BIOGEOGRAPHICAL STUDIES OF MARINE PHYTOPLANKTON*)

BY

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Introduction

Quantitative biogeographical studies of marine phytoplankton have lagged considerably following the appearance of GRAN's (1902) classical paper more than fifty years ago. In this work he outlined his scheme of "plankton elements" which supplanted CLEVE's (1897, 1900) concept of "plankton types" and has remained of fundamental importance to marine biogeography. Since significant progress has been made in floristic studies following Gran's publication, it seems appropriate at this time to consider these advances and arrive at some general features of phytoplankton biogeography. The fact that culture techniques in phytoplankton research is now a certainty also demands a renewed interest in biogeographical problems. It is clear that a satisfactory knowledge of the underlying biogeographical factors can be obtained only by combining floristic studies—where a species is found or what species are found in a given area—with culture studies—why a species is found in a given area and why it is abundant or unimportant. NORDLI's (1957) study on Ceratium reveals how successful this approach can be.

Results of experimental studies have served as standards in discussing or interpreting phytoplankton dynamics. Unfortunately most of the species thus far studied are among the less important in nature or are forms whose metabolic activities probably are not significantly representative. For example, the "guinea pig" Nitzschia closterium var. minutissima appears not to be a diatom at all but the chrysophycean Phaeodactylum tricornutum (HENDEY 1954). Biogeographical studies, however, can provide information as to what organisms are representative of the major thermal zones or specific ecological conditions. Following appropriate selection, experimental treatment then can provide data applicable to these environments or conditions. It is unlikely that one or two species can provide universally applicable data—the metabolism of an arctic

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representative undoubtedly differs from that of a tropical one. Furthermore, it is becoming especially important to know the distribution of a species since Braarud's (1951) observations suggest the existence of clones in nature: species common to the waters of Norway and North America may represent discrete physiological units.

Thus the author has attempted to summarize the more important concepts of phytoplankton biogeography as revealed in part by representative arctic, antarctic, tropical and cosmopolitan species. In mapping their distribution the investigation most representative of a given region was selected over minor studies, except when temperature and salinity data were included. These data were compiled irrespective of the accompanying degree of abundance of the species in question. Biogeographically, knowledge of the extremes of tolerable temperature and salinity is equally important to knowing optimal requirements.

The Distribution of Representative Phytoplankton Species and the Accompanying Temperature and Salinity Conditions

Antarctic Representative: Thalassiosira antarctica Comber

Thalassiosira antarctica is a characteristic and important component of the antarctic flora. Its distribution (Fig. 1) has been charted from the following sources:

Boden 1949; Hart 1934; Hendey 1937; Karsten 1905a; Mangin 1915, 1922; Manguin 1954.

T. antarctica appears to be circumpolar, a distribution favored by the prevailing current system (Sverdrup, Johnson and Fleming 1942, p. 615). Indeed, the majority of antarctic phytoplankton species are probably circumpolar considering the uniform environmental conditions within that area associated with the current systems. Latitudinally, T. antarctica is confined almost exclusively to waters within the Antarctic Convergence; occasionally it is encountered north of this boundary. Thus Hendey (1937) recorded T. antarctica near Cape Town and Cape Horn at temperatures of 8.4° and 17.2°C while Cleve (1901) found it in the "Southern Indian Ocean at 45°S, 26–34°E" at 6.5°C. However, the accompanying temperatures indicate that these occurrences undoubtedly resulted from current transport rather than local, independent stocks.

The conditions of temperature and salinity accompanying T. antarctica's occurrence are plotted (Fig. 2). The salient features of this relationship are probably applicable to antarctic phytoplankton in general. It is seen that in nature T. antarctic is stenothermal and stenohaline. The observed temperature

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range extends from $-1.77^\circ$ to $3.49^\circ$C. It is well represented at temperatures below $0^\circ$C, resulting in a mean of $-0.05^\circ$C for 228 observations (including those not plotted$^1$). Its observed salinity range is similarly narrow, 32.61–34.540/00. These salinity values reflect the influence of melting ice.

Except for localized conditions, antarctic species in general probably do not have to contend with marked salinity fluctuations or salinities much under 32.000/00. The degree of dilution resulting from ice-melting is limited because of the prevailing temperature conditions, and, in addition, the re-formation

$^1$ Those data not plotted for the species under consideration, as noted, include only those which were not accompanied by the corresponding temperature or salinity, or those which were duplicates.

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of ice imposes a limit on the reduction in salinity. These factors, coupled with the effects of turbulence, would maintain the high minimal salinity with which \textit{T. antarctica} and other antarctic species must contend.

The infrequency of \textit{T. antarctica} in adjacent northerly regions, even though transport is accessible, undoubtedly results from its "polar" requirements. Thus a thermal barrier confines \textit{T. antarctica} principally to the region within the Antarctic Convergence. Although specific differences in tolerance can be expected, temperature probably determines the northward extension of all antarctic species. But further observations are needed to establish whether the Antarctic Convergence circumscribes the natural habitat of all true antarctic species.

\textit{It may be concluded that for a species to thrive in antarctic waters it must be equipped to tolerate a high and fairly constant salinity and, more critically, extremely low temperatures.} Only a few dinoflagellates and perhaps no coccolithoporids can meet these requirements. Diatoms, on the other hand, are well represented. Other antarctic species include:

\begin{eqnarray*}
\text{Chaetoceros criophilus} \text{ Castr.} & \quad & \text{Fragilaria curta} \text{ V. H.} \\
\text{Chaetoceros neglectus} \text{ Karst.} & \quad & \text{Peridinium applanatum} \text{ Mangin} \\
\text{Eucampia balaustium} \text{ Castr.} & \quad & \text{Synedra reinboldii} \text{ V. H.}
\end{eqnarray*}

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Arctic Representative: *Thalassiosira hyalina* (Grunow) Gran

*Thalassiosira hyalina* has been selected to show the distribution of an arctic species (Fig. 3). The taxon as defined by Hustedt (1930) was used. The following sources were used in charting its distribution:

AIKAWA 1936; Bigelow 1926; Braarud 1935; Cleve and Grunow 1880; Damas and Koefoed 1909; Davidson 1931; Fish 1925; Gaarder 1938; Gran 1897a, 1897b, 1897c, 1900, 1902, 1929; Gran and Braarud 1935; Grøntved and Seidenfaden 1938; Hjort and Gran 1899; Jørgensen 1905; Kisselev 1925; Knudsen and Ostenfeld 1899; Marshall 1955; Ostenfeld 1910; Paulsen 1904; Ramsfjell 1957; Skvortzow 1931; Smayda 1958; Wirketiss and Kisselev 1935; Østrup 1895.

The principle features of *T. hyalina*’s distribution suggest an eastern arctic tendency, although additional data might reveal it as circumpolar. The pronounced arctic character of *T. hyalina* is readily discernible. It is resident in all the major polar currents and its distribution closely parallels their courses. It occurs in the East Greenland Current, through which it is in contact with the Labrador Sea stock. It has penetrated into Hudson Bay and through the Labrador Current has extended its range into the Gulf of St. Lawrence (Gran 1919) and south to Nova Scotia. Occasionally stray cells of *T. hyalina* are found in the Gulf of Maine proper and even at Cape Cod.

