Macrozooplankton diversity: how much do we really know?

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It is with respect and thanks that we dedicate this paper to dr. Koos den Hartog for his stimulating contribution, both scientific and organizational to the research in taxonomy, biodiversity and biogeography.

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Pelagic species are widely distributed in a horizontal plane and have three-dimensional distributions, since the sea covers about 70% of the surface of the earth, and on average 4 km deep.
For most macrozooplankton and micronekton groups there seems to be no great expectations of finding new taxa with the exception of gelatinous groups and of the deep sea, which is a relatively unknown especially in the benthopelagic zone close to the sea-bed.
However, we do not know very much about variation, either morphological or genetical, within so-called species in different parts of their range. We think we are dealing with single very broadly distributed species, which, in reality, are species complexes consisting of several more or less cryptic species or infraspecific categories. Examples are given in different animal phyla of the same phenomena e.g. that we find variation in consistent geographic patterns. The recognition of the true dimensions of the species diversity and variation in the ocean may give us a new view about the so-called species-poor pelagic system. Much more research is needed before we can have real confidence in our estimates of the numbers of species existing in the pelagic realm.

Introduction

Biogeography and biodiversity in the pelagic realm are not yet fully understood. At the present when we speak about taxonomic diversity, we usually mean the inventory of described species, or known species richness. In that sense the pelagic is indeed relatively poor, especially in relations to the immense volume of the pelagic biome, which is far and away the largest on earth and is truly three-dimensional.

At the higher taxonomic levels, biodiversity is much greater in the sea than on land, e.g. of the 34 animal phyla 29 occur in the sea and 14 are exclusively marine (Pearse & Buchsbaum, 1978; Funch & Kristensen, 1995). However, the pelagic realm harbours only 12 of these 29 phyla so here the diversity is comparable to that on the land (Angel, 1993).

Only about 15% of the recorded animal species are marine, and the pelagic realm is poorer in species than the benthic (May, 1994). For macrozooplankton groups the general opinion is that the epipelagic realm is relatively well documented. For most macrozooplankton and micronekton groups there seems to be no great expectations of finding new species with the exception of gelatinous groups and of the deep sea especially the benthopelagic zone within 100m or so of the seabed, which is an almost unknown habitat; there we can expect to find quite a number of new species. How-
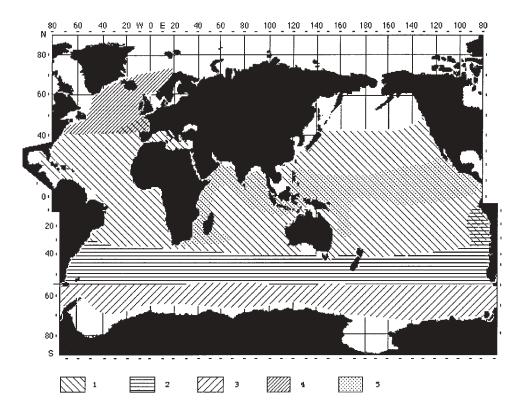
Fig. 1. The distribution pattern of the pteropod *Clio pyramidata*. 1 = *C. p.* forma *lanceolata*, 2 = *C. p.* forma *antarctica,* 3 = *C. p.* forma *sulcata* , 4 = *C. p.* forma *pyramidata,* 5 = *C. convexa*, (redrawn after Van der Spoel & Heyman).

ever, even the relatively well documented epipelagic and mesopelagic species show marked variations when we look closely at the various populations. Recent research of the genetic population structure of wide-spread zooplankton and micronekton species poses the question whether we are really looking at one highly variable species or to a species complex. In those species complexes the morphology of the components only show very slight sometimes hardly discernible differences in different geographic areas. The marked limitation in morphological variation may be the result of the constraints imposed by the environment, which allows little variation on the best possible morphological option, but the underlying genetic and physiological variation might be much greater than we perceive. This question is especially relevant for widely distributed species or for species with interrupted distributional ranges.

