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# Evidence of a high-productivity area off the coast of Málaga from studies of diatoms in surface sediments

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#### Abstract

The assemblages of diatoms contained in nineteen surface sediment samples recovered off the coast of Málaga province (Spain) between 5°W and 4°38′W have been analysed. The variations observed in the diatom assemblage point to the presence of nutrient-enriched waters, transported laterally from the centre of an upwelling that occurs to the west of the study area. The utility of species such as *Paralia sulcata, Thalassionema nitzschioides* and the spores of *Chaetoceros* spp. in the reconstruction of physico-chemical and biological characteristics and of the spatial structure of the upwelling is confirmed. © 1998 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

The Mediterranean behaves as a system of *antiestuarine* circulation with surface water entering from the Atlantic and leaving the Mediterranean at depth (Bormans et al., 1986). The gateway for the entry of water from the Atlantic is the Alborán Sea. When this water enters the Alborán Basin it is diverted to the northeast to form an anticyclonic gyre that occupies the whole of the western sector of the Alborán Sea, the western anticyclonic gyre (GAOC, Giro Anticiclonico Occidental) (Fig. 1). One of the most important oceanic fronts of the whole Mediterranean is defined in the northern and eastern areas of this gyre.

On the coast of Málaga, northeast of the Strait

of Gibraltar, upwelling of subsurface waters occurs, feeding the area in the proximity of the Spanish coast (Parrilla and Kinder, 1987). It is not known how these waters get there nor whether the upwelling process is local or also occurs elsewhere.

These nutrient-enriched waters enable the blooming of communities of phytoplankton. Generally, upwelling areas are characterised by abundant diatoms, as compared to oligotrophic areas in which this group is less represented (Estrada and Blasco, 1985). Even though only a minimal part of the frustules produced in the photic zone are preserved in the sediments (Calvert, 1974), the diatom abundance and distribution patterns observed in the sediments of nearby areas, such as Portugal, reflect presentday hydrography and productivity (Abrantes, 1988a, 1991a,b). The phytoplankton of coastal upwelling can be described as a sequence of assemblages

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Fig. 1. Studied area. Location of the predominant oceanographic features of the Alborán Sea, the anti-cyclonic gyre (GAOC) and the Almeria–Oran density Front (after La Violette, 1984).

that develop around the upwelling nucleus (Estrada and Blasco, 1985). Schuette and Schrader (1981), Abrantes and Sancetta (1985) and Abrantes (1988b) have recorded a spatial succession of diatom assemblages in surface sediments that is equivalent to the spatio-temporal succession observed by planktologists. The sequence of diatom assemblages in the sediment taphocoenoses includes, in the loci of the upwelling, small species of the genus Thalassiosira accompanied by small cells of Paralia sulcata and spores of Leptocylindrus, while proliferations of large diatoms (such as Coscinodiscus spp.) appear in the peripheral areas (Estrada and Blasco, 1985; Abrantes, 1988b). The presence of Chaetoceros resting spores (RS) in the taphocoenoses is indicative of fronts of major variability (Abrantes, 1988b).

The present work centres on the sphere of influence of the upwelling caused by the ascent of subsurface waters to the northeast of the Strait of Gibraltar (Fig. 1). The distribution of diatom thanatocoenoses recorded in the surface sediments of the area corroborates the presence of upwelling and in fact, allows the estimation of certain aspects of the spatial structure of the upwelling.

#### 2. Materials and methods

The nineteen surface sediment samples used in this study were collected from the continental shelf at Málaga, to the northeast of the Strait of Gibraltar, between San Pedro de Alcántara and Cape Calaburras (5°W and 4°38′W). They were collected during the oceanographic leg 'Proyecto Minero-Submarino de Málaga–Gibraltar' of the Spanish Oceanographic Institute (SOI) of the vessel *Jafruda Cresques* during autumn 1973. Samples were recovered with a Shypek dredge at depths from 10 to 110 m along three transects perpendicular to the coast (Fig. 2a).

Samples were subjected to complete chemical treatment: hot treatment with HCl and  $H_2O_2$  to eliminate CaCO<sub>3</sub> and organic matter. Following this, samples were neutralised with successive washes in demineralized water. The samples were sieved with

125 and 63  $\mu$ m mesh to eliminate the coarse fraction and the resulting residue was weighed and observed under the microscope to ascertain possible losses of larger diatoms as well as for the long pennates such as *Thalassionema nitzschioides* and/or *Thalassiothrix* spp. No evidence of losses was observed. The fraction smaller than 63  $\mu$ m was used for micropalaeontological analysis.

