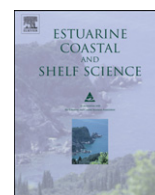




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Phytoplankton temporal changes in a coastal northern Adriatic site during the last 25 years

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ABSTRACT

There is an increasing awareness of the relationships among key phytoplankton groups and their role in biogeochemical cycles; however, less is known about the temporal scales of variability in biodiversity of the phytoplankton community. In the present study a long-term data set (1986–2010) of phytoplankton abundance is used to investigate the temporal variability of the phytoplankton community at a coastal site in the Gulf of Trieste (northern Adriatic Sea). The interannual variability of the phytoplankton community shows two major periods in terms of abundance and community composition. The first one, 1986–1994, was characterized by the highest abundances of microalgae and the dominance of phytoflagellates. The second period (1995–2007) showed lower abundances and a collapse of phytoflagellates. Lastly, an apparent new increase in abundances has been recorded during recent years (2008–2010). On a seasonal scale, a classical cycle with two maxima (spring and autumn) and a summer minimum is evident. Diatoms are the most abundant group of the late winter–early spring bloom whereas phytoflagellates, the most abundant group throughout the year, dominate the late spring blooms. Dinoflagellates and coccolithophores have low abundances and show their maxima in summer and autumn, respectively. The species composition has been analysed according to the Indicator Value Index, highlighting the more frequent and abundant taxa for each month. Results show that the winter months are characterized by coccolithophores, in spring small diatoms are dominant, dinoflagellates and larger diatoms are typical in summer, and coccolithophores and diatom colonies characterise the autumn.

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1. Introduction

Microalgae play a key role in regulating atmospheric carbon dioxide concentrations and in fuelling marine and freshwater food webs, and may be a useful index for recognising the consequences of climate change in coastal areas. The phytoplankton community can change even within a few weeks and therefore only long-term studies at coastal sites provide fundamental insights into the phytoplankton cycle (Smetacek and Cloern, 2008). The first study on the phytoplankton community in the Gulf of Trieste (northern Adriatic Sea) dates back more than a century (Steuer, 1903); subsequently, many taxa were described for the first time in this area (Schiller, 1933, 1937) and these early studies are still fundamental to the taxonomic knowledge of phytoplankton diversity.

Regular observations on plankton dynamics and environmental conditions began in the early 1970s; the results obtained indicated a high temporal variability in the ecosystem (Specchi et al., 1979; Fonda Umani et al., 1992), while information on the seasonal evolution of phytoplankton community structure was still lacking. More recently, in order to explain the mechanism controlling the phytoplankton variability, constant and consistent observations were started in the western (Cabrini et al., 1994, 2000) and eastern (Malej and Malačič, 1995; Mozetič et al., 1998, 2010) parts of the Gulf of Trieste. The analyses have shown a large spatial, seasonal and interannual variability in the phytoplanktonic community (Cabrini et al., 2000; Mozetič et al., 2002; Comisso et al., 2003) due to the influence of multiple drivers. In particular, the phytoplankton dynamics are influenced by physiological responses, by modifications in hydrological properties and by grazing pressures (Cataletto et al., 1993; Fonda Umani et al., 2005, 2007, 2012; Zingone et al., 2010a). Furthermore, since community composition and its temporal modification are the result of the synergy of multiple environmental conditions, they represent useful indicators for the definition of good environmental status (GES) as required by the European Marine Strategy Framework Directive (MSFD). The aim of

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this study is to identify the typical phytoplankton seasonal evolution and community structure of the Gulf of Trieste, using a 25-year data set (March 1986–September 2010) collected in a Long Term Ecological Research (LTER) coastal site.

2. Material and methods

2.1. Study area

The Gulf of Trieste is a shallow semi-enclosed basin, situated in the northern part of the Adriatic Sea, with a maximum depth of 25 m in the southern part. The surface area of the Gulf is about 600 km² with a volume of 9.5 km³ (Malej and Malačić, 1995). The main freshwater input is through the Isonzo River from the north-west coast (Comici and Bussani, 2007). The river inputs show a high temporal variability that affects salinity (Malačić and Petelin, 2001). The highest river discharges are generally observed in late spring and autumn and the lowest during winter and summer.

2.2. Sampling and analytical protocol

The sampling site (st. C1-LTER, 45°42′03″N, 13°42′36″E) is located in the Gulf of Trieste (North Adriatic Sea) 200 m from the coastline (bottom depth 18 m) (Fig. 1). Sampling by a research vessel has been ongoing since March 1986 with a monthly frequency (biweekly frequency from March 1986 to February 1987, from January to December 1990 and from August 2002 to September 2005). To determine phytoplankton, water samples were collected with 5-l Niskin bottles at four depths (0.5, 5, 10 and 15 m) and fixed with Ca(HCO₃)₂-buffered formaldehyde (0.8% final concentration; Thronsen, 1978). Here we present results focused on the surface layer for the period from March 1986 to September 2010.

Cell abundance and species composition of phytoplankton were estimated on 342 samples according to Utermöhl's method (1958), using an inverted microscope equipped with phase contrast, at 320–400× final magnifications. Variable volumes of seawater (25–50 ml, depending on cell concentrations) were settled for at least 48 h. Counting for dominant taxa was performed in random

fields or along transects. In addition, the whole sedimentation chamber was also examined for the less abundant taxa (Zingone et al., 2010b). Identifications were performed referring to Van Heurck (1899), Hustedt (1924, 1930, 1959), Schiller (1933, 1937), Taylor (1976), Dodge (1982), Sournia (1986), Ricard (1987), Balech (1988), Chrétiennot-Dinet (1990), Van den Hoek et al. (1995), Tomas (1997), Bérard-Therriault et al. (1999), Horner (2002), Young et al. (2003) and Malinverno et al. (2008). Phytoplankton taxa were ascribed to the following groups: diatoms, dinoflagellates, chlorophytes, chrysophytes, cryptophytes, dictyochophytes, euglenophytes, prasinophytes, prymnesiophytes both calcareous (coccolithophores) and non-calcareous, and undetermined phytoflagellates.

2.3. Data analysis

The seasonal cycle and interannual variability of total phytoplankton abundance and of the main groups (diatoms, dinoflagellates, coccolithophores and phytoflagellates) were calculated on the basis of monthly (seasonal cycle) and annual (interannual variability) median values from surface data for the period 1986–2010. Interquartile range (IQR) and minimum and maximum intervals of data were also calculated and are shown as box plots. A regime shift analysis (Rodionov and Overland, 2005) was applied to the total annual phytoplankton abundances in order to detect relevant periods. The analysis, which compares the year-by-year changes with the interannual variability, used the freely downloadable Matlab software “Stars” (<http://climatologic.com/stars.html>). The following parameters were used to set the analysis: series length-cutoff of 10 years, a significance level of $p = 0.025$ and the Huber weight function value of 1. The phytoplankton community structure was analysed by applying the Indicator Value Index (IndVal) proposed by Dufrene and Legendre (1997), grouping all samples per month (12 partitions). This indicator consists of the product of two independent parts A and B : $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$; A is the specificity, i.e. the ratio between the mean abundance of the species i sampled in month j and the sum of the mean abundances of the species over all of the months, and B is the fidelity, i.e. the ratio between the number of samples in which the species i is recorded and the total number of samples for month j . The number of species was selected using the rule of thumb, i.e. retaining up to the last species before the plot flattens, as generally used in principal component analysis (Jolliffe, 2002). In general, the specificity of the species i for a given month was high when the species was observed mainly in that month. On the other hand, the fidelity of the species i to a given month was high when the species was observed in all the samples of that month throughout the years. The analysis was performed on species observed in at least 0.5% of samples (Appendix 1).

The IndVal analysis was also applied to two distinct periods, identified on the basis of regime shift analysis, to test long-term differences in the structures of phytoplankton communities. Computation of the individual values and their significances was made by using the *indval.exe* software freely downloadable at <http://old.biodiversite.wallonie.be/outils/indval/home.html>.

The diversity (species richness, S) of diatoms (by far the largest group in the phytoplankton community, and also including the highest number of taxa) was evaluated by counting the number of species in spring (from March to May) and autumn (from September to November) samples and computing the seasonal mean value for each year. Shannon's diversity index H' (ln-based; Shannon, 1948) was calculated in order to represent the specific diversity of diatoms in spring and in autumn. The index takes into account the number of species and the evenness of their abundance; the mean H' for every year was considered. Bloom

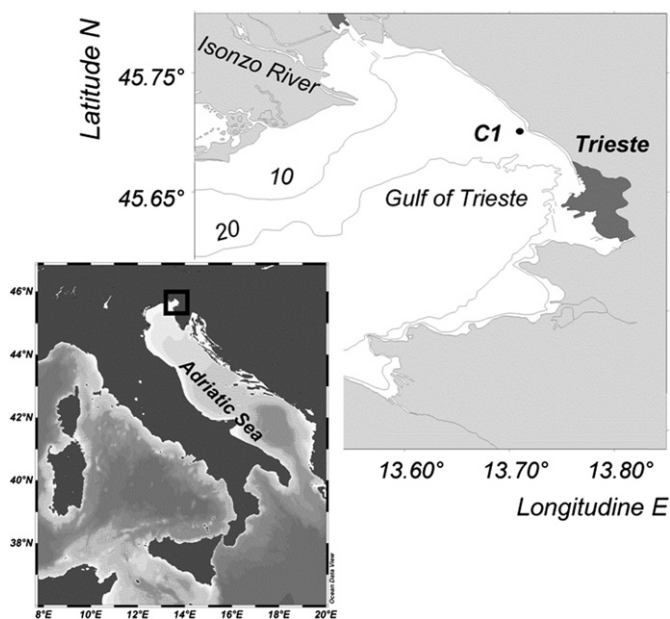


Fig. 1. Position of the sampling station C1-LTER in the Gulf of Trieste.

biodiversity was investigated, taking as “bloom” the total diatom cell abundance higher than 1×10^6 cells L^{-1} in spring and higher than 0.5×10^6 cells L^{-1} in autumn.

