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Spatial Distribution of Phytoplankton in Spring 2004 along a Transect in the Eastern Part of the North Sea

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We report the results from a 250 km long transect, from the Danish coast to the North Sea at 55°30′ N, which was sampled every 32 km in order to study the composition and distribution of phytoplankton, and their dependence on the distance from the coast, depth and other environmental factors. Altogether 144 species of algae were identified by light, epifluorescence and electron microscopy. Some ecological preferences were found on the basis of measured environmental parameters and compared with the literature. Possible controlling mechanisms for the distribution patterns of the plankton algae were analyzed by multivariate statistics. Only distance from the coast was found to be a significant factor for algal distribution along the transect. Three main areas of the transect were found: the coastal, middle and oceanic areas. Diatoms, mainly the centric ones, were the most abundant group of algae. The other less abundant groups were Dinophyceae, Dictyochophyceae, Prasinophyceae and Chlorophyceae. The pattern of distribution of diatoms and dinophytes along the transect was more or less similar, with larger numbers of cells found close to both the eastern and western parts of the transect, although the species composition was different. Some species were found to prefer coastal waters, other species were characterized as oceanic, and several species were found at all stations. *Porosira glacialis* showed an atypical distribution along the transect, with highest abundances at both coastal and oceanic stations.

Keywords:
· North Sea,
· phytoplankton,
· spatial distribution,
· algae,
· *Thalassiosira*,
· *Protoperidinium*,
· *Chaetoceros*,
· *Skeletonema*.

1. Introduction

The North Sea is a large, semi-enclosed sea on the continental shelf of north-west Europe, formed by flooding in the Holocene period, some 20,000 years ago. The total catchment area is 850,000 square kilometers (km^2). The sea is shallow (average depth 74 m), becoming deeper towards the north. Surface water temperature varies between 0 and 20°C, depending on the season and the part of the sea, with less variation in the north. Salinity displays few variations in the open North Sea (32–34.5‰). In the coastal areas of Skagerrak, salinity ranges between 25 and 34 and in the Wadden Sea it is usually less than 30. Temperature and salinity show variability at annual, seasonal and decadal scales (Ærtebjerg *et al*., 2001).

The North Sea is considered one of the world's most important fishing grounds, in part thanks to large, shallow parts of the sea, which provide extensive growth of benthic and planktonic communities and so make this part one of the most productive areas in the world. The sea is also rich in oil and gas. These facts result in intense pressure on the marine ecosystems; the most notable are effects of fisheries and eutrophication, caused by the presence of densely populated areas surrounding the sea (Ærtebjerg *et al*., 2001). Essential information regarding phytoplankton species composition in this area has been published e.g. by Heimdal *et al*. (1973), Drebes (1974), Dodge (1982) and Hartley (1986). Reviews of hydrographical, chemical and biological aspects of the North Sea have been published by Otto *et al*. (1990) and Reid *et al*. (1990).

The main aim of this study is to contribute to our knowledge of the species composition of the spring phytoplankton in the North Sea, and factors affecting distribution.

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2. Material and Methods

2.1 Sampling

The samples were collected along a 250 km long transect located in the eastern, shallow part of the North Sea. Sampling was carried out between 2nd and 4th of March 2004, with a total of nine sampling stations. The stations were regularly spaced along 55°30′ N, between 3°40′ E and 7°40′ E (Fig. 1). The distances between the stations were 30′ (circa 32 km). The collection took place on board the H/s DANA of the Danish Ministry of Food, Agriculture and Fisheries. At each station, a Rosette unit equipped with a CTD (conductivity-temperature-depth) profiler (Sea-Bird, model SBE11), an in situ fluorometer and six Niskin 5 L bottles were used to obtain temperature, salinity and fluorescence profiles down to about 3 m above the bottom, and water samples.

Two Niskin bottles (10 l water sample, collected 5 meters below the water level) were filtered through a 20 μm mesh sized plankton net and fixed by Lugol's iodine solution. These samples were later used for quantitative counts in the laboratory. Another 2 liters of water sample were filtered through a plankton net of 10 μm mesh size. The algal composition of the filtrate was observed directly using a light microscope on board ship and the relative frequencies of species found were estimated. From the sample filtered through a 10 μm net a small part was prepared for transmission electron microscopy (TEM): A single drop was placed on each of two Formvar-carbon coated grids. The grids were fixed by vapour from small drops of 4% osmium tetroxide on a Petri dish that was placed over the grids for approximately 10–15 min. The grids were allowed to dry, washed with distilled water for 30 minutes and allowed to redry.

Net samples were taken in combination with bottle samples. They were collected by towing a plankton net (mesh size 20 μm) through the water until discoloration was visible in the collecting bottle. Immediately thereafter, the main part of the sample was fixed with Lugol's iodine solution. These samples were used to estimate of relative frequencies of determined species, later in the laboratory.

2.2 Counting and species determination

Phytoplankton concentrations were estimated by counting in a Sedgwick–Rafter counting slide. The fixed water samples from the filtered 10 l surface water were used for quantitative counting. The samples were concentrated by sedimentation for several days and the water was pipetted off. The remaining water with cells was further sedimented in centrifuge tubes for 24 hours. After sedimentation, 1 ml containing all cells from 10 l of sample was transferred into the counting slide. Numbers of the algal cells of *Bacillariophyceae*, *Dinophyceae*, *Prasinophyceae*, *Chlorophyceae* and *Dictyochophyceae* were counted. A minimum of 400 cells or colonies were counted to obtain a standard deviation of ±10% (Lund *et al*., 1958). For more concentrated samples, 1 ml of suspension was taken from 2 ml of concentrated solution, and so in the calculation the final cell concentration was doubled. For less abundant groups of algae, more fields were counted to obtain a better estimate of cell concentration.

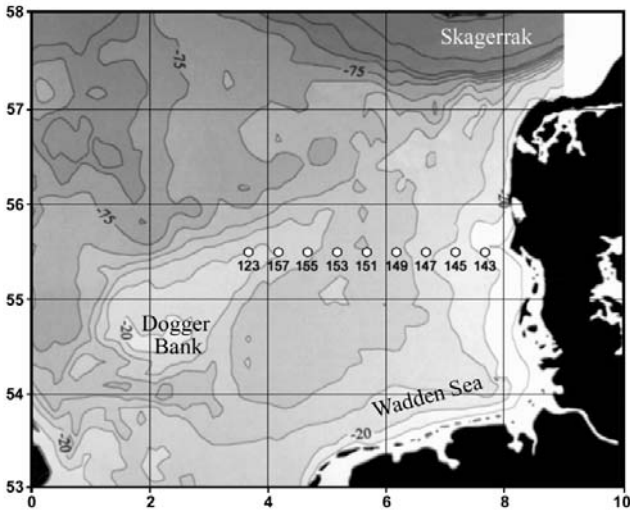


Fig. 1. Location of the sampling stations in the eastern part of the North Sea. Depth is given in meters.

When possible, organisms were identified to species level using the light microscope, whereby the relative frequency of individual species was noted on a scale from 1 (only one or few cells found) to 5 (the most abundant species), considered as live samples on board ship (2 l bottle water filtered by a 10 μm net) and Lugol-fixed samples (plankton net samples filtered by a 20 μm net). Transmission and scanning electron microscopy were also used in some cases. The frequency of organisms found only by means of electron microscopy was not enumerated.