For each of the samples used in the micropalaeontological study, the initial dry weight, the suspension volume, and the volume used to mount the slides were known. Three slides per sample were used in counting. Five to six transects per slide were studied, and in general more than 400 fields of view were observed. Magnification was ×1000. The recommendations of Schrader and Gersonde (1978) were used to count diatom valves. Due to the low number of diatoms per gram in most of the samples, a compromise between number to be counted and time spent had to be reached, but the number of valves identified for species identification was never less than 100 (Table 1). Samples 305, 307, 309 and 362 were not considered for species distribution due to the extremely low number of diatoms per gram.

Table 1
Number of diatoms counted per sample

All samples were assessed quantitatively for number of whole diatom valves, the number of fragments, silicoflagellates, sponge spicules, palynomorphs, phytoliths and radiolaria per gram of dry sediment (Table 1).

For evaluation of the state of preservation of diatom valves we followed the recommendations of Bárcena and Flores (1991).

## 3. Oceanographic aspects of the Alborán Sea

The Alborán Sea is the westernmost basin of the Mediterranean. All the water masses participating in exchanges through the Strait of Gibraltar circulate through the Alborán Sea: Atlantic Surface Water (ASW), Levantine Intermediate Water (LIW) and West Mediterranean Deep Water (WMDW). The circulation of the Alborán Sea is very energetic and is subject to strong seasonal variations related to the fluctuations in the intensity of water exchange through the Strait of Gibraltar (Pistek et al., 1985). Unlike most of the Mediterranean, the Alborán Sea has two systems of high biological productivity: the

Sample	Counted valves	Valves/g	Fragments/g	Porifera/g	Phytoliths/g	Palynomorphs/g	Preservation
297	104	10100	98100	5300	1200	2000	М
298	107	2900	26000	7700	0	300	М
299	100	6200	4400	2100	0	0	М
301	115	11100	85000	12300	1000	2500	М
304	102	16600	94600	9100	400	500	М
305	10	1100	24100	4500	300	600	
306	102	1100	6800	600	0	300	M–G
307	5	1000	9100	800	0	0	
308	256	18000	13000	1400	200	500	G
309	4	500	1300	200	0	0	
362	11	900	200	2000	200	0	
365	198	14500	70800	8200	400	600	M–G
368	102	6400	48900	6600	300	200	G
369	136	55200	458400	40700	400	9300	М
371	133	27200	225100	19600	1400	7400	М
428	313	59800	186900	1400	1900	7500	G
431	104	17600	148400	13000	1300	1300	M–G
432	108	56800	13000	8300	600	0	М
435	101	21800	222000	31000	2900	1500	М

Absolute abundances per gram of dry sediment of whole diatom valves, fragments of diatoms, porifera spicules, phytoliths and palynomorphs. Radiolarians and silicoflagellates were present in very low abundances and therefore they are not included in this table. Preservation is indicated as: G (good), M (moderate) and P (poor).



Fig. 2. Sampling localities and bathymetry. (a) Topography of the Málaga continental shelf according to the SOI. (b) Total content of biogenic and clay material (Hernandez-Molina, 1993).

system associated with the Almería–Oran density front and the GAOC. The later system is explored here. To the north of the GAOC there is an upwelling of subsurface waters. This vertical movement does not seem to be linked to regional atmospheric dynamics (La Violette, 1984) and is probably the result of instability created by lateral contact between the ASW and the LIW and the topography of the sea floor (Perkins et al., 1990). The deep, nutrientenriched waters rise following a continental slope (Ballester and Zavatti, 1983) and fertilise surface levels. In this way, a zone of high biological productivity is created. Moreover, the area receives an additional contribution of nutrients due to partial en-



Fig. 2 (continued). (c) Diatom abundances (valves/g of dry sediment) in the studied area.

richment of the ASW as it passes through the Gulf of Cadiz and the Strait of Gibraltar (Minas et al., 1984; Parrilla and Kinder, 1987).