Within the Norwegian Sea it is confined almost exclusively to the western half where it is a component of the “drift-ice flora”. Its absence from the eastern half, through which the warm Gulf Stream flows, is sharply defined. It is also absent along the western coast of Iceland where the warm Irminger Current passes. Neither does it occur off southern Iceland where warm Atlantic water is found; but it is a component of the East Icelandic Current. These features readily confirm its arctic character.

The isolated observations of *T. hyalina* in the Barents Sea, Kara Sea and off Japan probably form part of a continuous distribution. AIKAWA (1936) states *T. hyalina* to be common in northern Japanese waters, and Kisselev (1933) has noted the similarity in species composition between the Okhotsk Sea and the Arctic Polar Basin. Thus there is ample reason to believe that *T. hyalina* is more common in this region than its plotted distribution reveals.

The absence of *T. hyalina* along the Alaskan archipelago is unexpected. Cupp (1937) studied the phytoplankton at Scotch Cap, Alaska for seven years and failed to observe it. More modest observations have confirmed this (AIKAWA 1936; Motoda and Kawarada 1955). This condition, on the basis of the data available, persists even though AIKAWA (1936) claims that an active seeding of phytoplankton from northern Japanese waters takes place into this area—

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Fig. 3. The geographical distribution of *Thalassiosira hyalina*.

an avenue readily accessible to *T. hyalina*. Furthermore, the Japanese stock probably was derived originally from the Arctic and is still being supplemented\(^1\). Should this be a valid assumption, then one would expect that subsequent transport through the Bering Strait would lead to its establishment in the

\(^1\) The possibility that *T. hyalina* does not occur in Japanese waters must be kept in mind. Aikawa appears to be the only investigator to cite its presence by name. The predilection of Japanese students to lump species according to genus has made it impossible to check Aikawa’s claim. Skvortzow’s report that *T. hyalina* was found near Tsushima Island is suspect since his drawing also bears a resemblance to *T. rotula*, Meun.
eastern Pacific as well. But it remains for future observations to determine whether *T. hyalina* is found north of the Alaskan archipelago.

It is of interest to note that relatively higher temperatures prevail on the American side of the Bering Sea than in northern Japanese waters or the Bering Strait. This prompted Ekman (1953, p. 167) to state that “the American side of the Bering Sea is not distinctly arctic as regards temperature until we reach the Bering Strait”. Thus a thermal barrier might prevent *T. hyalina* and other strictly arctic species from inhabiting these waters. Mann (in Bigelow and Leslie 1930) reports *T. hyalina* from Monterey Bay, California. However, judging from its distribution pattern and temperature “requirements”, this is probably a misidentification.

In spite of suitable temperatures, *T. hyalina* appears to be only an unimportant visitor in isolated fjords along the Norwegian coast. It occurs consistently at the Lofoten Islands, and Gran (1902) also mentions its presence along the Finnmark coast, although no specific details are given. Stad, south of the Romsdalsfjord, represents its southern-most known extension. The question mark drawn in the Kattegat (Fig. 3) represents Cleve-Euler’s (1937) claim that *T. hyalina* occurs there. She attributed it as a visitor from the Baltic Sea and this led Gronntved (1950) to designate *T. hyalina* as having a bicentric distribution: found in the Arctic and Baltic Seas. However, numerous investigations in adjacent waters, including the Baltic, have failed to reveal *T. hyalina*. (Cleve-Euler (1917) reported this species from the Skagerrak as “united with *T. gravida*”). It seems likely that Cleve-Euler misidentified this species, and she herself professed uncertainty in her identification. Thus it is questionable if this species occurs in the Kattegat and Baltic, or that it has a bicentric distribution.

Hendey (1937) claimed to have found *T. hyalina* at two stations near Cape Town, Africa at temperatures of 13.97° and 15.33°C, respectively. He acknowledged that previously it was recorded only from northern waters and concluded “its occurrence off the coast of South Africa is somewhat unusual, it had probably been carried northeastwards from the neighborhood of Bouvet Island”. However, other investigations in the Antarctic have failed to record it as yet.

The few data available for the conditions of temperature and salinity under which *T. hyalina* has been encountered are presented (Fig. 4). The salient features of this relationship appear to be significantly representative of arctic phytoplankton in general (Smayda 1958). Like its ecological homologue *T. antarctica*, *T. hyalina* is both stenothermal and stenohaline. The temperatures accompanying its presence range from −1.35° to 9.03°C, the mean of 125 observations (including those not plotted) being 2.3°C.

The evidence is suggestive that those occurrences of *T. hyalina* at temper-
atures above 5°C represent remnants of earlier populations or merely a transport, rather than instances of active growth. For example, GRAN (1919) found this species during May in the Gulf of St. Lawrence, but not in June when the surface temperatures exceeded 5°C. DAVIDSON (1931) found only traces of T. hyalina during August and September in Hudson Bay at temperatures between 4.8° and 8.6°C. Other investigators likewise have found only stray cells of T. hyalina above 5°C.

Except for one observation at 27.11°/oo, T. hyalina has been observed only in waters above 31°/oo, the mean being 33.88°/oo. The mean value reflects the effect of melting ice and verifies the predominance of T. hyalina in polar oceanic water masses rather than neritic ones throughout its range. T. hyalina, hitherto, has been called a neritic species.

The conditions of existence as summarized for T. antarctica apply in general to T. hyalina as well. However arctic species do not have the uniformity of environmental conditions so typical of the Antarctic. The presence of warm Atlantic water within the Norwegian Sea not only renders a significant area uninhabitable but also divides the polar western Norwegian and Barents Seas to near Spitzbergen, ice-free only during the summer. As inhabitants of polar currents which flow away from the Arctic, arctic species are subjected to higher and more variable temperatures throughout their range as a whole than are antarctic species. This has contributed to an essential difference between the communities inhabiting the two polar regions. Whereas the seasonal antarctic flora is comprised principally of true antarctic forms (HART 1942), arctic
diatoms are in the minority and relatively unimportant in their habitat. In fact, *Chaetoceros furcellatus* Bail. is outstanding among arctic diatoms in that it appears to be the only one quantitatively significant throughout most of its range. This undoubtedly is related to its ability to withstand relatively higher temperatures than the other arctic forms (Table 1). But it is premature to ascribe temperature as the sole mechanism hindering the success of the arctic flora to attain the dominance enjoyed by its antarctic counterpart. Culture studies on representative forms are needed.

