Bathymetric Distribution of Chaetognaths[1]

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THE PRESENT REPORT on the vertical distribution of the Chaetognatha is based on a study of the collections of plankton made by the Scripps Institution of Oceanography expeditions in the Pacific (Fig. 1) and Indian oceans. Therefore, all the data included and discussed in this paper have been obtained by the author from studies and analysis of thousands of plankton samples from those oceans; and, when other sources of information are used in the discussion, the name and date of the corresponding authority and publication are given. The samples studied here that cover the Pacific and Indian oceans were taken at 140 m depth (oblique hauls), and at other various depths: 270, 300, 363, 600, 700 or 868 m (closing nets or vertical tows), down to 3000 m deep (mid-water trawls). The results obtained from these expeditions and from the material examined while studying the seasonal distribution of chaetognaths in the California waters, and also from previous work in the Atlantic, has made it possible to group the species of this phylum into several categories based on their distribution in depth.

The correlation between the distribution in depth of the species and the conditions affecting this distribution can only be reached through a knowledge of the two-dimensional distribution of each of the species, the factors involved in their distributional fluctuations, and the extent to which changes in those factors may affect the distributional pattern.

It was found, from these observations, that each individual species of chaetognaths occurs generally at about the same levels throughout the oceans, with the particular exception of *Eukrohnia hamata* (Möbius), as will be shown later in this paper. Therefore, these species can be grouped in three categories according to the strata they populate:

Epiplanktonic (upper 150–200 m)
Mesoplanktonic (200–1000 m)
Bathyplanktonic (below 1000 m level)

In each of these categories several series of stratification, or zonations, can be established. In the upper layers there is more zonation of the species than in the levels below 200 m. Because of the large number of species involved and the great variability of the conditions in the upper layers, the picture is a complex one. Migrations related to food, light, and seasonal changes may take place in the upper strata. In these upper layers competition is more active than in the deeper strata, and this is conditioned by the large number of species involved.

In general, the Chaetognatha decrease in number of species and in number of individuals per species with increase in depth, that is, the number of individuals per volumetric unit of water is larger in the upper layers than in deep waters. The species typical of waters below the 200 m level are one-fifth of the total of the phylum. Differences are found regarding this point, depending on the geographical localities under study. Thiel (1938) found more species and greater biomass of chaetognaths in the upper 50 m. Hida (1957) stated: "regardless of time of day of hauling, oblique hauls between the surface and 40m. yield larger numbers of chaetognaths and pteropods for m^3 of water strained than deeper hauls between the surface and 140m." A similar relation was found in the tropical Pacific (Hida and King, 1955). However, in both north and south high latitudes the layers below 200 m sustain a larger number of species of chaetognaths than do the upper strata. Whereas, as noted above, in other oceanic

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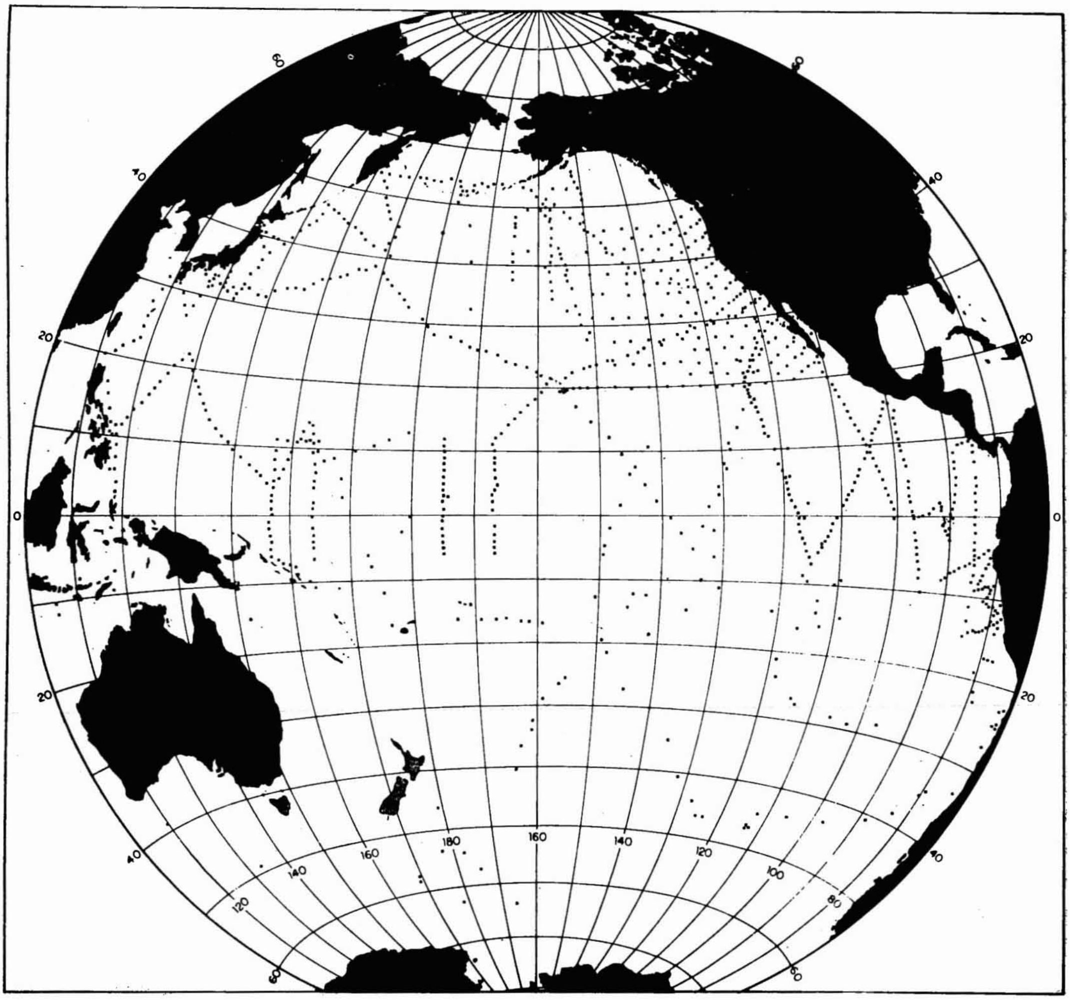

FIG. 1. Plan of the stations of the various expeditions in the Pacific.

regions the number of species in the upper 200 m exceeds the number of those in the deeper levels.

DISCUSSION

The Chaetognatha have six pelagic genera: *Bathyspadella* (recorded once, Tokioka, 1939), *Heterokrohnia, Eukrohnia, Krohnitta, Pterosagitta,* and *Sagitta.* The first two inhabit waters below the 1000 m level, *Eukrohnia* is mainly bathypelagic, with the exception of *E. hamata,* which changes its distribution in depth with latitude. *Pterosagitta* and *Krohnitta* populate the upper strata. The genus *Sagitta* is the most successful of the group: it appears to have the highest evolutionary level in the phylum, is the most abundant in species, and inhabits the greatest variety of environments throughout the oceans. Consequently, its species appear in each of the oceanic levels.

The species of Chaetognatha observed by the author in the samples studied from the Pacific and Indian oceans can be grouped as follows:

Epiplanktonic:
- *Krohnitta subtilis* (Grassi) 1881
- *K. pacifica* (Aida) 1897
- *Pterosagitta draco* (Krohn) 1853
- *Sagitta bedoti* Béraneck 1895

S. bierii Alvariño 1961
S. bipunctata Quoy and Gaimard 1827
S. elegans Verrill 1873
S. euneritica Alvariño 1961
S. ferox Doncaster 1903
S. gazellae Ritter-Zahony 1909
S. hexaptera d'Orbigny 1834
S. lyra Krohn 1853
S. minima Grassi 1881
S. pacifica Tokioka 1940
S. pseudoserratodentata Tokioka 1939
S. pulchra Doncaster 1903
S. regularis Aida 1897
S. scrippsae Alvariño 1962
S. tasmanica Thomson 1947

Mesoplanktonic:
Sagitta decipiens Fowler 1905
S. macrocephala Fowler 1905
S. marri David 1956
S. planctonis Steinhaus 1896
S. zetesios Fowler 1905
S. maxima (Conant) 1896[2]

Bathyplanktonic:
Eukrohnia bathyantarctica David 1958
E. bathypelagica Alvariño 1962
E. fowleri Ritter-Zahony 1909
E. hamata (Möbius) 1875 (in low latitudes)

[2] It also appears often in the upper layers, due to phenomena to upwelling.