Papers dealing with this subject show that there is more variation than we realise and that the so-called broadly distributed pelagic species might consist of a complex of species or infraspecific categories (Van der Spoel, 1967; 1971; Van Soest, 1975; Pierrot-Bults, 1976; Gibbs, 1986; Bucklin et al., 1996; Bucklin, 1996).

As Gibbs (1986) said: "We must look harder at the organisms we work with, ... there are more species out there than we realize".
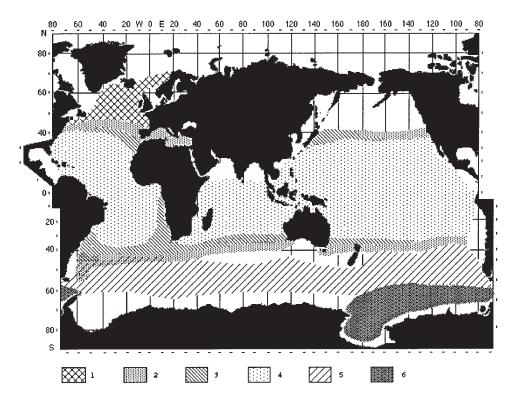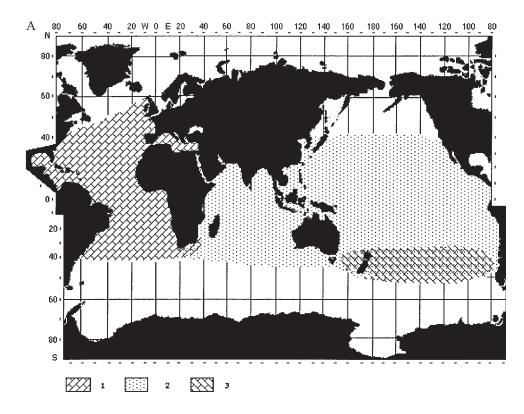
Fig. 2. The distribution pattern of the salps *Salpa fusiformis, S. thompsoni,* and *S. gerlachei,* muscle fibers number for the aggregate form: 1 = *S. fusiformis* with muscle fibers 60-70, 2 = *S. fusiformis* with muscle fibers 50-60, 3 = *S. fusiformis* with muscle fibers 40-50, 4 = *S. fusiformis* with muscle fibers 30-40, 5 = *S. thompsoni* with muscle fibers 130-235, 6 = *S. gerlachei* with muscle fibers 113-159 (redrawn after Van Soest, 1974; 1975).

In this paper the relation of wide distributions of either single species or groups of species with both morphological and molecular variation is discussed. Examples in macrozooplankton and micronekton from different phyla are given to illustrate the point that the patterns of geographic variation are similar in these various groups.

Very wide distribution patterns (70°N-70°S)

An example of a species in this category is the euphausid *Stylocheiron maximum* Hansen, 1908; it is described as having a very wide distributional range and yet lacks infraspecific variation (Van der Spoel & Heijman, 1983; Brinton et al., 2000).

Another species with a similar distribution pattern is the pteropod *Clio pyramidata* Linnaeus, 1767, but in this case the species shows geographic consistent variation in shell shape, and several formae have been established by Van der Spoel (1967) (fig. 1). Formae are infraspecific taxa, which are genetically different in their core geographic area, but gradually changes across the (broad) contact zones (Van der Spoel, 1971).

Fig. 3. The distribution pattern of the chaetognath *Sagitta serratodentata*-group. A: 1 = *S. serratodentata serratodentata,* 2 = *S. pacifica,* 3 = *S. serratodentata atlantica.*

The geographic areas in which these infraspecific taxa are distributed show the same boundaries as taxa, which are described at species level as discussed below.

