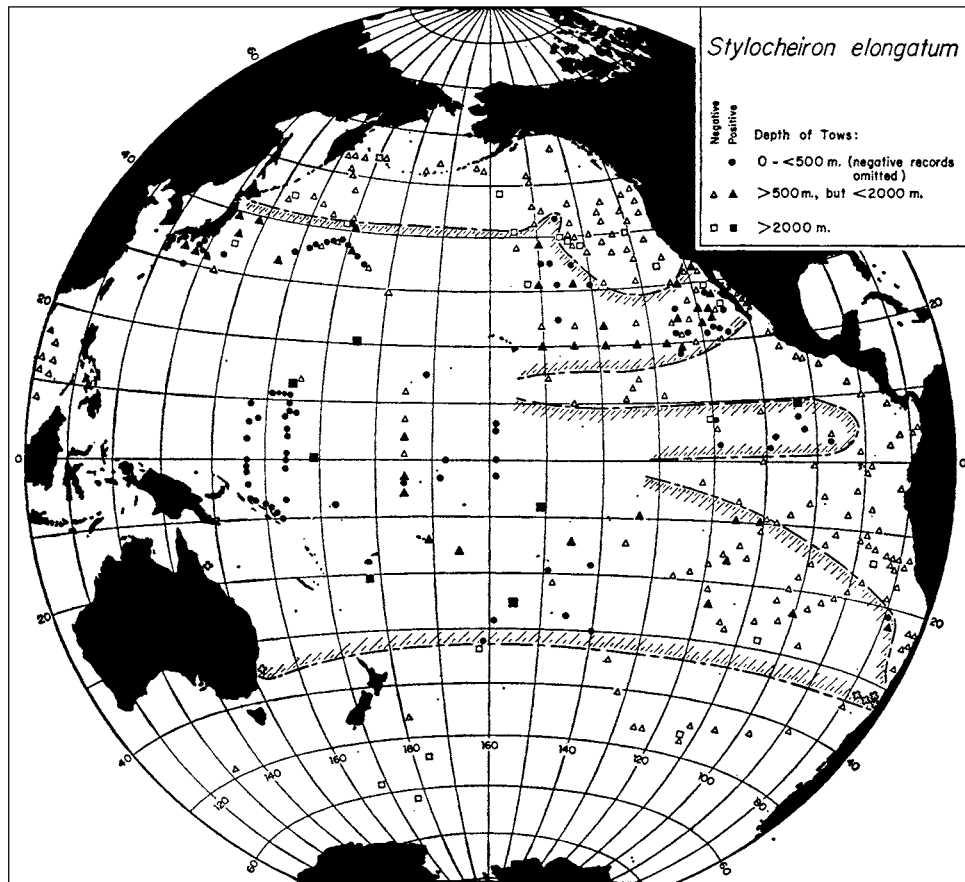
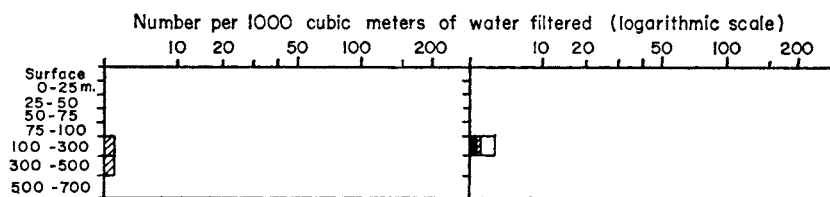


Fig. 90. Geographical distribution of *Stylocheiron elongatum*. Stations are not indicated unless a depth of at least 500 meters was reached by the net, except where a positive record was obtained from a shallower tow.

Stylocheiron elongatum

Vertical Distribution, Offshore Baja California, Pelagic Area

DAY NIGHT



Vertical Distribution, North Pacific (Transpacific, Norpac)

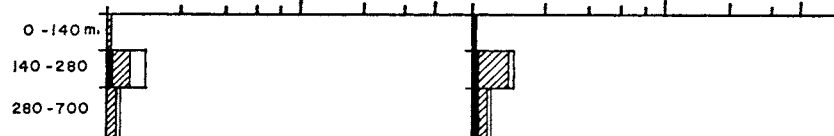


Fig. 91. Vertical distribution of *Stylocheiron elongatum*.

DIFFERENTIATION IN *STYLOCHEIRON AFFINE* HANSEN AND *S. LONGICORNE* G. O. SARS

The four species of the "*Stylocheiron longicorne* group" just discussed from the standpoint of distribution showed little or no morphological variability throughout their ranges. Two of these, *S. microphthalmia* and *S. suhmii*, have patterns of distribution, equatorial and central, respectively, that occur within each epipelagic euphausiid genus. *S. insulare* is known only from the region of the Indo-Australian Archipelago. *S. elongatum* has the broad distribution (ca. 40° N.–40° S.) characteristic of mesopelagic euphausiid species.

Two additional species complete the "*S. longicorne* group": *S. affine*, which has an extraordinarily broad geographical range (40° N.–40° S.) for an epipelagic euphausiid, and *S. longicorne*, living somewhat deeper, which ranges even more widely (45° N.–45° S.). During the examination of the Pacific collections of these two species it became evident that for each there was a range in variability in certain obvious morphological characteristics. It therefore seemed advisable to place the variability noted in each species on a quantitative basis.

Five forms of *S. affine* and two of *S. longicorne* were distinguished. Each kind of differentiation was consistent over a wide geographical area, and distinct from the level of differentiation found in adjoining areas. The possible systematic status of the forms is considered here in the light of the distributional ranges.

Stylocheiron affine Hansen

Hansen (1910) described *Stylocheiron affine* from the tropical western Pacific. He pointed out the differences between *S. affine* and *S. longicorne*:

The eyes are conspicuously lower in *S. affine* than in *S. longicorne*, less than twice as high as broad, somewhat pyriform, with the lower section from more than half as broad again to more than twice as broad as the upper part, in which, seen from the side, 4 or 5, rarely 6, crystal cones are plainly observed. . . . Sixth abdominal segment from considerably less to a little more than half as long again as deep, with the lower margin rounded somewhat flatly towards the end.

Forms of *S. affine* found in the Pacific differ from each other in one, or a combination of, the following three ways: (1) the ratio of the width of the lower part of the eye to the width of the upper part, (2) the size of the eye, (3) the ratio of the length of the sixth abdominal segment to the depth of the segment.

The shapes of the processes of the male copulatory organ and of the spines of the chaela are remarkably uniform in the "*S. longicorne* group," and have not often been of help in distinguishing the species or forms.

The *S. affine* variants are here given non-Latinized geographical names. The reasons for this provisional designation are discussed below. The ratios of the widths of the lower and upper parts of the adult eye and the length/depth ratios of the sixth abdominal segment are listed in table 12 for all of the known species and forms of the "*S. longicorne* group." Specimens were measured from several widely separated localities within the geographical range of each species (fig. 93a).

Stylocheiron affine, "California Current Form"(Figs. 92, *a* and *b*, 93a, 93b, 93c, 93d, 94, 95)

The lower (widest) part of the eye is nearly twice the width of the upper part (fig. 93b) measured at the top of the most distal, transverse row of crystalline cones (fig. 92, *l*). The sixth abdominal segment is more than twice as long as it is deep. The length of this segment is measured middorsally and the depth (middorsal to mid-ventral measurement) at the deepest place. The upper part of the adult eye has 4-6 cones in a transverse row.

TABLE 12
RANGES OF VARIABILITY IN CERTAIN MEASUREMENTS OF THE SPECIES AND
FORMS OF THE "*Stylocheiron longicorne* GROUP"

Species	No. crystalline cones in transverse row in upper eye	Length of adult (mm.)	Length of eye (mm.)	Length of eye Length of body	Width lower part Eye: Width upper part (B/T)	Length 6th Abd. seg.: Depth (L/D)
<i>S. microphthalmum</i>	2	6.1-6.9	.49-.54	.079-.087	2.50-3.00	1.46-1.60
<i>S. suhmii</i>	3	5.5-7.8	.57-.61	.077-.105	3.9-4.3	1.66-1.69
<i>S. insulare</i>	4-5	6.2-8.2	.70-.81	.118-.126	3.78-4.16	1.25-1.39
<i>S. affine</i>						
Calif. Current Form..	4-6	5.8-8.3	.67-.89	.101-.119	1.72-1.96	2.03-2.44
Eastern Equatorial Form.....	4-5	5.7-8.4	.61-.98	.097-.126	2.02-2.43	2.00-2.32
Western Equatorial Form.....	4-6	5.4-8.5	.75-.97	.114-.130	1.67-2.16	1.56-1.93
Central Form.....	5-8	6.0-8.0	1.00-1.25	.143-.160	1.45-1.74	1.40-1.58
Indo-Australian Form	4	5.5-7.3	0.62-.87	.100-.127	2.26-2.55	1.70-1.92
<i>S. longicorne</i>						
Long Form.....	9-19	7.1-11.3	0.90-1.46	.116-.149	0.86-1.37	2.00-2.35
Short Form.....	7-8	6.2-10.3	0.81-1.25	.127-.142	1.00-1.44	1.63-1.98
<i>S. elongatum</i>	13-16	12.5-18.5	1.40-1.67	.092-1.26	0.96-1.02	4.18-4.29

Differences between this and other forms, including those of *S. longicorne*, are graphically shown (fig. 93b) when the ratio of the length of the sixth abdominal segment to its depth (L/D) is plotted against the ratio of the width of the lower part of the eye to the width of its upper part (B/T). This form occurs in the southern part of the California Current and its center of abundance there is widely separated from that of the "Eastern Equatorial Form," most numerous south of 10° N.

It is evident from the scatter diagram (fig. 93b) that there is no obvious break separating the plot of points representing specimens of the "California Current Form" from the points representing the "Eastern Equatorial Form." However, *S. affine* collected in the zone of approximately 16°-21° N. was dominated (>50 per cent in each sample) by specimens having an eye B/T value near 2.00. These specimens

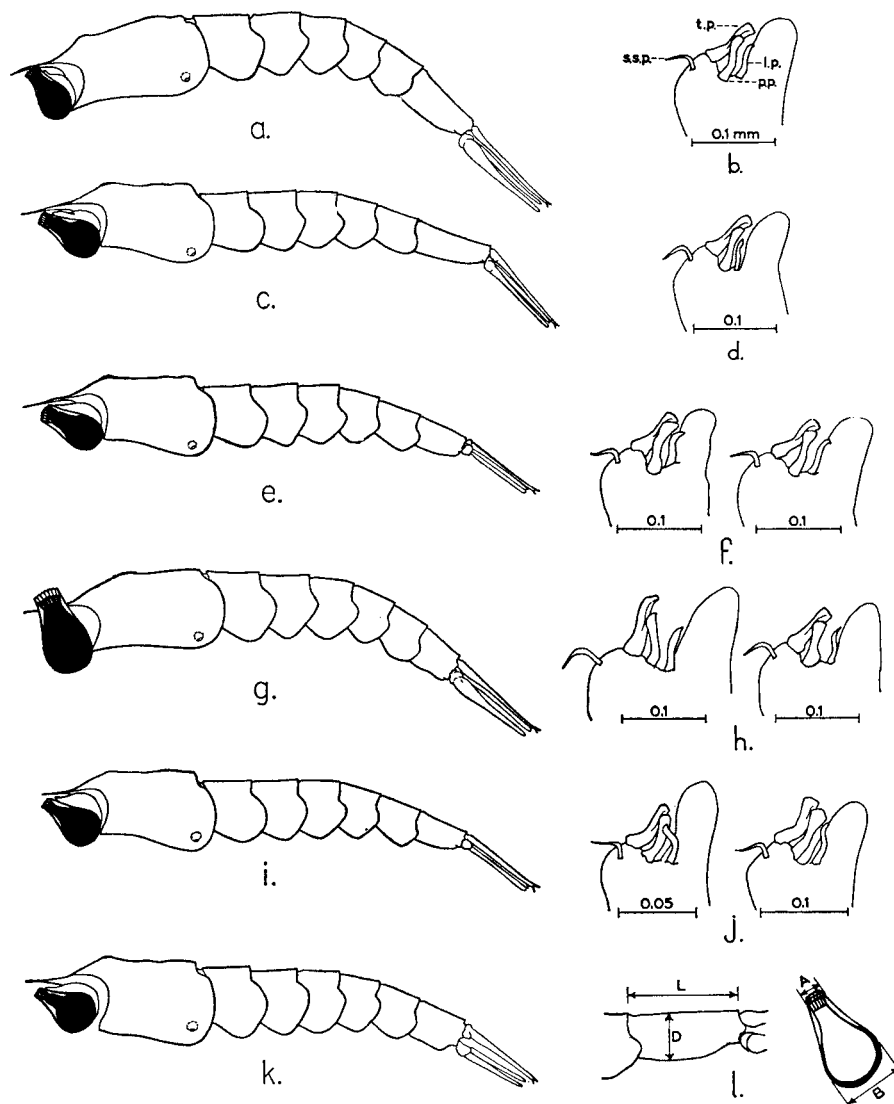


Fig. 92. Pacific forms of *Stylocheiron affine* in lateral aspect (not showing antennae or thoracic and abdominal appendages), and male copulatory organs (inner and median lobes) showing differences that cannot, at present, be regarded as significant. (Abbreviations: s.s.p., spine-shaped process; t.p., terminal process; p.p., proximal process; l.p., lateral process.) *a, b*. "California Current Form" (cop. organ of specimen 6.8 mm. long from "Norpac" exped. Sta. 95, 30° 20' N., 119° 27' W.). *c, d*. "East Equatorial Form" (cop. organ of specimen 7.0 mm. long from "Downwind" exped. Sta. 28, 27° 08' S., 72° 02' W.). *e, f*. "West Equatorial Form" (cop. organs of specimens 6.8 mm. long from "Naga" exped. Sta. 60-465, 13° 35' N., 111° 21' E., and 7.0 mm. long from "Downwind" exped. Sta. 9, 2° 08' S., 131° 27' W.). *g, h*. "Central Form" (cop. organs of specimens 7.2 mm. long from "Downwind" exped. Sta. 34, 28° 15' S., 96° 54' W., and 7.0 mm. long from "Norpac" exped. Sta. 115, 25° 39' N., 130° 22' W.). *i, j*. "Indo-Australian Form" (cop. organs of specimens 5.8 mm. long from "Naga" exped. Sta. 60-425, 9° 30' N., 103° 55' E., and 6.8 mm. long from "Troll" exped. Sta. 28A, 4° 28' N., 128° 20.5' E.) *k*. *Stylocheiron insulare*. *l*. Generalized lateral view of sixth abdominal segment and eye of "*S. longicorne* group" species showing parts measured in distinguishing the forms: L (length of sixth abdominal segment), D (depth of sixth abdominal segment), A (width of upper eye at distal limit of last complete row of enlarged cones), and B (width of widest part of lower eye).

are designated “intermediate” between the two forms (Intermediates “C.C.E.E.,” fig. 93b). Such intermediate forms were sometimes found within the California Current or Eastern Equatorial centers of abundance, but there they were always rare and mixed with a majority of the dominant form.

“Shellback” expedition stations occupied May 18–30, 1952 (fig. 93a), showed the zone of “intermediates” to be at 18° – 20° N. (fig. 93c), whereas “Eastropic” expedition

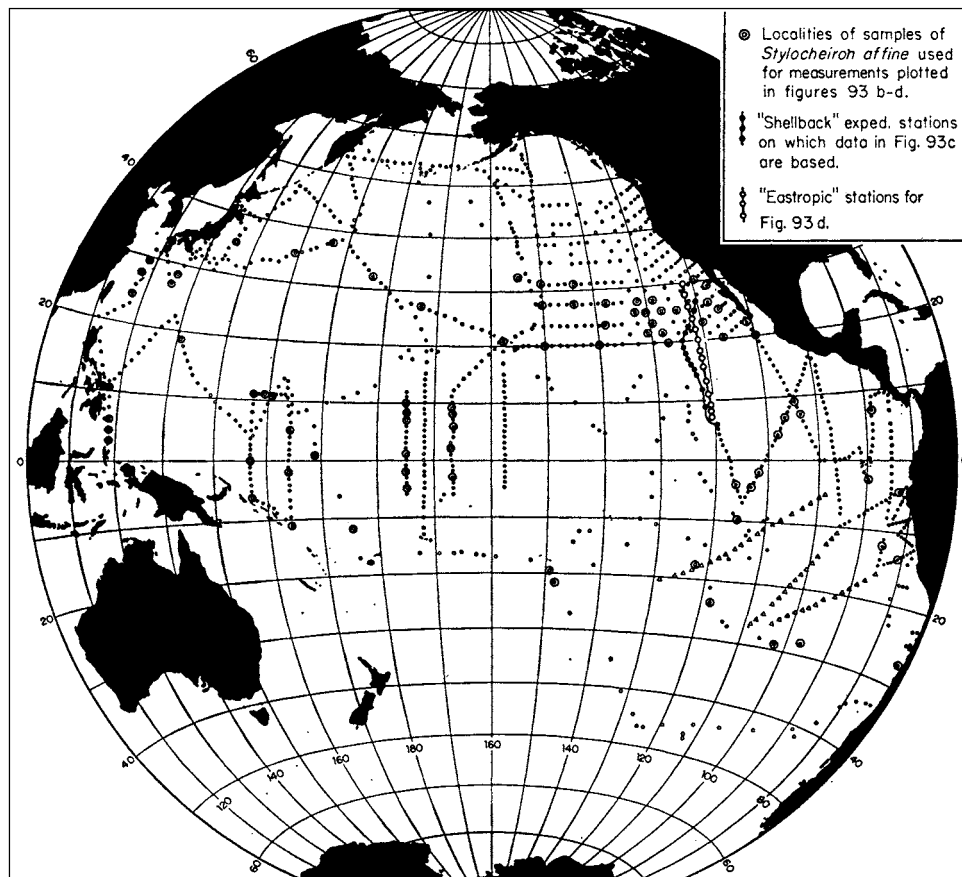


Fig. 93a. Positions of stations at which specimens of *Stylocheiron affine* plotted in figs. 93b–93d were collected.

samples collected October 3–10, 1955, showed the intermediate zone to be somewhat broader, 15° – 20° N. (fig. 93d).

Evidently, more mixing of populations takes place *within* each of the two regions (California Current and Eastern Equatorial) than takes place *across* (north-south) the boundary zone, 15° – 21° N. This possibility is supported by hydrographical findings: a frontal region was conspicuous at 17° – 19° N. during the “Shellback” expedition (Wooster and Cromwell, 1958), as shown by the temperature and oxygen profiles (fig. 93c). This may be a semipermanent, more western extension of a physical front frequently observed off the tip of Baja California. During the “Eastropic” expedition the front was broader and less abrupt.

In the above example of intergrading populations, as in other examples to be discussed below, it is evident that specimens morphologically intermediate between geographically adjacent forms were sometimes found outside of the boundary areas. Nevertheless, the highest *incidence* and *proportion* of morphological intermediates was always found in intermediate areas bounding the ranges of the designated forms (fig. 94).

Stylocheiron affine, "Eastern Equatorial Form"

(Figs. 92, *c-d*, 93a, 93b, 93c, 93d, 94)

In this form the width of the lower part of the eye is more than twice the width of the upper part (fig. 93b). The sixth abdominal segment is more than twice as long as it is deep. The upper part of the adult eye has 4–5 cones in a transverse row.

This form occupies the eastern equatorial basin, from 22° N. (May–August, 1952, "Shellback" expedition) to 33° S. (December, 1957, "Downwind" expedition), having a range much like that of *Euphausia distinguenda* (fig. 47). Westward extensions of the distribution were noted (1) near 10° N. in the North Equatorial Current and along an east–west thermal anticline at the northern edge of the Equatorial Countercurrent, (2) in the South Equatorial Current near the equator, and (3) along 10°–15° S.

The form intergrades at its northern limit with the "California Current Form." Intermediates between this and a "Western Equatorial Form" (discussed below) were distinguished (Intermediates "E.E.–W.E.," fig. 93b) on the basis of measurements made of specimens collected at four localities (fig. 94) in the region 4°–15° S., 109°–117° W. ("Shellback" and "Downwind" expeditions), which is geographically intermediate between the ranges of the two forms. These specimens were intermediate in respect to the proportions of the sixth abdominal segment (L/D). In addition, they fell within the lower limit of the range of the eye B/T ratio for the "Eastern Equatorial Form," and within the upper limit of the eye B/T ratio for the "Western Equatorial Form."

Thus, these specimens were intermediate in both selected proportions: the eye and the sixth abdominal segment. On the other hand, the "California Current"–"Eastern Equatorial" intergrades were intermediate only in respect to the ratio of the width of the lower part of the eye to the width of the upper part (B/T). The range of the sixth abdominal segment L/D ratio was nearly the same in both forms.

The northeast–southwest temperature gradient at a depth of 100 meters (fig. 7b) is very large, 16°–23° C., in the limited region where the "Eastern Equatorial"–"Western Equatorial" intermediates were found. This is a region of slow current, bordering on the Central Water Mass of the South Pacific.

The tongue of distribution centered at 10° N., where the "Eastern Equatorial Form" overlaps the range of the "Western Equatorial Form," is associated with cool water at a depth of 100 meters. No morphological intermediates were found here. The temperature gradient across the margins of the mid-Pacific tongue is still greater than that across the region farther south, where the morphological intermediates were found. Apparently the pattern of meridional and longitudinal flow in the equatorial current system establishes the extreme overlap in the ranges of the "Eastern Equatorial Form" and the "Western Equatorial Form." The intergradation

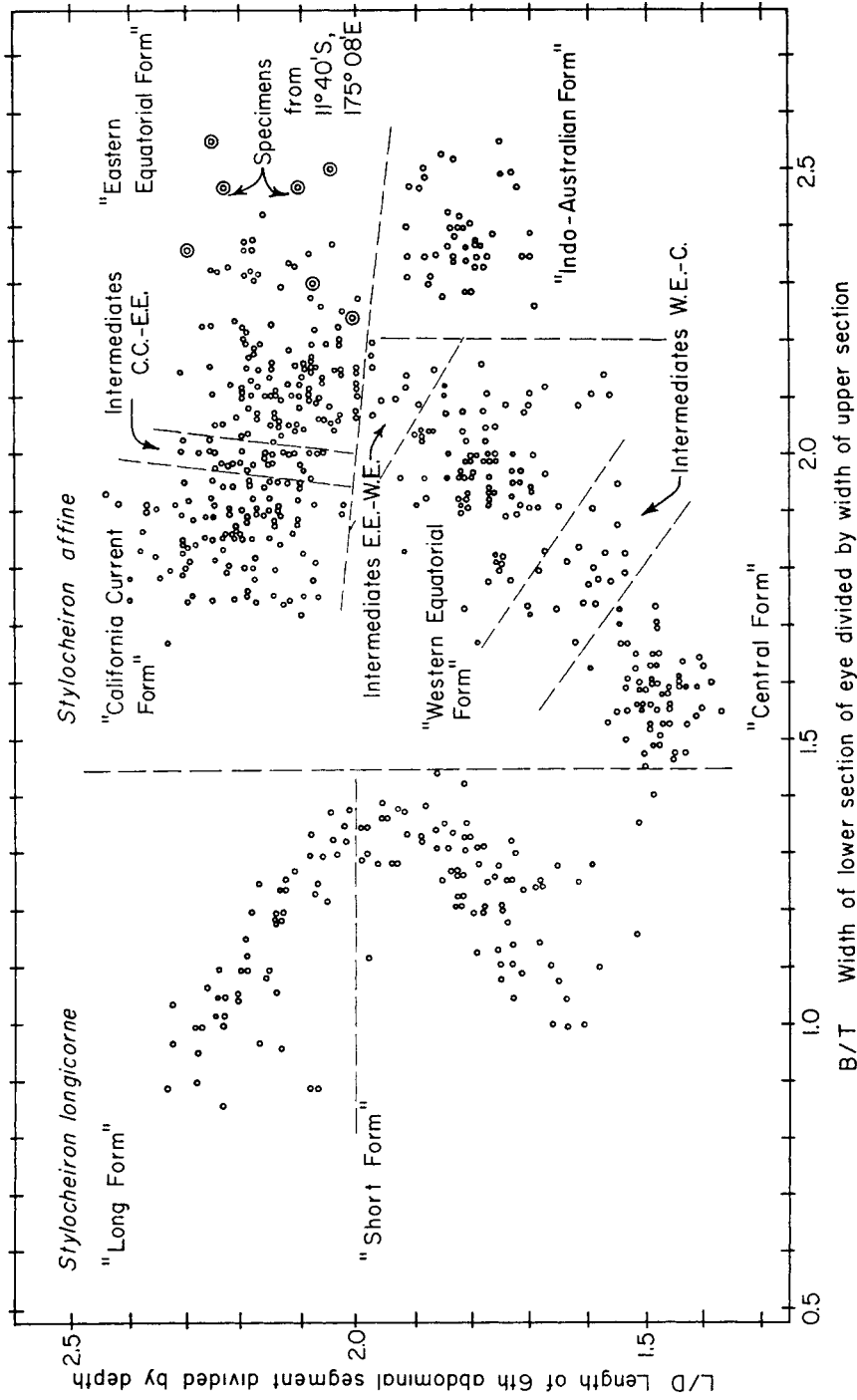


Fig. 93b. Method by which the five Pacific forms of *Stylocheiron affine* and the two Pacific forms of *S. longicornae* were distinguished. The ratio of the proportions of the sixth abdominal segment (length/depth is plotted against the ratio of the widths of the upper and lower parts of the bilobate eye (fig. 92, 1). The width of the upper part of the eye is measured at the most distal row of enlarged cones; the lower part of the eye is measured where it is widest. The localities for specimens designated "intermediate" between geographically adjacent forms are plotted in figures 94, 96, and 97.

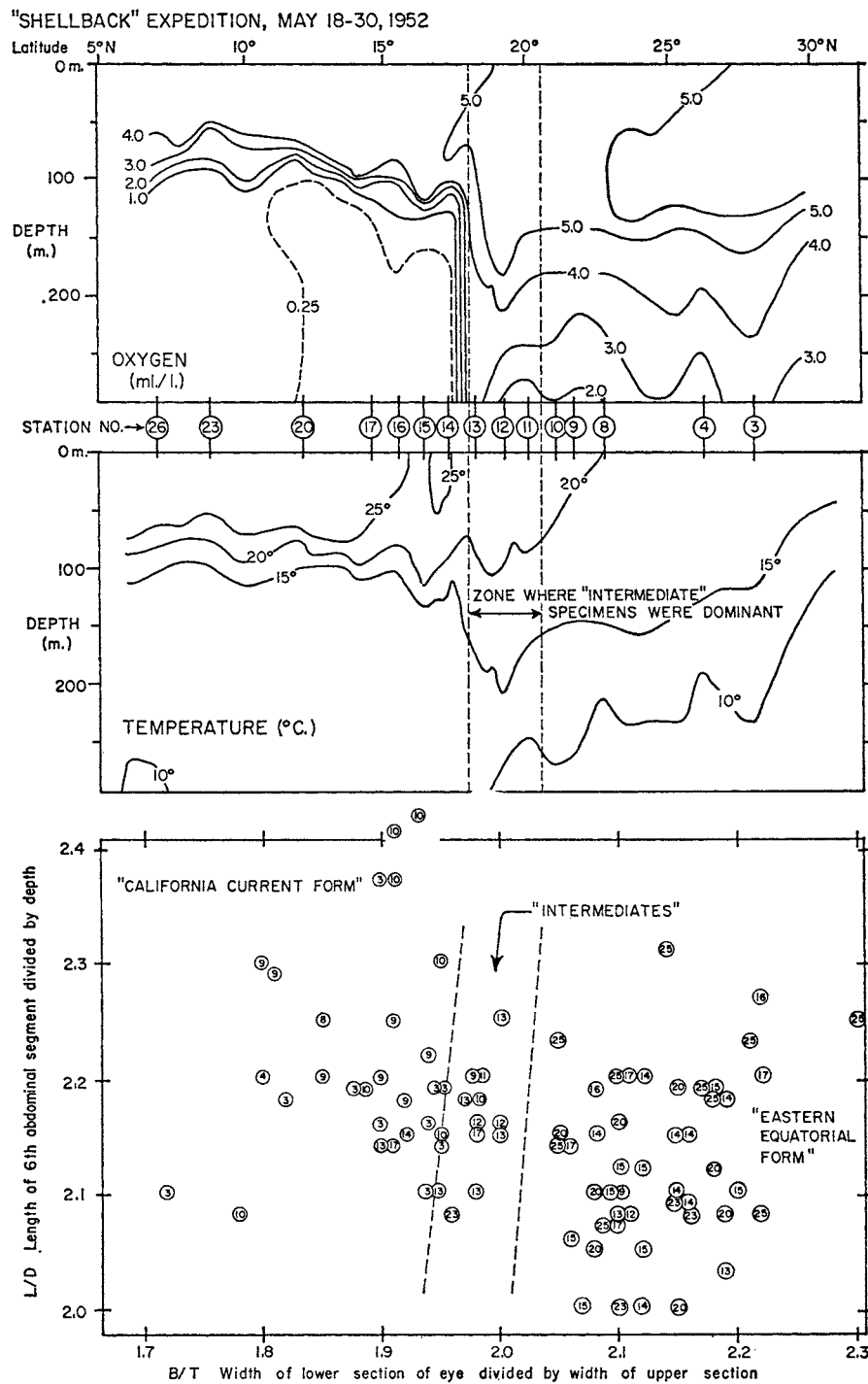


Fig. 93c. Profiles of the distribution of temperature and oxygen for "Shellback" expedition Stations 3–26, and plot of specimens of *Stylocheiron affine* from the same stations based on measurements of the sixth abdominal segment and the eye. Plots on scatter diagram include the number of the station at which the specimens were collected. Specimens designated "intermediate" were dominant at Stations 11–13. The "California Current Form" was dominant at Stations 3–10 and the "Eastern Equatorial Form" at Stations 14–26.

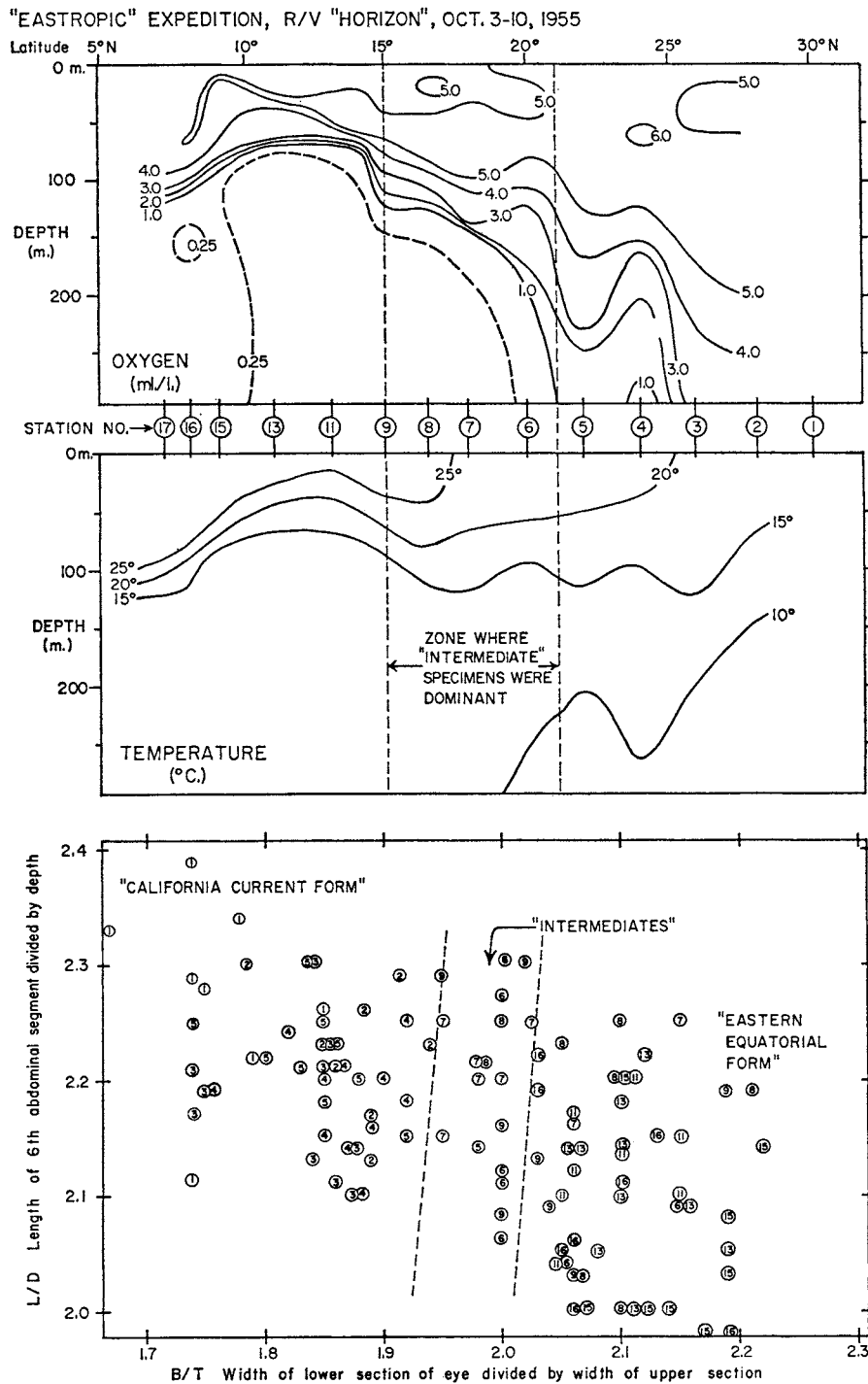


Fig. 93d. Profiles of the distribution of temperature and oxygen for "Eastropic" expedition Stations 1-17, and plot of specimens of *Stylocheiron affine* from the same stations based on measurements of the sixth abdominal segment and the eye. Plots on scatter diagram include the number of the station at which the specimens were collected. Specimens designated "intermediate" were dominant at Stations 6-8. The "California Current Form" was dominant at Stations 1-5 and the "Eastern Equatorial Form" at Stations 11-17.

is found where the overlap is least, that is, farther south, in a region where a given epipelagic population might retain its geographical position more readily than in the equatorial current system.

Seven specimens that agree with the "Eastern Equatorial Form" were found near 11° S., north of the Fiji Islands (figs. 93b, 94). It is not known whether these

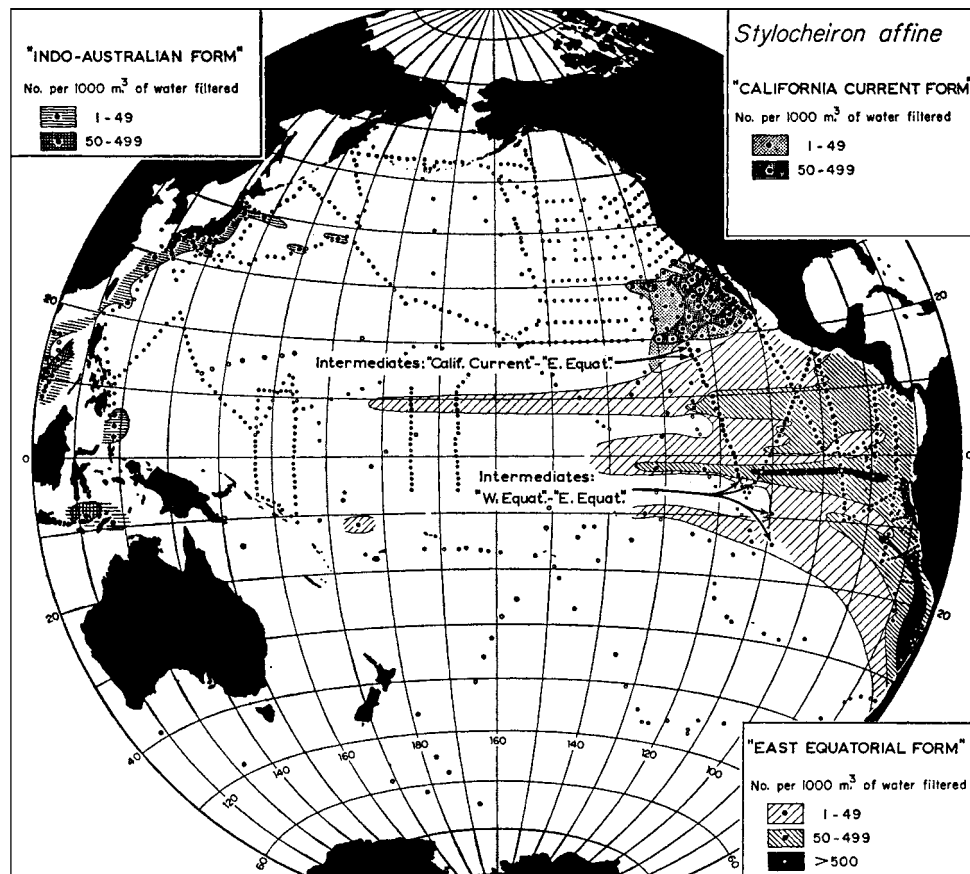


Fig. 94. Geographical distribution of the "California Current," "Eastern Equatorial," and "Indo-Australian" forms of *Stylocheiron affine*. The locations of records of specimens believed to be intergrades between adjoining forms are indicated.

were carried from the eastern Pacific, or represent a sixth form of *S. affine* centering in the southwestern Pacific, not yet sampled by the Scripps surveys.

