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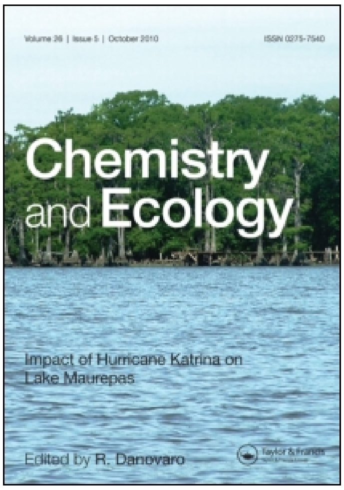

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Seasonal and interannual variations of phytoplankton in the Gulf of Venice (Northern Adriatic Sea)

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Spatial and temporal variations of phytoplankton community structure were studied in the Gulf of Venice (Northern Adriatic Sea) from February 1999 to December 2001 (INTERREG II, Italia–Slovenia project). Phytoplankton samples were collected, with a monthly frequency, at 11 stations in the basin. Abundance, biomass, and species composition were considered. Synthetic descriptors were used in order to evaluate the main succession pattern and to cluster communities that typify different hydrological conditions. A decreasing gradient of abundance and biomass was generally observed from west to east, passing from the land-influenced waters to offshore. The seasonal pattern and inter-annual variability of the main phytoplankton taxa are described and discussed in relation with the occurrence of a massive mucilage event and of a Po River flood.

Keywords: Phytoplankton; Seasonal pattern; Northern Adriatic; Mediterranean Sea

1. Introduction

The Northern Adriatic Sea (figure 1) is a shallow basin (mean depth 35 m) characterized by a prevalent cyclonic circulation of the water masses. The trophic state, the vertical structure of the water column, and the local circulation are deeply influenced by the inputs of many rivers from the Italian coast and by the highly saline and oligotrophic waters from the southern Adriatic basin [1, 2]. The Po, by far the largest Italian river, and the Adige give the major contribution to the total freshwater inputs in the basin. The average Po river discharge is about 1500 $m^3 s^{-1}$, but marked variations can occur within and among years. A pronounced seasonal variability is typically observed, with peaks in spring and autumn (up to 8000 $m^3 s^{-1}$), in response to mountain snow melting and heavy precipitation, and minima in summer (300–400 $m^3 s^{-1}$), after long dry periods [1, 3].

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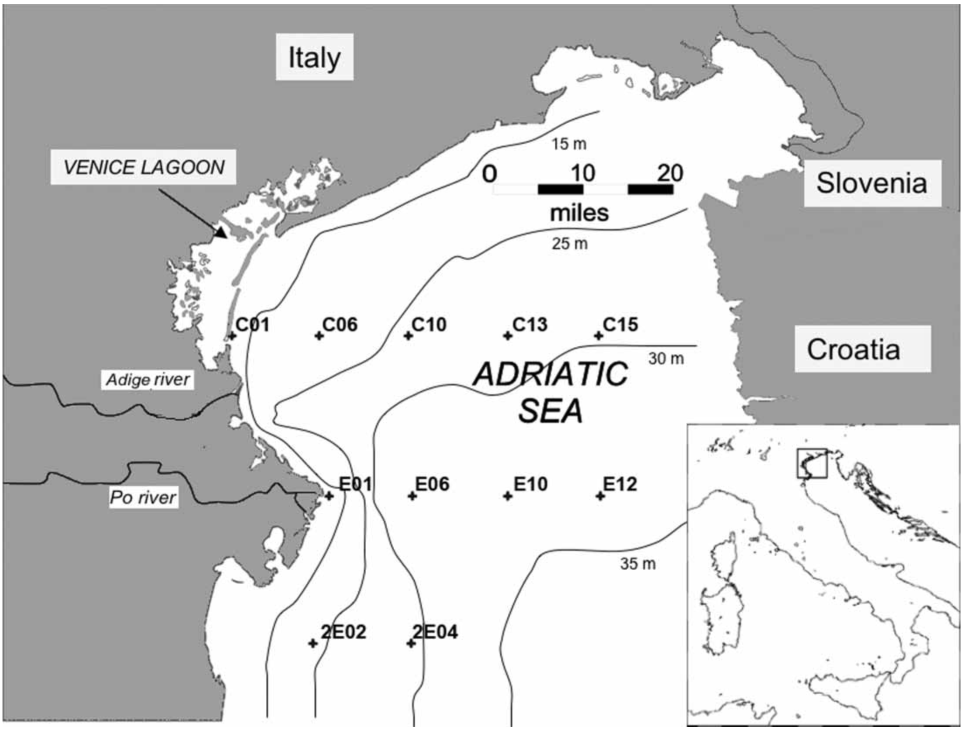