The diatom frustules were cleaned using the following procedure: 10 ml of the sample was mixed with 2 ml of 30% sulphuric acid (H_2SO_4) and 10 ml of saturated potassium permanganate ($KMnO_4$). After 24 hours, oxidation was induced by addition of 10 ml saturated oxalic acid ($H_2C_2O_4 \cdot 2H_2O$). The solution was rinsed 3 times with distilled water and a drop was placed onto a coverslip and dried. The coverslip was then placed onto a slide with a drop of Naphrax mounting medium. Finally, the slide was carefully heated to remove the toluene from the medium. To observe thecal morphology and plate tabulation of dinophyte species, the samples were stained with calcofluor white solution (Fritz and Triemer, 1985) and examined under the Olympus BX-60 microscope equipped

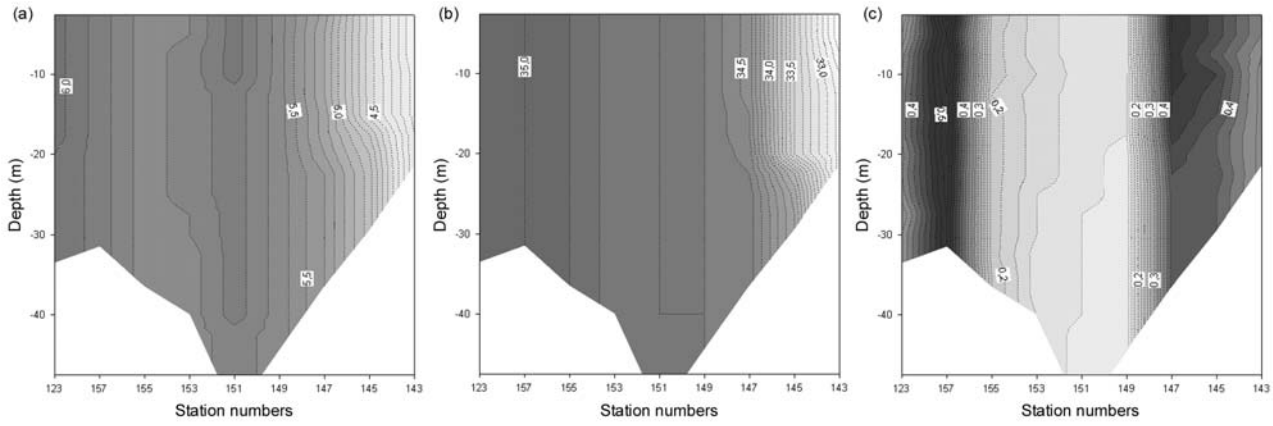


Fig. 2. Vertical profile of water temperature (a), salinity (b) and fluorescence (c), obtained along the transect.

with an epifluorescence illumination lamp Olympus U-RFL-T-200. The UV filter arrangement was for 330–380 nm excitation and 420 nm emission wavelength. (Calcofluor absorbs UV radiation in the 340–400 nm range and re-emits visible blue light.)

The species of choanoflagellates and diatoms were determined using a JEOL 1010 transmission electron microscope. Two sets of grids were used: grids made on board from the 10 μm sample and grids from acid-cleaned material. The later were used to examine frustules of small diatoms, which were observed without shadowcasting. The two samples with the greatest richness of dinophyte species were also examined with a JEOL JSM-6400 scanning electron microscope. The Lugol-fixed sample (1 ml) was washed in distilled water and mounted on 8 μm Millipore filters. Dehydration through an ethanol series (15 minutes in 30%, 50% and 70% ethanol, 20 minutes in 96% ethanol and 30 minutes in 99% ethanol and 99% ethanol with molecular sieves) was followed by critical-point drying with carbon dioxide (BAL-TEC CPD 030). Filters were mounted on 0.5″ aluminium specimen stubs (Agar scientific) and sputter-coated with platinum-palladium for 30 seconds using a JEOL JFC 2300 HR.

2.3 Data analyses

The data for species abundance and the environmental characteristics were statistically analyzed using a multivariate analysis routine in the program Canoco for Windows 4.5 (ter Braak and Šmilauer, 1998). The program CanoDraw for Windows 4.0 (ter Braak and Šmilauer, 2002) was used to construct of the ordination diagrams. Because of the short length of gradient—only 1.39 in the DCA (detrended correspondence analysis)—and the relative similarity of the stations, unimodal techniques were used in all analyses. Both indirect and direct analyses were used for the statistical evaluation of the data. The inner structure of the data was investigated using indirect PCA (principal component analysis), the relationship between the species composition of the stations and the environmental parameters was analyzed directly by means of RDA (redundancy analysis). The significance of independent variables was tested using Monte-Carlo permutation tests.

3. Results

3.1 Spatial variations of measured variables

Different horizontal gradients characterized the distribution of temperature, salinity and fluorescence (Fig. 2). No vertical gradients were noted along the transect due to well mixed water, except for the stations in the middle part of the transect, where a slight stratification was noted. The temperature varied from 4.0 to 6.1°C. The profile (Fig. 2(a)) showed a successive change of temperature along the transect, with cold coastal waters and warmer water near the oceanic part of the transect. A small increase in temperature was registered in the deepest part of the transect (station 151). Similar patterns of variation characterized the spatial distribution of salinity (Fig. 2(b)). The values varied between 32.7 and 35.0 PSU (approximately corresponding to ‰—Fotonoff and Millard Jr., 1983). Higher values were observed at the stations in the central part of the sea whereas low salinity was noted in the stations near the coast. This decrease is probably caused by the influence of the estuaries on the west coast of Denmark. A distinct fluctuation of fluorescence occurred along the whole transect (Fig. 2(c)). Values of chlorophyll a ranged from 0.13 to 0.54 mg·m^{-3}. The highest chlorophyll values were measured at stations 157 and 147, located in both western and eastern parts of the transect. Very low chlorophyll concentrations were found in the middle part of the transect.

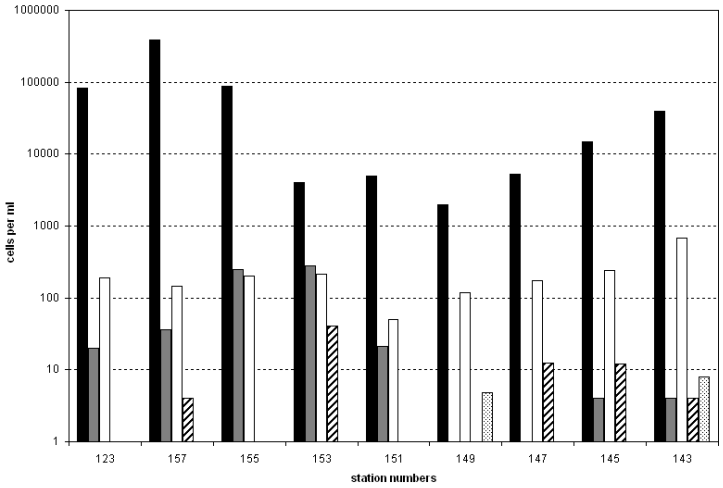


Fig. 3. Spatial distribution of cell concentration, shown for different phytoplankton groups—Bacillariophyceae (black bars), Dictyochophyceae (grey bars), Dinophyceae (white bars), Prasinophyceae (shaded bars) and Chlorophyceae (doted bars). The y axis is given in the logarithmic scale.