Stylocheiron affine, "Western Equatorial Form"

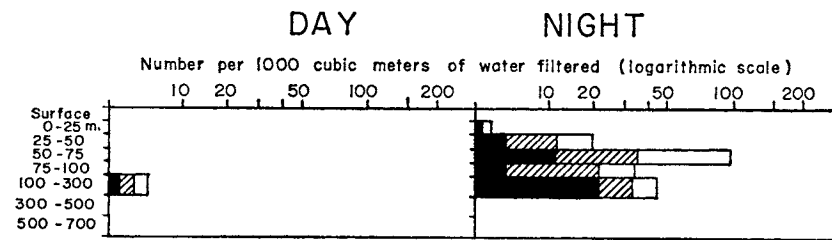
(Figs. 92, e-f, 93a, 93b, 96)

The lower part of the eye is 1.67–2.16 times as wide as the upper part. The upper part of the adult eye has 4–6 cones in a transverse row. The length of the sixth abdominal segment is 1.56–1.93 times the depth.

The axis of the distribution of this form is the equator. Small numbers are carried

Stylocheiron affine "California Current Form"

Vertical Distribution, Offshore Baja California Pelagic Area



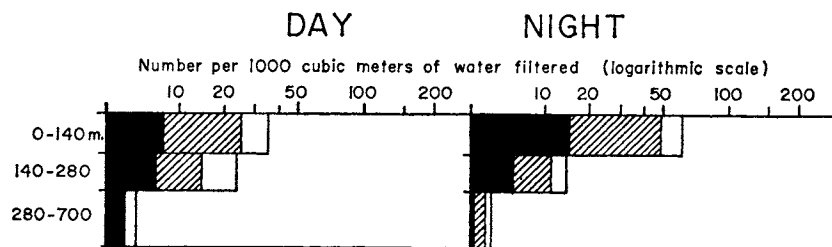
Vertical Distribution, Eastern North Pacific (Norpac)



a.

Stylocheiron affine "Central Form"

Vertical Distribution, North Pacific (Transpacific, Norpac)



b.

Fig. 95. Vertical distributions. a. The "California Current Form."
b. The "Central Form" of *Stylocheiron affine*.

northward near to Japan by the Kuroshio system; otherwise, the range lies entirely between 17° N. and 17° S. The occurrence of intergrades between this form and the "Eastern Equatorial Form" was described above. Specimens that may be intermediate (Intermediates "W.E.-C.," fig. 93b) between the "Western Equatorial Form" and a "Central Form" (discussed below) were found at four localities in the western Pacific (fig. 95). Three of these were widely separated geographically, but all were in regions where the range of the "Western Equatorial Form" slightly overlapped that of the "Central Form."

The "Western Equatorial"-"Central" intermediates (nineteen specimens in

all) were conspicuous because of the large size of the eye, 1.05–1.15 mm. long (agreeing with the “Central Form”), and the range of the sixth abdominal segment L/D values of 1.50–1.70—high for the “Central Form” and more in agreement with the “Western Equatorial Form.”

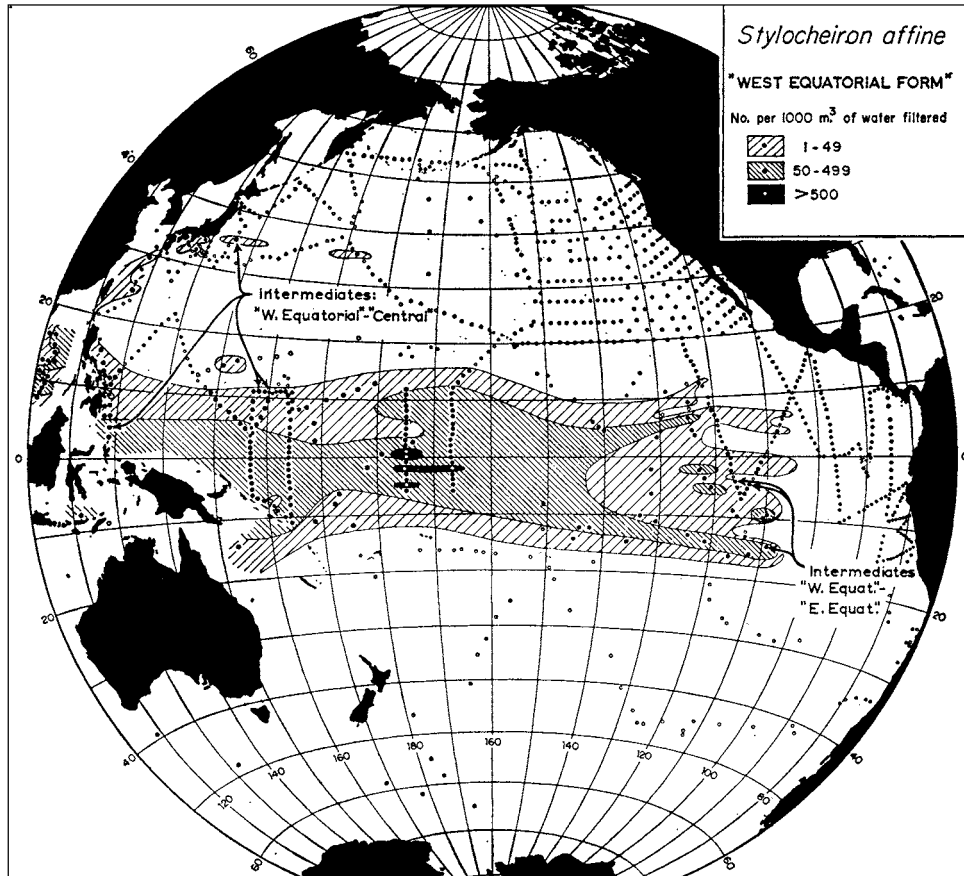


Fig. 96. Geographical distribution of the “Western Equatorial Form” of *Stylocheiron affine*. The locations of records of specimens believed to be intergrades between forms are indicated.

Stylocheiron affine, “Central Form”

(Figs. 92, g–h, 93b, 95, 97)

The eye of this form is larger than that of any of the other forms. The range of length of the eye, measured for adults from all parts of the distribution, was 1.00–1.25 mm. The sixth abdominal segment is shorter than in the other forms: the range of L/D values (1.40–1.58) scarcely overlapped the range of those values for the “Western Equatorial Form.” Similarly, there was little overlap in the sixth abdominal segment B/T ranges of these two forms: 1.45–1.78 for the “Central Form” and 1.67–2.16 for the “Western Equatorial Form.”

Specimens found in the western Pacific that are believed to be intermediate between the two forms were discussed in the preceding section dealing with the “Western Equatorial Form.”

The most westerly part of the range of the “Central Form” overlaps that of the “California Current Form,” but no specimen resembling an intergrade between the two has been found there. Rather, the “Central Form” of *Stylocheiron affine* bears a closer resemblance to a “Short Form” of *S. longicorne* (to be discussed) than to the “California Current Form” of *S. affine*.

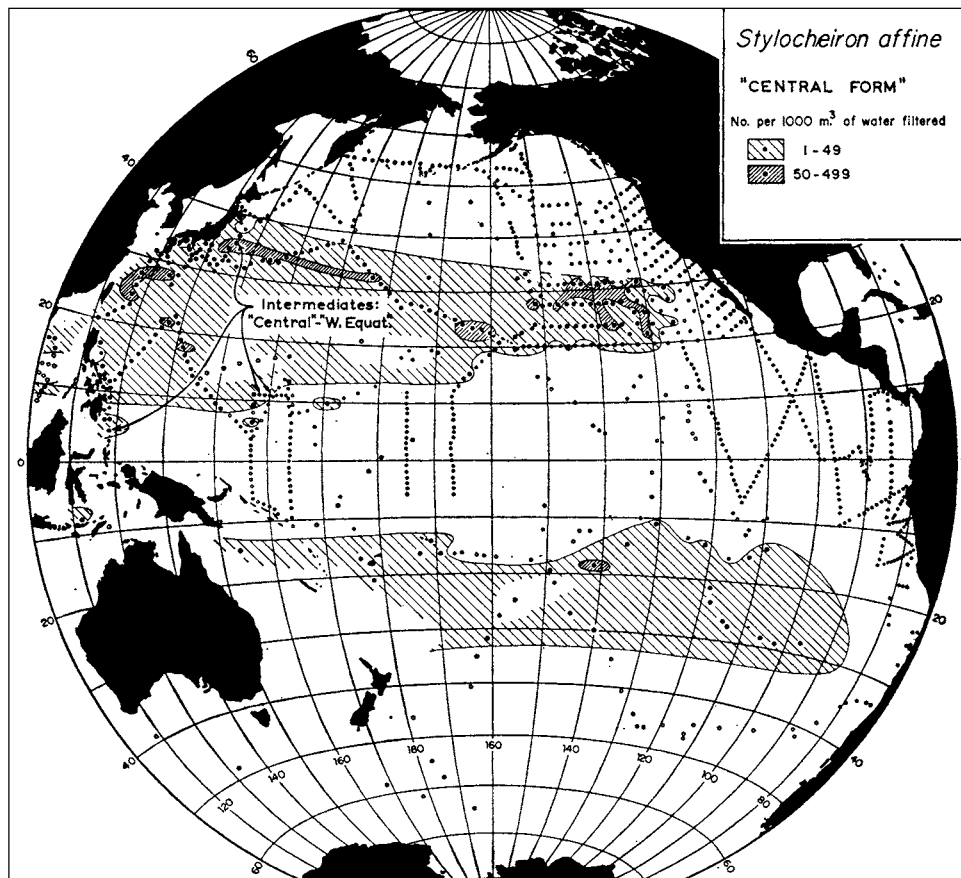


Fig. 97. Geographical distribution of the “Central Form” of *Stylocheiron affine*. The locations of records of specimens believed to be intergrades with the “Western Equatorial Form” are indicated.

Stylocheiron affine, “Indo-Australian Form”

(Figs. 92, *i-j*, 93b, 94)

The upper part of the eye is narrow in this form and bears no more than four crystalline cones in a transverse row. The lower part of the eye is 2.26–2.55 times as wide as the upper part. The length of the sixth abdominal segment is less than twice the depth of the segment. This form is smaller than the other forms of *S. affine*: the largest adult measured 7.3 mm.

A total of 36 specimens were found at 17 stations along the western edge of the Pacific sampled by the “Troll” and “Transpacific” expeditions. The most northerly records are from the region of the Kuroshio, west of Japan.

The “Western Equatorial” and “Indo-Australian” forms were both present in the “Naga” expedition material from the South China Sea, though there the “Western Equatorial Form” was dominant.

A more positive evaluation of the taxonomic status of the above geographical forms and of those found in the next species to be considered, *S. longicorne*, will be deferred until collections from the Atlantic and Indian oceans can be examined. The evidence presented here relating to the question of phenotypic vs. genotypic differentiation in *S. affine* is discussed further in the section on distribution and species formation.

Stylocheiron longicorne G. O. Sars

Sars (1885) described *Stylocheiron longicorne* from a single specimen collected by the *Challenger* south of the Cape of Good Hope. He specified: “Last caudal segment scarcely longer than preceding. Eyes rather large and much compressed, with cornea very narrow, oblong, but slightly contracted in its upper part.”

Hansen (1911) subsequently noted variability in this species, particularly in respect to the proportions of the eye and of the sixth abdominal segment. He stated of *S. longicorne*: “Eyes very high, somewhat more than twice as high as broad below the middle, with the upper third nearly as broad as, or, in large females, sometimes even broader than, the lower third. . . . Sixth abdominal segment from half as long again to more than twice as long as deep, with the lower margin rounded flatly upwards toward the end.”

The Scripps material on this species has been studied with attention to variation in these characteristics in relation to geographical distribution.

Two forms were noted (figs. 98, 99), as compared with the five found in *S. affine*. However, the distributional range of each form of *S. longicorne* is more extensive than that of any of the forms of *S. affine*. As for *S. affine*, the eye B/T ratio (width of lower part divided by width of upper part) was plotted against the sixth abdominal segment L/D ratio (length divided by depth) for adult specimens of *S. longicorne* collected at scattered localities throughout the range of the species (figs. 93b, 99).

Stylocheiron longicorne, “Short Form”

(Figs. 98, *c-d*, 99, 100)

The sixth abdominal segment is almost twice as long as its depth. The upper part of the eye is rarely wider than the lower part; the lowest B/T value found was 1.0, and most fell in the range 1.2–1.4. Sars’s type specimen was of this form.

Stylocheiron longicorne, “Long Form”

(Figs. 98, *a-b*, 99, 100)

The sixth abdominal segment is more than twice as long as its depth. The upper part of the eye is often wider than the lower part; the known range of B/T for this form is 0.85–1.48.

Adults from the cold-water part of the range commonly have 7–9 crystalline cones in the most distal transverse row in the upper eye. Large specimens from the western equatorial Pacific have up to 18 cones in that row.

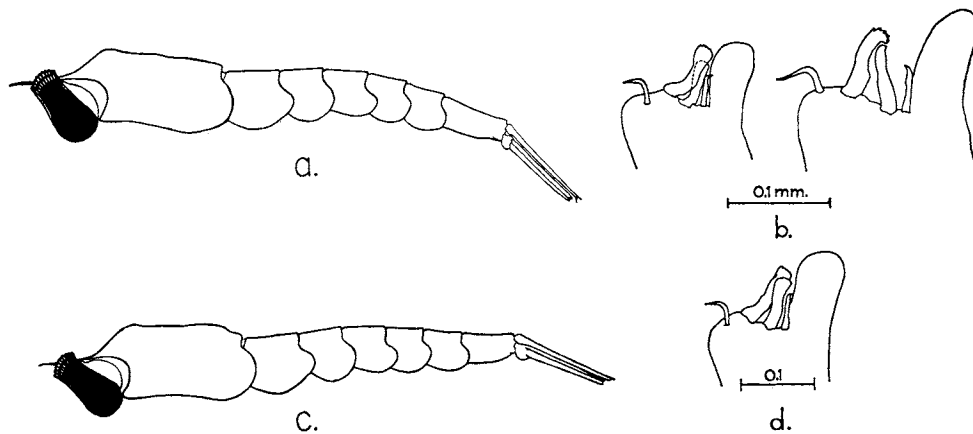


Fig. 98. Pacific forms of *Stylocheiron longicorne* in lateral aspect, and male copulatory organs. *a, b* "Long Form" (cop. organs of specimens 8.2 mm. long, $L/D = 2.14$ from "Naga" exped. Sta. 60-527, $9^{\circ} 54' N.$, $110^{\circ} 35' E.$, and 9.8 mm. long, $L/D = 2.20$, from "Norpac" exped. Sta. 157, $20^{\circ} 03' N.$, $150^{\circ} 01' W.$). *c, d.* "Short Form" (cop. organ from specimen 7.1 mm. long, $L/D = 1.92$, from "Norpac" exped. Sta. 80, $31^{\circ} 08.5' N.$, $143^{\circ} 39' W.$).

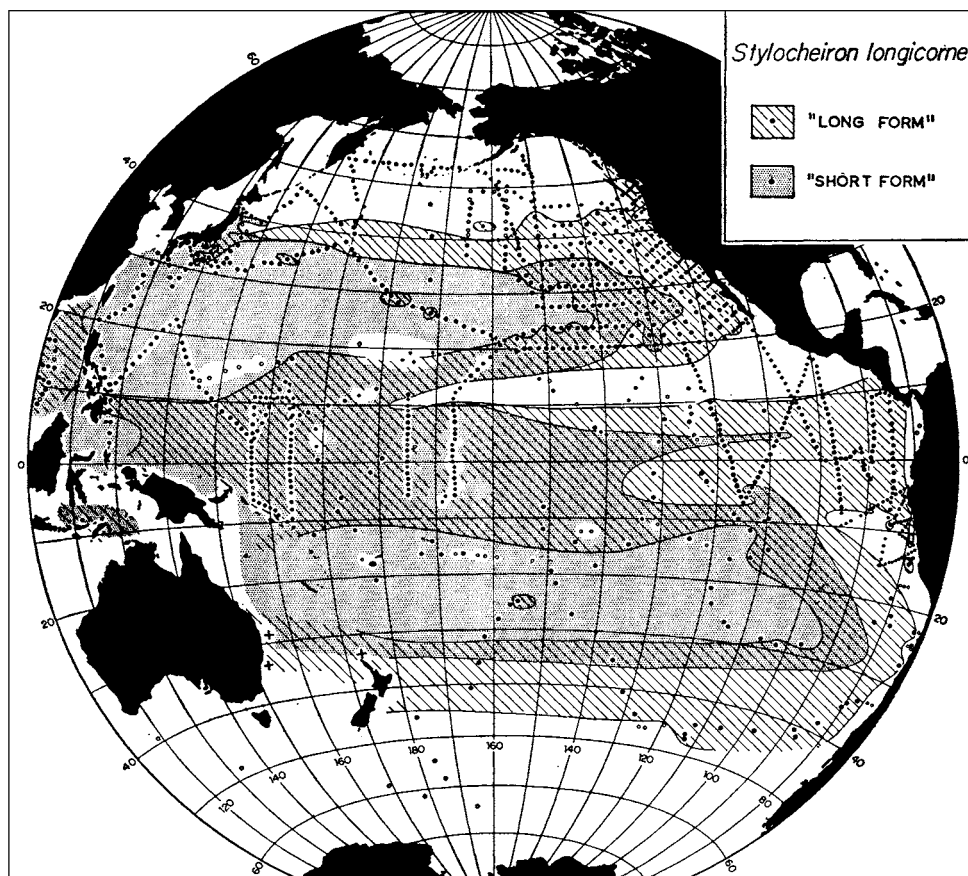
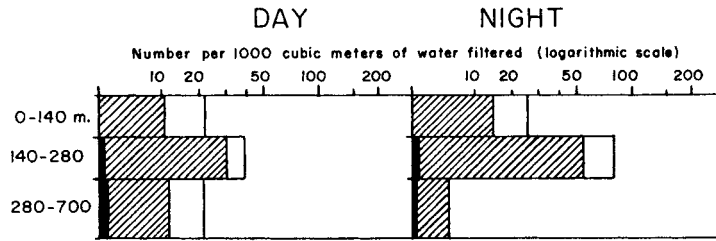


Fig. 99. Geographical distribution of two Pacific forms of *Stylocheiron longicorne*.

Stylocheiron longicorne "Short Form"

Vertical Distribution, North Pacific (Transpacific, Norpac)



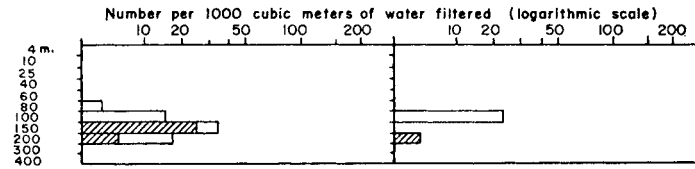
a.

Stylocheiron longicorne "Long Form"

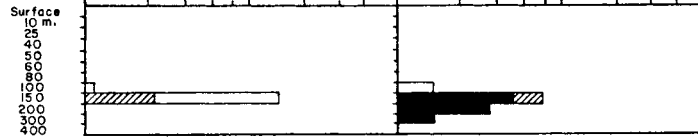
Vertical Distribution, Inshore Southern California

DAY NIGHT

C.C.O.F.I. Station 90.28, June 12-13, 1952



C.C.O.F.I. Station 90⁶.38, March 4-5, 1953



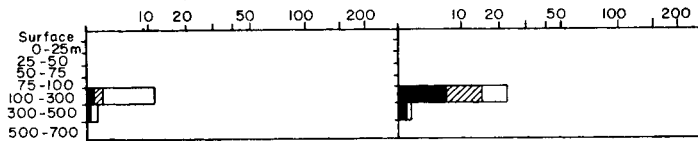
b.

Stylocheiron longicorne "Long Form"

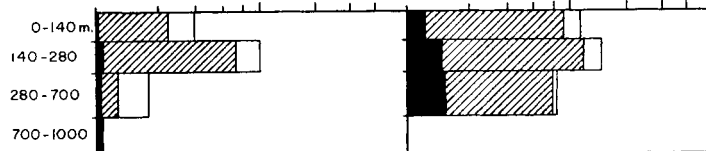
Vertical Distribution, Offshore Baja California Pelagic Area

DAY NIGHT

Number per 1000 cubic meters of water filtered (logarithmic scale)



Vertical Distribution, North Pacific (Transpacific, Norpac)



c.

Fig. 100. Vertical distributions of *Stylocheiron longicorne*.
a. "Short Form." b, c. "Long Form."

In specimens of *S. longicorne* having a very short sixth abdominal segment ($L/D < 1.75$), the upper part of the eye is relatively narrower ($B/T > 1.27$) than in specimens having longer sixth segments. For the long form of the species there is a scatter of points in figure 93b suggesting a relationship of B/T to L/D that is the converse of that found for the short form: when B/T is large in the long form, L/D is small; and when B/T is small, L/D is large. The position on the scatter diagram at which this trend is reversed ($L/D \sim 2.00$) was taken as the line of separation between the two forms.

Specimens having the widest upper parts of the eye were found most frequently in the warmest parts of the Central Water masses and in the most westerly part of the ocean. This was true of both the "Long Form" and the "Short Form" of the species. Apparently the "Long Form" lives somewhat deeper in these warm regions than in the cold-water part of the range; in the warm western equatorial region the adult was caught in the daytime only in tows reaching a depth of at least 300 meters. Thus, the wide upper eye appears to be associated with the warm-water part of the range of both forms of *S. longicorne*.

The relatively narrow upper eye ($B/T < 1.27$) was most frequently found in regions of the North and the South Pacific that are oceanographically analagous to each other: the eastern part of the North Pacific Central Water Mass, approximately 20° – 30° N., 130° – 145° W., and three "Downwind" expedition stations in the eastern South Pacific: $34^{\circ} 50'$ S., $135^{\circ} 53'$ W.; $14^{\circ} 17'$ S., $108^{\circ} 52'$ W.; $9^{\circ} 13'$ S., $109^{\circ} 42'$ W. These localities are in regions where intermediacy between the two forms is approached.

Thus, in each hemisphere the "Long Form" was found in the epipelagic region to the east of the zone of intergradation between the two forms, and in the cool waters of the West Wind Drift. It was found, though in smaller numbers, in cool subsurface waters near the equator. It was still rarer in the western Pacific where it appeared to have its greatest vertical range.

The "Short Form" of *S. longicorne* is adapted to the central regions of the Pacific. The northern and southern ranges coalesce in the mid-Pacific and the western Pacific. A few individuals were found in the eastern equatorial basin at the latitude of the Equatorial Countercurrent.

S. longicorne lives deeper than *S. affine*. Most of the population is below 140 meters during both day and night (fig. 100). *S. affine* was found mainly above 140 meters (fig. 95). Nevertheless, substantial numbers of both the "California Current" and "Central" forms of *S. affine* were caught at a depth of more than 140 meters during the "Norpac" and "Transpacific" expeditions; *S. longicorne* was frequently found at 0–140 meters, though the greater density of the population was at deeper levels.

VERTICAL ZONATION

The euphausiid species may be grouped according to their vertical ranges. Nearly all species were concentrated at greater depths during the day than at night. The diagrams of the average day and night vertical distributions (figs. 16, 18, etc.) show that the *Euphausia* species and certain *Nematoscelis*, *Nematobranchion*, and *Thysanopoda* species perform strong diurnal migrations that agree in amplitude with the known range of vertical movement of the deep sound scattering layer:

0–600 meters in clear central water, and 0–200 or 0–300 meters in northern waters and in the cold part of the California Current. The *Stylocheiron* species, *Bentheuphausia*, *Thysanopoda cornuta*, and *T. egregia* apparently do not migrate diurnally, yet they live in a habitat having an extensive vertical dimension—about 300

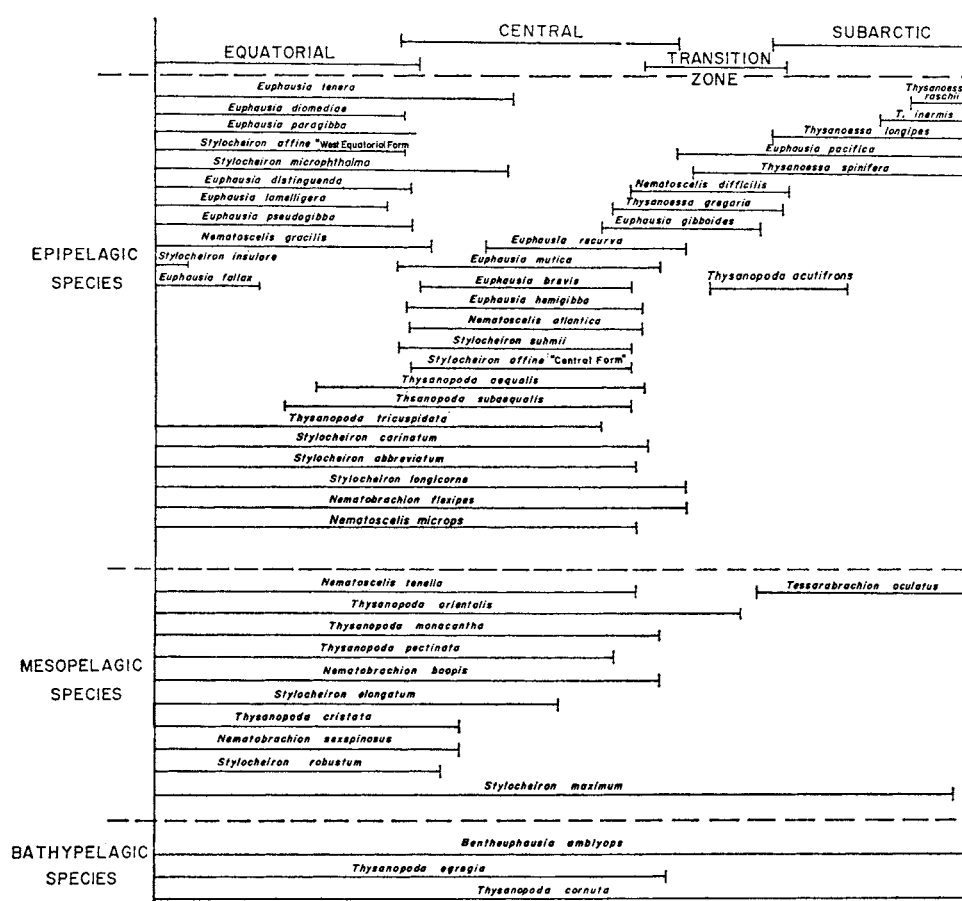


Fig. 101. Species composition of bathymetric euphausiid associations in the North Pacific. Relationships to horizontal zones are also indicated.

meters for *Stylocheiron affine* and *S. suhmii*, to 2,000 or more meters for the deepest-living *Thysanopoda* species.

The furcilia larvae of most species were concentrated above a depth of 280 meters at all times. Exceptions included furcilia of the mesopelagic *Stylocheiron elongatum* and *S. longicorne* and the bathypelagic *Thysanopoda cornuta*, *T. egregia*, and *Bentheuphausia amblyops*. Larvae of *B. amblyops* are not known. The vertical ranges of immature euphausiids were usually intermediate between the ranges of the adults and the furcilia. Groupings of the species according to bathymetric zones (figs. 101, 102) are based on the ranges of adult and immature specimens. These zones are distinguished as the sampled strata in which concentrations were found to be densest, that is, those strata through which the diurnal migration was typically carried out.

Vertical zones are identified for each of the geographical groupings of species—subarctic, transitional, central, and equatorial—to be summarized in the next section.

The epipelagic zone distinguished on the basis of euphausiid distributions is somewhat thicker than that recognized for the pelagic fauna as a whole.

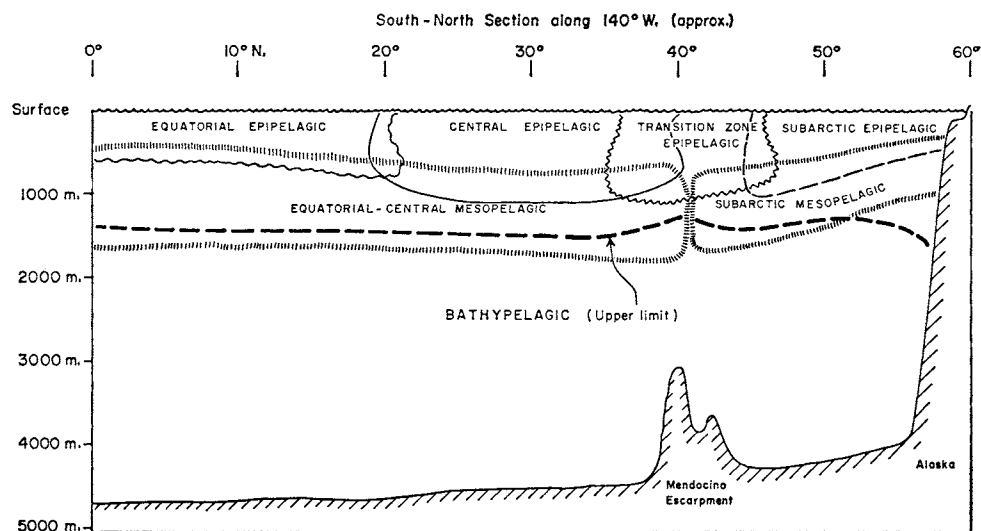


Fig. 102. Bathymetric and latitudinal zonation of associations of euphausiid species in mid-oceanic profile in the North Pacific.

Bruun (1957) described the epipelagic zone as the photic layer proper, about 200 meters thick in clear subtropical areas but sometimes thinner than 100 meters in regions of high productivity. Such a zone would therefore harbor those vertical migrants that descend only to a depth of 200 meters in the daytime. These would include larvae and immature stages of most euphausiids. However, 0–200 meters of depth would encompass only the nighttime habitat of adults of the many warm-water species that migrate between the surface and 300–700 meters of depth. Bruun gave the name *thermosphere* to the upper layer of tropical and subtropical seas that is warmer than 10° C. and he called the deeper cold zone the *psychrosphere*. The boundary between these zones is near 700 meters in warm waters. Thus, euphausiids associated with the deep scattering layers migrate within the thermosphere. Inasmuch as these species are near the surface at night and, during daylight hours, are believed to migrate vertically in response to the changing intensity of light (a dominating ecological feature of the epipelagic zone), they will be regarded here as epipelagic species.

Subarctic and coastal epipelagic species were found to inhabit the 0–280-meter layer. The psychrosphere is again found near the surface along the equator and the 10° N. parallel, where three equatorial euphausiid species appear to be limited to the 0–300-meter stratum. Epipelagic species inhabiting the warm deep pools of the Central Water masses have the most extensive vertical ranges, approaching 700 meters.

EPIPELAGIC ZONE

Subarctic epipelagic:	
<i>Thysanoessa raschii</i>	}
<i>T. inermis</i>	
<i>T. spinifera</i>	
<i>T. longipes</i>	
<i>Euphausia pacifica</i>	
	0-280 meters
Transition-zone epipelagic:	
<i>Nematoscelis difficilis</i>	}
<i>Euphausia pacifica</i>	
	0-280 meters
<i>Thysanoessa gregaria</i>	}
<i>Euphausia gibboides</i>	
<i>Thysanopoda acutifrons</i>	
	0-700 meters
Central epipelagic:	
<i>Thysanopoda obtusifrons</i>	}
<i>T. aequalis, T. subaequalis</i>	
<i>Euphausia brevis</i>	
<i>E. mutica</i>	
<i>E. recurva</i>	
<i>E. hemigibba</i> (North Pacific)	
<i>E. gibba</i> (South Pacific)	
<i>Nematoscelis atlantica</i>	
<i>N. microps</i>	
<i>Stylocheiron carinatum</i>	
<i>S. abbreviatum</i>	
<i>S. suhmii</i>	
<i>S. affine</i> "Central Form"	
<i>Nematobrachion flexipes</i>	
	0-700 meters
Equatorial epipelagic:	
<i>Euphausia tenera</i>	}
<i>E. distinguenda</i>	
<i>Stylocheiron microphthalmum</i>	}
<i>Thysanopoda tricuspidata</i>	
<i>Euphausia diomediae</i>	
<i>E. eximia</i>	
<i>E. lamelligera</i>	
<i>E. fallax</i>	
<i>Nematoscelis gracilis</i>	
<i>Stylocheiron affine</i>	
W. Equatorial Form"	
"E. Equatorial Form"	
"Indo-Australian Form"	
	0-700 meters

The mesopelagic euphausiid species occupy a stratum that overlaps the deeper part of the epipelagic zone. The upper limit of the mesopelagic zone may be as shallow as 140 meters in subarctic waters or as deep as 400-500 meters in the central region. Adults of the 13 species of this group do not migrate into the photic layer; their daytime habitat is typically between depths of 500 and 1,000 meters. According to Hedgpeth (1957) the mesopelagic zone lies between about 200 and 1,000 meters.

Most mesopelagic species are larger than their epipelagic counterparts. For example, *Thysanopoda orientalis* (25-35 mm.) and *T. pectinata* (25-40 mm.), both of which perform extensive vertical migrations, attain more than twice the

length of *Thysanopoda obtusifrons* or *T. aequalis*. Similarly the nonmigrating mesopelagic species *Stylocheiron maximum* and *S. elongatum* are much larger than the related epipelagic species *S. abbreviatum* and *S. affine*. The exception to the rule is *Thysanoessa parva*, which, though living at 500–700 meters, is the smallest species in its genus.

The horizontal ranges of mesopelagic species may be broad or narrow. In general they are broad. *Stylocheiron maximum* (fig. 81) has been found in all oceans but the Arctic, whereas *Thysanoessa parva* (fig. 59) is known to occur only in pockets of distribution in central waters, at the warm-water limits of the range of the allied species *T. gregaria*.

The subarctic species *Tessarabrachion oculatus* is provisionally included in the mesopelagic group. Adults are sometimes found in the 0–140-meter layer, but the vertical range of this species is greater than that of such typical epipelagic subarctic species as *Thysanoessa longipes* and *Euphausia pacifica*.

Seven mesopelagic species occupy both Central and Equatorial waters. In general, however, they are lacking in the belt 10°–20° N. in the eastern equatorial Pacific where the subsurface concentration of dissolved oxygen is extremely low. They are also lacking in the regions of the California and Peru currents but are found in the eastern equatorial basin in the zone of the Equatorial Countercurrent, 0°–10° N.

Three of the four mesopelagic species restricted to Central waters have similar patterns of distribution. (The more limited range of *Thysanoessa parva* is anomalous.) North Pacific and South Pacific ranges of *Nematobranchion sexspinosus* (fig. 74), *Thysanopoda cristata* (fig. 12), and *Stylocheiron robustum* (fig. 84) are widely separated in the eastern Pacific but merge in the western tropical Pacific.

MESOPELAGIC ZONE	
Cosmopolitan mesopelagic	
<i>Stylocheiron maximum</i>	140–1,000 meters
Subarctic mesopelagic	
<i>Tessarabrachion oculatus</i>	0–1,000 meters
Central-Equatorial mesopelagic (ca. 40° N.–40° S.)	
<i>Stylocheiron longicorne</i>	140–700 meters
<i>S. elongatum</i>	}
<i>Thysanopoda pectinata</i>	
<i>T. orientalis</i>	
<i>T. monacantha</i>	
<i>Nematoscelis tenella</i>	
<i>Nematobranchion boopis</i>	140–1,000 meters
Central mesopelagic:	
<i>Thysanoessa parva</i> (?)	}
<i>Nematobranchion sexspinosus</i>	
<i>Stylocheiron robustum</i>	
<i>Thysanopoda cristata</i>	
	280–1,000 meters
BATHYPELAGIC ZONE	
<i>Thysanopoda cornuta</i>	
<i>T. egregia</i>	
<i>T. spinicaudata</i>	
<i>Bentheuphausia amblyops</i>	

Both larvae and adults of *Thysanopoda cornuta* inhabit waters deeper than 500 meters. Adults were not caught unless the net reached a depth of at least 1,000 meters. Immature stages of *Thysanopoda egregia* and *Bentheuphausia amblyops* were exceedingly rare in the 140–280-meter layer, occurring typically deeper than about 500 meters. Adults of *B. amblyops* were not consistently caught unless a depth of at least 1,000 meters was sampled. The largest specimens of *T. egregia* (43–62 mm. in length), probably not yet mature, are known only from hauls reaching to at least 1,500 meters. The six known specimens of *T. spinicaudata* are all from hauls sampling to depths of 2,000 meters or more.