Other arctic species include:

- *Achnanthes taeniata* Grun.
- *Bacterosira fragilis* Gran
- *Chaetoceros furcellatus* Bail.
- *Fragilaria oceanica* Cl.
- *Ceratium arcticum* (Ehrbg.) Cl.
- *Navicula vanhöffenii* Gran

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Tropical Representative: *Planktoniella sol* (Wallich) Schütt

*Planktoniella sol* has been selected to show the distribution of a tropical form (Fig. 5). The following sources were used to chart its distribution:

- Aikawa 1930, 1936; Allen and Cupp 1935; Corlett 1953; Gaarder 1951; Gilbert and Allen 1943; Hart 1934; Hendey 1937; Hensen 1911; Hentschel 1932; Karsten 1907; Knudsen and Ostenfeld 1900; Krasske 1941; Lemmermann 1899; Mangin 1922; Ostenfeld 1898, 1902, 1915; Ostenfeld and Schmidt 1901; Pavillard 1925, 1931, 1935; Schröder 1906; Silva 1953, 1956a, 1956b; Skvortzow 1931; Subrahmanyan 1946; Takano 1955; Wandel and Ostenfeld, 1898; Wood 1950.

*Planktoniella sol* is a circumtropical diatom and found principally in oceanic regions. The gaps in its distribution within the tropics, as charted, reflect areas mainly uninvestigated. It is a component of all the major tropical current systems which ensures a wide distribution. After plotting *Planktoniella sol*'s
distribution it became apparent that it is not a tropical species in the strictest sense. Its range extends into subtropical regions and it is even found in the temperate Peruvian Current. It is unknown, however, whether it is a permanent component of this current or whether its occurrence coincides with maximum temperatures. It is also found near 60°N where it can be used as an indicator species of Gulf Stream water near its entrance into the Norwegian Sea.

The conditions of temperature and salinity accompanying *Planktoniella sol*'s occurrence in nature show it to be eurythermal and stenohaline (Fig. 6). Its temperature range extends from 1.9° to 30.5°C. HENDEY (1937) recorded *Planktoniella sol* at two stations where the temperature was 1.9° and 5.2°C. Since these occurrences undoubtedly resulted from current transport, they are
omitted in calculating a mean temperature of 19.2°C (101 observations, including those not plotted). The salinity range found for *Planktoniella sol*, 33.760/00 to 39.150/00, reveals its tropical character. A mean of 35.710/00 is obtained.

The ability of *Planktoniella sol* to withstand a wide temperature range, probably not shared to such a degree by the majority of tropical species, would account for its presence in extra-tropical areas. Since effective cell division is not expected to occur throughout this temperature spectrum, its observed tolerance of temperatures below 10°–15°C may represent sterile distributions. Were effective division possible at these lower temperatures, it would be expected that *Planktoniella sol* would be a more frequent member of the temperate phytoplankton.

Its absence from neritic areas may result from its salinity requirements in combination with some other factor. It is doubtful that salinity alone determines this exclusion.

*It may be concluded that in order for a species to inhabit the tropics it must be equipped to tolerate very high temperatures and, secondarily, high salinities. Coccolithophorids and dinoflagellates have been especially successful in meeting these requirements. There are relatively few true tropical pelagic diatoms, but a surprisingly large number of temperate species thrive in tropical waters. Some tropical species are:*

- *Chaetoceros laevis* Leud.-Fort.
- *Coccolithus sibogae* (Web. v Bos.) Schill.
- *Gossleriella tropica* Schütt
- *Hemiaulus membranaceus* Cl.
- *Peridinium elegans* Cl.
- *Rhizosolenia robusta* Norm.

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Cosmopolitan Representative: *Thalassionema nitzschioides* Grunow

*Thalassionema nitzschioides* has been selected to show the distribution of a cosmopolitan species (Fig. 5). The taxon as defined by Hustedt (1937) was used. The following sources were used to chart its distribution:

Aikawa 1930, 1936; Allen and Cupp 1935; Bigelow 1926; Braarud 1935, 1945a; Braarud and Bursa 1939; Braarud, Gaarder and Grøntved 1953; Cleve-Euler 1917, 1949; Corlett 1953; Cupp 1937; Czapek 1909; Davidson 1931; Ercegovic 1936; Fish 1925; Gaarder 1951; Gilbert and Allen 1943; Gran 1915; Gran and Braarud 1935; Grøntved 1952; Grøntved and Seidenfaden 1938; Gudmundsson 1937; Hagelstein 1939; Halldal 1953; Hasle 1956; Heiden and Kolbe 1928; Hentschel 1932; Iselin 1930; King 1950; Kisselev 1925, 1928; Krasske 1941; Manguin 1954; Margalef and Duran 1953; Mereschkowsky 1902; Motoda and Kawarada 1955; Ostenfeld 1913; Paulsen 1909, 1911; Pavillard 1925, 1931; Ramsfjell 1957; Reinhard 1910; Sabelina 1930; Schröder 1906; Silva 1949, 1952, 1953, 1956a, 1956b; Silva and Pinto 1948, 1952; Skvortzow 1931; Smayda 1957, 1958; Steemann Nielsen 1935; Subrahmanyan 1946; Takano 1955; Ussatchew 1935; Wirketiss and Kisselev 1935.

*Th. nitzschioides* is circumglobal and confined primarily to neritic areas. Its distributional pattern supports the contention of some investigators that neritic species can survive in oceanic environments if transported there. Its distribution in the Arctic is somewhat obscure due to the failure of early investigators to distinguish it from *Thalassiothrix frauenfeldii* Grun., a form also found there. *Th. nitzschioides* is ubiquitous and numerically important throughout the northern hemisphere. Additional investigations in the southern hemisphere probably will reveal a similar condition there as well.

An outstanding feature of *Th. nitzschioides*’ distribution is the failure to establish itself in the Baltic Sea. Although it occurs sporadically off Bornholm Island and near the Danzig Bay (Ostenfeld 1913), it is not stationary in the Baltic Sea. It is a pronounced euryhaline species (Fig. 7) occurring at salinities down to 4.13/00 in Portuguese Guinea (Silva and Pinto 1952) and 3.60/00 in Tscheskaja Bay in the Barents Sea (Wirketiss and Kisselev 1935). Except for the Gulfs of Finland and Bothnia where the salinity may decrease to 3.00/00 or less, much of the Baltic has a surface salinity of approximately 7.00/00 (Sverdrup, Johnson and Fleming 1942, p. 664). The salinity conditions in the Baltic, then, certainly would seem tolerable to *Th. nitzschioides*. It should be noted that the limnetic *Diatoma elongatum* (Lyngb.) Agardh closely resembles *Th. nitzschioides*. Välikangas (1926) classifies *D. elongatum*
as a "Meio- oder β-mesohalin" form showing its greatest development at salinities between 2.00–8.000%. The absence of *T. antarctica* from the Antarctic except along 120°W near the Antarctic Convergence (Hasle 1956) and Heard Island (Manguin 1954) is also strange considering that it occurs in the high Arctic at similar temperatures. It is also present in the Caspian Sea where it has persisted as a relict form. It is conceivable that morphological differentiation has accompanied *Th. nitzschioides*’ attainment of cosmopolitanism. The pluses drawn in on its distribution map (Fig. 5) represent finds recorded as varieties (Heiden and Kolbe 1928). Gaarder (1951) found this species to be variable and could distinguish between two valve types.

The distribution of *Th. nitzschioides* in relation to temperature and salinity (Fig. 7) reveals it to be pronouncedly eurythermal and euryhaline. Closer inspection shows the similarity in salinity but dissimilarity in temperature encountered by this species in different parts of its range. The stock found in tropical Portuguese Guinea (Silva and Pinto 1952) occurs at temperatures ranging from 22.2° to 30.7°C, the mean being 26.3°C (Fig. 7, open circles).

