

DISTRIBUTION PATTERNS IN CHAETOGNATHA

A C Pierrot-Bults and V R Nair

Introduction

Chaetognatha are holoplanktonic animals, except for the genera *Spadella*, *Bathyspadella* and *Krohnittella*. They are found in all oceans and seas, from coast to coast and from the surface to the bottom; they have even invaded estuarine habitats.

This chapter discusses only general distribution patterns and illustrates these patterns with selected species.

The factors that influence distribution patterns are present day water circulation, physiochemical and ecological parameters (temperature, prey abundance, behaviour of the animals themselves, and competing organisms), and historical events like past water circulation patterns, the morphology of ocean basins and the evolutionary history of the group. The first factors are to a large extent covered by the so-called water mass theory. The gross pattern of ocean circulation provides a set of quite distinct biological provinces as a result of climate and vertical circulation differences (Reid *et al.* 1978). The oceans are divided into cyclonic and anticyclonic gyres, with boundary currents and transitional zones in between. These transitional zones are the richest in species. For example, the subtropical convergence is a zone of congregation of tropical and cold water species. For chaetognaths the east and west Pacific boundary currents are the most diverse in species composition (Reid *et al.* 1978). Beklemishev (1971) divided the pelagic communities into cyclical, terminal, terminal/cyclical, and ice/neritec (Fig. 9.1). For general discussions about zooplankton distributions, see Reid *et al.* (1978); Van der Spoel and Pierrot-Bults (1979a); Boltovskoy (1981a); Van der Spoel and Heyman (1983); Pierrot-Bults *et al.* (1986).

The different water masses for the Atlantic Ocean, the Indian Ocean, and the Pacific Ocean are shown in Figure 9.2 (a-c).

The Pacific Ocean shows the greatest complexity and

the Indian Ocean the least in the amount of different water masses (Van der Spoel and Heyman 1983). Watermasses are horizontally and vertically defined, but species distribution seems to be more confined by the climatic zone than by the water mass *per se*. Diurnal vertical migrating populations cross different water masses every day, and thus encounter daily a wider range of environmental differences vertically than they would encounter horizontally in their range.

The historical component is difficult to study as we do not have a fossil record of chaetognaths. However, phylogenetic systematics, area-cladograms and knowledge about palaeo-oceanographic circulation patterns and palaeoclimate can provide insights into the history and phylogeny of the Chaetognatha and of pelagic distribution patterns (Pierrot-Bults and Van der Spoel 1979; Van der Spoel and Pierrot-Bults 1979a; Van der Spoel 1983; Van der Spoel and Heyman 1983).

The range of a species is another point of difficulty and should not be defined merely by presence or absence but also by numerical abundance and breeding. The area where sterile expatriates are found does not belong to the proper range of a species. Since knowledge of this is very scarce it is not yet possible to distinguish between the proper range and recordings of sterile expatriates.

The ocean is three-dimensional and ranges of oceanic species should be given in three dimensions. The most applied vertical division is the epipelagic, from 0–200 m, the mesopelagic from 200–1000 m (subdivided into the shallow mesopelagic from 200–600 m, and the deep mesopelagic from 600–1000 m) and the bathypelagic, which is deeper than 1000 m. These vast ranges give rise to horizontally and vertically separated communities and species (David 1963; Pierrot-Bults 1975a; 1979, 1982; and see Fig. 9.9). On the other hand, vertical migration might in some cases prevent actual speciation

fferent
1983).
efined,
ned by
Diurnal
water
wider
in they

as we
wever,
know-
atterns
history
pelagic
Spoel
an der

difficulty
nce or
breed-
1 does
Since
ible to
ngs of

ceanic
most
0-200
d into
deep
elagic,
s give
nunit-
1979,
ertical
iation

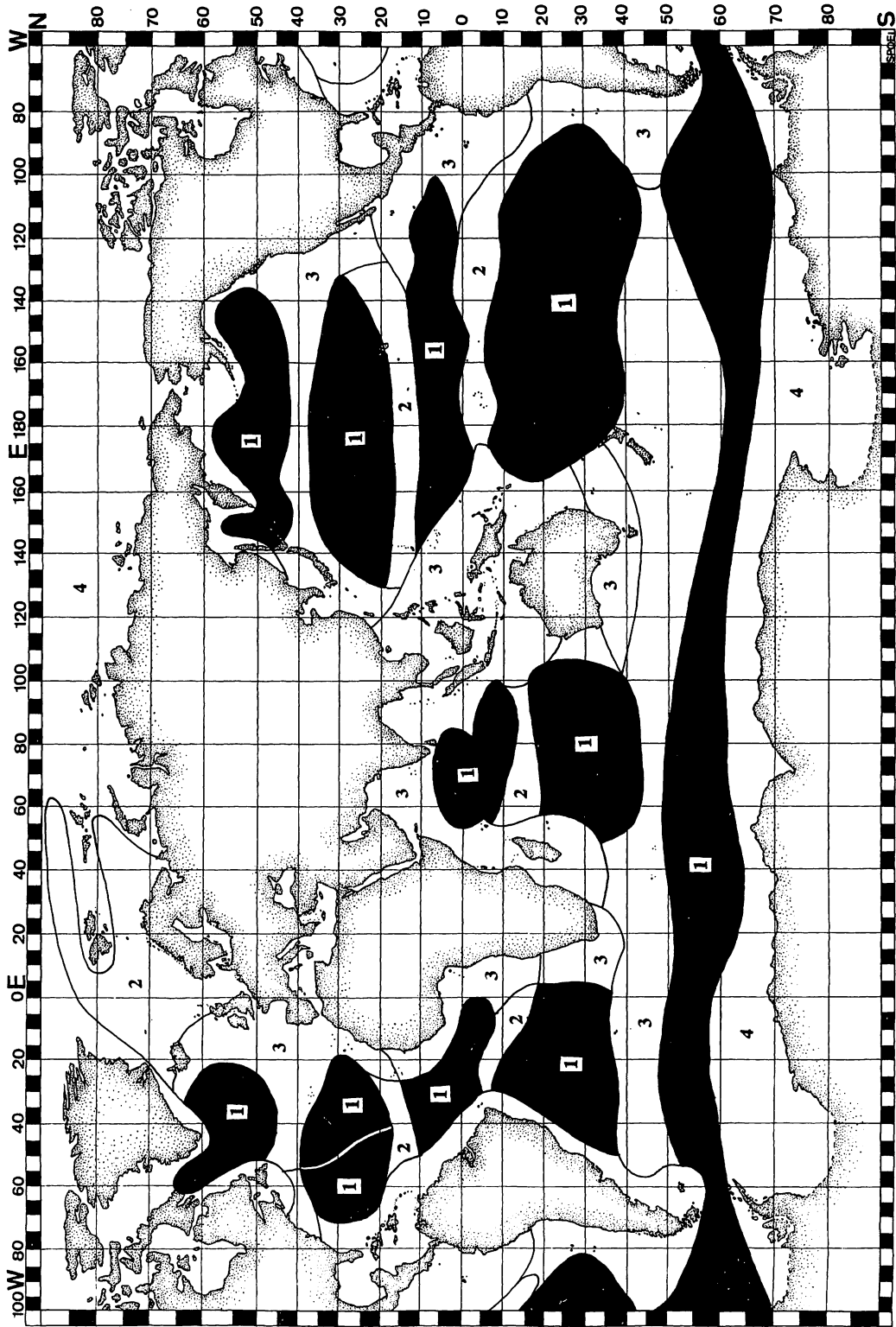


Fig. 9.1 Pelagic communities of the world ocean. 1, cyclical water; 2, terminal water; 3, terminal-cyclical water; 4, ice-neritic water. After Beklemishev (1971).

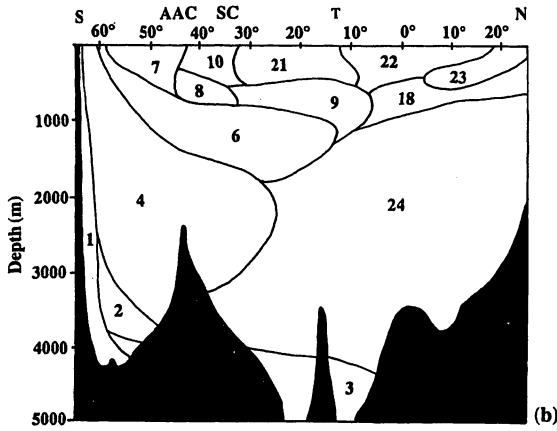
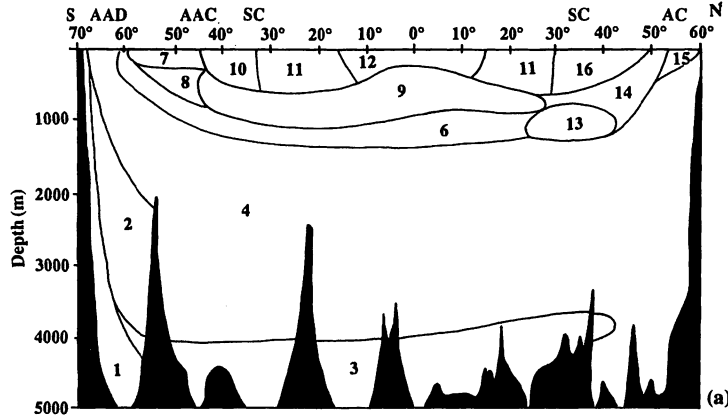
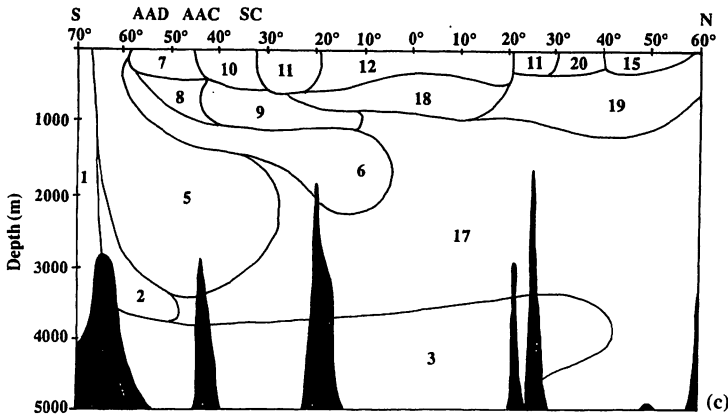


Fig. 9.2 A diagram of the watermasses of (a) the Atlantic Ocean, (b) the Indian Ocean, (c) the Pacific Ocean. 1, Antarctic slope water; 2, circum Antarctic deep water; 3, Antarctic bottom water; 4, Atlantic deep water; 5, Atlantic and Indian deep water; 6, Antarctic intermediate water; 7, Antarctic surface water; 8, intermediate mixed Antarctic water; 9, subantarctic intermediate water; 10, subantarctic surface water; 11, subtropical water; 12, tropical water; 13, Mediterranean water; 14, north Atlantic intermediate mixed water; 15, Arctic water; 16, north Atlantic surface water; 17, north Pacific deep water; 18, tropical intermediate water; 19, north Pacific intermediate water; 20, north Pacific surface water; 21, central Indian water; 22, north Indian water; 23, Red Sea and Persian Gulf water; 24, north Indian deep water. AAC, Antarctic convergence; AC, Arctic Convergence; AAD, Antarctic divergence; SC, subtropical convergence; T, thermal front. After Van der Spoel and Heyman (1983).



the Atlantic Ocean. 1, deep water; 3, deep water; 5, Atlantic deep water; 7, Antarctic subantarctic water; 13, intermediate mixed water; 17, deep water; 19, Pacific surface water; 23, deep water. convergence; divergence; T, 1983).

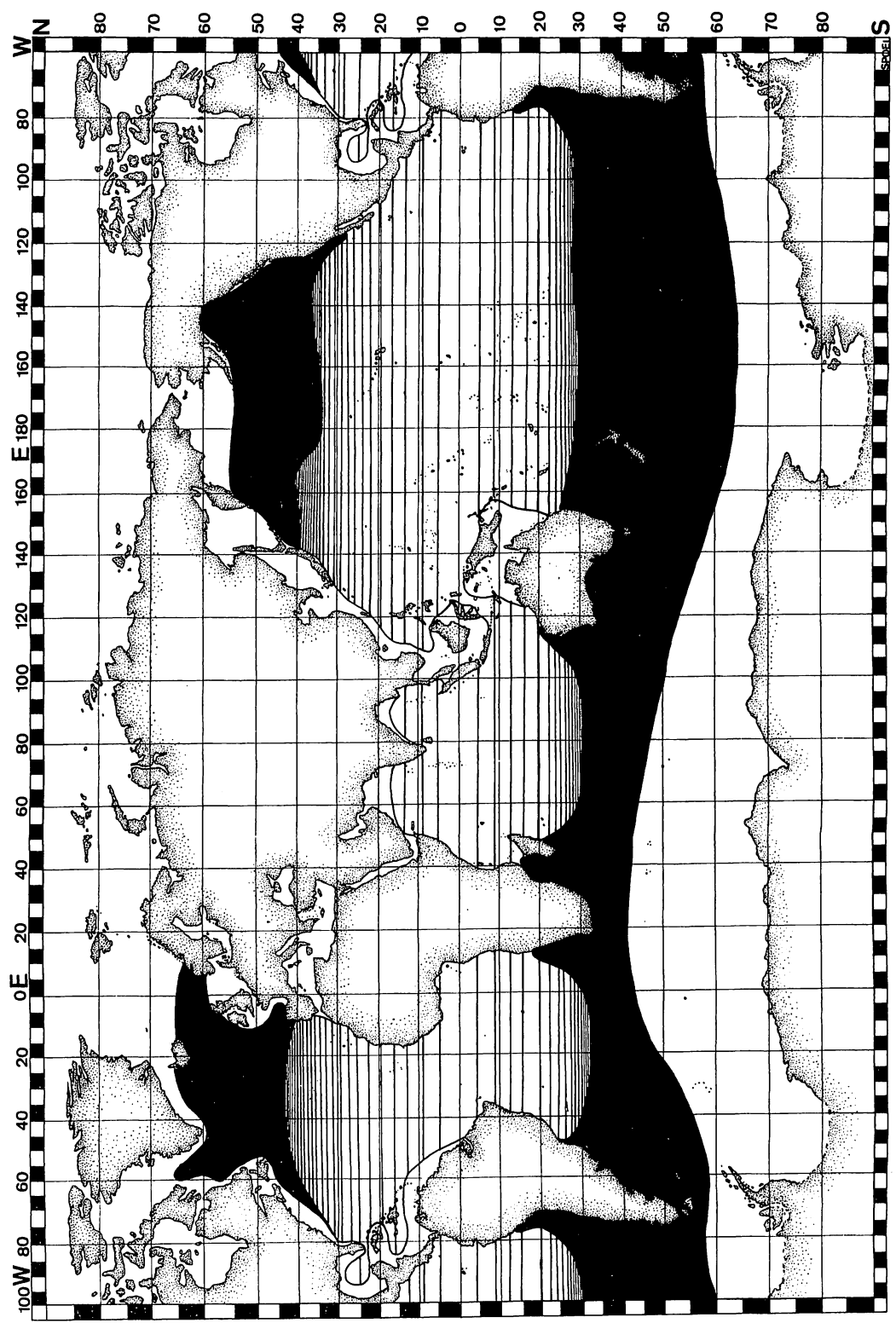


Fig. 9.3 Horizontal distribution of *S. planctonis* f. *zetesios*; striped area represents submergence. After Van der Spoel and Heyman (1983).