Thysanopoda cornuta and *Bentheuphausia amblyops* are cosmopolitan species of the bathypelagic zone, whereas *T. egregia* occurs only from 40° N. to 55° S. An explanation (p. 84) of the limited range of *T. egregia* was based on the fact that the larvae live at lesser depths than larvae of the other bathypelagic species, occurring most consistently in the 280–500-meter layer.

HORIZONTAL ZONATION

The biogeographical boundary often agrees with the limit of the physical province of the high seas, using the criterion of water mass. Water masses formed as a consequence of the sinking and mixing of water in specific local regions are identified over extensive areas by means of characteristic relationships of temperature to salinity, considered in detail by Sverdrup, Johnson, and Fleming (1942). The species boundary appears the more discrete, being based on presence or absence of organisms in a given sample. The water-mass boundary is recognized as a zone of convergence frequently associated with sharp horizontal gradients in temperature, the classical zoögeographical parameter. The distributions of subspecific forms (subspecies, races, ecophenotypes) may also correspond with physical zones. On the other hand, such forms are found sometimes in adjoining parts of one water mass, forming an allopatric complex. Nevertheless, each distribution is dependent upon a system of circulation, either an oceanic gyral or a current with associated countercurrents. These maintain both the water masses and the distribution of temperature that relates conspicuously to euphausiid distributions.

In the long run, planktonic species must depend for survival on ability to adapt to gradually changing oceanic climate. This may be accomplished if the distribution adjusts to new oceanic areas suitable from the standpoint of the tolerances of the species. If these new areas are not sustained by sufficiently closed current systems, species may become extinct where a tendency develops for populations to be swept downstream into waters mixed with those of a too-alien environment. The biological evolution of drifting organisms is believed to proceed according to the availability of habitats that can conserve a stock.

Furthermore, the vertical ranges of a number of planktonic species appear to correspond with the vertical extent of the water mass and its contained currents. For example, in temperate and tropical seas where many euphausiids perform diurnal vertical migrations between the surface and 300–800 meters of depth, the water masses are identified according to the temperature-salinity characteristics between depths of 200 and 1,000 meters or more. This layer is as thick as the mesopelagic zone, which also lies at about 200–1,000 meters.

Water masses arise in centers or zones where surface water sinks beneath lighter water along isopycnal interfaces giving rise to the uniform habitats that have both extensive breadth and depth. Temperature in relation to salinity defines the water mass. However, it is not to be underemphasized that temperature *per se* is a factor having a broad application to the ecology of plankton. Bruun (1957) stressed its important role in vertical zonation. The geographical ranges of species inhabiting the epipelagic or photic zone often appear to be limited by near-surface isotherms. Similarly, the boundaries of mesopelagic species conform with the positions of isotherms lying at some depth within the vertical range of the species. Inasmuch as many species have an extensive diurnal range that carries them through a vertical temperature gradient of as much as 10°–12° C., it is not possible, at present, to establish that a boundary isotherm can limit a horizontal range. However, limiting temperatures may be associated with feeding or physiological functions carried out at particular depths.

In each of the several systematic groups studied thus far in the oceanwide zoöplankton collections made by CalCOFI, POFI, and the Scripps Institution, certain species have been recognized as having geographical distributions that have a close analogy with the major water-mass provinces. Pelagic foraminifera (Bradshaw, 1959), chaetognaths (Bieri, 1959), and the euphausiid crustaceans discussed here each include species limited to subarctic, subtropical, and tropical zones. The ecological zones are designated *subarctic*, *central*, and *equatorial*, following the clear role played by the water masses in the physical zonation of the high seas. Ebeling's (in press) study of the melamphaeid fishes indicates that water masses are regulating factors in the distribution of bathypelagic vertebrates also.

A fourth Pacific faunal zone lies in temperate waters at the northern limit of the central region. In the western and mid-Pacific this is an area of transition between central and subarctic faunas, occupying water of the North Pacific Drift. In the eastern Pacific it encompasses the California Current and the associated deep and coastal countercurrents. This zone agrees geographically with a "Transition region" off California and Baja California, where Subarctic Water converges with Equatorial Water (Sverdrup and Fleming, 1941). In the western Pacific this transition zone is a narrow east-west belt in the region of 35°–45° N., but toward its eastern limit it diverges: a northern branch loses its identity in the eastern part of the Gulf of Alaska, and a southern branch is replaced by Equatorial Water off Baja California at 20°–30° N. Certain widely distributed species maintain their highest concentrations in this *transition zone*. Other species are endemic to it.

Another zone of transition lies in the southern hemisphere, 35°–45° S., reaching northward in offshore waters of the Peru Current. This belt includes the Subtropical Convergence and the northern part of the West Wind Drift. It is the habitat of endemic species and of certain antitropical species found also in the transition zone of the northern hemisphere.

THE PACIFIC SUBARCTIC SPECIES

The four subarctic euphausiids *Thysanoessa inermis*, *T. longipes*, *Tessarabrachion oculatus*, and *Euphausia pacifica* (*E. pacifica* lives also in the transition zone) are concentrated between 45° N. and 55° N., north of the North Pacific Drift. Three *Euphausia* species of the Southern Hemisphere (fig. 103) occupy a subantarctic belt between the Subtropical and Antarctic convergences. None of these, *Euphausia*

lucens, *E. longirostris*, and *E. vallentini*, or the allied Peru Current species *E. mucronata*, are found in the Northern Hemisphere. Similarly, the subarctic species are limited to the Northern Hemisphere. In the part of this paper dealing with isolating mechanisms it will be pointed out that probably neither subarctic nor subantarctic species have transgressed the equator since they became differentiated from parental stocks. Of the subantarctic distributions, that of *E. lucens* is most

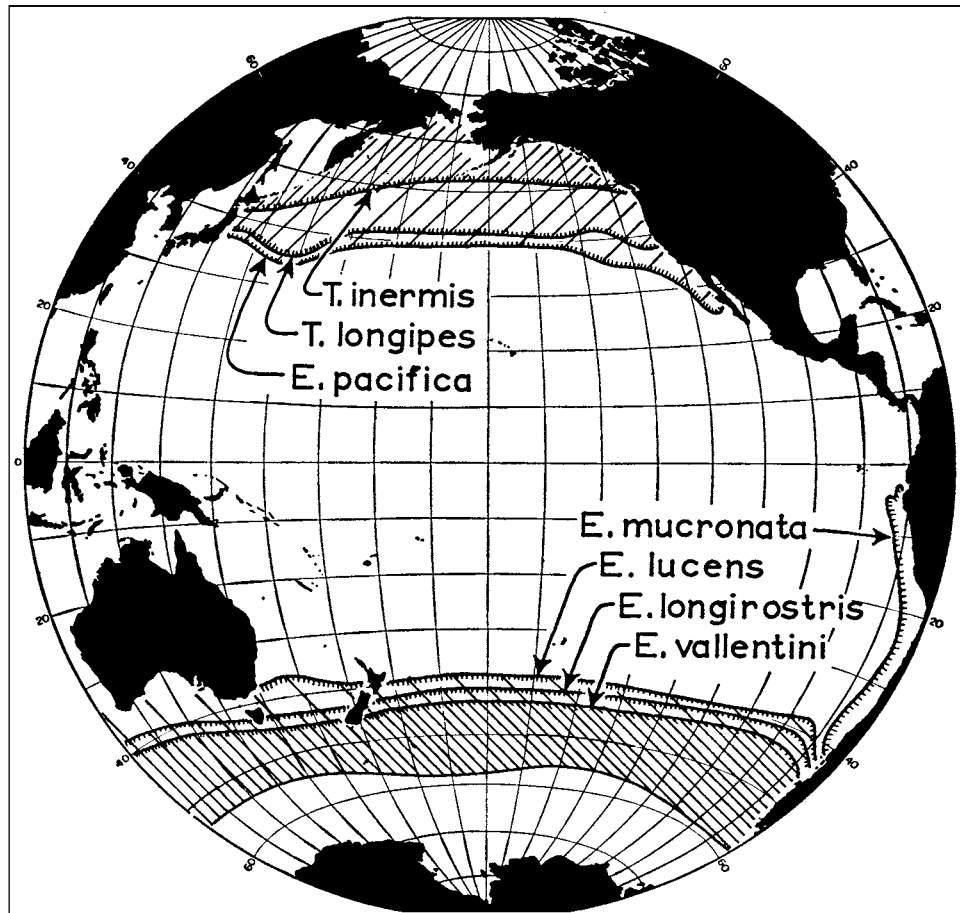


Fig. 103. Distributions of subarctic and subantarctic euphausiid species and *Euphausia mucronata*, a Peru Current species. None of these species is biantitropical (bipolar).

comparable geographically to the range of *E. pacifica* of the Northern Hemisphere. These are the two *Euphausia* species most similar in size and gross morphology. However, judging from the structure of the male copulatory organ, *E. lucens* is more closely related to the subantarctic and antarctic species *E. vallentini* and *E. superba* than to *E. pacifica*.

Other planktonic groups contain subarctic species. In the extreme western Pacific the copepod *Calanus tonsus* is abundant north of the convergence of the Oyashio and Kuroshio (Brodsky, 1955). Bogorov and Vinogradov (1955) included *Calanus cristatus*, *Sagitta elegans*, and the amphipod *Parathemisto japonica*

in the northern complex. Bieri (1959) showed that *Sagitta elegans* is limited to the subarctic zone throughout its North Pacific range.

Thysanoessa longipes (fig. 55) is a characteristic subarctic euphausiid. The “Spined Form” is more northern than the “Unspined Form” and is predominant in the Gulf of Alaska, and only the “Unspined Form” is found in the California Current, southward to 39°–40° N.

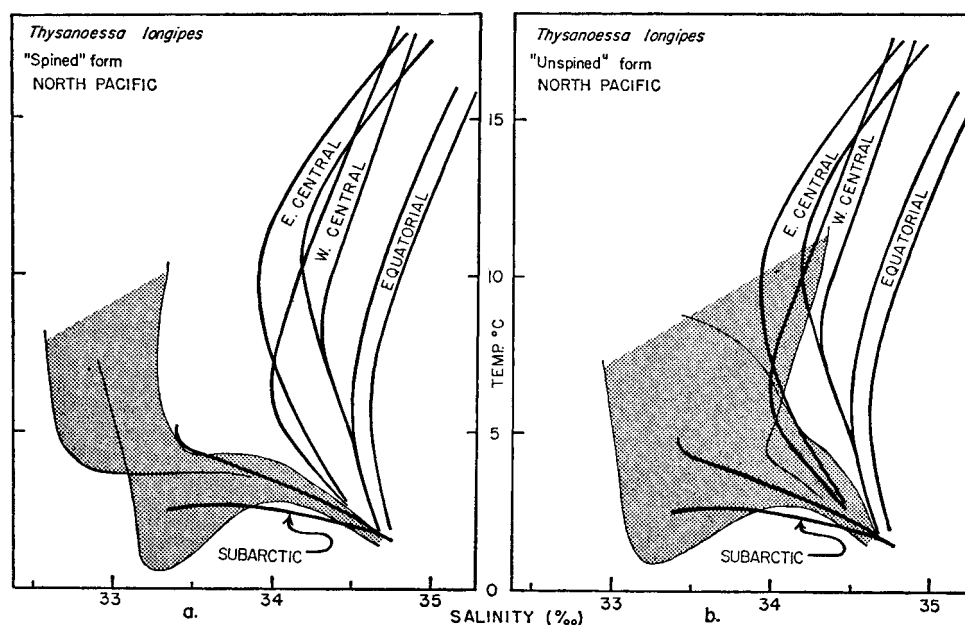


Fig. 104. Temperature-salinity characteristics below 100–150 meters in the subarctic habitat of *Thysanoessa longipes*, based on “Transpacific” and “Norpac” expedition observations. The shaded part is the T-S envelope enclosing T-S curves from stations at which *T. longipes* was caught. Certain extreme T-S curves are indicated as fine lines. The northern “Spined Form” (a) is seen to be more typically subarctic than (b) the “Unspined Form.” Water-mass envelopes are from Sverdrup, Johnson, and Fleming (1942).

Water-mass envelopes for *T. longipes* (fig. 104) confirm the subarctic nature of the water in which both forms of the species live. Water inhabited by “Spined” *T. longipes* is more nearly uniform with respect to the T-S relationship than that inhabited by the more southern “Unspined Form.” The environment of the latter, although remaining nearly subarctic in character below 300 meters, is strongly influenced above that depth by admixture of the North Pacific Drift. (The layer of maximum density of *T. longipes* during both day and night is 0–280 meters.) Populations of “Unspined” *T. longipes* are intermingled with the transition-zone species *Thysanoessa gregaria* (fig. 57) in the region 41°–45° N.

An area of abundance is evident in the distribution pattern of each form of *T. longipes*. The areas are separated from each other in mid-ocean by a belt of lower density having an east–west axis near 50° N., but converge off northern Japan at the western limit of both ranges. The two forms are tentatively regarded as ecophenotypes. It is not yet known whether they are genetically separate. The morphological distinctions, not evident in the young, appear to be brought about by

differences between the two environments: the temperature at 200 meters is below 4° C. in the range of the "Spined Form," but may be as high as 7° C. for the "Unspined Form."

Other northern species such as *Euphausia pacifica* have wider environmental tolerances, permitting them to range southward in the cool coastal waters off California. Such species persist until subarctic and upwelled components of the California Current become thoroughly mixed with Equatorial Water toward the south and with Central Water in the offshore region. The limits of the distribution of *E. pacifica* off Baja California fall where Subarctic and Equatorial waters are mixed in nearly equal proportions, according to the temperature-salinity characteristics of that region (Tibby, 1943). Seasonal variability in the southward extent of the distribution of *E. pacifica* in the California Current is to be discussed. This species is most closely allied with the subarctic region but inhabits much of the transition zone as well. There, its centers of distribution are in (1) Subarctic Water near the northern boundary of the North Pacific Drift, and (2) upwelled Subarctic Water of the California Current.

A relationship between the distribution of the aberrant polychaetous worm *Poebius meseres* and the Subarctic Water Mass was found by McGowan (1960). Though widely distributed in the 150–300-meter layer in the subarctic region, this species was caught at greater depths in the California Current and in the terminal part of the Peru Current between 6° S. and the Galápagos Islands (0° C.). Unlike *Euphausia pacifica*, *Poebius* submerges toward the southern limits of its range. The tropical records were of specimens believed to be sterile expatriates; it was suggested that their occurrence near the equator might be owing to a relationship between the Intermediate Water of the eastern tropical Pacific and Subarctic Water.

The part of the T-S curve representing the stratum of capture was used by McGowan to identify the water-mass habitat. This procedure is meaningful when the population maximum is encountered well within the column of water sampled. Stratified hauls carried out at 150-meter intervals by the "Transpacific" expedition made it possible to show a stratum of capture.

Records for most species are based on hauls made with open nets. Such hauls sometimes sample only the upper limits of an extensive vertical range, or may sample so thick a layer that the depth of capture cannot be determined. In these instances it may be useful to identify the water-mass habitat either by means of the full T-S curve, or by the part that relates to the usual vertical range of the species, if this is known.

THE TRANSITION-ZONE SPECIES

The region of transition between Subarctic Water and Central Water in the mid-Pacific and between Subarctic Water and Equatorial Water in the California Current is to be regarded as a biogeographical zone because it harbors (1) endemic species (*Nematoscelis difficilis* and the chaetognath *Sagitta scrippsae*), (2) antitropical species, limited, in the North Pacific, to this belt, and (3) maximum densities or regions of dominance of certain species having broader total ranges. A zone between the subantarctic and central regions in the Southern Hemisphere is distinguished in the same way.

In the western Pacific where the subarctic region is in contact with the warm Kuroshio and the Kuroshio Extension, a narrow transition zone has been recognized in which the copepod *Calanus pacificus* is particularly abundant (Bogorov and Vinogradov, 1955; Brodsky, 1955). In mid-ocean the transition zone was identified by Hida (1957) as an area of mixed fauna and variable biomass, usually characterized by large numbers of the

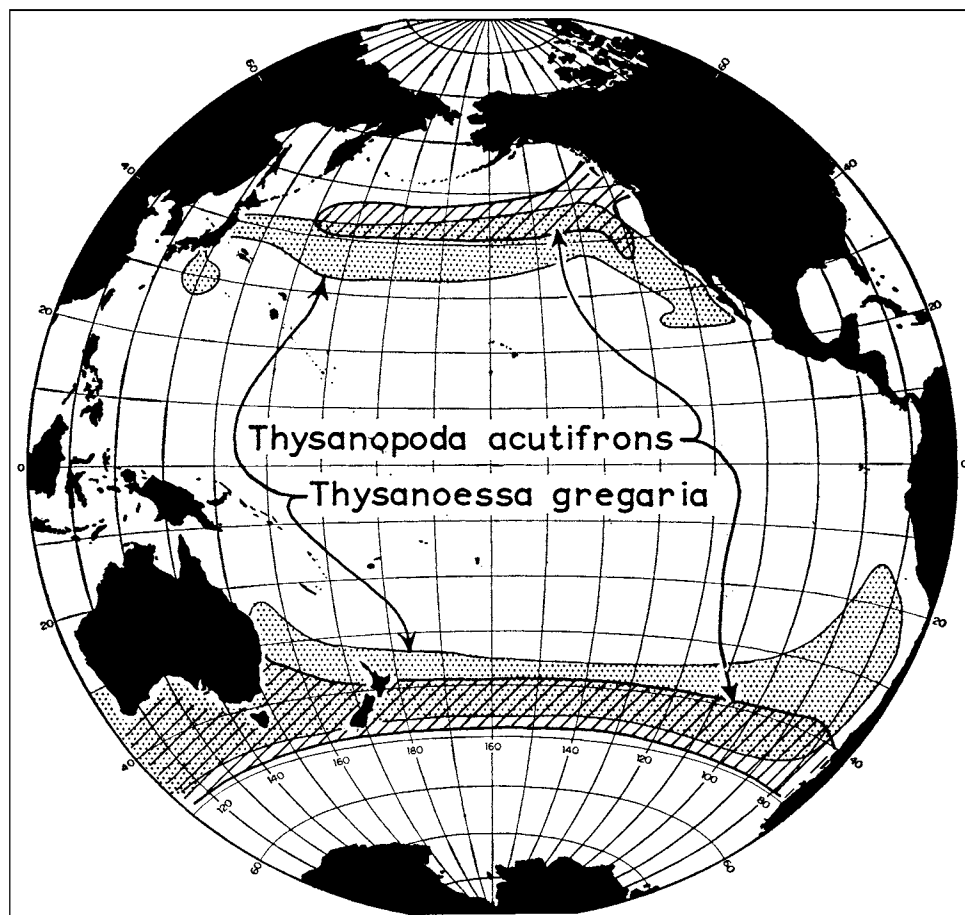


Fig. 105. Distributions of the transition-zone species *Thysanopoda acutifrons* and *Thysanoessa gregaria*. Species of this zone, which lies between subarctic (or subantarctic) and central waters, are all antitropical (bipolar).

pteropod *Limacina inflata*. A chaetognath identified by Hida as *Sagitta lyra* was abundant in the transition zone. This form, now distinguished from the more widespread *S. lyra* as *Sagitta scrippsae* (Alvariño, 1962), appears to be endemic to the transition zone.

The euphausiid *Nematoscelis difficilis* lives in this narrow belt made up by the North Pacific Drift and the California Current. *N. megalops*, a species very similar to *N. difficilis*, occupies the transition zone of the Southern Hemisphere and occurs in the Atlantic and Indian oceans as well. *N. megalops*, rather than *N. difficilis*, occupies the transitional belt in the North Atlantic.

The antitropical euphausiid *Thysanoessa gregaria* (fig. 105) lives in the transition zones of both hemispheres. Its mid-ocean, low-latitude boundaries are near the 33° parallels. In the eastern boundary currents the ranges reach toward the tropics until equatorial water is met. This is near 15° S. in the Peru Current and 18° N. in the California Current.

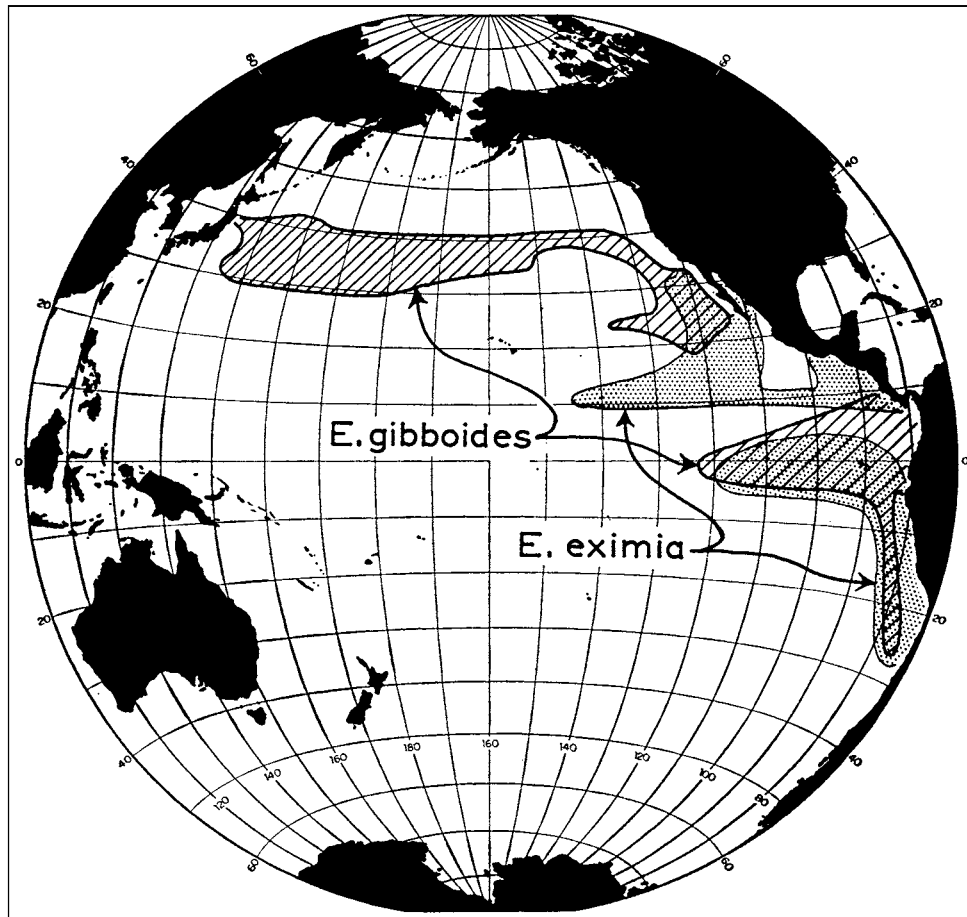


Fig. 106. Distributions of the large transition-zone–equatorial-zone *Euphausia* species *E. gibboides* and *E. eximia*, showing differences in ranges in the North Pacific and similarities in the South Pacific.

Thysanoessa gregaria and *Euphausia gibboides* are the euphausiids of the transition zone having the greatest tolerance for warm water, and *Thysanopoda acutifrons* (fig. 105) and *Euphausia pacifica* are the species of this group possessing the greatest tolerance for cold water, having affinities also with the subarctic zone. The *Nematoscelis difficilis*–*N. megalops* pair is intermediate with respect to temperature tolerance. *T. gregaria* is bounded in each hemisphere by the 7° C. and 11° C. isotherms at a depth of 200 meters, and the range of *T. acutifrons* is approximately circumscribed by the 4° and 8° C. isotherms at 200 meters. All transition-zone species are bitemperate (bipolar) (*N. difficilis* and *N. megalops*, representing an

early stage in specific differentiation, live in opposite hemispheres in the Pacific), whereas *none* of the subarctic or subantarctic species is bipolar.

A relationship between transition-zone and eastern equatorial habitats is suggested by a comparison of the distributions of *Euphausia gibboides* and *E. eximia* (fig. 106). These species are similar in size and general aspect, though the anatomy of the petasmas suggests that they are not closely related. The two species are much

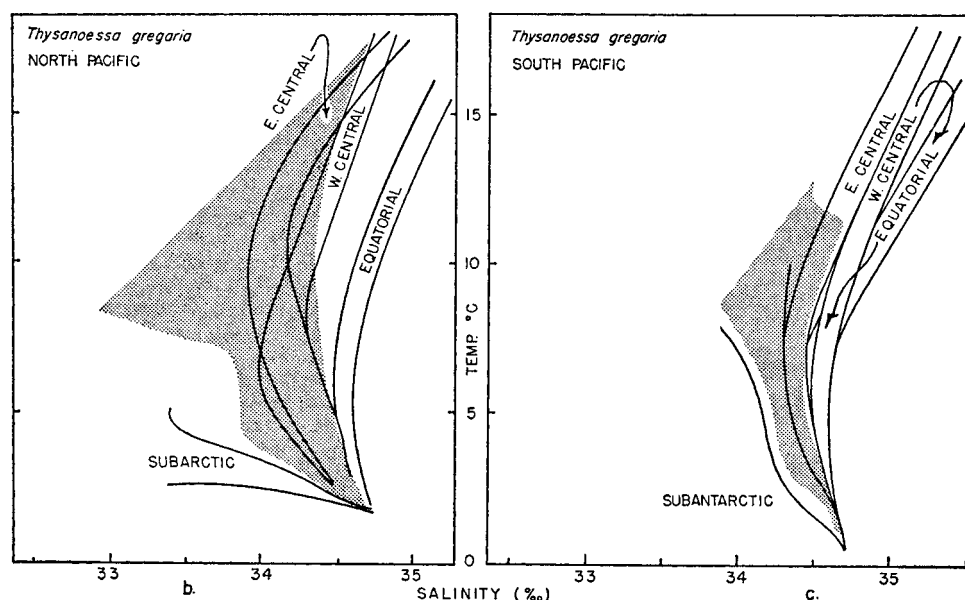


Fig. 107. Temperature-salinity envelope (shaded part) enclosing T-S curves below 100–150 meters for stations in the North Pacific and South Pacific habitats of *Thysanoessa gregaria*, compared with the T-S envelopes of the Pacific water masses.

larger than other euphausiids of the temperate and tropical waters. They have nearly the same distribution in the region of the Peru Current, though *E. gibboides* was found to be scarce south of 6° S. where *E. eximia* was abundant and reproductive. In the North Pacific, however, the two ranges overlap only off southern California and Baja California. From there, *E. gibboides* ranges northward and westward, and *E. eximia* ranges southward to the northern edge of the Equatorial Countercurrent, 11° N. Although its range is not specific to one water mass, *E. gibboides* lives in ecological zones that conform geographically with regions known to maintain other euphausiid species. It lives in a different zone in each hemisphere—the transition zone in the north, and the eastern equatorial zone in the south.

The similarities and differences in the distributions of *E. gibboides* and *E. eximia* point to the probable ecological importance of small temperature differences between habitats. The transition zone off the west coast of North America is cooler by 1° – 3° C. at 200 and 400 meters of depth than in the South Pacific. At 100 meters there is little difference in temperature between the transition zones of the two hemispheres. Evidently *E. eximia* and *E. gibboides* are adapted to similar, cool-water conditions, but their temperature and depth tolerances differ slightly. This may result in the apparent paradox of the similar and dissimilar ranges in the South and in the North Pacific respectively.

The temperature-salinity envelopes for *T. gregaria* (fig. 107) show that both the northern and southern habitats are intermediate in character between Equatorial Water and Subarctic (or Subantarctic) Water. In both habitats there is overlapping of the range with the Central water masses. In the South Pacific the T-S habitat of *T. gregaria* also extends into Subantarctic Water and modified Equatorial Water. The distributions of species living in the southern transition zone are closely related to the east-west belt of the Subtropical Convergence which curves northward as the South American continent is approached and becomes poorly defined in offshore waters of the Peru Current. Northward-reaching tongues in the distributions of *T. gregaria* and *N. megalops* are maintained, in part, by a northward-flowing subantarctic component of the Peru Current and a deeper remnant of southward-flowing Equatorial Water. The T-S curves indicate similarity of Equatorial Water to both South Pacific Central Water and Subantarctic Water.

The term "transition zone" is thus particularly descriptive of the North Pacific habitat of *T. gregaria*. There, the T-S envelope of the species falls in part *between* the typical envelopes of the Subarctic and Central water masses. In the South Pacific, it more nearly *overlaps* those envelopes. It is to be noted that the T-S habitat of *T. gregaria* in the North Pacific is characterized by a broader range of T-S curves than the South Pacific habitat. The differences between the zones lie mainly in the salinity property—the temperatures are nearly the same. It will be seen that the disjunct habitats of central species, when described in terms of the temperature-salinity relationship, differ from each other even more extremely than the antitropical transition zones. Evidently, differences of 2–3‰ in salinity, *per se*, have little direct effect in controlling the geographical distributions of oceanic species. Rather, the essential features of the oceanic habitat are (1) stability in the system of circulation (water mass), implying a nearly permanent place of origin of the water, (2) a range of temperature to which the species can adapt, and (3) an adequate food supply.

In an alternative explanation, there may already be genetic differences not yet morphologically discernible between the two populations of *T. gregaria*. Morphological differences in the *Nematoscelis difficilis–megalops* species pair already reflect presumed genetic differences. Geographically separate populations of a species will, in time, diverge genetically as a consequence of selective pressures that differ between the two environments. Differences in salinity of 2‰ between paired habitats may not influence distribution but might contribute to the development of dissimilar adaptations made by sibling species in the course of evolutionary time.

THE PACIFIC CENTRAL SPECIES

In common with the ranges of the species inhabiting transitional waters between the Subarctic (or Subantarctic) and Central water masses, or between Subarctic (or Subantarctic) and Equatorial water masses, those of species occupying the mid-latitudes (20°–40°) show differing amounts of antitropicality. The distributions are apparently related to the circulation that maintains the Central water masses of the North and South Pacific. The *central species* may be grouped according to the extent to which the distributional ranges conform with the range of the Central Water, as distinguished by its characteristic envelope of T-S curves.

Euphausia brevis (fig. 108), *E. hemigibba*, *Nematoscelis atlantica*, *Thysanopoda obtusifrons*, *Stylocheiron suhmii*, and *S. affine* "Central Form" are most numerous in the barren mid-parts of the North Pacific Central water masses. *E. brevis* and *N. atlantica* are bisubtropical, occurring also in South Pacific Central Water, whereas *E. hemigibba* is replaced in the Southern Hemisphere by *E. gibba*. The temperature-salinity envelopes

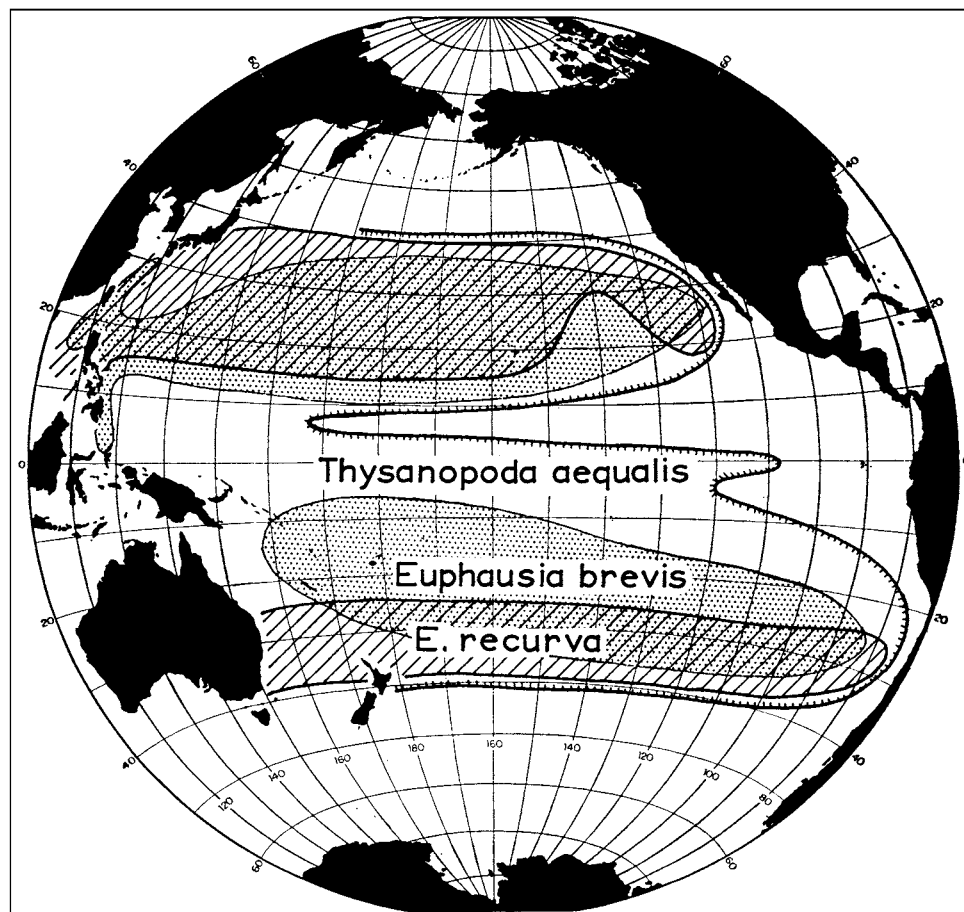


Fig. 108. Geographical distributions of three central-group euphausiid species showing different amounts of agreement with the position of the Pacific Central water masses (*cf.* fig. 2).

for central species, shown for *E. brevis* in figure 109, are in close agreement with the T-S characteristics of the Central Water Mass. *E. brevis*, *E. hemigibba*, and *Thysanopoda obtusifrons* are rare or absent in waters south and east of Japan. There, typical Central Water is modified by the Kuroshio system and submerging Subarctic Water.

Euphausia recurva and *Thysanopoda aequalis* (fig. 108) represent a second central group. They are found in low concentration toward the middle of the Central Water Mass region, and areas of abundance are associated with the margins of the ranges—places where the central environment impinges on more fertile and cooler water of the subarctic region, the eastern boundary currents, and the Equatorial

Water Mass. Of these species *E. recurva* inhabits only the higher latitudes of the central regions, 20°–42°, whereas *Thysanopoda aequalis*, like *Euphausia mutica* (fig. 35) and both forms of *Stylocheiron longicorne* (fig. 99), is found near the equator in the western Pacific as well as in the zones 20°–42°. The significance of such equatorial transgression is discussed below.

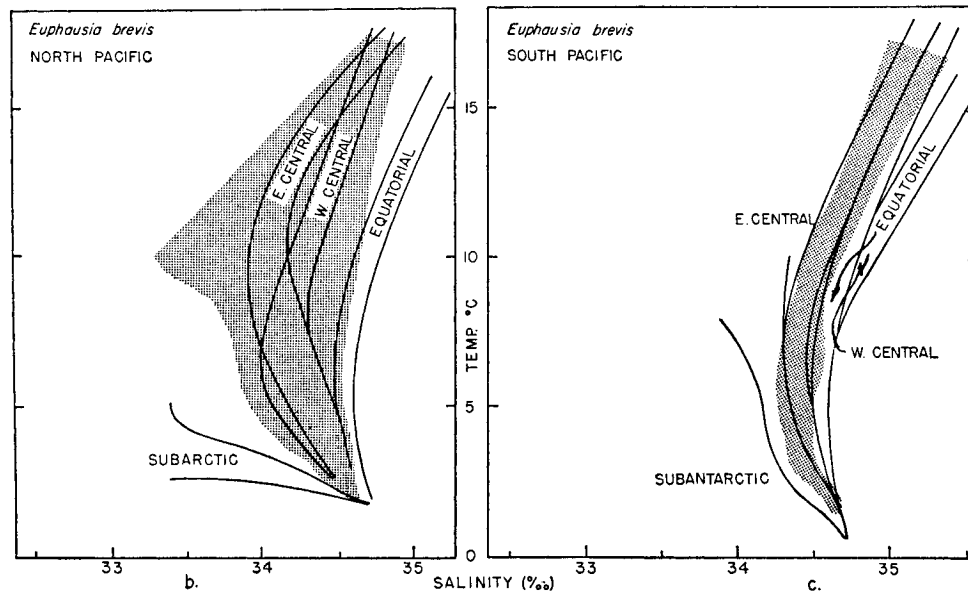


Fig. 109. Temperature-salinity envelope (shaded part) enclosing T-S curves below 100–150 meters for stations in the central habitat of *Euphausia brevis*, compared with T-S envelopes of the Pacific Water Masses.