Geographical variations were studied in the salp, *Salpa fusiformis* Cuvier, 1804, by Van Soest (1972; 1974) and shown to consist of several populations characterized by different numbers of muscle fibers inhabiting different latitudinal areas within its broad geographical range stretching from 70°N-40°S in all three oceans. Van Soest compared his results with those of Foxton (1961) who studied *S. thompsoni* Foxton, 1961, and *S. gerlachei* Foxton, 1961. *S. thompsoni* has a circum-subantarctic distribution, whereas *S. gerlachei* does not (fig. 2). Together these three species range from 70°N to 70°S. The most important difference between *S. fusiformis* and the other two species is in the numbers of muscle fibres. The number of muscle fibers in *S. fusiformis* increases with higher latitudes. *S. thompsoni* , a coldwater species, has a high number of muscle fibres, but *S. gerlachei,* which inhabits even colder waters does not entirely fit this pattern, it has higher numbers of fibres than *S. fusiformi*s, but lower numbers of muscle fibres than *S. thompsoni.*

Another example of a group of closely related species, which together show a 70°N-70°S distribution is the chaetognath *Sagitta serratodentata*-group. This group consists of five species *S. serratodentata* Krohn, 1853, *S. pacifica* Tokioka, 1940, *S. tasmanica*
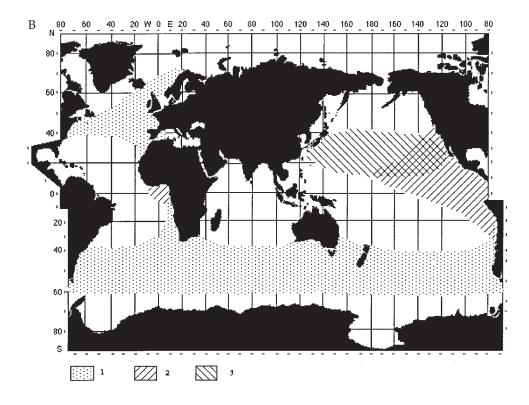
Fig. 3. The distribution pattern of the chaetognath *Sagitta serratodentata*-group. B: 1 = *S. tasmanica,* 2 = *S. bierii,* 3 = *S. pseudoserratodentata.*

Thomson, 1947, *S. bierii* Alvariño, 1961, and *S. pseudoserratodentata* Tokioka, 1939 (fig. 3). *S. serratodentata* is distributed in the tropics and subtropics in the Atlantic, and *S. pacifica* has an identical distribution in the Pacific. In Chaetognatha this is the only known example of a 40°N-40°S distribution with different species inhabiting the Atlantic and Pacific. Usually only species with a more restricted 30°N-30°S distribution show this phenomenon (Fleminger & Hülsemann, 1974; Van der Spoel & Heijman, 1983). *S. tasmanica* is a cold water species with a circumantarctic distribution in the south and a disjunct northern distribution occurring only in the North Atlantic. Whereas in the Pacific there is a transitional subspecies in the south *S. serratodentata atlantica,* and a transitional species in the North, *S. pseudoserratodentata.*

Another example in chaetognaths is the *S. lyra*-group, comprising *S. lyra* Krohn, 1853, *S. maxima* Conant, 1896, *S. gazellae* Ritter-Zahony, 1909, and *S. scrippsae* Alvariño, 1962 (fig. 4). *S. maxima* has a cold water distribution ranging from about 70°N-70°S submerging in the tropics to become a the deep-mesopelagic and bathypelagic species. Whether the northern and southern populations are uncertain. *S. gazellae* has a antarctic/subantarctic distribution, and shows a marked decline in abundance at the Antarctic Convergence. Moreover the populations on either side show morphological differences, viz. a small race occurs to the north and a large race south of the Conver-
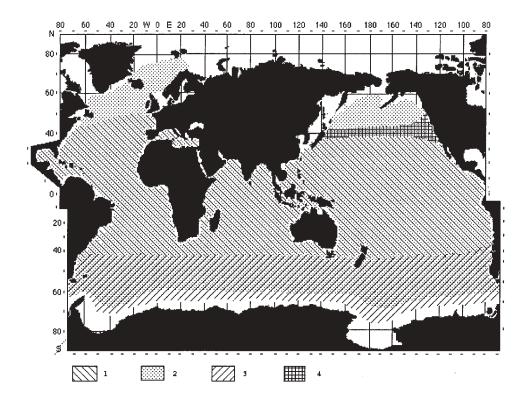
Fig. 4. The distribution pattern of the chaetognath *Sagitta lyra* group. 1 = *S. lyra*, 2 = *S. maxima*, 3 = *S. gazellae,* 4 = *S. scrippsae.*

gence (David, 1955) (fig. 5). The specimens of the large southern race of *S. gazellae* are the largest chaetognaths known.

