BULLETIN
ZOOLOGISCH MUSEUM
UNIVERSITEIT VAN AMSTERDAM

Vol. 5 No. 8 7-IV-1976

ZOOGEOGRAPHIC PATTERNS IN CHAETOGNATHS AND SOME OTHER PLANKTONIC ORGANISMS

A.C. PIERROT-BULTS

ABSTRACT

In this paper an attempt is made to give a general survey of our present knowledge about the relations between distribution patterns and diversity chiefly based on chaetognaths. Six main zoogeographic patterns are distinguished, viz. cosmopolitan, 40° N to 40° S circumglobal, 30° N to 30° S, bi-antitropical, circumpolar, and neritic; their relation with holoplankton diversity is discussed. Generally the more limited the distribution of a holoplanktonic species, the less infraspecific variation is observed. The most common pattern is the circumglobal from 40° N to 40° S. No obvious relations between distribution patterns and taxonomic categories could be traced.

INTRODUCTION

Studies on two widely distributed groups in chaetognaths, the *Sagitta planctonis*-group and the *Sagitta serratodentata*-group resulted in the recognition of bathymetric infraspecific categories in the *S. planctonis*-group, which shows a considerable horizontal as well as vertical distribution (Pierrot-Bults, 1969; 1970; 1975a; 1975b) and the recognition of species and subspecies in the *S. serratodentata*-group, which shows a more limited vertical but also a large horizontal distribution (Pierrot-Bults, 1974; 1976).

Chaetognaths are, with the exception of the genus *Spadella*, holoplanktonic animals, which occur from 0 to about 7000 m depth, dependent on the species. Moreover, a number of species shows vertical migration (Vinogradov, 1968). The considerable vertical distribution and the ability to migrate vertically affect horizontal distribution and speciation (David, 1961; Vinogradov, 1968).

The aim of this paper is the comparison of results of the studies on the *S. planctonis*-group and the *S. serratodentata*-group with phenomena occurring in other chaetognaths and some other holoplanktonic species.

REMARKS ON DISPERSAL

Currents in the sea have a major influence on the dispersal of holoplanktonic animals. Dependent though such animals, by definition, are on water movement, it is important to emphasize that this is not the only factor influencing dispersal; also the pattern of behaviour of the animals themselves is important. The distribution of epiplanktonic organisms is a product of prevailing hydrographic circulation, physicochemical limitations and innate behaviour patterns, which determine depth range and vertical migration (Cloud, 1961). This agrees in general with the opinion on the dispersal of terrestrial animals, in that not only the extrinsic factors like environmental temperature are important but that the intrinsic factors, such as the behaviour of the organisms also influence dispersal (Ekman, 1953; Mayr, 1963). Compared with the terrestrial one, the marine environment has some very specific characters. Besides the well-known characters of uniformity, stability in physical and chemical conditions and continuity, the oceans are three dimensional in space. Changes in the marine environmental conditions are gradual in time and space. Some authors commented on the general impression of a low speciation rate in the marine fauna (Zeuner, 1946; Day, 1963).

Insurmountable barriers for an organism are hard to detect in the marine environment. The classic hypothesis accounting for the dispersal of marine pelagic animals is that relatively small changes in environmental conditions are the limiting factors. Boundary zones in the marine environment are in general broad belts, inside which conditions change more abruptly than outside and where penetration by individuals is dependent on their specific tolerances. In very broad boundary zones taxa have sometimes developed that are restricted to the gradient of changing conditions. In that case the boundary regions are called transitional areas: biotopes with a special fauna. An example of a transitional area is found in the North Pacific between 38° N and 43° N (Bogorov, 1958). Well-known narrow boundary zones are the Subtropical and Antarctic convergences in the Southern Hemisphere.

The Subtropical convergence at about 40° S is the boundary for a large number of epipelagic species of chaetognaths (David, 1958; 1963), pteropods (Van der Spoel, in press), salps (Van Soest, 1975b), copepods (Frost & Fleminger, 1968), and euphausiids (Brinton, 1962; 1975). The convergence coincides roughly with the 15° C annual mean surface isotherm. Another boundary for the epipelagic fauna at about 30° N and 30° S coincides roughly with the 20° C annual mean surface isotherms.

The different ways in which barriers may effect animal distribution are discussed by David (1963): Either (1) the animals do not possess the adaptability to cope with the changing conditions and their distribution is limited by the boundary or (2) the animals are able to cross the boundary. The first possibility is shown by a great number of holoplanktonic species for which the 40° N and 40° S latitudes limit their distribution. The second possibility is shown by cosmopolitan species, remaining monotypic throughout their ranges, being apparently untouched by the conditions of the boundary regions or the conditions beyond them. There are relatively few monotypic cosmopolitan species. More numerous are the examples of species which are able to deal with the different conditions on both sides of the boundary region and with the changing conditions in the boundary region by adaptation and developing of infraspecific categories or which develop species-groups of vicariating closely related species on both sides of the boundary.

Different infraspecific categories may develop through the restricting influence of the boundary on gene flow, or through differences in selective pressure and the responses of the organisms to that pressure.

Different species may develop when the boundary is only occasionally crossed by individuals, so that populations on either side of the boundary are isolated for a sufficiently long period.

Vertical distribution has a considerable influence on horizontal distribution. In general it can be stated that epipelagic species are more restricted in their distribution than mesopelagic ones. Moreover, an organism which migrates vertically, crossing different water layers, must be able to tolerate a wider range of environmental conditions than an organism which lives at one depth level only. Vertical migrators are likely therefore to have a wider north-south range.

According to the nature of their vertical distribution, Vinogradov (1968) divided the chaetognaths into three groups: (1) species with their maximum abundance from 0 to 200 m depth, (2) species living at intermediate depths, from 200 to 1000 m, and (3) deep-sea species living below the

500 to 1000 m level. Only species with distributions within the 40° N to 40° S limits belong to the first group. The second group is often subdivided into two groups, one for the 200 to 600 m distributions and another for the 600 to 1000 m ones, and in this latter group many species execute diurnal vertical migrations.

David (1961) discussed the hypothesis of vertical migration being of selective advantage for marine organisms. The migration prevents the formation of too many species with restricted adaptibility and too little capacity to survive changes in the environment.

Cold water species with limited temperature tolerances may be epipelagic at high latitudes and mesopelagic at low latitudes. By occupying various appropriate depth ranges they can be distributed in all the oceans. This is the case in the chaetognath *Eukrohnia hamata* (Möbius, 1875) (cf. Thiel, 1938; Alvariño, 1964). The horizontal and vertical distributions of *Sagitta planctonis* Steinhaus, 1896 forma *zetesios* in the Atlantic Ocean is comparable to that of *E. hamata*. In *S. planctonis* a second forma (*planctonis*) occurs, more epipelagic from 40° N to 40° S. In this case the differences in vertical ranges led to the formation of bathymetric formae (Pierrot-Bults, 1975a). Another case of latitudinally changing vertical ranges is presented by *Sagitta maxima* Conant, 1896, showing a tendency to inhabit the deepest layers in the Subtropics (David, 1963).

HORIZONTAL DISTRIBUTION PATTERNS

In holoplanktonic animals six main zoogeographical patterns can be recognized: the cosmopolitan, the circumglobal tropical and subtropical, the tropical, the biantitropical, the circumpolar, and the neritic.

COSMOPOLITAN DISTRIBUTION

Though there are relatively few monotypic cosmopolitan holoplanktonic species one of the examples is thought to be the chaetognath *Eukrohnia hamata* (cf. Thiel, 1938; Alvariño, 1965; David, 1963) which is epipelagic at higher latitudes and mesopelagic at lower latitudes. But even here there are some indications of taxonomic differences within the species, for example the populations north and south of the Southern Subtropical convergence are different (David, 1963). *Sagitta macrocephala* Fowler, 1905 is another very widely distributed chaetognath; this monotypic species is inhabiting the layer of 500 to 1000 m, or even deeper.

Numerous species regarded monotypic and cosmopolitan show a great amount of infraspecific variation and have to be divided into infraspecific categories. For example the pteropods *Clio pyramidata* Linnaeus, 1767, which is composed of 7 formae and occurs from 70° N to 70° S (cf. Van der Spoel, 1967) and *Cavolinia tridentata* (Forskål, 1775), which is composed of 9 formae (fig. 2) (cf. Van der Spoel, 1974).