Like the transition-zone species (but unlike the subarctic and subantarctic species), central species (except *E. hemigibba* and *E. gibba*) occur in both hemispheres in the Pacific. Similarly, central species are generally found in both the Eastern and the Western Central water masses, as distinguished by Sverdrup, Johnson, and Fleming (1942). In the North Pacific, however, *Thysanopoda aequalis* is all but limited to the Eastern Central Water, while *T. subaequalis* lives mainly in the Western Central Gyral. In the South Pacific, the ranges of the two species more nearly overlap.

The mesopelagic euphausiids occupying the central zones transgress the tropics. This transgression is undoubtedly related to the uniformity of temperature across the tropical-subtropical midwater environment (cf. figs. 7c, 7d). The central-equatorial and central mesopelagic species fall into two groups (fig. 110), listed above (p. 197). The first group includes those species ranging across the breadth of the Pacific, exclusive (except for *Stylocheiron longicorne*) of the eastern boundary currents. These are found from 40° N. to 40° S., but are lacking in a wedge of oxygen-poor water extending westward from Mexico between 10° N. and 20° N., including the Gulf of California. They enter the eastern equatorial basin in the belt of the Equatorial Countercurrent, 0°–10° N.

The ranges of three species belonging to a second mesopelagic group are limited

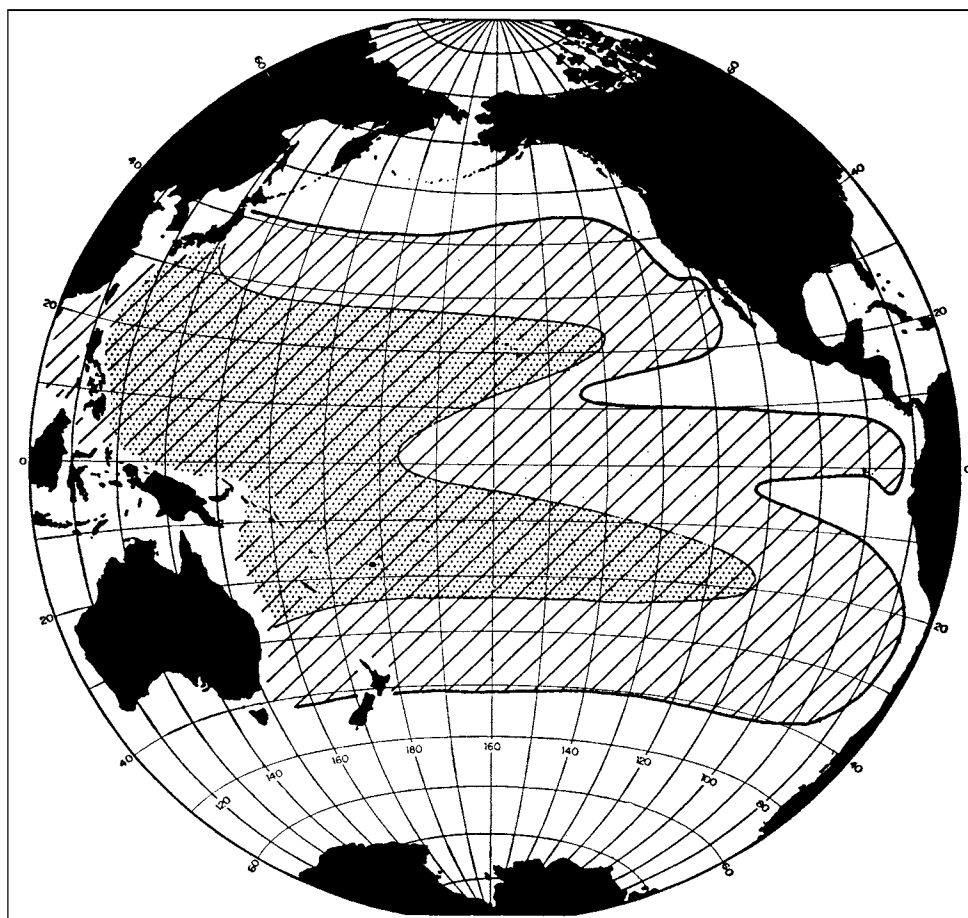


Fig. 110. Composite distribution patterns of the central-equatorial mesopelagic euphausiid species. Cross-hatched part: *Thysanopoda orientalis*, *T. monocantha*, *T. pectinata*, *Nematoscelis tenella*, *Nematobranchion boopis*, and *Stylocheiron elongatum*. Stippled part: *Nematobranchion sexspinosus*, *Thysanopoda cristata*, and *Stylocheiron robustum*.

to warmer water than those of the first group. These ranges are latitudinally disjunct in mid-ocean, but the northern and southern distributions merge in the western Pacific. The composite range of *Thysanopoda cristata*, *Nematobranchion sexspinosus*, and *Stylocheiron robustum* may be approximately circumscribed by the 16° C. isotherm at a depth of 200 meters, and is mainly allied with the province of the Central water masses.

THE PACIFIC EQUATORIAL SPECIES

Fifteen euphausiid species live in one part or another of the region of the Equatorial Water Mass. The ranges of five of these, *Nematoscelis gracilis*, *Stylocheiron microphthalmum*, *Euphausia diomediae*, *E. paragibba*, and *E. distinguenda*, agree best with that of the water mass, as it is mapped in *The Oceans* (Sverdrup, Johnson and Fleming, 1942)—20° N.–20° S. in the eastern Pacific and 10° N.–10° S.

in the western Pacific. These species occur in the equatorial part of the Pacific and Indian oceans, but are lacking in the Atlantic where there is no Equatorial Water Mass.

The first four of the above five species live across nearly the full east–west extent of the Pacific. Although the north–south dimension of the ranges (and of the

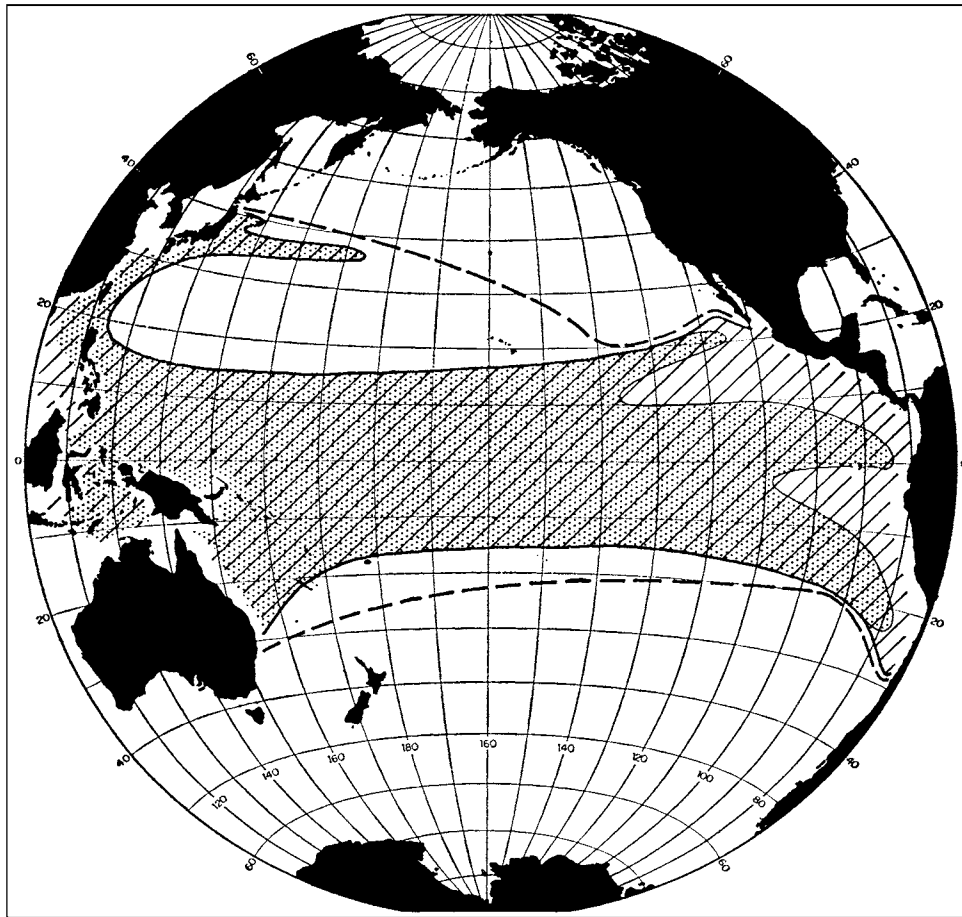


Fig. 111. Composite distributions of groups of epipelagic trans-equatorial euphausiid species. Cross-hatched part: *Euphausia diomediae* and *Nematoscelis gracilis*. Stippled part: *Thysanopoda tricuspidata*, *Euphausia paragibba*, and *Stylocheiron microphthalmum*. The dashed line indicates the limits of range of an equatorial–west central species, *Euphausia tenera*.

Equatorial Water Mass) is, for some species, narrowed in the western Pacific, these species are carried northward to Japanese waters along the western edge of the ocean by the Kuroshio System. The fifth species, *Euphausia distinguenda*, is limited to the most typical, eastern part of the Equatorial Water Mass. The most western parts of its bicornute range are in mid-ocean.

Thus the Pacific Ocean and Indian Ocean ranges of *E. distinguenda* are disjunct. The closely related species *E. sibogae* inhabits a geographically intermediate region in the Indo-Australian Archipelago. Also, *E. paragibba* is replaced in the

South China Sea by *E. pseudogibba*, so that its Pacific and Indian ocean habitats may not now be in communication with each other.

The three other Pacific–Indian Ocean equatorial species may, more probably, be carried between oceans across the basin-shelf waters of the Indo-Australian Archipelago. However, both larvae and adults of these species were not found in the extensive South China Sea–Gulf of Thailand shelf waters (“Naga” expedition records, October, 1960–June, 1961), suggesting that east–west exchange between populations of *Nematoscelis gracilis*, *Euphausia diomediae*, and *Stylocheiron microphthalma* is slight.

Thysanopoda tricuspидata and *Euphausia tenera* are two widespread tropical species having limits of distribution (the dashed line in fig. 111) that agree with the limits of the Equatorial Water Mass only in the eastern Pacific. To the west, these euphausiids range also into Central Water following the region circumscribed by the 25° C. summer surface isotherm. This is the typical pattern of distribution shown by shallow-living tropical plankton species. The ranges of *T. tricuspидata* and *E. tenera* are apparently determined by the temperature tolerances of their larvae, which live near the surface. The assemblage of this broad epipelagic habitat includes the chaetognath *Sagitta robusta* and the foraminiferan *Pulleniatina obliquiloculata*, and was called the equatorial–west-central fauna by Bieri (1959) and Bradshaw (1959).

The limit of penetration of the eastern equatorial basin by certain euphausiid species is shown in figure 111 by the easternmost tricornute part of the shaded area. These euphausiids include the equatorial–west-central species *Thysanopoda tricuspидata* and the equatorial species *Euphausia paragibba*, *Stylocheiron microphthalma*, and *Stylocheiron affine* “West Equatorial Form.” The eastward-reaching tongues of distribution of these species lie at (1) the boundary between the California Current and the Equatorial Water Mass, 18°–22° N. (no current is known to explain this tongue), (2) the zone of the Equatorial Countercurrent and the Cromwell Undercurrent, 0°–10° N., and (3) the region of mixing between Equatorial and South Pacific Central water, 10°–20° S., 80°–110° W.

Other euphausiid species may be grouped according to the relationship of their distributions to the eastern equatorial basin or to the Indo-Australian region. The eastern group (fig. 112) includes *Euphausia eximia*, *E. lamelligera*, *Nyctiphanes simplex*, and the “Eastern Equatorial Form” of *Stylocheiron affine*, in addition to *E. distinguenda*, discussed above. These distributions are, to a greater or lesser extent, cleaved along an east–west line by the zone of the Equatorial Countercurrent. Northern and southern parts of the ranges of *N. simplex* and *E. eximia* are completely separated, while the distributions of the three other species are separated toward their western limits. The composite range of this group of species extends westward at the southern edge of the North Equatorial Current (the belt of the thermal anticline) and in the South Equatorial Current.

The tropical species of the western Pacific are, for the most part, limited to nearshore waters. These species include *Euphausia sibogae*, *E. fallax*, *Pseudeuphausia latifrons*, *Nematoscelis lobata*, *Stylocheiron insulare*, and the “Indo-Australian Form” of *S. affine*. These species do not range far to the east (none of the major ocean currents of the region flows toward the east). The Equatorial Countercurrent

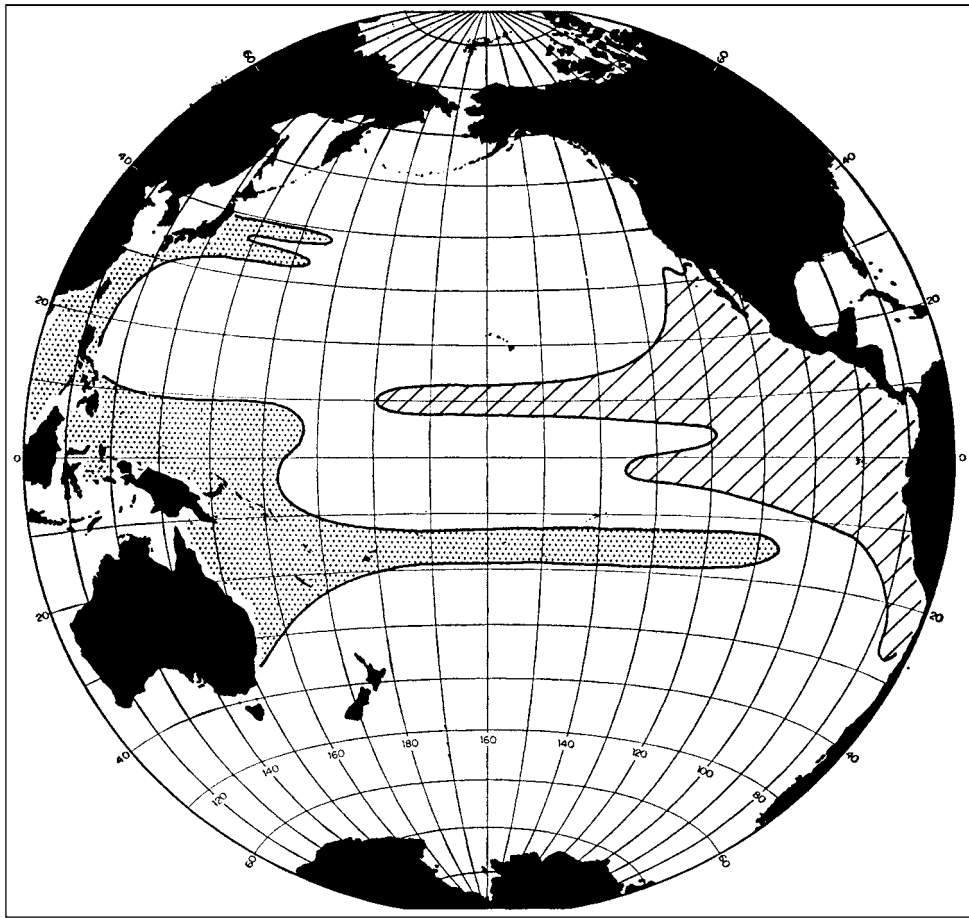


Fig. 112. Composite distributions. The western equatorial (Indo-Australian) group includes *Euphausia pseudogibba*, *E. fallax*, *E. sibogae*, *Pseudeuphausia latifrons*, *Nematoscelis lobata*, *Stylocheiron insulare*, and *S. affine* "Indo-Australian Form." The eastern equatorial group includes *Euphausia lamelligera*, *E. distinguenda*, *E. eximia*, *Stylocheiron affine* "East Equatorial Form," and *Nyctiphanes simplex*.

is believed to be undeveloped in the far western Pacific. *P. latifrons*, inhabiting tropical lagoons, is nevertheless found at Samoa in the South Pacific and at the Marshall Islands north of the equator.

Euphausia pseudogibba (fig. 40), though found at mid-ocean between 12° S. and 18° S., must be included in the Indo-Pacific group. This is the only species of the "*E. gibba* group" in the South China Sea and the Indo-Australian Archipelago, southward to the Great Barrier Reef. The anomalous eastward-reaching tongue in the distribution of *E. pseudogibba* occupies an extension of the warm-water environment of the Indo-Pacific region (cf. *Thysanopoda subaequalis*, fig. 23), as shown by the position of the 25° C. 200-meter isotherm (fig. 7c). This eastward extension of range is complementary to the westward-reaching habitat of *E. distinguenda*, *E. eximia*, and *Stylocheiron affine* "East Equatorial Form" that lies along the 10° N. parallel.

SPECIES OF THE ANTARCTIC OCEAN

Plankton of the Antarctic Ocean, though not considered in the distributional part of this paper, must be treated in the discussion of geographical isolation and mechanisms of speciation. Exhaustive work on the plankton of Subantarctic and Antarctic waters has long been carried out by the "Discovery" Commission.

The epipelagic niches of the Antarctic Ocean appear to have evolved in relation to four boundaries: the Antarctic continent, the edge of the pack ice, the Antarctic Convergence, and the Subtropical Convergence. The meridional component of Antarctic circulation, together with sinking of water masses at the Antarctic and Subtropical convergences, partially separates each zone from neighboring zones. Mackintosh (1937) noted that the limits of distribution of species of the Antarctic Ocean may be controlled by vertical migrations between surface water, which has a northward-moving component of flow, and southward-moving deep water.

John (1936) showed that *Euphausia crystallorophias* is associated with the coast of the Antarctic Continent, *E. superba* with the zone between the continent and the Antarctic Convergence, and *E. frigida* with the region between the ice-edge and the Antarctic Convergence. These may be regarded as species of the Antarctic Water Mass.

Three polychaetes, *Rhynchonerella bongraini*, *Vanadis antarctica*, and *Tomopteris carpenteri*, are believed to be endemic to waters south of the Antarctic Convergence (Tebble, 1960). No endemic subantarctic polychaetes were found, though the widespread *Vanadis longissima* (possibly a geographical race of *V. antarctica*, according to Tebble) has its southerly limit at the Antarctic Convergence.

Euphausia vallentini, *E. longirostris*, and *E. lucens* are subantarctic euphausiids, inhabiting a circumpolar belt bounded by the Subtropical and Subantarctic convergences. *E. spinifera* belongs to this group in the Pacific and Atlantic sectors of the Antarctic Ocean, though John found it north of the Subtropical Convergence in the Indian Ocean. An extensive study of *Euphausia triacantha* (Baker, 1959) demonstrated a close relationship between the maximum density of this species and the position of the Subantarctic Convergence. Smaller numbers were found on either side of the Convergence. There was little or no seasonal variability in the distribution.

Baker noted that the distributional pattern for *E. triacantha* was the reverse of that found by David (1955) for the chaetognath *Sagitta gazellae*. The chaetognath was found in both Antarctic and Subantarctic water, but was most scarce near the Antarctic Convergence. David described separate races of the species, one living north and the other south of the Convergence. These were based on consistent differences in size of the specimens: a "Large Southern Form" was antarctic, and a "Small Northern Form" was subantarctic.

THE BOUNDARY SPECIES

Eight euphausiid species are typically associated with boundary waters of the Pacific (fig. 114). Four of these, *Thysanoessa raschii* and *T. spinifera* of the northern Pacific rim, *Euphausia crystallorophias* of antarctic waters, and *Pseudeuphausia latifrons* of the western tropical Pacific, are most numerous in neritic waters. *Euphausia*

lamelligera, *E. mucronata*, and the two Pacific species of *Nyctiphanes* are often found in neritic waters, though their highest densities are usually subcoastal.

Zonation shown by these boundary species is remarkable in its similarity to the littoral zonation (fig. 113) recognized by Ekman (1953). *Thysanoessa raschii* is

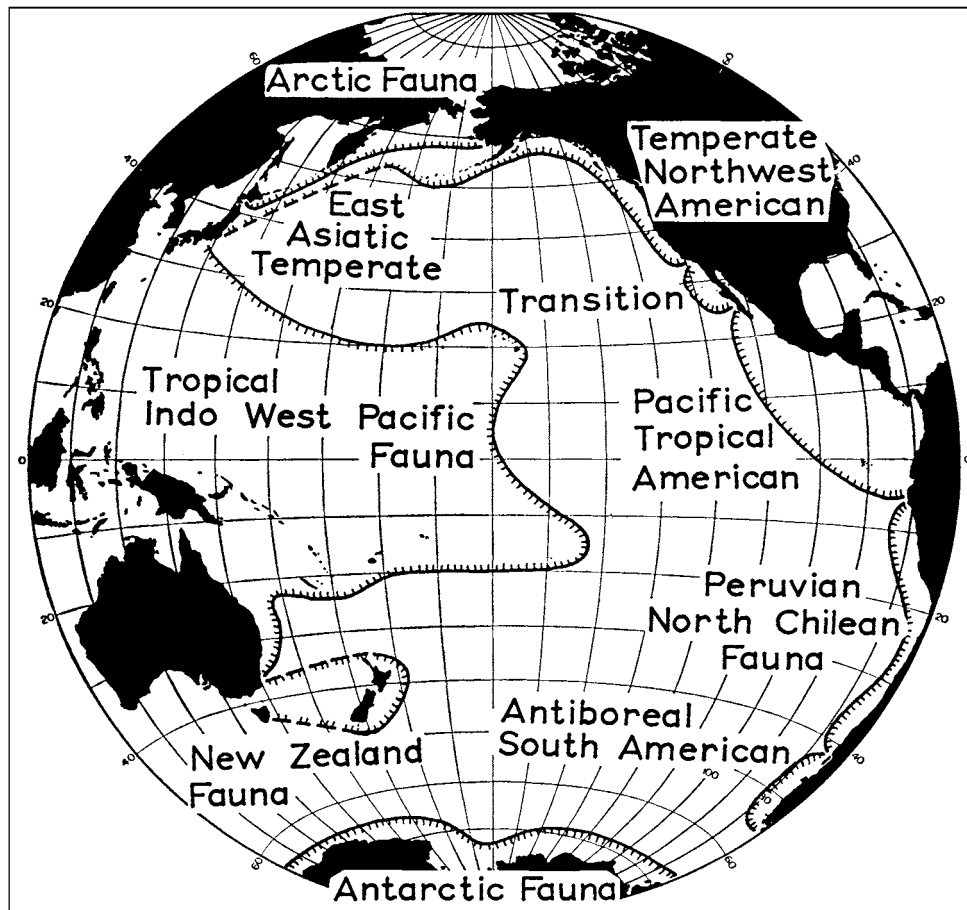


Fig. 113. Ekman's Pacific littoral faunas as summarized by Sverdrup, Johnson, and Fleming (1942).

Arctic, *T. spinifera* belongs to the Temperate Northwest American Fauna, and *Nyctiphanes simplex* may be considered part of the Transition Fauna, found between the temperate and tropical zones. The range of *Euphausia lamelligera* agrees with the zone of the Pacific Tropical American Fauna, and *E. mucronata* is found along the upwelling coast of South America occupied by the Peruvian North Chilean Fauna. *E. crystallorophias* is Antarctic, and *Nyctiphanes australis* is of the New Zealand Fauna. The range of *Pseudeuphausia latifrons* is similar to that of the Tropical Indo West Pacific Littoral Fauna, though this euphausiid has not—as far as is known—colonized neritic waters as far east as Hawaii or the Tuamotu Archipelago.

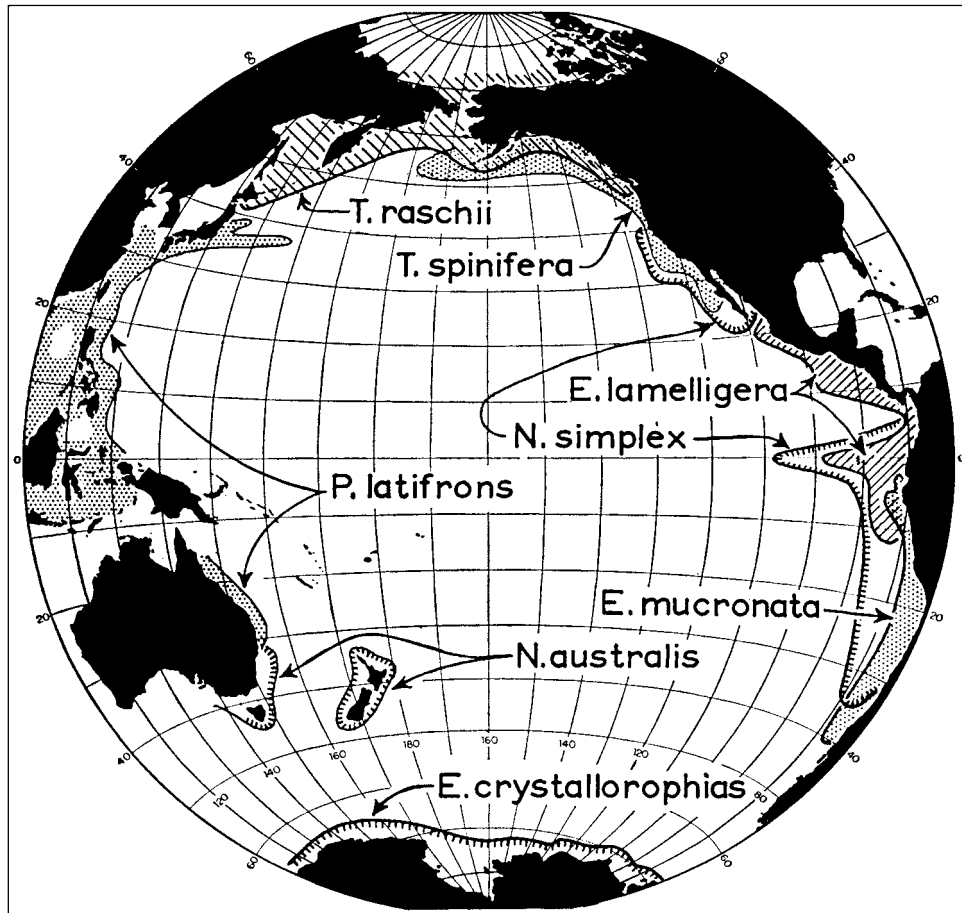


Fig. 114. The Pacific boundary species of euphausiids, showing close faunistic similarities to Ekman's littoral faunas.

Faunas of the high seas, as described for the euphausiids, are comparable in latitudinal extent with littoral and sublittoral provinces:

HIGH-SEAS EUPHAUSIID GROUPS	LITTORAL FAUNA (EKMAN)	EUPHAUSIID BOUNDARY SPECIES
<i>Thysanoessa longipes</i> "Spined," <i>T. inermis</i>	Arctic	<i>Thysanoessa raschii</i>
Subarctic Group	East Asiatic Temperate, Northwest American Temp.	<i>T. spinifera</i>
Transition-Zone Group, North	Transition	<i>Nyctiphanes simplex</i>
East Equatorial Group	Pacific Tropical American	<i>E. lamelligera</i>
West Equatorial Group	Tropical Indo West Pacific	<i>P. latifrons</i>
Trans-Equatorial Group		
Transition-Zone Group, South	Peruvian North Chilean	<i>E. mucronata</i>
Subantarctic Group	New Zealand	<i>N. australis</i>
Antarctic Group	Antiboreal South American	
	Antarctic	<i>E. crystallorophias</i>

Though the arctic-subarctic oceanic euphausiids *Thysanoessa longipes* “Spined” and *T. inermis* are found as far south as 50° N. in mid-ocean, they are regarded as the high-seas counterparts of the Arctic Littoral Fauna because, with the neritic species *T. raschii*, they are the euphausiids living in the Arctic Ocean and the Sea of Okhotsk.

No region of transition between littoral faunas of the west coast of South America was recognized by Ekman. Similarly, the euphausiid species of the oceanic transition zone of the South Pacific, *Nematoscelis megalops*, *Thysanoessa gregaria*, and *Thysanopoda acutifrons*, do not enter waters of the Peru Current near the coast of South America, the habitat of *Euphausia mucronata*. This is in contrast to the importance of *Nematoscelis difficilis* and *Thysanoessa gregaria* in the nearshore part of the California Current. In the same way, the spiny lobster of the transition zone of the North Pacific, *Panulirus interruptus*, is replaced in the transition zone off South America by *Jasus lalandii frontalis*, which is found only at offshore islands—to the west of the influence of the Peru Current.

It is therefore evident that only the North Pacific central and South Pacific central provinces, which scarcely impinge on coastal waters, have no littoral counter-parts. In the light of the many oceanic provinces, anticipated in certain general features by Steuer (1933), the observation of Ekman (1933, p. 319) that “the main faunistic regions in the high-oceanic pelagic fauna are more weakly characterized taxonomically than the main regions of the shelf” appears to be no longer meaningful.

ZOÖGEOGRAPHICAL AFFINITIES OF THE GENERA

Of the eleven euphausiid genera, five, *Thysanopoda*, *Euphausia*, *Thysanoessa*, *Nematoscelis*, and *Stylocheiron*, may be considered major genera from the stand-points of number of species and extent of oceanic area now occupied.

Of these, *Euphausia* has the largest populations and is the most widely distributed in the epipelagic zone today. It is, however, missing from the cold part of the North Atlantic, north of about 45° N. *Thysanopoda* has by far the greatest vertical range (from the surface to the greatest depths harboring euphausiids) and is the characteristic bathypelagic genus, but it is not found in arctic or antarctic waters. These two genera and *Nematoscelis*, which is intermediate in depth between *Euphausia* and *Thysanopoda*, all include species adapted to the horizontal faunal zones, transitional, central, and equatorial.

Thysanoessa, a cold-water genus, is dominant in the cold North Atlantic and North Pacific and is the only genus found in the Arctic Ocean. However, it shares importance with *Euphausia* in the Antarctic Ocean, but, in contrast to *Euphausia*, appears not to have colonized icebound waters south of the Antarctic Convergence. *Stylocheiron*, in spite of the broad range of *S. maximum* in deep water, is essentially an epipelagic tropical and subtropical genus which has achieved its maximum development in equatorial waters.

Six genera can be classified as minor. Four of these, all well-founded, are monotypic: *Bentheuphausia*, *Meganyctiphanes*, *Pseudeuphausia*, and *Tessarabrachion*. *Nyctiphanes* consists of four coastal species, and *Nematobrachion*, found consistently

in low numerical concentration in the zones 40° N.–40° S., contains three species.

Meganyctiphanes, *Nyctiphanes*, and *Pseudeuphausia* appear to be exclusively adapted to coastal habitats. Certain *Thysanoessa* species are coastal or neritic, and others are oceanic. It seems probable that *Nyctiphanes* arose as a temperate nearshore, upwelling-zone counterpart to boreal and antiboreal *Thysanoessa*. *Pseudeuphausia* is peculiarly suited to lagoons and insular and shelf waters of the western equatorial Pacific, the Indian Ocean, and the Red Sea.

Just as *Meganyctiphanes* is limited to the North Atlantic, *Tessarabrachion*, the curious genus not related to it, is confined to the subarctic North Pacific. Either *Tessarabrachion* arose subsequent to the height of Pleistocene glacial cooling, when a number of other species apparently developed antitropical distributions, or else oceanic cooling was never sufficiently intense to allow it access to the equatorial zone. In view of the endemic nature of other subarctic North Pacific species, the latter explanation is the more probable.

SEASONAL CHANGES IN DISTRIBUTIONS

Seasonal changes in boundaries or concentrations of species are not often evident when plotted on the scale of the oceanwide maps. Shifts in the positions of the boundaries may nevertheless be of the order of several hundred miles and of considerable local significance, reflecting changes in upwelling, amount of food, direction of current, and water temperature. Seasonal changes in euphausiid distribution have been observed in the Kuroshio, the California Current, the Peru Current, and the mid-equatorial Pacific. Data from these places and from the mid-Pacific part of the North Pacific Drift Current, crossed several times during the summer months by the Scripps expeditions, allow a consideration of time-change in the positions of the euphausiid boundaries.

THE REGION OF THE KUROSHIO AND THE EAST CHINA SEA

The northern limit of the influence of the Kuroshio system was at 40° N. in the eastern waters of Japan in September, 1953 ("Transpacific" expedition). This is the zone of convergence of the Oyashio and Kuroshio, discussed above (p. 67). Beklemishev and Semina (1956) found that the position of this convergence and the limits of the cold-water and warm-water plankton faunas were nearly constant, varying by a maximum of about three degrees of latitude between April, 1951, when it was observed off northern Hokkaido, and October, 1954, when it was farther south—off northern Honshu. May and June can be regarded as spring in waters north of the convergence, and August–October as the summer season in which the young of *Calanus cristatus* diminish the phytoplankton blooms by grazing (Bogorov and Vinogradov, 1955).

The southern boundary of the zone of *Calanus tonsus* (called the North Pacific temperate region by Brodsky, 1955) scarcely moved from July–August, 1953, to September, 1953, while the northern limits of tropical and subtropical species were slightly more northern during the September survey—by less than 100 miles in the region 150°–160° E. Semina (1958) found little change in boundaries of

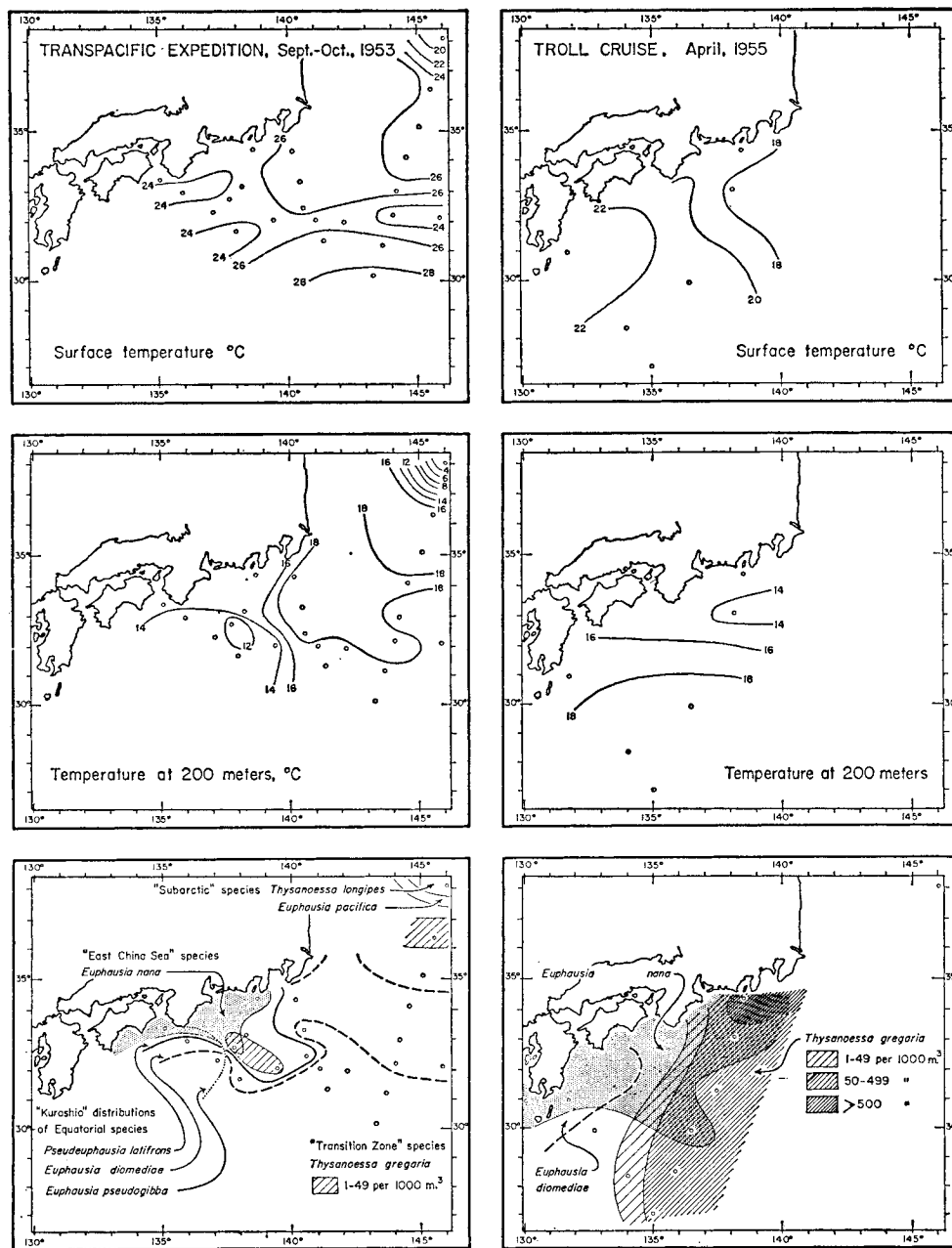


Fig. 115. Distributions of temperature and euphausiid species in the southeastern waters of Japan. "Transpacific" expedition, Sept.-Oct., 1953, and "Troll" expedition, April, 1955, data compared. Ranges of equatorial euphausiid species were broad during the September-October survey, and transition-zone species were widespread during the April survey.

phytogeographical zones in this region, but noted that the southern limit of the boreal province moved nearly two degrees northward in the late summer, while the northern limit of the tropical region was constant near 36° N. According to Beklemishev and Burkov (1958) the tropical fauna of the surface layer, bounded by the 15° C. isotherm, moves somewhat toward the north in the summer within the zone of 35°–40° N. Ponomareva and Beklemishev (1956) attributed the summer northward shift of the zoögeographical boundary to the influence of the changing monsoon. The summer faunas in the frontal region were mixed in the layer below 100–200 meters.