Tropical-subtropical patterns (40°N-40°S)

This area roughly corresponds to the regions of permanent stratification of the upper ocean (Longhurst, 1999).

This is a very common distribution type in macrozooplankton. An example showing this distribution is the chaetognath *Pterosagitta draco* Krohn, 1853.

An example of a similar distribution pattern is shown by the salp *Pegea confederata* (Forskål, 1775). However this species shows latitudinal variation in number of muscle fibres, where temperate specimens have two to three times as many fibres as tropical specimens (Van Soest, 1975).

In the pteropod genus *Diacria*, we see the same distribution patterns as in *Pterosagitta draco* but with far more variation. The *D. quadridentata* species group inhabits the same geographic area as *Pterosagitta draco,* but it has been differentiated into nine taxa. These are:

1. *Diacria danae* which occurs circumglobally between 40°N-40°S and has both an

equatorial and a central water form;

2. *D. costata* also represented by an equatorial and a central water form;

3. *D. quadridentata* an equatorial Indo-Pacific species;

4. *D. erythra* represented by the sub-species *crassa* endemic to the Red Sea and *erythra* found in the Red Sea and the adjacent Indian Ocean;

5. *D. schmidti* represented by a taxonomic distinct East Pacific population in the oxygen poor waters and a West Pacific population (Van Leyen & Van der Spoel, 1982). The differences between Equatorial and Central water forms in this group are probably explained by fertility differences of the two types of water masses.

In the *Diacria trispinosa* species group a complex development of colour patterns is found. By analyzing these colour patterns the *D. trispinosa* group can be considered to consist of seven species insistently recognizable by the colour
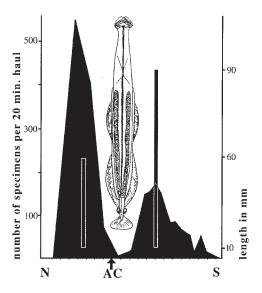

Fig. 5. The variation in the chaetognath *Sagitta gazellae* on either side of the Antarctic Convergence (AC), x-axis distance in hundreds of nautical miles, left y-axis number of specimens per 20 minute haul, right y-axis length in mm of the specimens sampled (redrawn after David, 1955).

patterns of their shells viz. *D. trispinosa* (De Blainville, 1821), *D. rampali* Dupont, 1979, *D. major* (Boas, 1886), *D. atlantica* Dupont, 1979, *D. maculata* Bleeker & Van der Spoel, 1988, *D. piccola* Bleeker & Van der Spoel, 1988, and *D. rubecola* Bontes & Van der Spoel. *D. piccola* is probably a sub-fossil species. *D. atlantica* is represented by two distinct forms, one in the North Atlantic, the other in the upwelling waters off west Africa, a pattern comparable to that of the mesopelagic fish *Benthosema glaciale* (Bontes & Van der Spoel, 1999). These separate taxa cover a range comparable to that of *Pterosagitta draco* the separate ranges are congruent with ranges in other species groups or single species (Bontes & Van der Spoel, 1999) (fig. 6).

Another species complex with an overall 40°N-40°S distribution is that of the copepods of the *Pontellina plumata* -group. Fleminger & Hülsemann (1974; 1977) attributed this group througout its global 40°N-40°S range to *P. plumata* Dana, 1849, but dividing it into a West Atlantic tropical species, *P. platychela* Fleminger & Hülsemann, 1974, an East Pacific species *P. sobrina* Fleminger & Hülsemann, 1974, and an Indo-Pacific species distributed from 30°N-30°S *P. morii* Fleminger & Hülsemann, 1974 (fig. 7).