Fig. 7. The temperature – salinity relationships of *Thalassionema nitzschioides*, the open circles represent the stock found in tropical Portuguese Guinea.
The salinity ranges from 4.13 to 34.34\%/oo with a mean of 25.04\%/oo. On the other hand, the stock found in the Oslofjord and Skagerrak (Braarud 1945a; Braarud and Bursa 1939; Cleve-Euler 1917) occurs at a mean temperature and salinity (185 observations) of 8.5°C and 28.86\%/oo, respectively. For northern European waters in general, Ostenfeld (1913) gives means of 7.7°C and 31.50\%/oo when Th. nitzschioides is “c and cc” (94 observations). The arctic and temperate stocks would be expected to have different temperature means as well. Thus within the cosmopolitan distribution of Th. nitzschioides we can distinguish between different thermal “clones”. These are stenothermal in the sense that they are subjected to only slight variations in temperature typical of that part of the range. Braarud (1945b) has found that at 10°C the Oslofjord Th. nitzschioides is capable of 1.2 divisions per day. It is important to determine whether its temperate and tropical counterparts would react similarly at that temperature.

The term cosmopolitan is used here for those species living in both cold-water and equatorial regions of all oceans. The most important prerequisite for the attainment of a cosmopolitan distribution by a phytoplankton species is a eurythermal tolerance. Unlike zooplankton and other animals, there can be no stenothermal, cold-water, cosmopolitan phytoplankton species because avoidance of the warm temperatures of sub-tropical and tropical regions requires a submergence below the euphotic zone. Salinity probably plays a subordinate role in such a distribution, although one can expect cosmopolitan species to have specific requirements.

Diatoms predominate among the known cosmopolitan species. Other cosmopolitan species include:

- Chaetoceros compressus Laud.
- Coccolithus huxleyi (Lohm.) Kpt.
- Exuviaella baltica Lohm.
- Leptocylindrus danicus Cl.
- Prorocentrum micans Ehrbg.
- Skeletonema costatum (Grev.) Cl.

**Bipolarity**

A bipolar distribution has been ascribed to a number of phytoplankton species. Thalassiothrix longissima Cleve et Grunow and Rhizosolenia hebetata Bailey f. semispina (Hensen) Gran are the classical examples given in the literature. Bipolarity, in its strictest sense, defines the occurrence of an element in both polar regions with its absence in the intervening tropical regions. The concept of bipolarity stresses a discontinuous distribution and actually it is indifferent whether the representative is a polar or subpolar species.

A number of zooplankton species claimed to be bipolar by early investigators have since been found to have a continuous longitudinal distribution. These
forms are tropically or equatorially submerged, inhabiting strata thermally similar to those inhabited in the polar regions. Although these discoveries refuted bipolarity for these species, they strengthened the viewpoint that migration is of cardinal importance in effecting a bipolar distribution (CHUN 1897, EKMAN 1953). Neither the "relict theories" of Theel, Pfeffer or Murray (cf. EKMAN 1953, p. 258) nor a polyphyletic origin can be accepted as an adequate explanation of bipolarity. It is unequivocal that the longitudinal migration of planktonic forms is essentially passive and dependent on currents.

Subscribing to the definition of bipolarity given above, we find that Th. longissima and Rh. hebetata f. semispira are not bipolar. Both are widely distributed throughout the tropics. In discussing the latter species, HENDEY (1937, p. 316) states "it was observed in all types of water, but more frequently in the waters of the tropical and subtropical zones". As for Th. longissima, it is found in the Mediterranean Sea (PAVILLARD 1925), in the Red Sea, Gulf of Aden, Malay Archipelago, Indian Ocean (OSTENFELD 1902) and South Equatorial Current (PAVILLARD 1935), to name a few of the localities. Admittedly, these species appear to be more important in the polar regions; nonetheless they inhabit and undergo active cell division in the tropics.

KARSTEN (1905a) listed 31 species of marine phytoplankton as being bipolar; but all of these are now known to live within the tropics as well. Indeed true bipolarity at the species level probably is not to be found among marine phytoplankton. The difficulties in establishing such a distribution appear to be insurmountable. Of prime importance in that it is the greatest obstacle is the problem of trans-tropical migration. To pass from one pole to the other entails being transported through the tropics. A stenothermal cold-water form like T. antarctica or T. hyalina (Figs. 2, 4) must successfully withstand tropical temperatures if it is to reach the opposite pole in a viable state. Unlike zooplankton, phytoplankton cannot take advantage of the suitable thermal conditions in the depths as these invariably lie under the euphotic zone. For a species to traverse these tremendous distances active cell division must take place and for this light is necessary.

It would seem that neritic species are well equipped to become bipolar since many produce resting spores, supposedly capable of withstanding the extremes of an environment. Resting spores having been formed, these might be carried to suitable habitats, germinate, develop resting spores anew and repeat the entire cycle again. Through this process the species could stepwise extend their range in the direction of the opposite pole. But as a general rule, only a small number of the vegetative cells of a given species capable of producing resting spores do so. Of these only a limited number, if any, would gain access to the proper current system. In addition, further dispersal during transport and loss due to sinking and grazing would continue to decimate this number.

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Admittedly, a species might succeed in establishing itself in a new area, but eventually it will be confronted with the problem of maintaining itself in a tropical environment as well. If it fails, then from the marginal areas of its range it must have its resting spores transported over a considerable distance to the opposite polar region. Even should these resting spores reach the opposite pole, a bipolarity is still not assured. There remains the problem of achieving a sufficient density enabling the species to withstand extinction due to grazing and assuring the production of resting spores. It is maintained that the attainment of a bipolar distribution through the mechanism of resting spores is ineffective for marine phytoplankton. This is borne out by the absence of a single known bipolar neritic species.

Above we assumed that the species would be unable to establish itself in the tropics. It is suggested, however, that in order for a species to thrive at both poles it must also become cosmopolitan. Successful trans-tropical transport leading to the establishment of a species at both poles will occur only when the species can maintain itself within the tropics as well. Karsten’s original list of “bipolar” species is offered in evidence.

Indicator Species and Visitors

The species making up the phytoplankton community during a seasonal cycle usually can be grouped into indigenous and visitor forms, or autochthonous and allochthonous species, respectively. Some of the visiting species are especially valuable in that they label the influence or presence of a specific water mass during its incursion into a given area. Such species are called indicator species. A valid indicator species of this type is one whose presence in a given area coincides with the introduction of a specific water mass of known origin. While it need not be an important component in its “native” water mass, it can not normally be found in the recipient one. It is irrelevant whether a phytoplankton indicator species is viable or dead upon its introduction.