Sampling to the south and east of Japan during the late summer of 1953 (“Transpacific” expedition) showed that the southern limit of the cold-water or subarctic zone, as indicated by *Thysanoessa longipes* and *Euphausia pacifica*, was near 38° N. (fig. 115). Numerous central species were present immediately south of the boundary of the subarctic province, and equatorial species such as *Euphausia diomediae* and *Pseudeuphausia latifrons* were widespread in the region of the eastward-bending Kuroshio, 32°–35° N. Tebble (1962) has shown that the ranges of subarctic and tropical polychaetes are also bounded at this convergence.

Surface temperatures off southern Japan were 2°–8° C. cooler during the “Troll” expedition, April, 1955, than during the summer survey of 1953 (fig. 115). Similarly, the temperature at a depth of 200 meters was 2°–3° C. cooler during the April period of observations. On the other hand, a patch of cold water observed near 32° N., 138° E. in October by the “Transpacific” expedition was not found by the “Troll” survey, made during a time when the entire region of the Kuroshio was generally cooler. The transition-zone species *Thysanoessa gregaria* was limited to the cold patch off southern Japan during the October, 1953, sampling period. It was more widespread and abundant in the area during April, 1955. Similarly, *Euphausia nana* ranged extensively off southern Japan during April, while the equatorial euphausiids such as *Euphausia diomediae* were then found only off southern Kyushu where the upper layers of the Kuroshio were warmest. Thus, the characteristic euphausiids in the Kuroshio off southern Japan were of the central and equatorial zones during the summer, and of the central and transition zones during April.

Two species, *Euphausia nana* and *E. similis*, have centers of distribution off southern Japan and in the East China Sea. According to the “Troll” expedition records (fig. 116), these ranged extensively into the southeastern water of Japan during the spring period. They were then reproductive and abundant. According to Mescheriakova (1954), spring enrichment of the surface plankton in the southern part of the Japan Sea occurs in March—earlier than in the northern part where enrichment takes place in May (Brodsky, 1941). During the summer-autumn sampling by the “Transpacific” expedition, *E. nana* and *E. similis* were not so numerous or so widespread off southern Japan as during the April series of observations.

Evidently the East China Sea maintains a system of circulation that permits retention of the breeding stocks of euphausiid species. The Tsusima Water Mass, formed where the Kuroshio sweeps the eastern slope of the broad shelf of the East China Sea (Uda, 1959), was found to harbor the larval populations of *Euphausia*

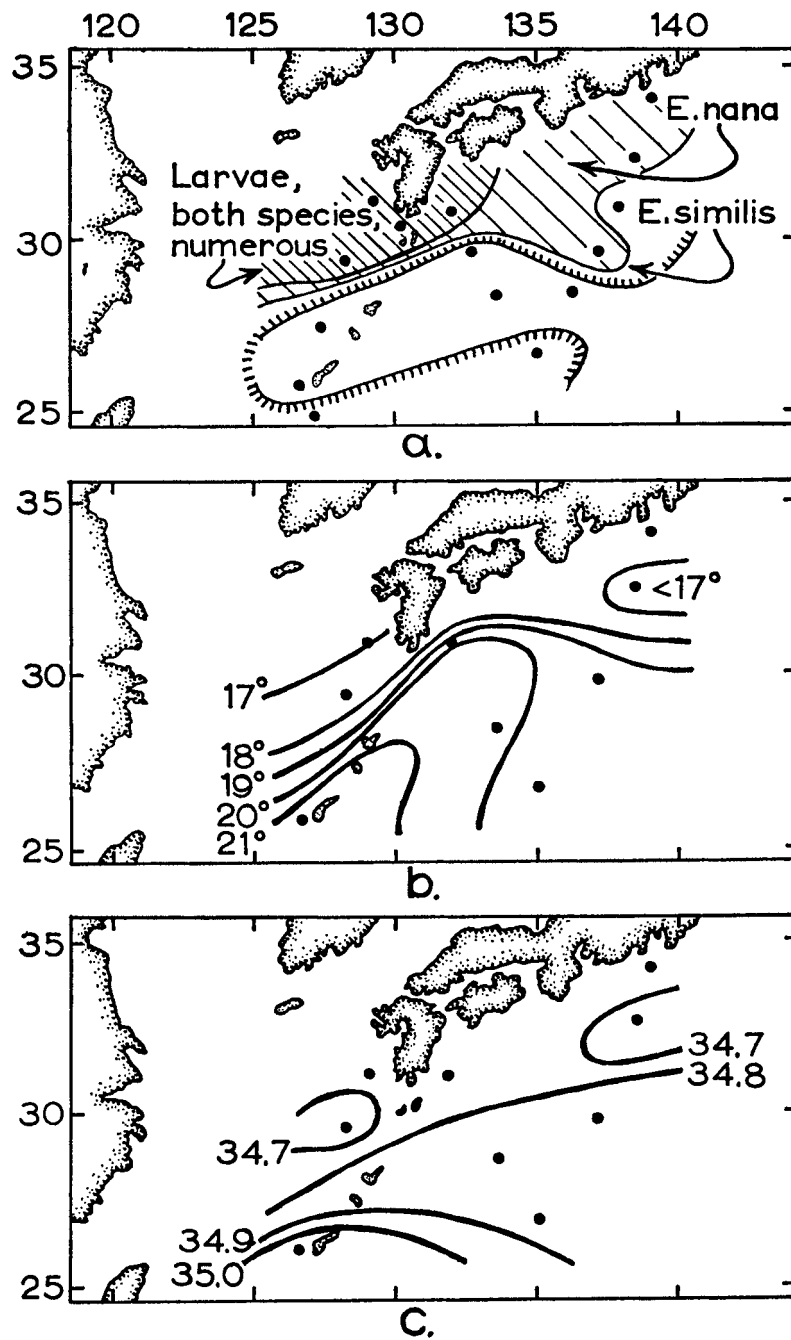


Fig. 116. Distribution. *a.* The East China Sea–Kuroshio species *Euphausia nana* and *E. similis* off southern Japan based on “Troll” expedition data. *b.* Temperature at 100 meters. *c.* Salinity at 100 meters.

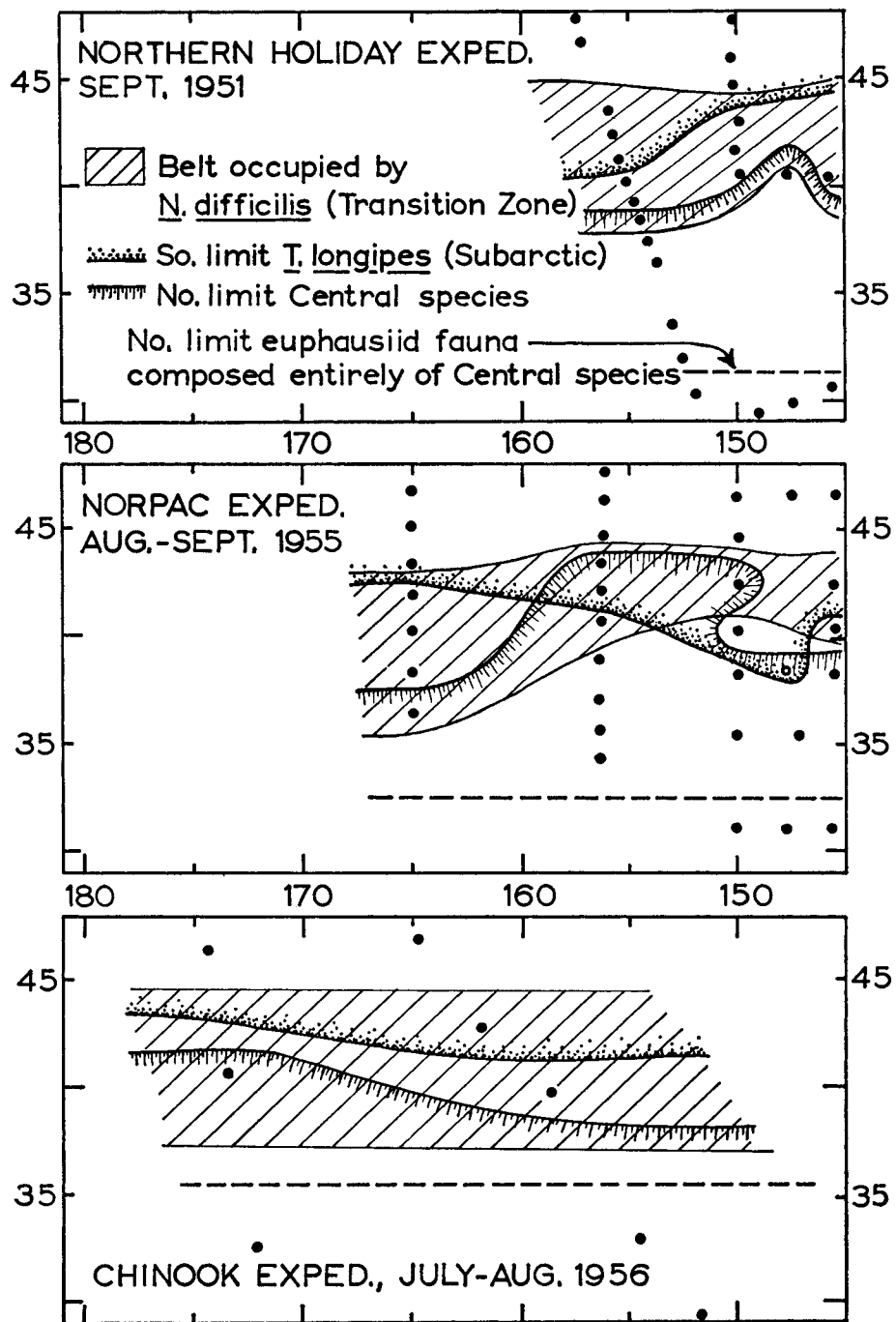


Fig. 117. Positions of the boundaries of subarctic, transition-zone, and central euphausiids in the mid-North Pacific. From "Northern Holiday," "Norpac," and "Chinook" expeditions.

nana and *E. similis*. Subsurface waters of the Kuroshio system then extend the ranges of the species toward the east. To judge from the “Troll” and “Transpacific” expedition data, it appears likely that here reproduction is seasonal, associated with the onset of the southwest monsoon which brings about the enrichment of the coastal waters of eastern Asia from the Sea of Japan to the South China Sea.

THE NORTH PACIFIC DRIFT CURRENT

Data from three cruises that crossed the North Pacific Drift Current during the summer months July to September indicate that the species boundaries associated with this east-west belt, 40°–45° N., are stable on an annual basis. The transition-zone euphausiid *Nematoscelis difficilis* was caught in mid-ocean between (1) 38° N. and 44° N. by the “Northern Holiday” expedition, September, 1951, (2) 36° N. and 44° N. by the “Norpac” expedition, August–September, 1955, and (3) about 39° N. and 43° N. by the “Chinook” expedition, July–August, 1956 (fig. 117). Similarly, the southern boundary of the subarctic species *Thysanoessa longipes* “Unspined Form” lay between 39° N. and about 44° N. during the eight crossings of the North Pacific Drift plotted.

The most northern influence of the central (subtropical) province is indicated in this region by the presence of *Euphausia mutica*, *E. recurva*, and *E. hemigibba*. The limit of these species was in the zone of 37°–44° N. during the summer surveys, while the northern limit of the zone composed *entirely* of central species lay consistently between 32° N. and 35° N.

THE CALIFORNIA CURRENT

The assemblages of euphausiid species in the eastern North Pacific (fig. 118) correlate geographically with the positions of the water masses (fig. 2) and current streamlines (fig. 119). The most extensive data from this quadrant of the ocean stem from the “Norpac” cruise of August–September, 1955, the CalCOFI section of which included the area bounded on the north by 46° N., on the south by 20° N., and on the west by 150° W. This part of the Pacific encompasses most of the California Current—a name applied to southward flow along the west coast of North America between 48° N. and about 23° N. Here Subarctic Water gradually converges with the Equatorial Water Mass. Water off central and southern California is generally regarded as transitional between the northern and southern types, and contains, in north-south transection, a progressively diminishing proportion of Subarctic Water. Equatorial Water diminishes in quantity toward the north, but was detected at 42° N. at 500–800 meters of depth during the “Norpac” cruise (Reid, Roden, and Wyllie, 1958).

The zone of transition between water masses coincides with the region occupied by euphausiid elements of the transition-zone fauna, *Nematoscelis difficilis*, *Thysanoessa gregaria*, and *Euphausia gibboides*, and with the more southern zone of the distributional range of *E. pacifica*. *E. pacifica*, inhabiting both the subarctic and the transition zones, is indicative of the latter only near the southern limit of the distributional range. There, it is usually lacking in the surface layer (p. 112 and table 11).

The total of the separate counts of species belonging to a particular geographical assemblage makes up a proportion of the euphausiid total at each station. Thus, the transition-zone species (when *E. pacifica* is included) make up the entire euphausiid fauna at the stations occupied off California and Baja California, 30°–40° N. (fig. 118). The distribution of the transition-zone group in the terminal part of the California Current indicates that the plankton component of the Current is carried westward in the zone 20°–25° N. There, it may be lost in unfavorable waters of the central region or dispersed along the boundary where the Equatorial and North Pacific Central water masses converge.

The surface current pattern and the distribution of temperature at a depth of 200 meters in the “Norpac” survey area (fig. 119) show correlations with euphausiid distributions. The 12° C. isotherm corresponds with the outer boundary of the transition-zone group. This isotherm is closely paralleled by a streamline (1.55 dynamic meters for 0/1,000 decibars) that bends westward at 24° N., coincident with the limit of the transition species.

The subarctic group, composed of *Tessarabrachion oculatus*, the northern populations of *Euphausia pacifica*, and the *Thysanoessa* species, *longipes*, *inermis*, and *raschii*, is dominant, north of 40°–45° N. These are the euphausiids that occupy waters north of about 45° N., except in coastal waters where there are also some records for species of the transition zone.

In the southern and offshore waters of the California Current the central euphausiid assemblage includes characteristic central species *Euphausia brevis*, *E. hemigibba*, *Nematoscelis atlantica*, and *Stylocheiron suhmii*, as well as the more widespread species *Thysanopoda aequalis*, *T. monacantha*, and *Stylocheiron carinatum*. The three last-named species transgress the equatorial region in mid-ocean, where they may not be considered to have affinities with central water. However, in the most eastern part of the Pacific they are lacking in part or all of the north-south breadth of the Equatorial Water Mass. To the north of their zone of absence in the Equatorial Water Mass, the centers of distribution of these species are in warm offshore central waters. Where they intrude from west to east into the California Current they must be regarded as elements of the North Pacific central fauna.

During the “Norpac” cruise, central species made up 100 per cent of the euphausiids at a distance of 400–700 miles from the coast of southern California. Some specimens belonging to this group were present at all but the most near-shore stations in the region. It is believed that these are sometimes carried toward the coast by lateral diffusion or by tongues of water drawn shoreward to replace offshore transport of upwelled water.

Equatorial euphausiids dominate to the south of about 20° N. In view of its total distribution (fig. 45), *Euphausia eximia* must be considered an equatorial species, though it is frequently numerous in the southern part of the California Current, 20°–30° N. The northward extension of the equatorial fauna in this region is characterized mainly by *E. eximia*, *E. distinguenda*, and *Nematoscelis gracilis*, and may be attributed to a northward trend in movements of the subsurface layers of the sea.

Seasonal change in the range of euphausiids of the California Current is here considered for the northern species *Euphausia pacifica* (figs. 120a–120f), the

central species *E. brevis* (figs. 120g–120i), and the equatorial species *E. eximia* (figs. 120j–120l). Data for February, April, and September reveal stability in the boundary of *E. pacifica* for the six years plotted. The southern limit of the range is consistent, falling within the zone 26°–32° N. off Baja California. The southernmost part of the distribution of this species, like that of another subarctic-transition-zone

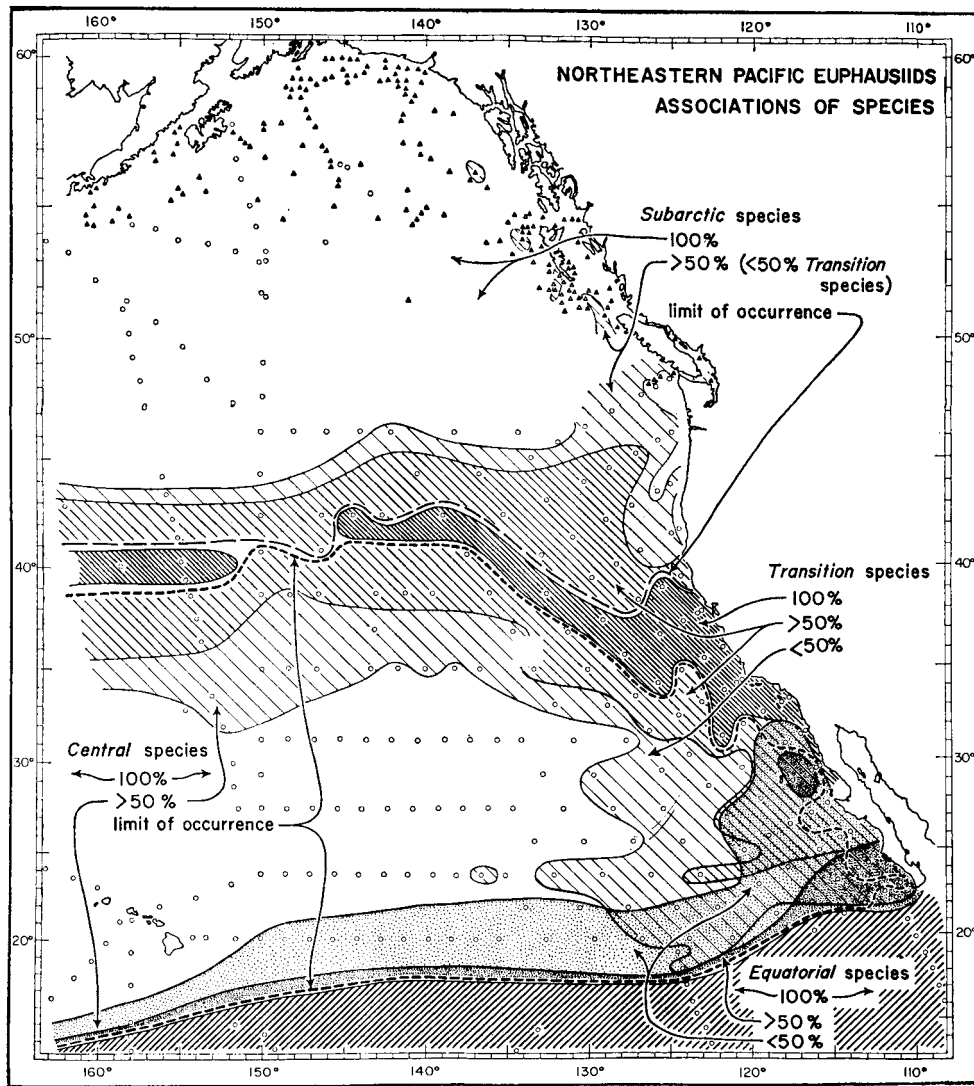


Fig. 118. Associations of euphausiid species in the northeastern Pacific based mainly on "Norpac" expedition, Aug.–Sept., 1955. The amount of a faunal group at a station is indicated as the percentage of the total euphausiid count (all species) made up by the summed counts of the species in that fauna. The northern stations, shown as triangles, are from Banner (1949).

species, *Thysanoessa spinifera* (fig. 53), is evidently related to the development of upwelling centers, (1) off central California, (2) south of Point Conception (Channel Islands region), and (3) off Punta Eugenia, Baja California. Normally, upwelling is intense in April, but may take place during any part of the year.

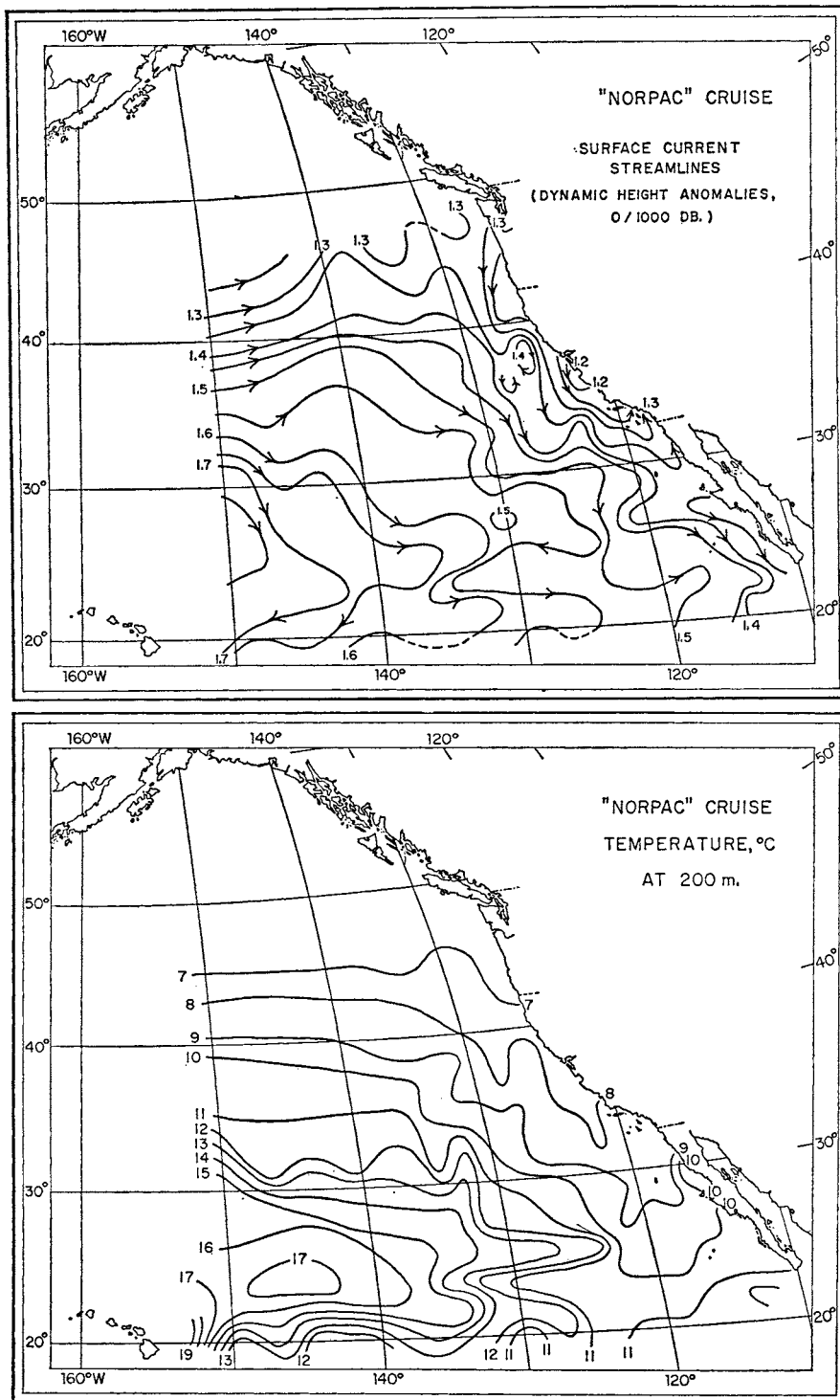


Fig. 119. Surface currents and temperatures at a depth of 200 meters in the north-eastern Pacific. From the "Norpac" expedition data.

Seasonal variability in the boundary of *E. pacifica* was less than annual variability during the period 1949–1958. This distributional range retreated from Baja California waters during the summers of 1949 and 1957, but not during the summers of 1950, 1952, 1954, and 1955 when *E. pacifica* persisted off Punta Eugenia and along the inshore waters of northern Baja California. During the 1957–58 warm-water period, *E. pacifica* and other cool-water species were generally lacking off Mexico, 25°–30° N.

Though the boundary of *E. pacifica* in the Punta Eugenia upwelling center was not atypical in 1954–55, the quantitative aspect of the distribution of this species was then different from earlier and later years studied. During 1954–55, cold-water euphausiids, including *E. pacifica*, were particularly numerous where the upper layers of water were cool in a divergent eddy off mid-Baja California. However, the *boundary* of the distribution of *E. pacifica* was little altered by this feature of the circulation.

Euphausia brevis, a central species, is usually found in the warm offshore part of the California Current. There, sampling has been carried out less consistently than in coastal waters. However, when the extent of sampling made it possible to draw the eastern limit of the range of this species, the boundary proved to be nearly constant (figs. 120g–120i). Eastward intrusions of *E. brevis*, noted in 1957–58, were only slightly or not at all greater than those plotted for 1949 and 1955.

Euphausia eximia of the eastern equatorial fauna and the southern part of the transition zone occupies an important place in the plankton of the terminal part of the California Current (figs. 120j–120l). The northern limit of the range of this species was commonly off San Diego, 32° N., during the period 1949–1955. Northward-reaching tongues of the distribution extended toward the Channel Islands, 33°–34° N. During the 1957–58 period of oceanic warming, *E. eximia* ranged into the waters of the Channel Islands and was found north of Pt. Conception in offshore waters—as far as 36° N.

THE PERU CURRENT

Seasonal and annual changes in the northern part of the Peru Current system are sometimes conspicuous, though not well understood. The destructive effect of warm water, “El Niño,” upon anchovetta and guano bird populations off Peru, and the intense fertility of the coastal region, 10°–15° S., are blights and blessings, respectively, to the Peruvian economy. The “Shellback” expedition sampled the Current, 4°–15° S., during June–July, 1952—probably a normal southern autumn (W. S. Wooster, personal communication). The “Downwind” expedition surveyed as far north as Callao, 12° S., in January, 1958—a southern summer during which “El Niño” was exceptionally severe and destructive. The plankton from these cruises indicated that zoogeographical changes accompanied the temperature changes (fig. 121).

During the January, 1958, onset of “El Niño” the coastal euphausiid *Euphausia mucronata* was maintained in the same northern center of abundance near Callao as in July, 1952, though surface temperatures were 22°–24° C. in January, as compared with 16°–18° C. during the July survey. The widespread warm-water

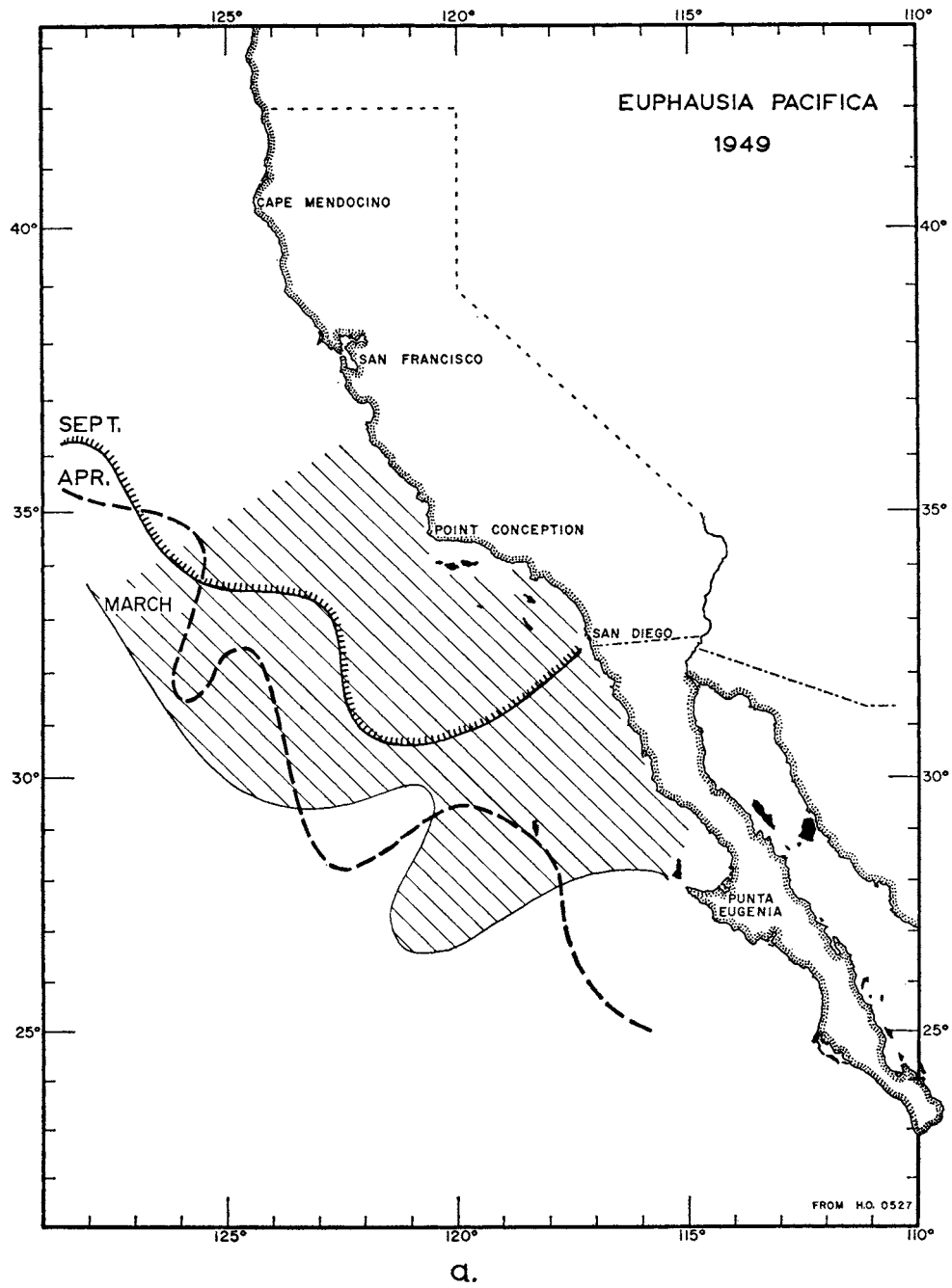


Fig. 120a. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1949. See also figs. 120b–120f.

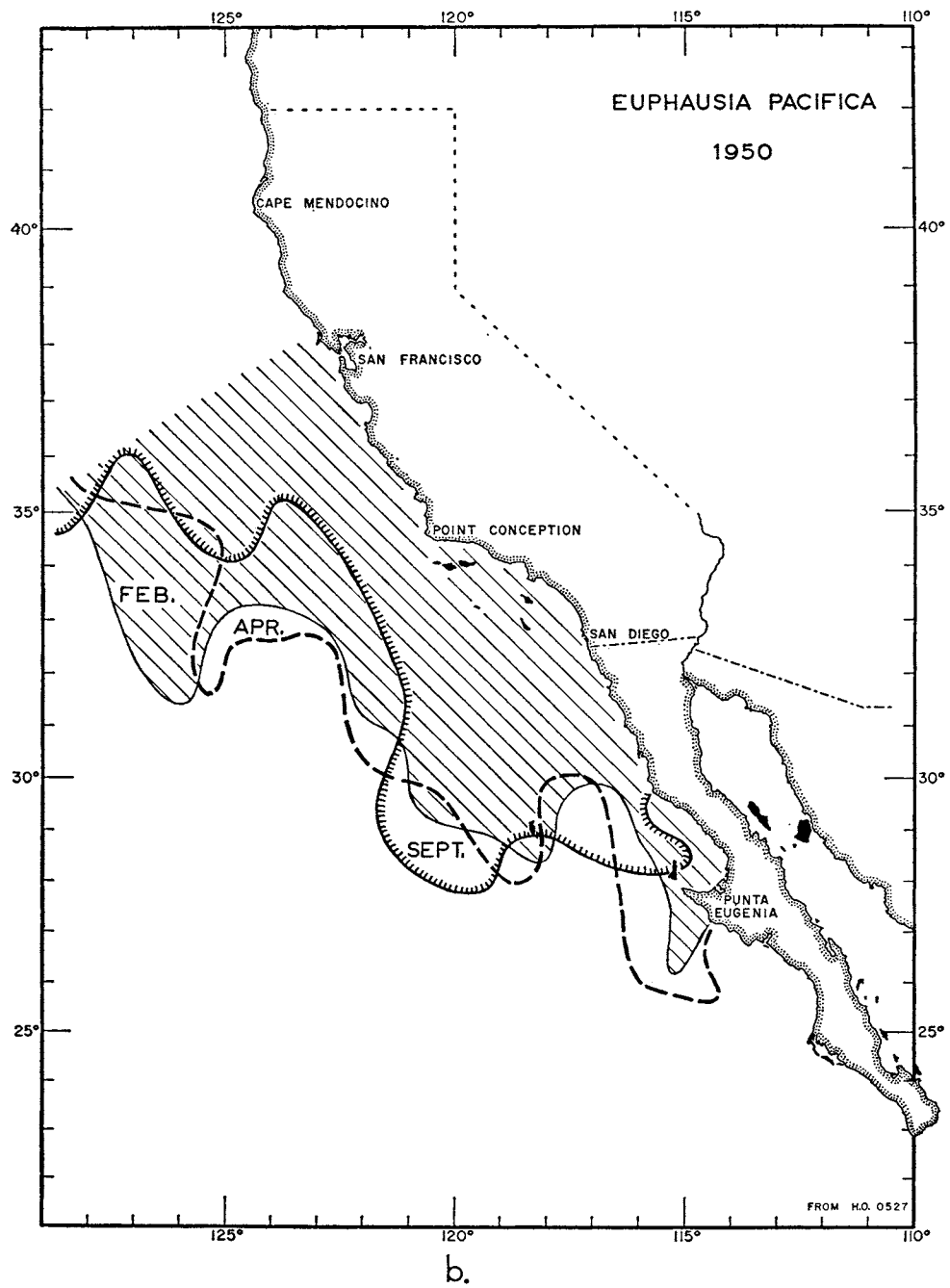


Fig. 120b. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1950.