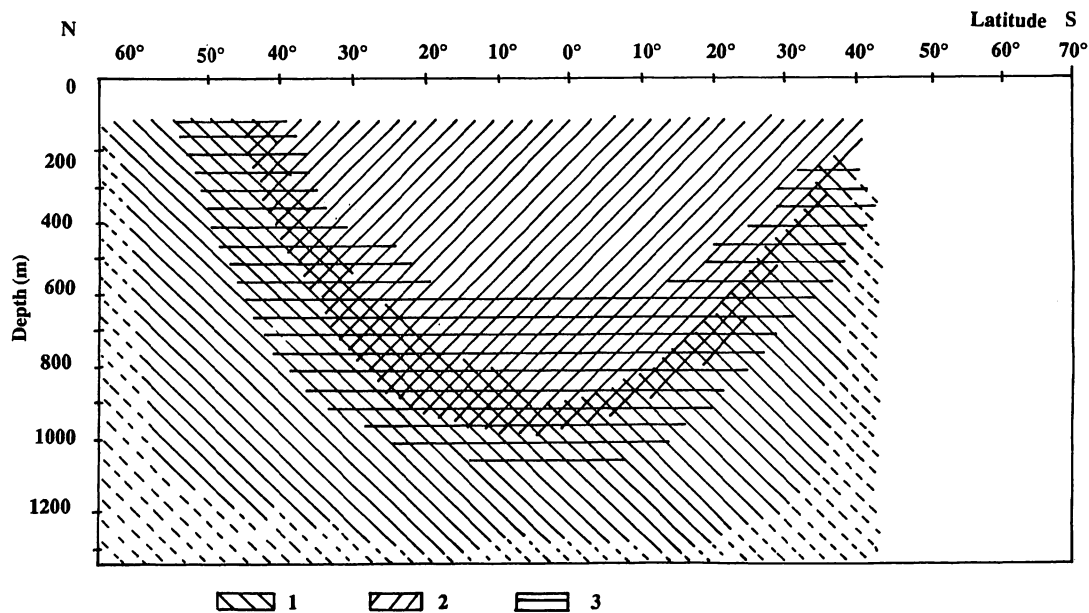


Fig. 9.4 Horizontal and vertical distribution of *Sagitta planctonis* f. *planctonis*, (1) *S. planctonis* f. *zetesios* (2), and intermediate (3). After Pierrot-Bults (1975).

by causing enough mixing of the populations to make at least some gene flow possible (David 1961).

Quantitatively, maximum population density of chaetognaths is confined to the photic zone (Pierrot-Bults 1982). In the tropics and subtropics the epipelagic is a warm biotope and the water column is usually stratified. At higher latitudes there is no permanent stratification and the division between epipelagic and mesopelagic fauna is often lost. Tropical submergence is shown when taxa that live in mesopelagic to bathypelagic layers in the (sub)tropics are epipelagic in the higher latitudes, an example is *Sagitta planctonis zetesios*

Fowler, 1905 (Figs. 9.3 and 9.4) and *Eukrohnia hamata* (Möbius, 1875) (Fig. 9.5). The border between stratified and non-stratified water is not only related to subtropical submergence in some species but also acts as a barrier to the distribution of species in the North Atlantic at about 43°N (Pierrot-Bults 1976a).

The latitudinal shift in bathymetric distribution of some chaetognath species (Fig. 9.6 a-e) shows the emergence of mesopelagic and bathypelagic species to the upper strata towards the subtropical convergence in the Indian Ocean (Nair 1978).

The mesopelagic is characterized by gradually dimin-

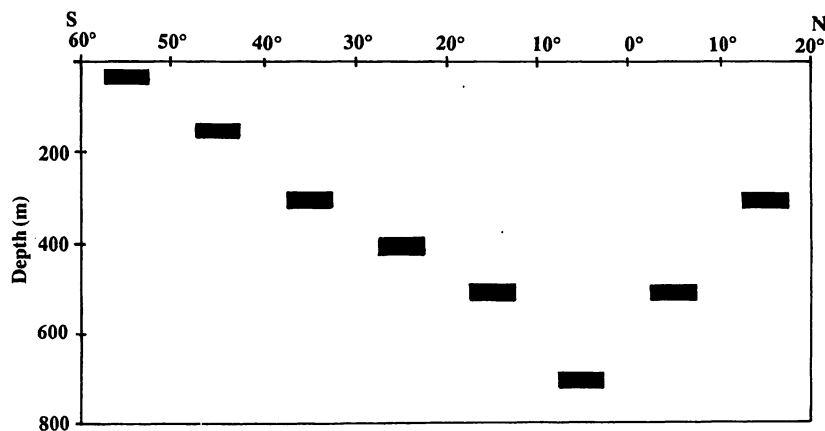


Fig. 9.5 Horizontal and vertical distribution of *Eukrohnia hamata* in the Atlantic Ocean. After Thiel (1938).

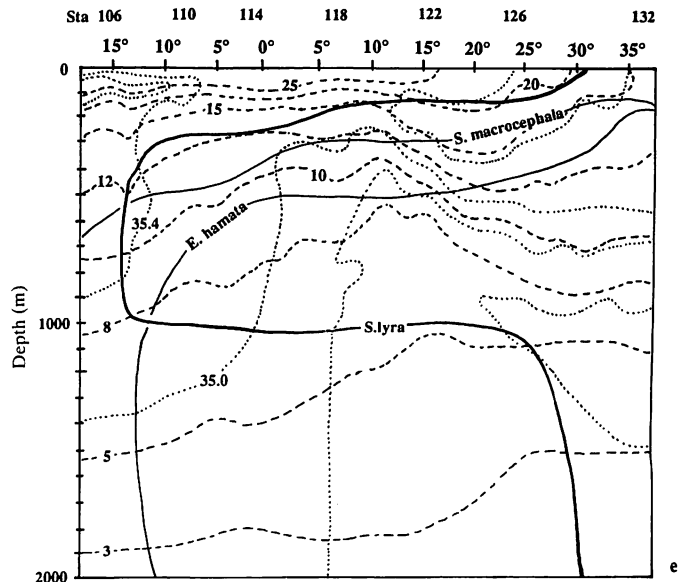
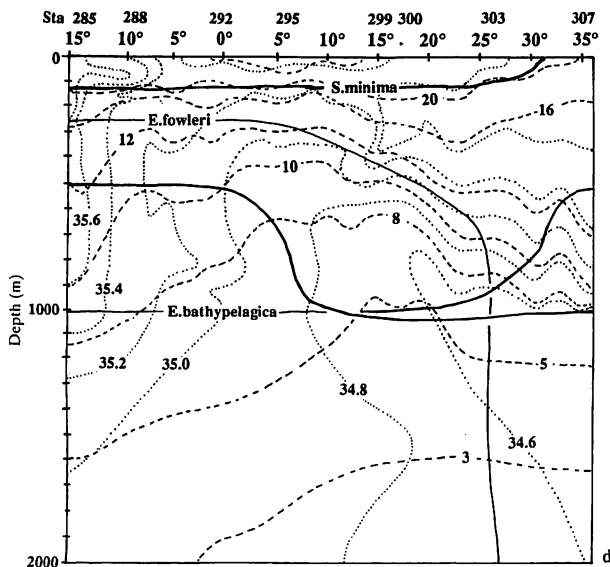
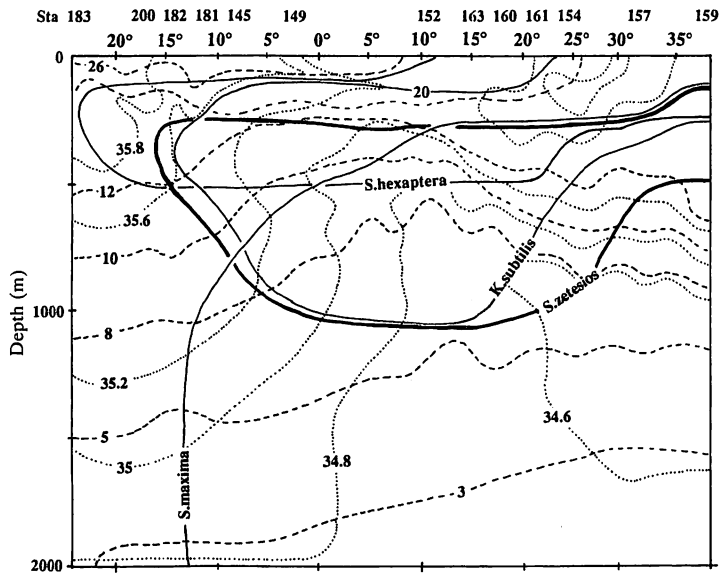
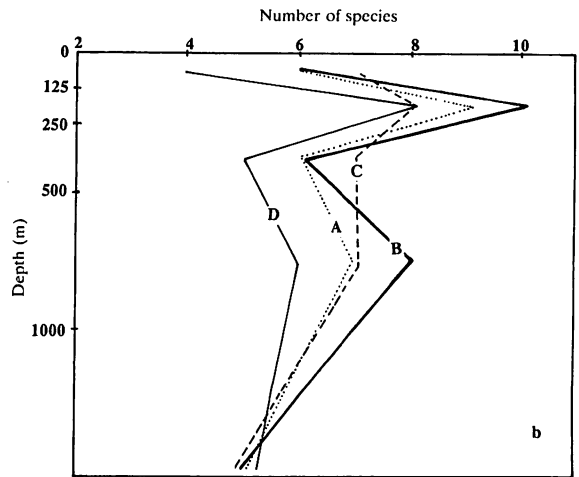
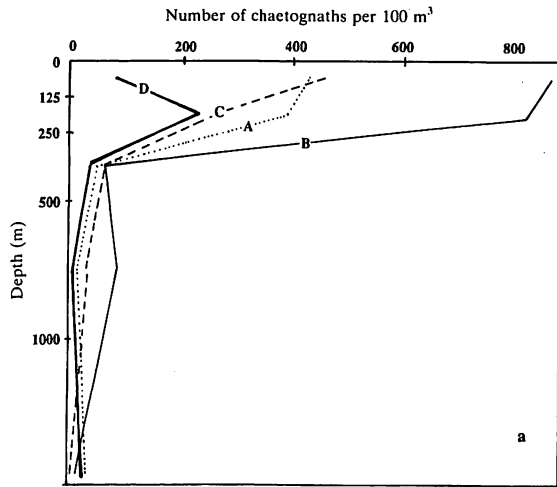


Fig. 9.6 Latitudinal shift in bathymetric distribution in the Indian Ocean. (a) number of chaetognaths, (b) number of species, (c) *Krohnitta subtilis*, *Sagitta hexaptera*, *S. maxima*, and *S. zetesios*, (d) *Eukrohnia bathypelagica*, *E. fowleri* and *Sagitta minima* and (e) *Eukrohnia hamata*, *Sagitta lyra* and *S. macrocephala*. A = entire area; B = north of the equator; C = between the equator and 20° s; D = south of 20° s. After Nair (1978).

le S
70°

intermediate
Eukrohnia
between
related to
also acts
the North
oution of
rows the
pecies to
vergence
ly dimin-

rtical dis-
ta in the
(1938).

ishing light. Most organisms living habitually in these layers perform diurnal vertical migration, living at mesopelagic depths in the daytime and in shallower water at night. Various hypotheses are put forward to explain vertical migrations, for example, the availability of food in the superficial layers and the advantage of lower metabolism at the deeper layers; avoidance of visual predation; horizontal dispersion and transport and breeding migrations (McLaren 1963; Pearre 1973, 1974, 1979b; Sameoto 1973; Longhurst 1976; Angel 1986; Schalk 1988). There are very few records of bathypelagic species performing diurnal vertical migrations; these are generally related to the light cycle (Longhurst 1976; Angel 1986).

Species diversity of chaetognaths gradually decreases from the lower epipelagic to the bathypelagic layers. Because of the overlap of epipelagic and mesopelagic species, maximum species diversity often lies at about 150–250 m, a comparable increase is seen at 800–1000 m as a result of extension of bathypelagic species in the

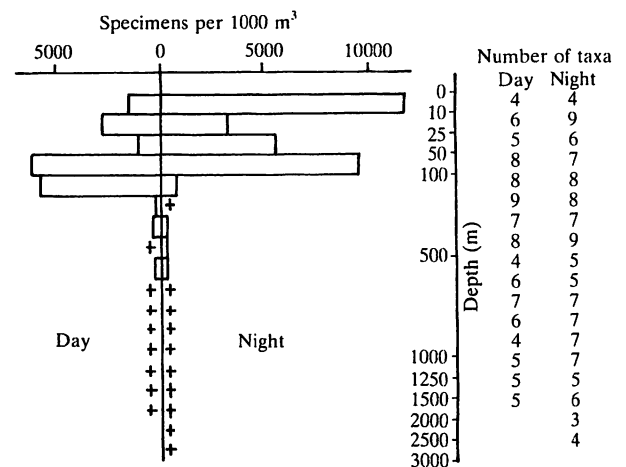


Fig. 9.7 Bathymetric distribution of the number of specimens per 1000 m³ and the number of taxa in the north-west Atlantic. After Pierrot-Bults (1982).

Table 9.1 Species observed at different strata in the Northern Indian Ocean (north of 10° S Lat)

Depth of haul (m)	Water masses found at particular stratum in the western side (west of 80°E long.)	Water masses found at particular stratum in the eastern side (east of 80°E long.)	Species
200–0	Arabian Sea surface water	Bay of Bengal surface water	<i>K. pacifica</i> , <i>K. subtilis</i> , <i>P. draco</i> , <i>S. bedoti</i> , <i>S. bipunctata</i> , <i>S. enflata</i> , <i>S. ferox</i> , <i>S. hexaptera</i> , <i>S. minima</i> , <i>S. neglecta</i> , <i>S. pacifica</i> , <i>S. pulchra</i> , <i>S. regularis</i> , <i>S. robusta</i> .
500–200	Persian Gulf water, Red Sea water	Bay of Bengal sub-surface water, Persian Gulf water	<i>K. subtilis</i> , <i>P. draco</i> , <i>S. bipunctata</i> , <i>S. decipiens</i> , <i>S. enflata</i> , <i>S. ferox</i> , <i>S. hexaptera</i> , <i>S. lyra</i> , <i>S. macrocephala</i> *, <i>S. maxima</i> , <i>S. minima</i> , <i>S. pacifica</i> , <i>S. regularis</i> , <i>S. zetesios</i> .
1000–500	Arabian Sea intermediate water, Equatorial intermediate water, Pacific water, Antarctic intermediate water	Bay of Bengal sub-surface water	<i>E. fowleri</i> , <i>E. hamata</i> , <i>S. decipiens</i> , <i>S. lyra</i> , <i>S. macrocephala</i> , <i>S. maxima</i> , <i>S. zetesios</i> .
2000–1000†	Arabian Sea intermediate water, Arabian Sea deep water		<i>E. bathypelagica</i> , <i>E. fowleri</i> , <i>E. hamata</i> , <i>S. decipiens</i> , <i>S. lyra</i> , <i>S. macrocephala</i> , <i>S. maxima</i> , <i>S. zetesios</i> .