3. Results

3.1. Phytoplankton annual cycle

Total phytoplankton abundance at the surface showed a pronounced interannual variability, highlighted by the large interquartile ranges (Fig. 2A); however, a seasonal pattern can be seen from the sequence of median values. The lowest median value was recorded in early winter (0.2×10^6 cells L^{-1} in January). In late winter and spring, cell abundance increased and the maximum median values were recorded in March (1.1×10^6 cells L^{-1}) and May (1×10^6 cells L^{-1}). During summer the abundance gradually decreased and a secondary peak was encountered in late summer

and autumn (0.8×10^6 cells L^{-1} in October; Fig. 2A). The highest abundances were reached by phytoflagellates and diatoms, which represented respectively 66% and 31% (as mean values) of the total phytoplankton abundance, while dinoflagellates (1.7%) and coccolithophores (1.3%) attained lower abundance. The diatom seasonal cycle was quite similar to the total phytoplankton evolution. The lowest abundance was found in December (median value 2.8×10^4 cells L^{-1}) and the annual peak was recorded in March (median value 5.7×10^5 cells L^{-1} ; Fig. 2B). The concentrations decreased sharply in late spring and summer (lowest median value 7×10^4 cells L^{-1} in May), and moderately increased in autumn (median value in October, 1.2×10^5 cells L^{-1}). The strongest seasonal signal in phytoflagellate dynamics was observed in spring, when abundance started to increase, with the highest cell concentration usually reached in May (median value 7.6×10^5 cells L^{-1}) following the late winter diatom bloom. Monthly variabilities were, however, very high, suggesting that the

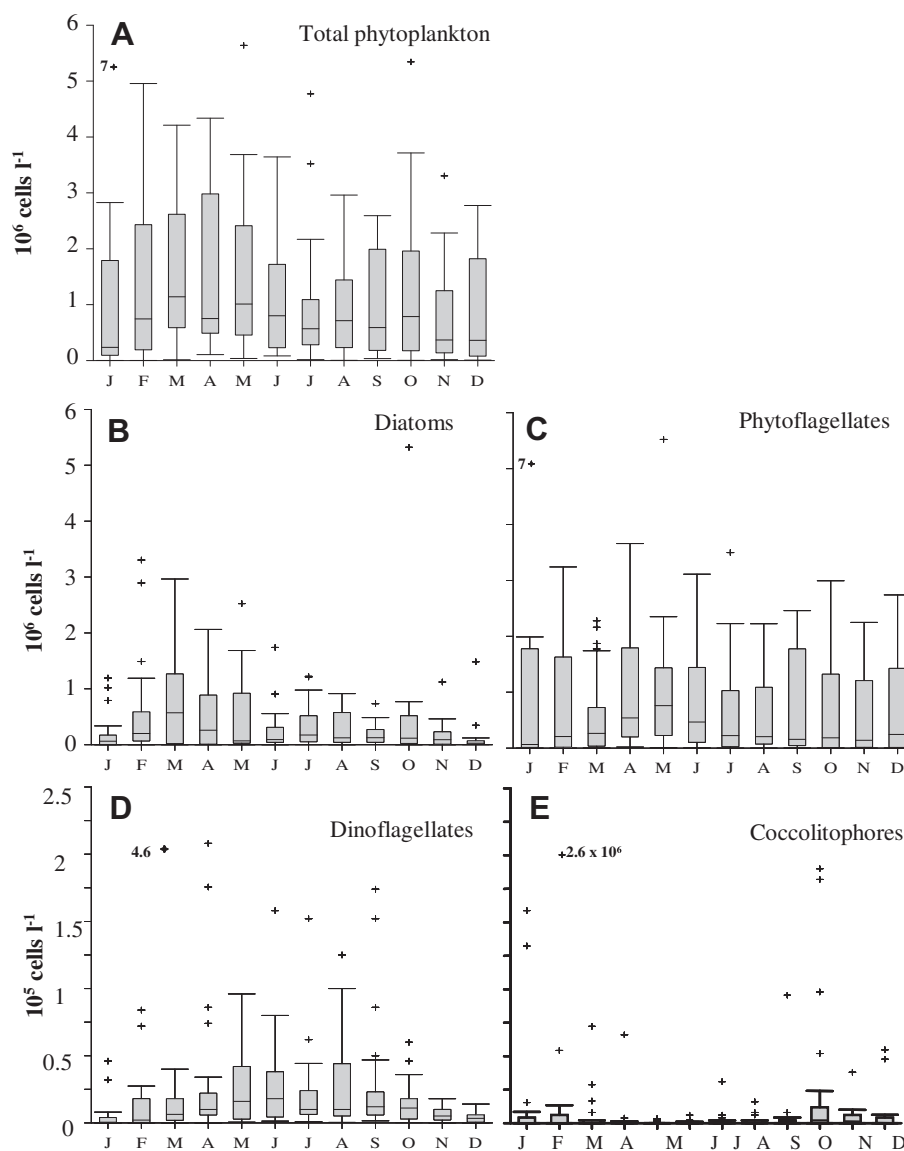


Fig. 2. Seasonal cycle of total phytoplankton (A), diatoms (B), phytoflagellates (C), dinoflagellates (D) and coccolithophores (E) during the period 1986–2010. Graphs report the data distribution with the median (horizontal line across the box), the interquartile range (grey box), the min–max range (vertical bars) and the outliers (crosses).

seasonal cycle of this group is characterized by a large unpredictability (Fig. 2C). Dinoflagellates showed the highest abundance in late spring and summer, with a maximum value in June (median value 2×10^4 cells L^{-1} ; Fig. 2D). Coccolithophores were typical of autumn and winter, with their highest median value of 2×10^3 cells L^{-1} recorded in October (Fig. 2E).

3.2. Phytoplankton community structure

A total number of 396 microalgal taxa were identified. They belonged to the diatoms (178), dinoflagellates (144), chlorophytes (2), chrysophytes (9), cryptophyceae (2), cyanophytes (1), dictyochophytes (9), euglenophytes (5), prasinophytes (6) and prymnesiophytes (22 coccolithophores and 9 other prymnesiophytes). The remaining taxa have uncertain classifications (6) or are general groupings not attributable to a specific taxon (3) (e.g. small phytoflagellates $< 10 \mu m$). The complete taxa list is reported in Appendix 1. The list includes harmful marine microalgae mainly belonging to dinoflagellates, in particular species belonging to genera *Alexandrium* (e.g. *Alexandrium pseudogonyaulax*), *Dinophysis* (e.g. *Dinophysis sacculus*) and *Prorocentrum* (e.g. *Prorocentrum lima*). Within diatoms some potentially toxic species of the genus *Pseudo-nitzschia* (e.g. *Pseudo-nitzschia delicatissima*) are reported.

The results of the IndVal analysis are graphically synthesized in Fig. 3, which reports only the species with the highest IndVal values for each month. The seasonal evolution presented some distinct characteristics. Coccolithophores (e.g. *Ophiaster hydroideus*) and dictyochophytes (e.g. *Dictyocha fibula*), despite the low cell abundance, presented remarkable high IndVal values in late autumn and winter (November, December and February). February was typically characterised by a late winter bloom of the diatom *Skeletonema marinoi*. Later (March–May), the community was represented mainly by the diatoms *S. marinoi* and the *Pseudo-nitzschia delicatissima* complex; in addition, dinoflagellates

(*Prorocentrum minimum* and *Prorocentrum micans*) and phytoflagellates (cryptophytes) were also well represented. In late summer–autumn, the high IndVal values of several taxa indicated that the phytoplankton community included diatoms (*Cyclotella* spp., *Proboscia alata*, *Cerataulina pelagica*, *Guinardia striata*, *Chaetoceros* spp.) and, among nanoflagellates, prasinophytes.

Within the phytoplankton community we focused on the diatom specific diversity in spring and autumn seasons, which are the typical bloom periods in the area of interest (Socal et al., 1992; Mozetič et al., 1998; Cabrini et al., 2000).

In spring the Shannon index (H') showed values ranging from 0.19 (in 1988) to 1.81 (in 2000), with a mean value of 0.97, and the species richness (S) ranged from 3.0 (in 1988) to 11.3 (in 2001 and in 2009) with a mean value of 7.1 (Fig. 4A). Higher values of the two indices were calculated for the autumn period: specifically, H' values ranged from 0.71 (in 1992) to 1.96 (in 2002) with a mean value of 1.49, and S values varied from 5.3 to 21.8 in the same years, with a mean value of 11.6 (Fig. 4B). However, during the first decade S rarely reached values higher than 7 and 10, respectively in spring and autumn, whereas during the last decade these values were often exceeded.