Heterokrohnia mirabilis Ritter-Zahony 1911 (recorded in the Pacific by Bieri, 1959; Tchindonova, 1955)

The species present below 200 m are cosmopolitan in distribution (inhabiting the Atlantic, Indian, and Pacific oceans), with the exception of *E. bathyantarctica* and *S. marri,* which were recorded circumpolarly in Antarctic waters; *E. bathypelagica* which appears to be restricted to the depths of the Pacific and Indian oceans, according to the present data (Alvariño, 1962, 196–*b*), and *Bathyspadella edentata,* represented by one specimen from the Pacific (Tokioka, 1939).

Sagitta elegans and *S. gazellae* typify the arctic-subarctic and the antarctic-subantarctic waters respectively (Fig. 2). The arctic constitutes an ecological individuality because of its uniform conditions. *S. elegans* is the typical chaetognath of the upper 100–150 m of this region, extending into the northern part of both the Pacific and the Atlantic. The extension of the distribution of *S. elegans* appears to be controlled by the concentration of oxygen in the water. *S. elegans* extends in the Pacific to 38°N. Here 297 plankton samples were studied from 182 stations distributed along this northern Pacific region. *S. elegans* was found in only 128 localities, and in each case it was concurrent

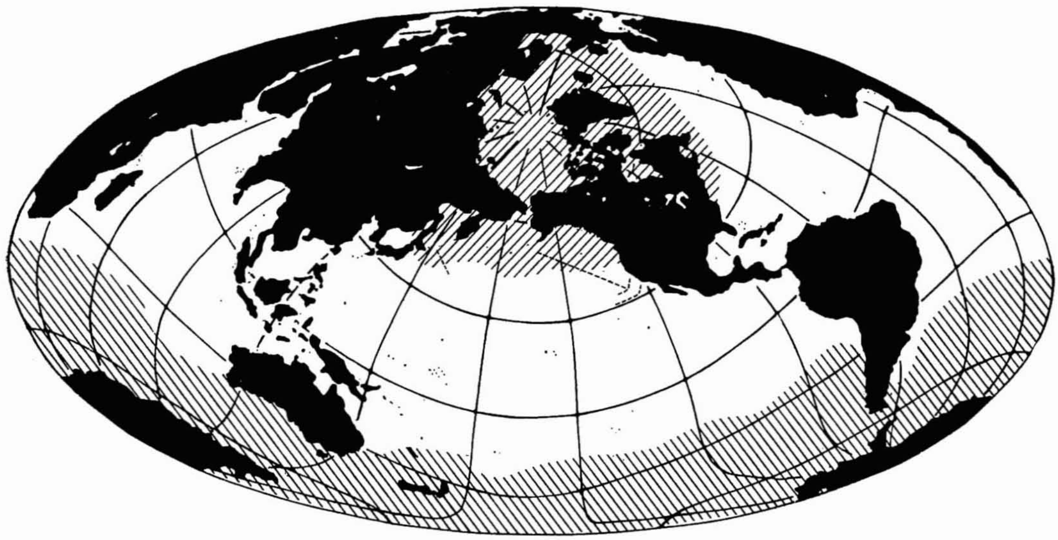

FIG. 2. World distribution of *S. elegans* and *S. gazellae.* Location of the profiles that appear in this paper.

TABLE 1

SPECIES OBSERVED AT DIFFERENT DEPTHS IN VARIOUS PACIFIC WATER MASSES

REGION	DEPTH OF HAUL[1] (meters)	SPECIES (author's data)
subarctic	upper 150	*E. hamata* *S. elegans*
	below 150	*E. bathypelagica* *E. fowleri* *E. hamata* *S. macrocephala* *S. maxima*
transition	upper 150	*S. elegans* *S. hexaptera* *S. scrippsae*
	300–150	*E. hamata* *S. maxima*
	below 300	*E. bathypelagica* *E. fowleri* *E. hamata* *S. macrocephala* *S. zetesios*
California waters	upper 150	*K. pacifica* *K. subtilis* *P. draco* *S. bedoti* *S. bierii* *S. bipunctata* *S. enflata* *S. euneritica* *S. ferox* *S. hexaptera* *S. minima* *S. neglecta* *S. pacifica* *S. pseudoserratodentata* *S. pulchra* *S. regularis* *S. robusta* *S. scrippsae*
	300–150	*S. decipiens* *S. hexaptera* *S. scrippsae* *S. zetesios*
	300–600	*S. decipiens* *S. macrocephala* *S. maxima* *S. zetesios*
	below 600	*E. bathypelagica* *E. fowleri* *E. hamata*

REGION	DEPTH OF HAUL[1] (meters)	SPECIES (author's data)
Kuroshio waters	upper 150	*K. pacifica* *K. subtilis* *P. draco* *S. bedoti* *S. bipunctata* *S. enflata* *S. ferox* *S. hexaptera* *S. lyra* *S. minima* *S. neglecta* *S. pacifica* *S. pulchra* *S. regularis* *S. robusta*
	150–600	*S. decipiens* *S. zetesios*
	below 600	*E. hamata*
northeast Pacific central waters	upper 150	*K. pacifica* *K. subtilis* *P. draco* *S. bierii* *S. bipunctata* *S. enflata* *S. ferox* *S. hexaptera* *S. minima* *S. pacifica* *S. pseudoserratodentata*
	280–150	*P. draco* *S. decipiens* *S. hexaptera* *S. scrippsae*
	868–280	*S. decipiens* *S. macrocephala* *S. zetesios*
	below 868	*E. bathypelagica* *E. fowleri* *E. hamata* *S. macrocephala* *S. maxima*

[1] It is obvious that the species recorded at the various depth-hauls may be listed in more than one place in these strata. For instance, *S. hexaptera* in California waters appears in both the upper 150 m and in hauls from 300 to 150 m. Similarly, *K. pacifica* in the northwest central Pacific waters appeared in samples from 150–326 m, etc. It should be understood that, broadly speaking, the species of chaetognaths belong to either the epi-, meso-, or bathyplanktonic domain, and that only in the particular cases previously explained, their bathymetric distribution appears to be altered because of currents (sinking of the waters, upwelling, etc.).

TABLE 1 (continued)

SPECIES OBSERVED AT DIFFERENT DEPTHS IN VARIOUS PACIFIC WATER MASSES

REGION	DEPTH OF HAUL[1] (meters)	SPECIES (author's data)
northwest Pacific central waters	upper 150	*K. pacifica* *K. subtilis* *P. draco* *S. bedoti* *S. bipunctata* *S. enflata* *S. ferox* *S. hexaptera* *S. minima* *S. pacifica*
	325–150	*K. pacifica* *S. decipiens*
	below 500	*E. bathypelagica* *E. fowleri* *E. hamata* *H. mirabilis*[2] *S. macrocephala* *S. maxima* *S. zetesios*
Pacific equatorial waters	upper 150	*K. pacifica* *K. subtilis* *P. draco* *S. bedoti* *S. bipunctata* *S. enflata* *S. ferox* *S. hexaptera* *S. neglecta* *S. minima* *S. pacifica* *S. pseudoserratodentata* *S. pulchra* *S. regularis* *S. robusta*
	600–300	*S. decipiens* *S. zetesios*
	below 600	*E. bathypelagica* *E. fowleri* *E. hamata* *H. mirabilis*[3] *S. macrocephala* *S. maxima* *S. macrocephala* *S. maxima*
southeast central Pacific waters	upper 140	*K. subtilis* *P. draco* *S. bipunctata* *S. enflata* *S. ferox* *S. hexaptera* *S. minima* *S. pacifica*
	500–140	*S. decipiens* *S. gazellae* *S. zetesios*
	below 500	*E. bathypelagica* *E. fowleri* *E. hamata* *S. macrocephala* *S. maxima*
subantarctic waters	upper 150	*E. hamata* *S. gazellae* *S. tasmanica*
	283–140	*E. hamata* *S. hexaptera*
	600–300	*E. hamata* *S. decipiens* *S. planctonis*
	below 600	*E. bathypelagica* *E. fowleri* *S. macrocephala* *S. maxima*
antarctic waters	upper 150	*E. hamata* *S. gazellae*
	600–150	*S. marri* *S. maxima* *S. planctonis*
	below 2000	*E. bathyantarctica*