* Found only in the northwestern Indian Ocean.

† No data available for this stratum from the northeastern Indian Ocean.

Table 9.2 Species observed at different strata in the central and southern Indian Ocean (between 10° S and 38° S lat.) and at the subtropical convergence (south of 38° S lat)

Depth of haul (m)	Central and Southern Indian Ocean		Subtropical convergence	
	Water masses found at particular stratum	Species	Water masses found at particular stratum	Species
200-0	Surface water	<i>K. subtilis</i> , <i>P. draco</i> , <i>S. bipunctata</i> , <i>S. enflata</i> , <i>S. ferox</i> , <i>S. hexaptera</i> , <i>S. minima</i> , <i>S. pacifica</i> , <i>S. regularis</i>	Antarctic water	<i>S. decipiens</i> , <i>S. lyra</i> , <i>S. maxima</i> , <i>S. serratodentata</i> <i>S. tasmanica</i>
500-200	Subsurface water	<i>E. hamata</i> , <i>E. fowleri</i> , <i>K. subtilis</i> , <i>P. draco</i> , <i>S. bipunctata</i> , <i>S. decipiens</i> , <i>S. enflata</i> , <i>S. lyra</i> , <i>S. macrocephala</i> , <i>S. maxima</i> , <i>S. minima</i> , <i>S. pacifica</i> <i>S. serratodentata</i> , <i>S.</i> <i>tasmanica</i> , <i>S. zetesios</i>	Deep Water	<i>E. bathypelagica</i> , <i>E. hamata</i> , <i>S. decipiens</i> , <i>S. lyra</i> , <i>S. maxima</i> , <i>S. serratodentata</i> <i>S. tasmanica</i> , <i>S. zetesios</i>
1000-500	Antarctic water, Pacific water	<i>E. bathypelagica</i> , <i>E. hamata</i> , <i>E. fowleri</i> , <i>S. decipiens</i> , <i>S. lyra</i> , <i>S. macrocephala</i> , <i>S.</i> <i>tasmanica</i> , <i>S. zetesios</i>	Deep Water	<i>E. bathypelagica</i> , <i>E. hamata</i> <i>S. decipiens</i> , <i>S. gazellae</i> , <i>S. lyra</i> , <i>S. macrocephala</i> , <i>S. maxima</i> , <i>S. zetesios</i>
2000-1000	Deep water	<i>E. bathypelagica</i> , <i>E. fowleri</i> , <i>E. hamata</i> , <i>S. macrocephala</i> , <i>S. tasmanica</i> , <i>S. zetesios</i>	Deep Water	<i>E. bathypelagica</i> , <i>E. hamata</i> <i>S. gazellae</i> , <i>S. macrocephala</i> , <i>S. maxima</i> , <i>S. zetesios</i>

mesopelagic domain (Nair 1978 (Indian Ocean); Pierrot-Bults 1982 (North Atlantic), (Fig. 9.7 and Tables 9.1 and 9.2)). Species diversity generally shows an increase from high to low latitudes, as in most other animal groups (Nair 1976; Pierrot-Bults 1976a; Nair and Madhupratap 1984).

The energy flux in the ocean is a vertical one. The deeper-living organisms are dependent on surface production and thus in the mesopelagic distributions the climate and distribution of surface parameters is still identifiable. The mechanisms determining bathypelagic distributions seem to be different from those which govern the epipelagic and mesopelagic ones (Fasham and Angel 1975; Angel 1979).

A feature of oceanic species is wide, continuous distribution. In these wide ranges geographic, infras-

pecific variation due to different selective pressures in the various parts of the range is frequently present (Van der Spoel 1973; Pierrot-Bults 1975a; Pierrot-Bults and Van der Spoel 1979). The exact taxonomic status of some chaetognath taxa is difficult to determine. Research on *Sagitta crassa* Tokioka, 1938, (Murakami 1959; Tokioka 1974a) has shown that, as a result of changing environmental conditions, considerable morphological differences occur in successive generations in the same population. The same phenomenon is described for *S. tasmanica* Thomson, 1947 from the south-east Pacific where, due to change of temperature and salinity, a gradual change to the *selkirki* form described by Fagetti (1958) as a species occurs (Fagetti 1958; 1968). The same occurs in the north-west Atlantic when *S. tasmanica* becomes trapped into a warm-core

Number of taxa
Day Night
4 4
6 9
5 6
8 7
8 8
9 8
7 7
8 9
4 5
6 5
7 7
6 7
4 7
5 7
5 5
5 6
3
4

Number of species
north-west

ata,
ata,
ata,
ata,

ata,

phala*,
ata,

ns,
ima,

hamata,
phala,

gulf stream ring (Fig. 9.8). The populations of *S. setosa* Müller 1847 show differences in the different parts of the range. *S. batava* Biersteker and Van der Spoel, 1966 from the Oosterschelde is conspecific with *S. setosa*. *Sagitta euxina* Moltchanoff, 1909 from the Black Sea, described as a close relative of *S. setosa*, might prove not to be a valid species when populations of the whole range of *S. setosa* are studied (Pierrot-Bults 1976a).

It is to be expected that detailed variation studies will reveal more of these differences. According to Gibbs (1986) we should be suspicious of the many so-called species that have circumglobal distributions, as they might prove to consist either of different species or infraspecific taxa. Studies on copepods show that there exist genetic differences between populations (Bucklin and Marcus 1985; Carillo *et al.* 1974).

For the same reason, species with disjunct distributions like *S. tenuis*, *S. tasmanica* and *S. bierii* need further study to see whether the disjunct parts of the range are inhabited by populations with different genetic structures. Different species and higher taxonomic groups have different tolerances to transitions and change in environmental circumstances. This is reflected in the distributions of the different groups of organisms. A survey of faunal boundaries of ranges of

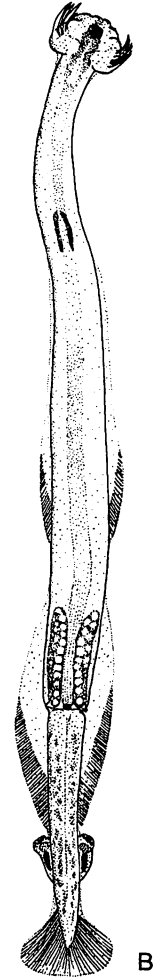
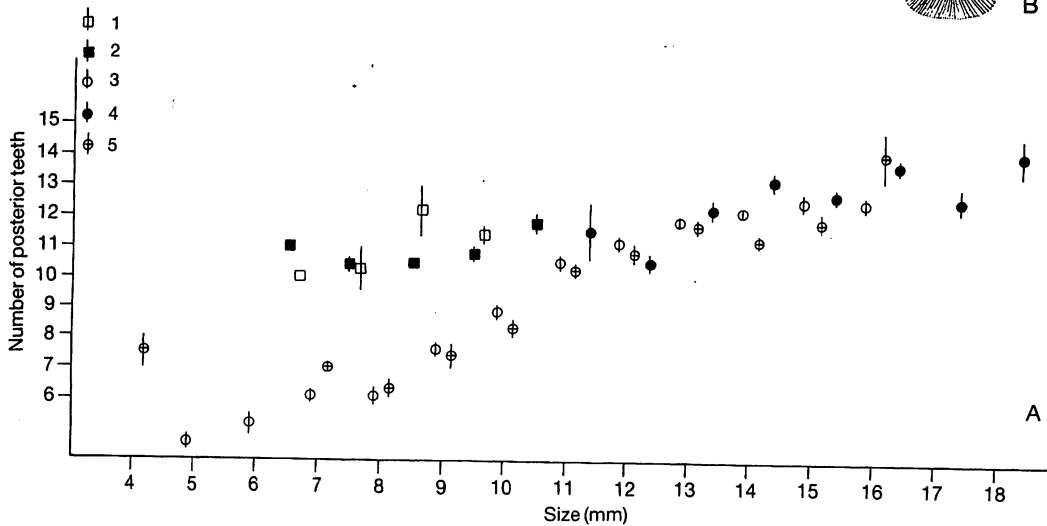


Fig. 9.8 (A) Relation between size in mm (x-axis) and number of posterior teeth (y-axis) in *Sagitta tasmanica* from the north-west Atlantic, (B) *Sagitta tasmanica* (*selkirki* form) from the north-west Atlantic Gulf Stream warm core ring. 1, *Sagitta tasmanica* (*selkirki*) from the south-east Pacific; 2, *Sagitta tasmanica* (*selkirki*) from the north-west Atlantic; 3, *Sagitta tasmanica* from the north-east Atlantic; 4, *Sagitta tasmanica* from the south-east Atlantic; 5, *Sagitta tasmanica* from the north-west Atlantic.



different groups of pelagic organisms shows a general correlation of distribution patterns with water masses, but the precise positions of the distribution boundaries show a gradual change from less tolerant to more tolerant taxa (Van der Spoel and Heyman 1983). Both horizontal and vertical distributions of different species seem to be spatially separated. Figure 9.9 shows the horizontal and vertical distribution of 21 species in the southern Indian Ocean. It is clear that, although there is considerable overlap, the main distribution of each species is different from that of the others (David

1963). The same is seen in the vertical distribution of 18 taxa in the North Atlantic, there is a spatial difference in the distribution of the taxa (Fig. 9.10) (Pierrot-Bults 1982).

The list of species discussed in this paper, along with their distributional ranges in the world oceans, is presented in Table 9.3. These species are chosen because they are considered to be representative of certain patterns of distribution. For a more complete list of chaetognath species see Chapter 11.

Types of distribution

The subtropical gyral regions within the ocean circulation system show the greatest stability in environmental parameters and in stratification of the water column.

Frost and Fleminger (1968) and Fleminger and Hulsemann (1973) recognized latitudinal patterns in the distribution of copepods. They found two main patterns; species occurring from 40°N–40°S and species occurring from 30°N–30°S. The first group showed monotypic species with a circumglobal distribution, the latter showed provincialism with different taxa in the Indo-Pacific and in the Atlantic. Pierrot-Bults (1976a)

compared chaetognath and other holoplanktonic distribution patterns. North–south and east–west discontinuities and ocean connections are important in determining the planktonic distribution patterns, of which latitudinal belt-shaped patterns are most dominant. Van der Spoel (1983) and Van der Spoel and Heyman (1983) divided pelagic distribution patterns further into belt-shaped and non-belt-shaped patterns.

In this paper the above patterns are compared with the distribution patterns of chaetognaths. The distribution maps are reconstructed after Tokioka (1952,

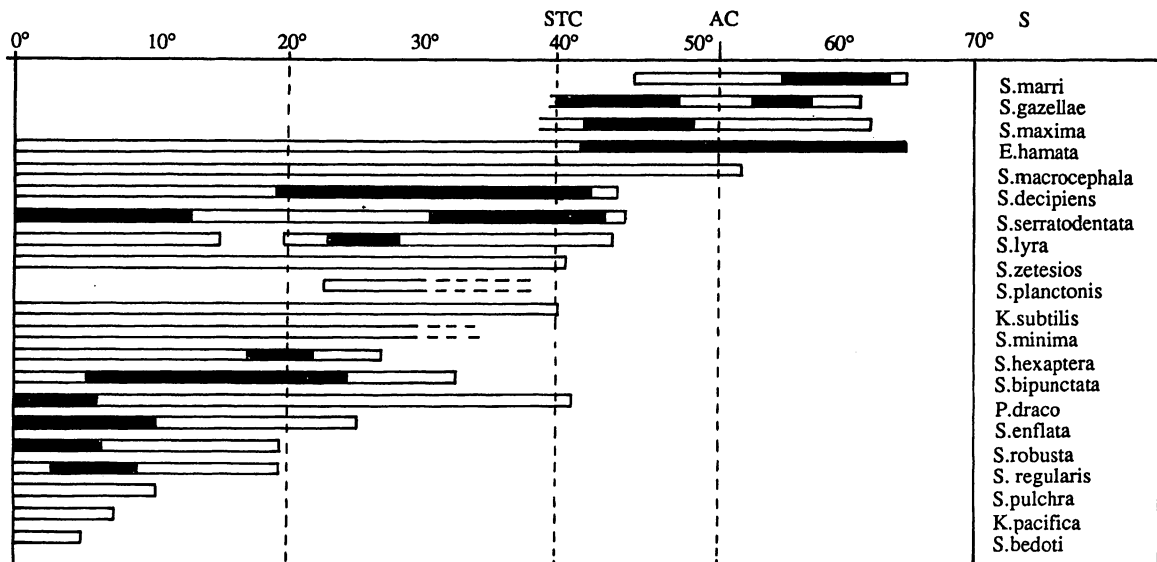


Fig. 9.9 Distribution of 21 chaetognath species in the Indian Ocean. AC = Atlantic convergence, STC = subtropical convergence, S = south. After David (1963).

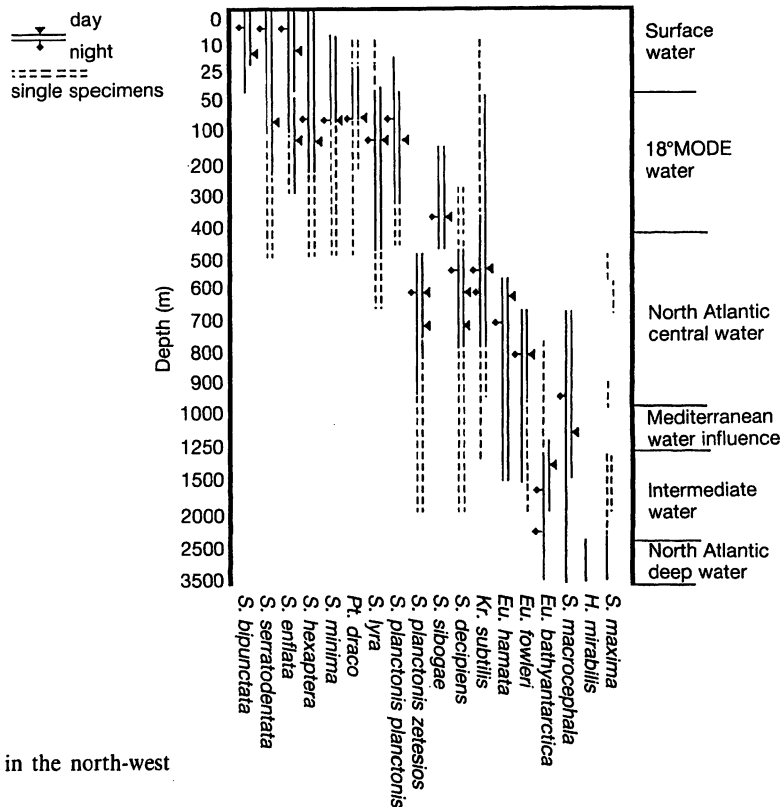


Fig. 9.10 Vertical distribution of 18 taxa in the north-west Atlantic. After Pierrot-Bults (1982).