Figure 1. Study area and location of the 11 stations along the three transects.

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A temporal succession of two different hydrodynamics patterns is typically recognized in this area:

(1) In winter, from November to March, heat losses and mechanical stirring by winds lead to vertical mixing of the water column, characterized by highly saline waters. The Po river outflow remains confined near the western coast and spreads southwards, and is separated from offshore waters by a persistent frontal system.
(2) For the rest of the year, a temperature and salinity vertical gradient leads to a highly stratified water column with different density layers at the surface and at the bottom.

A trophic gradient, decreasing from north-west to south-east, is commonly observed in the Northern Adriatic Sea: the nutrient-rich waters coming from the rivers are mainly spread southward and eastward from the Italian coast [1, 2]. The amount and the distribution of the diluted waters in the northern Adriatic basin are highly variable and they have a marked influence on phytoplankton communities, mainly through the supply of inorganic nutrients and seston, and through the control of the vertical stability of the water column [1, 4]. In particular, concurrent enrichment (mainly by river) and depletion (by phytoplankton uptake) of both DIN and P can cause rapid and marked variation of the N/P ratio [3].

The meteo-ocenographic conditions, the patterns of currents, and the nutrient limitation (in particular by P) are considered to be the general environmental conditions that seem to favour mucilage formation in the Northern Adriatic basin [5]. This phenomenon has been observed, at least at its early stage, almost every year since the 1990s and with a huge development in the years 1991, 1997, 2000, and 2002. Mucilage starts in late spring/early summer, when the stratification strengthens, and the exchange of water masses between the northern and

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the middle basin slows down [6]. However, there is no evidence of changes in the dominant species composition of microphytoplankton in the years when massive mucilage aggregates were observed [7].

The Utermöhl fraction of the phytoplankton community (cells $> 3\,\mu\text{m}$ as a maximum linear dimension) has been extensively studied in the Northern Adriatic Sea in the past [7–15]. The community is mainly made up by diatoms (*Skeletonema marinoi*, previously identified as *S. costatum*, *Chaetoceros* spp., *Thalassiosira* spp., and *Pseudo-nitzschia* spp.) and by small flagellates (nanoflagellates and cryptophyceans). The following seasonal pattern has been generally recognized: a late-winter/early-spring diatom bloom, related to the increase in day length and irradiance and to high nutrient inputs from the rivers; a late-spring/summer decline, when the community is mainly sustained by nutrient regeneration; a late autumn/winter minimum, mainly related to the decrease in light and temperature.

Although these seasonal fluctuations are common to other coastal seas [13, 16], the dynamic of phytoplankton in the Northern Adriatic Sea shows marked spatial and temporal heterogeneity and both seasonal and inter-annual fluctuations related to the freshwater inputs and to their distribution in the basin.

The Gulf of Venice is located at the north-western side of the Northern Adriatic (figure 1). It is an area characterized by a remarkable variability of the trophic gradient, at both the spatial and temporal scales: it encompasses the permanently meso-eutrophic coastal area, the highly dynamic transition zone between mesotrophic and saline oligotrophic waters, and, at its eastern side, an offshore, mostly oligotrophic area.

Beside some long-term studies that considered only the coastal belt of the Gulf of Venice [15], information about the phytoplankton community of this area is quite sporadic [9, 17]. In the present study, we examine the phytoplankton community structure and dynamics in the Gulf of Venice, over three years (February 1999 to December 2001). We aim, first of all, to define the phytoplankton composition in the different hydrographic conditions encountered in the basin; then, we analyse the prevalent seasonal pattern in the area; finally, we consider the interannual variations of the phytoplankton community structure, with emphasis on the occurrence of a massive mucilage event (May–August 2000) and of a flood of the Po River (October 2000).