[2] Tchindonova and Tokioka records.
[3] Bieri's records.

with oxygen values of more than 6 ml/l. The presence of *S. elegans* was expected in the rest of the localities of this region (because of the characteristics of the waters); however, it was noteworthy that every negative station and sample for *S. elegans* corresponded to oxygen values below 6 ml per liter. Consequently it was found in these studies that *S. elegans* does not occur in the Pacific in waters with less concentration of oxygen than the amount stated above; and this could also be the limiting factor in the spreading of this chaetognath to deeper levels. *S. elegans* is present in the Oyashio waters, but when these waters collide with the Kuroshio, its southern distribution is abruptly interrupted, even at deep levels, in the region where the two bodies of water meet.

The conditions are also more or less uniform in antarctic waters in the west–east direction (Baker, 1954), while the gradients change from south to north. It is well known that the plankton (and this is true for the Chaetognatha population according to our data) follows a rather homogeneous circumpolar distribution in the antarctic belt. *S. gazellae* is the typical chaetognath in the upper layers of these waters. It extends along the antarctic and subantarctic regions spreading northward from the subtropical convergence in deep waters.

S. gazellae was observed in the present study at MacMurdo Sound (samples were kindly sent by Mr. J. L. Littlepage), in a current from ice-water interface to 7, 10, and 72 m depth; extending along the upper 200 m in the south Pacific to 30°S. and to 21°S. at about 400 m depth. *S. gazellae* was also observed in the upper 200 m, in the samples taken by the Drake Expedition (material kindly sent from Argentina by Dr. E. Balech) at 55° S to 60° S and 60° W to 62° W to 63° 33′ W.

The typical mesoplanktonic Chaetognatha occupy different layers. Thus *S. decipiens* inhabits the upper part of the mesoplanktonic region, while *S. zetesios* and *S. planctonis* occupy the core, and *S. macrocephala* and *S. marri* extend from the lower levels of the mesoplankton to the upper part of the bathyplanktonic domain, and *S. maxima* changes its depth distribution with latitude. The fact that David (1956), Moore (1949), and Thomson (1947) reported *S. planctonis* in surface waters could be due to upwelling processes. *S. planktonis* Steinhaus and *S. zetesios* Fowler are easily distinguished (although many authors failed to separate them), by using morphological characteristics that are constant, instead of the meristic characteristics related to hooks, teeth, etc. For example, reliable morphological characteristics for this identification are: length of tail segment in relation to the total length, and the shape and position of the lateral fins. In *S. planctonis* the tail segment is shorter than in *S. zetesios*. The posterior fins in *S. planctonis* are triangular in shape, while those in *S. zetesios* are roundish. In *S. planctonis* the anterior end of the anterior fins reach up to the level of the ventral ganglion,whereas in *S. zetesios* they reach only to the level of the posterior end of the ventral ganglion. In order to verify this, here are the quotations from the respective species' authors. Steinhaus (1896): "Vorderflossen sehr sehmal bis zur mitte des Bauchganglion"; and Fowler (1905): "anterior fin well separated from the posterior, longer and narrower than posterior, wider behind than in front, not quite or only reaching the hinder end of the ventral ganglion."

In the samples studied here, *S. marri* was found only at levels below 200 m, south of parallel 50° S, in 59% of the samples from stations located between 50° S and 65° S, in the south Australian waters and the south Pacific.

S. planctonis was observed in the present studies distributed along the subantarctic waters, in a region limited by the subtropical convergence and the antarctic convergence.

S. hexaptera, S. regularis, and *K. pacifica* are also found very often extending (present data) to the lowest strata of the epiplankton and even to the upper strata of the mesoplankton.

S. bipunctata is an oceanic cosmopolitan species, which inhabits the epiplanktonic region, extending in the Pacific from the 40° N to the 35° S (Alvariño, in press *a*). Bieri (1959) suggested it is an antiequatorial species, as he did not find it within 5° to 10° on either side of the Equator. *S. bipunctata* was observed in the present studies in the upper 150 m in 46 stations along the Pacific equatorial belt, in a band of a width extending from 10° N to 15° S. (The stations correspond to the following expeditions: Equapac Horizon, Equapac Stranger, Shellback, Monsoon, Capricorn, Downwind, Troll, Tethys.)

The bathyplanktonic domain is populated by *E. fowleri, E. bathyantarctica, E. bathypelagica, H. mirabilis,* and *B. edentata.*

Some species, such as *E. hamata, E. fowleri, E. bathypelagica, H. mirabilis, S. maxima,* and *S. macrocephala,* are common to both the arctic-subarctic and antarctic-subantarctic waters. They are cosmopolitan in the most complete sense, with the exception of *E. bathypelagica,* connecting both polar or subpolar regions along the depths of the oceans. Thus, the isolation of the arctic and antarctic is relative (Barnes, 1957). *E. hamata* populates the Atlantic, Pacific, and Indian oceans at different depths, and the upper layers of the arctic and antarctic (various authors and personal unpublished data). *E. fowleri* also inhabits the three oceans, extending in the Pacific from 53° 57′ N to 46° S (several authors, and personal unpublished notes). *E. bathypelagica* (personal studies) extends in the Pacific from 53° 56′ N to 46° S. *H. mirabilis,* reported by Bieri (1959), David (1958*b*), Ritter-Zahony (1911), and Tchindonova (1955), was observed in samples taken respectively from 2300 m, 3000–2000 m, 2000–3423 m, and 5000 m. *S. macrocephala* (personal records) appeared in the Pacific from 40° N to 46° S. *S. maxima* was observed in the present material from 45° N to 46° S. However, observations obtained up to the present show that the antarctic and subantarctic waters have three indigenous chaetognaths: *S. gazellae* in the upper layers, and *E. bathyantarctica* and *S. marri* in deep waters. The antarctic belt also has indigenous siphonophores: *Diphyes antarctica, Marrus antarcticus,* and *Pyrostephos vanhoeffeni,* and one species, *Dimophyes arctica,* which is common to the arctic and antarctic waters, extending to deep levels at low latitudes (author, unpublished data). The arctic-subarctic region has *S. elegans* as a chaetognath of its own, and no siphonophore restricted exclusively to this region.

In the Pacific from 40° N to 40° S at least 20 species of oceanic Chaetognatha are present in the upper 200 m. In this same span, two other species of *Sagitta* are found at depths below the 200 m level: *S. decipiens,* extending from 200 or 600 m deep; and *S. zetesios,* from 300 to 800 m, besides the other species that cover the same span but extend both northward and southward. This zonation in depth is also observed for both species in the Atlantic and Indian oceans (author, unpublished data).

The mesoplanktonic domain can be subdivided into three zones: upper, median, and low, each having its characteristic species. The indications are that each species may have its own vertical range, a region in which to find optimal conditions. The zonation in the strata varies, not only for the different species but also for the respective individuals at different stages of maturity. The type of distribution for some species may vary with latitude, season, etc. Thus it is necessary to emphasize that the above established classification must be further subdivided into other types of vertical stratification or zonations. These are:

1. Vertical distribution related to latitude.
2. Vertical distribution affected by the circulation in the oceans.
3. Ontogenic vertical distribution.
4. Seasonal and diurnal vertical distribution.

With the exception of zonation in relation to seasonal or diurnal migration, a problem that merits special attention in another study, these points will now be discussed.