Hydrographic evidence of a narrow divergence to the north of the front, close to 5°W, has been found in several SOI legs (Parrilla and Kinder, 1987). Upwelling waters have been reported by Gil (1986) in the northwest region of the Alborán Sea. Minas et al. (1984) observed areas of maximum chlorophyll-a with concentrations > 3.0  $\mu$ g/l to the west of the 5°W meridian. High, although less significant, values (2.0 to 1.0  $\mu$ g/l) were found to the east. New evidence of blooming in this area was offered by Packard et al. (1988). These authors recognised a zone with minimum oxygen levels, a direct consequence of the biological consumption of the gas, and underscored the importance of this divergence to the northwest of the gyre as a mechanism for pumping the nutrients necessary to maintain the high productivity off the coast of Málaga.

The presence of low temperatures and high salinities, high concentrations of chlorophyll-a, and of a zone of minimum  $O_2$  levels permit one to entertain the notion that subsurface waters rich in nutrients consistently appear at the surface, close to the Spanish coast, to the northeast of the Strait of Gibraltar. It is not known how such waters reach this site, whether the upwelling process is local or happens elsewhere, and where these nutrient-enriched waters come from, but several models have been proposed (Bormans et al., 1986; Parrilla and Kinder, 1987; Packard et al., 1988).

#### 4. Results

The number of valves per gram of dry sediment is in general low, relative to those reported by Abrantes (1988b, 1990) on the coast of Portugal. The samples with maximum values are found in the westernmost two transects (Table 1, Fig. 2c) with values higher than  $20 \times 10^3$  valves per gram. These two transects also feature the highest values for diatom fragments and sponge spicules per gram of sediment. By contrast, lower values were recorded in the easternmost transect. Preservation of diatom valves varies from sample to sample. In general, the best preservation is seen in the two westernmost sectors.

There is a relatively high percentage of biogenic and clay material (between 25 and 50% in weight), the percentage of these sediments increasing towards the west (Fig. 2b; Hernandez-Molina, 1993). Our data indicate that the proportion of the non-carbonate fraction of >63  $\mu$ m is higher in the eastern sector (mean values 30%) (Fig. 3), than in the central and western sectors (about 10%). Furthermore, the



Fig. 3. Relative abundance of sandy carbonate-free sediment (>63  $\mu$ m) and abundance of diatoms/g of dry sediment on the studied samples.

highest values in diatoms/g are also found in the central and western sectors (Fig. 3). Sand content and diatom abundance are not directly related, but there is some indication of higher diatom content in less coarse samples (Fig. 3).

A total of 70 diatom taxa were recognised in the samples. The taxa were grouped as a function of their ecological significance into planktonic, neritic, benthic, fresh-water and reworked categories, following Abrantes (1988a,b). Likewise, those resistant to dissolution were included in a single group. The diatom assemblage is dominated by *T. nitzschioides*, *P. sulcata*, spores of *Chaetoceros*, and planktonic and neritic forms associated with areas of coastal upwelling (Hasle and De Mendiola, 1967; Sancetta, 1979, 1982; Schuette and Schrader, 1981; Abrantes, 1988a,b) (Fig. 4g–i).

The most common resedimented diatom is *Denticulopsis hustedtii*. This is a Miocene form identified in the Guadalquivir Basin (Berggren et al., 1976) and in the Lorca series by Gersonde (1980). Other reworked forms found are *Thalassiosira plicata*, *Fragilariopsis cylindrica/fossilis* group, *Actinocyclus ingens* and the triangular form of *Fragillaria*. The reworked group in general attains values below 10% of the entire diatom assemblage (Fig. 4e, Table 2).

The percentage values of the fresh-water forms are not significant (<3%), with a few exceptions (Table 2). These samples also contain high values of phytoliths and palynomorphs (Table 1).

Species such as *Azpeitia nodulifer*, *Coscinodiscus marginatus*, *P. sulcata*, and *Chaetoceros* spores form the group of resistant species. They occur in values lower than 33% except in samples 299 and 308 where they represent 48 and 58% of the assemblage (Fig. 4d, Table 2). It should be noted that both *P. sulcata* and *Chaetoceros* spores are important components of the meroplankton.