3.2 Distribution of the algal abundance

There was a distinct gradient in phytoplankton concentration of cells per ml along the whole transect (Fig. 3). At all sampling stations, the most abundant group was diatoms. However, the number of cells varied greatly among the stations. The highest abundance of diatoms was observed in the eastern and western stations of the transect. In the eastern part of the transect, cell numbers increased sharply at station 157, where almost 400,000 cells of diatoms occurred in 1 ml. The abundance was much lower (on average 4000 cells per ml) in the central part of the transect. This horizontal gradient of diatom abundance is thought to correspond with the measured fluorescence values, as shown in Fig. 2(c). The quantity of dinoflagellate cells showed a similar pattern, but the absolute number of cells was much lower. Two abundance peaks were observed in the spatial distribution of Dinophyceae: a large peak at station 143 (almost 700 cells per ml) and a much smaller one in the eastern station of the sampling transect. Similarly to diatoms, the lowest abundance of dinoflagellates occurred in the middle part of the transect. The spatial variation of the third most abundant group, Dictyochophyceae, showed a clearly different pattern. Cells of *Dictyocha* species had the highest relative frequencies at stations 153 and 155, where their abundance reached more than 250 cells per ml. Cells of *Dictyocha* species were scarce in the rest of the transect. Likewise, most cells of prasinophycean algae were found at station 153 in the middle of the transect. The representatives of the class *Chlorophyceae* occurred only in the eastern part of the transect in relatively low abundance (only circa 6 cells per ml).

3.3 Phytoplankton composition of the transect

A total of 144 different species were found at all stations along the whole transect. The species list with values of relative frequencies at all stations is given in Table 1.

With 85 species found, the diatoms were the most abundant algal group in the transect. Generally, centric diatoms occurred in larger numbers. The diatoms *Skeletonema marinoi* (Fig. 4), *Paralia sulcata* (Fig. 5) and *Porosira glacialis* (Fig. 6) were present at all stations in relatively high abundance. In the western part of the transect, filaments of *Skeletonema marinoi* produced a bloom, apparent as a high levels of fluorescence in this area. The genera with the highest number of species were *Chaetoceros* and *Thalassiosira*. A total of 12 species of *Chaetoceros* was found along the whole transect (Figs. 7–19). A distinct horizontal gradient of species composition was observed. The species *C. contortus* (Fig. 8) and *C. convolutus* (Fig. 9) had high relative frequencies in the western part of the transect, whereas *C. danicus* (Fig. 10) and *C. diadema* (Figs. 13 and 14) appeared in the eastern part of transect, near the coast. *Chaetoceros subtilis* (Fig. 19) was observed at the stations in both eastern and western parts of the transect, but not in the middle part. The genus *Thalassiosira* was represented by 10 species (Figs. 20–35). The two most abundant species, *T. angulata* (Fig. 20) and *T. eccentrica* (Figs. 26 and 27), had maximum relative frequency in the middle part of the transect. The number of pennate diatom species was clearly lower than centric ones (only 25% of all species), although some species occurred in high abundance. Among the most abundant species were *Nitzschia*

Table 1. Relative frequencies of species at the stations studied. The species codes correspond to Fig. 58.