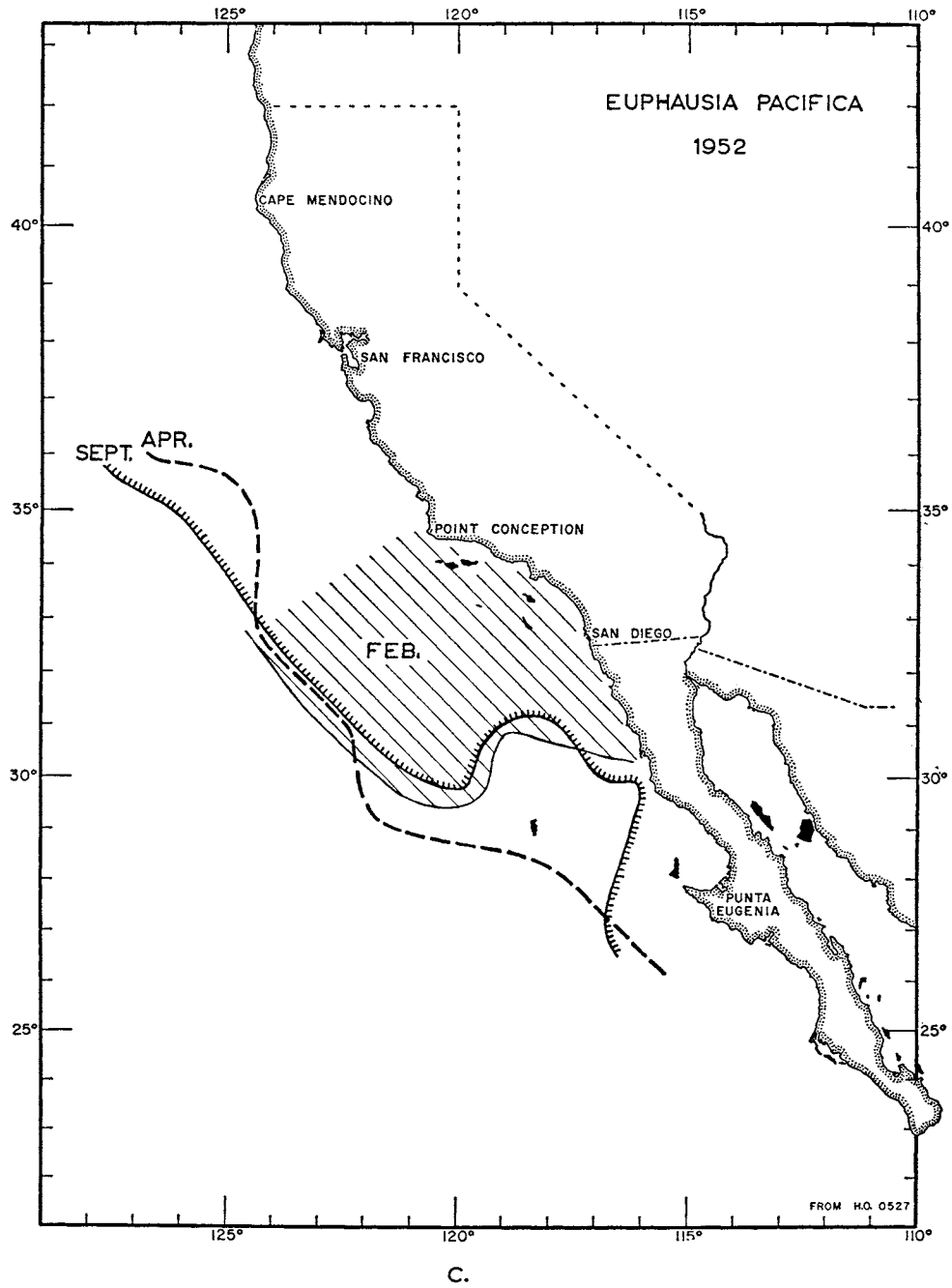


Fig. 120c. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1952.

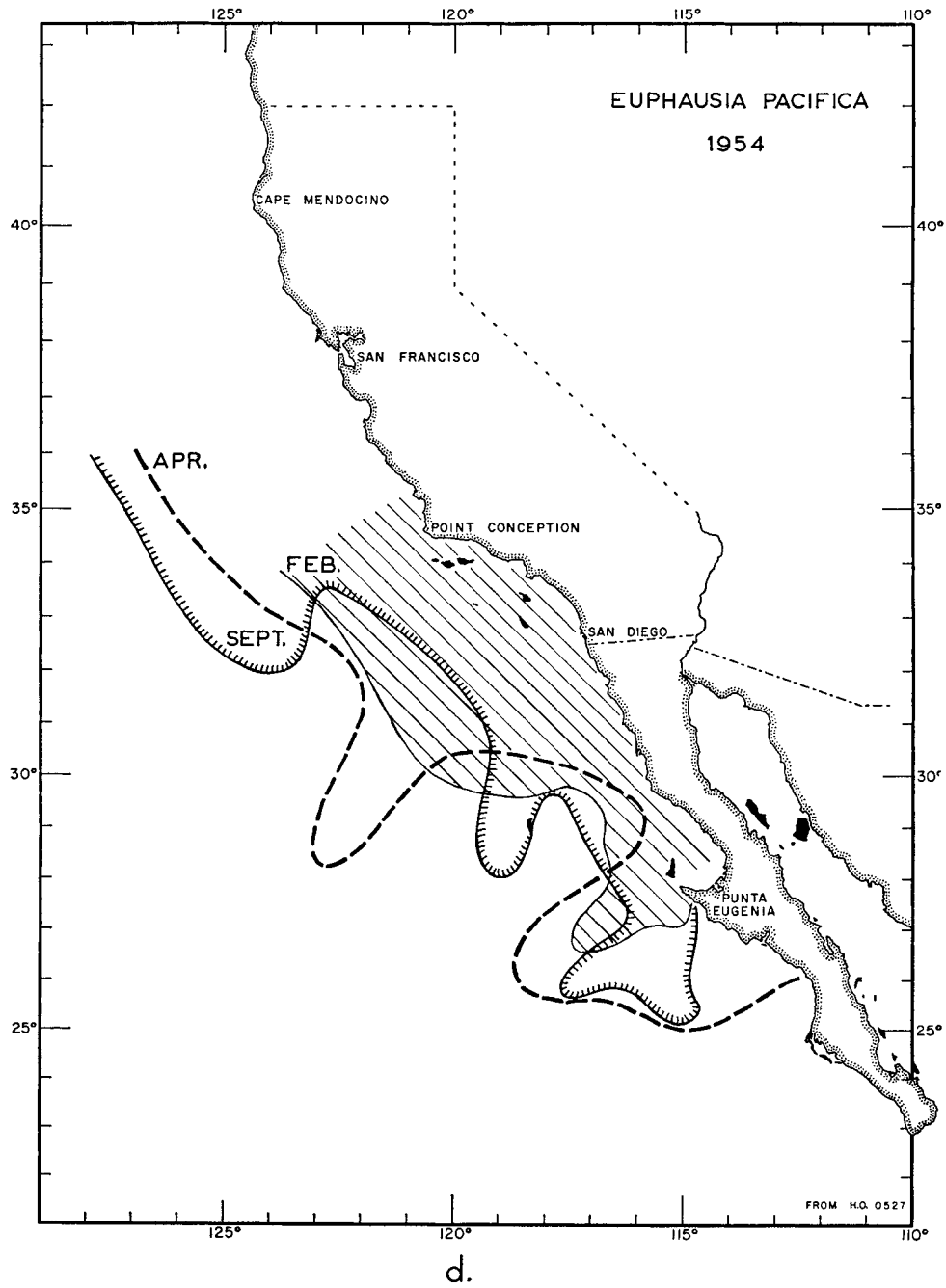


Fig. 120d. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1954.

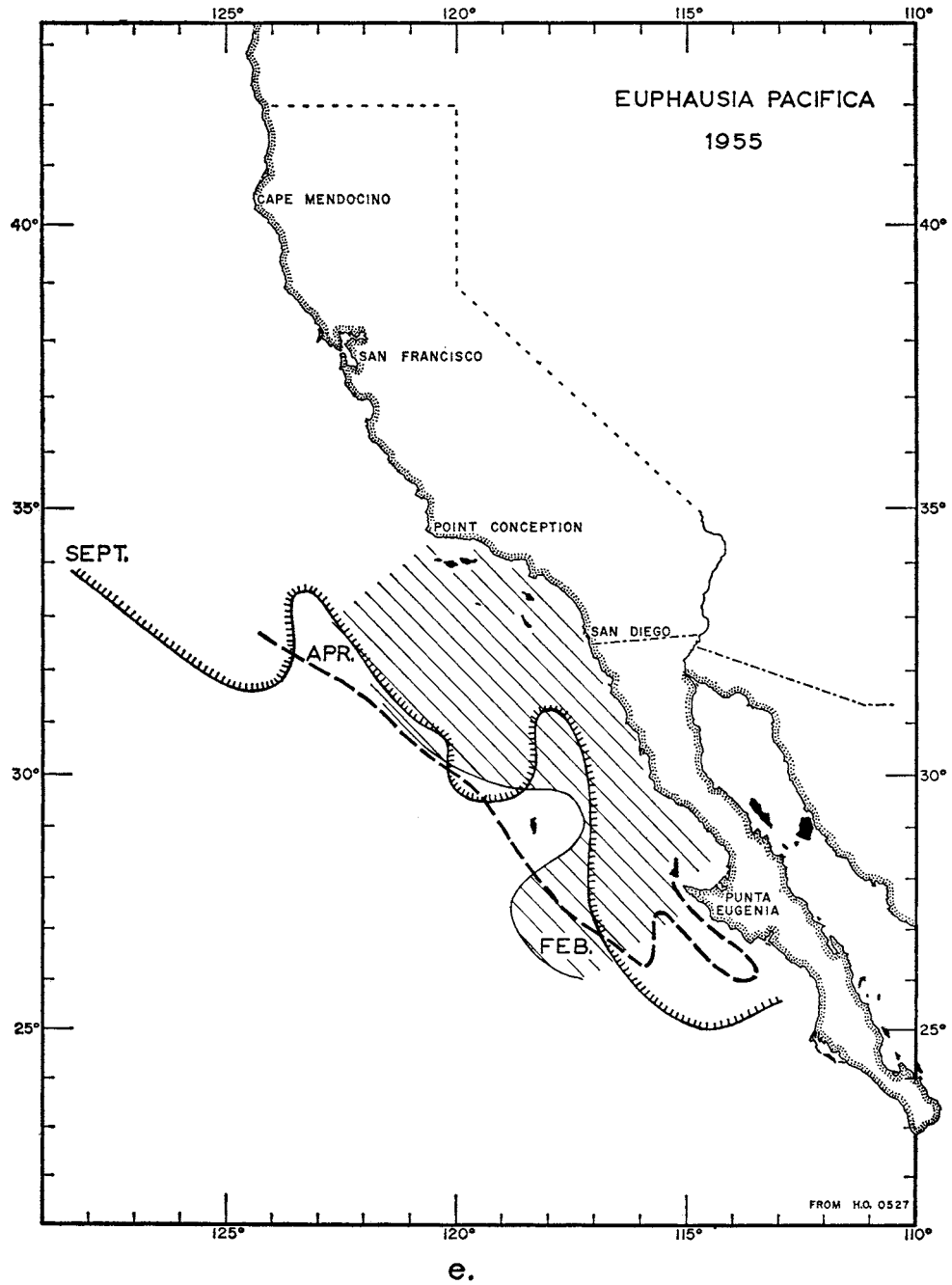


Fig. 120e. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1955.

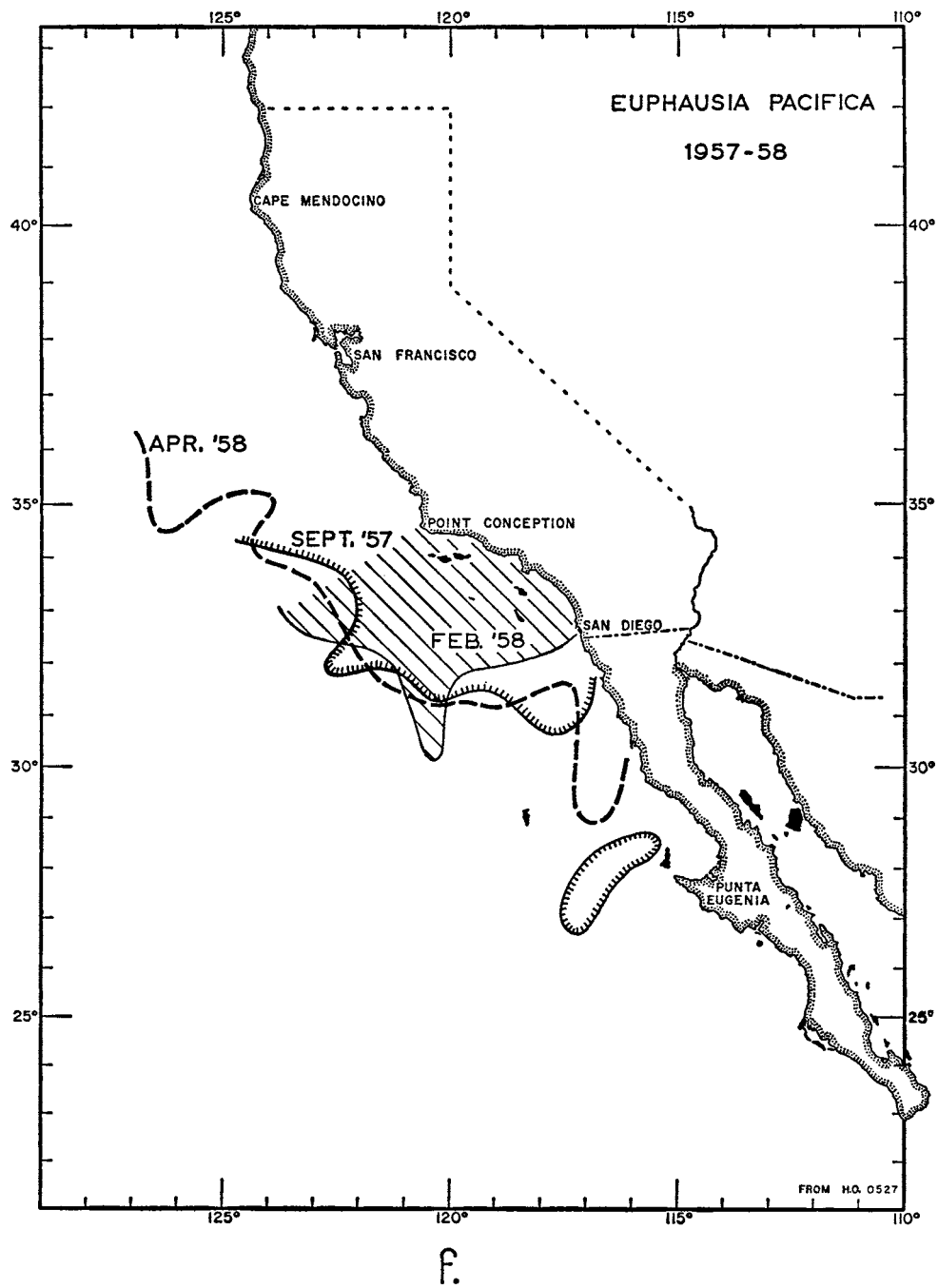


Fig. 120f. The boundary and the winter, spring, and summer distributions of *Euphausia pacifica* in the California Current, 1957-58.

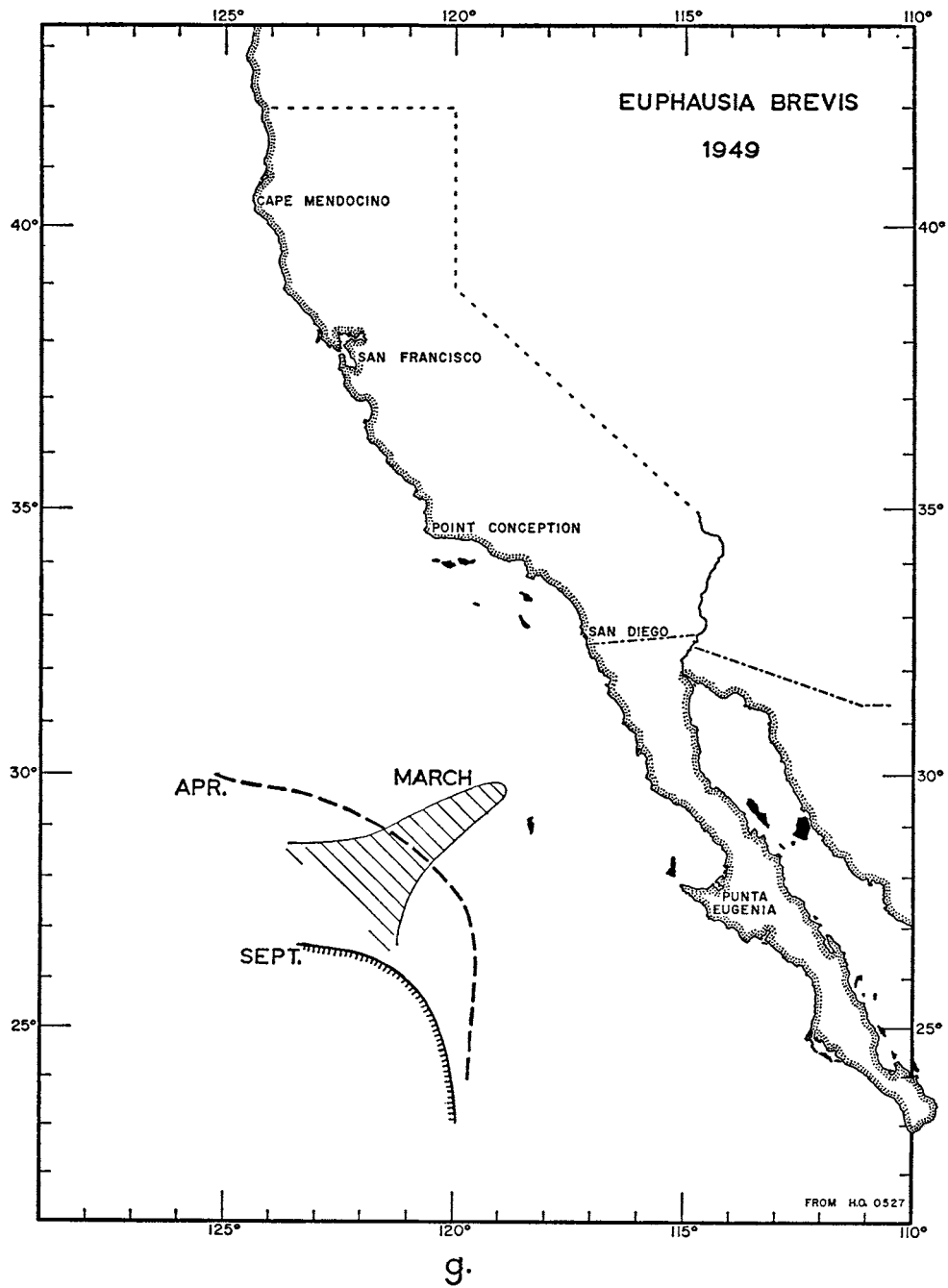


Fig. 120g. The boundary and the winter, spring, and summer distributions of *Euphausia brevis* in the California Current, 1949. See also figs. 120h and 120i.

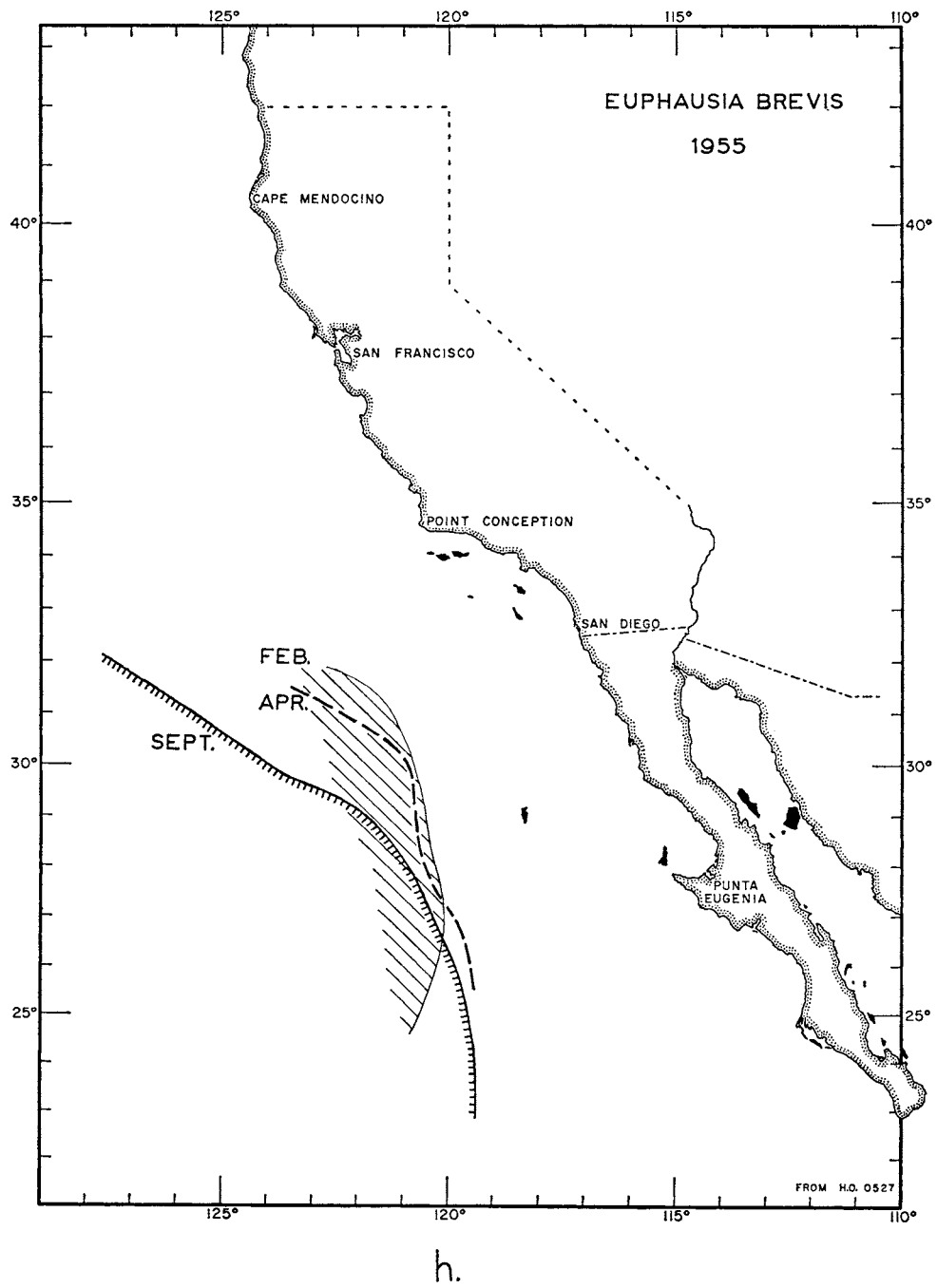


Fig. 120h. The boundary and the winter, spring, and summer distributions of *Euphausia brevis* in the California Current, 1955.

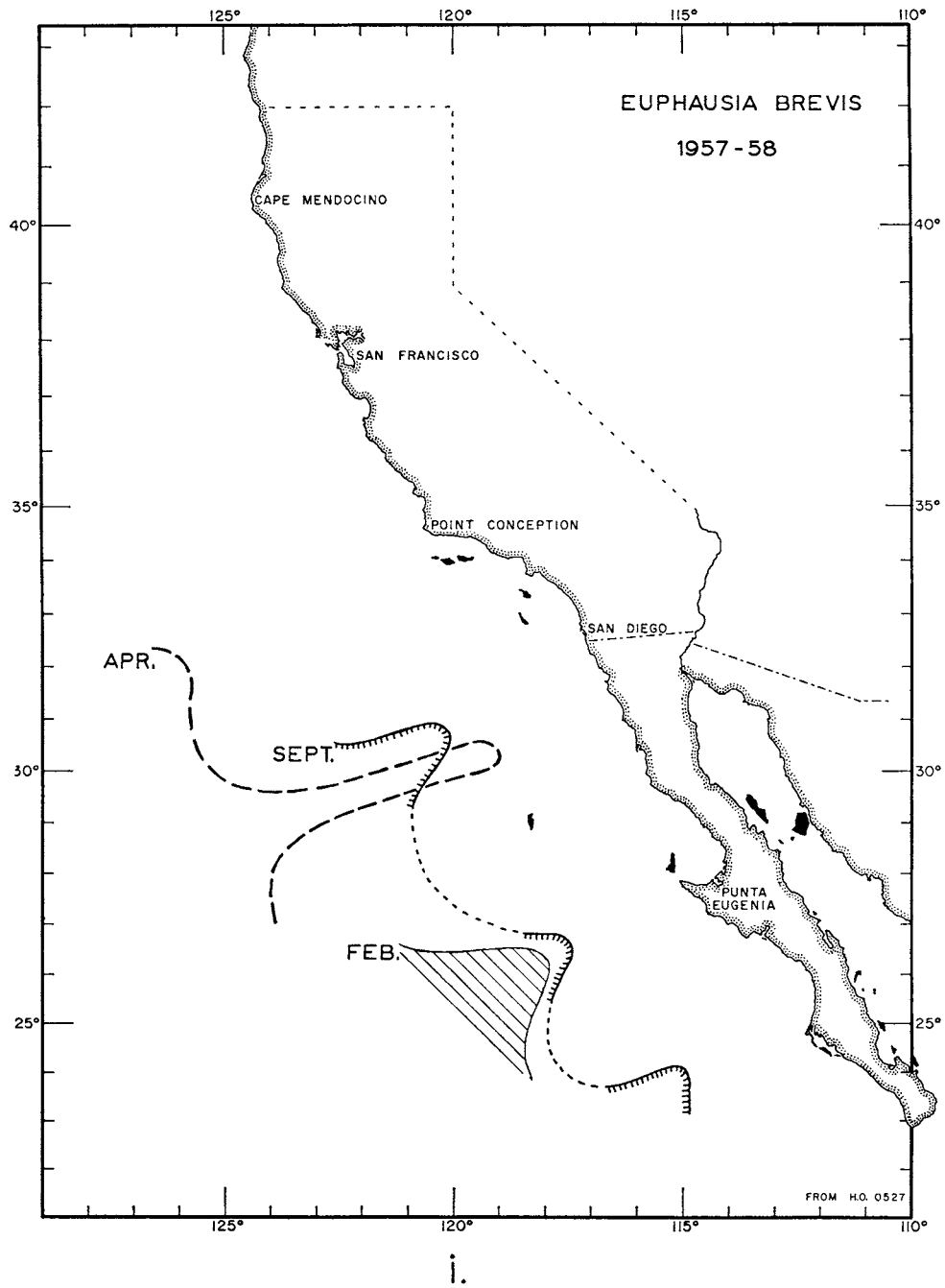


Fig. 120i. The boundary and the winter, spring, and summer distributions of *Euphausia brevis* in the California Current, 1957-58.

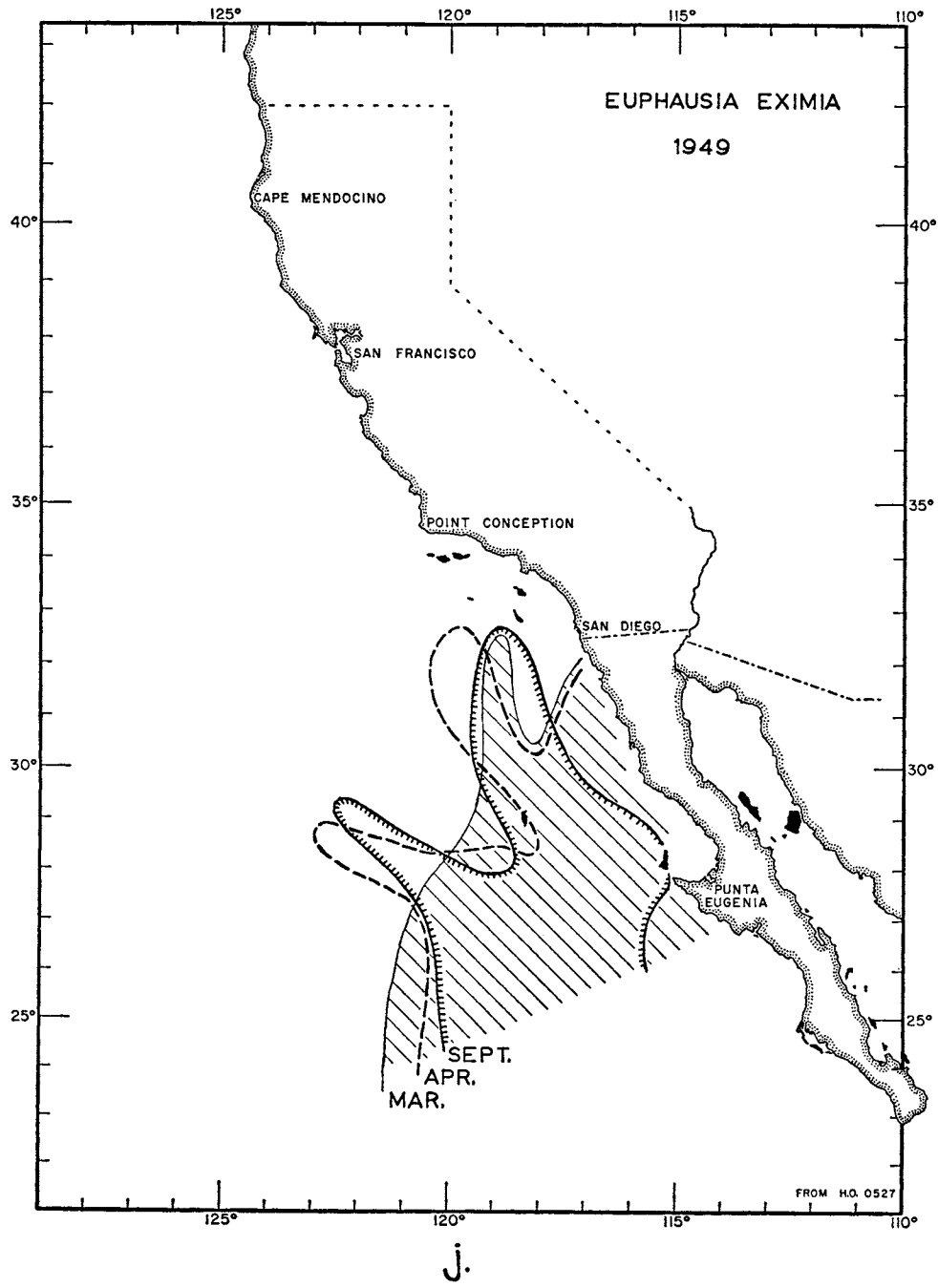


Fig. 120j. The boundary and the winter, spring, and summer distributions of *Euphausia eximia* in the California Current, 1949. See also figs. 120k and 120l.

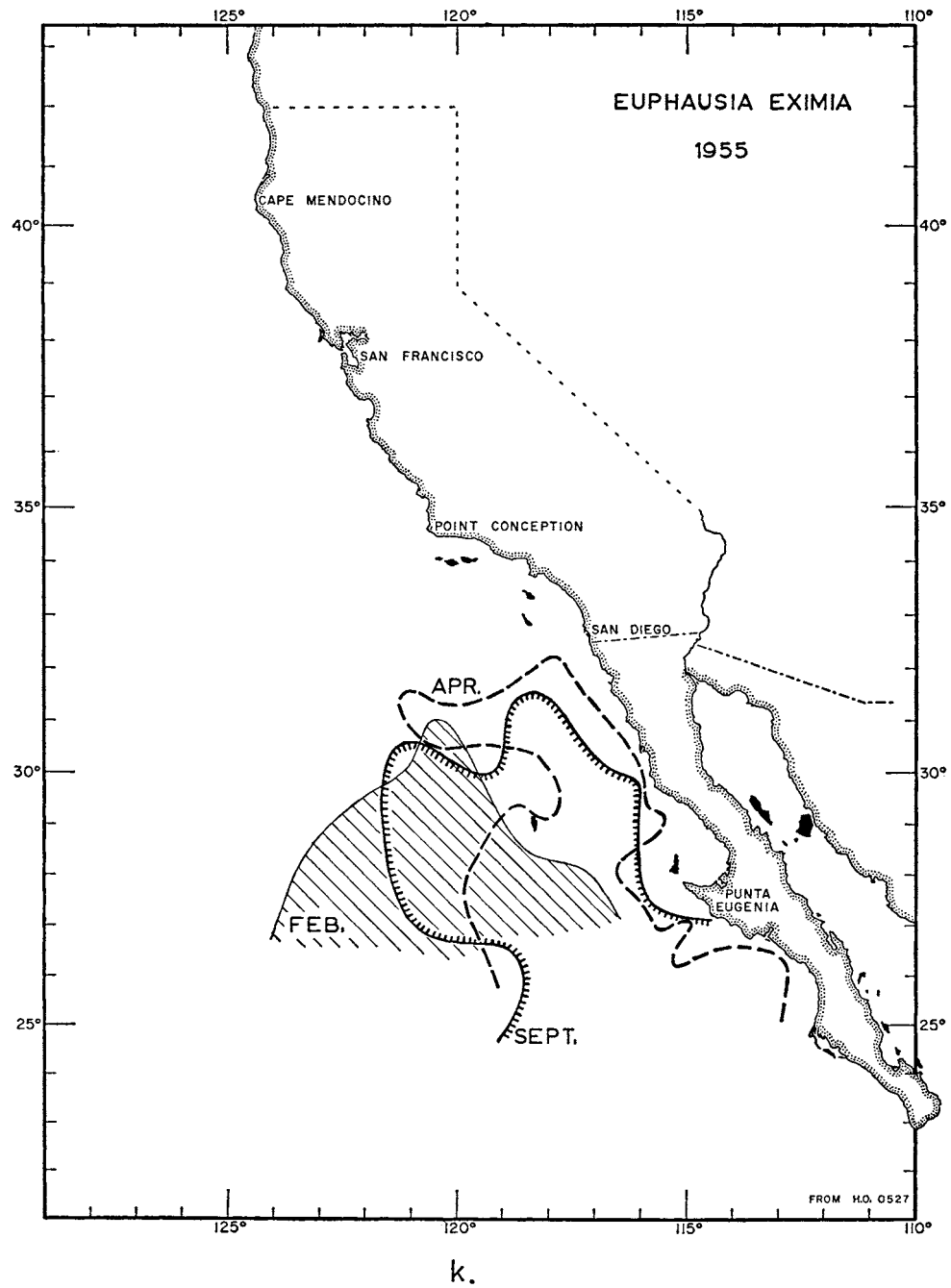


Fig. 120k. The boundary and the winter, spring, and summer distributions of *Euphausia eximia* in the California Current, 1955.

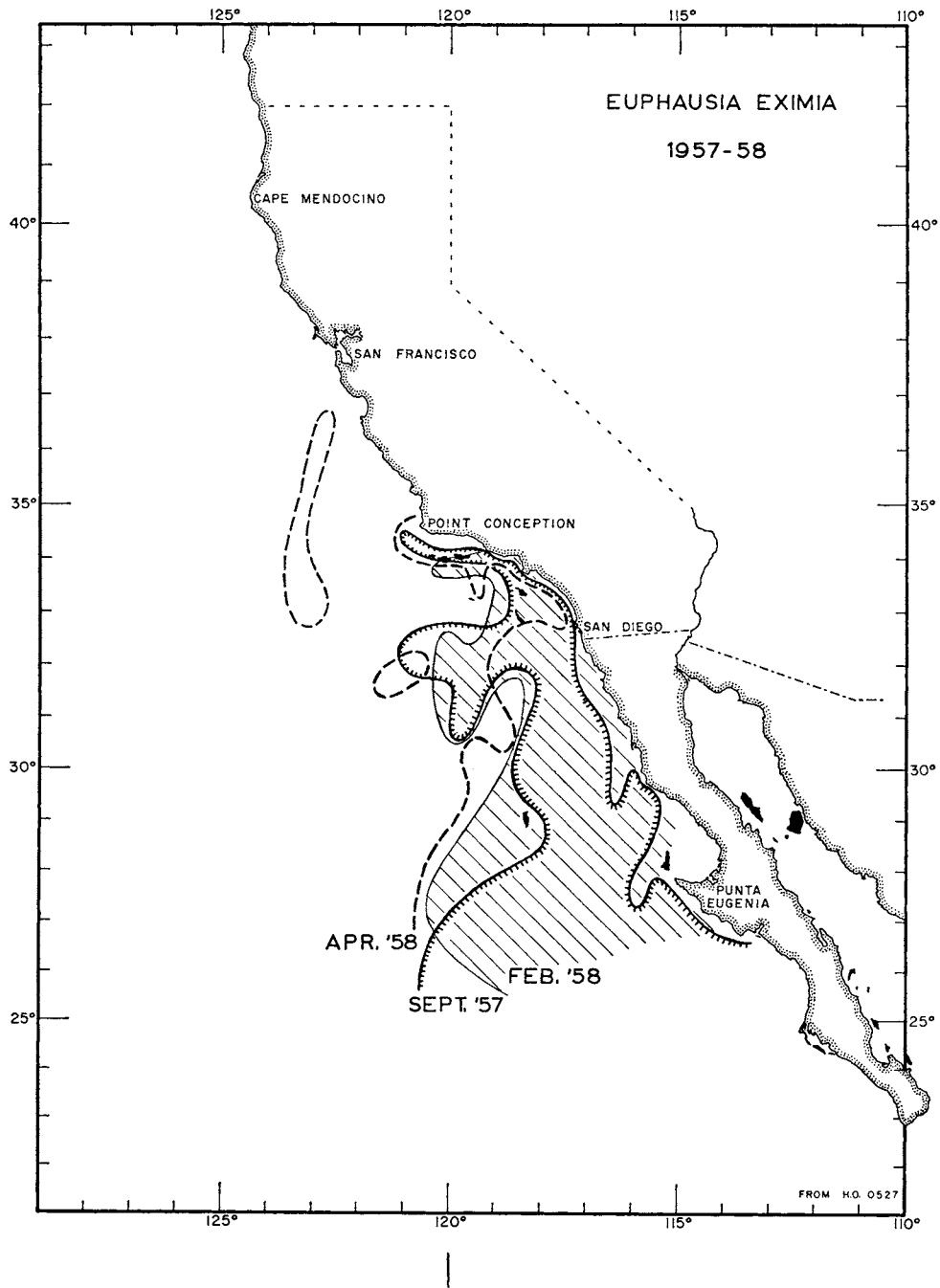


Fig. 1201. The boundary and the winter, spring, and summer distributions of *Euphausia eximia* in the California Current, 1957-58.