Examples of widely distributed groups in chaetognaths are the *Sagitta planctonis*-group consisting of a species composed of two bathymetric formae throughout the Atlantic Ocean and another species in Antarctic waters (fig. 1) (cf. Pierrot-Bults, 1975a) and the *Sagitta serratodentata*-group composed of 5 species, one being divided into two subspecies (fig. 3) (cf. Pierrot-Bults, 1974). A widely distributed species group in salps is the *Salpa fusiformis*-group (cf. Van Soest, 1974b) though it is suggested in a later paper (Van Soest, 1975b: 200) that *Salpa gerlachei* Foxton, 1961 could be a clinal form of *S. thompsoni* Foxton, 1961 as these taxa differ only biometrically and show intermediates.

CIRCUMGLOBAL DISTRIBUTION COVERING TROPICS AND SUBTROPICS

Two main patterns in copepod distribution are distinguished by Frost & Fleminger (1968): a first of broad and a second of narrower latitudinal ranges. The first group consists of tropical and subtropical species breeding regularly from 40° N to 40° S. According to these authors the species tend to be monotypic, circumglobal in distribution and probably maintain gene flow around South-Africa.

A considerable number of holoplanktonic animals remains monotypic by strong gene flow or by homeostasis. The chaetognaths *Sagitta enflata* (Grassi, 1881), *S. minima* (Grassi, 1881), *Pterosagitta draco* (Krohn, 1853) and *Krohnitta subtilis* (Grassi, 1881) show such a distribution and monomorphy (cf. Bieri, 1959; Alvariño, 1965). In other groups, similar examples are seen; in the pteropods *Hyalocylis striata* (Rang, 1828) and *Styliola subula* (Quoy & Gaimard, 1827) (cf. Van der Spoel, 1967); in the euphausiid *Euphausia tenera* Hansen, 1905 (cf. Brinton, 1975); in the copepod *Clausocalanus mastigophorus* (Claus, 1863) (cf. Frost & Fleminger, 1968) and in the salp *Salpa aspera* Chamisso, 1819 (cf. Van Soest, 1974b).

If gene flow is restricted by extrinsic barriers or if merely differences in selective pressure are effective infraspecific categories may arise. Examples are: the circumglobal salp species *Thalia democratica* (Forskål, 1775) composed of two formae (cf. Van Soest, 1975b); the pteropods *Cuvierina columnella* (Rang, 1827) composed of three formae (cf. Van der Spoel, 1967) and *Diacria quadridentata* (ms. Lesueur, De Blainville, 1821) composed of two subspecies, subdivided into 6 formae (cf. Van der Spoel, 1971a); the euphausiid *Stylocheiron affine* Hansen, 1910 (cf. Brinton, 1962) composed of 5 infraspecific categories in the Indo-Pacific Ocean (fig. 4); and the phronimid *Phronima colletti* Bovallius, 1887 composed of two infraspecific categories in the Pacific Ocean (cf. Shih, 1969).

Evolution above subspecies level, due to successive isolations and reinvasions may result in groups of closely related species. Within such groups eurythermal species ranging from 40° N to 40° S tend to show circumglobal distribution while more stenothermal species tend to have a noncircumglobal distribution with close relatives in the different oceans. The chaetognaths of the *Sagitta hispida*-group (Ibañez, 1969) are examples of such a distribution pattern (cf. Bieri, 1959; Alvariño, 1965; Tokioka, 1974). Copepods of the *Eucalanus elongatus*-group with 5 species (fig. 5) (cf. Fleminger & Hulsemann, 1973) and of the *Clausocalanus arcuicornis*-group with 5 species (fig. 6) (cf. Frost & Fleminger, 1968) are two well studied examples. In salps the *Cyclosalpa pinnata*-group (cf. Van Soest, 1974a) and in euphausiids the *Euphausia brevis*-group (cf. Brinton, 1975) are known to represent these patterns.

TROPICAL SPECIES

A second category recognized by Frost & Fleminger (1968) consists of species breeding regularly from 30° N to 30° S. According to these authors this group is characterized by absence of gene flow around the continents and by non-circumglobal distribution. Moreover, there may be one or more close relatives in tropical waters of the major oceans. The examples mentioned by Fleminger & Hulsemann as non-circumglobal tropical species all form part of a circumglobally distributed species-group, with provincialism.

Exceptions to the pattern found by Frost & Fleminger (1968) and Fleminger & Hulsemann (1973) are disjunct species without recognizable differences between populations in different oceanic basins. Such an example is the chaetognath *Krohnitta pacifica* (Aida, 1897) (cf. Alvariño, 1965), the heteropod *Oxygyrus keraudreni* (Lesueur, 1817) (cf. Van der Spoel, in press), the salps *Cyclosalpa danae* Van Soest, 1975 and *Brooksia rostrata* (Traustedt, 1893) (cf. Van Soest, 1975a), and the euphausiid *Thysanopoda tricuspidata* H. Milne-Edwards, 1837 (cf. Brinton, 1975).

In widely distributed species groups, the species with a distribution from 40° N to 40° S thus tend to show circumglobal distribution while the more restricted tropical species consist of close relatives in the major oceans. This is found in chaetognaths of the *Sagitta hispida*-group (Ibañez, 1969) where *Sagitta bipunctata* Krohn, 1853 is found circumglobally from 40° N to 40° S, whereas the more tropical *S. hispida* Conant, 1869 is confined to the tropical Atlantic Ocean and *S. robusta* Doncaster, 1902 occurring only in the tropical Indo-Pacific Oceans (cf. Bieri, 1959). In the *Sagitta serratodentata*-group, *S. serratodentata serratodentata* Krohn, 1853 is found in the Atlantic Ocean and *S. pacifica* Tokioka, 1940 in the Indo-Pacific Oceans, though these distributions reach somewhat beyond the 30° N to 30° S limits (cf. Pierrot-Bults, 1974). The salp *Ritteriella retracta* (Ritter, 1906), distributed from 40° N to 40° S, is circumglobal while the more tropical *Ritteriella picteti* (Apstein, 1904), is only known from the Indo-Pacific (cf. Van Soest, 1974b). In copepods of the *Pontellina plumata*-group, the Indo-Pacific species *P. moreii* Fleminger & Hulsemann, 1974 is replaced in the Atlantic by *P. platychela* Fleminger & Hulsemann, 1974, while the more widely distributed *P. plumata* Dana, 1849 is again circumglobal (cf. Fleminger & Hulsemann, 1974) (fig. 7). In copepods of the *Eucalanus elongatus*-group, *E. hyalinus* Giesbrecht, 1892 is circumglobal, but *E. inermis* Giesbrecht, 1892 and *E. bungii* Giesbrecht, 1892 are Pacific species while *E. elongatus elongatus* (Dana, 1849) is an Indo-West Pacific (cf. Fleminger & Hulsemann, 1973) taxon.

A well-known phenomenon among tropical species is the east-west-diversity. In the chaetognaths of the *Sagitta hispida*-group (Ibañez, 1969), *Sagitta crassa* Tokioka, 1938 is found in the West-Pacific while *S. tenuis* Conant, 1896 is found in the East-Pacific Ocean. In euphausiids east-west diversity is seen in the closely related species *Euphausia sanzoi* Torelli, 1934, which is restricted to the Indian Ocean and Western Pacific and *E. gibboides* Ortmann, 1893, which only occurs in the Eastern and Northern Pacific and Atlantic Ocean, as well as in the species *Euphausia sibogae* Hansen, 1908 from the Western Pacific and *E. distinguenda* Hansen, 1911 from the Eastern Pacific (cf. Brinton, 1975). East-west diversity within a single species in known for the two infraspecific categories of the euphausiid *Stylocheiron affine* Hansen, 1910: the Indo-Australian form and the east-equatorial form (cf. Brinton, 1962). For Pacific salps east-west diversity is recorded from *Cyclosalpa quadriluminis* Berner, 1955 with the forma *quadriluminis* in the Indian and West-Pacific oceans and the forma *paralella* in the northern West-Pacific (cf. Van Soest, 1974a). The pteropods *Cavolinia tridentata* forma *teschi* Van der Spoel, 1974. and *C. tridentata* forma *occidentalis* Dall, 1908 show a comparable east-west diversity (cf. Van der Spoel, 1974). The same holds true for the phronimid *Phronima colletti*, which shows one form in the Indo-West Pacific and another form in the East Pacific (cf. Shih, 1969). In copepods the same pattern is shown by *Eucalanus elongatus elongatus* in the Indo-West Pacific and *E. inermis* in the Eastern Pacific (cf. Fleminger & Hulsemann, 1973).