Spring and autumn diatom community composition was analysed in order to investigate the biodiversity in two contrasting seasonal conditions (Table 1). Spring and autumn diatom blooms differed both in terms of abundance and in terms of biodiversity. In spring, diatom abundances were higher than 1×10^6 cells L^{-1} and were due to one or two taxa; from 1986 to 2000 diatom blooms were due mostly to the species *Skeletonema marinoi* and to the genus *Pseudo-nitzschia*. Thereafter, they were completely replaced by the genus *Chaetoceros*. In autumn diatom abundance generally did not exceed 0.5×10^6 cells L^{-1} and there was a higher biodiversity, as also shown by the Shannon index (Fig. 4B and Table 1). It is remarkable that in several years no blooms were recorded; in particular, after 2003 no autumn bloom was recorded.

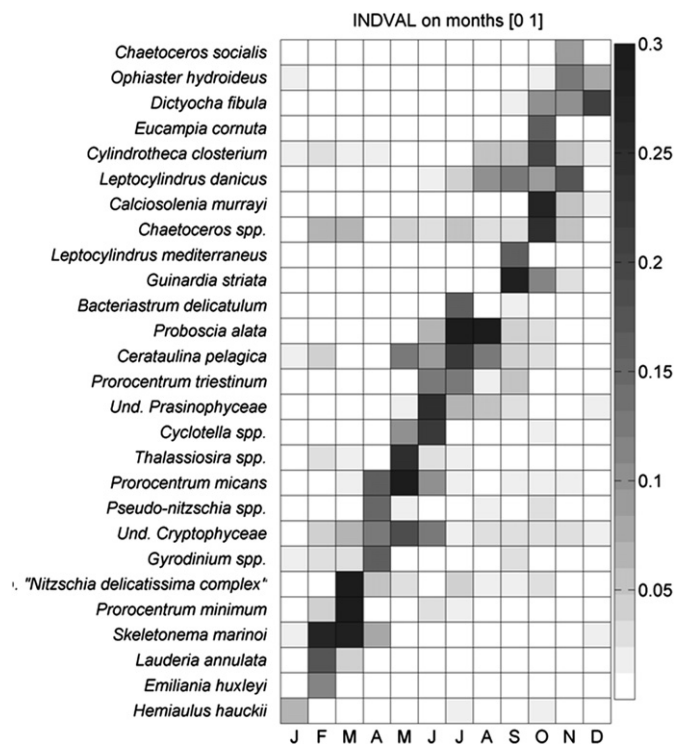


Fig. 3. List of phytoplankton taxa characterized by the highest and significant IndVal for each month; taxa are ordered to show the seasonal succession through the year.

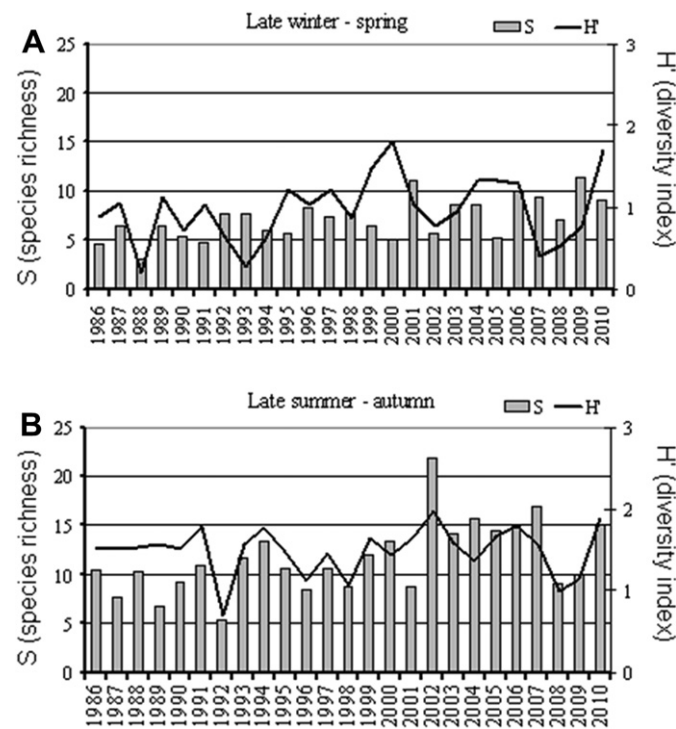


Fig. 4. Diatom species richness (S) and diversity index (H') in spring (A) and autumn (B). The left axis shows species richness (S) and the right axis shows diversity index (H').

Table 1
Diatom species composition of spring and autumn blooms; values in brackets show cell abundance $\times 10^3$ (cells L^{-1}).

	Late winter–early spring bloom	Autumn bloom
1986	<i>Pseudo-nitzschia</i> spp. (1674)	<i>Pseudo-nitzschia</i> spp. (328) <i>Leptocylindrus danicus</i> (80) <i>Guinardia striata</i> (40)
1987	<i>Skeletonema marinoi</i> (1994) <i>Thalassiosira angulata</i> (1452)	–
1988	–	–
1989	<i>Skeletonema marinoi</i> (1080)	–
1990	<i>Thalassiosira</i> spp. (1880) <i>Pseudo-nitzschia</i> spp. (520)	<i>Pseudo-nitzschia</i> spp. (580) <i>Pseudo-nitzschia seriata</i> (66)
1991	<i>Pseudo-nitzschia</i> spp. (1524) <i>Skeletonema marinoi</i> (1180) <i>Chaetoceros</i> spp. (920)	<i>Pseudo-nitzschia</i> spp. (290) <i>Chaetoceros curvisetus</i> (68) <i>Chaetoceros</i> spp. (64) <i>Chaetoceros decipiens</i> (62) <i>Leptocylindrus danicus</i> (68)
1992	<i>Pseudo-nitzschia</i> spp. (3420) <i>Skeletonema marinoi</i> (2580)	<i>Leptocylindrus danicus</i> (1060)
1993	<i>Skeletonema marinoi</i> (1912)	<i>Eucampia cornuta</i> (257) <i>Chaetoceros</i> spp. (233) <i>Cerataulina pelagica</i> (88)
1994	–	<i>Pseudo-nitzschia delicatissima</i> (180) <i>Asterionellopsis glacialis</i> (54) <i>Proboscia alata</i> (50) <i>Thalassiothrix</i> spp. (50) <i>Chaetoceros</i> spp. (48)
1995	–	–
1996	–	<i>Pseudo-nitzschia seriata</i> (178) <i>Thalassiothrix mediterranea</i> (104) <i>Chaetoceros</i> spp. (88)
1997	<i>Pseudo-nitzschia delicatissima</i> (2282)	<i>Chaetoceros</i> spp. (393) <i>Bacteriastrum</i> spp. (224) <i>Pseudo-nitzschia seriata</i> (82)
1998	<i>Pseudo-nitzschia delicatissima</i> (2436) <i>Thalassiosira</i> spp. (1628)	–
1999	<i>Lauderia annulata</i> (849)	<i>Pseudo-nitzschia seriata</i> (358) <i>Guinardia striata</i> (120) <i>Chaetoceros</i> spp. (66) <i>Chaetoceros curvisetus</i> (66)
2000	<i>Skeletonema marinoi</i> (2646) <i>Chaetoceros</i> spp. (603)	<i>Chaetoceros</i> spp. (4646) <i>Leptocylindrus danicus</i> (148) <i>Pseudo-nitzschia seriata</i> (78) <i>Skeletonema marinoi</i> (68)
2001	–	–
2002	–	<i>Chaetoceros socialis</i> (302) <i>Chaetoceros</i> spp. (256)
2003	<i>Chaetoceros</i> spp. (1170)	<i>Chaetoceros</i> spp. (866)
2004	<i>Chaetoceros</i> spp. (1073)	–
2005	–	–
2006	<i>Chaetoceros</i> spp. (1010)	–
2007	–	–
2008	–	–
2009	<i>Chaetoceros</i> cf. <i>single</i> (2267)	–
2010	<i>Chaetoceros</i> cf. <i>single</i> (640)	–

3.3. Long-term changes in the phytoplankton community

Results of the regime shift detection analysis showed the presence of two distinct periods (Fig. 5A): the first from 1986 to 1994 with high phytoplankton abundance values, in which phytoflagellates were dominant, and the other from 1995 to 2007 with low cell concentrations and prevalence of diatoms (Fig. 5B and C). Furthermore, the analysis showed that the last years, from 2009 to 2010, might have been different from the previous period. In fact, from 2009, phytoflagellates became prevalent again and total cell abundance increased, reaching values similar to those observed during the first period (Fig. 5A–E). However, the shortness of this

period (2009–2010) precludes distinction between a fluctuation and the beginning of a new regime.

Regarding diatom abundance, the highest median value was registered in 1991 (6×10^5 cells L^{-1}). With the exception of this year, median diatom abundances were generally lower than 4×10^5 cells L^{-1} , and an exceptional event was recorded in 2000 (October, *Chaetoceros* spp.) (Fig. 5B). Phytoflagellates showed a dynamic similar to the total phytoplankton one, with the maximum median value recorded in 1991 (2×10^6 cells L^{-1}); very low median abundances were recorded from 1995 to 2008 (median value $< 5 \times 10^5$ cells L^{-1}) and an evident increase was observed in 2010 with the maximum median value of 1×10^6 cells L^{-1} . An exceptional value of 7×10^6 cells L^{-1} was recorded in 1994 (January, undetermined phytoflagellates) (Fig. 5C). Dinoflagellates were usually scarce, with median values of abundance generally lower than 2×10^4 cells L^{-1} , with the exception of 2002 and 2010 (maximum median values 2.5×10^4 cells L^{-1}). In 2009 an exceptional maximum value of 4.6×10^5 was recorded (March, early bloom of *Prorocentrum minimum*) (Fig. 5D). Coccolithophores were generally very scarce, with median values less than 100 cells L^{-1} until 2000; there was an increase from 2001 and the highest concentrations were reached in 2004 and 2010 (median values respectively 4×10^3 and 3×10^3 cells L^{-1}); a very high peak was recorded in 1995 (February, exceptional bloom of *Emiliania huxleyi*) (Fig. 5E).