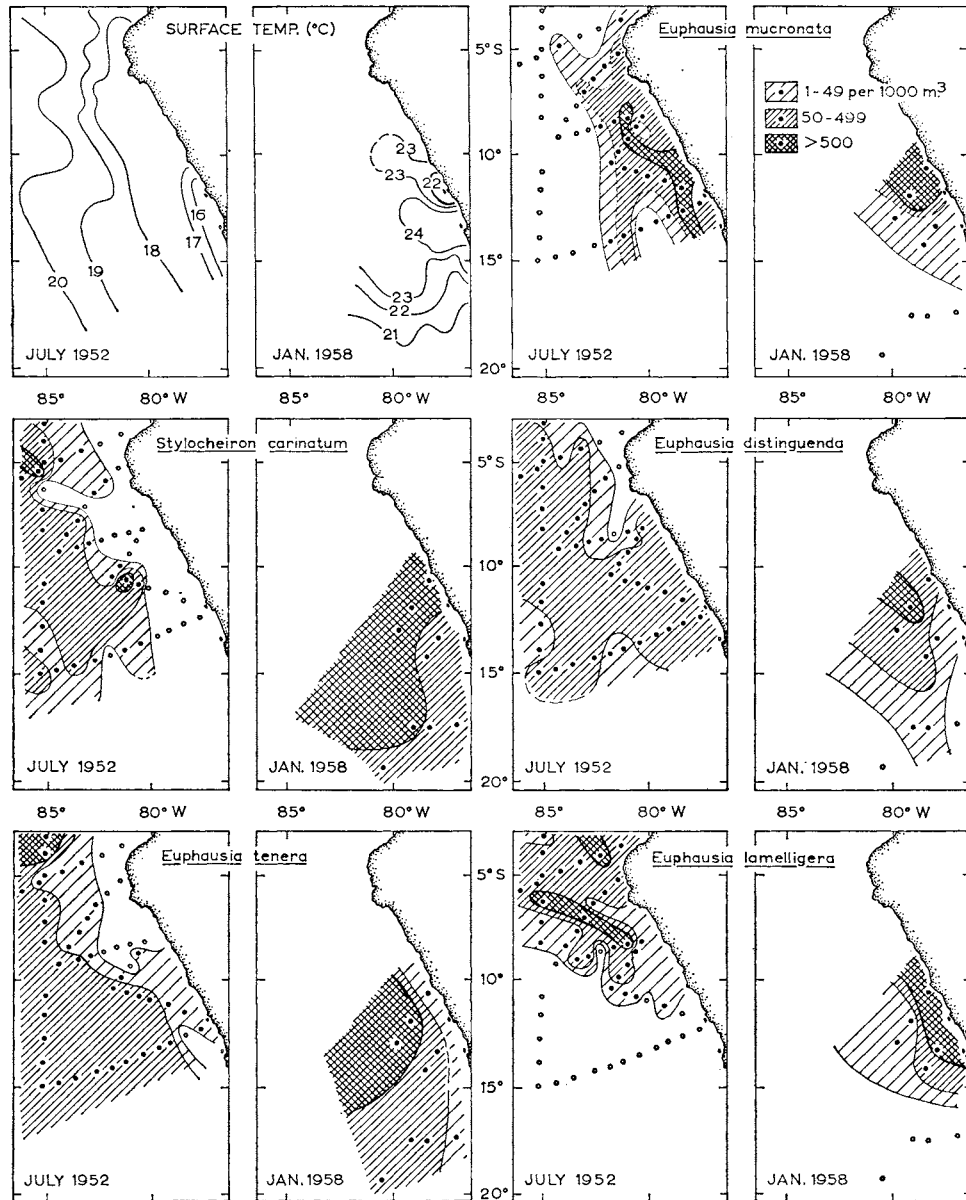


Fig. 121. Distributions of surface temperature and euphausiid species in the northern part of the Peru Current. July, 1952 ("Shellback" exped.) and January, 1958 ("Downwind" exped.) data compared.

species *Stylocheiron carinatum* was abundant in coastal waters during the warm January, 1958, period but was lacking from the main part of the Current, cooler than 18° C., in July, 1952. High densities of the eastern equatorial species *Euphausia distinguenda* and *E. lamelligera* extended farther south into the Peru Current during "El Niño" than during the survey carried out in the southern winter. Similarly, *E. tenera* was numerous off Callao in January, 1958, but not in July, 1952.

A widely accepted conception of "El Niño" holds that warming of the region of the Current takes place as a consequence of a southward shift of the tropical rain belt, bringing about a disruption of upwelling and a southerly deflection along the coast, of water from the Equatorial Countercurrent. These changes are initiated in December, according to Sverdrup, Johnson, and Fleming (1942), but the peak period of warming is February and March.

A second kind of incursion of warm water, discussed by Gunther (1936), may take place during the upwelling season when tongues of saline offshore water, bounded at their northern and southern limits by cooler waters, move shoreward across the current system.

The differences in the euphausiid distributions suggest that in January, 1958, the water off Peru was generally warm but was not dominated by strong currents. During the "Downwind" expedition the Current was nearly static from the standpoint of water movement. Temperatures off Callao were 5°–8° C. higher than at the time of the "Shellback" survey. The species composition of the euphausiid fauna of the region was constant for the two survey periods, though the dominating equatorial species were observed to be numerous farther south (e.g., *E. lamelligera*) and nearer to shore (*Stylocheiron carinatum*) during the "Downwind" expedition than during the "Shellback" expedition, which was carried out when upwelling prevailed.

Other important species of the Peru Current region, for example *Nyctiphanes simplex* (fig. 25) and *Nematoscelis gracilis* (fig. 70), were also numerous and present in several stages of development during the "Niño" period, suggesting that warming and stability of the rich Peru Current is tolerable, if not optimal, for euphausiids of the region.

It is inferred from this interpretation of "El Niño" that the fish upon which the guano birds depend withdraw from the waters of the Peruvian coastal islands as a result of high temperatures rather than because of insufficient food. Cool-water plankton species such as *Euphausia mucronata*, however, have sufficient vertical range to allow them to persist in the northern part of the Peru Current despite the collapse of upwelling. At the same time, the typical equatorial fauna of the offshore part of the Current moves somewhat shoreward and toward the south.

THE EQUATORIAL MID-PACIFIC

The equatorial mid-Pacific, 160° E. to 130° W., is characterized by an east-west belt of species belonging mainly to the equatorial assemblage. In mid-ocean, the equatorial group includes *Euphausia diomediae*, *E. paragibba*, *E. distinguenda*, *Nematoscelis gracilis*, *Stylocheiron affine* "East Equatorial Form," and *S. affine* "West Equatorial Form," but not the equatorial–west-central species *Thysanopoda*

tricuspidata, *E. tenera*, and *S. microphthalmalma*. The region in which more than 50 per cent of the euphausiids are equatorial in the northern winter (as indicated by the data for POFI Cruise 8, January–March, 1951) extended as far north as 8° N., south of Hawaii (fig. 122a).

Summer data indicate that in this region the central euphausiid group (*Euphausia recurva*, *E. mutica*, *E. brevis*, *E. hemigibba*, *Nematoscelis atlantica*, *Stylocheiron suhmii*, and *S. affine* “Central Form”) recedes somewhat to the north of the position occupied during the winter, and that the belt dominated by equatorial species is then correspondingly broader, reaching 14° N. (fig. 122b).

Farther west, near 172° W., the major boundary between central and equatorial species is indicated by the winter data (“Troll” and “Capricorn” expeditions) to be at 8° N. and by the summer data (“Equapac” expedition) to be at 9°–11° N.

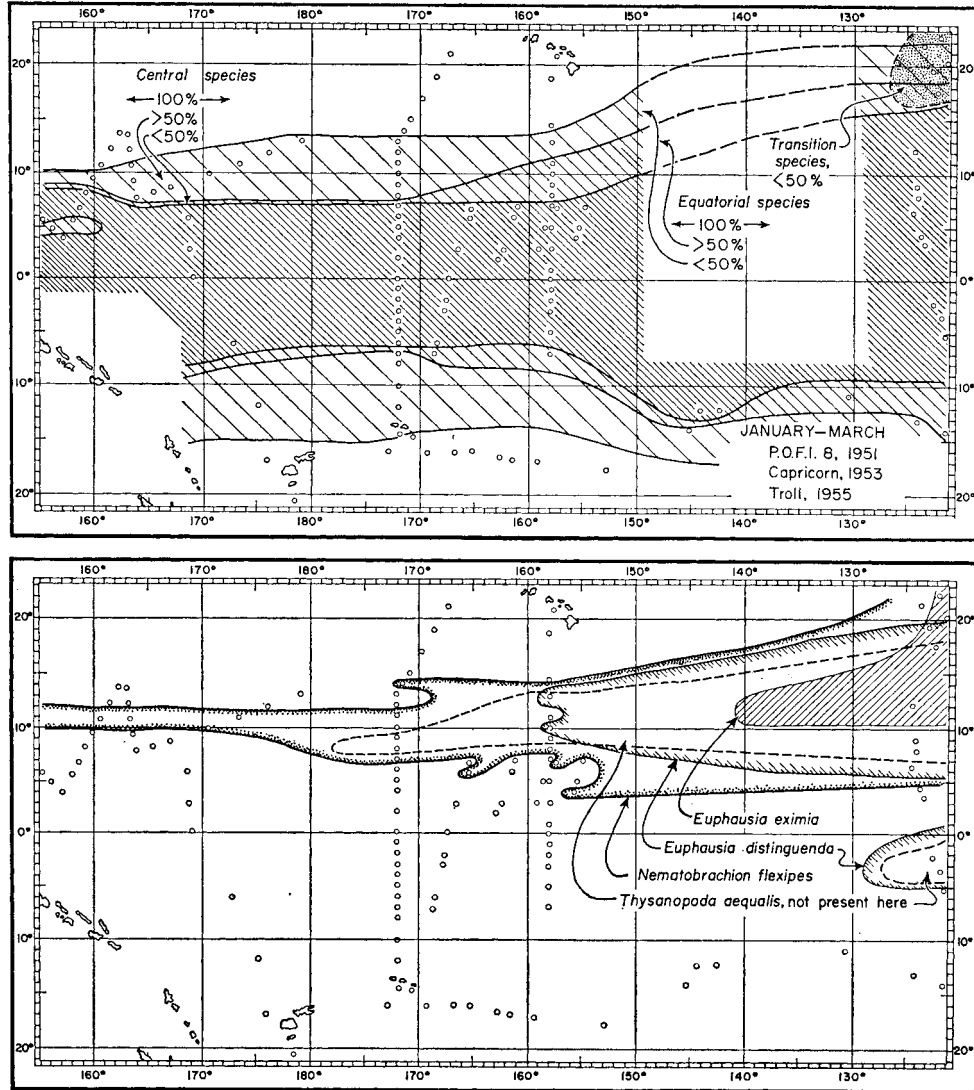
The northern boundary of the Equatorial Countercurrent at longitude 172° W. was near 10° 30' N. during the winter, 1951, POFI cruise (Cromwell, 1953). At this latitude, the euphausiid fauna was then dominated by central species, though equatorial species were included in small numbers (fig. 122a). Here the widespread tropical-subtropical species *Nematobrachion flexipes* was present in the region of the boundary between the Countercurrent and the North Equatorial Current, although *Thysanopoda aequalis*, generally occurring widely in the equatorial mid-Pacific, was not.

Farther to the east, intrusions into the mid-Pacific region by *Euphausia eximia* and *E. diomediae* may be regarded as indicating transport from the eastern equatorial basin. Tongues of distribution of these species lay in the latitude of the North Equatorial Current, but also along the belt of the thermal anticline at the Countercurrent–North Equatorial Current boundary.

During the summer of 1950 (POFI Cruise 5), Cromwell found the northern boundary of the Countercurrent farther south than in the winter—near 9° N., as compared with 10° 30' N.—at longitude 158° W. These boundaries are within the east-west belt entirely dominated by equatorial species. The abrupt boundary between central and equatorial species was then farther north, at 14° N., as compared with 8° N. for the winter survey. To the south, the cooler part of the North Equatorial Current and the thermal anticline were indicated by the absence of *Thysanopoda aequalis* and the presence of *Euphausia distinguenda* and *Nematobrachion flexipes* (fig. 122b).

GEOGRAPHICAL ISOLATION AND SPECIATION

Barriers that have isolated elements of once-common populations from each other are often more easily recognized on the land than in the ocean. For example, land masses are separated from each other by water. Inasmuch as some water masses are separated from each other only by regions of oceanographic convergence and divergence that cannot absolutely isolate populations, the role of oceanographic boundaries in evolutionary processes is uncertain. Only the three north–south continental land masses that partition the seas into the Atlantic, Pacific, and Indian oceans can be readily recognized as barriers between the pelagic habitats of low or mid-latitudes. Populations of certain warm-water euphausiid species are, today, isolated from each other by these barriers.



Figs. 122a. (above) and 122b (facing page). Euphausiid assemblages in the equatorial mid-Pacific, based upon (122a) January–March sampling and (122b) July–September sampling. Percentages of total euphausiids belonging to central, equatorial, and transition-zone groups are plotted. Terminal parts of the distributions of two eastern equatorial species, *Euphausia eximia* and *E. distinguenda*, and a tongue of distribution of the widespread species *Nematobrachion flexipes* are shown. The area from which *Thysanopoda aequalis* is excluded is indicated to illustrate complementary zoögeographical effects in the region of the North Equatorial Current.

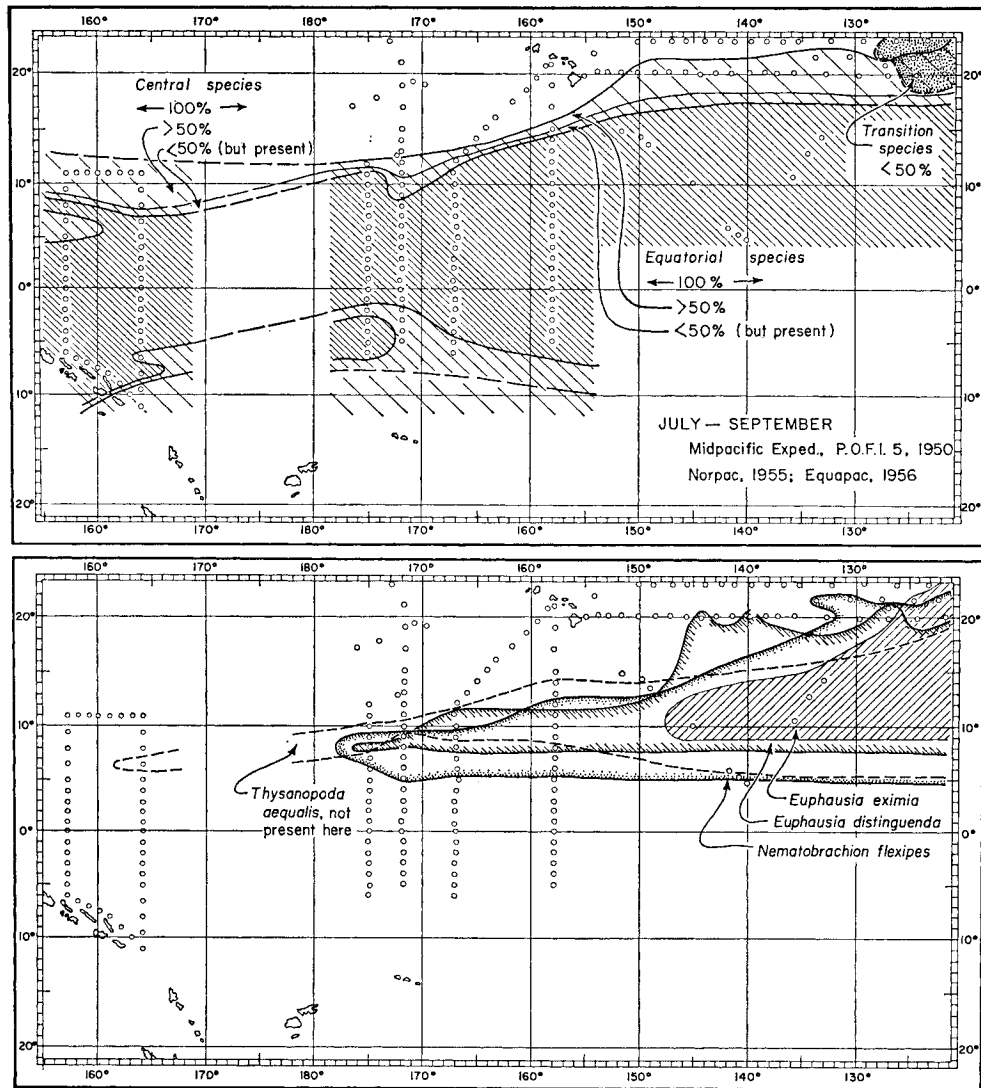


Fig. 122b. Euphausiid assemblages in the equatorial mid-Pacific, based upon July-September sampling.

A number of references were made in the foregoing sections to *forms of uncertain taxonomic rank*. These are species or subspecific forms that may or may not be sufficiently distinct genetically to be incapable of interbreeding or, if able to interbreed, of producing viable offspring. Such forms include the “Spined” and “Unspined” forms of *Thysanoessa longipes*, the *Thysanopoda aequalis*–*T. subaequalis* species pair, the “Large Southern” and “Small Northern” forms of the chaetognath *Sagitta gazellae*, the polychaete species pair *Vanadis antarctica*–*V. longissima*, and the several forms of the two euphausiids *Stylocheiron affine* and *S. longicorne*. McGowan (in press) has discussed the possible ecotypic basis of differentiation in *Limacina helicina*, showing that forms of this pteropod are associated with subarctic and transition zones of the North Pacific.

In such examples the closely related forms live on opposite sides of convergences or other oceanographic boundaries and are incompletely isolated from each other. Therefore, it is not certain to what extent such forms can diverge genetically. However, when sibling forms are geographically separated from each other it is certain that the splitting-up of the parent population has brought about reproductive isolation. The species pairs *Nematoscelis difficilis*–*N. megalops* (north–south disjuncts) and *Euphausia distinguenda*–*E. sibogae* (east–west disjuncts) have widely separated ranges.

The argument to be presented here is not that of Mayr (1942) —that absolute isolation is essential for speciation. Far too little is yet known about the genetics of plankton species to suggest this. Rather, it will be shown that the paired roles of continental and tropical barriers could have repeatedly split up euphausiid populations in the past (just as such barriers are partitioning the distributions of species today), giving rise to existing groups of species as a consequence of independent selective adaptations.

The immense size of zoöplankton populations may be conducive to a slow evolutionary rate. Bowman (1955) pointed out that owing to the size of these oceanic populations—enormous compared with most terrestrial populations—genetic drift is virtually absent. Buzzatti-Traverso has alternatively suggested (personal communication) that the large size of plankton populations is accompanied by a high absolute incidence of mutations, including a greater frequency of those permitting individuals to colonize new environments than would occur in a small population. Johnson (1939) suggested that species development in a group of North Pacific *Eucalanus* copepods may have been associated with such colonization of successive habitats along paths of the clockwise circulation of the North Pacific.

The role of colonization of neighboring waters, as compared with the role of absolute geographical isolation, in the differentiation of zoöplankton species must remain an open question. In any event, gene flow between populations within a distributional range is encouraged by the mixing action of oceanic currents. The time required for the exchange of genetic material between geographical extremes in the range may be of the order of many years, but not units of time significant to evolutionary processes.

Temperature will be used in this discussion to describe the ancient habitats of species. Temperature reflects obvious responses of the ocean to climatic change. Certainly, it is a significant ecological parameter in the epipelagic part of the

ocean. Habitats are, as yet, best described in terms of the distributions of the animals and the isotherms, shallow and deep, that relate to their boundaries.

Isotherm positions may be extrapolated for any postulated amount of general oceanic warming or cooling. It would be a more complicated matter to extrapolate the positions of ancient water masses.

It is well known (e.g., Durham, 1950; Hubbs, 1952) that ocean temperatures have changed in the course of geological time. The distributions of animals have surely changed according to the migrations of limiting isotherms or associated parameters, where transport by currents allowed. The persistence of belts of oceanic productivity, as measured in the sediments by Arrhenius (1955), suggests that the positions of some major currents must have remained nearly constant since the close of the Tertiary epoch. However, if the water-mass zones have similarly persisted, it is unlikely that plankton distributions have migrated in strict harmony with latitudinal migrations of isotherms. When oceanwide warming or cooling compelled a species to occupy a new geographical environment within the range of physical, nutritional, and chemical features to which it could adapt, this new environment also had to contain a sufficiently closed current system to maintain the population.

BIANTITROPICAL PANOCEANIC DISTRIBUTIONS

A characteristic type of distribution in the Pacific consists of a disjunct pair of oceanwide belts, one situated in mid-latitudes in the Northern Hemisphere and the other at the same latitudes in the Southern Hemisphere. Long known as bipolarity, this phenomenon was shown by Hubbs (1952) to be concerned with latitudinal discontinuities in distribution that might be wide, narrow, or even incomplete in some parts of the ocean. He proposed the more inclusive term "antitropicality" to augment "bipolarity." Antitropical species living in both Northern and Southern hemispheres will here be called "biantitropical."

No euphausiid species is bipolar in the strict sense of occurrence only in the Arctic and Antarctic oceans. Disjunct ranges most widely separated in terms of latitude are found in the distributions of *Thysanopoda acutifrons* (fig. 14) and *Thysanoessa gregaria* (fig. 57). Incipient antitropicality is suggested in the distributions of the central species *Thysanopoda aequalis* and *T. subaequalis* (fig. 23), *Euphausia mutica* (fig. 35), and *E. brevis* (fig. 37). With progressive warming of the cool equatorial water mass (figs. 2, 7c, 7d) these separated distributions would be expected to coalesce further, near the equator, rather than to withdraw from the equatorial belt. Subsequent general cooling, perhaps associated with a glacial epoch, would then bring about retreat of the species to the warmest parts of the central water masses, increasing the degree of antitropicality. On the other hand, this same cooling would be expected to bring the species of the transitional zone, for example *Thysanoessa gregaria*, nearer to the tropics. A species having such a distribution might then colonize an analogous habitat in the opposite hemisphere, establishing a distribution that could become antitropical during the following warm epoch. If, before the tropical transgression, the distribution were already biantitropical, the subsequent exchange of genetic material across the composite

reunited range would retard or prevent genetic differentiation between the northern and southern populations.

It is significant that the antitropical euphausiids, and most of the *Euphausia* species occupying the central water masses of the oceans, are also panoceanic, occurring in the Atlantic and Indian oceans as well as in the Pacific. In contrast, subarctic euphausiids (excepting the two most northern species, *Thysanoessa inermis* and *T. raschii*, which appear to have passed between the Atlantic and Pacific oceans by way of the Arctic Ocean, and the most tropical species, e.g., *Euphausia americana* of the Atlantic and *Nematoscelis gracilis* of the Indo-Pacific Equatorial Water Mass) do not occur in both the Atlantic and the Indian–Pacific oceans, but are endemic to one or the other. All antarctic species (living south of the Antarctic Convergence) and subantarctic species (living between the Subtropical and Antarctic convergences) are confined to the Antarctic Ocean and are circumpolar.

Given sufficient time, the separated populations of biantitropical species would be expected to undergo independent selective adaptations. *Nematoscelis difficilis* and *N. megalops* are examples of biantitropical evolutionary divergence in an early stage. Another transition-zone species, *Thysanoessa gregaria*, ranges somewhat farther into warm waters than *N. difficilis* or *N. megalops*—by about 1° C., interpreting 100-meter isotherms as limiting. Its northern and southern populations may have exchanged genetic material across the tropics more recently than the precursor of *N. difficilis*–*megalops*. At any rate, *T. gregaria* of the Northern Hemisphere is still morphologically indistinguishable from *T. gregaria* of the Southern Hemisphere.

It appears likely that this is the means by which other groups made up of species having similar or overlapping distributions, such as *E. recurva* (fig. 34), *Euphausia mutica* (fig. 35), and *E. brevis* (fig. 37), have differentiated from their respective common stocks. In such a group, which consists of related, though not sibling, species, the splitting-up of the ancestral population between hemispheres or between oceans occurred much earlier (perhaps at the close of the Tertiary epoch, when the equatorial zone is believed to have become differentiated) than, for example, the splitting-apart of the population of the precursor of *N. difficilis* and *N. megalops*, which are still very similar today and may be regarded as siblings. Relatively recent Pleistocene latitudinal oscillations of isotherms, discussed below, could have brought about subsequent recolonization of each of the widely separated, zoögeographically analogous areas by more than one of the daughter species, after the daughter species had diverged morphologically in their respective native oceans or hemispheres.

The relative merits of the three possible origins of biantitropical panoceanic euphausiid distributions may be considered in turn.

The first hypothesis suggests that the tropics were—and in some areas may still be—traversed by organisms in deep water along isothermal surfaces, with emergence in high latitudes. The plankton sampling carried out by the Scripps surveys has been adequate to show that, although many deep-living widely-ranging species provide evidence of emergence in high latitudes (e.g., *Nematobrachion boopis*, fig. 75), the northern and southern segments of the dual ranges of many other species

are, in fact, widely separated. It is with these biantitropical distributions that we are concerned.

A second explanation assumes that the northern and southern populations are relict bands of broad distributions which were occupied by the species during the part of the early Tertiary epoch when the world climate is believed to have been more uniform and the deep sea was warmer than today (Emiliani, 1954). Subsequent equatorial warming, or cooling, brought about a latitudinal split in the distributions. This postulate seems more plausible when applied to the generic than to the specific level. The genus *Thysanoessa* is, in fact, biantitropical and consists of different groups of species occupying only the cooler waters of each hemisphere. As pointed out above, however, it seems more probable that the breaking up of the Tertiary temperature uniformity led to biantitropical *speciation* as a consequence of biantitropical distribution, rather than to biantitropical *distributions* within modern species. Evolution in zoöplankton may be slow. However, it is not likely that separated populations have continued undifferentiated, or have undergone parallel evolution since the Eocene and Oligocene epochs some 50 million years ago.

A third explanation of biantitropicality, advocated by Berg (1933) and Hubbs (1952), assumes that tropical waters were transgressed during Pleistocene periods of global cooling. Durham (1950) concluded from a study of the distribution of coral reef types that there has been a gradual southward recession of tropical temperatures in the northeastern Pacific since the Oligocene epoch. Coastal assemblages in California indicate that there were northward and southward fluctuations of Pleistocene marine isotherms, but it is believed that these were only of the magnitude of 2°–3° of latitude from their present positions.

To account for tropical transgression of oceanic zoöplankton species it must be postulated either that *seasonal* extremes in temperature produced more extreme fluctuations in isotherms than those indicated by the *average* fluctuation corresponding to 2°–3° of latitude, or that oceanic fluctuations (as contrasted with the littoral temperature changes deduced from the coastal assemblages) were more extreme than near-shore fluctuations. Another possibility is that general Pleistocene temperature changes would be less accurately reflected in an area of upwelling, such as the coast of California studied by Durham, than in the surface waters of a now-stable water mass, such as the western Central American pool, across which equatorial transgression might take place. If coastal upwelling were reduced off California during the ice ages, the slightly lowered coastal temperatures (corresponding to 2°–3° of latitude) which have been demonstrated could reflect greater cooling outside of the coastal area.

Hubbs (1952) suggested that if the surface shore waters of the eastern Pacific were 8° C. cooler in the winter than during present winters, and 3° C. cooler in the summer, continuity and exchange between faunas now antitropically separated would have been possible. He adduced corroborative evidence for such a past north–south connection in the present paucity of the eastern equatorial fish fauna, which, he suggests, was much reduced by Pleistocene cold-water transgressions.

Surface waters off Central America in the zone of 0°–18° N. are not substantially fed by either the California or Peru currents, having perhaps greater affinities with the Equatorial Countercurrent than with any other outside area. While

near-shore cooling doubtless allowed temperate coastal populations access to the tropics, north–south Pleistocene exchanges between temperate pelagic faunas may have occurred offshore. Illustrating this possibility is a reconstructed Pleistocene distribution for *Thysanoessa gregaria* (fig. 123), based upon 2½–3° C. of cooling at 200 meters of depth, using Recent isotherm patterns. The 7° C. and 11° C. isotherms at 200 meters are associated with the limits of the Recent range of *T. gregaria*. The oceanwide temperature change required to sufficiently cool the warm Central American pool would have made the California Current extremely cold. The antitropical transition-zone fauna of the California Current would then have moved so far offshore that it would no longer have transport-access to the eastern equatorial basin. As a result of the cooling, the coastal fauna in the region 20°–30° N. would then have consisted of subarctic species (*Euphausia pacifica*, fig. 28; *Thysanoessa longipes*, fig. 55; *Tessarabrachion oculatus*, fig. 60), none of which occurs in both hemispheres, not having transgressed the equator.

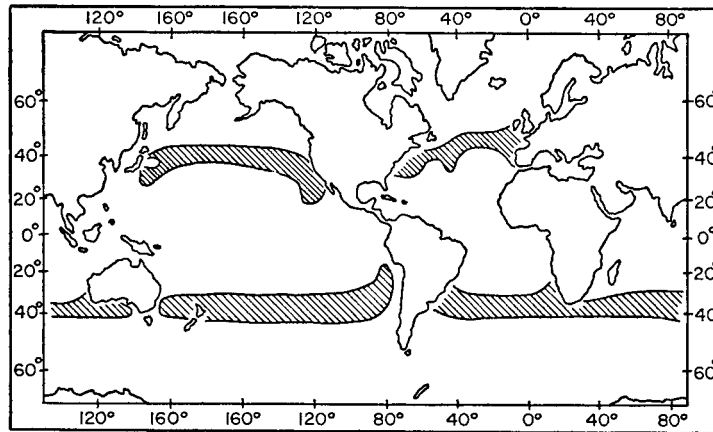
Similarly, the distribution of the Peru Current species *Euphausia mucronata* (fig. 49), like that of its California Current analogue *E. pacifica*, indicates that the highest temperature it can tolerate (e.g., 9° C. at 200 meters) is still lower than the upper limit for *Thysanoessa gregaria*, a biantitropical species with high tolerance for cold water. Even though *E. mucronata* ranges northward to 5° S. in the cold coastal part of the Peru Current, it appears not to have crossed the equatorial region. On the other hand, *T. gregaria*, which in the Southern Hemisphere now reaches northward only to about 15° S., was able to cross, by virtue of living in warmer water, farther offshore. The postulated distribution of *T. gregaria* under circumstances of oceanic cooling (fig. 123c) resembles that of *Sagitta minima* today (Bieri, 1959, fig. 21), whereas with oceanic warming (fig. 123b) its postulated range is like the present range of *Thysanopoda acutifrons* (fig. 14).

When continuity was established between northern and southern habitats of the Pacific species of the transition zone, north–south coalescence may also have been brought about in ranges of the same species in the Atlantic. Such continuity may have occurred more recently in the Atlantic than in the Pacific: *Nematoscelis megalops* is present in the transition zones of both the North and the South Atlantic, whereas *N. difficilis* of the North Pacific has differentiated from *N. megalops* of the South Pacific.

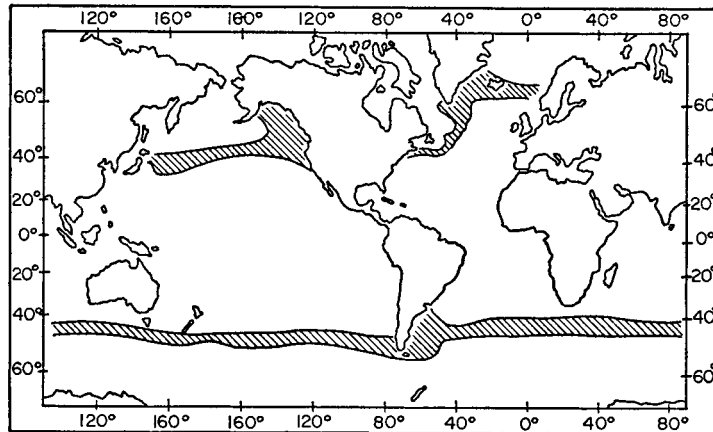
Figure 123 does not clearly show how the merging of North Atlantic and South Atlantic populations could have taken place with cooling of only 3° C. at 200 meters. However, *Thysanoessa gregaria*, like another biantitropical transition-zone species, *Thysanopoda acutifrons*, submerges to a depth of about 700 meters near the warm limits of its present range. In this way it may have crossed the barrier of warm water off northwestern Africa.

Both the 400-meter and the 200-meter temperatures are 5° C. warmer at 20° N. in the eastern Atlantic than in the eastern Pacific. The deep thermal barrier off Africa may be responsible for the absence of all *Euphausia* species from the cold North Atlantic north of 45° N. and for the endemic status of the genus *Meganycitiphanes* there.

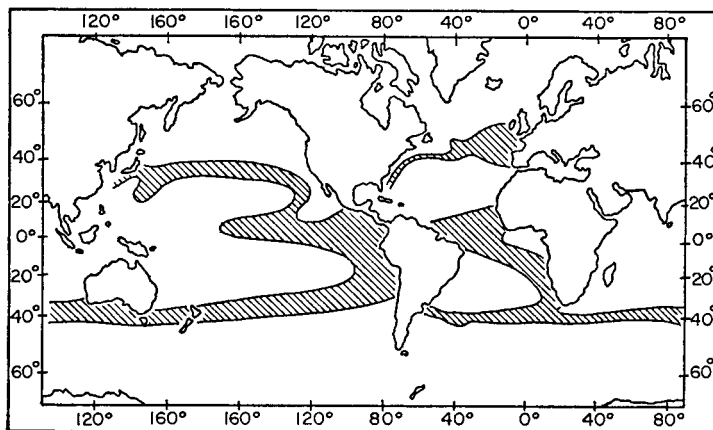
Interglacial warming of the oceans must have been of equal importance to oceanic cooling in developing and maintaining biantitropical distribution. It is to



a. *Thysanoessa gregaria*, present distribution



b. Postulated distribution, with 2 1/2° warming (at 200 m.)



c. Postulated distribution, with 2 1/2° cooling (at 200 m.)

Fig. 123. Recent distribution of the transition-zone species *Thysanoessa gregaria*, and postulated distributions under circumstances of oceanwide temperature change. Present limiting (boundary) isotherms are used to extrapolate hypothetical distributions.

be emphasized that the subsurface equatorial region is characterized by a belt of cool water that extends across the ocean. Although the transition-zone species required cooling of the eastern Pacific to cross the tropics, the central species, such as *Euphausia brevis*, presumably crossed in the western Pacific during epochs of general oceanic warming. *Stylocheiron suhmii* and *Thysanopoda subaequalis* transgress the equator in the western Pacific today. Figure 124 illustrates how northern and southern populations of *E. brevis* may have been in communication in the western Pacific when the oceans were uniformly warmed.