The distribution of the benthic, neritic and planktonic groups of diatoms is shown in Fig. 4a–c (Table 2). The benthic group is less well represented than the other two, with values lower than 20%, except in four samples (299, 306, 365 and 432) where they represent more than 23% of the assemblage. The planktonic and neritic groups (Fig. 4a,b) are the most significant. However, their distribution seems to be inverted in the sense that the planktonic forms show higher percentages in the samples taken

Table 2 Relative abundances of the diatom groups studied as well as selected diatom taxa

Sample	Planktonic	Meroplanktonic	Benthic	Resistent	Fresh-water	Reworked	Chaetoceros RS	P. sulcata	T. nitzschioides
297	48	27	11	14	1	13	4	12	39
298	52	33	8	5	1	6	5	11	42
299	0	77	23	48	0	0	31	34	0
301	38	38	11	19	1	11	4	24	31
304	35	35	18	29	4	7	5	25	29
306	19	47	30	4	1	3	19	16	14
308	7	74	17	58	2	0	48	9	5
365	35	24	30	25	2	8	1	20	27
368	63	21	8	20	1	7	5	13	50
369	67	17	1	12	1	13	3	5	50
371	70	15	2	10	1	12	2	5	54
428	30	38	19	24	8	6	5	18	23
431	65	20	1	11	5	9	3	7	45
432	16	43	38	28	1	1	31	0	8
435	73	16	3	30	2	5	5	3	53

close to the coast, while the neritic forms are better represented in the deeper samples.

Regarding the pattern followed by some taxa individually, the following observations are of interest.

(1) *P. sulcata* has higher values in the eastern sector, reaching values greater than 20% (Fig. 4g, Table 2). In the central sector this species is most abundant in deeper samples but decreases towards the coast (Fig. 4g). The same kind of behaviour is seen in the western sector.

(2) *T. nitzschioides* is well represented in all three sectors although it appears with greater regularity in the central and eastern sectors (Fig. 4h, Table 2).

(3) *Chaetoceros* RS is best represented in the deeper samples of the eastern sector. However, in samples 299, 308 and 432 it represents 31, 48 and 31%, respectively (Fig. 4i, Table 2).

#### 5. Discussion

#### 5.1. Reworking evidence

Miocene diatomaceous formations are spread wide along the North Betic gateway (Martinez and Rodriguez, 1946; Toumarkine and Boli, 1973; Berggren et al., 1976; Gersonde, 1980; Sierro et al., 1989). The oldest formations (early-middle Tortonian) are located in the western part of the Guadalquivir Basin (Toumarkine and Boli, 1973; Berggren et al., 1976), becoming younger to the east. Sierro et al. (1989) dated the 'Arroyo Saladillo Formation' located in the centre of the basin as middle-late Tortonian, while Gersonde (1980) and Gersonde and Schrader (1984) attributed a Messinian age to the easternmost formations. Diatom assemblages observed in the central and eastern formations (Gersonde, 1980; Sierro et al., 1989) are not similar to those studied here.

'El Cuervo section' (western Guadalquivir Basin) has many of the species reported in this study, in the same general levels of abundance (Berggren et al., 1976). However, ratios of several important taxa are not the same, suggesting that 'El Cuervo section' cannot be the sole source of our material. For instance, the diatom assemblage recognised in the present study is dominated, in most of the samples, by T. nitzschioides (Table 2), while T. longissima is scarcely represented. Also, high values of D. hustedtii do not correlate with high values of P. sulcata or with the highest values of T. nitzschioides (Table 2) as they should if most of them were reworked. Furthermore, the dominant assemblage is not considered reworked because of the clear difference in preservation observed between the extinct forms that are certainly reworked, and the dominant forms.

Thus, the occurrence of Miocene diatoms in surface sediments could be the result of reworking sediments from the North Betic gateway. The presence of *D. hustedtii* indicates that sediment has come



Fig. 4. Distribution patterns as percent of the total assemblage. (a) Planktonic group. (b) Meroplanktonic (neritic) group. (c) Benthic group. (d) Resistant group. (e) Reworked group. (f) Fresh-water group.

from the westernmost diatomitic deposits (El Cuervo section).

The existence of extensive Tertiary diatomitic deposits in the Guadalquivir Basin but the lack of such formations in coastal areas implies the erosion of these older sediments by the rivers of the Guadalquivir Basin and subsequent transport and deposition by the ASW on the coast of Málaga.

The influence of the small rivers discharging in the study area (Verde and Real rivers) (Fig. 4f) could explain the low presence of fresh-water diatoms. Higher values were recorded in samples 431 and 428 (Table 2) located off the Verde river mouth.

# 5.2. Evidence for upwelling from diatom assemblages

In general, the phytoplankton of an upwelling area is characterised by the dominance of diatoms and the development of a succession of species around the upwelling core (Estrada and Blasco, 1985).