1. Variations in the vertical distribution in relation to latitude.

The sampling at different depths unfortunately does not cover the Pacific conveniently. Although in most of the cases the plankton samples were taken at different depths in each of the stations distributed throughout the Pacific (Fig. 1), in only half of the cases were the stratified samples taken with closing nets. However, with the data at hand it could be observed that the distribution in depth varies for some species with the geographical location. Species that appear only in deep layers in one region, are found in shallower depths or in surface waters in other areas.

E. hamata is unique in this respect; it covers the epi-, meso-, or bathyplanktonic categories in relation to latitude. It lives at great depths in the tropical and subtropical regions of the oceans, but in the subarctic and subantarctic regions it gradually rises near the surface toward

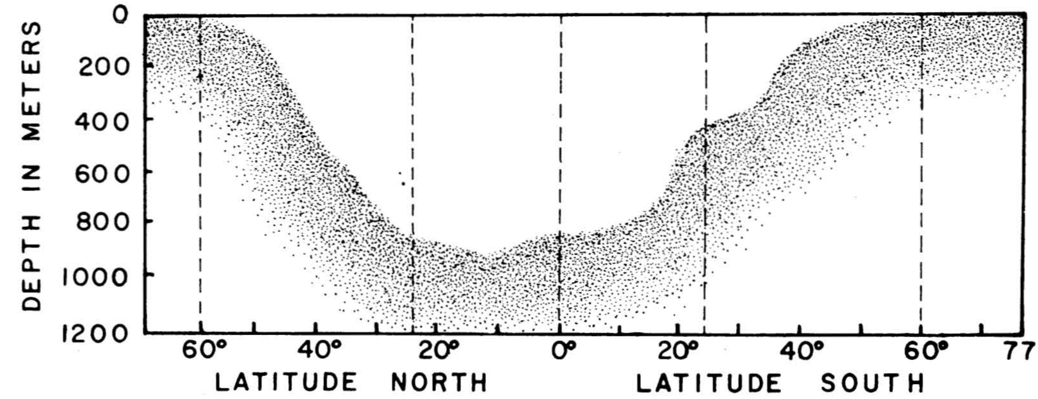

FIG. 3. Distribution in depth of *E. hamata* in the Pacific, from the Bering Sea to MacMurdo Sound in the Antarctic.

both poles (Fig. 3). This diagram is very similar to that of Thiel (1938) for the same species, covering from 60° S to 20° N in the Atlantic. This schematic diagram showing the distribution of *E. hamata* in the Pacific from arctic to antarctic waters was made by combining the data obtained from the study of more than 4,000 samples taken by the Scripps Expeditions in the Pacific from 1952 to 1962 (Fig. 1), and the monthly CalCOFI cruises for 1954 and 1958. It is important to notice in the present diagram the incipient emergence of *E. hamata* in the equatorial region. This emergence was also found for *E. fowleri* and *S. maxima;* while *S. bipunctata* occasionally submerged slightly in some locations of this region. For example, at station 49 of the Transpacific Expedition (47° 35.7′ N—167° 44.8′ E), the maximum number of individuals of *E. hamata* was found at about 225 m depth (Figs. 4, 5). In this locality the number of specimens or the volume of chaetognaths will be larger at this depth than at any other layer in this column of water, although the chaetognath population is represented by only one species. However, if these data were combined with the data from several other localities, the large amount of specimens at this layer will be shown in the results. This may be the case in Leavitt's (1947) surprising results.

S. maxima follows a pattern rather similar to *E. hamata* in its respective vertical distribution in the Pacific; it was observed in the present studies from 45° N to 46° S, although it reaches levels below those occupied by *E. hamata* in both high latitudes. *S. maxima* was observed 20 times in California waters, at about 140 m depth, in regions where upwelling was evident. However, it is found in these waters normally at depths below 140 m (author, unpublished data).

The adjacent seas isolated from the depths of the ocean by shallow regions do not have representatives of the bathyplanktonic species. *E. hamata* is recorded along the narrow Aleutian passes that connect the Bering Sea with the Pacific, as this species extends into the surface layers in that region. However, in other areas, where the population of *E. hamata* does not inhabit the upper strata and the connecting sill with neighboring waters is above its vertical distribution level, it does not pass to adjacent seas. This could be the case in the Mediterranean, where the Gibraltar sill at a depth of 320 m and the outward undercurrent make a barrier to the inward migration of the chaetognaths which in those latitudes inhabit layers below the threshold. A similar picture was found for the Siphonophorae (Bigelow and Sears, 1936); for the deep water Medusae (Kramp, 1924), and for the euphausiids (Ruud, 1936). Germain and Joubin (1916) reported *E. hamata* and *S. planctonis* from six and four localities respectively in the Mediterranean. Germain (1930–1932) includes *E. hamata* in the fauna list of the Mediterranean and explains that *S. macro-*

cephala does not enter these waters. I examined the literature on the Chaetognatha of the Mediterranean and the following authors did not find either of these species in the Mediterranean: Alvariño (1957*a*), Baldasseroni (1913, 1914), Furnestin (1953*a, b,* 1955, 1956, 1957, 1958*a,* b), Ghirardelli (1950, 1952), Hamon (1952), Ramult and Rose (1945), Rose and Hamon (1953), Scaccini and Ghirardelli (1941), Trégouboff (1958*a, b*). Ghirardelli (1950) says: "Il prof. Trégouboff mi segnala di aver pescato una sola volta un unico esemplare di *E. hamata* che disgrazatamente è andato perduto." Rose (in Trégouboff and Rose 1957:482) says: "*E. hamata* est rarissime, elle n'a été vue qu'une fois à Villefranche par M. Trégouboff . . ." and that "*S. planctonis* est très rare et vit à grande profondeur. Nous ne l'avons jamais recoltée." Furnestin (1953*a*) says that certain species of chaetognaths (*S. hexaptera, S. setosa, S. planctonis, P. draco, Spadella cephaloptera,* and *Spadella profunda*) were not found in the samples she analyzed, although they were reported by other authors, and she considers some of those species "extrêmement rares et d'autres demanderaient même confirmation de leur présence, comme c'est le cas pour *S. planctonis, Spadella profunda, E. hamata.*"

All this information suggests that either only a few individuals of *S. planctonis* and *E. hamata* enter the Mediterranean occasionally, which might happen when the outflow slows down and the Atlantic inflow conveys into the Mediterranean stray members of the respective chaetognath populations from regions in the Atlantic where these chaetognaths appear in the epiplanktonic layers; or the positive records reported are erroneous due to contamination, or mislabeling of the samples, or other error. *E. hamata* has been observed (Alvariño, 1957*b*) over the Iberian Atlantic continental shelf, at depths from 5 to 10 m, in regions of upwelling (author, unpublished notes), and at less than 50 m at 46° and 47° N in the Bay of Biscay (author, unpublished data).

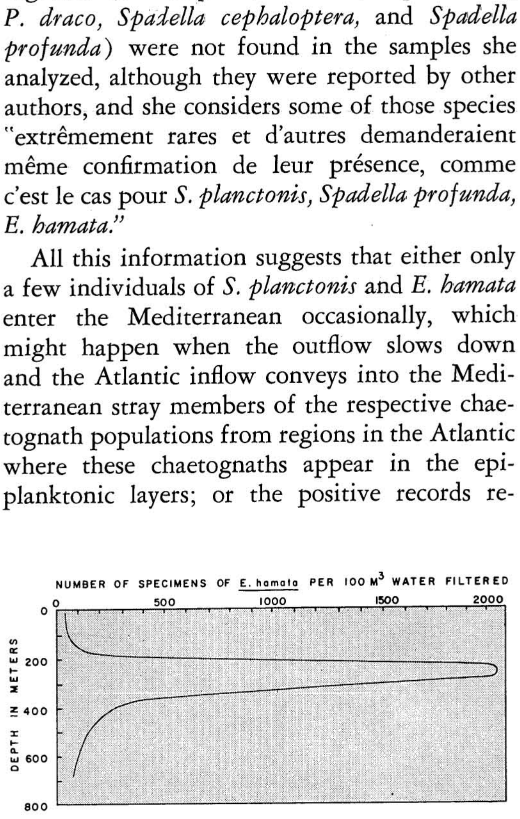

FIG. 4. Quantitative distribution in depth of *E. hamata* in the northwest Pacific, at Station 49 of the Transpac Expedition (47° 35.7′ N, 167° 44.8′ E).