In chaetognaths, as in many other planktonic groups, the majority of the tropical species is restricted to the Pacific region. Of the eight tropical chaetognath species only one is known from the Atlantic (*Sagitta hispida*). *Krohnitta pacifica* is circumglobal and the remaining six (*Sagitta bedoti* Beraneck, 1895; *S. ferox* Doncaster, 1902; *S. neglecta* Aida, 1897; *S. pulchra* Doncaster, 1902; *S. tenuis* Conant, 1896) are all confined to the Indo-Pacific or have their main distribution in the tropical Malayo-West-Pacific region. This area is the richest in chaetognath species. Temperature fluctuations in the Pacific Ocean during the Pleistocene period were not as pronounced as elsewhere in the world, the waters remaining tropical during the glaciations (Ekman, 1953; Briggs, 1975).

BIANTITROPICAL DISTRIBUTION

When the distribution of a species is disjunct, and the taxon is absent in the tropics but present in the Northern and Southern Hemispheres, the distribution is called biantitropical (Brinton, 1962). The term biantitropical covers the concepts bisubtropical, biboreal and bipolar. Biantitropical species have a tendency to develop into two or more taxa in the North and in the South.

A number of species do not show recognizable differences between their northern and southern populations. This is the case in the chaetognath *Sagitta tasmanica* Thomson, 1947 (cf. Pierrot-Bults, 1974), the pteropods *Limacina lesueuri* (d'Orbigny, 1836) and *L. trochiformis* (d'Orbigny, 1836) (cf. Van der Spoel, 1967), and in the euphausiids *Thysanoessa gregaria* G.O. Sars, 1883 (cf. Brinton, 1962) and *Euphausia brevis* Hansen, 1905 (cf. Brinton, 1975). According to Brinton (1962) euphausiid species from the transition zone are all biantitropical while subarctic species are not biantitropical.

In chaetognaths, *Sagitta maxima* Conant, 1896 is thought to show differences between the northern and southern populations (cf. David, 1963). The same is true for the pteropod *Limacina helicina* (Phipps, 1774) which comprises one subspecies in Arctic/Subarctic waters, the latter is subdivided into one forma (*helicina*) in the North Atlantic and into two formae (*pacifica* and *acuta*) in the North Pacific Ocean, while the subspecies *antarctica* is represented in Antarctic and Subantarctic waters by two formae (*antarctica* and *rangi*) (cf. Van der Spoel, 1967) (fig. 8).

Some populations appear to have been isolated sufficiently long to develop closely related species in the North and in the South. For example the closely related chaetognaths *Sagitta pseudoserratodentata* Tokioka, 1939 and *S. serratodentata atlantica* Thomson, 1947 are biantitropical (Pierrot-Bults, 1974). A comparable distribution is seen in the euphausiids *Nematoscelis difficilis* Hansen, 1910 and *N. megalops* Hansen, 1910 (cf. Brinton, 1962) and in *Euphausia hemigibba* Hansen, 1910 and *E. gibba* G.O. Sars, 1883 (cf. Brinton, 1975) (fig. 7).

The phenomenon that species are biantitropical in one ocean and not in the other is seen in chaetognaths, *Sagitta tasmanica* is biantitropical in the Atlantic and not in the Pacific Ocean (cf. Pierrot-Bults, 1974). Certain euphausiids show the same: *Euphausia recurva* Hansen, 1905 is biantitropical in the Pacific, but not in the Atlantic Ocean (cf. Brinton, 1975) and this also holds true in certain copepods: *Clausocalanus arcuicornis* Dana, 1849 and *Eucalanus hyalinus* which are biantitropical in the Pacific but not in the Atlantic Ocean (cf. Fleminger & Hulsemann, 1973).

ARCTIC AND CIRCUMANTARCTIC DISTRIBUTIONS

Species occurring south of 40° S are generally circumantarctic in distribution while species in Arctic and Subarctic waters often show differentiation into a North Pacific and a North Atlantic population, or they show endemism in either of these two oceans.

The chaetognath *Sagitta tasmanica* occurs in the North Atlantic and is circumantarctic, but it is absent from the North Pacific Ocean (Pierrot-Bults, 1974). The pteropod *Limacina helicina* has developed different formae in the North Atlantic and North Pacific Ocean while other formae in the South show a circumantarctic distribution (cf. Van der Spoel, 1967).

There are, however, species which are identical in both the North Pacific and North Atlantic, for example the chaetognath *Sagitta elegans* Verrill, 1873 and the euphausiids *Thysanoessa inermis* (Krøyer, 1846) and *T. raschii* (M. Sars, 1863) (cf. Brinton, 1962).

NERITIC DISTRIBUTION

Tokioka (1974) discussed species groups of chaetognaths which have both neritic and closely related oceanic taxa. He considered the species *Sagitta crassa* composed of three categories as in *S. bedoti*. In his opinion *S. tenuis* comprises four categories, among which *S. friderici* Von Ritter-Zahony, 1911, *S. euneritica* Alvariño, 1961 and *S. peruviana* Sund, 1961 originally were considered valid species. In this light the possibility that more infraspecific categories may be defined within this group is postulated by Tokioka (1974).

Another group of neritic chaetognath species is the *Sagitta setosa*-group, with different taxa in the North Sea coastal area (*S. batava* Biersteker & Van der Spoel, 1966) and Black Sea (*S. euxina* Moltschanoff, 1909). The mediterranean populations of *S. setosa* J. Müller, 1847 resemble the coastel North Sea *batava*, the latter is considered an infraspecific category. *S. euxina* is morphologically intermediate between *S. setosa* from the North Atlantic and *batava*. The taxonomic relationships of these taxa are still uncertain. The Black Sea populations may be a relict from the Sarmatic basin (Ekman, 1953), which were linked in the past with their North Atlantic relative *S. setosa*. The categories of *S. elegans* constitute also a group of closely related taxa with an oceanic category (*elegans*), an Arctic category (*arctica*) and a neritic category in the Baltic (*baltica*).

The neritic taxa in general have a great deal of tolerance to environmental conditions. They may be regarded as being less closely adapted and capable of surviving fluctuating conditions (David, 1963).

CLINAL VARIATION

Clines were described and discussed by Huxley (1939), who distinguished various types of clines, viz. discontinuous or continuous, stepped or smooth. According to Mayr (1963: 361) clines are the product of two conflicting forces: selection and gene flow. Selection tends to make every population optimally adapted to its local environment and gene flow tends to make all members of a species identical. The result of both is a gradual change of characters.

Clines are character gradients and within one species several clines may be recognized in various directions. There may be, however, a rather strong correlation among several characters (Mayr, 1963).

Planktonic species with a large continuous north-south distribution tend to show clinal variation in several characters mostly correlated with latitude. If the distribution continues in latitudes higher than about 40°, the variation is gradual between the 40° N to 40° S limits and shows discontinuities at these limits. These discontinuities then result in the development of infraspecific categories. In addition, species without latitudinal variation are often seen to be restricted by the 40° N boundary zone, whereas species with latitudinal variation develop special taxa in the transition zone with related taxa in Subarctic and central waters.

Thus at the boundaries of the 40° N and 40° S latitudes, different steps in the speciation process can be observed. Depending on the species concerned this finds its expression in stepped clines or even real speciation.

Species showing discontinuities in clinal variation at about 40° latitude are the salps *Salpa fusiformis* Cuvier, 1804, *Pegea confoederata* (Førskal, 1775), and *Thalia democratica* (Førskal, 1775) where a cline in the number of muscle fibres exists (Van Soest, 1972; 1975b).