The values of absolute abundance as valves per gram of dry sediment obtained in the present study are relatively high for the Mediterranean Sea, but lower than those reported by Abrantes (1988b, 1990) for the coast of Portugal. These data reflect the existence of a coastal upwelling on the coast of

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Fig. 4 (continued). (g) Paralia sulcata. (h) Thalassionema nitzschioides. (i) Chaetoceros RS.

Málaga, although the system may be less productive than the Portuguese one. Fig. 2c and Fig. 3 show the distribution of diatom abundance, with higher values in the westernmost sector and a tendency to decrease towards the east.

This east/west difference could reflect a genuine gradient in production, but could also result from different conditions of sedimentation and transport. Available oceanographic evidence indicates that upwelling and production are more common to the west (Minas et al., 1984; Gil, 1986; Parrilla and Kinder, 1987), in agreement with our data. However, grainsize differences suggest that the lower abundance of diatoms in the eastern sector could be a function of differential transport (diatoms being removed from coarser sediments) or of preservation (with dissolution greater in more porous sediments) Abrantes (1988b).

Species distribution in coastal upwelling regions is defined by the constant presence of neritic assemblages in areas close to the coast line and a pelagic assemblage offshore (Estrada and Blasco, 1985). However, this distribution may be altered by the presence of currents. The distribution of the groups of species considered here (planktonic and neritic-benthic) points to a reversal in distribution patterns. In the eastern sector, the distribution of these groups is clearly altered by factors of preservation. However, in the central and western sectors the planktonic forms are more abundant towards the coast line while the neritic-benthic forms are better represented in the offshore samples (Fig. 4a-c). Fresh-water diatoms also show an inverse distribution, with higher values recorded for deeper samples (Fig. 4f). This inversion in distribution was also reported by Blasco et al. (1981), who suggested that the spreading of neritic-benthic forms towards distal areas points to the existence of a subsurface current towards the outer shelf. If the surface currents were to flow towards the proximal shelf, pelagic species would appear close to the coast. A similar type of situation can be present in the study area, although physical evidence to corroborate these inferences from the diatom distribution is not available.

#### 5.3. Evidence from key species

The variations observed in diatom assemblages can be used to differentiate conditions of strong/permanent upwelling from conditions of occasional upwelling and/or production from river discharge (Abrantes, 1990). They also serve to explain the differences in characteristics of upwelling water masses and the horizontal motion responsible for nutrient distribution (Margalef, 1978).

*Paralia sulcata* is a neritic species characteristic of coastal upwelling conditions and has been widely used as an indicator of high primary production (Margalef, 1978; Margalef et al., 1979; Abrantes, 1988b, 1990, 1991a). Blasco et al. (1980) reported that *P. sulcata* and benthic forms adapted to low light intensity dominate assemblages off northwest Africa during strong-wind conditions. Owing to its persistent presence in the sediments of the Portuguese margin, and its resistance to dissolution, the preservation state of the species has also been used as an indicator of the general state of preservation (Abrantes, 1988a,b, 1990). Its distribution in the samples studied here offers evidence of the presence of a productive area off the coast of Málaga. Also, its higher abundance in the eastern sector points to an enhancement of more resistant forms due to differential dissolution. The higher abundance of the species in deeper samples is probably due to displacement by bottom currents.

Another significant taxon is Thalassionema nitzschioides. This form is associated with occasional upwelling and/or river discharge (Blasco et al., 1981; Pokras and Molfino, 1986; Pokras, 1987; Abrantes, 1988b, 1990). In the studied area, the scanty presence of fresh-water diatoms makes it unlikely that river discharges could be responsible for a significant nutrient input. The values of phytoplankton productivity (concentration of chlorophyll-a) recorded in the study area range between 3 and 1  $\mu$ g/l (Minas et al., 1984). These are lower than those recorded off northwest Africa (5 µg/l) (Estrada and Blasco, 1985) or off Peru (11.2  $\mu$ g/l) (Packard et al., 1984). These observations are consistent with the suggestion of Blasco et al. (1981) that under low-intensity upwelling conditions T. nitzschioides becomes a dominant species. This species is more abundant in the central and eastern sectors (Fig. 4h), which is consistent with the idea that the core of the upwelling lies to the west of the zone and that nutrients are transported laterally towards the east.