No *E. fowleri, S. macrocephala,* or *S. zetesios* have been observed in the Mediterranean, and perhaps, according to the references above, also *E. hamata* and *S. planctonis* could be included in this group.

The Gulf of California connects with the Pacific along the deep open sea, and *E. hamata* was observed there in samples taken from 700 m depth.

The restriction of *E. bathyantarctica* and *S. marri* to antarctic waters could be due to the fact that they inhabit the belt of great depths occurring in those waters (Baker, 1954), in a region well defined by the antarctic West Wind Drift. Their distribution pattern is probably related to the circulation systems of the antarctic regions; thus they appear to be confined to the waters of the subantarctic West Wind Drift.

2. *Vertical distribution affected by the oceanic circulation.*

Each of the species of chaetognaths occupies different zones in the corresponding epi-, meso-, or bathyplanktonic domains. The levels each species occupies change somewhat under the effects of the geographical location, and there is evidence of stratification associated with size and maturity of the individuals, which will be discussed later.

Sometimes a given species does not follow the normal distribution pattern, and it appears to assume a stratification dependent upon the prevailing currents and turbulence. In certain localities, species typical of the upper layers are recorded at deeper levels than usual, apparently due to the sinking of the water masses they populate, or deep water species may appear in the upper layers because of upwelling. These phenomena are detected throughout the examination of the chaetognath population and are correlated with hydrographic data (Alvariño, 1962, in press *a*).

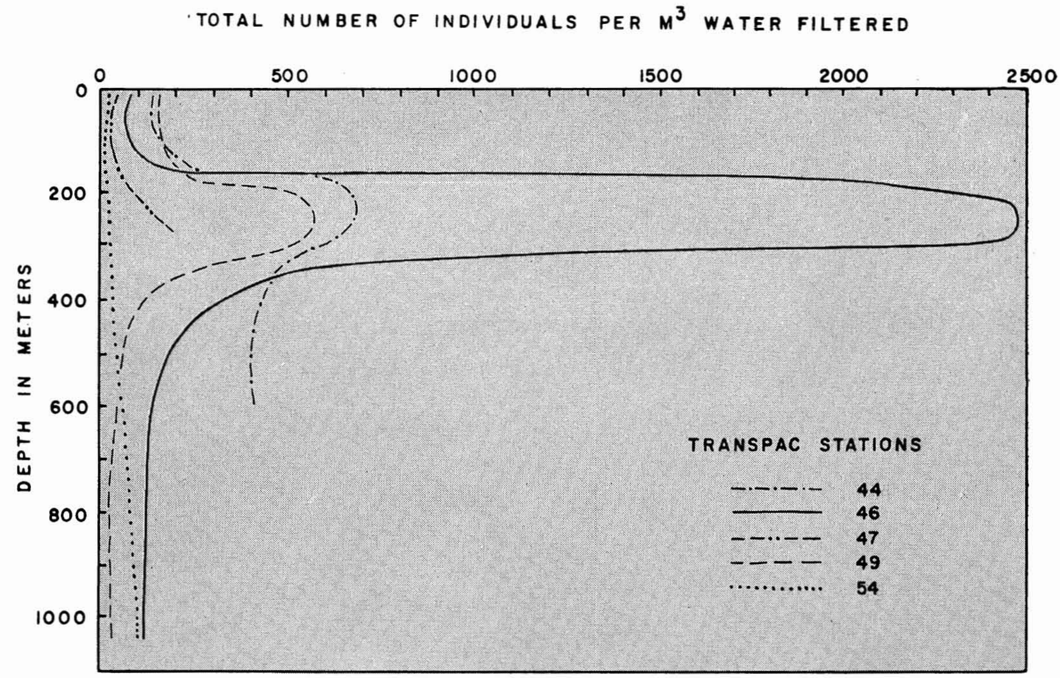

FIG. 5. Quantitative distribution in depth of chaetognaths in the Transpac Stations 44–54. Sta. 44, 53° 40.8′ N, 161° 55.5′ E; Sta. 46, 51° 13.0′ N, 164° 34.3′ E; Sta. 47, 49° 50.1′ N, 165° 49.2′ E; Sta. 49, 47° 35.7′ N, 167° 44.8′ E; Sta. 54, 40° 34.5′ N, 170° 02.3′ E.

Figure 5 is a quantitative profile of the distribution of the chaetognaths in the northwest Pacific, off the Kurile Trench. This diagram shows that the number of specimens, mainly of *E. hamata* (see also Fig. 4) is highest at about 200-300 m. The pattern formed at stations 52 and 54 (Fig. 6) is probably due to the turbulence and piling up of the central Pacific waters against the northern waters. At stations 52 and 54 (Fig. 6) eight species of chaetognaths were observed in the upper 200 m, six were observed from 510 m to 200 m, and four species below 510 m; whereas at stations 44–50 *S. elegans* and *E. hamata* were the only chaetognaths recorded in the upper 200 m and the latter in the strata below these levels. At stations 52 and 54 in the upper 200 m converge *S. elegans* (arctic-subarctic); *S. scrippsae* (transition); *S. minima, S. hexaptera, P. draco, K. subtilis* (central Pacific), and *S. bedoti* (typical in those longitudes of Kuroshio waters). Between 510 m and 300 m *S. scrippsae, S. minima* and *K. subtilis* are still found, with *S. decipiens, S. zetesios* and *E. hamata.* Below 510 m occur *S. decipiens, S. zetesios, S. macrocephala* and *E. hamata.* In these stations (52 and 54) more species are found in the upper 200 m and mid-levels than in the deep layers.

The southern boundary of *S. elegans'* distribution in the eastern Pacific and the northern boundary of *S. scrippsae* overlap (Fig. 7). *S. scrippsae,* an epiplanktonic and typical chaetognath of the Transition Area (between central Pacific and subarctic waters), the Alaska gyral, and the California Current (Alvariño, 1962, in press *a*), modifies its distribution in depth with the geographical region and with the age of the individuals. *S. scrippsae* extends along the upper 200 m in its main distributional region; but in the southernmost boundaries of the California Current, where these waters meet the warm inflow from the south and southwest, the population of *S. scrippsae* sinks with the cold waters (Fig. 8), reaching to a depth of 600 m in the outermost edges of the distributional region. This means that, although *S. scrippsae* has in general an epiplanktonic distribution, it sinks to deeper levels in the southernmost part of the California Current and disappears in these sinking waters. In this case, the distribution of *S. scrippsae* in the lowest levels of the epiplanktonic domain or in upper layers of the mesoplanktonic region is due to the geographical location that is related to the oceanic circulation.

From station 25 southward (53° 32.5′ N—163° 20.8′ W to 35° 46.8′ N—130° 02.5′ W) the waters in the upper 200 m are inhabited by several species of *Sagitta* (Fig. 7): *S. elegans* from 41° N northward (station 13), and *S. scrippsae* (outstanding as an "indicator" of the California Current) from 46° N southward; and, from 40° N southward, also were present *S. bierii, S. pacifica, S. pseudoserratodentata, S. bipunctata, S. hexaptera, S. enflata, K. subtilis,* plus 10 other species that populate the low latitudinal regions of the California waters. In this section (Fig. 7) can be observed the progressive sinking of *E. hamata* toward the low latitudes, and the stratification of *S. decipiens, S. zetesios,* and *S. macrocephala* (see also Fig. 9).

S. decipiens extends in the Pacific from the southern boundary of the subarctic waters to the subtropical convergence in the southern hemisphere. It populates the mesoplanktonic layers, and occasionally is found in the upper 140 m hauls, in which case its occurrence is an evidence of upwelling in that particular location, confirmed in every case by the hydrographic data (Alvariño, in press *a*).