Another candidate species that requires critical re-examination is the widespread euphasiid species *Stylocheiron abbreviatum* G.O. Sars, 1883. It has a similar 40°N-40°S distribution to that of the chaetognath *Pterosagitta draco*, with the exception of its absence from the Eastern-Pacific oxygen-poor waters. The specimens from the Red Sea and from the nearby Mediterranean of *Stylocheiron abbreviatum* are morphologically distinct. The populations in the Red Sea are thought to be of Indian Ocean origin while those in the
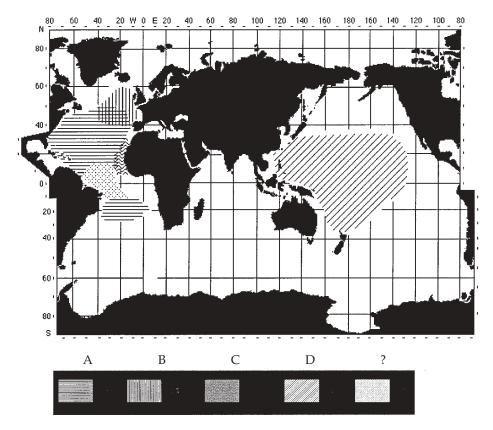
Fig. 6. The distribution pattern of the pteropod *Diacria trispinosa*-group. A = *D. rubecula*, B = *D. atlantica*, C = *D. atlantica* dark form, D = *D. maculata*.

Mediterranean are of Atlantic origin. At the moment there is no evidence that migration through the Suez Canal linked these populations (Casanova, 1990). *S. abbreviatum* is a member of the *S. maximum* species group, which shows the broad 70°N-70°S distribution.

Probable cryptic species have also been described in decapod crustaceans. In his study of *Acanthophyra pelagica* (Risso, 1816) and *Sergestes arcticus* Krøyer, 1855, which occur both in the Mediterranean and in the Atlantic Ocean Casanova (1977) found slight but consistent morphological differences between specimens from the two areas (Casanova, 1977). Whether or not these differences indicate there are cryptic species or merely phenotypic and ecological responses to the rather different environmental conditions prevailing either side of the Strait of Gibraltar has to be established. Both species might be expected to be able to pass through the Strait from the Atlantic, since at night they migrate to shallow depths, but can such migrants survive the warmth of the Mediterranean's mesopelagic zone? These and other species living in both the Atlantic and the Mediterranean have either invaded since the last glaciation, or have survived the Quaternary events and have become adapted to life in waters which are very different from the Atlantic Ocean (Casanova & Rampal, 1998).
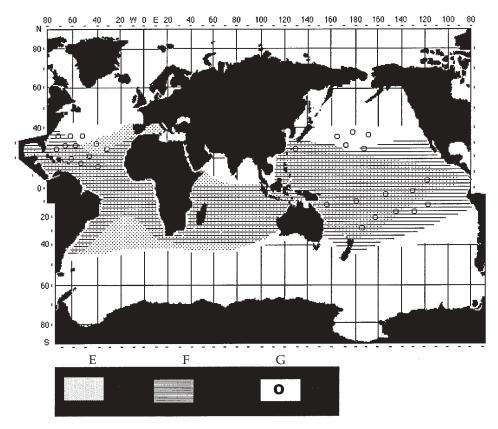
Fig. 6. The distribution pattern of the pteropod *Diacria trispinosa*-group. E = *D. trispinosa*, F = *D. rampali*, G = *D. major* (after Bontes & Van der Spoel, 1998).

That differentiation and speciation can be expected in *Sergestes* is evident as shown by Judkins (1978) who described the *Sergestes edwardsii* species group that as a whole occupies the same geographic area as *Pterosagitta draco* does.