*Planktoniella sol* is an indicator species of the Gulf Stream near its entrance into the Norwegian Sea (Fig. 5). Its specificity for this current is revealed by the salinity values accompanying its occurrence in that region (Fig. 6, open circles). These values concentrate about 35.350/00, ranging from 35.21 to 35.440/00, in close agreement with the mean of 35.300/00 characteristic of inflowing Gulf Stream water (SVERDRUP, JOHNSON and FLEMING 1942, p. 655). The corresponding temperatures range from 6.6° to 12.5°C, representing *Planktoniella’s* occurrence from March through November (WANDEL and OSTENFELD 1898; KNUDSEN and OSTENFELD 1900). *Planktoniella sol* serves also as an indicator species of intrusive offshore water masses in the coastal regions.

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bordering the Benguela Current (HART 1953) and Peru Current (GUNTER 1936, quoted by HART). The fact that Planktoniella sol is easily identifiable, a characteristic of most indicator species, has contributed to its being used as an indicator species so frequently.

SCHÜTT (1893) maintained that each current system possesses its own characteristic flora. Although many species are possessed in common with other currents, the different assemblages often can be used to delimit the currents and areas of their influence within a given thermal zone. But as the currents pass through different regions, thermal changes and admixture take place resulting in considerable changes in composition. The ability of a species to maintain itself in spite of these changes increases its chances of becoming an indicator species. It will suffice to state that relatively few species can be used as indicators of hydrographic phenomena.

Species belonging to a local flora may also be used as indicators of some specific element in their environment. Eutreptia lanowi Steuer, for example, serves as an indicator of polluted waters in the inner Oslofjord (BRAARUD 1945a) and the Grand Canal of Venice. The presence of certain diatoms, such as Thalassiosira baltica (Grun.) Ostf., indicates a specific salinity range, while others, Cyclotella caspia Grun., signal fresh-water dilution. The abundance of the eurythermal Chaetoceros wighami Btw. and Ch. subtilis Cl. appears to be inversely related to the degree of salinity; these species attaining maximum concentrations in the Baltic and Caspian Seas. That limnetic and brackish diatoms are excellent indicators of the degree of salinity (more specifically Cl ion concentration) enabled KOLBE (1932) to formulate his “Halobion system”. The results of culture studies will probably warrant a similar classification for marine forms, if not for total salinity then for specific inorganic ions.

The flora and its seasonal cycle are remarkably constant for a given area. Thus, to an experienced observer, the composition of the phytoplankton community and their relative abundance are a measure of the community’s stage of development and previous history, and even relate something about the “natural fertility” of the environment. In many temperate inshore areas, for example, Skeletonema costatum (Grev.) Cl. initiates the late-winter or spring flowering, is succeeded by Thalassiosira spp., which in turn are replaced by Chaetoceros spp., and so on. But the community is likewise sensitive, and any significant environmental changes will become manifested in terms of composition and abundance. Comparison of waters contaminated with domestic and industrial pollutants with non-polluted ones readily reveals this.

As contrasted to hydrographic indicator species, visitor species or guests may indicate the influence of different water masses but give no concrete information as to their origin. The presence of visitor species usually represents a temporary extension of range corresponding to the seasonal changes in

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temperature. Thus, within a given area, we can distinguish between its local flora and warm or cold-water visitors. The visitors often become important components in the community at times when sub-optimal temperatures suppress active growth of the local representatives.

Cleve (1897) overemphasized the role of visiting species in contributing to and molding the seasonal phytoplankton cycle. Justly, he concluded that phytoplankton can be grouped into thermal units, called “plankton-types”, which have centers of abundance within their respective thermal zones. Accordingly, cold-water forms are concentrated in the polar regions and warm-water ones in the tropics. These plankton-types, he maintained, are constantly “migrating” and in the process serially seeding the areas through which they pass, resulting in the domination of the community by these newly arrived visitors. Thus, he attributed the seasonal changes in composition and dominance of the community to the periodic recruitment of species from these different areas. As an example, he claimed the spring flowering in the Skagerrak to be the result of a seeding by water emanating from the Arctic, while the summer flora was derived from southerly waters. Cleve’s viewpoint denied the existence of a stationary population in these waters made possible through the production of resting spores (Gran 1902) or other means. In propounding his concept, Cleve also failed to recognize the importance of the environment in molding the biological conditions, so aptly described by Gran (1912): “when the conditions of existence in the flowing water-masses gradually alter, it is the new conditions of existence that decide the character of the flora, since the species best qualified to endure them will very soon get the upper hand over the others.” A fact well established today. In reality, the seasonal composition of a developing population is derived primarily from a local stock and secondarily from visitors. Some visitors are certain to appear each year and be of secondary importance. Others are sporadic in occurrence and may suddenly appear in great numbers like Asterionella japonica Cl. did along the Norwegian coast in 1927 (Gran 1929). One visitor, Biddulphia sinensis Grev., a “tropical-neritic Indo Pacific form” suddenly appeared in 1903 off Hamburg and quickly spread to much of the North Sea where it has since established itself (Ostenfeld 1909).

**Concepts of Neritic, Oceanic, Meroplanktonic and Holoplanktonic**

Hensen’s (1887) coinage of the term plankton replaced the then current Auftrieb. But plankton as defined by Hensen was no improvement over Auftrieb since it included both swimming and planktonic forms. It remained for Haeckel (1890) to divide up the composite plankton and introduce the

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classification which persists today: benthos, nekton and plankton. In the same work he introduced the terms neritic, oceanic, meroplanktonic and holoplanktonic.

Neritic and oceanic were established by HAECKEL (1890, p. 22) to characterize the horizontal distribution of plankton: "oceanisches Plankton ist dasjenige des offenen Weltmeeres, mit Ausschluss des schwimmenden Küsten Bioso; ... das neritische Plankton umfasst die schwimmende Fauna und Flora der Küsten Regionen, sowohl der Contiente, als der Archipele und Inseln." Those organisms independent of the sea bottom he termed holoplanktonic—"Organismen welche gar keine Beziehung zum Benthos haben", and those dependent on it meroplanktonic. It is surprising that Haeckel did not attempt to relate neritic with meroplanktonic, and oceanic with holoplanktonic.

GRAN (1902) noticed that many diatom species forming resting spores were confined primarily to coastal waters, the non-producers to oceanic waters. This observation led him to redefine neritic and oceanic (p. 75–76): "neritisch sind alle Arten, die in irgend einer Weise von der Küste, d. h. vom Meeresboden der seichteren Küstenmeere abhängig sind; sie können z. B. Dauersporen haben; ... oceanisch sind dagegen alle Arten, die vom Meeresboden in ihrem ganzen Lebenscyklus unabhängig sind". Gran then concluded: "nach dieser Definition sind also die Begriffe neritisch und oceanisch mit den ebenfalls von Häckel aufgestellten Begriffen meroplanktonisch und holoplanktonisch vollständig kongruent". Gran's modification of Haeckel's classification has persisted ever since.