The pteropod *Limacina helicina* developed the forma *pacifica* in the transition zone in the North Pacific with another forma in Subarctic waters (cf. Van der Spoel, 1967). The copepod *Eucalanus bungii* is represented by the subspecies *californicus* in the transition zone and the subspecies *bungii* in Subarctic waters and the related species *E. hyalinus* in central waters (cf. Fleminger & Hulsemann, 1973). The euphausiid *Thysanoessa longipes* Brandt, 1851 shows a spined and an unspined category in Arctic and Subarctic waters respectively and the related species *T. gregaria* in the transition zone (cf. Brinton, 1962). The chaetognath *Sagitta serratodentata serratodentata* shows clinal variation in the number of teeth, is distributed from 40° N to 35° S and is represented in higher latitudes by the closely related species *S. tasmanica* (cf. Pierrot-Bults, 1974). The chaetognath *S. elegans* Verrill, 1873 comprises an infraspecific taxon in the Arctic and Subarctic (*arctica*) with another taxon (*elegans*) in boreal waters (cf. Von Ritter-Zahony, 1911). *S. lyra* Krohn, 1853 with a 40° N to 40° S distribution is represented in the North Pacific transition zone by the category *scrippsae* (cf. Tokioka, 1974) and is replaced by *S. gazellae* Von Ritter-Zahony, 1909 in the Antarctic (cf. David, 1958).

DISCUSSION

The most common distribution pattern in chaetognaths is the circumglobal distribution from 40° N to 40° S. The same is found for a great number of other holoplanktonic groups (cf. Briggs, 1975). Few planktonic species are specific for restricted watermasses (cf. Bieri, 1959; Briggs, 1975), but in some species several infraspecific categories correlated with watermasses have been established, for example in pteropods (cf. Van der Spoel, 1967) and euphausiids (cf. Brinton, 1962; 1975).

Biological discontinuities in continuous ranges are explained in different ways by various authors. Brinton (1962) takes the view that the infraspecific categories seen in the euphausiid *Stylocheiron affine* are phenotypical responses to the environment and Van der Spoel (1969; 1971b) and Van Soest (1975b) described some infraspecific categories (as formae sensu Van der Spoel, 1969) in pteropods and salps, respectively, thus interpreting the variation as genetically determined. Bathymetric formae are described in the chaetognath *S. planctonis* (cf. Pierrot-Bults, 1975a). Formae are supposed to have a genetic basis and arise through differences in selective pressure and different responses of the organisms to that pressure. There is no restriction to interbreeding which results in broad intergrading zones between formae.

Huxley's concept of a stepped cline (Huxley, 1939: 494; 1940: 29; 1942: 210) breaking up into "dependent subspecies" or "non-isolated subspecies" seems to cover the concept of Van der Spoel (1969; 1971b) of discontinuous clinal variation forming series of formae. If the assumption that clines are caused by selective pressure and gene flow is correct, then individuals in one part of the cline show a gene complex different from those in another part of the cline. If clinal variation shown by several characters is correlated, as happens frequently (Mayr, 1963), a distribution pattern of biological discontinuities may be seen within a continuous range of interbreeding populations. In this "stepped cline" the gene complexes of the "steps" are different from each other.

The term "independent subspecies" or "isolated subspecies" is used by Huxley (1940; 1942) for groups of populations wholly or partially isolated by extrinsic barriers. This will result in narrow belts of intergrading zones or no intergrading zones between the populations of different subspecies. Unfortunately breeding experiments to prove that plankton formae have a genetic base are not possible yet.

In general it can be stated for holoplanktonic animals that the more limited the distribution of a species the less infraspecific variation is seen. (1) Species with a wide distribution are in the advantage when having a high degree of variability and develop infraspecific taxa, coping with the differences in environmental conditions and selective pressure. (2) Species with a restricted oceanic distribution show phenotypically monomorphic adaptations based on balanced and buffered gene complexes. This can be demonstrated by comparing heteropods and pteropods. Heteropods have a limited north-south range and a limited penetration into deeper layers, while pteropods extend from the Arctic to the Antarctic and show a wider vertical range. Pteropods show a considerable amount of infraspecific variation (both formae and subspecies) while most heteropods do not show series of formae (cf. Van der Spoel, 1972; in press). Salps are restricted mainly to the warmer and temperate areas and do not penetrate into the deeper layers. Few infraspecific taxa have been described and only the more widely distributed taxa show clinal variation with discontinuities at about 40° N and 40° S (Van Soest, 1975b).

Widely distributed chaetognaths show changes in vertical distribution and/or infraspecific variation in horizontal or vertical direction (David, 1963; Alvariño, 1965; Vinogradov, 1968; Pierrot-Bults, 1975a).

Widely distributed species groups consisting of closely related species of probably monophyletic origin, show that active speciation has occurred in the past. The taxonomic and geographic relations between taxa of most species groups in chaetognaths need more intensive study. For example the species of the genus *Eukrohnia* Von Ritter-Zahony, 1911 (*E. hamata*; *E. fowleri* Von Ritter-Zahony, 1911; *E. bathyantarctica* David, 1958; *E. bathypelagica* Alvariño, 1962; *E. minuta* Silas & Shrinavasan, 1968) and the *Sagitta maxima*-group consisting of *S. maxima*, *S. lyra*, *S. gazellae* and *S. scrippsae*, present such a situation. Infraspecific variation is mentioned for *S. gazellae* (cf. David, 1958), whereas Tokioka (1974) considered *scrippsae* an infraspecific category of *S. lyra*.

In contrast to oceanic species, neritic species show a more limited distribution with more variation and mixing of populations. Tokioka (1974) considered many neritic chaetognath "species" (which are closely related to species in adjacent water masses) not tenable but of infraspecific rank. There is a tendency for offshore species to branch off several lower taxa in the neritic zone due to adaptive radiation rather than to isolation. This phenomenon was earlier described by Colebrook & Robinson (1963) for plankton around the British Isles.

There seems to be a correlation between speciation and distribution, the wider the distribution the larger the diversity of a group. Distributional patterns show, however, no correlation with taxonomic categories as these patterns seem to differ from group to group.

REFERENCES

ALVARIÑO, A., 1964. Bathymetric distribution of chaetognaths. Pacif. Sci., 18 (1): 64-82, figs. 1-12.

-------, 1965. Chaetognaths. Oceanogr. mar. Biol., 3: 115-194, figs. 1-17.

BIERI, R., 1959. The distribution of the planktonic chaetognatha in the Pacific and their relationship to the watermasses. Limnol. Oceanogr., 4 (1): 1-28, figs. 1-26.

BOGOROV, B.G., 1958. Biogeographical regions in the plankton of the north-western Pacific Ocean and their influence on the deep sea. Deep-sea Res., 5 (2): 149-161.

BRIGGS, J.C., 1975. Marine zoogeography: 1-475 (McGraw-Hill, New York).

BRINTON, E., 1962. The distribution of Pacific Euphausiids. Bull. Scripps Instn Oceanogr., 8 (1): 51-269, figs. 1-126.

-------, 1975. Euphausiids of south-east Asian waters. Naga Rep., 4 (5): 1-287, figs. 1-139.

CLOUD, E., 1961. Paleobiogeography of the marine realm. Publs Am. Ass. Advmt Sci., 67: 151-200, figs. 1-12.

COLEBROOK, J.M. & G.A. ROBINSON, 1963. Ecological differentiation in the plankton of the waters around the British Isles. Publs Syst. Ass., 5: 157-169, figs. 1-9.

DAVID, P.M., 1958. The distribution of the Chaetognatha of the southern ocean. Discovery Rep., 29: 199-228, pl. X, figs. 1-13.

-------, 1961. The influence of vertical migration on speciation in the oceanic plankton. Syst. Zool., 10 (1): 1-16.

-------, 1963. Some aspects of speciation in the Chaetognatha. Publs Syst. Ass., 5: 129-143, figs. 1-5.

DAY, J.H., 1963. The complexity of the biotic environment. Publs Syst. Ass., 5: 329-493, tab. 1-3.

EKMAN, S., 1953. Zoogeography of the sea: i-xiii, 1-417, figs. 1-121 (Sidgwick & Jackson, London).

FLEMINGER, A. & K. HULSEMANN, 1973. Relationships of Indian Ocean epiplanktonic calanoids to the world oceans. In: B. Zeitschel, ed., The biology of the Indian Ocean: 339-347, figs. 1-7 (Springer Verlag, Berlin, Heidelberg, New York).