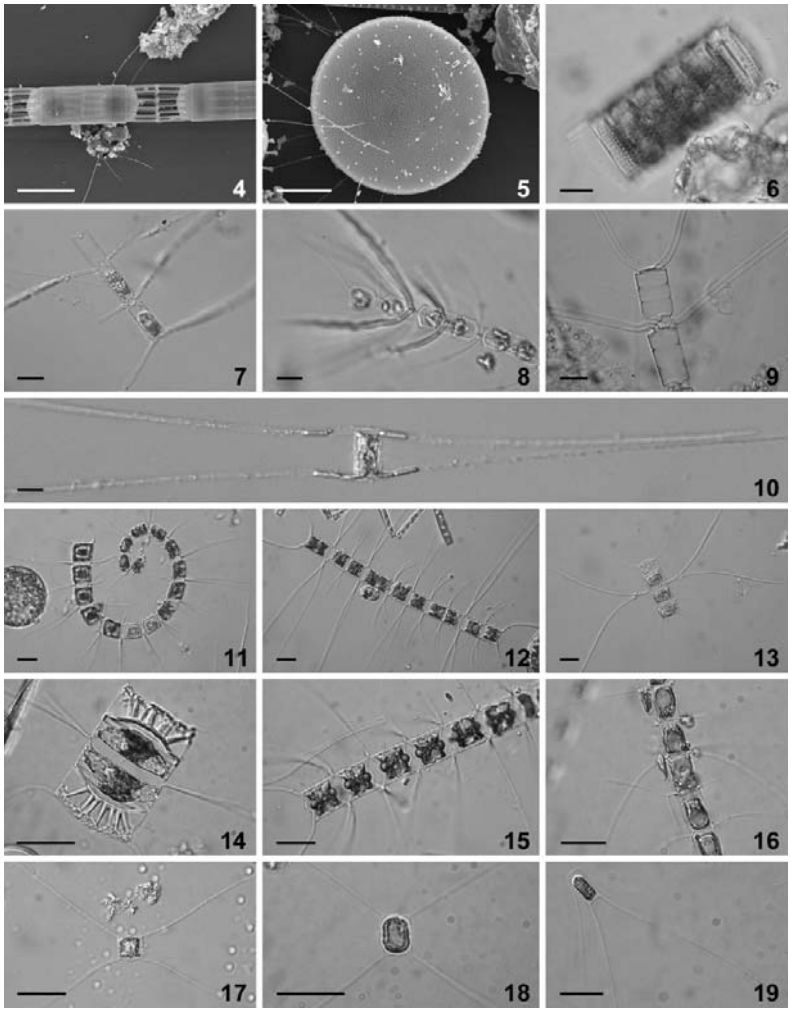
Species found in sampling sites	Codes	123	157	155	153	151	149	147	145	143
Craspedophyceae										
Calliacantha simplex Manton and Oates		—	—	—	1	—	—	—	—	—
Parvicorbicula socialis (Meunier) Deflandre		1	—	—	—	—	—	—	—	—
Chrysophyceae										
Meringosphaera mediterranea Lohmann		1	—	—	—	—	—	—	—	—
Prymnesiophyceae										
Emiliania huxleyi (Lohmann) Hay and Mohler	*Emi hux*	—	—	—	—	—	2	4	1	1
Dictyochophyceae										
Dictyocha crux Ehrenberg		—	—	—	—	—	1	—	—	—
Dictyocha fibula Ehrenberg	*Dic fib*	—	—	1	1	2	2	1	1	1
Dictyocha speculum Ehrenberg	*Dic spe*	2	1	3	3	3	1	1	—	1
Bacillariophyceae										
Actinocyclus octonarius Ehrenberg		1	1	2	3	1	1	1	1	1
Actinoptychus senarius (Ehrenberg) Ehrenberg	*Act ser*	—	1	1	1	2	2	2	2	3
Amphora ovalis (Kützing) Kützing	*Amp ova*	1	1	1	—	—	—	—	—	—
Asterionellopsis glacialis (F. Castracane) F.E. Round	*Ast gla*	—	—	2	4	2	—	1	1	1
Asterionellopsis kariana (Grunow) F.E. Round		1	—	—	—	—	1	—	—	1
Aulacodiscus argus (Ehrenberg) A. Schmidt	*Aul arg*	—	—	—	—	—	—	—	—	1
Bacillaria paxillifer (O.F. Müller) Hendey	*Bac pax*	—	2	1	1	1	1	—	—	—
Bellerochea malleus (Brightwell) Van Heurck		—	—	—	—	—	2	—	—	—
Biddulphia cf. *rhombus* (Ehrenberg) W. Smith		—	—	—	—	—	1	—	—	1
Brachysira cf. *aponina* Kützing		—	—	—	—	—	—	1	—	—
Brockmanniella brockmannii (Hustedt) Hasle		—	—	3	—	—	—	—	—	—
Chaetoceros borealis J.W. Bailey		—	—	1	1	2	1	—	—	—
Chaetoceros contortus Schütt	*Cha cnt*	1	2	2	2	—	1	—	—	—
Chaetoceros convolutus Castracane	*Cha cnv*	2	2	3	2	2	—	—	—	—
Chaetoceros danicus Cleve	*Cha dan*	—	1	—	—	2	1	1	2	2
Chaetoceros debilis Cleve	*Cha deb*	—	—	—	—	—	—	—	1	2
Chaetoceros decipiens Cleve	*Cha dec*	—	—	—	1	2	—	—	—	1
Chaetoceros diadema (Ehrenberg) Gran	*Cha dia*	—	—	—	—	—	3	3	3	4
Chaetoceros didymus Ehrenberg	*Cha did*	—	—	—	—	—	—	—	—	1
Chaetoceros pseudocrinitus Ostenfeld	*Cha pse*	2	2	—	—	—	—	—	—	—
Chaetoceros cf. *similis* Cleve		1	2	—	—	2	—	—	—	—
Chaetoceros socialis Lauder		—	—	—	—	1	—	—	—	—
Chaetoceros subtilis Cleve		2	1	1	2	—	—	2	1	1
Cocconeis sp.		—	—	1	—	—	—	—	—	—
Corethron criophilum Castracane	*Cor cri*	2	2	1	2	1	1	—	—	—
Coscinodiscus asteromphalus Ehrenberg		1	1	1	1	1	1	1	1	1
Coscinodiscus wailesii Gran and Angs	*Cos wai*	—	—	—	1	1	1	1	1	1
Diploneis smithii (Brébisson) Cleve	*Dip smi*	1	1	1	1	—	—	1	—	—
Diploneis cf. *coffaeiformis* (Schmidt) Cleve		—	—	—	—	—	—	—	1	—
Ditylum brightwellii (T. West) Grunow	*Dit bri*	—	—	—	2	4	2	1	2	3
Entomoneis sp.	*Ent* sp.	1	1	1	1	—	—	—	—	—
Eucampia zodiacus Ehrenberg	*Euc zod*	—	—	—	—	—	—	—	2	2
Fallacia forcipata (Greville) Stickle and Mann		—	1	1	1	—	—	—	—	—
Fragilaria cf. *islandica* Grunow ex Van Heurck		—	—	—	—	—	—	1	—	—
Fragilariopsis cf. *cylindrus* (Grunow) Krieger		1	2	2	1	1	—	—	1	1
Guinardia flaccida (Castracane) H. Peragallo		—	—	1	—	2	—	—	1	1
Guinardia striata (Stolterfoth) G.R. Hasle	*Gui str*	1	1	—	—	—	—	—	—	—

Table 1. (continued).

Species found in sampling sites	Codes	123	157	155	153	151	149	147	145	143
Gyrosigma fasciola (Ehrenberg) Griffith and Henfrey	*Gyr fas*	1	1	1	1	—	1	—	—	—
Leptocylindrus danicus Cleve		—	2	1	—	—	—	—	—	1
Minidiscus trioculatus (F.J.R. Taylor) Hasle		1	—	1	—	—	—	—	—	—
Navicula distans (W. Smith) Ralfs	*Nav dis*	2	2	2	2	2	1	1	—	—
Navicula cf. *duerrenbergiana* Hustedt		1	1	—	—	—	—	1	—	—
Navicula cf. *meniscus* Schumann		—	—	—	—	1	—	—	—	1
Navicula notha Wallace		1	—	1	—	—	1	—	—	—
Navicula cf. *pavillardii* Hustedt		1	1	—	—	—	—	1	—	—
Navicula peregrina (Ehrenberg) Kützing		2	—	—	1	—	—	—	—	—
Navicula perminuta Grunov		—	—	1	1	—	—	—	—	—
Navicula scopulorum Brébisson ex Kützing	*Nav sco*	—	2	1	—	—	—	—	—	—
Navicula cf. *transitans* Cleve		2	2	3	2	1	—	—	1	—
Neostreptotheca subindica von Stosch		—	—	—	—	—	—	1	—	—
Nitzschia constricta (Kützing) Ralfs	*Nit con*	3	1	4	3	—	1	1	—	—
Nitzschia cf. *dissipata* (Kützing) Grunow		1	1	1	1	1	—	—	—	1
Nitzschia cf. *fasciculata* Ehrenberg	*Nit fas*	2	1	1	—	1	—	—	—	—
Nitzschia longissima (Brébisson in Kützing) Ralfs		5	2	2	2	2	4	4	—	2
Nitzschia panduriformis var. *minor* W. Gregory		—	1	—	—	—	—	—	—	—
Nitzschia pusilla Grunow	*Nit pus*	2	2	2	1	—	—	—	—	—
Odontella aurita (Lyngbye) C. A. Agardh	*Odo aur*	—	—	1	2	1	1	1	—	2
Odontella mobiliensis (J.W. Bailey) Grunow	*Odo mob*	1	—	2	2	2	2	1	1	2
Odontella sinensis (Greville) Grunow	*Odo sin*	—	—	—	1	1	1	1	1	1
Paralia sulcata (Ehrenberg) Cleve		2	2	2	1	4	5	3	2	3
Pleurosigma cf. *lanceolatum* Donkin	*Ple lan*	2	2	2	1	1	—	—	—	—
Pleurosigma normanii Ralfs		1	1	2	1	1	1	1	1	1
Podosira stelliger (J.W. Bailey) Mann	*Pod ste*	1	1	1	2	2	2	2	2	1
Porosira glacialis (Grunow) E. Jorgensen	*Por gla*	5	5	3	1	1	1	2	3	5
Proboscia alata (Brightwell) Sündstrom		—	—	1	—	1	—	—	—	—
Pseudo-nitzschia pungens (Grunow ex Cleve) Hasle	*Pse pun*	1	3	3	1	2	1	—	—	1
Rhaphoneis amphiceros (Ehrenberg) Ehrenberg		2	2	3	2	2	3	2	1	2
Rhizosolenia polydactyla Castracane		—	—	—	—	—	—	—	1	—
Rhizosolenia pungens Cleve-Euler	*Rhi pun*	—	1	1	1	2	1	1	1	2
Rhizosolenia styliformis Brightwell	*Rhi sty*	—	—	1	1	1	1	—	—	—
Skeletonema marinoi Sarno et Zingone	*Ske mar*	5	5	5	4	3	1	1	2	3
Thalassionema nitzschioides (Grunow) Mereschkowsky	*Ths nit*	3	3	4	5	2	4	5	5	5
Thalassiosira angulata (Gregory) Hasle	*Tha ang*	1	—	1	3	4	5	4	4	3
Thalassiosira anguste-lineata (Schmidt) Fryxell et Hasle		—	—	—	—	—	2	—	—	—
Thalassiosira curviseriata Takano		—	2	4	—	—	—	—	—	1
Thalassiosira constricta Gaarder	*Tha con*	—	—	—	—	—	—	—	—	1
Thalassiosira eccentrica (Ehrenberg) Cleve	*Tha ecc*	2	2	2	5	4	3	3	2	1
Thalassiosira cf. *lineata* Jousé	*Tha lin*	—	—	—	—	—	—	—	—	1
Thalassiosira nordenskioeldii Cleve	*Tha nor*	—	—	—	—	—	—	—	3	4
Thalassiosira pacifica Gran and Angst		1	1	1	1	2	2	1	1	2
Thalassiosira pseudonana Hasle and Heimdal		1	—	1	—	—	—	—	—	1
Thalassiosira punctigera (Castracane) Hasle	*Tha pun*	—	—	1	1	2	2	1	2	2
Thalassiosira tenera Proschkina-Lavrenko		1	1	1	1	—	1	—	1	1
Triceratium alternans J.W. Bailey		1	1	1	—	1	2	2	1	1
Triceratium favus Ehrenberg		—	—	—	—	—	—	1	—	—
Dinophyceae										
Alexandrium tamarense (Lebour) Balech	*Ale tam*	2	2	2	3	2	2	2	—	—
Amphidoma caudata Halldal	*Amh cau*	1	—	1	2	2	1	—	—	1
Amylax triacantha (Jørgensen) Sournia	*Amy tri*	—	—	1	1	1	1	1	1	—