S. zetesios extends in the Pacific from 46° N to 36° S, and *S. planctonis* from about 30° S southward. It appears from the author's data that the first species is more abundant than the latter.

S. macrocephala was observed from the Aleutian Trench region to 46° S in the Pacific (personal data).

The record of a particular species at greater depths than usual may be due to different factors, as already explained. Therefore, the difference is clear between truly deep water species like *E. fowleri,* midwater *S. decipiens, S. macrocephala,* and *E. hamata* (epiplanktonic in high latitudes, bathypelagic in low latitudes), or *S.*

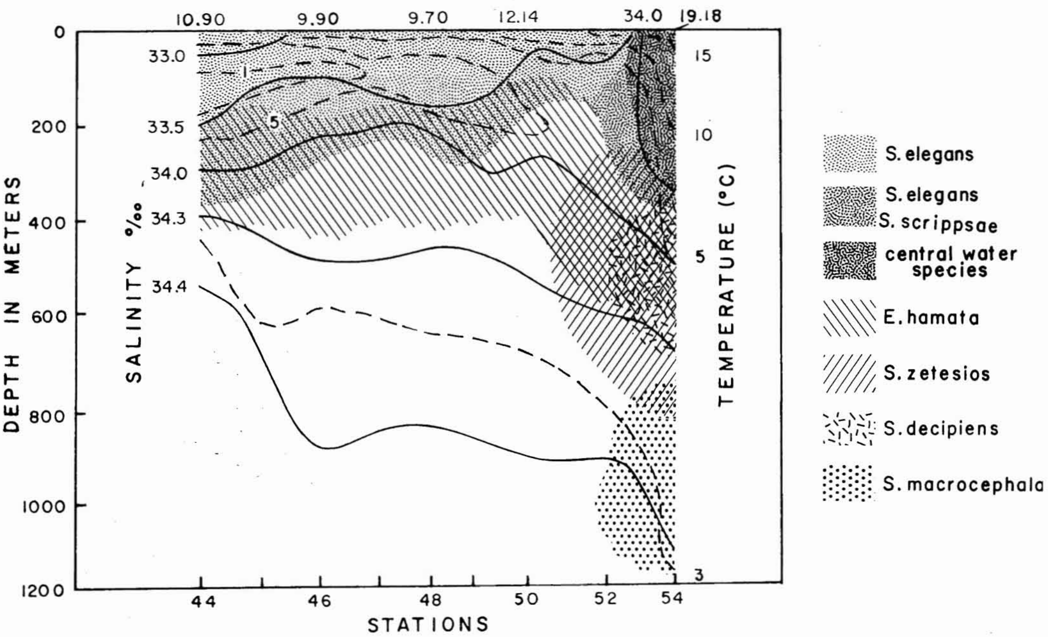

FIG. 6. Profile Stations 44–54 of the Transpac Expedition (53° 40.8′ N, 161° 55.5′ E to 40° 34.5′ N, 170° 02.3′ E).

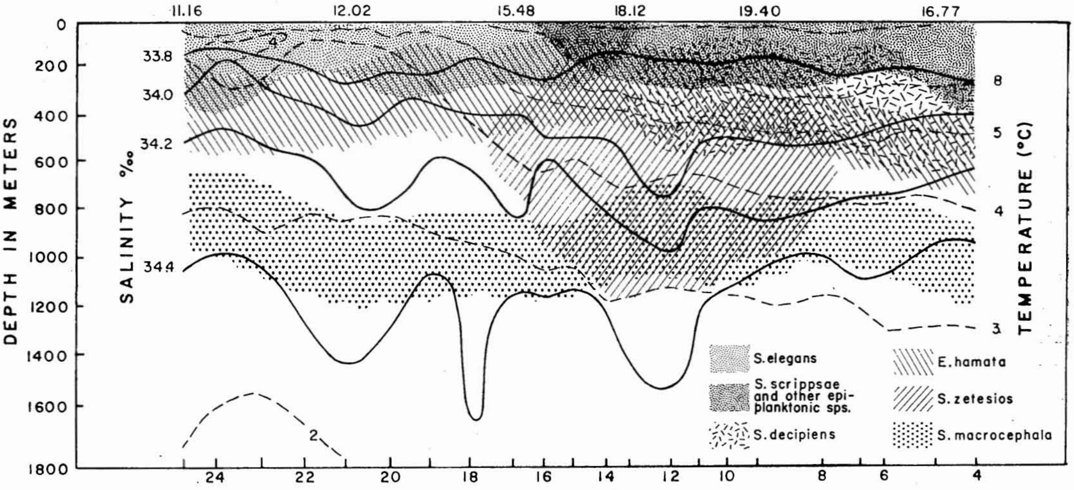

FIG. 7. Profile of the Transpac Expedition, Stations 4–24 (35° 46.8′ N, 130° 02.5′ W and 53° 15.0′ N, 161° 55.0′ W).

scrippsae (epiplanktonic, although at the southernmost part of its distribution region this species sinks with the waters it populates).

Epiplanktonic species appearing at deeper layers than usual may indicate a convergence. An illustration of this point was found by the author in a region in the south central Pacific, where the respective northern and southern boundaries of distribution of *S. gazellae* and *S. pacifica* coincide at depths below 200 m. This overlapping in the distribution of *S. gazellae* and *S. pacifica* was obtained from the examination of samples from the Downwind and Monsoon expeditions. The stations of the Downwind Expedition used in this case extended from 23° 30′ N—125° 05′ W to 46° 25′ S—123° 38′ W and 125° 03′ W (October 1957 to December 1957), and from 10° 01.5′ N—118° 58′ W to

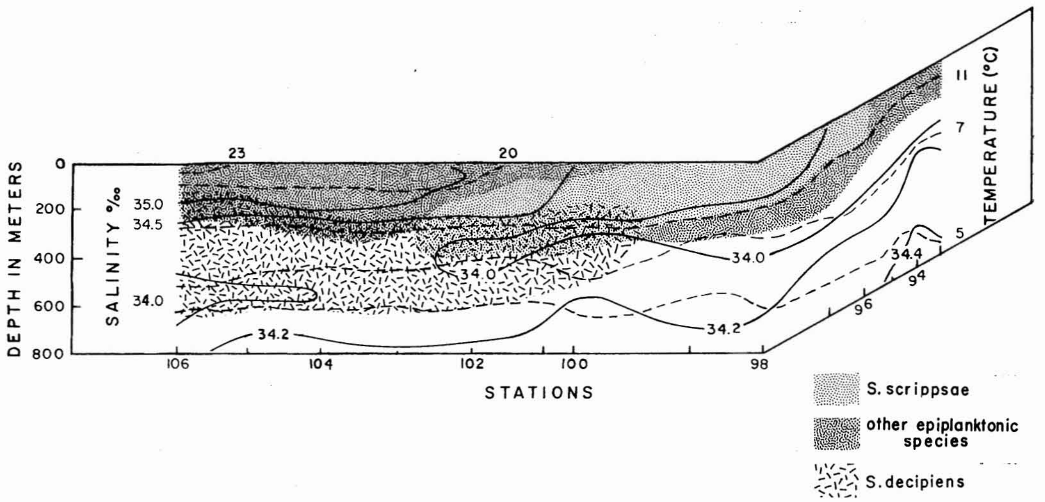

FIG. 8. Profile Stations 94–106 of the NORPAC CalCOFI Expedition (31° 01′ N, 118° 07′ W to 27° 25′ N, 150° 00′ W). The distribution of *S. scrippsae* has been disclosed from the other species that occur in the same region.