-------, 1974. Systematics and distribution of the four sibling species comprising the genus Pontellina Dana (Copepoda, Calanoida). Fish. Bull., 72 (1): 63-120, figs. 1-39.

FROST, B. & A. FLEMINGER, 1968. A revision of the genus Clausocalanus (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. Bull. Scripps Instn Oceanogr., 12: 1-235, pls. 1-67, figs. 1-6.

HUXLEY, J.S., 1939. Clines: an auxilliary method in taxonomy. Bijdr. Dierk., 27: 491-520, figs. 1-9.

-------, 1940. Towards the new systematics. In: J.S. Huxley, ed., The new systematics: 1-46 (Oxford University Press).

-------, 1942. Evolution, the modern synthesis: 1-645 (George Allen & Unwin, London).

IBAÑEZ, J.J., 1969. Application de l'analyse factorielle en planctologie: écologie et taxonimie numérique. Univ. Paris sta. zool. Villefranche-sur-Mer, thèse, 12: 1-130, figs. 1-10.

MAYR, E., 1963. Animal species and evolution: i-xiv, 1-797 (Bellknap Press, Harvard University Press, Cambridge, Mass.).

PIERROT-BULTS, A.C., 1969. The synonymy of Sagitta planctonis and Sagitta zetesios (Chaetognatha). Bull. zool. Mus. Univ. Amsterdam, 1 (10): 125-129, figs. 1-12.

-------, 1970. Variability in Sagitta planctonis Steinhaus, 1896 (Chaetognatha) from West African waters in comparison to North Atlantic samples. Atlantide Rep., 11: 141-149, figs. 1-4.

-------, 1974. Taxonomy and zoogeography of certain members of the "Sagitta serratodentata-group" (Chaetognatha). Bijdr. Dierk., 44 (2): 215-234, figs. 1-11.

-------, 1975a. Taxonomy and zoogeography of Sagitta planctonis Steinhaus, 1896 (Chaetognatha) in the Atlantic Ocean. Beaufortia, 23 (297): 27-51, figs. 1-14.

-------, 1975b. Morphology and histology of the reproductive system of Sagitta planctonis Steinhaus, 1896 (Chaetognatha). Bijdr. Dierk., 45 (2): 225-236, figs. 1-19.

-------, 1976. Histology of the seminal vesicles in the "Sagitta serratodentata-group" (Chaetognatha). Bull. zool. Mus. Univ. Amsterdam, 5 (4): 19-30, figs. 1-13.

RITTER-ZAHONY, R. VON, 1911. Revision der Chätognathen. dt. Südpol. Exped., 13 (Zool., 5, 1): 1-71.

SHIH, C.T., 1969. The systematics and biology of the family Phronimidae (Crustacea: Amphipoda). Dana Rep., 74: 1-100, figs. 1-22.

SOEST, R.W.M. VAN, 1972. Latitudinal variation in Atlantic Salpa fusiformis Cuvier, 1804 (Tunicata, Thaliacea). Beaufortia, 20 (262): 59-68, figs. 1-2.

-------, 1974a. Taxonomy of the subfamily Cyclosalpinae Yount, 1954 (Tunicata, Thaliacea), with the descriptions of two new species. Beaufortia, 22 (288): 17-55, figs. 1-20.

-------, 1974b. A revision of the genera Salpa Forskål, 1775, Pegea Savigny, 1816 and Ritteriella Metcalf, 1919 (Tunicata, Thaliacea). Beaufortia, 22 (293): 153-191, figs. 1-15.

-------, 1975a. Observations on taxonomy and distribution of some Salps (Tunicata, Thaliacea), with descriptions of three new species. Beaufortia, 23 (302): 105-130, figs. 1-13.

-------, 1975b. Zoogeography and speciation in the Salpidae (Tunicata, Thaliacea). Beaufortia, 23 (307): 181-215, figs. 1-12.

SPOEL, S. VAN DER, 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda): 5-375, figs. 1-366 (J. Noorduyn & Zoon, Gorinchem).

-------, 1969. Two new forms of Cavolinia uncinata (Rang, 1829) (Pteropoda, Gastropoda). Beaufortia, 16 (220): 185-198, figs. 1-9.

-------, 1971a. New forms of Diacria quadridentata (De Blainville, 1821), and Cavolinia uncinata (Rang, 1829) from the Red sea and the East-Pacific Ocean (Mollusca, Pteropoda). Beaufortia, 19 (243): 1-20, figs. 1-21.

-------, 1971b. Some problems in infraspecific classification of holoplanktonic animals. Zeitschr. zool. Syst. EvolForsch., 9: 107-138, figs. 1-7.

-------, 1972. Notes on the identification and speciation of Heteropoda (Gastropoda). Zool. Meded., 47: 545-560.

-------, 1974. Geographical variation in Cavolinia tridentata (Mollusca, Pteropoda). Bijdr. Dierk., 44 (1): 100-112, figs. 1-6.

-------, 1976 (in press). Euthecosomata, Gymnosomata and Heteropoda. (Oosthoek, Scheltema & Holkema, Utrecht.)

THIEL, M.E., 1938. Die Chaetognathen Bevölkerung des Süd-Atlantischen Ozeans. Wiss. Ergebn. dt. Atlant. Exped. "Meteor", 13 (1): 1-110.

TOKIOKA, T., 1974. On the specific validity in species pairs or trios of plankton animals, distributed respectively in different but adjoining water masses, as seen in chaetognaths. Publ. Seto mar. biol. Lab., 21 (5-6): 393-408.

VINOGRADOV, M.E., 1968. Vertical distribution of the oceanic zooplankton: 1-339, figs. 1-84. (English transl. Israel Program for scientific Translations, Jerusalem, 1970).

ZEUNER, F.E., 1946. Dating the past, an introduction to geochronology: i-xviii, 1-474, pls. 1-24 (Methuen, London).

A.C. PIERROT-BULTS
Institute of Taxonomic Zoology
University of Amsterdam
Plantage Middenlaan 53
Amsterdam - The Netherlands