1959, 1962, 1979); Hida (1957); Bieri (1959); Alvarinho (1964, 1969, 1974); Nair and Rao (1973); Pierrot-Bults (1974, 1975a, 1982); Nair (1978); Furnestin (1979); Rao (1979); and Boltovskoy (1981a).

Belt-shaped patterns

Belt-shaped patterns follow the latitudinal or climatological belts and can be divided into wide ranges, and warm water and cold water distributions.

Wide ($\pm 70^{\circ}\text{N}$ – $\pm 65^{\circ}\text{S}$) ranges -(epipelagic/mesopelagic species)

There is no epipelagic chaetognath species with a very wide, belt-shaped distribution.

Mesopelagic species with a wide, belt-shaped distribution (*Eukrohnia hamata* (Fig. 9.5) and *Sagitta planctonis zetesios* (Figs. 9.3 and 9.4) show (sub)tropical submergence. *Sagitta planctonis zetesios* is replaced in the epipelagic and shallow-mesopelagic of the lower

(< 40°) latitudes by its close relative *S. planctonis planctonis* Steinhaus, 1896 (Pierrot-Bults 1975a). Recently, a bathypelagic species belonging to this group has been found in the Atlantic (Chidgey, personal communication). *Eukrohnia fowleri* Ritter-Záhony, 1909 is a mesopelagic species without submergence. Because of competition, its vertical distribution might be influenced by the distribution of *E. hamata* (Pierrot-Bults 1982). In the northern Indian Ocean (north of 20°S) *E. fowleri* dominates the bathypelagic realm but it is replaced by *E. hamata* in subtropical waters (Nair 1978).

Warm water ($\pm 40^{\circ}\text{N}$ – $\pm 40^{\circ}\text{S}$) ranges (epipelagic/mesopelagic species)

Many epipelagic chaetognaths show a tropical–subtropical range (from 40°N – 40°S) broad enough to enable the species to have a circumglobal distribution and maintain gene flow around South Africa (Fleminger and Hulsemann 1973; Pierrot-Bults 1976a). Examples

Table 9.3 List of species and their distribution in the oceans (species of very restricted distribution excluded)

	Species	Ocean		
		Pacific	Indian	Atlantic
Surface water				
8°MODE water	Neritic			
	<i>S. bombayensis</i>		x	
	<i>S. crassa</i> f. <i>crassa</i>	x		
	<i>S. crassa</i> f. <i>naikaiensis</i>	x		
	<i>S. crassa</i> f. <i>tumida</i>	x		
	<i>S. bedotii</i> f. <i>litoralis</i>	x		
North Atlantic central water	<i>S. johorensis</i>	x		
	<i>S. demipenna</i>	x		
	<i>S. tropica</i>	x	x	
	<i>S. oceania</i>	x	x	
Mediterranean water influence	<i>S. pulchra</i>	x	x	
	<i>S. tenuis</i>	x	x	x
	<i>S. friderici</i>	x		x
Intermediate water	<i>S. hispida</i>			x
	<i>S. helenae</i>			x
North Atlantic deep water	<i>S. setosa</i>			x
	Epipelagic			
	<i>S. bedotii</i> f. <i>bedotii</i>	x	x	
	<i>S. bedotii</i> f. <i>minor</i>	x	x	
	<i>S. ferox</i>	x	x	
	<i>S. neglecta</i>	x	x	
	<i>S. regularis</i>	x	x	
	<i>S. robusta</i>	x	x	
	<i>S. pacifica</i>	x	x	
	<i>S. pseudoserratodentata</i>	x		
	<i>S. serratodentata serratodentata</i>		x	x
	<i>S. serratodentata atlantica</i>	x		
	<i>S. tasmanica</i>	x	x	x
	<i>S. bierii</i>	x		x
planctonis (1975a).	<i>S. bipunctata</i>	x	x	x
g to this	<i>S. minima</i>	x	x	x
lgey, per-	<i>S. enflata</i>	x	x	x
i Ritter-	<i>Pt. draco</i>	x	x	x
without	Mesopelagic/*cold water			
ritical dis-	<i>S. lyra</i>	x	x	x
tion of E.	<i>S. hexaptera</i>	x	x	x
rn Indian	<i>S. decipiens</i>	x	x	x
he bathy-	<i>S. sibogae</i>	x	x	x
amata in	<i>S. planctonis</i> f. <i>planctonis</i>	x	x	x
	<i>S. planctonis</i> f. <i>zetesios</i>	x	x	x
	<i>K. pacifica</i>	x	x	x
	<i>K. subtilis</i>	x	x	x
	<i>K. mutabbii</i>			x
	<i>E. hamata</i>	x	x	x
	<i>E. fowleri</i>	x	x	x
c/	* <i>S. gazellae</i>	x	x	x
	* <i>S. marri</i>	x	x	x
subtrop-	Bathypelagic			
o enable	<i>S. maxima</i>	x	x	x
ion and	<i>S. macrocephala</i>	x	x	x
eminger	<i>E. bathypelagica</i>	x	x	x
xamples	<i>E. bathyantartica</i>	x	x	x
	<i>H. mirabilis</i>	x	x	x

of this type of distribution are *Pterosagitta draco* (Krohn, 1853), (Fig. 9.11), *S. minima* (Grassi, 1881) and *S. enflata* (Grassi, 1883). Whether the monotypy in these species is due to gene flow or is a result of homeostasis is not known. The possibility exists that future research on the different populations of wide-spread so-called monotypic species will reveal different taxa (Pierrot-Bults 1976a; Gibbs 1986). *Sagitta bipunctata* Quoy and Gaimard, 1827 is a species with a circumglobal 40°N–40°S distribution. It is most abundant in the central water masses, is abundant in the tropical belt of the Indian Ocean (Nair 1977), and is rare or absent in the tropics in the Pacific (Bieri 1959). Casanova and Andreu (1989) did not find it abundant in the tropical Indian Ocean and the abundance pattern in the Atlantic is not clear; it might show the same pattern as the pteropod *Limacina lesueuri* (d'Orbigny, 1938) (Fig. 9.12). *Sagitta lyra* (Krohn, 1853, *S. hexaptera* (d'Orbigny, 1851), *S. sibogae* (Fowler, 1906), non-*S. decipiens*, (Pierrot-Bults, 1979), and *Krohnitta subtilis* (Grassi, 1881) are examples of shallow, mesopelagic belt-shaped distributions. *Sagitta decipiens* Fowler, 1905 is a shallow to deep mesopelagic species with a latitudinal wide distribution. Unfortunately, most authors treat *S. sibogae* and *S. decipiens* as one species and so it is difficult to tell the exact distribution of either. Tokioka (1959) described *S. neodecipiens* (= *S. decipiens*) from the North Pacific Equapac and Shellback expeditions in samples from 400 m to the surface.

The two representatives of the *S. serratodentata* group, *S. serratodentata serratodentata* Krohn, 1853 and *S. pacifica* Tokioka, 1940, have a 40°N–40°S distribution, but they show the non-circumglobal tropical pattern as discussed below (Pierrot-Bults 1974) (Fig. 9.13).

Warm water ($\pm 30^{\circ}\text{N}$ – $\pm 30^{\circ}\text{S}$) ranges

The species with a restricted tropical range cannot maintain gene flow because the land masses act as physical barriers. According to Fleminger and Hulsemann (1973) this category is characterized by non-circumglobal distributions and different close relatives in the different oceans, usually an Indo-Pacific and an Atlantic species. An exception to this is the epipelagic–shallow mesopelagic *Krohnitta pacifica* (Aida, 1897) (Fig. 9.14) which shows no recognizable differences between the Atlantic and the Indo-Pacific populations, although it might consist of two different species as proposed by Alvaríño (1969) who described the Atlantic populations as *Kr. mutabii*.

Cold water ranges

Chaetognath species occurring at latitudes higher than 40°S are usually circumantarctic. Such is the case for *Sagitta tasmanica*, *S. gazellae* Ritter-Záhony 1909, *S. maxima* Conant, 1896, and *S. marri* (David 1956) (Fig. 9.15).

More provincialism is seen in the northern temperate zone. *S. tasmanica* occurs in the North Atlantic but not in the North Pacific. *S. elegans* Verrill, 1873 occurs in both oceans (Fig. 9.16). It shows infraspecific variation, with different subspecies in the Arctic (*S. elegans arctica* Aurivillius, 1896) in the subarctic (*S. elegans elegans*) and in the Baltic (*S. elegans baltica* Ritter-Záhony, 1911). Whether the northern and southern hemisphere populations of *S. tasmanica* belong to the same species or not is still an unsolved question (See Fig. 9.15). *S. maxima* has a cold water distribution. It shows tropical submergence but a deep tropical connection between the northern and the southern hemisphere populations has not been found. Differences between the northern and southern populations have been mentioned (David 1963; Pierrot-Bults 1976a) and Bieri (personal communication) proposes a different species for the Antarctic populations.

Patterns derived from belt-shaped patterns

Central water patterns

The only chaetognath species confined to central waters is *S. pseudoserratodentata* Tokioka, 1939 which is found in the North Pacific central water mass (Bieri 1959).

A species with a circumglobal 40°N–40°S distribution, but most abundant in the central water masses of the Pacific and rare or absent in the tropics is *S. bipunctata* (Bieri 1959). In the Indian Ocean it is distributed in the tropics (Nair 1977) but David (1963) records it more abundant from 5–25°S than from the equatorial region. There are no records for abundance in the Atlantic; it might exhibit a distribution pattern similar to that shown in Figure 9.12.

According to Beklemishev (1981) the Pacific equatorial and central waters differ more from each other than is the case in the other oceans, so a more even distribution in the Indian and Atlantic Oceans could be expected. However, the pattern of *S. bipunctata* does not conform with the patterns of other planktonic species, such as the euphausiid *Stylocheiron suhmi* G. O. Sars, 1883, which does not extend into the northern Indian Ocean (Van der Spoel and Pierrot-Bults 1979a; Beklemishev 1981; Van der Spoel and Heyman 1983).

Interocean connections

Interocean connections are possible for cold water species in the Arctic. *S. elegans* and *E. hamata* are distributed in both the North Pacific and the North Atlantic. In the southern hemisphere the cold water and subtropical distributions are circumglobal. The neritic species *S. friderici* Ritter-Záhony, 1911 is distributed in the east Pacific and east Atlantic, including the Mediterranean and is sparsely distributed in the Gulf of Mexico (Fig. 9.17). *S. tenuis* Conant, 1896 shows the same distribution but has a greater representation in the Gulf of Mexico and a narrower distribution in the east Pacific (Fig. 9.18) (Tokioka 1979). This pattern possibly reflects the Panama connection, present until 3.5 mya. Tokioka (1979) records that *S. tenuis* inhabits warmer and more saline water than *S. friderici* and states that *S. tenuis* is the inlet water form of *S. friderici*, but most authors treat both species as valid species. Alvariño (1961) considers the east Pacific populations of *S. friderici* to be a different species, *S. euneritica*.

The exchange between the Indian and the Pacific Ocean through the Indo-Malayan archipelago is predominantly from the Pacific towards the Indian Ocean (Gordon 1986). In the Banda Sea, strong and deep vertical mixing occurs, causing vertical displacement of organisms (Van der Spoel and Schalk 1988), thus creating dispersal possibilities for deeper-living organisms to reach the Indian Ocean. Most (distant) neritic tropical species are distributed in the Indo-Pacific.

Species which occur both in the Red Sea and in the Mediterranean are usually cosmopolitan (Furnestin 1979). *S. neglecta* Aida, 1897 is an example of an Indo-Pacific species which might have reached the Mediterranean through the Suez Canal. It is only recorded in the south-east Mediterranean (Furnestin 1979).

Non-belt-shaped patterns

Oceanic species

Sagitta bierii Alvariño, 1961, in the east tropical Pacific Ocean, has a restricted distribution related to oxygen-poor water (Bieri 1959). Specimens probably belonging to *S. bierii* were found in waters off West Africa, so it is possible that this species is found in both the east Pacific and east Atlantic waters (Ducret 1968; Pierrot-Bults 1974).

S. pseudoserratodentata is another example. It is

distributed in the north Pacific central water (Bieri 1959) and was recently recorded by Andreu *et al.* (1989) in the south-west Indian Ocean. *S. serratodentata atlantica* Thomson, 1947 is distributed in the south Pacific transitional water. It is not yet clear whether there is a connection with the Atlantic *S. serratodentata serratodentata* populations through the south Indian Ocean, although a connection is mentioned by Alvariño (1974) (See Fig. 9.13).

S. ferox Doncaster, 1902, *S. robusta* Doncaster, 1902, and *S. regularis* Aida, 1897 are endemic Indo-Pacific species (Bieri 1959; Nair and Rao 1973; Nair 1978). They have no close relatives in the tropical Atlantic (Fig. 9.19).

S. scrippsae Alvariño, 1962 has a north-east Pacific distribution. It is a member of the *S. maxima* group and is most closely related to, or a synonym of, *S. lyra*. The latter species shows a circumglobal 40°N–40°S distribution (Alvariño 1962a, 1969).

Neritic species

Each oceanic coast has, in principle, its own neritic fauna. The patterns can be divided roughly into a warm water neritic pattern (from 50°N–40°S) and a cold water neritic pattern (at latitudes higher than 30°) and show latitudinal zonation. The neritic zonation of the world oceans is shown in Figure 9.20 (Van der Spoel and Heyman 1983). The chaetognath neritic distribution patterns are all warm water patterns.