Also in fishes we see similar patterns. Miya & Nishida (1997) presented the case of the "monospecific" *Cyclothone alba* Brauer, 1906 (Family Gonostomatidae); a shallow mesopelagic (300-500 m) micronektonic with a distribution in all three oceans from about 30°N to 30°S. The authors carried out an analysis of 16S ribosomal RNA of specimens from different locations of *C. alba* and found five genetically distinct subgroups within *C. alba* with complete congruency between molecular differences and geography (fig. 8). The central North Pacific specimens are more closely related to the western North Atlantic, and the western North Pacific specimens are more closely related to the eastern equatorial Indian Ocean populations than either of these to the other Pacific specimens. The authors explain this by the connection through the Panama isthmus of the tropical Pacific and Atlantic about three million years BP. They also compared these results with analyses for two other *Cyclothone* species. The genetic differences within *C. alba* were as great as those between *C. alba* and *C. signata* Garman, 1899, and *C. braueri*
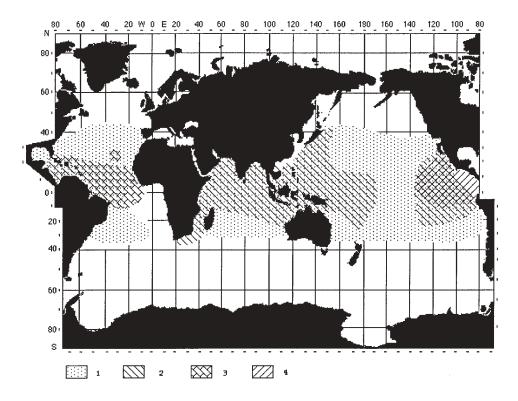
Fig. 7. The distribution pattern of the species of the copepod genus *Pontellina* (redrawn after Fleminger & Hülsemann, 1974). 1 = *P. plumata*, 2 = *P. morii,* 3 = *P. platychela*, 4 = *P. sobrina.*

Jespersen & Tåning, 1926, its closest relatives, both of which have more restricted allopatric ranges. Together these species show a 40°N-40°S distribution (fig. 9).

Other examples of variation correlated with geographic distribution are found in myctophid fishes. A study of the circumglobal myctophid *Ceratoscopelus warmingii* (Lütken, 1892) (= *C. townsendi* Eigenmann & Eigenmann, 1889) by Badcock & Arujo (1988) revealed six morphological variants and thirteen geographically and meristically distinct populations. Badcock & Arujo (1988) concluded albeit reluctantly that despite these variations they should still be regarded as one species, but recognizing that new evidence may ultimately prove them wrong. Gartner (1998) concluded after revisiting the literature in the context of his own data on age and growth patterns, meristics, morphometrics and reproductive biology, that not all variation appears to be ecophenotypic, and called for molecular studies of this "species" to establish whether or not these variants are genetically distinct.

Gibbs (1986) studied the mesopelagic genus *Eustomias* Vaillant, 1888, subdividing it into about a hundred species whereas before in 1983 only about 47 were recognized .The bases for splitting these species were that the minor morphological variations which were not only consistent in both sexes but also showed geographical consistency.

For example Gibbs (1986) divided two species (recognized in 1964) into 24 species
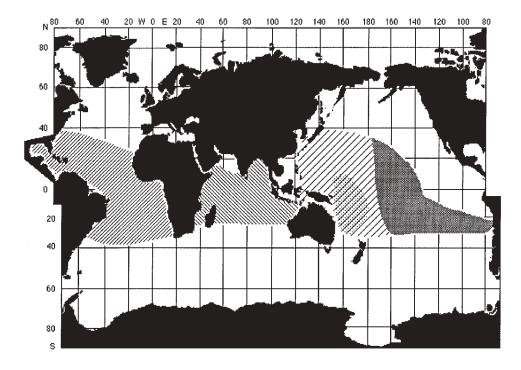
Fig. 8. The distribution pattern of the 5 different populations of the fish *Cyclothone alba*. (redrawn after Miya & Nishida, 1997).

after detailed examination of the morphology of specimens from different parts of the ocean. The ranges of these species are the same as for other distinctive mesopelagic species, which have relatively restricted geographical range.

A comparable case is that of the pteropod *Cavolinia longirostris* which had earlier been considered to show minor variations, but a critical re-examination by van der Spoel has resulted in the description of a new genus *Diacavolinia* with 24 species. In this case the species complex has an overall 40-40 distribution together with an oceanic/epipelagic pattern.