Received: 2 March 1976

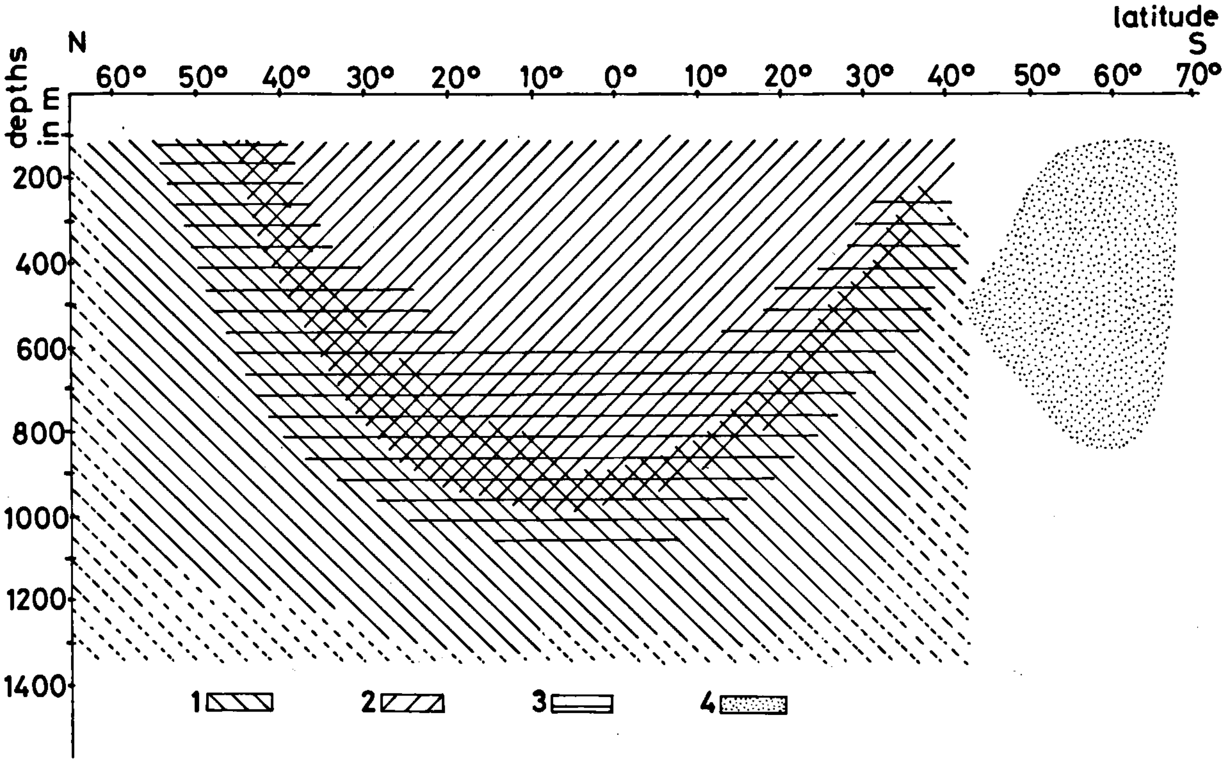
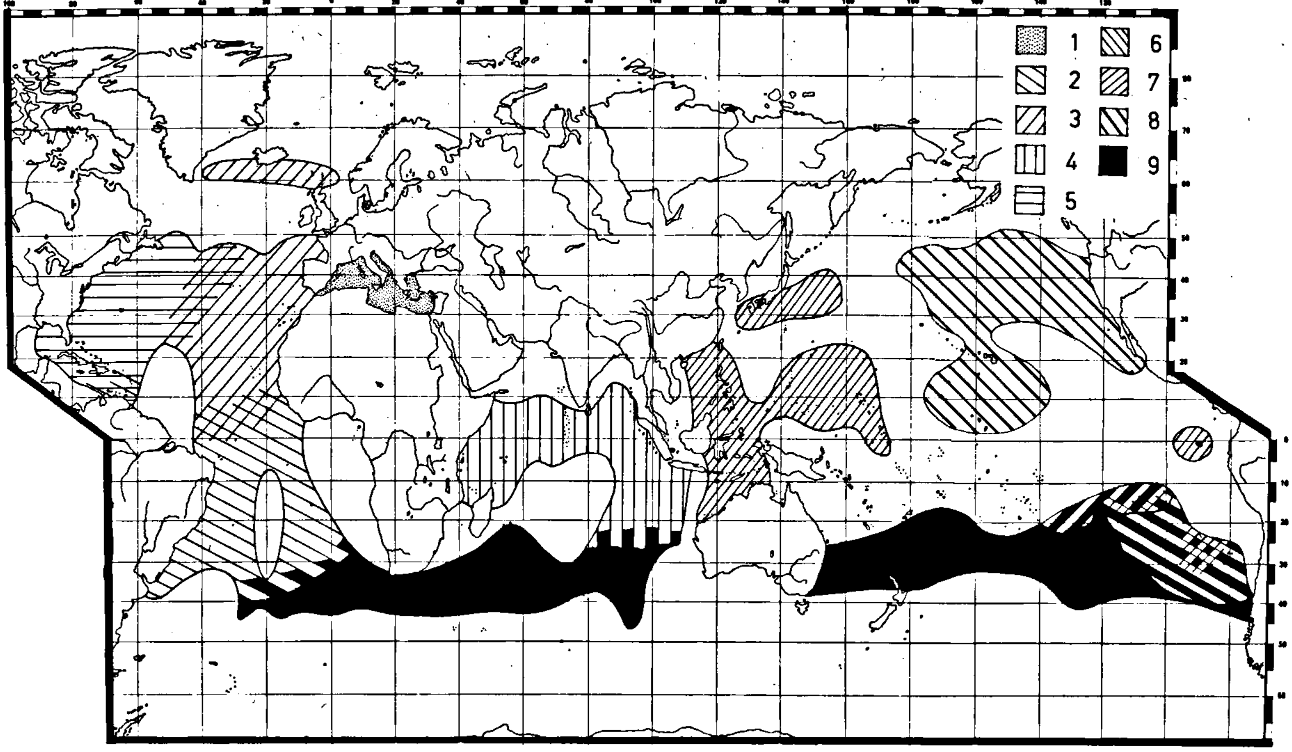


Fig. 1. Latitudinal difference in vertical distribution of chaetognaths of the *Sagitta planctonis*-group. 1 = *zetesios*; 2 = *planctonis*; 3 = *intermediates*; 4 = *marri* (after Pierrot-Bults, 1975).



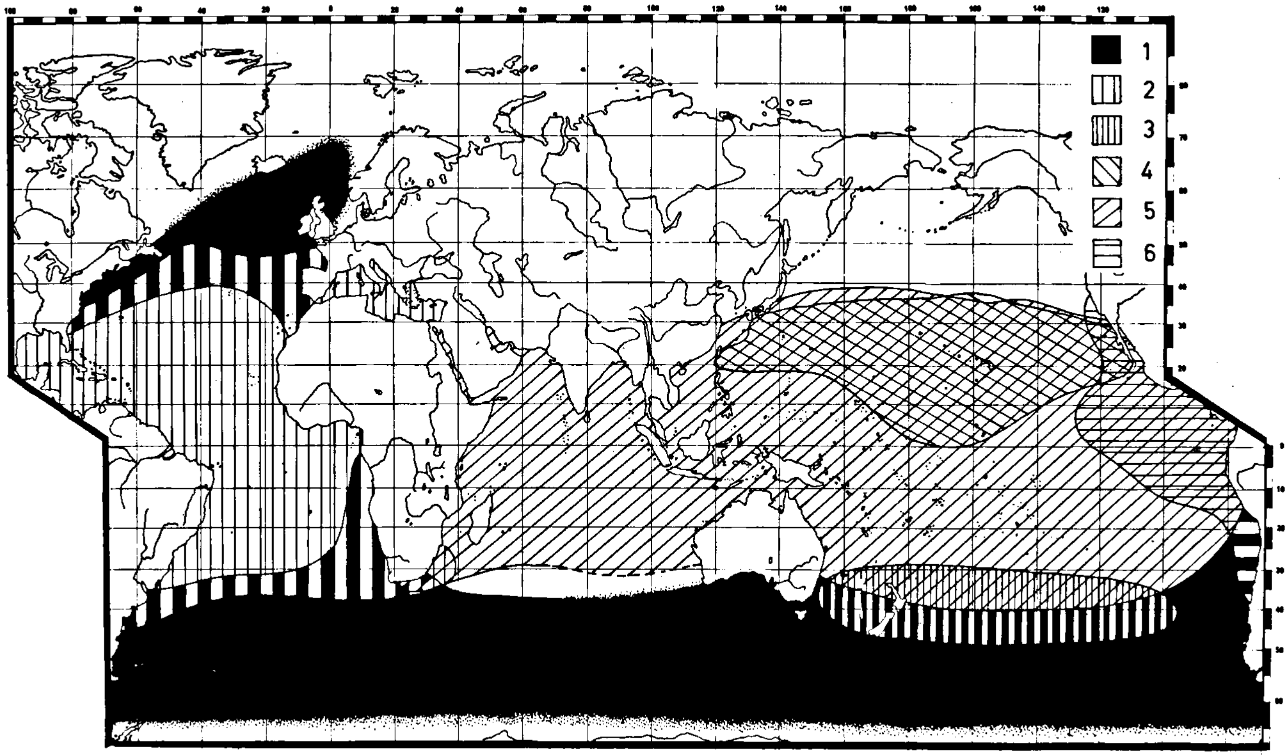
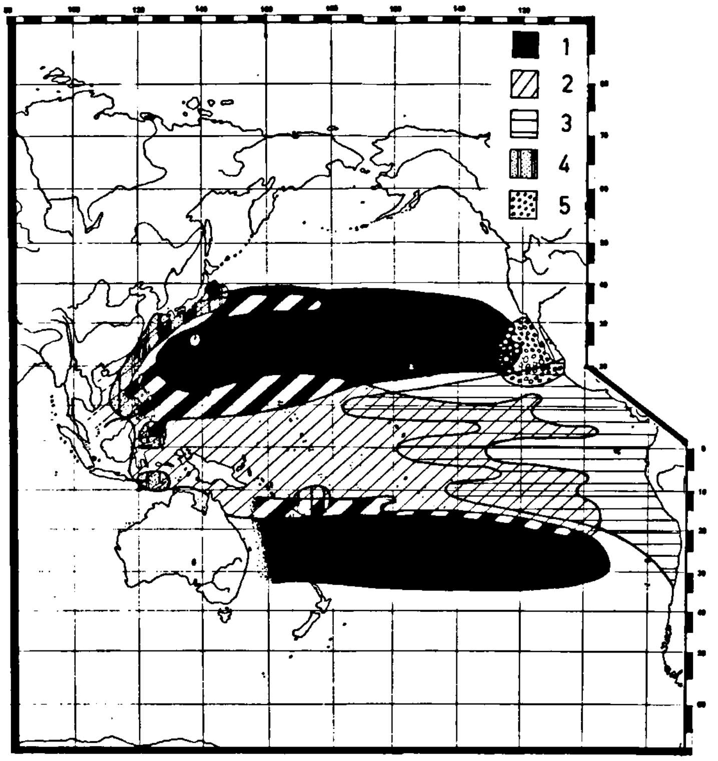


Fig. 2. Distribution of the pteropod *Cavolinia tridentata* with 9 formae. 1 = *tridentata*; 2 = *atlantica*; 3 = *dakarensis*; 4 = *danae*; 5 = *bermudensis*; 6 = *affinis*; 7 = *teschi*; 8 = *occidentalis*; 9 = *kraussi* (after Van der Spoel, 1974).