Neritic species have a more restricted distribution than the oceanic ones. It is to be expected that the separated populations show genetic and taxonomic differences because of the more restricted means of contact between neritic regions. For example, differences have been described between the North Sea and the Oosterscheldt populations of *S. setosa*, the populations described as *S. batava* Biersteker and Van der Spoel, 1966, and also between North Sea and Mediterranean *S. setosa* populations (Furnestin 1979). It is also thought that the Black Sea species *S. euxina* might be conspecific with *S. setosa*, as might *S. bedoti bedoti* Beraneck, 1895 and *S. bedoti minor* Tokioka, 1942, which are distant neritic forms, and *S. bedoti f. littoralis* Tokioka and Pathansali, 1965, which is the inlet water form (Tokioka 1979) (Fig. 9.21). The neritic *S. crassa* shows several inlet water forms from different parts of its range, for example, *S. crassa f. crassa* Tokioka, 1938, *S. crassa f. naikaiensis* Tokioka, 1939 and *S. crassa f. tumida* Tokioka, 1939, (Tokioka 1979). It is to be expected that, with more research into infraspecific

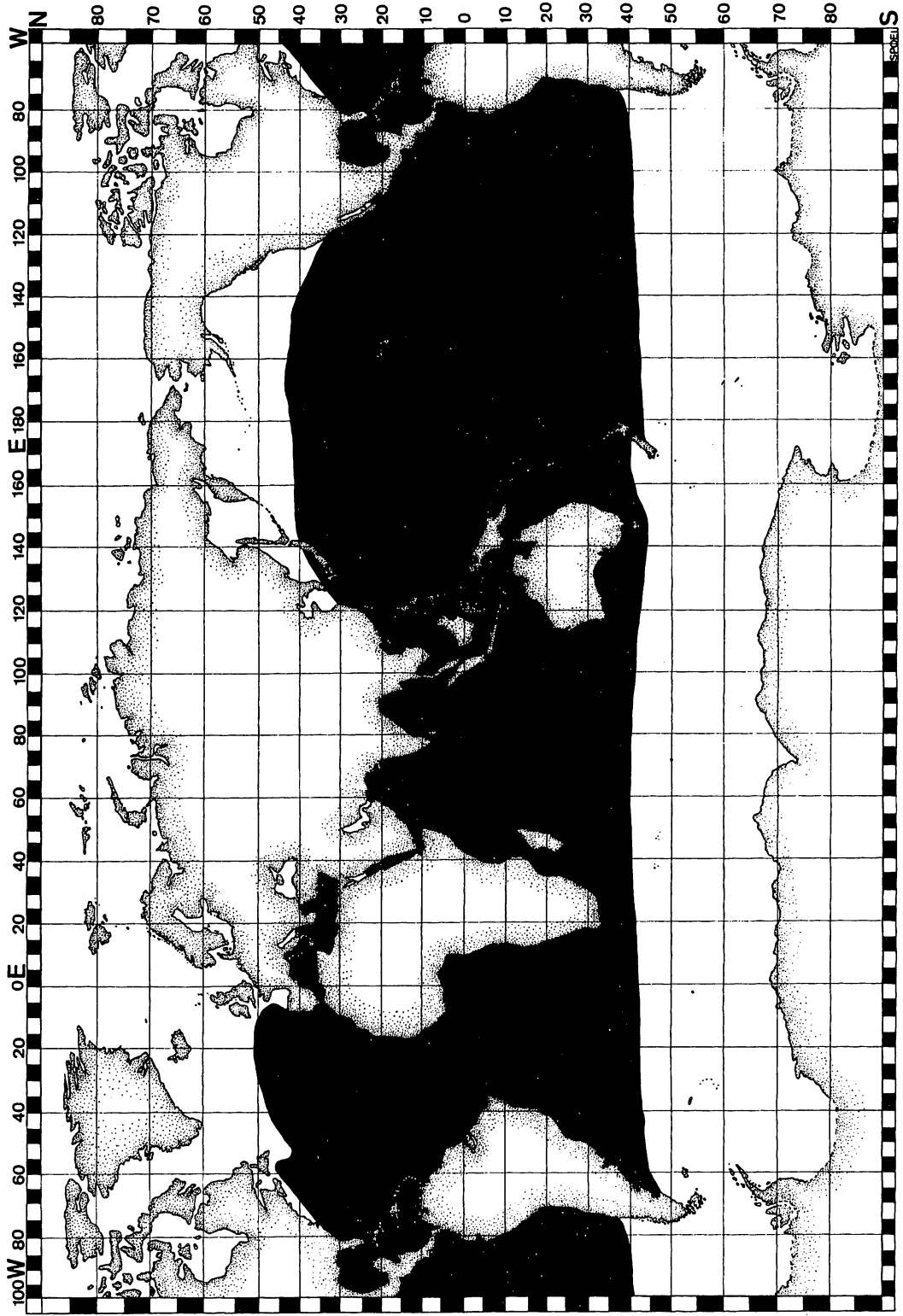


Fig. 9.11 Distribution of *Pterogorgia draco*.

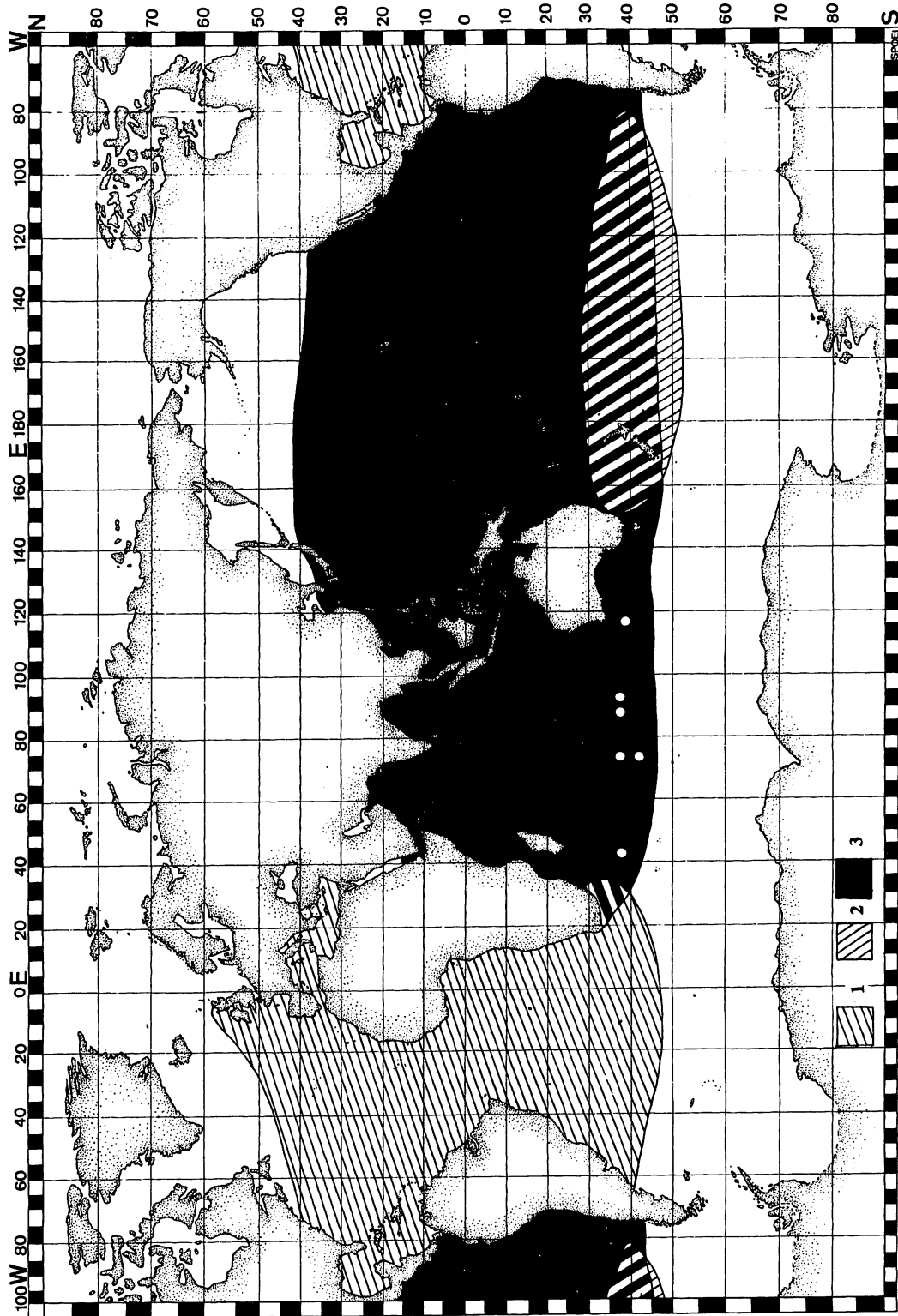


Fig. 9.13 Distribution of 1, *Sagitta serratodentata serratodentata*; 2, *S. serratodentata atlantica*; 3, *S. pacifica*. White dots in the South Indian Ocean represents *S. serratodentata* according to Alvarino (1972).

FIG. 7.15 Distribution of 1, *Sagitta serratodentata serratodentata*; 2, *S. serratodentata atlantica*; 3, *S. pacifica*. White dots in the South Indian Ocean represents *S. serratodentata* according to Alvarino (1972).

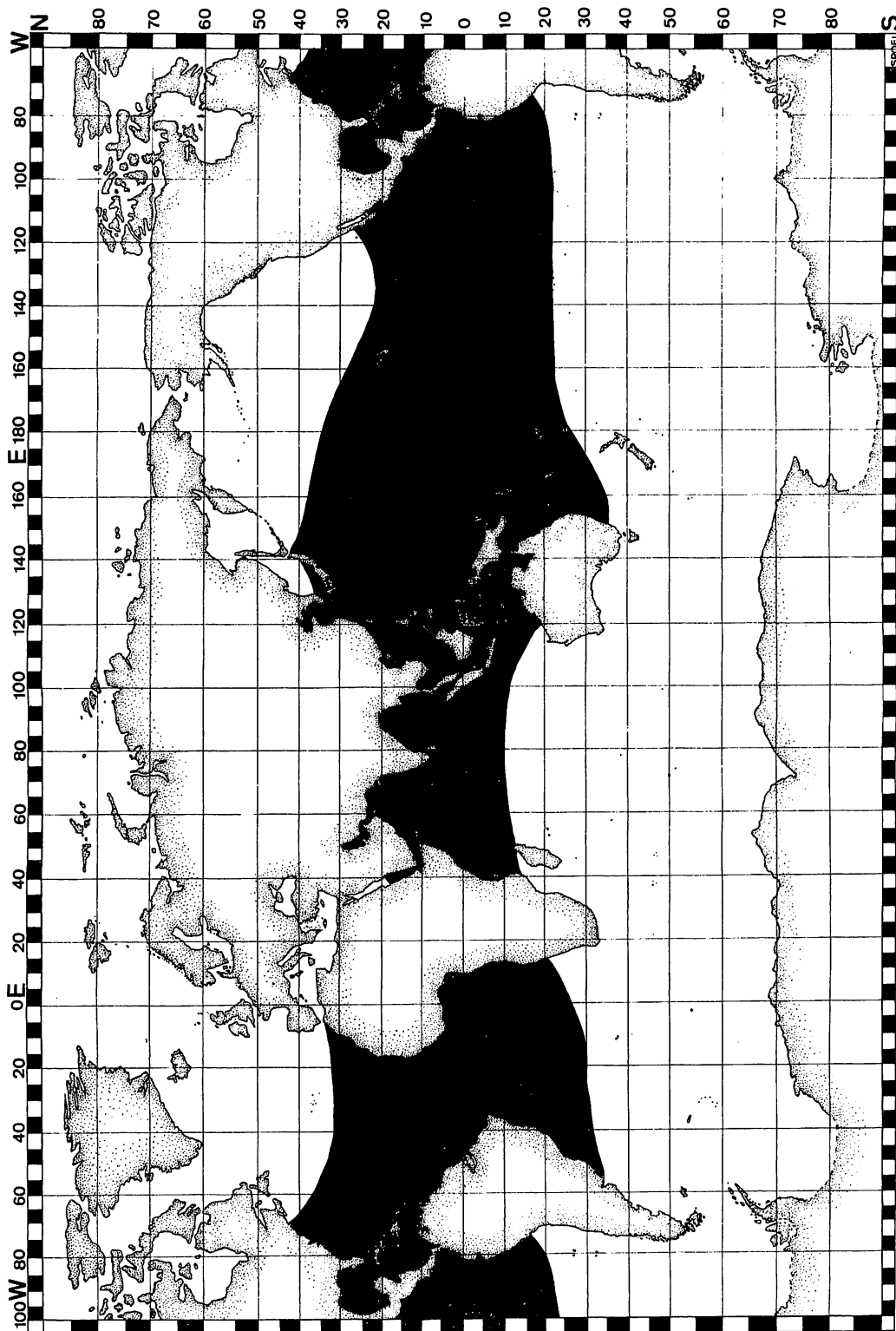


Fig. 9.14 Distribution of *Krohnia pacifica*.

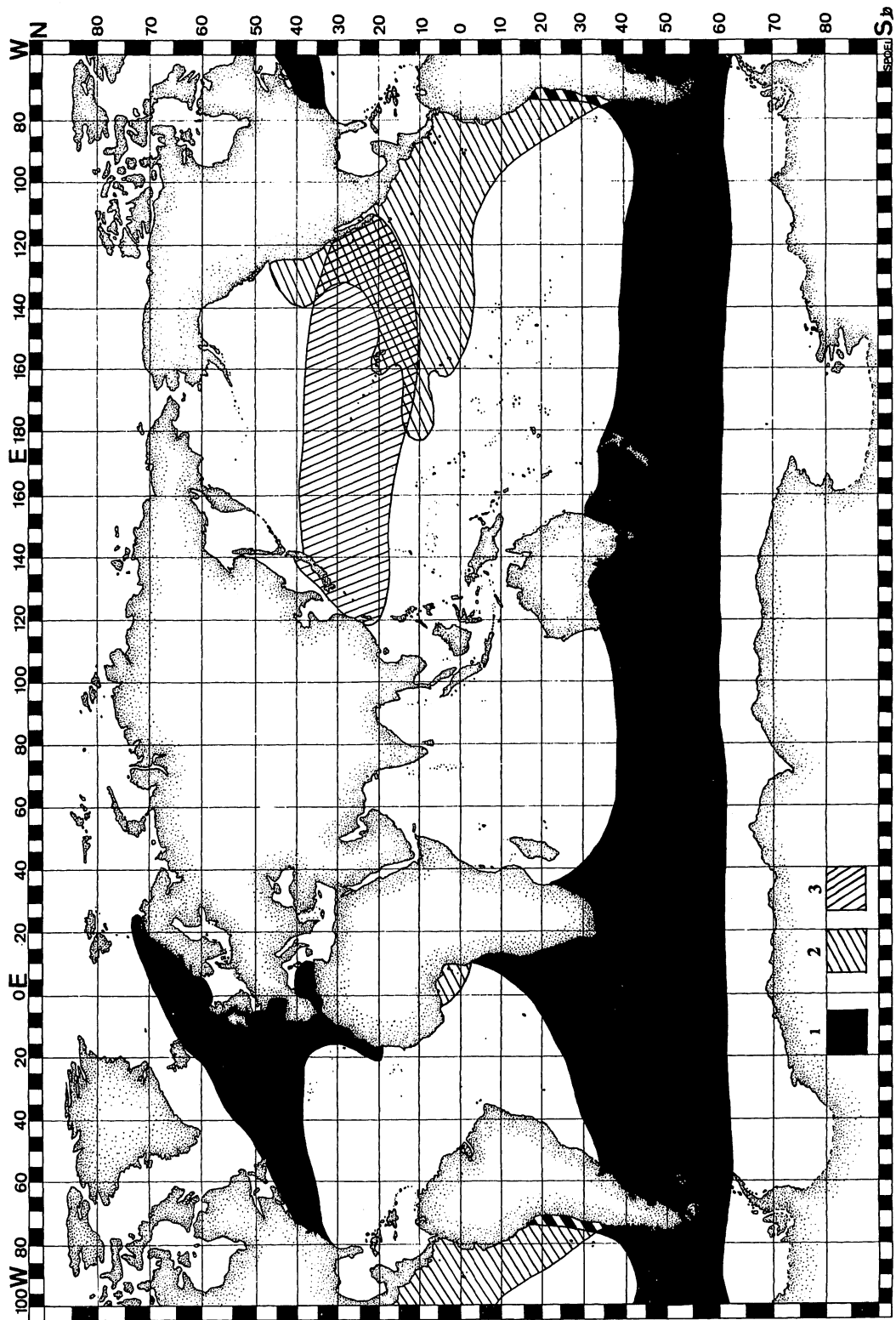


Fig. 9.15 Distribution of 1, *Sagitta tasmanica*; 2, *S. bierii*; 3, *S. pseudoserratodentata*.