2. Materials and methods

The investigation was carried out in the Gulf of Venice in the frame of an INTERREG II initiative, onboard of the RV *U. D'Ancona*, on 11 stations along three transects (C, E, and 2E) at a distance from the Italian coast between 2 and 40 nautic miles (figure 1). From February 1999 to December 2001, with a monthly frequency, phytoplankton sampling was performed using 5 1 Niskin bottles, at the surface layer of each station. At two stations (C10, maximum depth 28 m, and E06, maximum depth 30 m; figure 1), discrete samples were also gathered at five depths along the water column (0, 1, 5, 15 m, and near-bottom layer) to analyse the phytoplankton vertical distribution. The two stations are considered as being representative of the hydrological and trophic variability of the area [18–20].

At each sampling, transparency (Secchi disk), PAR irradiance (Biospherical quantum scalar irradiance meter), temperature, salinity, dissolved oxygen, and pH (Idronaut Ocean Seven 316 multiprobe) were measured. Inorganic dissolved nutrients (N-NH_3, N-NO_2, N-NO_3, Si-SiO_4, and P-PO_4) were analysed according to Grasshoff *et al.* [21], chlorophyll *a* was determined by spectrofluorimetry [22], and particulate organic carbon (POC) and particulate nitrogen

(PN) were analysed with Perkin Elmer 2004 CHN elemental analyser, following Hedges and Stern [23].

The abundance, biomass, and species composition of phytoplankton were estimated on 441 samples using an inverted microscope equipped with phase contrast (model Zeiss Axiovert 35), at a magnification of 400×. Samples were fixed with exametilentetramine-neutralized formaldehyde to a final concentration of 4%. Sub-samples from 5 to 50 ml were allowed to settle for 12–24 h and examined [24]. A variable transect number was observed until at least 200 (but often more than 500) cells were counted for each sample [25].

Species composition was defined according to Tomas [26] and references therein. The undetermined organisms belonging to cryptophyceans, chrysophyceans, prymnesiophyceans (except coccolithophorids), prasinophyceans, and chlorophyceans, whose sizes varied between 3 and 4 μm, were all included in the group 'nanoflagellates'. Cell size and volume were determined according to Strathmann [27], and species diversity was calculated after Shannon and Weaver [28].

Univariate and multivariate analyses were applied to cluster communities, typifying different environmental conditions. Data were processed by Analysis of Variance (SPSS version 12.0), using Tukey's multiple comparison after $\log_{10}$ transformation of phytoplankton data [29]. When variances were heterogeneous, Welch's test and Dunnet's T3 multiple comparison procedure [30] were used in place of standard analysis of variance. Linear correlation analysis was performed using Statistica by Statsoft. In order to obtain information about the interannual variation of phytoplankton, original data of abundances were used to produce data matrices and perform multivariate analyses, using P.R.I.M.E.R. software [31]. This software, born for benthos community studies [32, 33], has been used successfully to describe the phytoplankton distribution in ecosystem characterized by a marked salinity gradient [34–36]. After standardizing and transforming data in a double-square root, on matrices of Bray–Curtis similarity index, hierarchical agglomerative clustering (Q mode) was carried out with the group-average link [31]. Clustering of taxa (R mode) was obtained using Hellinger distance [37]. Finally, in order to find the best combination between Q mode and R mode analyses, the sum of the abundances of each taxon clustered in the R mode was calculated for each cluster of samples (Q mode). A subsequent cumulative sum of these values among the species was also obtained, leading to a single abundance value for each cluster of species (R mode) and for each cluster of samples (Q mode). In this way, we can identify which cluster of species was dominant in a corresponding cluster of samples, thus obtaining a combination between the list of the taxa and the list of the samples.

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3. Results

3.1 *Environmental variables*

The sampling area showed significant hydrological differences, mainly determined by the extension of the Po River plume in the basin, which were more evident in spring and autumn, when the Po River discharge attained its maximum (between 3000 and 6000 m^3s^{-1}). The large ranges, the averages, and the standard deviations of hydrochemical and biological data (table 1) evidenced the high variability and the complexity of this ecosystem. The whole data set was divided into three subsets, characterized by three density classes, on the basis of the T/S diagram (figure 2).