Table 1. (continued).

Species found in sampling sites	Codes	123	157	155	153	151	149	147	145	143
Ceratium furca (Ehrenberg) Claparède et Lachmann	*Cer fur*	—	—	—	1	1	1	1	2	1
Ceratium fusus (Ehrenberg) Dujardin		—	—	—	—	1	1	2	1	—
Ceratium horridum (Cleve) Gran		—	—	—	—	2	—	—	—	—
Ceratium lineatum (Ehrenberg) Cleve	*Cer lin*	—	—	—	1	1	1	—	—	—
Ceratium longipes (Bailey) Gran	*Cer lon*	—	—	—	2	1	1	2	2	1
Ceratium macroceros (Ehrenberg) Vanhöffen	*Cer mac*	—	—	—	1	1	—	—	—	—
*Ceratium tri*pos (O.F. Müller) Nitzsch	*Cer tri*	—	1	—	2	1	1	—	—	—
Dinophysis acuminata Claparède et Lachmann		—	—	—	1	—	1	1	—	—
Diplopelta bomba Stein ex Jorgensen	*Dpl bom*	—	—	1	2	2	3	3	2	1
Dissodinium pseudolunula Swift ex Elbrächter et Drebes		—	—	—	—	—	—	1	—	—
Gonyaulax spinifera (Claparède et Lachmann) Diesing	*Gon spi*	1	—	1	1	1	—	1	—	—
Gymnodinium sp.		—	—	1	1	—	1	1	—	—
Gyrodinium cf. *undulans* Hulbert		1	—	—	—	2	2	1	—	2
Gyrodinium sp.		—	—	—	—	1	—	—	—	—
Minuscula bipes Lebour		1	1	2	2	1	2	2	2	1
Noctiluca scintillans (Macartney) Kofoid et Swezy	*Noc sci*	—	—	—	—	—	—	—	1	1
Pentapharsodinium dalei Indelicato et Loeblich	*Pen dal*	1	1	2	3	3	2	2	1	1
Phalacroma cf. *mitra* Schütt		—	—	—	—	—	—	—	1	—
Phalacroma rotundatum (Claparède et Lachmann) Kofoid et Michener	*Pha rot*	1	—	—	—	1	1	2	2	1
Prorocentrum micans Ehrenberg	*Prr mic*	—	—	—	2	1	3	1	1	1
Proterythropsis vigilans Marshall	*Ptr vig*	—	—	—	1	—	—	—	—	—
Protoceratium reticulatum (Claparède et Lachmann) Butschli	*Ptc ret*	—	1	1	2	3	—	—	—	—
Protoperidinium achromaticum (Levander) Balech	*Pro ach*	1	—	—	2	2	2	3	4	4
Protoperidinium brevipes (Paulsen) Balech		—	1	1	1	1	—	1	1	—
Protoperidinium cerasus (Paulsen) Balech	*Pro cer*	1	1	1	—	—	—	—	—	—
Protoperidinium conicum (Gran) Balech	*Pro con*	—	—	—	1	1	—	—	1	—
Protoperidinium denticulatum (Gran et Braarud) Balech	*Pro den*	—	—	—	1	1	—	—	—	—
Protoperidinium depressum (Bailey) Balech	*Pro dep*	—	1	1	2	1	—	—	—	—
Protoperidinium excentricum (Paulsen) Balech		—	—	—	—	—	—	—	1	—
Protoperidinium cf. *granii* (Ostenfield) Balech	*Pro gra*	—	1	1	—	—	—	—	—	—
Protoperidinium leonis (Pavillard) Balech	*Pro leo*	—	—	1	2	—	1	—	—	—
Protoperidinium marielebouriae (Paulsen) Balech		—	—	—	—	—	—	—	2	—
Protoperidinium oblongum (Aurivillius) Parke et Dodge		—	—	1	1	—	1	—	—	—
Protoperidinium pellucidum Bergh	*Pro pel*	2	2	1	2	2	2	1	1	1
Protoperidinium pentagonum (Gran) Balech		1	—	—	—	—	1	1	—	—
Protoperidinium pyriforme (Paulsen) Balech	*Pro pyr*	1	1	2	2	2	—	—	—	—
Protoperidinium subinerme (Paulsen) Loeblich	*Pro sub*	—	—	—	1	1	1	1	—	—
Protoperidinium sp.		—	—	—	—	—	—	1	—	—
Protoperidinium sp. B Hansen and Larsen		—	—	—	—	1	—	—	—	—
Pyrophacus horologium Stein		1	—	—	1	1	1	—	1	—
Zygabikodinium lenticulatum Loeblich Jr. and Loeblich		1	1	1	1	1	1	1	2	1
Prasinophyceae										
Halosphaera viridis Schmitz	*Hal vir*	1	1	1	—	2	—	—	—	—
Pterosperma cristatum Schiller	*Pte cri*	—	—	1	2	1	1	2	2	1
Pterosperma moebii (Jørgensen) Ostenfeld	*Pte moe*	—	—	—	1	1	—	—	—	—
Pterosperma polygonum Ostenfeld	*Pte pol*	—	—	—	1	1	—	—	—	—
Pterosperma vanhoeffenii (Jørgensen) Ostenfeld	*Pte van*	—	—	—	1	2	1	—	—	—
Chlorophyceae										
Pediastrum boryanum (Turpin) Meneghini	*Ped bor*	—	—	—	1	1	1	1	1	1
Pediastrum cf. *kawraiskyi* Schmidle		—	—	—	—	—	—	—	—	1
Scenedesmus sp.		—	—	—	—	—	—	—	1	—