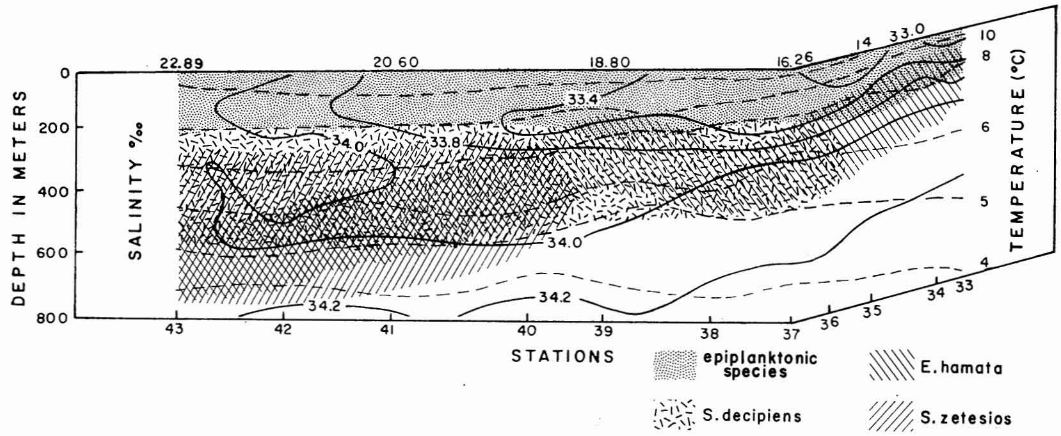

FIG. 9. Profile Stations 33–43 of the NORPAC CalCOFI Expedition (41° 45′ N, 124° 29′ W to 38° 35′ N, 149° 59′ W); with the distribution in depth of the mesoplanktonic species in the California waters. Notice the offshore sinking of *E. hamata.*

46° 44′ S—113° 09′ W (December 1957 to February 1958). The data from Monsoon Expedition covered from 64° 11′ S—165° 56′ W and 63° 05′ S—178° 31′ E to 11° 03′ N—142° 28′ W (February 1961 to April 1961). The data for *S. gazellae* at latitudes higher than 64° S are from MacMurdo Sound. The bathymetric distribution of *S. pacifica* northward from 20° N was obtained by studying records from the Capricorn, NorthPac, Equapac, Transpac, Shellback, and Tethys expeditions.

There is no doubt of the proper identification of both species. *S. gazellae* can be well separated from its close relatives (see Alvariño, 1962, and references. For *S. pacifica* see Alvariño, 1961, and references).

S. gazellae extends from the antarctic waters to 29° S in the Pacific, spreading farther north at mid-depths at stations where *S. pacifica* was also recorded in deeper layers than usual. *S. pacifica,* an inhabitant of the upper 100 m in the tropical and equatorial Pacific, extending from 40° N to 20° S, and from here to 35° S, was observed at levels below 200 m down to 400 m. These two species, one recruited from the tropical Pacific (*S. pacifica*), and other from the antarctic-subantarctic waters (*S. gazellae*), populate the upper 100 m in their respective dis-

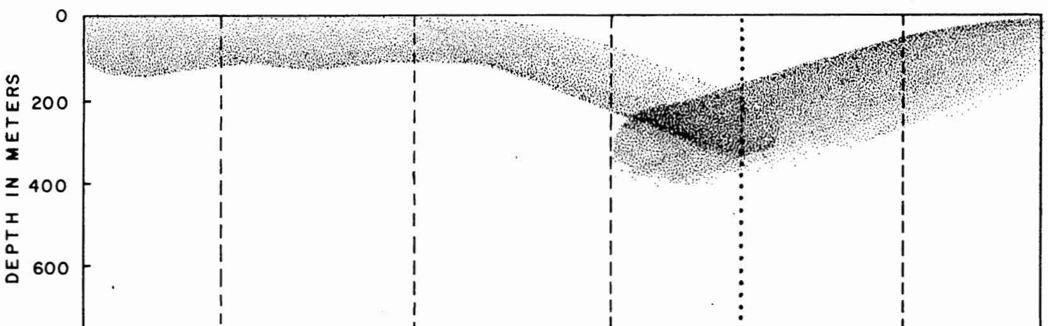

FIG. 10. Latitudinal bathymetric distribution of *S. pacifica* and *S. gazellae.*

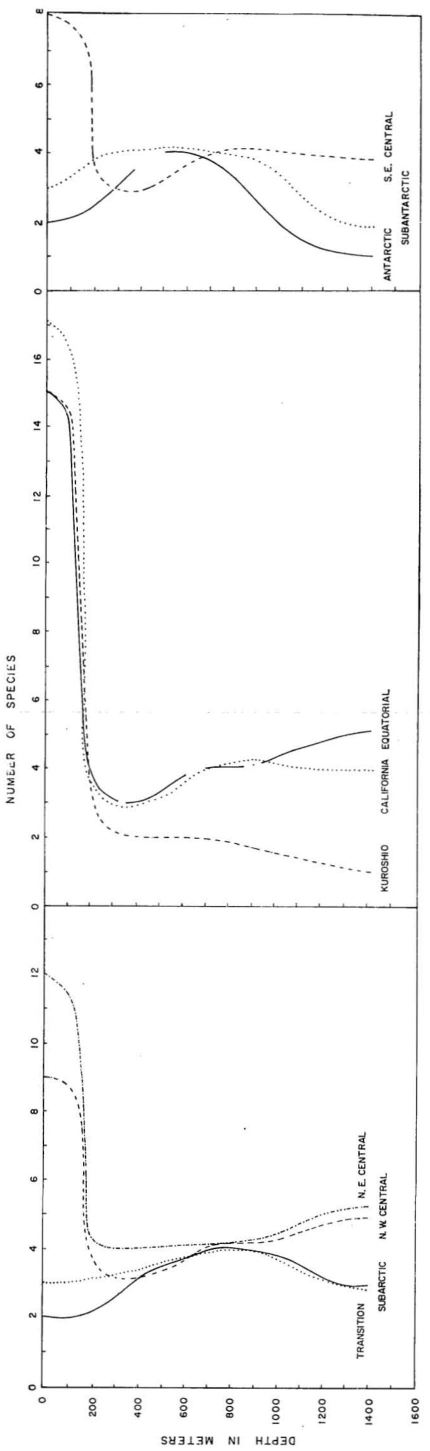

FIG. 11. Quantitative specific vertical distribution in the different Pacific water masses.

tributional region, and their corresponding southernmost and northernmost edges of their respective domains overlap in deep waters (Fig. 10), indicating a region of convergence in the respective distribution of the species—a convergence that partially coincides with the region of the hydrological convergence. *S. hexaptera, S. bipunctata, S. enflata, K. subtilis,* and *P. draco* (cosmopolitan species inhabiting the Pacific central waters) were recorded in the upper layers of that region of convergence, whereas at levels below 300 m *S. gazellae, S. pacifica, S. decipiens, S. macrocephala, E. fowleri, E. bathypelagica, E. hamata,* and *S. zetesios* were recorded. The specimens of *S. gazellae* recorded in this region were less than 20 mm long, at early Stage I of maturity. The boundary of the subtropical convergence also marks the northern limit of the distribution of *S. tasmanica* and *S. planctonis.*

In other instances, when two masses of water pass one above the other, then the typical cold water species sink with the waters while the warm water species extend throughout the upper layers.

S. tasmanica inhabits the upper 150 m in the Atlantic and in the southernmost part of the Indian Ocean (author, unpublished data). It enters the Pacific along with the subantarctic West Wind Drift, and its northward spread into the south Pacific stops at the region of the subtropical convergence. It extends westward, turning northward off the southern part of South America. This is demonstrated by the records of this species off Chile and at the southern part of Peru. It does not progress in the main Peru Current. The author's data on the distribution of *S. tasmanica* in the Indian and Pacific oceans were obtained from samples collected by the Scripps Expeditions in both oceans (paper in preparation). Unfortunately, David (1958, 1959) did not explain if the *serratodentata* he recorded is *S. serratodentata* Krohn or *S. tasmanica* Thomson; although the locations of the records correspond to the distributional region of the latter.

S. planctonis extends along the mid-depths of the Atlantic and Indian oceans, and enters the south Pacific with the subantarctic West Wind Drift, spreading to the subtropical convergence (personal data).