Manifest in the concept of neritic and oceanic, in Gran's sense, are two diverse elements. Firstly, a geographical orientation is included which vaguely defines the normal distribution of an organism relative to the coast or open ocean. Secondly, a biological concept is included which characterizes the type of life cycle innate to the organism. Accordingly, neritic, as pertaining to phytoplankton, has come to mean an organism confined to coastal or "inshore" regions and possessing a sedentary stage (resting spore); oceanic designates an organism inhabiting a deep sea environment in a continuously pelagic state. A causal relationship and interdependence of concepts is implied. But, in fact, a neritic species need not be meroplanktonic (i. e. spore producing) nor need a meroplanktonic species be neritic. The same applies to the apparent oceanic—holoplanktonic relationship. Some organisms, including Asterionella japonica Cl., Guinardia flaccida (Castr.) Perag., Skeletonema costatum (Grev.) Cl. and Thalassionema nitzschioides Grun., appear to be confined to coastal waters yet fail to form resting spores. Other species do not form resting spores, such as Nitzschia delicatissima (Ehrbg.) Sm. and Thalassiosira decipiens (Grun.) Jörg., but are equally successful in neritic or oceanic regions. Many species normally inhabiting oceanic regions are periodically introduced into inshore areas where

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they become active participants in the community. Likewise, many resting spore producers have been found in active growth in oceanic waters. Some, like *Thalassiosira gravida* Cl. and *T. nordenskioeldii* Cl., have a center of abundance in oceanic regions. These two species are found in the ice-floe region of the Norwegian Sea. Even though the ice packs may simulate a neritic environment in providing an effective surface for the deposition of resting spores or congealed vegetative cells, the hydrographic conditions nonetheless reveal an oceanic character. These examples support the contention that using the possession or absence of a resting spore stage as a criterion in delimiting the environment inhabited by a species, and indirectly defining its milieu, is neither completely reliable nor satisfactory. Contrary to Gran’s viewpoint, *neritic and meroplanktonic are not synonymous, nor are oceanic and holoplanktonic*. Braarud (*Braarud, Gaarder and Grøntved 1953*) also has pointed out the heterogeneity of the concepts of neritic and oceanic and the ensuing difficulties in using them in the sense of Haeckel and Gran.

Thus we have two unrelated sets of terms classifying phytoplankton; one representing a geographical or environmental concept, neritic—oceanic, the other a biological phenomenon, meroplanktonic—holoplanktonic. It is now necessary to consider the fitness of these terms as applied to phytoplankton.

Without doubt, as Haeckel recognized, the distribution of plankton bears some relevance to the coast (“neritisches Plankton”) or open ocean (“ozeanisches Plankton”). But, nonetheless, the terms neritic and oceanic, as applied to phytoplankton to describe such a distribution, are of little biogeographical value. They are at best vague generalizations of an environment which does not exist *per se*, and which in reality represents a multitude of environments. The classification of a species as Arctic, for example, conveys a fairly comprehensive picture of its general thermal requirements and distribution. But now the classification of this species as neritic or oceanic is essentially meaningless, for whereas the designation Arctic is a specific and definable biogeographical unit, neritic and oceanic are heterogeneous and not distinguished by any specific element. How, then, does one define neritic and oceanic? Are the parameters used to distinguish between them of importance to the phytoplankton? A species, for example, may be confined to either the neritic or oceanic province, or found in both, because of the absence or presence of a resting spore or sedentary stage, a nutritional reason or a physiological reason other than nutrition. An adequate definition must take into account the nature of the organisms to be classified. Indeed one can arbitrarily select the edge of the continental shelf or a particular depth (see *Hedgpeth 1957*) as the boundary between the neritic and oceanic provinces. But while this may be appropriate for some aspects of oceanography, it has no value when applied to phytoplankton. Here is also a source of confusion resulting from the usage of neritic

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and oceanic in all disciplines within oceanography, but with different meanings. *We must recognize, therefore, that the classification of a phytoplankton species as neritic or oceanic places it in an undefined region and tells nothing of its life cycle, or why it is found there.* Neritic and oceanic either should be rejected as biogeographical terms for phytoplankton, or subdivided to accommodate the different ecological groups whose distribution is related to coastal or oceanic waters in some manner. The former alternative would seem preferable.

The terms meroplanktonic and holoplanktonic, in general, appear to be quite satisfactory. Many phytoplankton species possess a resting spore stage and must be considered as meroplanktonic. In fact a fundamental and natural biological category exists among phytoplankton based on the production of resting spores. The possibility that holoplanktonic species also possess a pelagic dormant stage in their life cycle can not be dismissed. KARSTEN (1905a) contended that some of the open ocean species actually possess just such a stage, which he called “Schwebesporen”. Should this be the case, then the production of a resting stage need not necessarily mean a dependence on the sea bottom.

For most of the diatoms there is little doubt which species produce resting spores and which do not. Gran could use his classification legitimately only for the diatoms, since little was known about the biology of the other components. It is now known that a number of dinoflagellates form resting spores, including representatives of *Ceratium* (JOLLOS 1910) and *Goniaulax* (NORDLI 1951) as well as many *Peridinium* species. Resting spores have also been encountered among the coccolithophorids (KAMPTNER 1937; GAARDER 1954). Thus here is a feature common to certain representatives of the principal groups comprising the phytoplankton.

It appears that certain diatoms must be considered as meroplanktonic even though they do not form resting spores. Their life cycle has been said to include a vegetative sedentary stage, so that one can consider them analogous to tychopelagic species. The essential difference here is that unlike the true tychopelagic forms they are normally planktonic and capable of active cell division at that time. Now the evidence that such species exist is very scanty. OSTENFELD (1913), especially, mentions such species, among which are *Asterionella japonica* Cl., *Eucampia zoodiacus* Ehrbg., *Leptocylindrus danicus* Cl., *Skeletonema costatum* (Grev.) Cl. and *Thalassionema nitzschioides* Grun. But at no time does he cite any actual observations to support his claims. This problem is certainly worthy of investigation.

It is commonly observed that many of those species claimed by Ostenfeld to have a sedentary vegetative stage become abundant, decline to trace concentrations and then often become abundant again. Frequently this temporary loss of vigour can not be attributed to nutrient deficiency or any other factor.
Nor is it known whether these cells are in a vegetative or dormant phase, although cytological study should clarify this.

An adequate definition of meroplanktonic and holoplanktonic, as pertaining to phytoplankton, must take into account the considerations discussed above. Hence it is proposed that *meroplanktonic* be retained for those organisms which either produce a resting spore, or possess a sedentary stage or dormant pelagic phase, and hence are *pelagic vegetatively*, except for reproductive stages, *only during part of their life cycle*. *Holoplanktonic* embraces those organisms not producing a resting spore, or possessing a sedentary or dormant pelagic phase, but being *pelagic vegetatively*, except for reproductive stages, *throughout their life cycle*. These definitions emphasize a biological feature—how they live—and have no geographical connotation.

An adequate biogeographical classification of phytoplankton is dependent on culture studies. Following the systematic study of the requirements for and tolerances of certain parameters by phytoplankton in *vitro*, these parameters should be measured in the natural environment. Then by comparing the normal distribution and dynamics of the organisms in relation to these with what has been found in the laboratory, a satisfactory classification should be possible. Such a classification is not imminent. Thus in the interim it seems advisable to have a provisional classification which recognizes that phytoplankton do have a real, definable horizontal distribution. The inadequacy of the concepts of neritic and oceanic to define this has been pointed out.