Neritic/distant neritic patterns

Distribution patterns in neritic and distant neritic regions are far more geographically restricted than in the open ocean. Boundaries to species distributions roughly coincide at the same latitudes as the oceanic boundaries e.g. polar, subpolar, subtropical and tropical, but because of more possibilities of isolation, certainly in the east-west ranges, there is a tendency to local endemism.

An example of a distant neritic species for which infraspecific variation is recorded is the chaetognath *Sagitta elegans* Verrill, 1873, with 3 subspecies, *S. elegans elegans*, *Sagitta elegans arctica* Aurivillius, 1896, and *Sagitta elegans baltica* Ritter-Zahony, 1911,
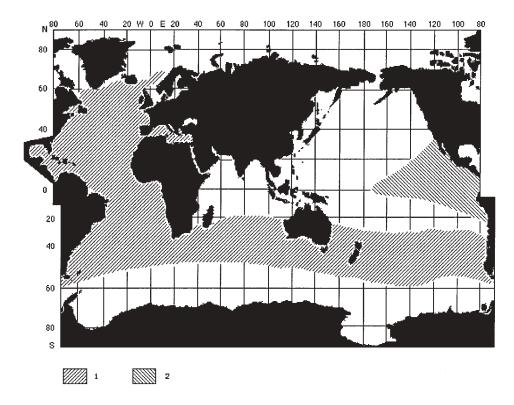
Fig. 9. The distribution of the fishes (1) *Cyclothone signata*. and (2) *Cyclothone braueri* (redrawn after Miya & Nishida, 1997).

which are distributed in the Subarctic, Arctic and Baltic respectively. Research on genetic variation is urgently needed here to determine the exact taxonomic status of these taxa.

The North-Atlantic copepod *Nannocalanus minor* shows a distant neritic distribution, but in this species no subspecies were recorded. However, recent research on mitochondrial 16S rRNA in these copepods revealed population genetic structure correlated with distribution patterns and dispersal routes (Bucklin et al., 1996). *Nannocalanus minor* shows two different genetic types in different parts of the North Atlantic Ocean congruent with ocean current patterns in that part of the ocean (Bucklin, 1998) (fig. 10).

The copepod *C. finmarchicus* (Gunner, 1736) has a widespread distribution in the northern part of the North Atlantic. However, critical examination of populations within various parts of this range established that *Calanus finmarchicus* has a large scale population genetic structure which is correlated with geographic patterns related to the physical circulation in the North Atlantic (Bucklin et al., 1996).

Molecular analysis has started on the genetic structure of the neritic chaetognath species *Sagitta setosa* Krohn, 1853 (Peijnenburg et. al., in press). This species has a disjunct distribution with populations in the North Sea and others in the Mediterranean and Black Sea (fig. 11). Morphological differences, mainly length related, have been
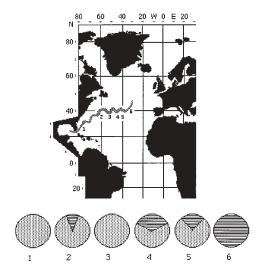
previously reported (Peijnenburg & Pierrot-Bults, in press) but have not been conclusive. Molecular analyses by Peijnenburg et al. (in press) have recently shown clear distinctions between the North Sea and the Mediterranean populations, and the Black Sea specimens form a distinct group within the Mediterranean. Whether this disjunct distribution was caused by glacial cycles is as yet unclear.

Discussion

Species in different phyla show similar distribution patterns. If we look at the distribution patterns of the species-groups discussed above we see that the integrated ranges of the separate taxa within each closely related species group match the patterns of the very widely spread species. According to Van der Spoel & Heijman (1983) species groups with a global distribution are composed of: an Indo-Pacific warm-water taxon (30°N-30°S), a circumglobal tropical-subtropical taxon (40°N-40°S), and a group of central water taxa or transitional water taxa.