The IndVal analysis was repeated for the two relevant periods detected on the basis of regime shift analysis (Fig. 5A) in order to identify possible changes in the typical seasonal species composition. Fig. 6A and B shows that 20 taxa were representative for the first period (1986–1994) and 26 taxa for the second one (1995–2007). Only a few species showed high IndVal in both periods: *Skeletonema marinoi* in early spring, *Cerataulina pelagica* and *Prorocentrum micans* in late spring–summer, *Proboscia alata* in summer, *Dictyocha fibula* in autumn and the *Nitzschia delicatissima* complex which, however, was observed prevalently in late summer until 1995 but mainly in late winter and spring thereafter. However, considering the differences between the two periods, May was characterized by only two phytoplankton taxa (*C. pelagica* and *P. micans*) in the period 1986–1994 as opposed to seven taxa (*Thalassiosira* spp., *Cyclotella* spp., *Neoceratium fusus*, *P. micans*, *Eutreptiella* spp., Und. Chlorophytes and Und. Cryptophytes) in the period 1995–2007. Strong differences between the two periods were also observed in summer: the 1995–2007 period was characterized by a higher number of species; in particular, high IndVal values were observed for diatoms *P. alata* and *C. pelagica* and dinoflagellates *Neoceratium tripos* and *Prorocentrum triestinum*.

Moreover, the diatom *Leptocylindrus danicus*, typical of late summer and late autumn in the first period, disappeared in the second one, whereas the genus *Chaetoceros* characterized late autumn only in the second period, and coccolithophores, which are typical of late autumn and winter, showed a detectable signal only after 1995 (Fig. 6A and B).

4. Discussion

In the Gulf of Trieste, the phytoplankton mean annual cycle is characterized by a two-peak (late winter–early spring, and autumn) and two-trough (summer and early winter) pattern. The first annual bloom, late winter–early spring, is based on diatoms which trigger off mainly monospecific blooms, a typical feature of the Adriatic Sea (Caroppo et al., 1999; Totti et al., 2000; Bernardi Aubry et al., 2004; Cerino et al., 2011) as well as of the Mediterranean Sea (Leblanc et al., 2003; Ribera D'Alcalà et al., 2004; Zingone et al., 2010a). With the progress of the seasons, at the end of spring

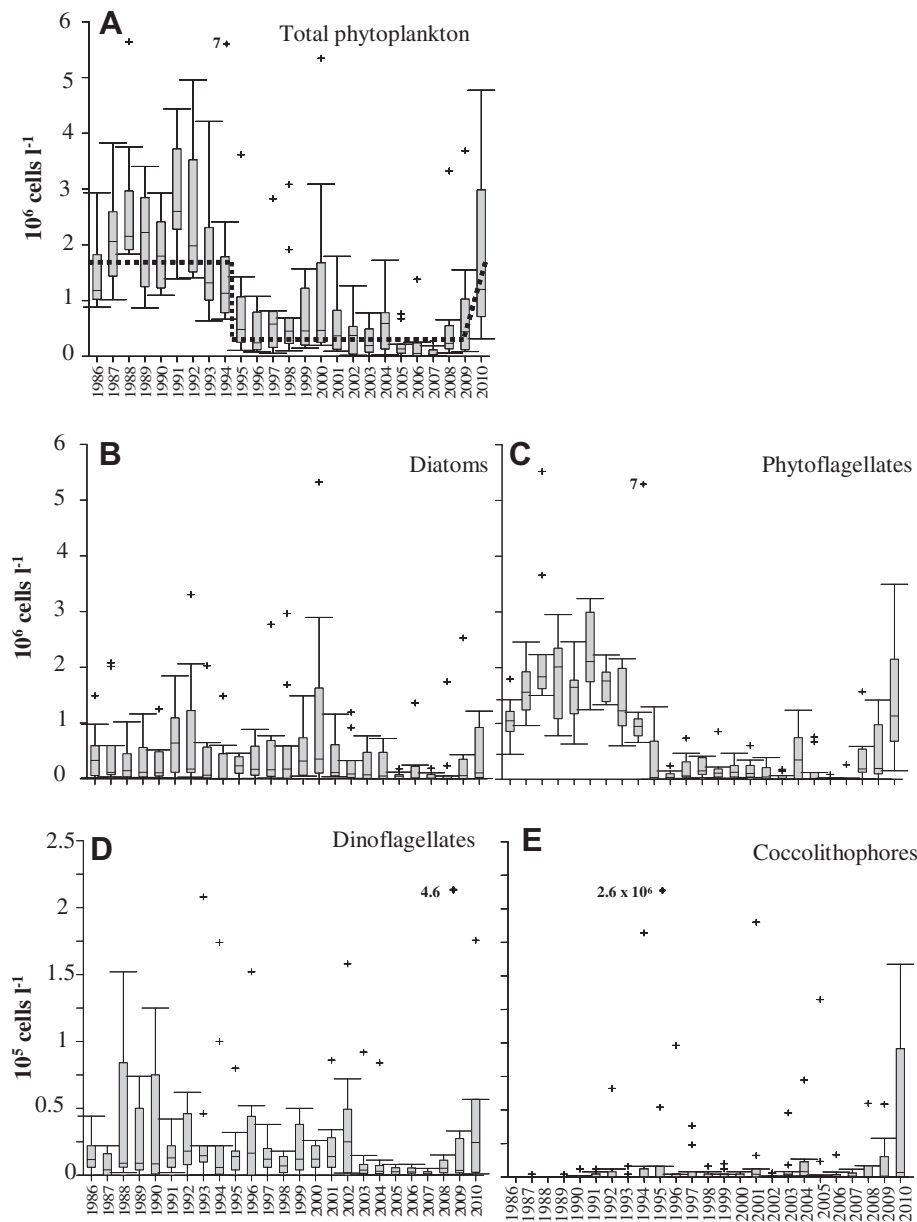


Fig. 5. Time series of total phytoplankton (A), diatom (B), phytoflagellate (C), dinoflagellate (D) and coccolithophore (E) abundance (cells L⁻¹) during the period 1986–2010. Graphs report the data distribution with the median (horizontal line across the box), the interquartile range (grey box), the min–max range (vertical bars) and the outliers (crosses). The dotted line represents the regime shift.

a shift is observed from a phytoplankton community which is diatom-based to a mainly small flagellate-based one. Dinoflagellates are generally scarce and mainly observed in late spring and summer. In summer, total phytoplankton abundance is generally low, while in early autumn there is a second increase in species abundance which is often associated with less intense blooms which are determined by the presence of three or more diatom species, usually of large cell size. The late winter–early spring bloom is characterized by cell abundance higher than the autumn one. The two diatom blooms have different implications for the carbon cycling in the ecosystem. In particular, the intense late winter diatom blooms are mostly exported to the bottom and only partly grazed by microzooplankton and mesozooplankton; on the other hand, the autumn bloom is mainly consumed by intense grazing activities (Fonda Umani et al., 2012).

The development of the two diatom blooms (Fig. 2B) can be ascribed to the seasonal evolution of the main driving biogeochemical and physical forcings. In particular, the first bloom, typically monospecific (Table 1), is triggered by the seasonal increase in total irradiance, seawater temperature, stratification of the water column (Malačić and Petelin, 2001) and nutrient availability (Solidoro et al., 2007; Lipizer et al., 2011; Cossarini et al., 2012) delivered by the main input source, i.e. the Isonzo River (Cozzi et al., 2012). The summer decline in phytoplankton abundance may be consequent to the depletion of nutrient contents (Cossarini et al., 2012) and to intense grazing activities (Fonda Umani et al., 2012). Despite the low abundance, the summer–early autumn community is well diversified. New nutrient input (Cozzi et al., 2012) forces the autumn bloom which is, however, typically lower (Fig. 2B) and characterized by higher biodiversity than the late winter–spring