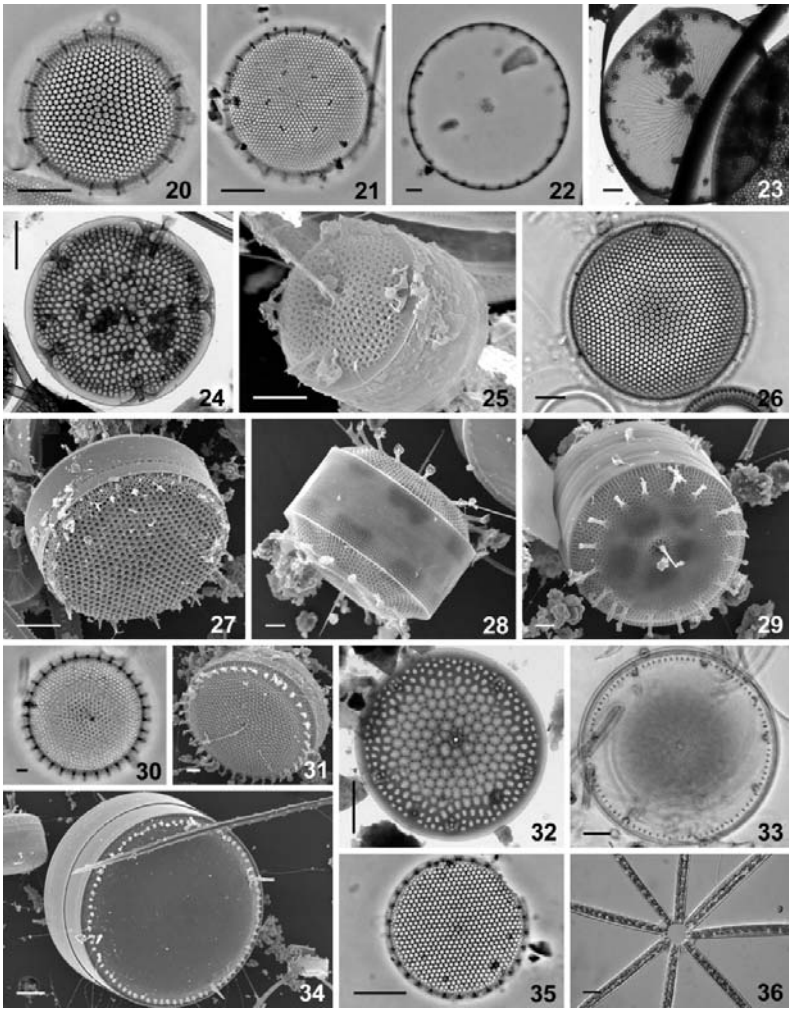


Figs. 4–19. Main and interesting species found along the transect (1). 4. *Skeletonema marinoi*. 5. *Porosira glacialis*. 6. *Paralia sulcata*. 7. *Chaetoceros borealis*. 8. *Chaetoceros contortus*. 9. *Chaetoceros convolutus*. 10. *Chaetoceros danicus*. 11. *Chaetoceros debilis*. 12. *Chaetoceros decipiens*. 13, 14. *Chaetoceros diadema*. 15. *Chaetoceros didymus*. 16. *Chaetoceros pseudocrinitus*—17, 18. *Chaetoceros* cf. *similis*. 19. *Chaetoceros subtilis*. Scale bars: Figs. 4–6: 10 μm; Figs. 7–19: 20 μm.

longissima and *Thalassionema nitzschioides* (Fig. 36). High levels of fluorescence in the eastern part of the transect were probably partially caused by their blooms.

In comparison to diatoms, only 44 of the species found were dinoflagellates. Twenty five of these were heterotrophic and therefore did not contribute to the measured fluorescence. The most abundant species were *Alexandrium tamarense* (Fig. 37) in the western part, *Protoperidinium achromaticum* and *Diplopelta bomba* (Fig. 38) in the eastern part, and *Pentapharsodinium dalei* (Fig. 39) at all stations along the transect, with maximum abundance in the central area. At all stations, *Minuscula bipes*, *Protoperidinium pellucidum* and *Zygabikodinium lenticulatum* occurred in relatively constant abundance. Most of the dinoflagellate species found belong to the thecate genera *Ceratium* and *Protoperidinium*. With 17 species found, the genus *Protoperidinium* was the richest genus of algae, and was found throughout the transect (Figs. 40–52). *P. achromaticum* (Fig. 40), the most numerous species, was very abundant at stations 143 and 145, located near the coast. However, no cells were found in the western stations of the transect.

Other algal groups were much less abundant, with the exception of *Dictyocha speculum* (Fig. 53), which commonly occurred at almost all stations. Two species of colorless flagellates—*Calliacantha simplex* (Fig. 54) and *Parvicorbicula socialis* (Fig. 55)—were found by transmission electron microscopy. A small bloom of *Emiliania huxleyi* (Fig. 56) was registered in the eastern part of the transect. This coccolithophorid alga was mainly abundant