Fig. 3. Distribution of chaetognaths of the *Sagitta serratodentata*-group. 1 = *S. tasmanica*; 2 = *S. serratodentata serratodentata*; 3 = *S. serratodentata atlantica*; 4 = *S. pseudoserratodentata*; 5 = *S. pacifica*; 6 = *S. bierii* (after Pierrot-Bults, 1974).



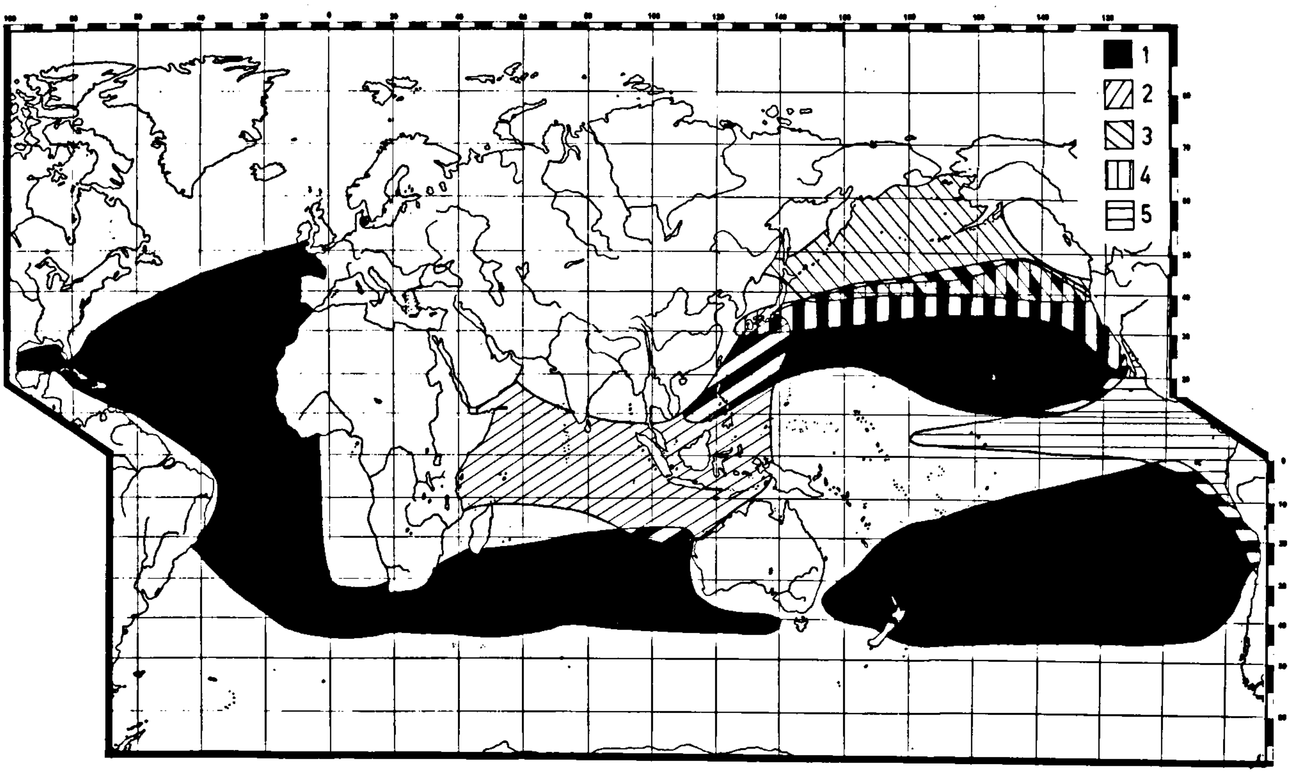


Fig. 4. Distribution of the 5 Pacific categories of the euphausiid *Stylocheiron affine*. 1 = central forms; 2 = western equatorial forms; 3 = eastern equatorial forms; 4 = Indo-Australian forms; 5 = California current forms (after Brinton, 1962).

Fig. 5. Distribution of copepods of the *Eucalanus elongatus*-group. 1 = *E. hyalinus*; 2 = *E. elongatus*; 3 = *E. bungii bungii*; 4 = *E. bungii californicus*; 5 = *E. inermis* (after Fleminger & Hulsemann, 1973).