A total number of 38 samples (9% of the total samples) were grouped in the first subset (group 1: $\gamma_t < 21\,kg\,m^{-3}$), which included all the surface samples of the coastal stations (C01 and E01) and samples of some stations far from the coast (E06 and C06, 2E02), when the river

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Table 1. Range, averages and standard deviations of the main hydrobiological parameters in the Gulf of Venice.

	Min	Max	M	S.D.
Po river discharge (m^3 s^{-1})	486	6430	1822	1282
Temperature (°C)	5.8	28.7	18.0	5.7
Salinity	8.7	38.5	35.1	4.1
Anomaly of density (γ_t; kg m^{-3})	5.5	29.9	25.2	3.5
Oxygen (%)	32.9	176.9	103.8	13.8
pH	7.9	8.7	8.2	0.1
N-NH$_3$ (µM)	0.01	23.2	1.5	3.0
N-NO$_2$ (µM)	0.01	2.86	0.40	0.58
N-NO$_3$ (µM)	0.01	197.3	9.0	24.1
DIN (µM)	0.11	221.5	10.9	26.7
SI-SIO$_4$ (µM)	0.01	115.3	7.3	13.4
P-PO$_4$ (µM)	0.01	2.00	0.12	0.24
POC (µg dm^{-3})	29.1	3040.8	242.8	274.7
TPN (µg dm^{-3})	5.1	370.1	40.7	42.3
Chlorophyll *a* (µg dm^{-3})	0.01	25.6	1.7	2.2
Total phytoplankton abundance (cells dm^{-3})	45882	34515231	1672349	3266475
Total phytoplankton biomass (µgC dm^{-3})	1	1897	79	160

plume is more widespread through the cyclonic gyre. Most of the samples (244 samples, 55% of the total samples) fell in the group 2 ($\gamma_t 21 - 27\,\mathrm{kg\,m^{-3}}$), which included all the samples gathered at the surface during water-column stratification (from late spring to late summer), in most of the basin. The rest of the samples (158 samples, 36% of the total samples) fell in the high-density group (group 3: $\gamma_t > 27\,\mathrm{kg\,m^{-3}}$), which clustered several summer deep samples and the late autumn and winter samples of the offshore stations (>20 nautical miles from the coast).

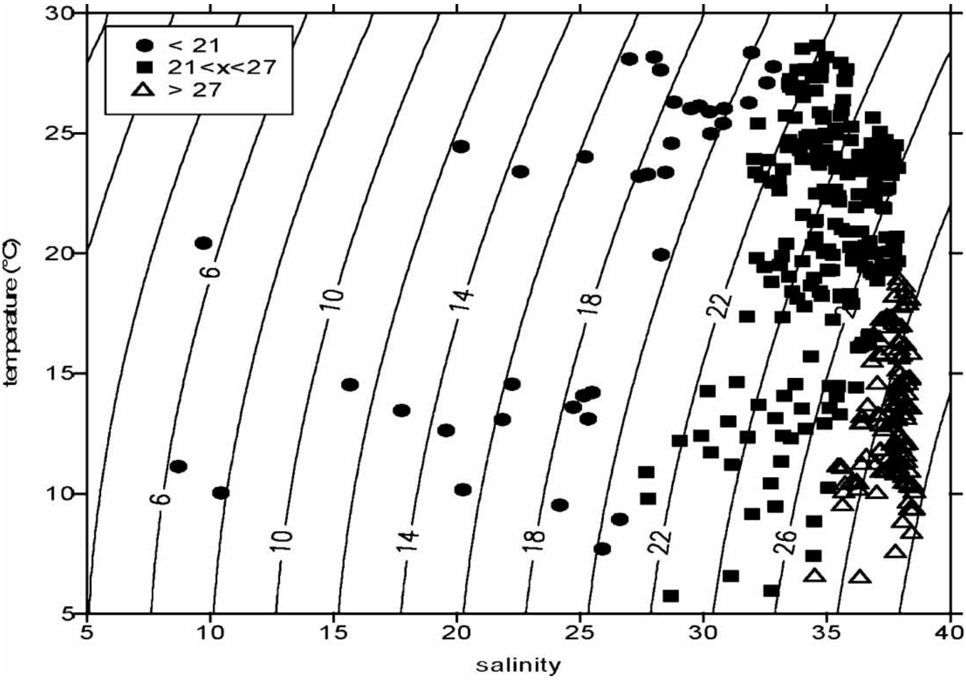

Figure 2. Distribution of samples according to the T/S diagram.