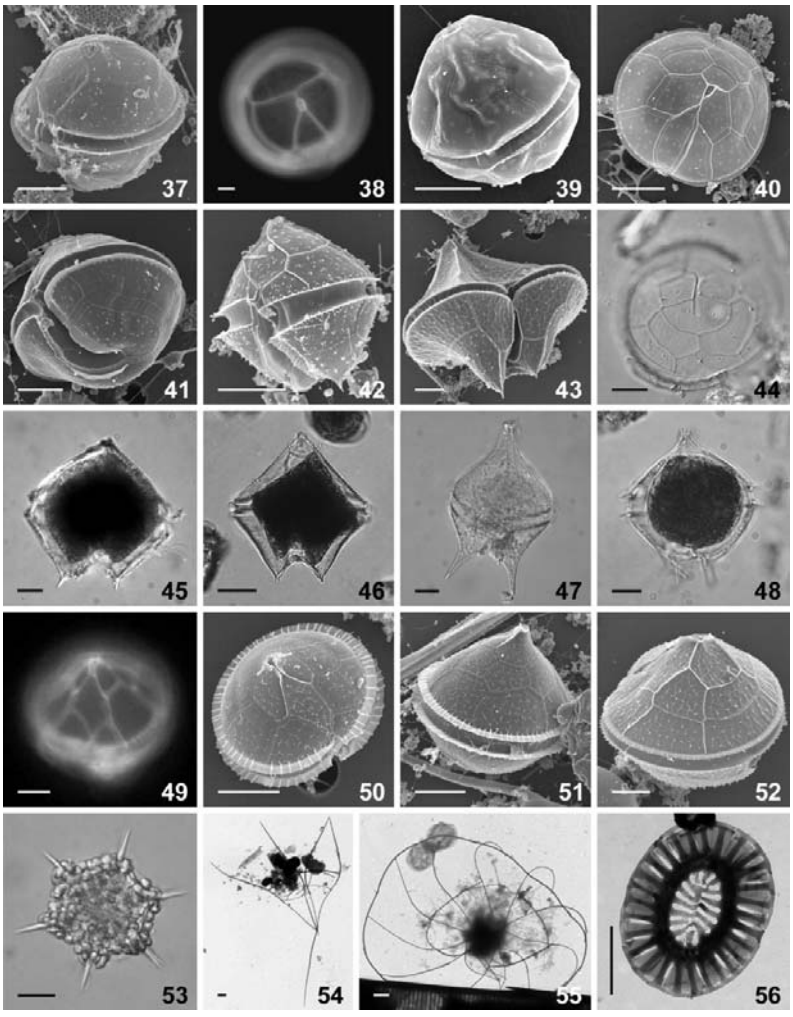
Figs. 20–36. Main and interesting species found along the transect (2). 20. *Thalassiosira angulata*. 21. *Thalassiosira angustelineata*. 22, 23. *Thalassiosira constricta*. 24, 25. *Thalassiosira curviseriata*. 26, 27. *Thalassiosira eccentrica*. 28, 29. *Thalassiosira nordenskioeldii*. 30, 31. *Thalassiosira pacifica*. 32. *Thalassiosira pseudonana*. 33, 34. *Thalassiosira punctigera*. 35. *Thalassiosira tenera*. 36. *Thallassionema nitzschioides*. Scale bars: Figs. 20–21, 26–27, 33–36: 10 μm; Figs. 22–25, 28–31: 2 μm; Fig. 32: 1 μm.

at station 147, where together with *Thalassiosira angulata* and *Thalassionema nitzschioides*, it was one of the most dominant algae.

3.4 Results of statistical analyses

An indirect gradient analysis PCA was used to detect the inner structure of the data obtained. The two first ordination axes together explained 60% of the total variability. The positions of the samples in the space of these two axes are illustrated in Fig. 57. On the ordination diagram, the sampling localities are arranged more or less in correspondence to their physical order along the transect, forming the shape of an inverted letter U. The sampling stations form three distinct groups in the diagram: The group of coastal stations 143, 145, 147 and 149; the group of oceanic stations 123, 155 and 157; and the group of two stations 151 and 153, situated in the middle part of the transect. The distinct separation of these three groups along the first ordination axis reflects the important role of the distance from the coast for the species composition at each station. However, the uneven arrangement of the stations along the first axis indicates the considerable changes of phytoplankton composition in the areas between stations 149–151 and 153–155. The second ordination axis dividing the stations 151 and 153 from all others is linked positively with sea depth and negatively with fluorescence.

The influence of several environmental characteristics on species composition was tested statistically using RDA analysis. Separate analyses were performed to de-



Figs. 37–56. Main and interesting species found along the transect (3). 37. *Alexandrium tamarense*. 38. *Diplopelta bomba*. 39. *Pentapharsodinium dalei*. 40, 41. *Protoperidinium achromaticum*. 42. *Protoperidinium brevipes*. 43. *Protoperidinium 0conicum*. 44. *Protoperidinium denticulatum*. 45. *Protoperidinium leonis*. 46. *Protoperidinium marielebouriae*. 47. *Protoperidinium oblongum*. 48, 49. *Protoperidinium pellucidum*. 50, 51. *Protoperidinium pyriforme*. 52. *Protoperidinium subinerme*. 53. *Dictyocha speculum*. 54. *Calliacantha simplex*. 55. *Parvicorbicula socialis*. 56. *Emiliana huxleyi*. Scale bars: Figs. 37–53: 10 μm; Figs. 54–56: 1 μm.

tect the influence of temperature, salinity, fluorescence, distance from the coast, depth and the total abundance of algae. Only the influence of distance from coast proved to be significant, with a p-value of 0.001. All other characteristics were found not to be statistically significant for the transect. The relation of individual species to the coastal or oceanic environment is shown in Fig. 58. The first ordination axis, characterizing the influence of coast distance, explained almost 35% of the total variability. *Chaetoceros diadema*, *Chaetoceros danicus*, *Emiliania huxleyi*, *Protoperidinium achromaticum*, *Actinoptychus senarius*, *Thalassionema nitzschioides* and *Pediastrum boryanum* belong among the typical coastal species. Similarly, the majority of *Thalassiosira* species were positively correlated with the coastal environment. The species *Chaetoceros convolutus*, *Chaetoceros contortus*, *Pleurosigma lanceolatum*, *Gyrosigma fascicola*, *Skeletonema marinoi* and *Nitzschia* species show an affinity for the oceanic environment. Species displayed in the upper part of the diagram showed no relation to either coastal or oceanic areas. These species (e.g. *Ceratium macroceros*, *Ceratium lineatum*, *Thalassiosira eccentrica*, *Pentapharsodinium dalei* and all species of *Pterosperma*) occurred only or in highest abundance in the middle part of the transect, at stations 151 and 153, respectively. *Porosira glacialis* has a distinctive place on the ordina-

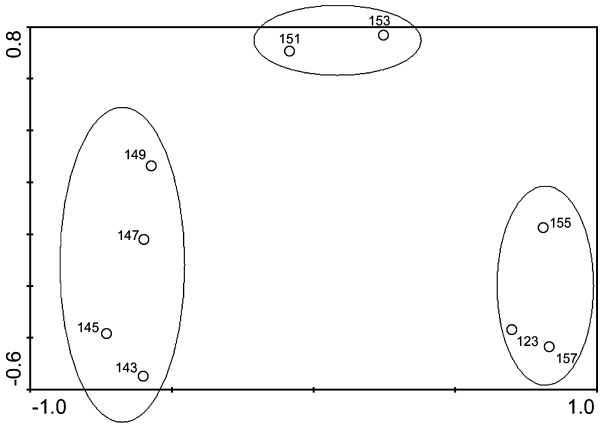


Fig. 57. PCA ordination diagram showing position of the samples in the space of the first two ordination axes. Separation of sampling stations into three groups is illustrated.

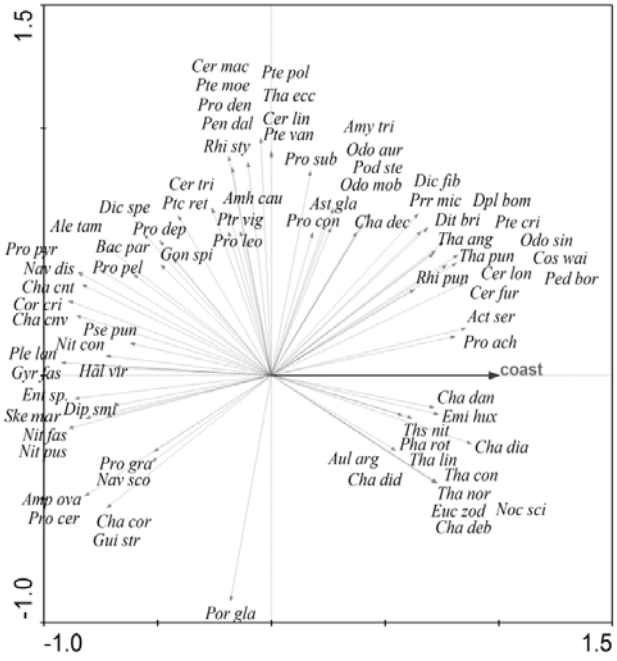


Fig. 58. RDA ordination diagram showing positions of the species and their relation to the coastal or oceanic environment in the space of the first two ordination axes. See Table 1 for species codes. Only the 78 most fitted species are displayed.

tion diagram. Only this species showed an atypical distribution along the transect, with highest abundances at both coastal and oceanic parts.