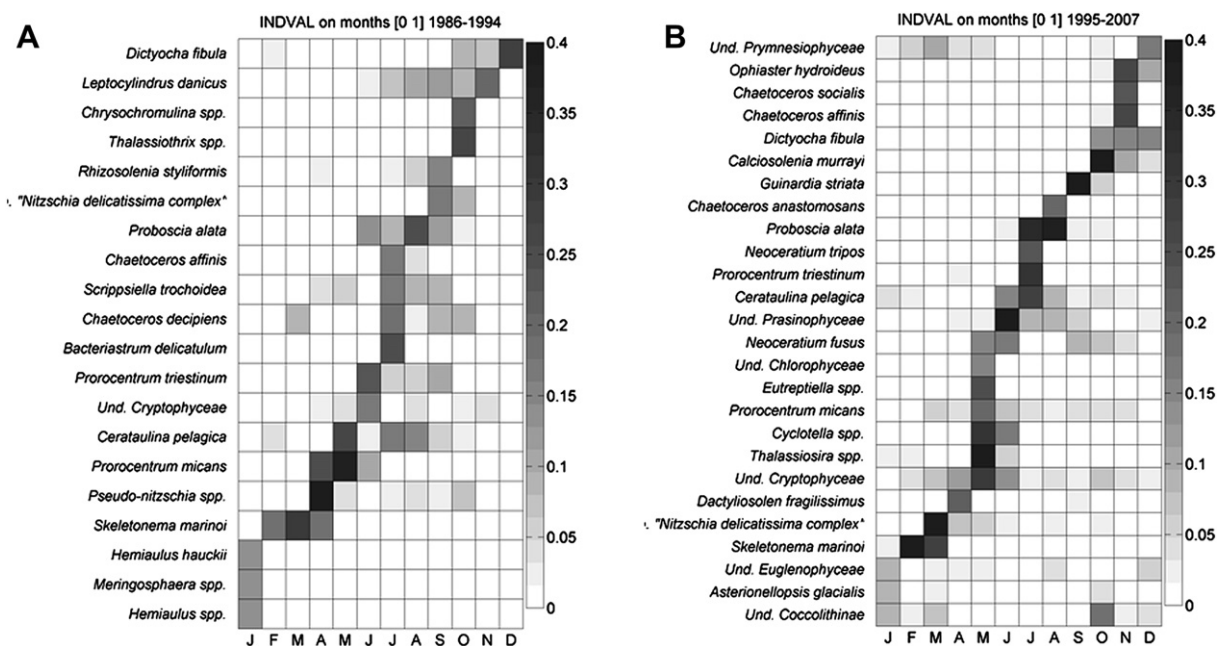


Fig. 6. List of phytoplankton taxa characterized by the highest and significant IndVal for each month; taxa are ordered to show the seasonal succession through the period 1986–1994 (A) and 1995–2007 (B).

one (Table 1, Fig. 4), possibly due to less favourable environmental conditions such as rapidly decreased irradiance and onset of vertical mixing of the water column. In contrast, on the eastern side of the Gulf of Trieste the autumn bloom showed typically higher abundances than the spring one, which generally occurred with a certain delay (May until 2003 and July until 2009) (Mozetič et al., 2012), showing that, even in a small coastal area such as the Gulf of Trieste, substantial spatial variability of biological features is an inherent characteristic.

Over the wider North Adriatic Sea, the first annual phytoplankton bloom is typically recorded in late winter–spring in the Gulf of Trieste (western coast), in the Gulf of Venice (Bernardi Aubry et al., 2004) and at Croatian sites (Marić et al., 2012). For the whole Mediterranean Sea, in fact, the late winter bloom has been defined as a unifying feature for phytoplankton (Ribera D'Alcalà et al., 2004).

The occurrence of a late winter–early spring bloom is an inherent feature of the Gulf of Trieste ecosystem as it has been recorded consistently during the 1986–2010 period. However, the species responsible for the bloom changed, highlighting possible variations in the trophic status of the ecosystem. From 1986 until 2000 the diatom *Skeletonema marinoi* was the main species of late winter–early spring blooms, with occasional contributions from *Pseudo-nitzschia* spp. and *Thalassiosira* spp. From 2003, late winter blooms were due only to the genus *Chaetoceros* (Table 1), but bloom intensities were lower than those due to *S. marinoi*.

Skeletonema marinoi is a ubiquitous species; it is a dominant diatom in Norwegian and Scottish fjords (Gilpin et al., 2004) and in many other coastal planktonic ecosystems. In the middle Adriatic it is responsible for the largest annual bloom, a regular winter event (Totti et al., 2000); the same species also forms blooms in the South (Caroppo et al., 1999) and in the North-West Adriatic, where it is the major contributor to the total particulate organic carbon and to the high chlorophyll values (Harding et al., 1999; Bernardi Aubry et al., 2006). The importance of *S. marinoi* has also been ascertained along the North Eastern Adriatic coast in the earlier period (1972–1999); however, its frequency decreased in the successive monitored years (Marić et al., 2012). Several

studies regarding the silicon requirement of *Skeletonema costatum*, a physiologically similar species to *S. marinoi*, showed that this species needs a concentration of 0.56–2 µg Si per cell, which is lower than other diatoms (Paasche, 1973); therefore, *S. marinoi* would be expected to prevail because of its low silicon requirement. In fact, silica limitation seemed to have been the prevailing feature in the Mediterranean since the early 1980s (Ludwig et al., 2009). More recently, the results of mesocosm experiments also confirmed that in limited silicon conditions *S. costatum* dominated in terms of both cell abundance and biomass (Gilpin et al., 2004). On the other hand, the disappearance of *S. marinoi* since the late 1990s may also be a consequence of the reduction in the availability of another nutrient, i.e. phosphorus, due to its restriction for agricultural and industrial use under Italian law from 1988 and to the general improvement in sewage treatment. The dominance of *Chaetoceros* spp. from 2003 to 2010 could be favoured by their greater affinity for low nutrient concentrations than other diatoms. In fact, the small-sized *Chaetoceros* spp., due to a favourable surface-to-volume ratio, is able to grow at low nutrient concentrations and even at high N/P ratios (Lagus et al., 2004 in; Mozetič et al., 2010).

Besides the modification in the specific composition of the blooms, a relevant interannual variability has also been recognised during the period 1986–2010, with the presence of a regime shift in 1995.

Using a shorter period of the present timeseries, a decrease of phytoplankton in the early '90s was first observed by Fonda Umani et al. (2004) and a regime shift was detected in 1993 (Kamburska and Fonda Umani, 2009). Our study, based on a much longer timeseries, confirms that the sharp decrease of phytoplankton abundances in the early '90s represents the most important long-term signal within the whole period (1986–2010), but identifies the year of the regime change in 1995. It must be, however, considered that the detection of the precise time of a regime shift would always suffer of a degree of subjectivity, since it depends on the length of the timeseries and, to a certain extent, on the sensitivity of the parameters chosen for the analysis. Nevertheless it is evident from ours and from previous results that a sharp change in the ecology of the Gulf occurred in the early 1990s.

Other important taxonomical differences such as the major prevalence of diatoms in the second period showed that this functional group could better adapt to changing environmental conditions. On the other hand, dinoflagellates decreased in abundance and the red tides, which in the past sporadically occurred in the Gulf during the summer, gradually disappeared since the Gulf began to be affected by recurrent appearances of large mucilaginous aggregates (Sellner and Fonda Umani, 1999). Although in the 2003–2007 period phytoplankton abundance was strongly reduced, there was an evident higher specific diversity revealed by IndVal analyses. Biodiversity is a useful indicator of ecosystem functioning because higher species richness indicates a higher efficiency in resource exploitation (Gravel et al., 2011). Therefore, in conditions of reduced resources, increase in biodiversity may be favoured. Evidence of processes of oligotrophication for the northern Adriatic Sea is provided by Solidoro et al. (2009) reporting biogeochemical parameters and by Mozetič et al. (2010) reporting chlorophyll data. The reduction in P concentration in North Adriatic coastal areas seems the largest factor responsible, with a consequent alteration in the N/P ratio (Bernardi Aubry et al., 2004; Mazziotti and Cabrini, 2004). Several studies demonstrate that an increase of the N/P ratio may shape phytoplankton community structure, favouring more opportunistic species (Bulgakov and Levich, 1999; Finkel et al., 2010). Therefore, the modifications in bloom-specific composition we observed are a further indirect indication of the substantial modifications that are underway in the northern Adriatic ecosystem. In particular, oligotrophication in the gulf can be ascribed to a reduction in outflow from the Isonzo River which was observed during the 1986–2010 period, with the occurrence of dry years in the latter part of the period in 1994, 2003, 2005, 2006 and 2007 (Mozetič et al., 1998; Comici and Bussani, 2007; Cozzi et al., 2012). Concomitant with dry years, our timeseries showed the absence of some spring (1994, 2005 and 2007) and autumn (2005, 2006 and 2007) blooms, highlighting the possible direct relationship between the external input and the productivity of the ecosystems.

Finally, the long-term timeseries of phytoplankton abundance at station C1 in the Gulf of Trieste allowed detection and description of a new species, i.e. *Scrippsiella spinifera* (Honsell and Cabrini, 1991), recognition for the first time of some harmful marine microalgae belonging to genera *Alexandrium* and *Dinophysis* (Honsell et al., 1992; Cabrini et al., 2001) which can negatively influence the mussel farms located along the coasts, and identification of non-indigenous species (NIS) which have probably been introduced into the Gulf of Trieste by ballast waters (David et al., 2007). In fact, for an initial assessment of the risk of NIS introduction, measures of ballast water management are important (Gollasch, 1998). Only the availability of long-term monitoring offers the possibility of recording NIS events inside the phytoplankton community, even if the cause of this introduction remains an open question.