Instead, a binary classification (Table 2) is proposed which distinguishes between three distributional types: paractic (Gr. παράκτιος, of the coast), anoictic (Gr. ανοικτός, in the open sea) and adiaphoric (Gr. ἀδιάφορος, indifferent). These are then used in combination with the prefix of the term defining the life cycle innate to a given species: meroplanktonic, holoplanktonic. It must be emphasized that paractic, anoictic and adiaphoric do not represent environments. Paractic is conceived of as a concept which recognizes that a given species is bound to, and normally distributed in, certain waters because of

<table>
<thead>
<tr>
<th>Mero-</th>
<th>Paractic</th>
<th>Anoictic</th>
<th>Adiaphoric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cerataulina bergoni -</td>
<td>Chaetoceros laciniatus</td>
<td>Rhabdosphaera spinosa</td>
<td>Ditylum brightwellii (?)</td>
</tr>
<tr>
<td>Guinardia flaccida -</td>
<td>Gonialax polyedra</td>
<td>Stephanopyxis turris</td>
<td>Thalassiosira decipiens</td>
</tr>
<tr>
<td>Rhizosolenia fragilissima -</td>
<td>Skeletonema costatum (?)</td>
<td>Coccolithus huxleyi</td>
<td>Exuviaella baltica</td>
</tr>
<tr>
<td>Chaetoceros atlanticus</td>
<td></td>
<td></td>
<td>Nitzschia delicatissima</td>
</tr>
</tbody>
</table>

Table 2.

A Classification of Marine Phytoplankton.

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requirements attributable to coastal influences. The nature of this attraction is unknown, but may be due to shallowness, nutrients, growth factors or other parameters, singly or in combination. Anoictic defines a distribution limited to those waters free from coastal influences, and adiaphoric is restricted to those species whose requirements and tolerances permit an existence in both types of water.

Thus a mero-paractic species is one which has a dormant or sedentary stage and is distributed in waters modified by coastal influences. Mero-anoictic represents a species with a similar life cycle, but found in waters free from coastal influences, while a mero-adiaphoric species is found in both types of water. Holo- denotes a species pelagic vegetatively throughout its life cycle.

**Factors Affecting the Distribution of Phytoplankton**

The distribution of marine phytoplankton is governed by essentially the same variables that effect their abundance. Actually there is no marine habitat where a phytoplankton species can not find favorable conditions in some part of its ecological spectrum. But it is the combined effect of these variables which determine distribution, and it is usually difficult to single out the most important one in a given situation.

The spatial relations of phytoplankton distribution can be thought of as three-dimensional, consisting of a latitudinal, longitudinal and vertical component. Using this as a model, the various factors affecting this pattern of distribution can be analyzed.

1. *Light*: The vertical distribution of marine phytoplankton is regulated almost exclusively by light. Under certain conditions thermal stratification or turbulence may cause a gradient in vertical distribution, but these are indirect effects in that they do not elicit a physiological response directly controlling vertical distribution as does light. There is little doubt that phytoplankton have specific light requirements, both qualitatively (Baatz 1940) and quantitatively, but little is known. The vertical distribution of certain dinoflagellates appears to be related in some way to light as these show marked diurnal movements (Hasle 1950, 1954). But light is probably not the sole factor involved as certain ions also influence phototaxis (Haldal 1957). A "shade flora" consisting of diatoms, including Planktoniella sol, and dinoflagellates has been claimed to inhabit the greater depths within the tropics (Karsten 1907; Steemann Nielsen 1934, 1939). Steemann Nielsen (1939) distinguished between three groups of Ceratium spp. which he termed oligophotic, mesophotic and euphotic.

Light also governs the longitudinal distribution of phytoplankton, principally through its absence. Because of the "midnight sun" phenomenon and presence
of ice, atheric conditions exist periodically or continually throughout much of the polar regions. But whether this precludes the existence of a community is not certain; for Rodhe (1955) has found an abundant flagellate population in certain ice-covered arctic lakes. A number of arctic diatoms appear to have low light requirements and are capable of active growth on the under side of ice (see SMayda 1958). The periodic colonization in those waters where ice-melting accompanies the “midnight sun” is well marked.

2. Temperature: That the distribution of phytoplankton is a function of temperature is manifest in their division into arctic, boreal, temperate or tropical species. Thus temperature regulates the longitudinal distribution of phytoplankton, as shown here more specifically for T. antarctica and T. hyalina. Unfortunately the classification of phytoplankton as to their thermal requirements is based exclusively on biogeographical data. In many instances insufficient data were had resulting in the classification of an organism inconsistent with its presently known distribution.

The belief that dinoflagellates as a group are warmth-loving organisms is now being borne out by experimental studies. Barker (1935) found the optimal temperatures of a number of species to lie between 18° and 25°C, of which Peridinium triquetrum (Ehrbg.) Leb. (18°C) and Prorocentrum micans Ehrbg. (25°C) can be mentioned. Nordli (1953) obtained a temperature optimum of 15°C for Ceratium furca (Ehrbg.) Clap. et Lach. and 20°C for Ceratium fusus (Ehrbg.) Duj. Diatoms likewise have been studied in vitro (Schreiber 1927; Braarud 1937, 1945b), but the results are fragmentary. For example, Braarud (1937) found Thalassiosira nordenskioeldii Cl. to be very prolific at 10°C, although in nature it attains a maximum between 2° to 3°C, and disappears at slightly higher temperatures (Gran and Braarud 1935, SMayda 1957). A species’ ability to thrive at different temperatures appears to be related to the amount of nutrients available. Braarud (1945a) found boreal diatoms in active growth at 20°C in polluted waters of the Oslofjord, whereas growth was negligible in non-polluted areas.

3. Salinity: This factor controls distribution primarily in inshore areas, latitudinal distribution, where considerable fluctuations and differences are common. Experimental studies indicate, however, that representative dinoflagellates and coccolithophorids are more or less euryhaline (Braarud 1951; Braarud and Pappas 1951; Braarud and Rossavik 1951; Nordli 1957; Mjaaland 1956). The dinoflagellates tolerated salinities from 5 to 45‰, and one clone of Peridinium trochoideum (Stein) Lemm. even 55‰ (Braarud 1951). In all instances, the individual species were characterized by a low optimum, the lowest optimum being 10‰ (Exuviaella baltica Lohm.) and the highest 25‰ (Ceratium furca Ehrbg.).

These results, coupled with what can be inferred from biogeographical data,
suggest that salinity is more important in governing abundance rather than
distribution within the marine environment. It may be that total salinity is not
so important a factor of distribution as are specific ions (DROOP 1958; PROVA-
SOLI, MCLOUGHLIN and PINTNER 1954). DROOP (1958) draws the tentative
conclusion that Na tolerance may be the most important parameter distin-
guishing between “neritic and supra-littoral or estuarine species”.