Fig. 9.15 Distribution of 1, *Sagitta tasmanica*; 2, *S. bieri*; 3, *S. pseudoserratodentata*.

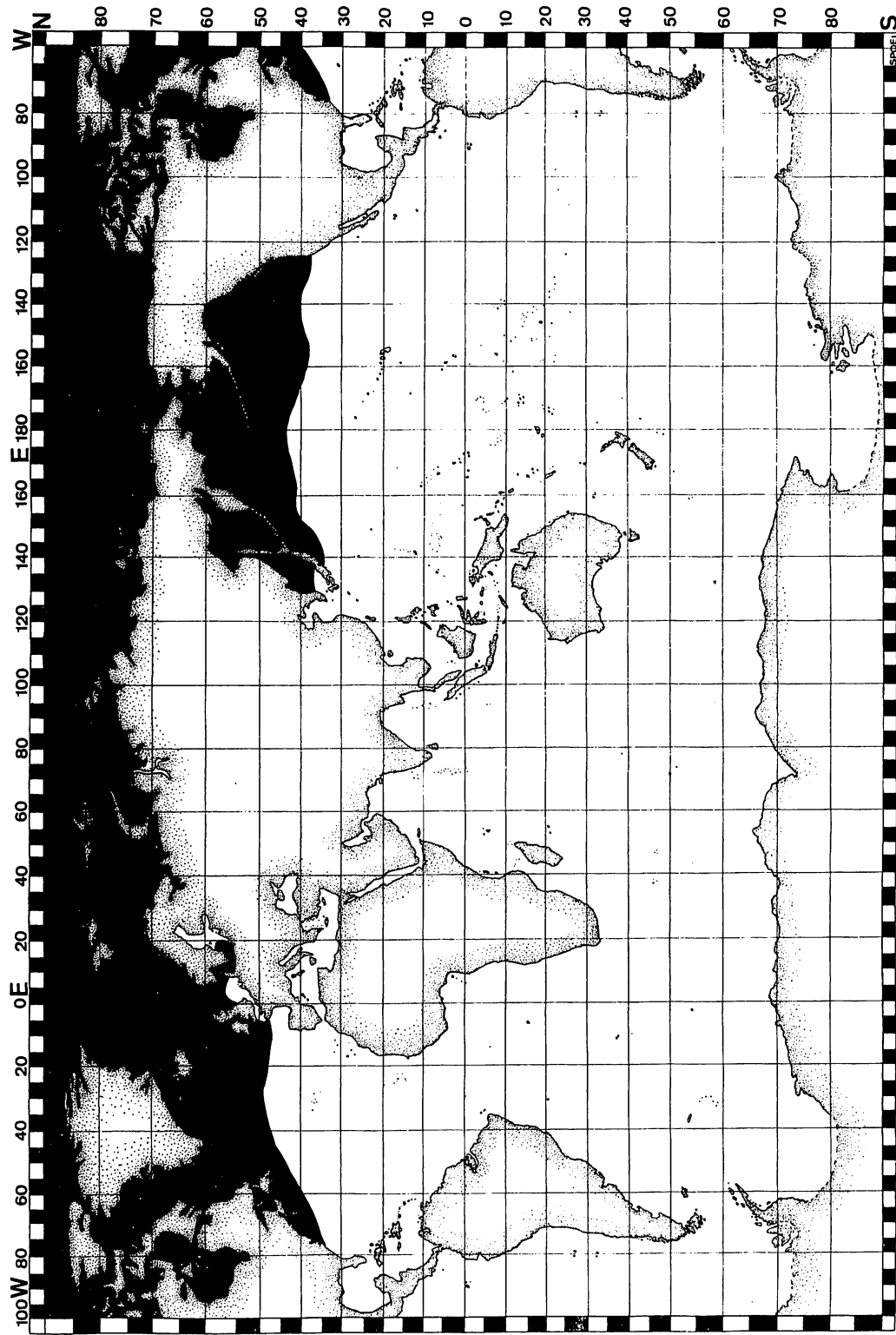


Fig. 9.16 Distribution of *Sagitta elegans*.

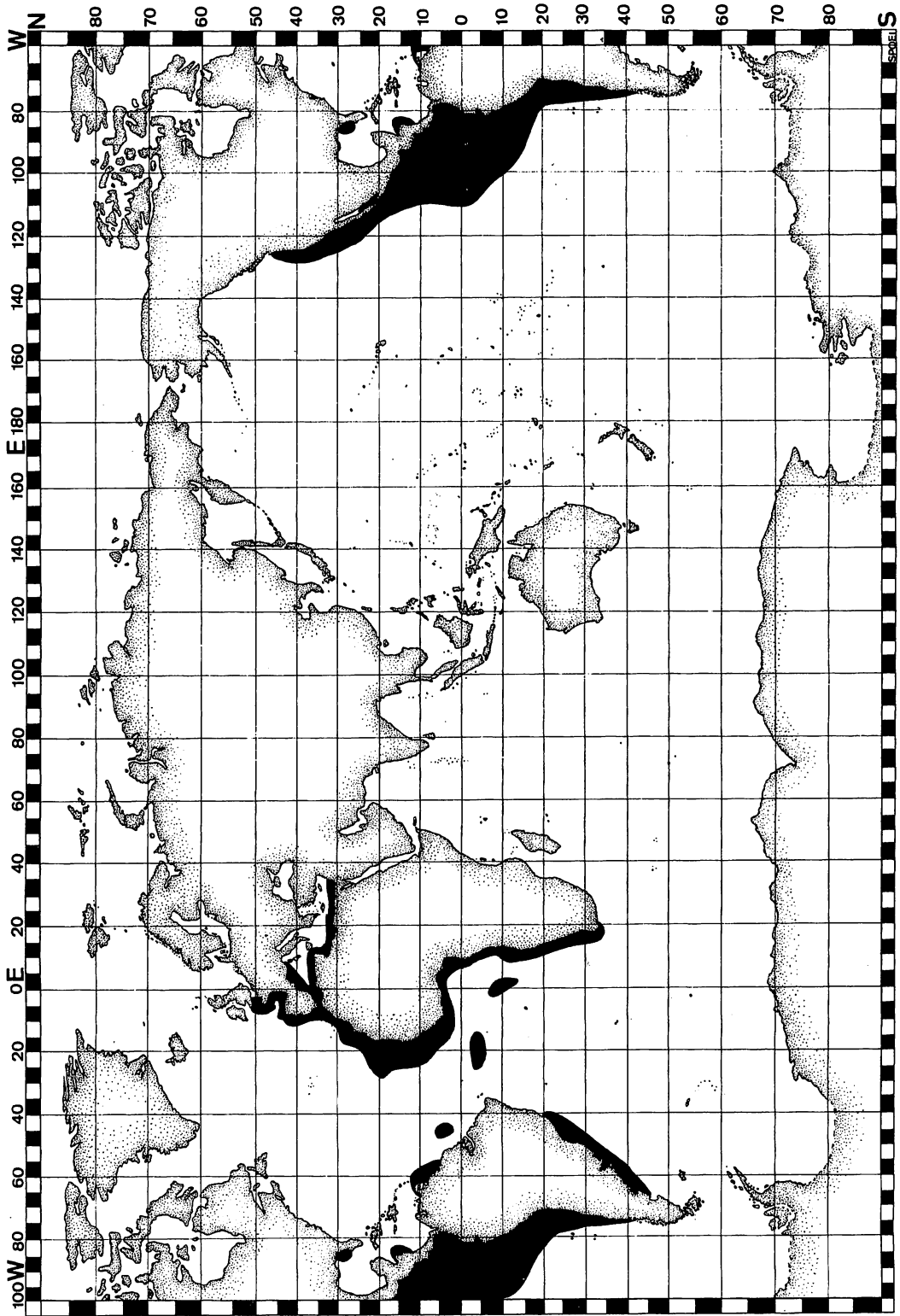


Fig. 9.17 Distribution of *Sagitta friderici*.

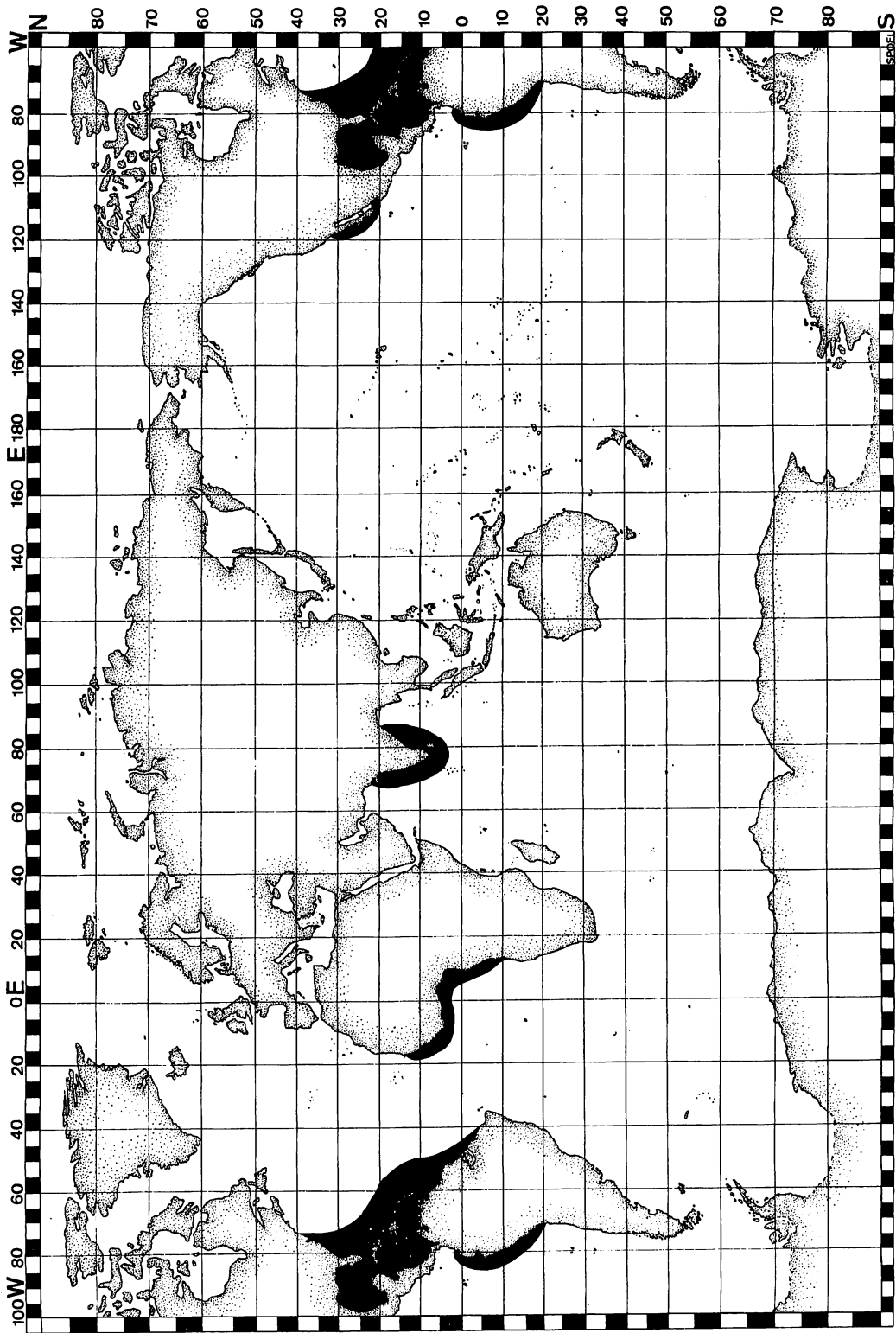


Fig. 9.18 Distribution of *Sagitta tenuis*.

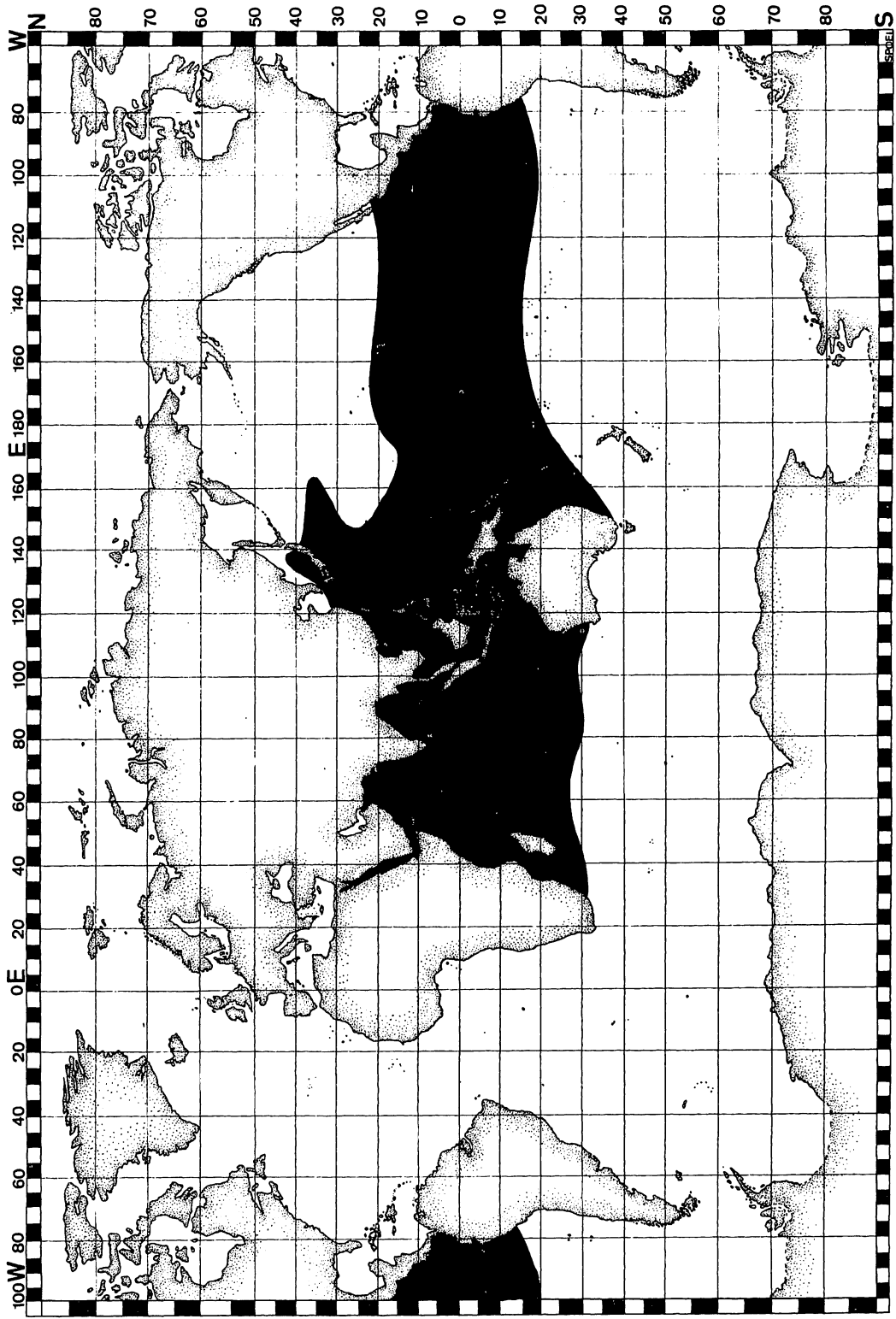


Fig. 9.19 Distribution of *Sagitta regularis*.