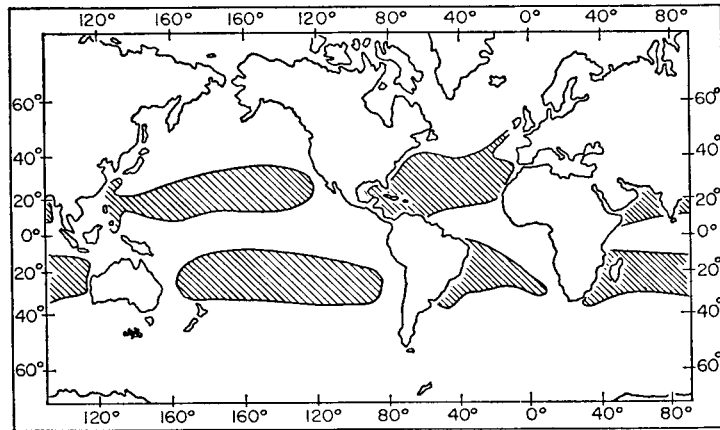
The distributions of the four *Nyctiphanes* species suggest that a period of oceanic cooling, more extreme than subsequent ones, occurred before the beginning of their isolation and differentiation. *N. couchii* (coastal Europe), *N. capensis* (coastal South Africa), *N. australis* (coast of New Zealand and southeast Australia) are now widely separated from each other and from *N. simplex* (fig. 25), but are present in analagous situations where upwelling prevails. In view of the extreme separation of the distributions of these species and their advanced differentiation compared with any that may have taken place in biantitropical species or species pairs, it seems reasonable to suppose that the distribution of the parent *Nyctiphanes* may have been split up at the onset of an exceptionally long and intense warm epoch. Alternatively, the more localized and variable habitats of these nearshore species may have accelerated adaptive differentiation, not yet detectable in the geographically separated parts of the distributions of most biantitropical oceanic species.

Northern and southern regions of distribution of *N. simplex* are now separated from each other in the eastern Pacific. Genetic exchange between these isolates would be expected to be associated with slightly lowered temperatures along the coast of Central America. This surely happened during glacial periods, or more recently. In the less widely separated ranges of *Euphausia lamelligera* (fig. 48), north-south population exchange probably takes place intermittently today, across the terminal part of the Equatorial Countercurrent.

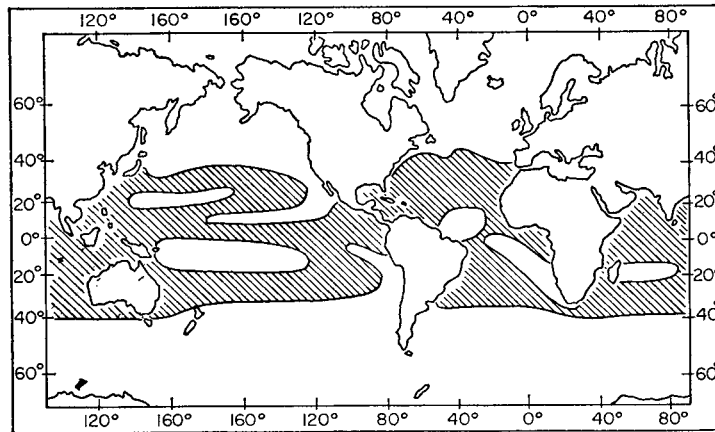
The panoceanic (Atlantic, Pacific, and Indian oceans) occurrence of biantitropical species may stem from Interglacial migrations between oceans in the Southern Hemisphere, around the tips of continents. It is improbable that Recent species date from the time of the Central American Seaway (to be discussed below when equatorial distributions are considered).

It is doubtful whether central euphasiid species pass between the Indian and Atlantic oceans around the tip of South Africa (35° S.) today. The subtropical convergence is believed to occur near 35° S. in this region, but subantarctic euphausiids (e.g., *Euphausia lucens*, *E. spinifera*, and *E. similis*) are abundant as far north as the Cape of Good Hope, 34° S. (John, 1936). The warm southwestward-flowing Agulhas Current is dissipated at the Cape into the cold Benguela Current and the West Wind Drift. The West Wind Drift, flowing along the zone 38°–45° S., carries species of the transition zone (*Thysanoessa gregaria*, *Nematoscelis megalops*, and perhaps *Euphausia gibboides*) between the two oceans, but probably no central panoceanic species now ranges into this high-latitude belt of the southern hemisphere.

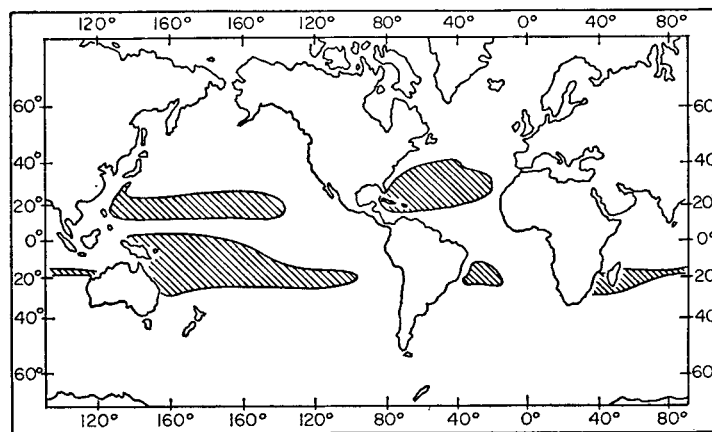
The tip of South America is a still more distinct east–west barrier to all but antarctic and some subantarctic species. Australia, like South Africa, probably



a. *Euphausia brevis*, present distribution



b. Postulated distribution, with 2 1/2° warming (at 200 m.)



c. Postulated distribution, with 2 1/2° cooling (at 200 m.)

Fig. 124. Recent distribution of the central species *Euphausia brevis*, and postulated distributions under circumstances of oceanwide temperature change. Present limiting (boundary) isotherms are used to extrapolate hypothetical distributions.

prevents the east-west passage of most antitropical species. Exceptions are the transition-zone species *Thysanoessa gregaria*, which may occur south of the continent, and the central species *Euphausia mutica*, which may pass through insular waters to the north. Cooling of the oceans could have made possible the passage of other central species across the waters of the East Indian Archipelago, and oceanic warming could have established tolerable habitats for these species south of the continents.

EQUATORIAL DISTRIBUTIONS

The distributions of Pacific equatorial euphausiids can not be described in terms of deep, limiting isotherms alone. Certain 200-meter temperatures that bound the ranges of the central species *Euphausia mutica* and *E. recurva* could also circumscribe, in lower latitudes, the range of *E. diomediae*. This reemphasizes that watermass habitats have more dimensions than is implied when ancient distributions are postulated in the framework of movements in the positions of isotherms.

Two factors appear to have been instrumental in the rise of the Pacific-Indian Ocean equatorial fauna: (1) The current systems of the environment are sufficiently closed to maintain endemic populations, and (2) the Pacific and Indian ocean equatorial regions are characterized by a unique combination of cool temperatures at intermediate depths (13°–14° C. at 200 meters) and very warm (26°–27° C.) temperatures near the surface, to which the furcilia larvae of the species are adapted. These conditions prevail in all but the southern part of the Indian Ocean. The northern part is a zoögeographical cul-de-sac (which suggests that the Indian-Pacific equatorial euphausiid fauna may have arisen there). Moore (1952) postulated such a dual temperature control for Atlantic euphausiid distribution: a superficial isotherm limits distribution in view of night activities of a species near the surface, and a deep temperature is limiting at the level of an isolume where the downward daytime migration stops.

There is no equatorial euphausiid assemblage in the Atlantic, although there are two endemic tropical Atlantic species, *Euphausia americana* and *E. krohnii*. These belong to a group of three related species. The third species, *E. eximia*, lives in the eastern tropical Pacific and is isolated from the other two. Neither *E. americana* nor *E. krohnii* is as restricted to low latitudes as *E. eximia* (fig. 45), which ranges from 30° N. to 30° S. in the California and Peru currents.

Euphausia diomediae, *E. distinguenda*, *E. paragibba*, *Nematoscelis gracilis*, and *Stylocheiron microphthalmum* are the Pacific-Indian Ocean equatorial species, limited to the regions of the equatorial water masses. A habitat for an equatorial assemblage may be lacking in the Atlantic because of the pattern of equatorial currents: the South Equatorial Current feeds the Gulf Stream, and the east-west breadth of the equatorial part of the ocean is narrow owing to the asymmetrical configuration of the continents in low latitudes. It is not possible to say whether equatorial species are lacking in the Atlantic because there is no Atlantic equatorial water mass, or because Pleistocene fluctuations in sea temperature were insufficient to permit the passage of such species as *E. diomediae* westward around the Cape of Good Hope.

Thus, the characteristically tropical species are different on each side of the Central American Isthmus. (Equatorial-west-central species, such as *Euphausia*

tenera, *Thysanopoda tricuspidata*, and *Nematoscelis microps* which range from 35° N. to 35° S. in the mid-Pacific, occur in all three tropical oceans.) Nygren (1950) believed that the Bolivar Seaway, a Cretaceous passage across northern South America, was already closed during the mid-Miocene, but Simpson (1950) found evidence for a Miocene barrier to land mammals between the North and South American continents.

Burkenroad (1936) may have reconciled these points of view by indicating, on the basis of Penaeid distributions, that only shallow neritic-like connections existed between the Atlantic and Pacific oceans during the Cenozoic. It appears probable that high-seas plankton has not been transported across these connections since the Cretaceous.

Differentiation in the *Euphausia americana-eximia-krohnii* complex may date from the closing of the Bolivar Seaway. Populations of a parent species could have been isolated at the breakup of a widespread distribution into restricted tropical habitats in the Atlantic, Pacific, and Indian oceans.

EUPHAUSIIDS OF THE INDO-AUSTRALIAN ARCHIPELAGO

Four euphausiid species are endemic to the region of the Indo-Australian Archipelago and the Philippines. These are *Euphausia sibogae* (fig. 47), *E. fallax* (fig. 32), *Stylocheiron insulare* (fig. 89), and *Nematoscelis lobata*. Equatorial species (e.g., *Euphausia diomediae*, *Nematoscelis gracilis*) are also present here, but the zoöplankton faunas of the Pacific and Indian oceans are in limited communication in this region by reason of the currents and shallow depths of certain of the insular waters. The Arafura Sea north of Australia and the Strait of Malacca at Singapore are scarcely 100 fathoms deep today. Pacific-Indian Ocean exchange can only take place through a circuitous north-south passage through deep waters of the Timor, Banda, and Moluccan or Celebes seas. Such seas may have once provided semi-isolated environments in which plankton species of the Archipelago arose.

THE CENTRAL-EQUATORIAL GROUPS OF FOUR SPECIES

The three temperate epipelagic euphausiid genera each include four species that appear to form a natural group. In each genus the four species are more closely related to each other than to any other species. In *Euphausia*, *E. brevis*, *E. mutica*, and *E. recurva* are central panoceanic species, whereas *E. diomediae* is equatorial, occurring only in the Pacific and Indian oceans. In *Nematoscelis*, *N. atlantica* is central, and *N. tenella* and *N. microps* are central but range also into the western equatorial region. All three are panoceanic. A fourth species, *N. gracilis*, is equatorial in the Pacific and Indian oceans.

In *Stylocheiron*, three species of the natural group are panoceanic. Of these *S. suhmii* is essentially central, whereas *S. affine* and *S. longicorne* are central-equatorial. *S. microphthalma* remains equatorial and, like *Euphausia diomediae* and *Nematoscelis gracilis*, is limited to the Pacific and Indian oceans. Thus, there is one equatorial Indo-Pacific species with three more-or-less central species in each of the above groups.

We can envisage in, for example, *Euphausia*, a common ancestor of *brevis*, *mutica*, *recurva*, and *diomediae* having a broad distribution in the warm mid-Cretaceous seas. In this hypothetical view there was intercommunication between the

Pacific and the Atlantic through the Bolivar Seaway, and between the Atlantic and Indian oceans by way of the Tethys Sea. By the end of the postulated wide-spread climatic uniformity of the Tertiary epoch, oceanic communication between the Atlantic and the Pacific had been cut off. The Tethys Sea had nearly vanished during the late Cretaceous period. With the late Oligocene breakdown of the uniform world-climate and emergence of the tropical-equatorial region as an environment with unique habitats, four oceanic areas achieved a high degree of isolation from each other: the Atlantic, the North Pacific, the South Pacific, and the Indian Ocean.

The present large extent of the equatorial region of the Indian Ocean, and its relative isolation, being bounded within the tropical zone by the Afro-Asian land mass, suggests that *E. diomediae* may have differentiated there and subsequently spread to the Pacific following the development of a communicating waterway. With a 2°–3° C. cooling of the oceans at 200 meters of depth, the distribution of *E. distinguenda* would resemble that of *E. diomediae* today; whereas, with a 2°–3° C. warming, the distribution of *E. diomediae* would be like that of *E. distinguenda* at present (fig. 125). Thus, these zoogeographically complementary species may have alternately filled the equatorial habitat during glacial and interglacial epochs, respectively.

The extensive vertical and horizontal spread of warm waters in the Atlantic (particularly the North Atlantic) compared with the Indian and Pacific oceans may have been the environment in which the most characteristically central species, *E. brevis*, became differentiated. *E. recurva* and *E. mutica* might then have evolved in the North Pacific and the South Pacific.

The “*Euphausia gibba* group” may be regarded as a fourth natural group-of-four. The present distributions (fig. 40) of these species suggest that, as in the foregoing groups, pockets of isolation evolved in separate oceans, splitting up the once-widespread distribution of a common ancestor. The present distribution of *E. paragibba* is equatorial and limited to the Indian and Pacific oceans. *E. hemigibba* is found throughout the North Pacific central region, has been reported from 9° N. and 26°–30° S. in the Indian Ocean, and is widespread in the central waters of the Atlantic. *E. gibba* is restricted to the South Pacific central zone. *E. pseudogibba* inhabits western equatorial waters of the Pacific and Atlantic oceans, and is present in the tropical part of the Indian Ocean.

Evidently *E. paragibba* is the Indian-Pacific equatorial species in this group, while *E. hemigibba* and *E. gibba* are central. (But, here, *E. gibba* is not pan-oceanic.) *E. pseudogibba* can scarcely be considered a third central species, however, though it ranges far to the east in the Pacific along the boundary between equatorial and central waters. In the hypothetical pattern of origin already suggested for the “groups of four,” *E. gibba* may have been isolated in the South Pacific where it remains, *E. hemigibba* in the North Pacific (from which it spread to the Indian and Atlantic oceans during interglacial warming of the Equatorial Water Mass), *E. pseudogibba* in the Atlantic where its north–south range is extensive, and *E. paragibba* in the semi-enclosed tropical Indian Ocean.

The mutually exclusive nature of the distributions of these four species in the Pacific implies a degree of similarity in ecological requirements that does not exist

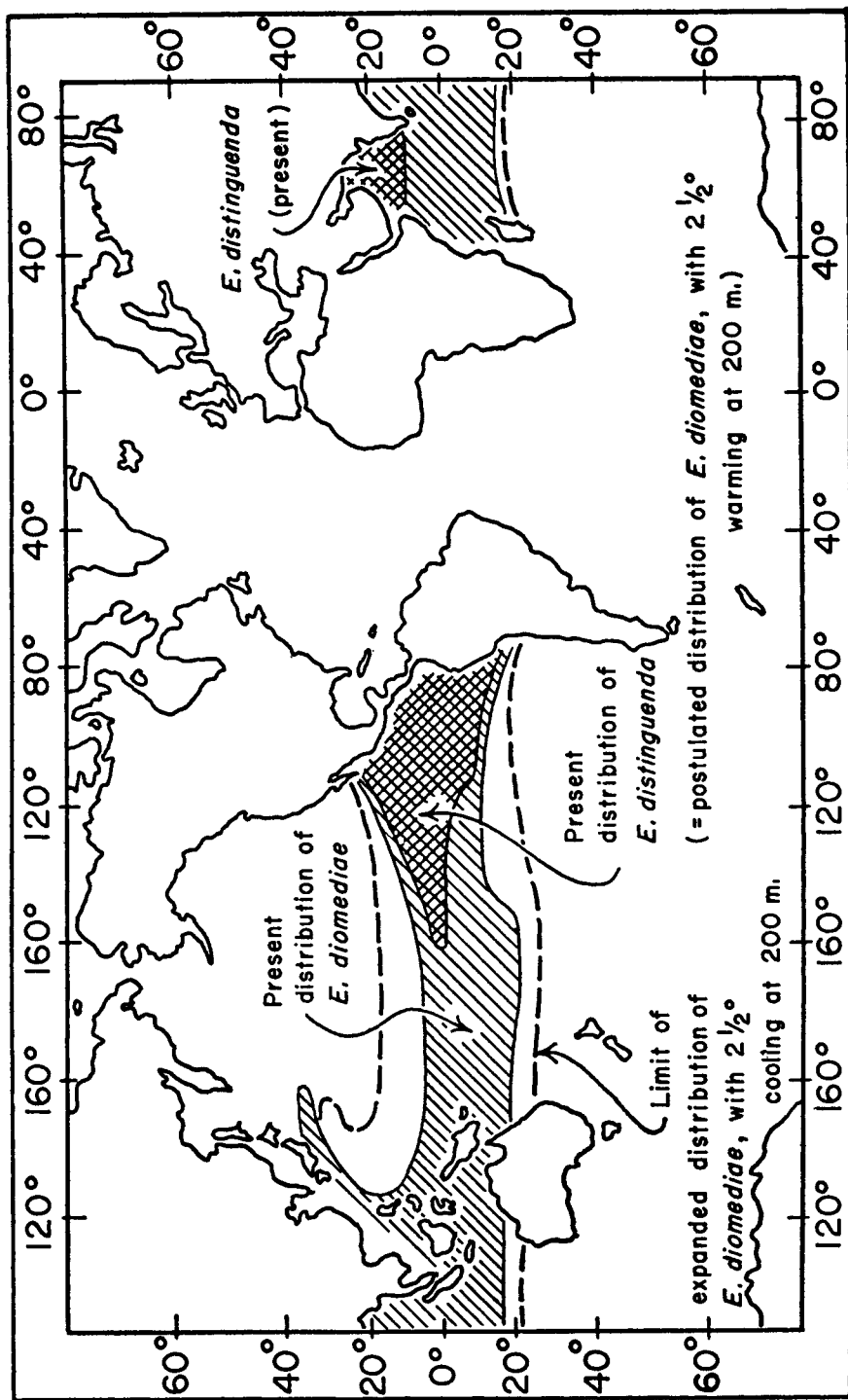


Fig. 125. The present distributions of the equatorial species *Euphausia diomediae* and *E. distinguenda*, and postulated distributions under circumstances of general change in oceanic climate. Present limiting isotherms are used to extrapolate hypothetical distributions.

among the species of the other groups of four. The possible role of competition is indicated here to account for the maintenance of the separateness of the present distributions.

THE MESOPELAGIC GROUPS OF THREE SPECIES

Three euphausiid genera contain natural groups of three species. The genus *Nematobranchion* contains only three species, *N. boopis*, *N. flexipes*, and *N. sexspinosus*. Three *Thysanopoda* species, *T. acutifrons*, *T. orientalis*, and *T. microphthalma*, are a clear natural group (Hansen, 1910) as are *Stylocheiron maximum*, *S. abbreviatum*, and *S. robustum*. These species inhabit depths down to 1,000–1,500 meters, though *N. flexipes*, *T. acutifrons*, and *S. abbreviatum* are associated with the deeper part of the epipelagic zone, rather than with the mesopelagic zone. In mid-water there are only three geographically isolated oceans. The Equatorial Water Mass cannot be considered a barrier to species that can live below 700 meters. The subtropical-tropical Pacific, therefore, represents a single habitat for species living at intermediate depths. This habitat is geographically isolated from comparable habitats of the Atlantic and Indian oceans.

Of the 17 mesopelagic euphausiid species, 15 are contained by waters between the northern and southern subtropical convergences (40° N.–40° S.) and by the continental boundaries of the Atlantic, Pacific, and Indian oceans. The groups of three may have evolved as a consequence of the isolation provided by the three oceans during an epoch of climatic stability. More recently, most of the nine species have spread to all subtropical oceans during periods of fluctuations in ocean temperature.

SUBARCTIC DISTRIBUTIONS

The extent of exchange or intercolonization that has taken place between North Atlantic and North Pacific populations is important to a consideration of the subarctic pelagic fauna. Records of land mammal migrations led Simpson (1947) to conclude that a land bridge connected the Asiatic and American continents across the Bering Strait during the large part of geologic history, including much of the Cenozoic period. The bridge was submerged during the middle Eocene and middle-to-late Oligocene, and perhaps also in the early Pliocene, but was above water during the Pleistocene glaciations.

Of the six subarctic Pacific species, four, *Euphausia pacifica*, *Thysanoessa longipes*, *T. spinifera*, and *Tessarabrachion oculatus*, are endemic to the North Pacific. The two other species *Thysanoessa raschii* and *T. inermis*, (both arctic-subarctic) are common to the North Atlantic and the North Pacific. Two species, *Thysanoessa longicaudata* and *Meganctiphanes norvegica*, are endemic to the subarctic North Atlantic.

Thysanoessa is, today, the characteristic subarctic genus, but it is evident from the biantitropical distribution of the genus (*T. vicina* and *T. macrura* occur in the Antarctic Ocean) and of the species *T. gregaria*, that the genus once inhabited low latitudes. There are reasons to believe that *Thysanoessa* arose in deep waters. The bilobate eye of *T. longipes*, *T. gregaria*, and *T. parva* appears to be an adaptation to a deep oceanic habitat. The eye of *Thysanoessa* may now be undergoing modification toward roundness in the neritic species of the genus, *T. raschii* and *T. spinifera*. *T. parva*, the deepest-living species of the genus, is known only from the Atlantic and Pacific oceans, and has only residual pockets of distribution.

The species of *Thysanoessa* tend to submerge as they approach the warm-water margins of their ranges, indicating stenothermy but relatively little depth specificity, compared with other genera. Einarsson found *T. longicaudata* only in the surface layers in the area north of the 10° C. surface isotherm, whereas according to Leavitt (1938) this species was found as deep as 2,500 meters and was lacking in the surface layers, near the southern limit of its north Atlantic range. Perhaps *Thysanoessa* evolved at depth in the warm Cretaceous seas, and subsequently emerged into cool post-Tertiary waters of high latitudes.

T. longipes became differentiated as an oceanic subarctic species in the Pacific and *T. longicaudata* in the Atlantic. *T. raschii*, *T. spinifera*, and *T. inermis* filled cold epipelagic environments of low salinity, which may have been more widespread immediately following glacial epochs than they are today. Successive emergence and submergence of the Bering Strait land-bridge undoubtedly played an important role in the geographical isolation of infant-species in that area. Drobysheva (1960) shows that semi-isolated stocks of *Thysanoessa raschii* and *T. inermis* exist in the Barents Sea today.

Monotypic *Tessarabrachion* presents a puzzle. Its confinement to the subarctic Pacific suggests that it arose and differentiated in its present mesopelagic habitat.

ANTARCTIC OCEAN DISTRIBUTIONS

The relationships and distributions of the species of *Euphausia* in the Antarctic Ocean may be considered in relation to the question of whether or not zoöplankton species give rise to daughter species across purely oceanographic barriers. John (1936) stated: “

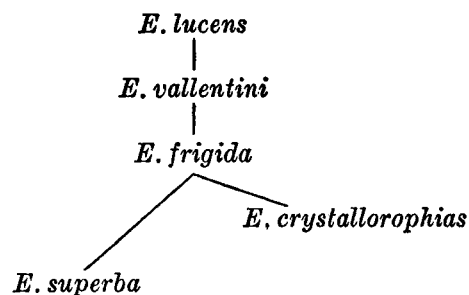
. . . nine of the ten Antarctic species . . . form two natural groups and . . . if it be supposed that the genus *Euphausia* arose in warm waters, the existence of these groups and the order of occurrence of their members show that the genus has colonized the cold southern waters along two distinct lines. Along one line the colonization has not been completed; although the southernmost member occurs in the ice-free water of the Antarctic Zone, it does not appear to breed successfully there. Colonization has been completed along the other line; every niche has been occupied to the farthest south; there is a neritic species along the coasts of the Antarctic continent.

The two groups are:

- (1) *E. hanseni*, *E. spinifera*, *E. longirostris*, *E. triacantha*
- (2) *E. lucens*, *E. vallentini*, *E. frigida*, *E. superba*, *E. crystallophias*. . . .

Although John apparently did not consider it to be a member of group 1, the structural evidence suggests that *E. similis* is closer to the four species in it than to any other species, even considering those outside of the Antarctic Ocean.

John believed the structural evidence sufficient to diagram the colonization of Antarctic waters by group 2 in the following way:



In both groups the species are sharply separated from each other by many structural characters. All have undergone extensive differentiation from any common ancestor that might be postulated.

The zones of the Antarctic Ocean are bounded by convergences or by the Antarctic land mass. The meridional circulation partially separates each of the epipelagic zones from its neighbors. Nevertheless, complete isolation of adjacent habitats, particularly in the relatively homogeneous waters 500–1,000 meters deep, is lacking.

Evolution of the Antarctic and Subantarctic lines might have taken place in mid-latitudes within the Atlantic, Pacific, and Indian oceans during periods of temperature fluctuations. The land masses would then have been barriers separating segments of populations. The clear relationship of *E. pacifica* of the Northern Hemisphere to the *E. lucens*–*E. frigida* line of the Antarctic Ocean indicates that the parent species of this branch occupied low latitudes or transgressed the tropics some time during the evolution of the genus. Subsequent to the separation of the northern and southern parts of the parent stock, *E. pacifica* or its precursor was geographically confined by the Asian-American land masses and did not give rise to more than this species and *E. nana*. (It was discussed earlier how *E. nana* may have arisen in the East China Sea.) In contrast, the Antarctic line evolved in midlatitudes of the South Atlantic, South Pacific, and South Indian oceans during alternating periods of extreme oceanic cooling and warming in the Southern Hemisphere.

It was postulated above that the antitropical distributions of Recent species were established during the Pleistocene. The period of cooling that brought about the equatorial transgression of the ancestor of *E. pacifica* from the south (or of the ancestor of such species as *E. lucens* and *E. frigida* from the north) must have been much earlier—possibly at the same time that the genus *Thysanoessa* became antitropical. This may have been at the close of the temperature uniformity of the Tertiary epoch, or earlier.

DIFFERENTIATION WITH INCOMPLETE ISOLATION: A POSSIBLE RELATIONSHIP BETWEEN OCEANOGRAPHIC BARRIERS AND EVOLUTIONARY PROCESSES

It has been stressed in the foregoing paragraphs that opportunities for speciation may be a consequence of biantitropical distribution or isolation of populations in separate oceans. Such opportunities have been repeatedly provided in the pelagic environment in the course of evolutionary time. Successive climatic revolutions might, therefore, be accompanied by an increasing rate of species formation, were it not likely that few climatic changes have been of sufficient magnitude or geographical extent to allow time for the differentiation of species. Successive epochs may not always have been separated sufficiently to have permitted allopatric differentiation before coalescence again occurred, either around the tips of continents or across the tropics. Of course, environments may have been so altered by climatic change that species unable to adapt to the changing conditions became extinct.

Less may be inferred about the possible effectiveness of oceanographic barriers in isolating plankton populations from one another. The finding of the geographical

racess or subspecies suggests the possibility that morphological differentiation may sometimes arise in segments of the over-all population of a species, in each of a series of communicating regions.

Differentiation found in *Stylocheiron affine* and *S. longicorne*, and between *Thysanopoda aequalis* and *T. subaequalis*, involved characteristics other than those usually considered to be of major taxonomic significance in euphausiids. There is a striking similarity between the distributions of *T. aequalis* and *S. longicorne* "Long Form" and between those of *T. subaequalis* and *S. longicorne* "Short Form" (figs. 23, 99).

The "Spined" and "Unspined" forms of *Thysanoessa longipes* may have differentiated in isolation from each other in the Arctic Ocean and Bering Sea-North Pacific, respectively. "Spined" *T. longipes* now lives in the Arctic Ocean, but occurs farther south as well. The young of the two forms are indistinguishable, and the male copulatory organs appear to be identical. They may, therefore, be geographical races. Specimens of *T. longipes* having abdominal armature intermediate between that of the two forms have not been found.

The *neglecta* and *inermis* forms of *Thysanoessa inermis*, discussed in detail by Einarsson (1945), appear not to be comparable to the forms of *T. longipes*, inasmuch as the "Unspined Form" of *T. longipes* attains full maturity without metamorphosing into the "Spined Form." Einarsson was of the opinion that the form *neglecta* is a transitory form in the development of *T. inermis*, rarely retained in the adult. He stated, further:

It is of great interest that in the genus *Thysanoessa* the two forms (*inermis* and *neglecta*) are found, so to speak, in pure culture. Two species, *T. raschii* and *T. spinifera*, are of the *inermis* form, while the remaining species of the genus, with the exception of *T. inermis*, are of the *neglecta* form. It is most probable that *T. inermis* has originated from one of the "typical" species of *Thysanoessa*, with the second pair of legs elongate and with divided eyes, and the development of the species may therefore be considered an interesting example of the recapitulation of the phylogeny of the ontogeny of the species.

Of the euphausiid genera, *Stylocheiron* appears to show the greatest degree of morphological instability (or intraspecific variability). It is not clear whether the cause of differentiation at the level of the forms of *S. affine* is genetic or environmental (physiological), or both.

Two interpretations of the distributions will be considered. In the first the forms are regarded as valid species. These differentiated, owing to a minimum of exchange of water (and populations) between habitats, (1) where a "new" water mass was colonized by a population already occupying an adjoining one, or (2) where parts of the over-all range of the parent species were on opposite sides of oceanographic fronts or zones of environmental transition, or (3) where segments of the range were completely isolated from each other geographically. Hybridization subsequently took place at the coalescences of boundary areas of more than one of the sibling species, not yet reproductively isolated from each other. The amount of hybridization was limited by the small geographical extent of breeding-spawning-rearing habitats compatible with both young species. This interpretation is supported by the fact that intergrading individuals between forms of *S. affine* were found only in small parts of the overlapping ranges, except for the connecting

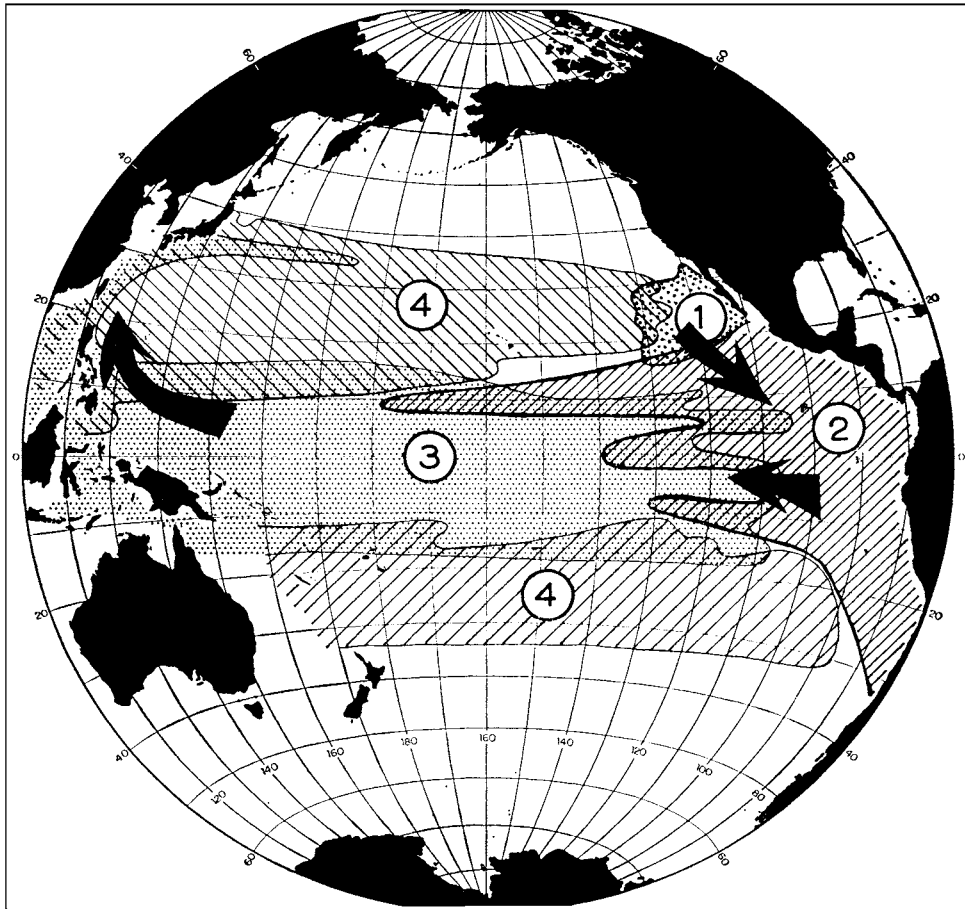


Fig. 126. A generalized picture of the distribution of four of the five Pacific forms of *Stylocheiron affine*: (1) "California Current Forms," (2) "Eastern Equatorial Forms," (3) "Western Equatorial Forms," (4) "Central Forms." The "Indo-Australian Form," found along the western rim of the ocean, is not shown. Specimens believed to be intermediates between forms have been found in areas of overlap of ranges between (1) and (2), (2) and (3), and (3) and (4), but not between (4) and (1). Arrows indicate prevailing current directions in places where intermediate specimens were found. The arrow in the southern part of the California Current applies only to the zone of overlap between forms (1) and (2), and not to the zone 10° – 18° N. where the North Equatorial Current arises.

zone between the "California Current" and "Eastern Equatorial" forms which was occupied mainly by intergrades.

In the second interpretation the forms are considered to be geographical races. The characteristic morphology of each form is a consequence of the effects of environmental differences upon growth. The relatively uniform distribution of physical properties within an oceanographic region or water mass gave rise to the morphological adaptation made. Intermediates then were found where growth and development took place within boundary areas. There, the properties of the local environment are transitional, intergrading between those of the two broader environments that shaped adjacent forms of the species. Each intermediate individual,

like the large populations of the species-forms, is an ecophenotype reflecting environmental influences rather than genetic constitution.

Sibling species, each having become differentiated in isolation from the others, might have coalesced in the pattern of distribution shown (fig. 126) if competition between them had played a role in limiting the amount of overlap of neighboring ranges. This possibility was suggested above in the discussion of the Pacific distributions of species in the "*Euphausia gibba* group." However, the more likely possibility appears to be subspeciation as a consequence of partial ecological isolation. It seems desirable to retain that part of the species concept that holds that interspecific breeding does not occur in a natural environment, or that if it does occur, the hybrids will be sterile or nonviable.

It may be possible, however, that the kind of differentiation observed in *S. affine* has something to do with speciation in the ocean. The degree of tolerance for the boundary environment by populations living near the limits of the distributional range of a species is believed to have an important influence on the likelihood of survival of each pelagic species. Tolerance of the boundary environment is established by natural selection for characters that tend to increase geographical range. The small, long-term temperature changes that are believed to have taken place in the ocean, and that have been accompanied by corresponding adaptations (or extinctions) of species, may be compared to the changes that take place, for example, in the western part of the ocean where a continuous stream of zoöplankton is propelled from the warm Kuroshio into the similarly warm, but not physically or biologically identical, waters of the western North Pacific central gyral—where the "West Equatorial Form" of *S. affine* impinges on the "Central Form" (fig. 126). In the past, before the "Central Form" was established, the "West Equatorial Form" was sometimes able to survive in the Pacific central gyral owing to physiological adaptations in local populations. It subsequently occupied the central regions as a result of a genetic modification for "potential central water colonization" incorporated into the entire species. However, this genetic modification would be advantageous only where transport-access provided the greatest opportunities for colonization of the central areas. Selective pressure for this result would be greatest in the downstream region, less in the mid-Pacific, and least in the eastern equatorial basin where there is relatively little mixing of Central and Equatorial waters.

In spite of the once-common genetic constitution of the parent species, differential selection may have taken place in the composite range, each partly isolated form becoming adapted for colonization of those areas toward which it had transport-access. Ultimately, genetic differentiation may have been brought about at the geographical extremes (California Current and North Pacific Central region) of a chain of subspecies or races, owing to the cumulative inhibiting effects upon upstream gene flow of a series of partial geographical isolations of neighboring populations. These processes may be continuing.

If the areas where intergradation occurs are as localized as this study suggests, relatively small-scale oceanographic changes might separate elements of the subspecies complex. For example, if reduced Peru Current upwelling or a change in climate were to upset the ecological balance in the part of the South Equatorial

Current where intergrades between the "Eastern Equatorial" and "Western Equatorial" forms are found, separation of the breeding components of the two forms might be brought about, further decreasing gene flow between the extremes ("California Current Form" and "Central Form") of the postulated race-circle. If the two extreme forms are not already sufficiently different to be reproductively isolated from each other, even short-term separation of links of the five-form chain might be sufficient to bring about further differentiation.

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