5. Conclusions

This work has attempted to draw the seasonal and long-term dynamics of the phytoplankton community structure in the Gulf of Trieste through the analysis of a long timeseries of cell abundance and community composition data. Despite the high interannual variability, a regular seasonal succession of different functional groups was observed in the Gulf of Trieste. The early winter community was scarce in terms of abundance and characterized mainly by nanoflagellates and coccolithophores; with the progress of the season an intense, mainly monospecific, late winter–early spring bloom developed and was sustained by small diatoms such as *Skeletonema marinoi* until 2000 and *Chaetoceros* spp. thereafter. Phytoplankton abundance decreased in summer, when dinoflagellates mostly appeared, while in late summer–autumn a second bloom, of lower abundance, developed, usually characterized by a higher biodiversity than the previous one and mainly due to large diatoms. On the basis of phytoplankton abundance and community composition, two main different periods were identified during the 1986–2010 timeseries. The first period, from 1986 to 1994, was characterized by higher total phytoplankton abundances and dominance of phytoflagellates, which drastically decreased from 1995. In the second period, from 1995 to 2007, phytoplankton abundance sharply decreased and diatoms became prevalent. Lastly, from 2009 phytoflagellates showed a new pronounced increase, becoming in 2010 the prevalent functional group. The observed long-term changes could be related to the more general oligotrophication of the northern Adriatic Sea. Specifically for the Gulf, the direct influence of the discharge from the Isonzo River may have had a direct impact on the changes in abundance and community composition. The observed changes in phytoplankton community could have significant implications for food web transfer and could be used as a proxy to assess the quality status of coastal waters as required by the Marine Strategy Framework Directive (MSFD) and in the framework of conservation biology.

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Appendix 1. List of phytoplankton taxa and frequency of occurrence (percentage out of 342 samples).

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Bacillariophyceae (Diatoms)	%	Chaetoceros lacinosus Schütt	1.4	Diploneis spp.	6.9
<i>Achnanthes brevipes</i> Agardh	0.3	<i>Chaetoceros lauderi</i> Ralfs	1.0	<i>Ditylum brightwellii</i> (West) Grunow	2.1
<i>Achnanthes</i> spp.	0.7	<i>Chaetoceros lorenzianus</i> Grunow	1.4	<i>Entomoneis</i> sp.	0.3
<i>Amphora</i> spp.	2.4	<i>Chaetoceros messanensis</i> Castracane	0.3	<i>Eucampia cornuta</i> (Cleve) Grunow	4.8
<i>Asterionellopsis glacialis</i> (Castracane) Round	8.6	<i>Chaetoceros peruvianus</i> Brightwell	0.3	<i>Eucampia</i> spp.	1.0
<i>Asteromphalus hookeri</i> Ehrenberg	0.3	<i>Chaetoceros pseudocurvisetus</i> Mangin	1.7	<i>Eucampia zodiacus</i> Ehrenberg	0.3
<i>Asteromphalus</i> spp.	5.9	<i>Chaetoceros similis</i> Cleve	0.3	<i>Fragilaria</i> spp.	0.3
<i>Bacteriastrium biconicum</i> Pavillard	0.3	<i>Chaetoceros socialis</i> Lauder	2.4	<i>Fragilariopsis</i> spp.	2.8
<i>Bacteriastrium cf. delicatulum</i>	0.3	<i>Chaetoceros</i> spp.	59.0	<i>Grammatophora marina</i> Kützing	1.4
<i>Bacteriastrium delicatulum</i> Cleve	8.6	<i>Chaetoceros</i> spp. <10µm	0.3	<i>Grammatophora</i> spp.	0.3
<i>Bacteriastrium</i> spp.	8.6	<i>Chaetoceros</i> spp. <20µm	2.1	<i>Guinardia delicatula</i> (Cleve) Hasle	9.0

(continued)

<i>Biddulphia alternans</i> (J.W. Bailey) Van Heurck	0.3	<i>Chaetoceros subtilis</i> Cleve	0.3	<i>Guinardia flaccida</i> (Castracane) Peragallo	25.9
<i>Campylodiscus</i> spp.	0.3	<i>Chaetoceros tenuissimus</i> Meunier	1.7	<i>Guinardia</i> spp.	0.3
<i>Campylosira</i> spp.	0.3	<i>Chaetoceros teres</i> Cleve	0.7	<i>Guinardia striata</i> (Stolterfoth) Hasle	20.0
<i>Catacombas gaillonii</i> Williams & Round	0.3	<i>Chaetoceros throssenii</i> (Marino, Montresor and Zingone)	1.7	<i>Guinardia tubiformis</i> (Hasle) Hasle	0.7
<i>Cerataulina pelagica</i> (Cleve) Hendey	60.7	Marino, Montresor and Zingone		<i>Gyrosigma acuminatum</i> Rabenhorst	1.0
<i>Cerataulina</i> spp.	0.3	<i>Chaetoceros tortissimus</i> Gran	0.7	<i>Haslea</i> cf. <i>wawrikae</i>	0.3
cf. <i>Attheya</i> spp.	0.3	<i>Chaetocers</i> cf. <i>simplex</i> Ostefeld	1.7	<i>Haslea wawrikae</i> (Husedt) Simonsen	3.4
cf. <i>Cylindrotheca closterium</i>	1.4	<i>Cocconeis placentula</i> Ehrenberg	0.7	<i>Hemiaulus hauckii</i> Grunow	23.8
cf. <i>Fragilariopsis</i> spp.	0.3	<i>Cocconeis</i> spp.	2.1	<i>Hemiaulus sinensis</i> Greville	1.4
cf. <i>Lauderia annulata</i>	0.3	<i>Corethron criophilum</i> Castracane	0.3	<i>Hemiaulus</i> spp.	1.7
cf. <i>Nitzschia fruticosa</i>	0.3	<i>Coccinodiscus</i> spp.	6.2	<i>Lauderia annulata</i> Cleve	5.9
cf. <i>Proboscia alata</i>	0.3	<i>Cyclotella</i> spp. <20µm	0.7	<i>Leptocylindrus</i> cf. <i>danicus</i>	0.3
cf. <i>Thalassiosira</i> spp.	0.3	<i>Cyclotella</i> spp.	20.0	<i>Leptocylindrus</i> cf. <i>minimus</i>	0.7
<i>Chaetoceros affinis</i> Lauder	9.3	<i>Cylindrotheca closterium</i> (Ehrenberg) Lewin & Reimann	39.0	<i>Leptocylindrus danicus</i> Cleve	48.6
<i>Chaetoceros anastomosans</i> Grunow	2.8	<i>Cylindrotheca fusiformis</i> Lewin & Reimann	7.2	<i>Leptocylindrus mediterraneus</i> (Peragallo) Hasle	4.1
<i>Chaetoceros atlanticus</i> Cleve	1.7	<i>Cymbella</i> spp.	0.7	<i>Leptocylindrus minimum</i> Gran	8.3
<i>Chaetoceros castracanei</i> Karsten	1.0	<i>Dactyliosolen blavyanus</i> (H.Peragallo) Hasle	1.4	<i>Licmophora abbreviata</i> Agardh	1.4