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The main hydrological features differed significantly among the three groups of samples (table 2): group 1 was characterized by a low salinity and by a high concentration of inorganic nutrients, organic matter (POC, PN), and chlorophyll *a*. Higher salinity and lower concentrations of inorganic nutrients and chlorophyll *a* distinguish the other two groups; group 3 shows the lowest temperature, chlorophyll *a*, POC, and PN concentrations.

3.2 *Phytoplankton community*

The spatial variability of phytoplankton abundance and biomass was very pronounced. The highest abundance and biomass (often $>10^7$ cells dm^{-3} and >300 µg C dm^{-3}) were generally

Table 2. Average abundance of the main phytoplankton class and of some related parameters in three density groups, evidenced by the T/S diagram (see figure 2).

	Group 1		Group 2		Group 3			
	M	S.D.	M	S.D.	M	S.D.	*N*	Sign
Temperature (°C)	20.1	6.9	20.8	4.7	13.2	2.7	441	**
Salinity	25.1	6.2	35.1	1.9	37.6	0.8	441	**
Anomaly of density (γ_t; kg m^{-3})	17.0	3.9	24.5	1.6	28.3	0.7	441	**
DIN (µM)	57.5	63.7	7.1	14.8	5.7	10.4	419	**
SI-SIO$_4$ (µM)	31.7	32.0	4.5	6.5	5.7	5.9	419	**
P-PO$_4$ (µM)	0.45	0.58	0.08	0.13	0.10	0.15	419	**
POC (µg dm^{-3})	681.5	424.3	241.5	253.4	132.9	79.0	418	**
TPN (µg dm^{-3})	117.0	75.8	38.7	31.6	24.2	15.8	412	**
Chlorophyll *a* (µg dm^{-3})	4.5	4.5	1.5	1.9	1.4	1.3	426	**
Diatoms (cells dm^{-3})	4 191 062	7 382 953	756 054	1 864 850	307 127	2 767 281	441	**
Dinoflagellates (cells dm^{-3})	39 263	45 073	100 395	732 818	14 018	547 514	441	**
Coccolitophorids (cells dm^{-3})	15 303	23 227	25 524	38 387	50 704	57 464	441	**
Silicoflagellates (cells dm^{-3})	377	1414	93	664	555	1240	441	**
Nanoflagellates (cells dm^{-3})	1 064 985	864 078	613 367	592 234	337 468	621 583	441	**
Total Phytoplankton (cells dm^{-3})	5 476 744	7 660 206	1 674 996	2 678 617	753 262	3 266 475	441	**
Diatom biomass (µgC dm^{-3})	214	361	66	122	28	149	441	**
Dinoflagellate biomass (µgC dm^{-3})	11	15	11	43	2	33	441	**
Coccolitophorid biomass (µgC dm^{-3})	1	2	2	3	2	3	441	n.s.
Silicoflagellate biomass (µgC dm^{-3})	0.3	1.2	0.1	0.6	0.4	0.9	441	**
Nanoflagellate (µgC dm^{-3})	4	4	2	2	1	2	441	**
Total phytoplankton biomass (µgC dm^{-3})	234	373	84	137	34	160	441	**

Note: Results of one-way ANOVA are also reported. Values that are significantly different are shown. *N*: number of samples; n.s.: not significant.
$^{**}p < 0.01$; $^{*}p < 0.05$.

found in the diluted Po river waters (included in group 1), intermediate values in the surface offshore waters (around 10^6 cell dm^{-3} and 80 $\mu\mathrm{g\,C\,dm}^{-3}$; group 2), and the lowest abundance and biomass (minima around 4×10^4 and 1 $\mu\mathrm{g\,C\,dm}^{-3}$; group 3) in the oligotrophic, high saline bottom waters. The spatial heterogeneity of phytoplankton abundance was permanently observed at the surface, both during diatom blooms (e.g. *Skeletonema marinoi*, in February 2001) and in low standing stock conditions (e.g. November 1999), with the relative maxima always located in the southern branch of Po river plume (figure 3), with the exception of some minor peaks that were observed far from the coast.