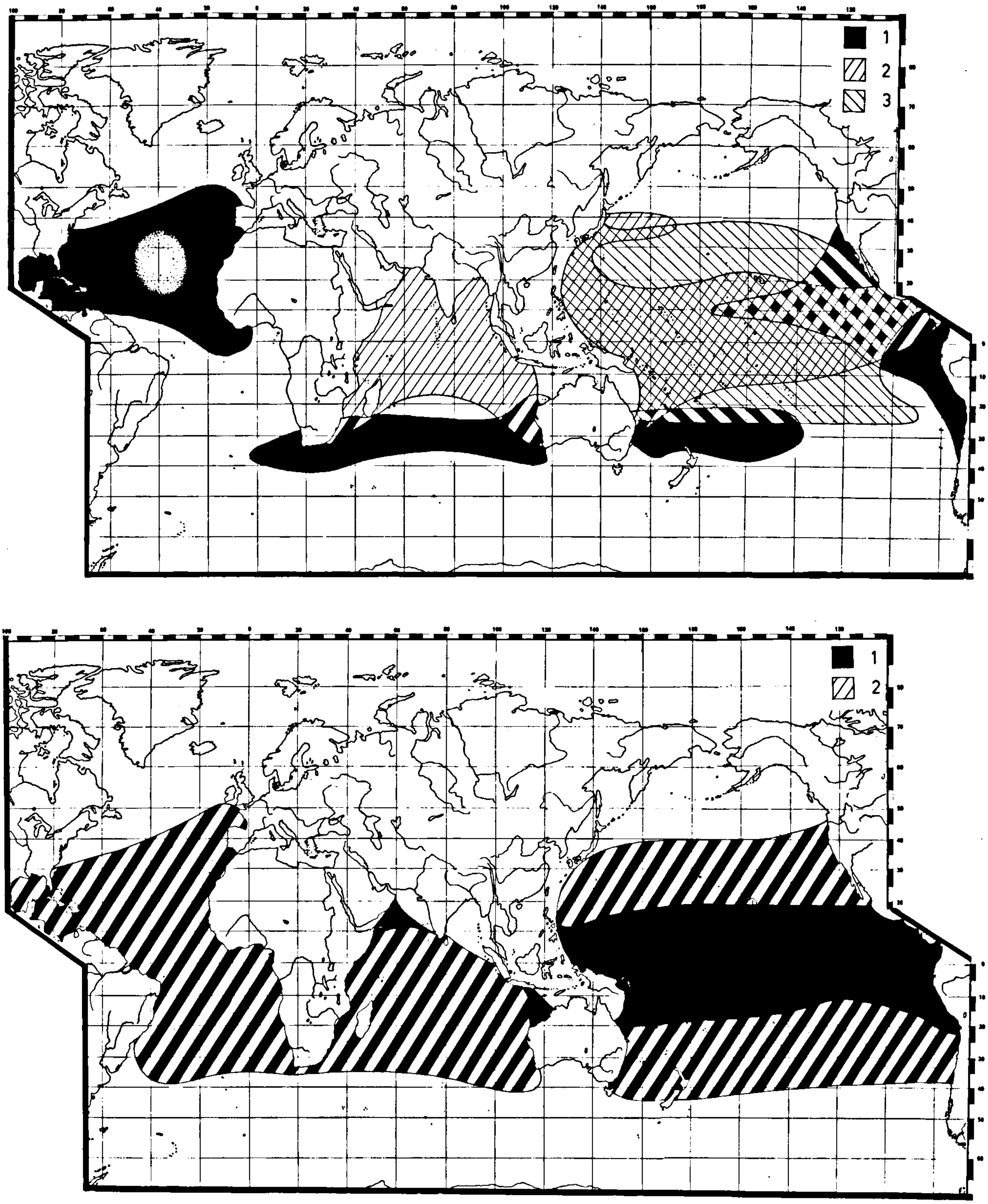
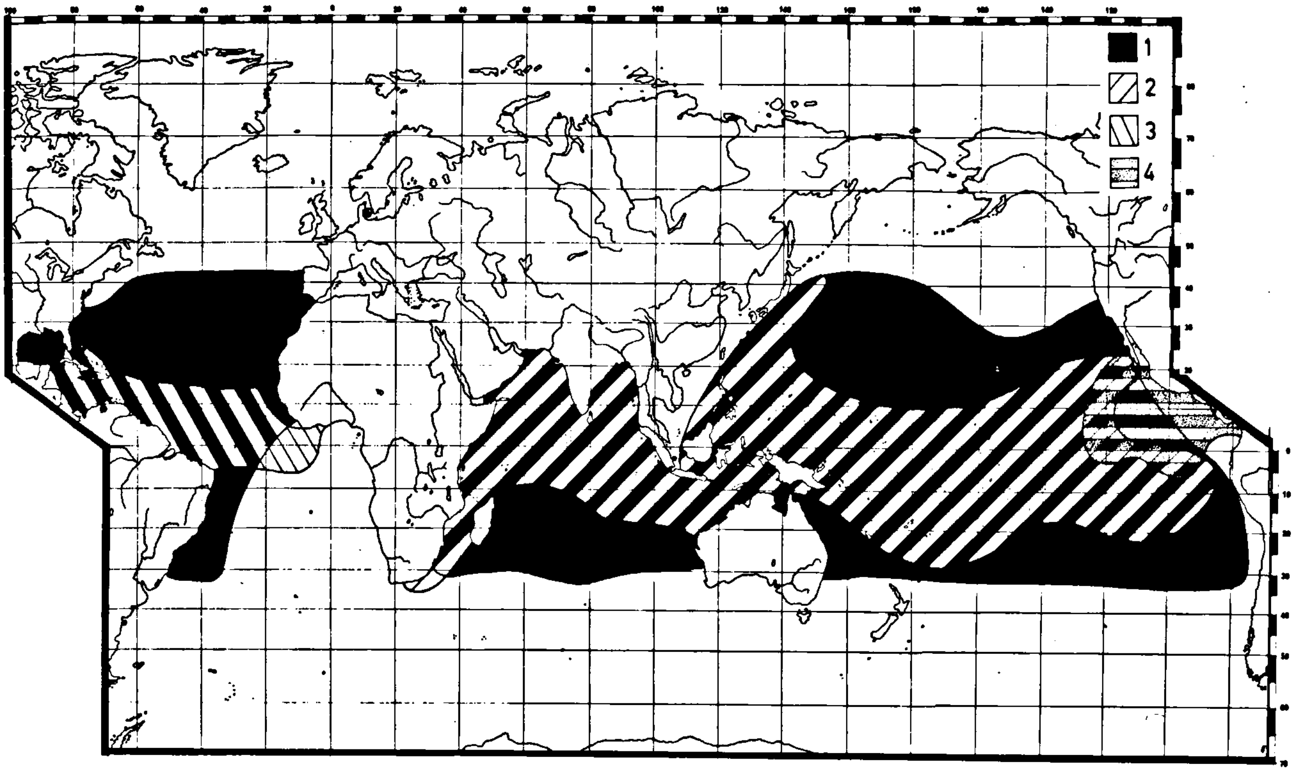


Fig. 6. Distribution of copepods of the *Clausocalanus arcuicornis*-group. A: 1 = *C. jobei*; 2 = *C. minor*; 3 = *C. farrani*. B: 1 = *C. paululis*; 2 = *C. arcuicornis* (after Frost & Fleminger, 1968; Fleminger & Hulsemann, 1973).



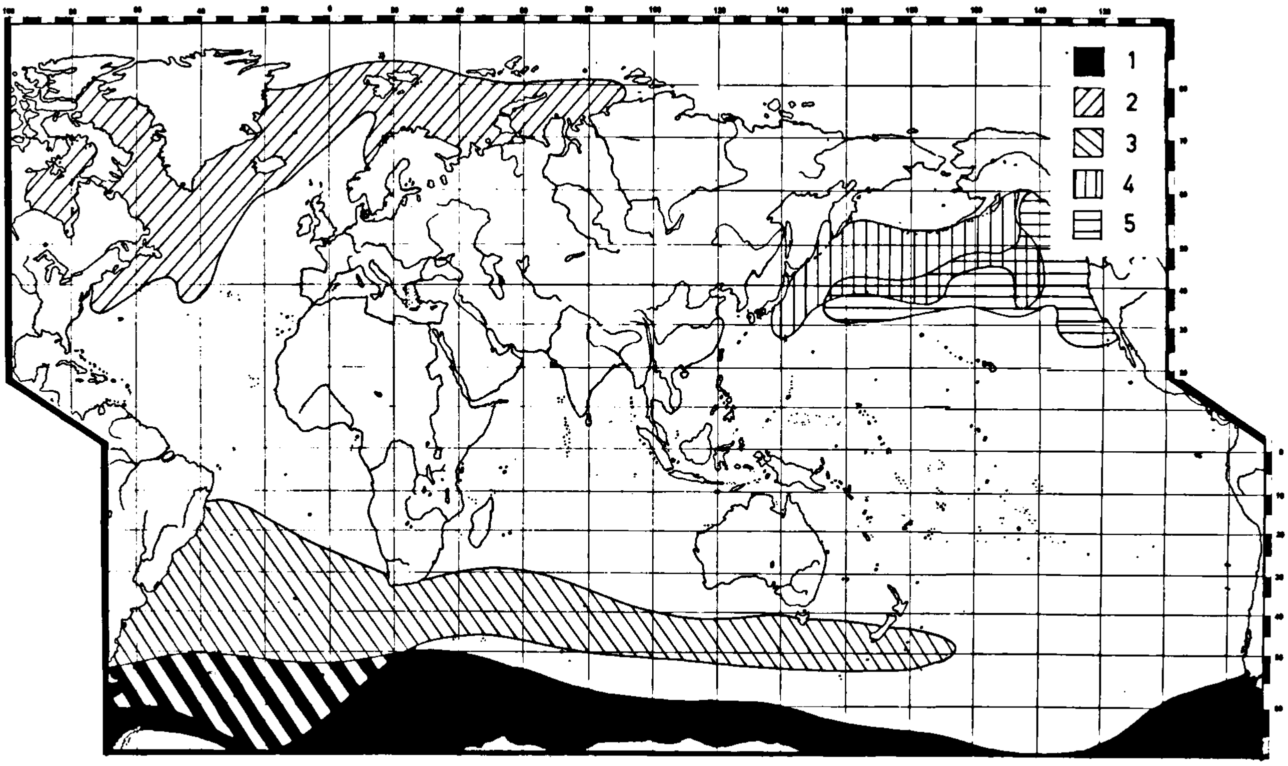


Fig. 7. Distribution of copepods of the *Pontellina plumata*-group. 1 = *P. plumata*; 2 = *P. morei*; 3 = *P. platychela*; 4 = *P. sobrina* (after Fleminger & Hulsemann, 1974).

Fig. 8. Distribution of the pteropod *Limacina helicina* with 5 formae. 1 = *antarctica*; 2 = *helicina*; 3 = *rangi*; 4 = *acuta*; 5 = *pacifica* (after Van der Spoel, 1967).