<i>Chaetoceros</i> cf. <i>atlanticus</i>	0.3	<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle	16.9	<i>Licmophora flabellata</i> (Grev.) Agardh	0.3
<i>Chaetoceros</i> cf. <i>brevis</i> Schütt	0.3	<i>Dactyliosolen phuketensis</i> (Sundström) Hasle	1.0	<i>Licmophora gracilis</i> Grunow	2.8
<i>Chaetoceros</i> cf. <i>gracilis</i> Schütt	0.7	<i>Diatoma elongatum</i> Agardh	0.3	<i>Licmophora</i> spp.	11.0
<i>Chaetoceros contortus</i> Schütt	0.7	<i>Diatoma</i> spp.	1.0	<i>Lioloma</i> cf. <i>elongatum</i> (Grunow) Hasle	0.3
<i>Chaetoceros curvisetus</i> Cleve	15.5	<i>Dimerogramma marinum</i> Ralf in Pritchard	1.4	<i>Lioloma pacificum</i> (Cupp) Hasle	3.4
<i>Chaetoceros dadayi</i> Pavillard	1.4	<i>Dimerogramma</i> spp.	0.3	<i>Melosira moniliformis</i> Agardh	1.4
<i>Chaetoceros danicus</i> Cleve	1.4	<i>Diploneis bombus</i> Ehrenberg	4.1	<i>Melosira nummuloides</i> Agardh	0.7
<i>Chaetoceros decipiens</i> Cleve	23.8	<i>Diploneis crabro</i> Ehrenberg	0.3	<i>Melosira</i> spp.	1.0
<i>Chaetoceros didymus</i> Ehrenberg	0.3	<i>Diploneis smithii</i> Cleve	0.3	<i>Navicula</i> cf. <i>directa</i>	0.7
<i>Navicula cryptocephala</i> Kützing	0.3	<i>Rhabdonema</i> spp.	0.3	Chlorophyceae	
<i>Navicula directa</i> Ralfs	2.4	<i>Rhizosolenia</i> cf. <i>fallax</i> Sundström	0.3	<i>Oltmannsiella</i> spp.	3.1
<i>Navicula pygmaea</i> Kützing	0.3	<i>Rhizosolenia</i> cf. <i>hebetata</i>	0.3	Und. Chlorophyceae	5.5
<i>Navicula</i> spp.	25.2	<i>Rhizosolenia</i> cf. <i>styliformis</i>	0.7		
<i>Neocalyptrella robusta</i> (G.Norman ex Ralfs)	0.3	<i>Rhizosolenia hebetata</i> Bailey	0.3	Chrysophyceae	
Hernández-Becerril & Meave del Castillo		<i>Rhizosolenia imbricata</i> Brightwell	3.1	<i>Dinobryon</i> cf. <i>faculiferum</i>	0.7
<i>Nitzschia</i> cf. <i>distans</i> Gregory	0.3	<i>Rhizosolenia</i> spp.	10.3	<i>Dinobryon coalescens</i> Schiller	0.3
<i>Nitzschia</i> cf. <i>fruticosa</i> Hustedt	0.3	<i>Rhizosolenia styliformis</i> Brightwell	10.3	<i>Dinobryon faculiferum</i> (Willén) Willén	0.3
<i>Nitzschia</i> cf. <i>lorenziana</i>	0.3	<i>Skeletonema marinoi</i> Sarno & Zingone	31.0	<i>Dinobryon</i> spp.	4.5
<i>Nitzschia longissima</i> (Brébisson in Kützing) Ralfs	22.4	<i>Skeletonema</i> spp.	0.7	<i>Meringosphaera mediterranea</i> Lohmann	8.3
<i>Nitzschia lorenziana</i> Grunow	2.1	<i>Striatella unipunctata</i> (Lyngbye) Agardh	1.4	<i>Meringosphaera</i> spp.	2.8
<i>Nitzschia sigma</i> Smith	0.7	<i>Synedra fulgens</i> Smith	0.3	<i>Meringosphaera tenerria</i> Schiller	4.5
<i>Nitzschia</i> spp.	18.6	<i>Synedra</i> spp.	0.7	<i>Ollicola vangorii</i> (Conrad) Vørs	2.8
<i>Paralia solcata</i> Cleve	3.1	<i>Thalassionema</i> cf. <i>nitzschiioides</i>	0.3	Und. Chrysophyceae	3.4
<i>Pinnularia</i> spp.	0.7	<i>Thalassionema frauenfeldii</i> (Grunow) Hallegraeff	10.7		
<i>Plagiotropis</i> spp.	1.4	<i>Thalassionema nitzschiioides</i> (Grunow)	18.3	Cryptophyceae	
<i>Pleurosigma angulatum</i> Smith	5.2	Mereschkowsky		<i>Hillea fusiformis</i> (Schiller) Schiller	0.3
<i>Pleurosigma directum</i> Grunow	0.3	<i>Thalassionema</i> spp.	4.5	Und. Cryptophyceae	65.5
<i>Pleurosigma</i> spp.	13.1	<i>Thalassiosira angulata</i> (Gregory) Hasle	3.4		
<i>Proboscia alata</i> (Brightwell) Sundström	42.1	<i>Thalassiosira gravida</i> Cleve	1.0	Cyanophyceae	
<i>Proboscia indica</i> (Peragallo) Hernández-Becerril	3.8	<i>Thalassiosira mendiolana</i> Hasle & Heimdal	0.3	Und. Cyanophyceae	0.3
<i>Pseudo-nitzschia</i> cf. <i>delicatissima</i>	0.7	<i>Thalassiosira rotula</i> Meunier	2.1		
<i>Pseudo-nitzschia</i> cf. <i>fraudolenta</i>	0.7	<i>Thalassiosira</i> spp. <10µm	0.3	Dictyochophyceae	
<i>Pseudo-nitzschia</i> cf. <i>galaxiae</i> Lundholm and Moestrup	0.7	<i>Thalassiosira</i> spp.	29.7	<i>Apedinella</i> spp.	4.8
<i>Pseudo-nitzschia</i> cf. <i>pungens</i> (Grunow ex Cleve) Hasle	2.4	<i>Thalassiothrix mediterranea</i> Pavillard	1.7	cf. <i>Apedinella spinifera</i> (Thronsen) Thronsen	0.3
<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden	24.5	<i>Thalassiothrix</i> spp.	2.4	<i>Dictyocha crux</i> Ehrenberg	2.4
<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle	1.0	Und. centric diatoms	3.8	<i>Dictyocha fibula</i> Ehrenberg	18.6
<i>Pseudo-nitzschia multistriata</i> (Takano) Takano	1.0	Und. centric diatoms <10µm	0.3	<i>Dictyocha speculum</i> Ehrenberg	4.5
<i>Pseudo-nitzschia pseudodelicatissima</i> (Hasle) Hasle	4.8	Und. centric diatoms <15µm	0.3	<i>Dictyocha speculum</i> var. <i>septen.</i> Ehrenberg	2.1
<i>Pseudo-nitzschia seriata</i> (Cleve) Peragallo	22.8	Und. centric diatoms <20µm	1.7	<i>Dictyocha staurodon</i> Ehrenberg	0.3
<i>Pseudo-nitzschia</i> spp.	22.8	Und. centric diatoms >20µm	1.7	<i>Octactis octonaria</i> (Ehrenberg) Hovasse	3.8
<i>Pseudo-nitzschia</i> spp. "Nitzschia delicatissima complex"	13.4	Und. pennate diatoms	16.9	Und. Dictyochophyceae	0.7
<i>Pseudo-nitzschia</i> spp. "Nitzschia seriata complex"	15.5	Und. pennate diatoms <20µm	2.8		
<i>Pseudo-nitzschia subfraudulenta</i> Hasle	1.0	Und. pennate diatoms >20µm	5.2		
<i>Pseudosolenia calcar-avis</i> (Schultze) Sundström	10.0	Und. Diatoms	30.3		
Dinophyceae (Dinoflagellates)		<i>Dinophysis</i> spp.	2.8	<i>Neoceratium inflatum</i> (Kofoid)	0.3
<i>Alexandrium</i> cf. <i>minutum</i> Halim	0.3	<i>Dinophysis tripos</i> Gourret	0.3	Gómez, Moreira & López-García	
<i>Alexandrium pseudogonyaulax</i> (Biecheler)	1.0	<i>Diplopsalis</i> "group"	11.4	<i>Neoceratium longipes</i> (Bailey)	1.4
Horiguchi ex Kita & Fukuyo		<i>Glenodinium foliaceum</i> Stein	0.3	Gómez, Moreira & López-García	
<i>Alexandrium</i> spp.	23.4	<i>Gonyaulax</i> cf. <i>fragilis</i> (Schütt) Kofoid	0.7	<i>Neoceratium longirostrum</i> (Gourret)	0.3