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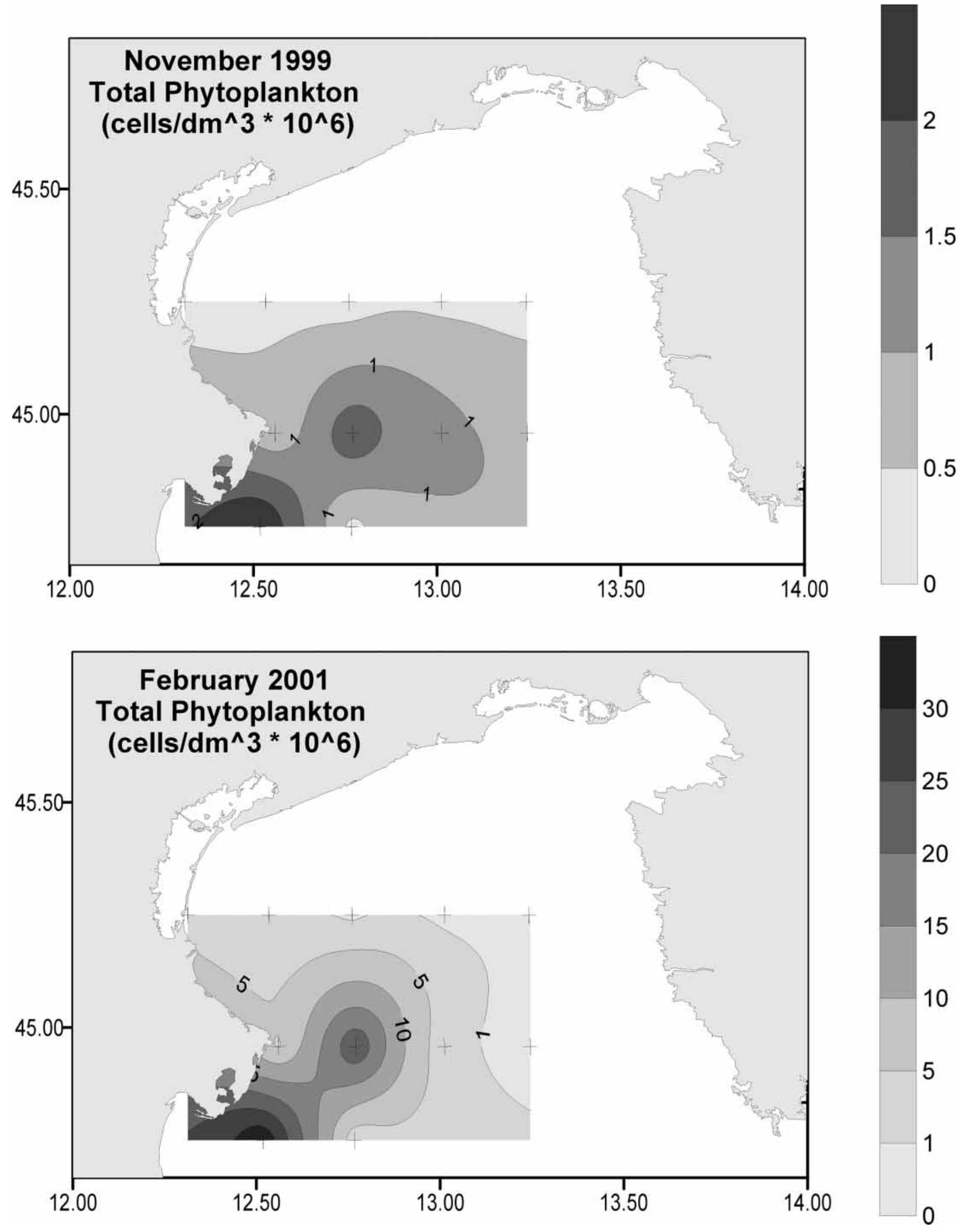

Figure 3. Surface distribution of phytoplankton abundance observed in two dates in different seasons.