The best known example of where salinity is a barrier to distribution is the
Baltic Sea. The salinity of the Kattegat near the entrance into the Baltic Sea
is approximately 150/00. At nearby Bornholm Island, lying within the Baltic,
the salinity is only 7 0/00 (DIETRICH and KALLE 1957, p. 417). A number of
diatoms that occur in the Kattegat at 150/00 are absent at Bornholm Island,
presumably because of the decreased salinity (OSTENFELD 1913). Some of the
species that can be assumed to have a minimal salinity requirement between
70/00 and 150/00 are:

*Chaetoceros decipiens* Cl.  
  - *laciniosus* Sch.  
*Guinardia flaccida* (Castr.) Perag.  
*Lauderia borealis* Gran  
*Leptocylindrus danicus* Cl.  

*Rhizosolenia alata* Btw.  
  - *setigera* Btw.  
  - *styliformis* Btw.  
*Thalassiosira nordenskioeldii* Cl.  
  - *gravida* Cl.

NORDLI (1953) has shown that the low salinities of the Baltic prevent the
occurrence of *Ceratium fusus*, *C. furca* and *C. tripos*, although they show good
growth at 150/00. SEGERSTRÅLE (1951) has found that the salinity of the Baltic
is rising, and thus it would be most desirable to follow the ensuing changes in
phytoplankton composition.

4. *Pollution*: Pollutants have become important factors of distribution in
localized areas. The nature of the pollutant determines whether it will be
toxic or beneficial, and may be highly selective in molding the community.
In any respect, pollutants are accompanied by changes in composition and
abundance. BRAARUD (1945a) concluded that although no organisms could be
used as totally specific indicators of domestic pollution in the Oslofjord, in
certain cases the species composition and response illustrated different degrees
of pollution. RYThER (1955) showed that the effluent from duck farms had a
profound effect on the phytoplankton composition in Moriches Bay. BRAARUD
and PAPPAS (1951) found that small amounts of sewage stimulated the growth
of *Peridinium triquetrum*, whereas concentrations greater than 75 ml/l retarded
growth. ØDEGAARD (1942) found marine diatoms to differ in their resistance to
domestic and industrial pollutants.

5. *Fertility*: This represents the gamut of substances having nutritional or
other biological significance, and effecting the distribution of phytoplankton.
They may be distinguished from certain pollutants in being naturally occurring

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substances in a given water mass. Insight into "fertility" as a factor of distribution is dependent upon culture studies of the requirements for and, more important, tolerances of these substances. Basic nutrients, for example, may be present in concentrations inhibitory to certain species, as shown for certain limnetic forms (Rodhe 1948). Peters (1934) claimed that the distribution of certain Ceratium spp. was governed by nitrate and phosphate concentrations. Organic factors undoubtedly affect distribution, including indirectly by acting as chelators or forming other complexes allowing the presence of species at nutrient concentrations that normally would be inhibitory (Fogg and Westlake 1955). Steemann Nielsen (1934) postulated that the horizontal distribution of Ceratium is governed by organic metabolic substances (Stoffwechsel-produkte). The ultimate distinction between pararctic, anoictic and adiophoric species may be in their requirements for and tolerances of specific substances.

6. Currents: Currents are important, physical factors of distribution. Above all, they provide a species with a range in accordance with the biological factors enumerated above.

Acknowledgements

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Summary

1. The distribution of representative arctic, antarctic, tropical and cosmopolitan phytoplankton species was charted. The accompanying temperature—salinity conditions were also presented.

2. Both polar species, Thalassiosira antarctica and Thalassiosira hyalina, are stenothermal and stenohaline. T. antarctica is circumpolar and confined primarily to those waters within the Antarctic Convergence. T. hyalina shows an eastern arctic tendency and has an irregular longitudinal distribution. Whereas the seasonal antarctic flora is comprised principally of true antarctic species, arctic diatoms are relatively unimportant in their habitat.

3. The tropical Planktoniella sol is eurythermal and stenohaline in its distribution. It is circumtropical and can be used as an indicator species of the Gulf Stream near its entrance into the Norwegian Sea.

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4. *Thalassionema nitzschioides* was selected as the cosmopolitan species. It is both eurythermal and euryhaline. Within the range of a cosmopolitan species one can distinguish between different thermal "clones". There can be no stenothermal cold-water cosmopolitan phytoplankton species.

5. The existence of bipolarity claimed for certain phytoplankton species is reconsidered, and the conclusion arrived at that true bipolarity is not to be found among marine phytoplankton at the species level. It is postulated that the presence of a species at both poles is enabled only by the attainment of a cosmopolitan distribution.

6. The different types of phytoplankton indicator species are discussed. The distinction between indicator and visitor species is also considered, and the role of visitor species in the community commented upon.

7. The interrelationships between meroplanktonic and neritic, holoplanktonic and oceanic phytoplankton, as advanced by Gran, are re-evaluated. It is shown that these terms are not synonymous. It was argued that neritic and oceanic have no biogeographical value and should not be used for phytoplankton. The terms meroplanktonic and holoplanktonic were redefined. A meroplanktonic species is one which is pelagic vegetatively only during part of its life cycle; holoplanktonic is pelagic vegetatively throughout its life cycle. It is maintained that a satisfactory biogeographical classification is dependent on culture studies. A provisional, binary classification of marine phytoplankton is then proposed.

8. The roles of light, temperature, salinity, pollution, fertility and currents as factors of distribution are then discussed.

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Addenda

The occurrence of *Thalassiosira hyalina* north of the Alaskan archipelago (Kawarada and Ohwada 1957) and Okhotsk Sea (Jousé 1957) has been reported. These observations confirm the presence of *T. hyalina* in Pacific waters and indicate a circumpolar distribution.

Only Hendey's (1937) report of *T. hyalina* in the southern hemisphere was briefly discussed earlier, as all other known reports (Boden 1950; Krasske 1941; Zacharias 1906) were deemed not to warrant discussion. But as they might be offered in evidence against *T. hyalina’s* arctic nature or in support of the existence of bipolarity of marine phytoplankton at the species level, a brief discussion of these reports is in order. Boden appears not to have found *T. hyalina* along the west coast of South Africa; the inclusion of this species in his hand-
book stems from HENDEY's claim that it is present in those waters. KRASSKE's viewpoint that *T. hyalina* and *T. decipiens* are identical can not be accepted. Hence, *T. hyalina* probably does not occur along the Chilean coast. ZACHARIAS' claim that he found *T. clevei* (a synonym of *T. hyalina*) in the Gulf of Valparaiso, and also in the Adriatic Sea, seems improbable.

LEWIN (1958) has reinvestigated the taxonomic position of *Phaeodactylum tricornutum* and concluded that it is a diatom rather than a chrysophycean. She has also compiled a bibliography of those investigations employing *P. tricornutum*, but erroneously identified as *Nitzschia closterium* or its *minutissima* form.

GRAN and ANGST (1931) report *Planktoniella sol* from Puget Sound, Washington, its most northerly known extension in the eastern Pacific. The criticism has been received that the literature has not been thoroughly searched in mapping the distributions of the species considered herein. It must be stressed that it was not the purpose to record every known observation of these species, but rather to provide an insight into the general features of distribution and the accompanying temperature and salinity conditions. Accordingly, a single, reliable report of occurrence from a given area was frequently selected over other confirmatory observations. However, all known reports containing applicable temperature and salinity data were used in calculating the respective means of occurrence.

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