4. Discussion

Distinct horizontal gradients of algal concentration and species composition were found along the transect. Three groups of stations were found, based on different phytoplankton composition: Most of the species were most abundant either at the coastal or at the oceanic part of the transect, while some species occurred mainly at stations located in the deeper area in the middle of the transect. High concentrations of diatom cells per ml were noted in both eastern and western parts of the transect, although a much higher concentration was discovered at station 157. However, different algal composition were found at stations situated in the eastern and the western part of the transect, respectively. Generally, the highest species diversity of all algae groups was found at stations 151 and 153, with low numbers of algae per ml. This phenomenon is known not only in the marine environment but also under all types of natural conditions (Levin *et al.*, 2001).

The level of temperature and salinity was more or less constant along the whole transect, apart from two stations at the west coast of Denmark (stations 143 and 145), where the water was colder and less saline, probably due to the influence of fresh water from estuaries along the coast of Denmark. A very different pattern was found in the spatial distribution of fluorescence values. Two distinct peaks of fluorescence occurred at stations 157 and 147, located at the opposite ends of the transect. Very low chlorophyll concentrations were found in the middle part of the transect. This chlorophyll distribution was obviously associated with water depth. High chlorophyll levels were measured in the shallow parts of the transect, while the lowest concentration was found in the deepest part (station 151). While the eastern part of the transect was influenced by coastal proximity, the shallow depth in the western part of the transect was caused by the vicinity of the shallow Dogger Bank area (Johns and Reid, 2001). These two zones were separated by an area with depths of 35–40 meters. The high algal abundance in both eastern and western parts of the transect was probably caused by the nutrient richness in shallow, mixed parts of the sea, which evoked the phytoplankton bloom. However, we did not measure any nutrient concentrations to support this hypothesis.

In both eastern and western parts of the transect, the high values of fluorescence were probably caused by the large number of diatoms, which are typical organisms of spring blooms in marine environments (Johns and Reid, 2001). However, we could not rule out that these values were caused by other organisms, for example by nanoplanktonic ones. They could contribute to the measured values of fluorescence but they were not found because of the sampling method. However, diatoms were found in huge numbers, for example circa 400 million cells per liter of sampled water at station 157. Moreover, the diatom blooms at the different parts of the transect were produced by different species.

The bloom of *Skeletonema marinoi* in the sea far from the coast is quite surprising. The occurrence of *Skeletonema* species is usually associated with coastal areas; blooms have been reported very frequently during spring from the coastal areas in Norway (Braarud *et al*., 1973; Erga and Heimdal, 1984), Canada (Conover and Mayzaud, 1984), Alaska (Waite *et al*., 1992) and British Columbia (Haigh *et al*., 1992). Furthermore, *Skeletonema* species are suggested to grow best in semi-enclosed waters and are not often found in high concentrations in oceanic environments (Smayda, 1957; Sarno *et al*., 2005). In our study, high abundances were noted at stations near the coast. However, the highest abundance of this species was observed in the western stations, in the middle part of the North Sea. Additionally, the diatom cell concentration in this part of transect was 10× higher than the bloom near the coast. The high production of *Skeletonema marinoi* in the open sea might be caused by the relatively shallow water in this part of the sea, which simulates coastal conditions, and the slightly warmer water temperature. The higher oceanic abundance could be also associated with eddies reflecting the coastal origin of the water (Batten and Crawford, 2005). However, our data did not support the strict ecological preference of *Skeletonema* for semi-enclosed, coastal waters.

The spatial distribution of dinoflagellates was similar to that of diatoms. However, the highest number of dinoflagellate cells was found at station 143, whereas the highest bloom of diatoms was observed at station 157. The lowest abundance of dinoflagellates was found in the middle of the transect (station 151), increasing again toward the oceanic part of the transect. The species compositions of the coastal and oceanic stations of transect were also different. For example, *Protoperidinium achromaticum* was mainly found at the stations near the cost. This species has previously been found by e.g. Dodge (1982) round British Isles, by Trigueros *et al*. (2000) in the estuary of Urdaibai in northern Spain and by Hoppenrath (2005) from Helgoland. It seems that this species is a typical representative of coastal phytoplankton.

Three distinct groups of stations were found based on differences in species composition—three stations in each eastern and western part of the transect, and two stations in the middle. Different algal species dominated in each group. Spatial differences of phytoplankton composition along the transect were significant in RDA analysis, showing differences between coastal and oceanic species. Reid *et al*. (1978), who investigated the spatial distribution of phytoplankton of California, published similar results. They found that the plankton composition at stations 100 km apart in the along-shore direction was more similar that at stations hundreds of meters apart in the offshore direction.

Many species showed one of four types of distribution along the transect, as shown in Fig. 58 (coastal, oceanic, with a maximum of abundance in the middle part of the transect, or more abundant in both eastern and western part of the transect). Most of the species occurred in either the eastern or the western part of the transect, in coastal or open oceanic environments, respectively. With the exception of *Skeletonema*, the ecological preferences of most other species correspond with published data. A preference for a coastal environment has previously been published for e.g. *Coscinodiscus wailesii* (Edwards and Johns, 2004), *Emiliania huxleyi* (Yang *et al*., 2001), and *Thalassiosira angulata* and *T. nordenskioeldii* (Reigstad *et al*., 2000). The genus *Chaetoceros*, similar to the genus *Thalassiosira*, is generally considered to be coastal (Cupp, 1943). We observed some species of *Chaetoceros* in coastal waters only, but other species were found to be close to the oceanic part of the transect (for details see Fig. 18). Among the oceanic species were *Ch. contortus*, *Ch. convolutus* and *Ch. pseudocrinitus*. However, *Ch. contortus* has previously been reported only from coastal areas (Rines, 1999).

Several species (e.g. *Pterosperma* species and *Thalassiosira eccentrica*) were found only in the middle part of the transect. We assume that the distribution of these species is correlated with the water depth, although it was not significant in the RDA analysis. This result of the analysis was probably caused by different phytoplankton composition in both eastern and western parts of transect, where the water depth was similar. The atypical distribution of *Porosira glacialis*, with highest abundances in both coastal and oceanic parts of transect, may suggest the existence of two cryptic species with similar morphology but different ecological preferences.

In conclusion, we observed a distinct gradient in distribution of many species along the transect, corresponding to their ecological preferences to the coastal or oceanic environment, respectively. Detection of species ecology needs much more investigation in various localities throughout the world. Nevertheless, we believe that this investigation contributes to the knowledge of habitat preferences of marine phytoplankton species.

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