Another interesting observation is the scanty presence of *Chaetoceros* RS (Fig. 4i). This group appears in the last stages of the biological succession, where the nutrients of the photic zone are decreased (Blasco et al., 1980, 1981) and it dominates fossil assemblages at the edges of the areas affected by permanent strong upwelling (Schuette and Schrader, 1981; Abrantes, 1988b). In these samples, its distribution does not follow the patterns of diatom absolute abundance (Fig. 2c and Fig. 4i). Since the spores are robust, poor preservation cannot account for their rarity in our samples. We suggest that the low abundance of *Chaetoceros* RS is an accurate reflection of the intermediate levels of production in this region; upwelling is weak or sporadic so that sustained periods of production, leading to a well developed species succession, do not occur.

#### 6. Conclusions

(1) The presence of diatoms in the surface sediments of the continental shelf at Málaga reflects the existence of a coastal upwelling in the area. The absolute values recorded (in the order of  $10^4$  valves/g) are one order of magnitude lower than those obtained by Abrantes (1988b, 1990) ( $10^5$  valves/g) on the Portuguese coast, indicating a less productive system.

(2) The sediments in the easternmost sector are sand-sized which hinders preservation of the fossil diatom assemblage. The preservation of diatoms is better in the central and western sectors, where the sediments are finer.

(3) Inversion of the distribution patterns of the planktonic, neritic-benthic groups suggests that there is a subsurface current towards the outer shelf. The presence of pelagic species on the proximal shelf is suggestive of the existence of a surface flow towards the coast.

(4) The spatial distribution of certain diatom taxa in surface sediments offers an approximation of the structure of the upwelling in the upper layers of the water column.

(5) *Paralia sulcata* indicates the presence of a productive area off the coast of Málaga. Its increased presence in the eastern sector would reflect a differential dissolution of less silicified taxa, favouring the presence of more resistant forms.

(6) *Thalassionema nitzschioides* seems to be a dominant species in low-intensity upwelling conditions and/or in areas of lateral nutrient transport towards the east.

(7) The scanty presence of *Chaetoceros* spores suggests that the area studied is not occupied by waters strongly enriched in nutrients; it also suggests the absence of variability fronts of an upwelling.

The waters bathing the area are certainly not typical of an upwelling core but rather of peripheral areas. In addition, preservational factors may hinder interpretation.

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#### Appendix A. Taxonomic appendix

The diatom taxa recorded in this study are listed below. The taxa were grouped as a function of their ecological significance as described in the text. The cited bibliographic references can be found in Round et al. (1990).

#### A.1. Planktonic group

Azpeitia Peragallo 1912

- A. nodulifer (Schmidt) Fryxell and Sims 1986. Fryxell, Sims and Watkings 1986, pp. 18–19, figs. 16, XXX-2.
- Coscinodiscus Ehrenberg 1840

C. marginatus Ehrenberg 1841. Hustedt 1930, pp. 416-414, fig. 223.

C. radiatus Ehrenberg 1840. Hustedt 1930, pp. 420-421, fig. 225.

Nitzschia Hassall 1845

*N. bicapitata* Cleve 1900. Kaczmarska and Fryxell 1986, p. 237, figs. 4–6, 9–10.

- Rhizosolenia (Ehrenberg) Brightwell 1858 R. styliformis Brightwell 1858. Sundström 1986, pp. 15–19, figs. 5, 47–56.
- Thalassionema Grunow ex Hustedt 1932 T. nitzschioides (Grunow) Grunow 1881. Hasle and Mendiola 1967, pp. 111–112, figs. 5, 11–17, 27–34, 39–44.
- Thalassiosira Cleve 1873

T. lineata Jousé 1968. Hasle and Fryxell 1977, pp. 22–23, figs. 15–25.

*T. oestrupii* (Ostenfeld) Hasle, 1972. Fryxell and Hasle 1980, pp. 805–810, figs. 1–10.

Thalassiothrix Cleve and Grunow 1880

*T. longissima* Cleve and Grunow 1880. Hasle and Semina 1987, pp. 177–181, figs. 1–25.