Fig. 10. The distribution of two different genotypes in different populations of the copepod *Nannaocalanus minor* in the North Atlantic Ocean. The numbers in the map correspond with the numbers in the circles below representing the proportion of the genotypes in the different areas. 1 = Florida Strait, 2-5 are from within the North Atlantic current, 6 = NE Atlantic (redrawn after Bucklin, 1996).
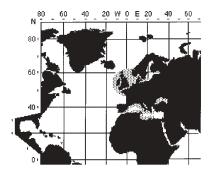
Infraspecific variants show geographic patterns similar to the ranges of single species. The examples given above show that pelagic species, which are widely distributed, probably consist of complexes of genetically different entities which may either be infraspecific or cryptic species (Van der Spoel, 1967; 1971; Van Soest, 1975; Pierrot-Bults, 1976; Bucklin et al., 1996; Bucklin, 1998, Miya & Nishida, 1997, Peijnenburg et. al., in press). Van Soest (1975) pointed out that in the open ocean it takes time to spread genetic information across the immense species ranges in salps giving rise to infraspecific categories, which may lead to species. Another example of morphological variation is the *D. trispinosa* -group, which on closer analysis revealed a consistent geographic pattern and is, therefore, considered to be more than mere phenotypic variation.

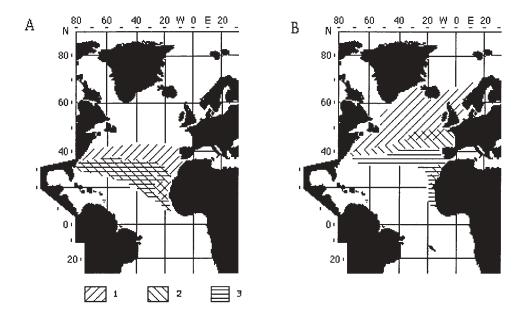Fig. 11. The distribution of the chaetognath *Sagitta setosa*.

Fig. 12. The distribution of water masses during (A) the last ice-age (approximately 18000 years BP) and (B) recent (after Angel, 1976). 1 = subpolar; 2 = transitional; 3 = subtropical.

Even within the closely related species groups mentioned in this paper there are questions left unanswered. The morphological differences found in *Sagitta gazellae* and the probable discontinuous distribution of *Sagitta maxima* (both *Sagitta lyra*-group), and the discontinuous distribution of *Sagitta tasmanica* (*Sagitta serratodentata*-group) raises the question whether they really are one species or whether there are several cryptic species involved (Pierrot-Bults, 1998).

The biogeographic patterns in different groups are rather similar, indicating that environmental factors play a major role. That these patterns are formed in different groups by different kinds of taxa, either species, subspecies, formae, or races, may be explained by differences in reproductive behaviour in those groups. However, in one group as shown by pteropods e.g. *Diacria*, species, subspecies, forms and ecotypes may constitute the components of a pattern.

The possible mechanisms of isolation and speciation, whether intrinsic (genetically determined) or extrinsic (historical and environmentally determined), are not well understood.

To find out whether genetic differences also mean genetic isolation one should study the interactions and interbreeding of the taxa or populations in the different groups.

Speciation rates in the pelagic environment have been thought to be slow (Pierrot-Bults & Van der Spoel, 1976), but the more detailed morphological and molecular studies mentioned in this paper point to more variation and more cryptic species than currently recognized. Apparently the pelagic environment plays an important role in the way the patterns develop. Consequently effects of watermass boundaries and cli-

matic zones on genetic population structure of marine populations need to be studied. At the moment we do not know oceanic macrozooplankton species which are endemic to a single watermass, except in the Antarctic (the East Pacific water mass distribution is considered a distant neritic type of distribution). Longhurst's (1998) division in oceanic faunal provinces based on productivity regime modelling cannot be traced by single species distributions. However, Beaugrand et al. (2002) did find similar divisions in the North Atlantic Ocean based on faunal assemblages of copepods.

Much more research is needed to come to a definite estimation of the number of species existing in the pelagic realm.

More knowledge about genetic diversity might also support Longhurst's faunal division and give more insight in functional aspects of diversity.

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