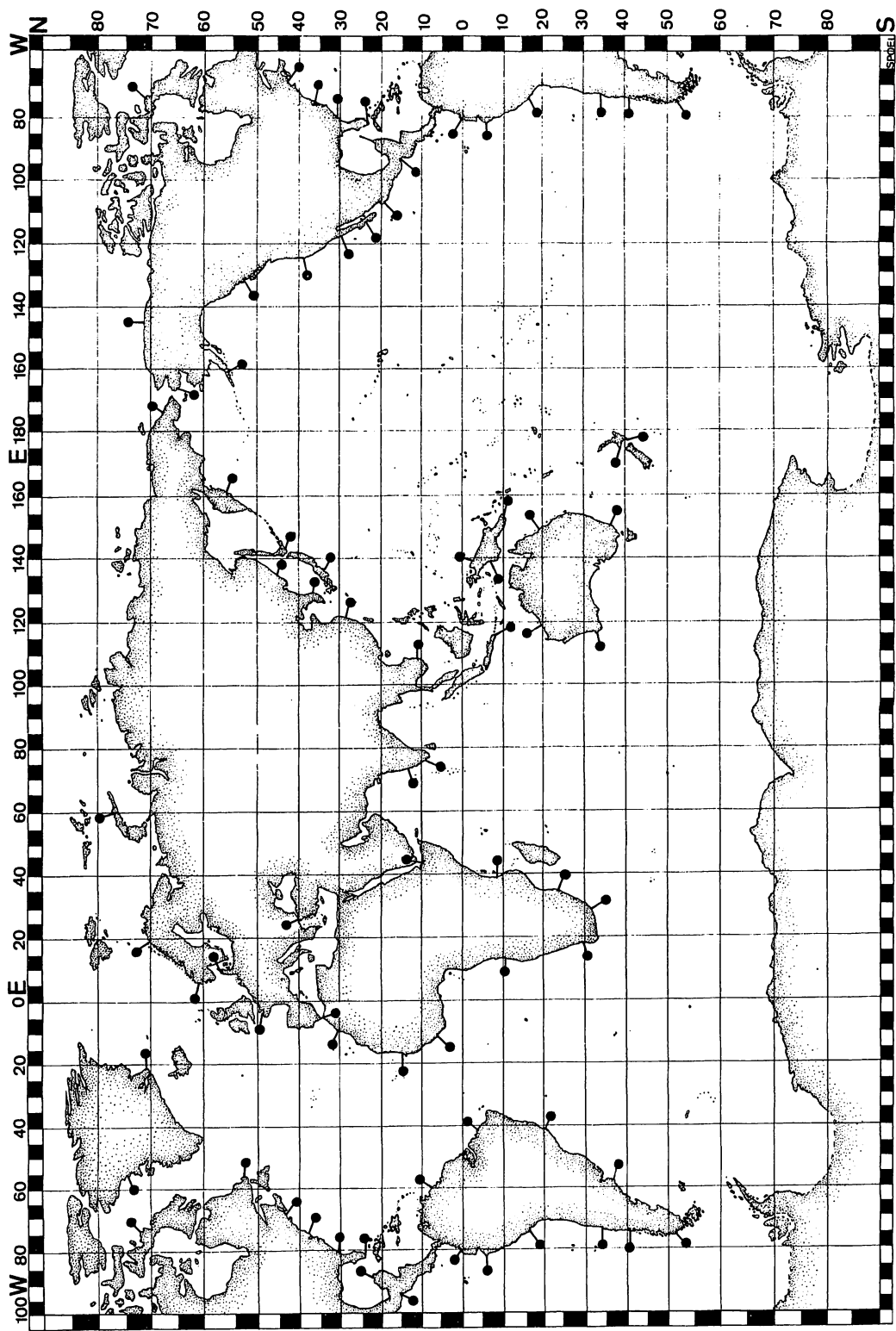


Fig. 9.20 The neritic zonation of the world oceans. After Van der Spoel and Heyman (1983).

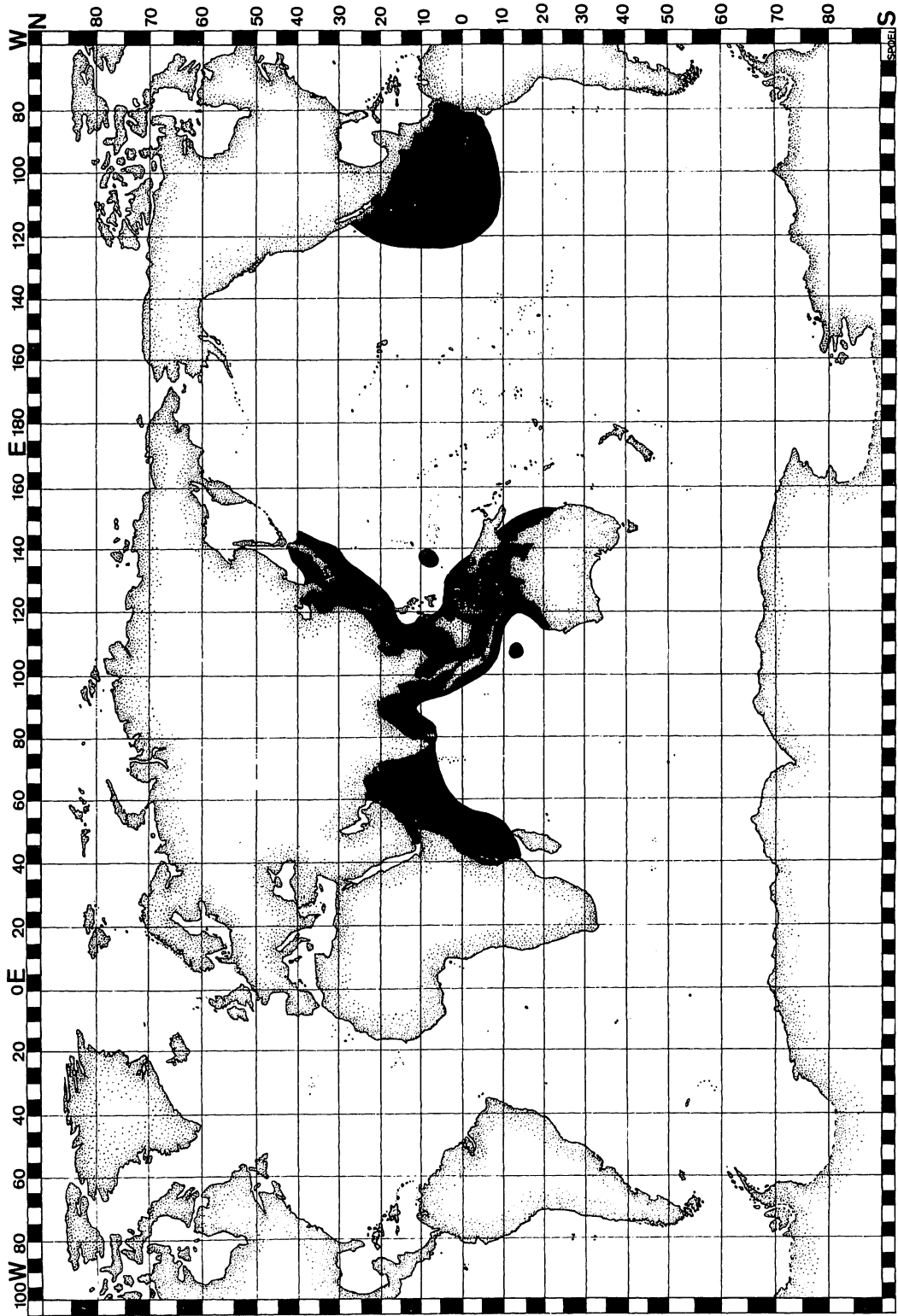


Fig. 9.21 Distribution of *Sagitta bedoti*.

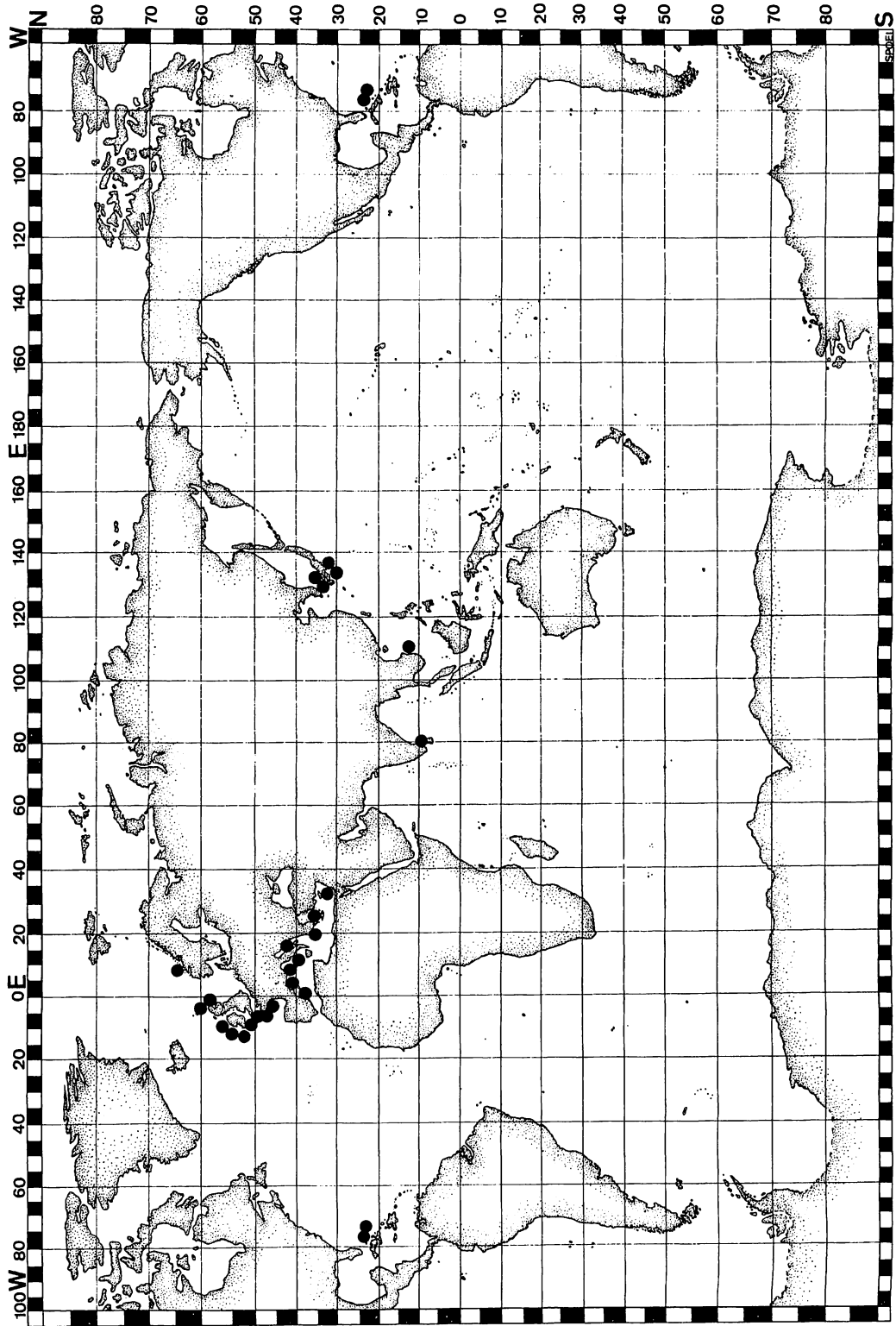


Fig. 9.22 Distribution of *Spadella cephaloptera*.

variation differences between populations in different regions, other neritic species will be found. The Spadellidae are dealt with under benthic patterns.

Warm water patterns

The greatest diversity, especially in neritic species, is seen in the Indo-Malayan region (Tokioka 1959, 1962, 1965b; Reid *et al.* 1978). *S. bedoti* is found in the Indian Ocean, the west Pacific, and the east Pacific (Fig. 9.21). The populations on both sides of the Pacific are isolated by distance and it would be interesting to look for infra-specific differences between these populations. The same applies for the west and east Atlantic populations and for those *S. tenuis* populations of the west Atlantic and east Pacific (see Fig. 9.18). The first two have a distance barrier and the last two the Panama isthmus barrier.

Tokioka (1979) discusses neritic taxa from the Indo-West Pacific—*S. bedoti litoralis*, *S. bedfordii* Doncaster, 1902, *S. crassa*, *S. crassa* f. *naikaiensis*, *S. crassa* f. *tumida*, *S. delicata* Tokioka, 1939, *S. johorensis* Pathansali and Tokioka, 1963 and *S. demipenna* Tokioka and Pathansali, 1963. They all can be considered inlet water forms from bays and lagoons. *S. bombayensis* Lele and Gae, 1936 is an endemic species confined to the near-shore waters of Bombay (Nair 1974).

S. oceania Gray 1930 and *S. tropica* Tokioka, 1942 occur in inlet waters of islands in the Pacific and estuarine zones of India (Nair 1974). *S. bedoti* f. *bedoti* and *S. bedoti* f. *minor* are taxa of the open neritic waters. In general the specimens from inlet waters are much smaller than those from the open neritic waters. This phenomenon is seen in the cold water species *S. elegans* and in the warm water species *S. bedoti*.

S. neglecta is a neritic/distant neritic species of the tropical Indo-Pacific. *S. hispida* Conant, 1896 is distributed in the north and central west Atlantic.