The greatest number of specimens for the smallest number of species per unit volume of water filtered was found in the arctic-subarctic and antarctic-subantarctic regions and in some localities of the transition and neritic areas (personal data). The greatest specific diversity with a small number of specimens was found in the subtropical, tropical, and equatorial waters, and in regions of mixing of waters from the above extreme geographical regions.

To emphasize the importance of the ocean's circulation with respect to zonation in depth of chaetognath species, diagrams from the different geographical localities and zones of dynamic disturbances have been prepared (Fig. 11). These diagrams show in general the quantitative specific distribution in depth of the Chaetognatha in the different water masses of the Pacific. The results obtained do not preclude the possibility that in the future, with more detailed studies, some slight variations may be observed. The California region includes the species recorded there from latitude 42° N to the southernmost tip of Baja California. This region appears to have the greatest number of species of chaetognaths in the upper 200 m, and the study of those species indicates the various origins of the inflows into the region. In Figure

TABLE 2

ONTOGENIC VERTICAL DISTRIBUTION OF *S. scrippsae*

LATITUDE N	DEPTH (meters)	MAXIMUM SIZE (millimeters)
46°	140	<30
	200	40
	300	50
	below 300	60
39°	170	<30
	340	40
	510	50
	680	60

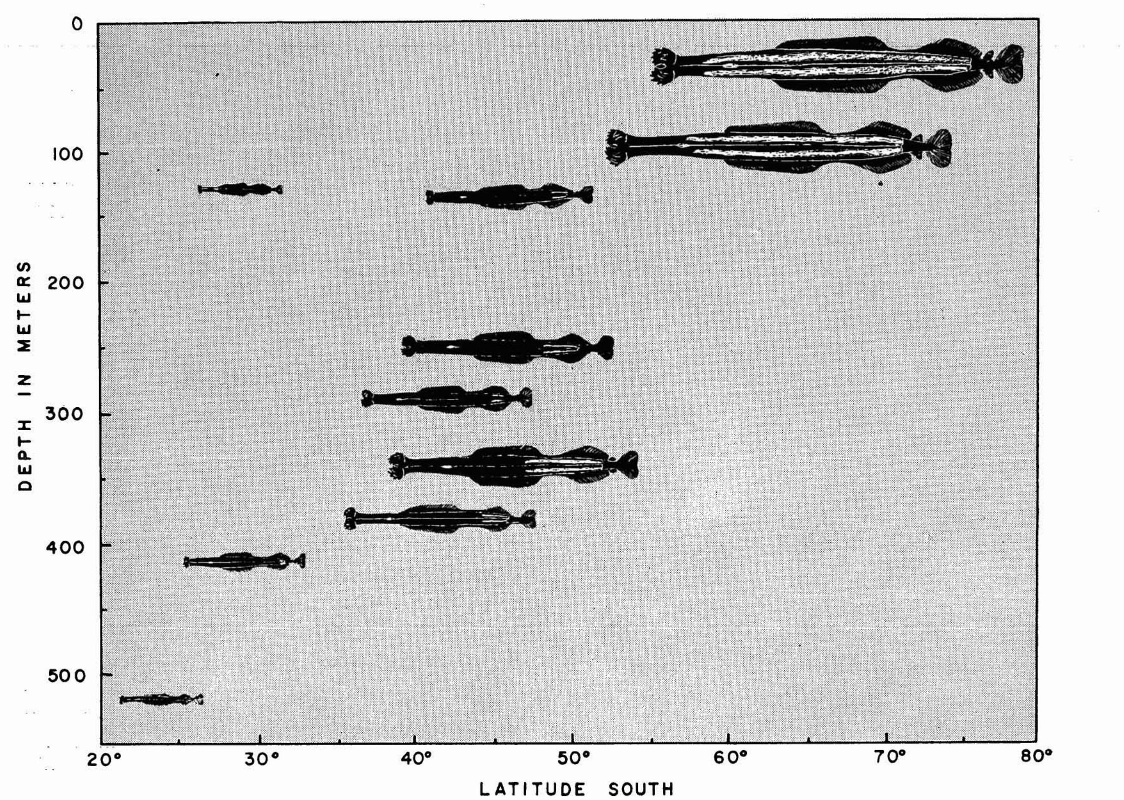

FIG. 12. Ontogenic vertical and latitudinal distribution of *S. gazellae*.

TABLE 3

ONTOGENIC VERTICAL DISTRIBUTION OF *S. gazellae*

LATITUDE S	DEPTH (meters)	MAXIMUM SIZE (millimeters)
MacMurdo Sound (77°)	7,10,72	90
46°	140	40
	283	50
	346	60
42°	283	40
	400	45

11 the southern part of the subarctic waters is called the transition area.

S. pseudoserratodentata and *S. bierii* are typical of the northeast Pacific central waters; and *S. lyra* of the northwest central waters, mainly the Kuroshio. Probably there are species typical of either southeast central and southwest central Pacific waters. Here are included our data from only the southeast central Pacific waters, because of the few data at hand from the southwest central Pacific region.

3. *Ontogenic distribution of the chaetognaths with depth*

Bigelow (1926), Huntsman (1919), and Russell (1931) found that the young of *S. elegans* appear in more superficial waters than do the adults. Fowler (1905) reported similar behavior for *E. hamata.* These records agree with my personal observations for the above species

TABLE 4

ONTOGENIC LATITUDINAL DISTRIBUTION OF *S. scrippsae*

LATITUDE N	MAXIMUM SIZE RANGE RECORDED (millimeters)
46°	60
44°	60
42°	60
40°	60
38°	46–50
36°	40–45
34°	40–45
32°	32–45
30°	28–45
28°	24–40
26°	15–36
25°	10–34
24°	10–20

TABLE 5

ONTOGENIC LATITUDINAL DISTRIBUTION OF *S. gazellae*

LATITUDE S	MAXIMUM SIZE RANGE RECORDED (millimeters)
77°	90
64°	85
57°	60
54°	50
46°	50
44°	50
42°	45
40°	25–45
38°	25–45
36°	30
34°	30
32°	25
30°	20
28°	15–30
26°	20
24°	20
22°	20
21°	<20

and for *S. scrippsae, S. gazellae, S. zetesios, E. fowleri, S. minima, S. planctonis,* and *S. macrocephala.*

The life history of these species might possibly reflect the history of the phylum. It appears that the older genera and species have been relegated to the deep strata. The young genera and the young of each of the species are represented by a large number of species and individuals respectively per volumetric unit of water; while the old genera and species have fewer species and individuals respectively, in those parameters.

The movement of the adults to deep layers could also be related to increase in weight of the individuals, associated with ripening of the sexual products. Further observations on this type of behavior might show if the Chaetognatha respond to a change in density like *Daphnia pulex* (Eyden, 1923), which decreases in specific gravity when emptying its brood pouch. A similar regulation in pelagic fishes has been observed by several authors.

A size stratification is usually found; sometimes the mature specimens do not invade the deep strata. Mature *S. scrippsae,* 50–60 mm in length were found in the upper 140 m collections, at 43° 46.5′ N—125° 08.5′ W to 43° 26.5′ N—125° 08.5′ W.

Personal observations on the ontogenic distribution of *S. gazellae* are shown in Figure 12. This agrees with David's (1955) ontogenic distribution of this species.

Adults as well as young *S. scrippsae* were found in the transition region and in the main part of the California Current, while only the young were recorded at the outer edges and southernmost boundaries of these water masses. The structure of the population of *S. scrippsae* shifts with latitude along with the extension of the inflow of the respective water mass (Alvariño, in press).

It was observed that only the young of *S. gazellae* (present data) and *S. scrippsae* spread to the outer edge of their distributional region.

The young of *S. zetesios* appeared in the northeast Pacific at about 300 m, whereas the adults were found only at depths below 500 m.

In station 46 of the NORPAC CalCOFI (38° 20′ N—127° 05′ W) specimens of *S. minima* of a size larger than usual were found from 700 to 280 m depth.

Studies of the life history of the species, mainly those of particular interest as "indicators," will give some understanding of their ecological needs, and of their relation to oceanographic concepts.

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