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<i>Amphidinium acutissimum</i> Schiller	0.7	<i>Gonyaulax</i> cf. <i>gracilis</i> Schiller	0.7	Gómez, Moreira & López-García	
<i>Amphidinium curvatum</i> Schiller	0.7	<i>Gonyaulax</i> cf. <i>scrippsae</i>	0.3	<i>Neoceratium macroceros</i> (Ehrenberg)	5.5
<i>Amphidinium lanceolatum</i> Schroder	0.3	<i>Gonyaulax digitale</i> (Pouchet) Kofoid	0.3	Gómez, Moreira & López-García	
<i>Amphidinium longum</i> Lohmann	3.4	<i>Gonyaulax hyalina</i> Ostenfeld & Schmidt	0.7	<i>Neoceratium massiliense</i> (Gourret)	0.3
<i>Amphidinium schroederi</i> Schiller	0.3	<i>Gonyaulax polygramma</i> Stein	6.6	Gómez, Moreira & López-García	
<i>Amphidinium</i> spp.	10.3	<i>Gonyaulax scrippsae</i> Kofoid	1.4	<i>Neoceratium trichoceros</i> (Ehrenberg)	7.6
<i>Amphidinium stigmatum</i> Schiller	0.3	<i>Gonyaulax spinifera</i> (Claparède & Lachmann) Diesing	3.4	Gómez, Moreira & López-García	
<i>Amphidoma caudata</i> Halldal	0.7	<i>Gonyaulax turbynei</i> Murray & Whitting	0.3	<i>Neoceratium tripos</i> (Müller)	2.1
<i>Ceratoperidinium</i> sp. Margalef ex Loeblich III	0.3	<i>Gonyaulax</i> spp.	6.6	Gomez, Moreira & Lopez-Garcia	
cf. <i>Alexandrium</i> spp.	4.1	<i>Gymnodinium agiliforme</i> Schiller	0.7	<i>Noctiluca scintillans</i> (Macartney) Kofoid & Swezy	2.8
cf. <i>Enciculifera carinata</i> Matsuoka, Kobayashi & Gains	0.7	<i>Gymnodinium corii</i> Schiller	0.3	<i>Oblea</i> spp.	1.7
cf. <i>Gonyaulax</i> spp.	0.3	<i>Gymnodinium</i> spp.	38.3	<i>Oxyphysis oxytoxoides</i> Kofoid	1.0
cf. <i>Gyrodinium fusiforme</i>	0.3	<i>Gyrodinium flagellare</i> Schiller	0.3	<i>Oxytoxum caudatum</i> Schiller	0.3
cf. <i>Lingulodinium polyedrum</i>	0.3	<i>Gyrodinium fusiforme</i> Kofoid & Swezy	23.8	<i>Oxytoxum</i> cf. <i>gracile</i> Schiller	0.3
cf. <i>Mesoporos</i> spp.	0.3	<i>Gyrodinium</i> cf. <i>lachryma</i> (Meunier) Kofoid & Swezy	4.8	<i>Oxytoxum</i> cf. <i>laticeps</i>	0.3
cf. <i>Oblea</i> spp.	0.7	<i>Gyrodinium pingue</i> (Schütt) Kofoid & Swezy	1.0	<i>Oxytoxum</i> cf. <i>milneri</i> Murray & Whitting	0.3
cf. <i>Prorocentrum compressum</i>	0.3	<i>Gyrodinium</i> spp.	23.1	<i>Oxytoxum laticeps</i> Schiller	2.1
cf. <i>Prorocentrum triestinum</i>	0.3	<i>Kofoidinium velleioides</i> Pavillard	0.3	<i>Oxytoxum longipes</i> Schiller	0.7
cf. <i>Protoperidinium</i> spp.	0.3	<i>Lessardia elongata</i> Saldarriaga & Taylor	2.1	<i>Oxytoxum scolopax</i> Stein	0.7
cf. <i>Scripsiella</i> spp.	0.3	<i>Lingulodinium polyedrum</i> (F.Stein) Dodge	6.2	<i>Oxytoxum</i> spp.	6.6
cf. <i>Scripsiella trochoidea</i>	0.3	<i>Mesoporos</i> cf. <i>perforatus</i> (Gran) Lillick	0.3	<i>Oxytoxum variabile</i> Schiller	1.0
<i>Cochlodinium</i> spp.	0.7	<i>Mesoporos</i> spp.	0.7	<i>Oxytoxum viride</i> Schiller	0.3
<i>Corythodinium</i> cf. <i>michaelsarsii</i> (Gaarder) Taylor	0.3	<i>Neoceratium candelabrum</i> (Ehrenberg)	1.7	<i>Peridinium</i> cf. <i>balticum</i> (Levander) Lemmermann	0.3
<i>Corythodinium</i> cf. <i>tesselatum</i> (Stein)	0.3	Gómez, Moreira & López-García	0.3	<i>Phalacroma rotundatum</i> (Claparède & Lachmann)	2.1
Loeblich Jr. & Loeblich III		<i>Neoceratium candelabrum</i> var. <i>dep.</i> (Ehrenberg)	0.3	Kofoid & Michener	
<i>Dinophysis acuminata</i> Claparède & Lachmann	0.7	Gómez, Moreira & López-García	0.3	<i>Podolampas palmipes</i> Stein	2.1
<i>Dinophysis acuta</i> Ehrenberg	0.3	<i>Neoceratium carriense</i> Gómez, Moreira & López-García	2.1	<i>Podolampas spinifera</i> Okamura	0.3
<i>Dinophysis caudata</i> Saville-Kent	8.6	<i>Neoceratium extensum</i> Gómez, Moreira & López-García	0.7	<i>Podolampas</i> spp.	0.3
<i>Dinophysis</i> cf. <i>acuminata</i>	0.3	<i>Neoceratium furca</i> (Ehrenberg)	31.7	<i>Pronoctiluca acuta</i> (Lohmann) Schiller	0.3
<i>Dinophysis</i> cf. <i>saccula</i>	1.0	Gómez, Moreira & López-García	29.3	<i>Pronoctiluca pelagica</i> Fabre-Domergue	0.3
<i>Dinophysis fortii</i> Pavillard	3.4	<i>Neoceratium fusus</i> (Ehrenberg)	0.3	<i>Pronoctiluca</i> spp.	0.3
<i>Dinophysis ovum</i> Schütt	0.3	Gómez, Moreira & López-García	0.3	<i>Prorocentrum aporum</i> (Schiller) Dodge	1.7
<i>Dinophysis parva</i> Schiller	0.3	<i>Neoceratium hexacanthum</i> (Gourret)	0.3	<i>Prorocentrum balticum</i> (Lohmann) Loeblich III	1.0
<i>Dinophysis saccula</i> Stein	7.2	Gómez, Moreira & López-García	4.8	<i>Prorocentrum</i> cf. <i>dactylus</i> (Stein) Dodge	1.0
<i>Prorocentrum</i> cf. <i>lima</i>	0.7	<i>Torodinium</i> spp.	5.5	Prymnesiophyceae calcareous (Coccolithophores)	
<i>Prorocentrum</i> cf. <i>triestinum</i>	1.0	Und. naked dinophyceae <20µm	3.8	<i>Acanthoica quattropsina</i> Lohmann	7.6
<i>Prorocentrum compressum</i> (Bailey) Abé ex Dodge	9.0	Und. naked dinophyceae >20µm	6.2	<i>Acanthoica</i> spp.	0.7
<i>Prorocentrum cordatum</i> (Ostenfeld) Dodge	0.3	Und. thecate dinophyceae <20µm	3.8	<i>Calciosolenia brasiliensis</i> (Lohmann) Young	11.7
<i>Prorocentrum gracile</i> Schütt	4.1	Und. thecate dinophyceae >20µm	55.9	<i>Calciosolenia murrayi</i> Gran	14.1
<i>Prorocentrum lima</i> (Ehrenberg) Dodge	0.3	Und. Dinophyceae	0.3	<i>Calciosolenia</i> spp.	2.8
<i>Prorocentrum micans</i> Ehrenberg	45.5	Und. Cysts	0.3	<i>Coronosphaera</i> spp.	0.3
<i>Prorocentrum minimum</i> (Pavillard) Schiller	26.9	Euglenophyceae	0.3	<i>Emiliana huxleyi</i> (Lohmann) Hay and Mohler	6.6
<i>Prorocentrum nanum</i> Schiller	0.7	<i>Euglena</i> spp.	2.8	<i>Emiliana</i> spp.	0.3
<i>Prorocentrum</i> spp.	14.5	<i>Eutreptia</i> spp.	3.1	<i>Halopappus</i> spp.	0.7
<i>Prorocentrum triestinum</i> Schiller	16.9	<i>Eutreptiella eupharyngea</i> Moestrup & Norris	12.1	<i>Michaelsarsia adriaticus</i> (Schiller)	1.0
<i>Protoperidinium bipes</i> (Paulsen) Balech	18.3	<i>Eutreptiella</i> spp.	19.7	Manton, Bremer and Oates	
<i>Protoperidinium bispinum</i> (Schiller) Balech	0.3	Und. Euglenophyceae	0.3	<i>Michaelsarsia elegans</i> (Gran) Menton	0.3
<i>Protoperidinium cerasus</i> (Paulsen) Balech	0.3	Prasinophyceae	0.3	<i>Ophiaster formosus</i> Gran	0.3
<i>Protoperidinium</i> cf. <i>depressum</i>	0.7	<i>Pachisperma</i> sp.	0.3	<i>Ophiaster hydroideus</i> (Lohmann) Lohmann	11.0
<i>Protoperidinium conicum</i> (Gran) Balech	0.3	<i>Pseudoscourfieldia marina</i> (Thonsden) Manton	2.4	<i>Rhabdosphaera clavigera</i> Murray and Blackman	9.3
<i>Protoperidinium crassipes</i> (Kofoid) Balech	2.4	<i>Pterosperma</i> sp.	0.3	<i>Rhabdosphaera</i> spp.	1.7
<i>Protoperidinium curtipes</i> (Jørgensen) Balech	0.3	<i>Pyramimonas</i> spp.	4.8	<i>Rhabdosphaera tignifer</i> Schiller	0.7
<i>Protoperidinium depressum</i> (Bailey) Balech	0.3	<i>Tetraselmis</i> spp.	2.4	<i>Syracosphaera</i> cf. <i>pirus</i> Haldall and Markali	0.3
<i>Protoperidinium diabolium</i> (Cleve) Balech	5.2	Und. Prasinophyceae	35.5	<i>Syracosphaera histrica</i> Kamptner	0.3
<i>Protoperidinium divergens</i> (Ehrenberg) Balech	2.1	Prymnesiophyceae non - calcareous	1.4	<i>Syracosphaera prolongata</i> Gran ex Lohmann	0.3
<i>Protoperidinium leonis</i> (Pavillard) Balech	0.3	cf. <i>Corymbellus aureus</i>	0.3	<i>Syracosphaera pulchra</i> Lohmann	2.4
<i>Protoperidinium mediterraneum</i> (Kofoid) Balech	0.7	<i>Chrysochromulina</i> cf. <i>hirta</i>	0.3	<i>Syracosphaera</i> spp.	16.2
<i>Protoperidinium mite</i> (Pavillard) Balech	0.3	<i>Chrysochromulina hirta</i> Manton	1.7	Und. Coccolithophores	22.1
<i>Protoperidinium oblongum</i> (Aurivillius) Parke & Dodge	0.7	<i>Chrysochromulina parkeae</i> Green & Leadbeater	1.4	Incertae sedis	
<i>Protoperidinium ovum</i> (Schiller) Balech	0.3	<i>Chrysochromulina polylepis</i> Manton & Parke	0.3	<i>Commation</i> sp.	1.0
<i>Protoperidinium pallidum</i> (Ostenfeld) Balech	0.3	<i>Chrysochromulina</i> spp.	3.1	<i>Ebria tripartita</i> (Schumann) Lemmermann	1.4
<i>Protoperidinium pyriforme</i> (Paulsen) Balech	0.3	<i>Corymbellus aureus</i> Green	1.4	<i>Hermesinum adriaticum</i> Zacharias	3.4
<i>Protoperidinium</i> spp.	16.6	<i>Phaeocystis</i> spp.	1.7	<i>Leucocryptos marina</i> (Braarud) Butcher	3.4
<i>Protoperidinium steinii</i> (Jørgensen) Balech	7.9	Und. Prymnesiophyceae	31.0	<i>Paulinella ovalis</i> (Wulff)	3.8
<i>Pseliodinium vaubanii</i> Soumia	3.4			Johnson, Hargraves & Sieburth	
<i>Pyrocystis lunula</i> (Schütt) Schütt	0.3			Und. Ebridea	0.3
<i>Pyrocystis noctiluca</i> Murray ex Haeckel	0.3				

(continued)

<i>Scrippsiella spinifera</i> Honsell & Cabrini	1.0		
<i>Scrippsiella</i> spp.	9.3		
<i>Scrippsiella trochoidea</i> (Stein) Balech ex Loeblich III	18.6		
		Other groups	
		Und. phytoflagellates <5µm	1.7
		Und. phytoflagellates <10 µm	90.0
		Und. Choanoflagellida	3.8

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