Benthic patterns

The only benthic species which is recorded frequently is *Spadella cephaloptera* Busch, 1851, (Fig. 9.22). There is doubt whether the Atlantic and Pacific populations of *S. cephaloptera* are really conspecific or whether they belong to other species (Bieri, personal communication). The distribution of the other spadellidae is not sufficiently known to speculate about their distribution pattern. The hypothesis is that they will fall into

the neritic patterns following a latitudinal succession, as shown in Figure 9.20.

Rarely recorded species

There have been descriptions of a number of species whose taxonomic position and distribution is not yet clear because of the scarcity of samples. Casanova (1985a) described the epipelagic *Sagitta erythraea* from the Red Sea and (1985b) the two mesopelagic species *S. lucida* and *S. adenensis* from the north-west Indian Ocean. From the tropical west Atlantic between 0°–8°S Casanova (1986c) described *Eukrohnia macroneura* and *E. flaccicoeca* from a depth of more than 300 m. Marumo and Kitou (1966) described the bathypelagic *Heterokrohnia bathybia* from the western North Pacific and Dawson (1968) described *H. involucrum* from the Arctic basin. *H. curvichaeta*, *H. davidi*, *H. heterodonta*, and *H. murina* from the north Atlantic have been described by Casanova (1986a) and Casanova and Chidgey (1987) described *H. furnestinae*. From the Antarctic *H. fragilis* and *H. longidentata* have been described by Kapp and Hagen (1985) and Hagen and Kapp (1986) described *H. longicaudata*, also from the Antarctic.

Casanova (1986b) described a new genus and species, *Archeterokrohnia rubra*, from the North Atlantic and another species *A. palpifera*, from the Mediterranean (Casanova (1986e). According to Kapp (1991a) *Archeterokrohnia* is synonymous with *Heterokrohnia*.

Species groups

Several species groups are recognized within the chaetognaths, for example the *S. maxima* group, the *S. planctonis* group, and the *S. serratodentata* group.

The *S. planctonis* group consists of *S. planctonis planctonis*, which has a shallow mesopelagic distribution; *S. planctonis zetesios*, which has a deep mesopelagic distribution from 40°N–40°S and an epipelagic/mesopelagic distribution in higher latitudes; and *S. marri*, which is endemic in the Antarctic (see Figs. 9.3 and 9.4), although there is doubt about the taxonomic position of this last species (see Conclusions).

Nearly the same pattern of distribution is shown by the members of the *S. maxima* group (*S. maxima*, *S. lyra*, *S. gazellae* and *S. scrippsae*). *S. maxima* is distributed at high latitudes. It shows submergence but a deep tropical connection has not been found, the antarctic populations might be a different taxon (David 1963;

Bieri, personal communication). *S. lyra* shows a shallow mesopelagic distribution from 40°N–40°S. The endemic Antarctic species is *S. gazellae*. There is an endemic Pacific species described for the north-east Pacific, *S. scrippsae*, but this taxon might be conspecific with *S. lyra*.

The *S. serratodonta* group consists of *S. serratodonta serratodonta* and *S. pacifica*, which had a 40°N–40°S distribution in the Atlantic and Pacific respectively. *S. serratodonta atlantica* has a south Pacific transitional water distribution, *S. pseudoserratodonta* a north

Pacific central water distribution, *S. tasmanica* a north Atlantic cold water and circumglobal subantarctic distribution, and *S. bierii* a tropical east Pacific and east Atlantic distribution (See Fig. 9.15).

The distribution of members of a species group fall within the patterns of restricted distributed species. There is little overlap in distributions within a group. In the opinion of some scientists these species groups are of generic level (Tokioaka 1965a; see also Chapter 11).

Conclusions

The same basic distribution patterns (belt-shaped, distant neritic, etc.) are found in different plankton groups, with a minority not distributed like the rest (Johnson and Brinton 1963; Brinton 1962; Fleminger and Hulsemann 1973; Pierrot-Bults 1976a; Van der Spoel and Pierrot-Bults 1979a; Beklemishev 1981; Van der Spoel and Heyman 1983). These distribution patterns are not only reflected in species but also in infraspecific categories (Pierrot-Bults 1976a).

The epipelagic chaetognath fauna of the Atlantic shows little endemism. Only *Sagitta helenae*, *S. hispida* and *S. setosa*, all neritic species, are endemic for the Atlantic. *S. serratodonta serratodonta* is the only oceanic taxon restricted to the Atlantic, while *S. serratodonta atlantica* is confined to the south Pacific (Pierrot-Bults 1974). *S. bombayensis* an endemic species in the Indian Ocean, is also neritic. The Pacific shows the maximum number of endemic taxa, both neritic and oceanic.

Oceanic endemic taxa are *S. scrippsae*, *S. pseudoserratodonta* and *S. bierii*, although there is some doubt about the last two. The distribution of *S. bierii* may also extend to the east-Atlantic (Ducret 1968; Pierrot-Bults 1974) and *S. pseudoserratodonta* is also recorded from the north-west Indian Ocean (Andreu *et al.* 1989). *S. scrippsae* is a north-east Pacific taxon, which is thought to be conspecific with *S. lyra* by some authors (see Chapter 11). Neritic Pacific taxa are *S. delicata*, *S. crassa* f. *crassa*, *S. crassa* f. *naikaiensis*, *S. crassa*, f. *tumida*, *S. bedoti* f. *litoralis*, *S. johorensis* and *S. demipenna*.

Oceanic Indo-Pacific species are *S. robusta*, *S. neglecta*, *S. ferox*, *S. bedoti bedoti*, *S. bedoti minor*, *S. regularis* and *S. pacifica*. *S. pulchra* is a distant neritic Indo-Pacific species and *S. oecania* and *S. tropica* are

neritic species. Only endemics from the Antarctic are known for the epipelagic/mesopelagic taxa: *S. gazellae* and *S. marri*.

Most endemic species are (distant) neritic, while among oceanic species endemic species are subantarctic. This pattern was also found for other planktonic groups (Beklemishev 1981) (See Table 9.3).

The bathypelagic chaetognaths are thought to be widely distributed, although it is not clear if this is true for all bathypelagic species because of the scarcity of samples. *Sagitta macrocephala* is a cosmopolitan deep mesopelagic/bathypelagic species.

Eukrohnia bathyantarctica, *E. bathypelagica* and *Heterokrohnia mirabilis* are species with a circumglobal bathypelagic distribution. The very deep-living, abyssal benthoplanktonic species of *Heterokrohnia*, recently described for the North Atlantic and the Antarctic, might represent provincialism.

Relations of distribution patterns to the relative geological age of the water masses are difficult to ascertain. Following the formation of the different water masses in geological time, only the earliest possible moment for the development of certain taxa can be given.

Van der Spoel and Heyman (1983) put forward a hypothesis for the development of faunas (Fig. 9.23). Related to plate tectonics and the development of the ocean basins, it is postulated that the central water faunas are the oldest possible, while the cold water faunas and the deep sea faunas could only be developed later; cold water taxa are usually ancestral to deep water taxa. Warm water taxa split into equatorial, central water and general warm water taxa. The general warm water taxa can be distinguished as living in the 40°N–40°S belt and the 30°N–30°S belt. It is postu-

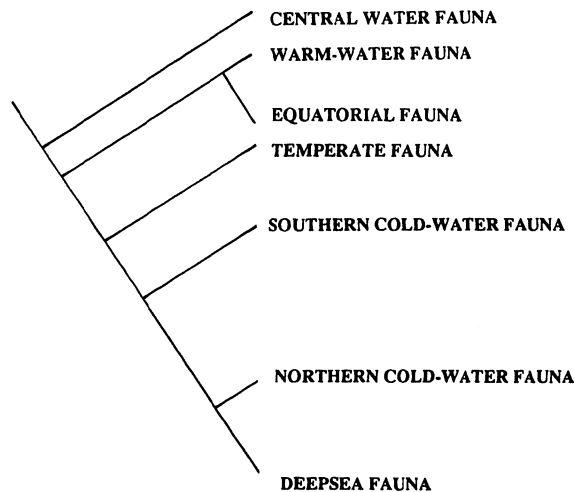


Fig. 9.23 Geocladogram of the major planktonic faunas. After Van der Spoel and Heyman (1983).

lated that the 30°N–30°S distributions developed out of the 40°N–40°S distributions in the Eocene–Oligocene, when global temperatures dropped. Some taxa show a limited east Pacific distribution and it is supposed that this pattern is more recent, judging by the taxonomic level of the endemics in this region (Van der Spoel and Heyman 1983).

It is expected that cold water and deep sea fauna elements are more derived than warm and central water elements. The Antarctic endemics are thought to represent the most recent development (Pierrot-Bults and Van der Spoel 1979; Van der Spoel and Heyman 1983). White (1987) postulates that periodic episodes of anoxic events occurring primarily in the mid- to late Cretaceous, Eocene and Miocene caused the developments of the mesopelagic and deep sea faunas.

The splitting of a northern and southern hemisphere cold water fauna is of rather recent origin judging from the close relation of subarctic and subantarctic taxa. Pierrot-Bults and Van der Spoel (1979) discussed the speciation in macrozooplankton. They assumed that the Chaetognatha are oceanic in origin. From the shallow Pacific they dispersed into the Indian and Atlantic Oceans, from tropics to higher latitudes and from the epipelagic to the mesopelagic zone, following the development of the ocean basins and the water masses therein. The bathypelagic realm was the latest to develop, the oldest deep water basin is the North Atlantic. It is usually accepted that the organisms

inhabiting the bathypelagic are derived from cold water ancestors. So the tropical and subtropical plankton of the Pacific is the oldest plankton. Chaetognatha show their greatest diversity in this Ocean (Tokioka 1965b). For chaetognaths only one central water taxon is present (*S. pseudoserratodentata*). General warm water 40°N–40°S distributions are the most common oceanic distribution pattern in Chaetognatha and east Pacific taxa are also present (*S. bieri*, *S. bedoti*). For Chaetognatha, oceanic equatorial taxa are only present in the Indo-Pacific (*S. robusta*, *S. regularis*). Salvini-Plawen (1986) stated that (among others) primitive characters in chaetognaths are a long tail (> 40 per cent of the total body length), a great number of teeth, a short fin situated only on the tail and the presence of gut diverticula.

If the *Sagittas* are divided on the presence or absence of gut diverticula, then the division shown in Table 9.4 is reached.

The elongation of the gut in other groups, such as Crustacea, can be an adaption to poor food conditions (Vinogradov 1970) but since most of the chaetognath species with gut diverticula are neritic or epipelagic, living in areas of high productivity this character is considered not to be adaptive but of phylogenetic importance.

Species with gut diverticula show predominantly epipelagic warm water Indo-Pacific distributions, with the exception of *S. minima*, which shows a circumglobal warm water distribution, and *S. hispida*, a warm water Atlantic species. *S. sibogae*, *S. decipiens*, and *S. planctonis* are mesopelagic species with gut diverticula. Contrary to the epipelagic species with gut diverticula these show a circumglobal distribution. Species with a circumglobal warm water distribution (except *S. minima*), and Antarctic species are all without gut diverticula. The question arises here whether *S. marri* really belongs to the *S. planctonis* group. This species has no gut diverticulum and the position and shape of the fins is quite different from *S. planctonis planctonis* and *S. planctonis zetesios* (Fig. 9.24). The hypothesis is that the division of *Sagitta* into a group with and a group without gut diverticula took place before the Cretaceous, since the formation of the mesopelagic water masses started in the mid- to late Cretaceous and both groups have mesopelagic taxa.

If Salvini-Plawen's (1986) hypothesis about the primitive nature of the presence of a gut diverticulum, a long tail, and a short fin restricted to the tail segment is correct, then the genus *Sagitta* is more derived than the genus *Pterosagitta*. The latter genus is a monospe-

Table 9.4 Distribution of taxa with and without gut diverticula

	P*	I*	A*	P	I	A	Antarctic
	warm	warm	warm	cold	cold	cold	
With gut diverticula							
<i>S. johorensis</i>	n*						
<i>S. demipenna</i>	n						
<i>S. delicate</i>	n						
<i>S. bedfordii</i>	n	n					
<i>S. crassa</i>	n	n					
<i>S. neglecta</i>	o*	o					
<i>S. oecania</i>	o	o					
<i>S. regularis</i>	o	o					
<i>S. tropica</i>	o	o					
<i>S. robusta</i>	o	o					
<i>S. ferox</i>	o	o					
<i>S. hispida</i>			n				
<i>S. minima</i>	o	o	o				
<i>S. decipiens</i>				o	o	o	
<i>S. sibogae</i>				o	o	o	
<i>S. pl. planctonis</i>				o	o	o	
<i>S. pl. zetesios</i>				o	o	o	
<i>S. elegans</i>				o		o	
Without gut diverticula							
<i>S. bombayensis</i>		n					
<i>S. pseudoserratodentata</i>	o						
<i>S. scrippsae</i>	o						
<i>S. pulchra</i>	n	n					
<i>S. pacifica</i>	o	o					
<i>S. bedoti</i>	n	n	n				
<i>S. tenuis</i>	n	n	n				
<i>S. friderici</i>	n	n?	n				
<i>S. bipunctata</i>	o	o	o				
<i>S. bierii</i>	o	o	o				
<i>S. enflata</i>	o	o	o				
<i>S. s. atlantica</i>	o	o	o				
<i>S. s. serratodentata</i>			o				
<i>S. helenae</i>			n				
<i>S. setosa</i>			n				
<i>S. hexaptera</i>				o	o	o	
<i>S. lyra</i>				o	o	o	
<i>S. maxima</i>				o	o	o	
<i>S. macrocephala</i>				o	o	o	
<i>S. tasmanica</i> northern form						o	
<i>S. tasmanica</i> southern form							o
<i>S. gazellae</i>							o
<i>S. marri</i>							o

* I, = Indian Ocean; P = Pacific Ocean; A, = Atlantic Ocean; n, = neritic; o, = oceanic.

cific genus distributed in the tropical/subtropical epipelagic, so the distribution pattern also points to a primitive genus. (See Fig. 9.11).

Another hypothesis following from the distribution patterns is that the mesopelagic and/or bathypelagic genera *Krohnitta*, *Eukrohnia*, and *Heterokrohnia* are more derived than both *Pterosagitta*, which is epipelagic, and *Sagitta*, which is epipelagic, mesopelagic and bathypelagic.

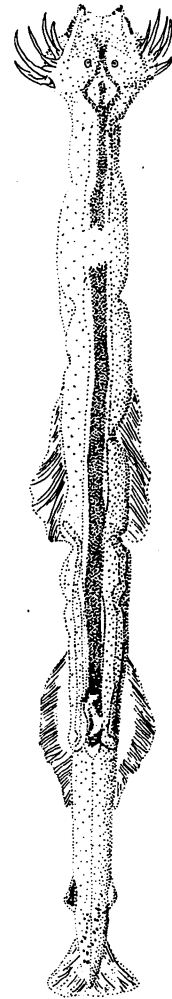


Fig. 9.24 *Sagitta marri*. After Pierrot-Bults (1975).