# A.2. Neritic group

Actinocyclus Ehrenberg 1837 A. octonarius Ehrenberg 1861. Hendey 1964, p. 83, pl. 24, fig. 3. Actinoptychus Ehrenberg 1839 A. senarius (Ehrenberg) Ehrenberg 1843. Hustedt 1930, p. 475, fig. 264. Chaetoceros Ehrenberg 1844 Chaetoceros spores (RS). Spores of all Chaetoceros taxa were grouped together. Leptocylindrus Cleve 1889 Delphineis Andrews 1977 D. surirella (Ehrenberg) Andrews 1977. Hustedt 1930, pp. 173-174, fig. 679 (as syn.: Rhaphoneis surirella). Navicula Bory 1822 N. directa (Smith) Ralfs 1861. Peragallo, 1897-1908, pp. 90-91, pl. XII, fig. 6. Nitzschia Hassall 1845 N. panduriformis Gregory. Peragallo, 1897-1908, pp. 268-270, pl. LXX, figs. 1-13. Paralia Heiberg 1863 P. sulcata (Ehrenberg) Cleve 1873. Hustedt 1930, pp. 276-279, figs. 118-120 (as syn.: Melosira sulcata). Thalassiosira Cleve 1873 T. eccentrica (Ehrenberg) Cleve 1903-1904. Fryxell and Hasle 1972, pp. 300-308, figs. 1-18 A.3. Benthic group Achnantes Bory 1822 A. brevipens Agardh 1824. Hustedt 1959, pp. 424-426, figs. 876-877. Amphora Ehrenberg 1840 Amphora spp. (not determined to species level) Cocconeis Ehrenberg 1837 Cocconeis spp. (not determined to species level) Diploneis Ehrenberg 1844 D. smithii (Brébisson) Cleve 1894. Hustedt 1959, pp. 647-654, figs. 1051-1052 Gomphonema Agardh 1824 Gomphonema spp. (not determined to species level) Grammatophora Ehrenberg 1839 Grammatophora spp. (not determined to species level) Trachyneis Cleve 1894 T. aspera (Ehrenberg) Cleve 1894. Hendey 1964, p. 236, pl. 29, fig. 13. Triceratium Ehrenberg 1841 T. antidiluvianum (Ehrenberg) Grunow 1870. Hustedt 1930, pp. 810-812, figs. 472-473 A.4. Reworked group

Actinocyclus Ehrenberg 1837

A. ingens Rattray 1890, p. 149, pl. 11, fig. 7. Denticulopsis Simonsen 1979 *D. hustedtii* (Simonsen and Kanaya) Simonsen 1979. Akiba and Yanagisawa 1985, p. 488, pl. 17, figs. 4–5, 7–23; pl. 18, figs. 1–10; pl. 19, figs. 1–5; pl. 7, figs. 16–29; pl. 9, figs. 1–9.

*Thalassiosira plicata* (Grunow) Schrader 1974. Schrader 1974b, p. 917, pl. 4, figs. 1, 2, 4–9.

Fragilariopsis Hustedt 1913

F. cylindrica/fossilis group

Fragilaria Lyngbye 1819

Fragilaria sp. triangular form

Rouxia Brun and Héribaud 1893

Rouxia spp. (not determined to species level)

#### A.5. Fresh-water group

Aulacoseira Thwaites 1848

A. granulata (Ehrenberg) Thwaites 1848. Hustedt 1930, p. 248, fig. 104 (as syn.: *Melosira granulata*).

Cyclotella Kützing ex Brébison 1838

C. kútzingiana Thwaites 1848. Hustedt 1930, pp. 338–339, fig. 171.

C. ocellata Pantocsek 1902.. Hustedt 1930, pp. 40-341, fig. 173.

Epithemia Brebisson 1838

Epithemia spp. (not determined to species level)

Fragilaria Lyngbye 1819

F. capuccina Desmazieres 1825. Williams and Round 1987, p. 268, figs. 3–4, 7.

#### A.6. Resistant group

Azpeitia Peragallo 1912

*A. nodulifer* (Schmidt) Fryxell and Sims 1986. Fryxell, Sims and Watkings 1986, pp. 18–19, figs. 16, XXX-2.

Chaetoceros Ehrenberg 1844

*Chaetoceros*-spores (RS). Spores of all *Chaetoceros* taxa were grouped together.

Coscinodiscus Ehrenberg 1840

*C. marginatus* Ehrenberg 1841. Hustedt 1930, pp. 416–414, fig. 223.

Leptocylindrus Cleve 1889

Leptocylindrus spores (RS).

Paralia Heiberg 1863

*P. sulcata* (Ehrenberg) Cleve 1873. Hustedt 1930, pp. 276–279, figs. 118–120 (as syn.: *Melosira sulcata*).

Stephanopyxis Ehrenberg 1844

Stephanopyxis spp. (not determined to species level)

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