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Throughout the study, 212 distinct phytoplankton taxa were detected; 143 of them were identified to the species level. Cell volume ranged from 15 μm^3 (nanoflagellates, *Nitzschia frustulum*) to 3×10^5 μm^3 (*Rhizosolenia* spp., *Coscinodiscus* spp., and *Ceratium* spp.). Phytoplankton diversity varied between 0.2 and 3.3 (average 1.9), with quite irregular patterns in both space and time.

The abundance and biomass of the main phytoplankton taxa have been clustered and averaged according to the three density classes described above. Some species were common to the three density groups, but they showed a different relative importance (table 3). The most important species (40 species making up to 95% of the total biomass and 63% of the total

Table 3. Average abundances (cells dm^{-3}) of the most important taxa in each density group (evidenced by the T/S diagram; see figure 2).

	Group 1		Group 2		Group 3	
	cells dm^{-3}	%	cells dm^{-3}	%	cells dm^{-3}	%
Asterionellopsis glacialis	**19 607**	**63**	4567	15	6937	22
Skeletonema marinoi	**2 714 377**	**91**	210 025	7	63 899	2
Thalassionema nitzschioides	**25121**	**73**	6824	20	2588	7
Thalassiosira sp.	**188 760**	**72**	59 417	23	13 234	5
Pseudo-nitzschia delicatissima group	**183 590**	**58**	112 940	35	22 213	7
Bacteriastrum sp.	**2922**	**57**	1738	34	480	9
Cerataulina pelagica	**170 860**	**63**	94 377	35	6129	2
Cyclotella sp.	**30 702**	**78**	8004	20	879	2
Leptocylindrus danicus	**32 305**	**61**	15 555	30	4841	9
Pleurosigma sp.	**1509**	**49**	1295	42	298	10
Protoperidinium diabolus	**229**	**60**	109	29	41	11
Chaetoceros compressus	**259 920**	**87**	31 403	10	8419	3
Chaetoceros decipiens	**44 230**	**53**	20 948	25	18 925	23
Chaetoceros sp.	**214 616**	**66**	85 643	26	25 546	8
Dactyliosolen fragilissimus	**37 090**	**70**	9981	19	6137	12
Guinardia striata	**4449**	**56**	2739	35	717	9
Hemiaulus hauckii	**52 822**	**60**	14 278	16	20 782	24
Prorocentrum minimum	6275	8	**68 134**	**91**	807	1
Scrippsiella trochoidea	305	16	**1481**	**78**	118	6
Rhabdosphaera clavigera	511	32	**990**	**62**	91	6
Syracosphaera pulchra	1983	33	**3261**	**54**	777	13
Ceratium furca	46	42	**50**	**46**	13	12
Ceratium fusus	93	36	**117**	**46**	45	18
Gyrodinium sp.	379	10	**2243**	**60**	1147	30
Prorocentrum micans	450	32	**846**	**61**	101	7
Cylindrotheca closterium	24 972	43	**27 771**	**48**	5280	9
Proboscia alata	1973	39	**2359**	**47**	708	14
Gymnodinium sp.	14 985	37	**17 855**	**44**	7405	18
Und. Cryptophyceae	138 376	40	**168 837**	**48**	41 102	12
Guinardia flaccida	93	25	**194**	**53**	80	22
Diploneis crabro	62	4	64	4	**1427**	**92**
Nitzschia longissima	26	7	67	17	**290**	**76**
Pseudo-nitzschia seriata group	12 475	13	9336	9	**76 839**	**78**
Calciosolenia murrayi	29	2	478	36	**831**	**62**
Emiliania huxleyi	10 109	14	16 423	23	**44 709**	**63**
Dictyocha fibula	283	39	69	10	**367**	**51**
Octactis octonaria	0	0	21	17	**100**	**83**
Lioloma pacificum	13	3	219	46	**248**	**52**
Ophiaster hydroideus	0	0	732	48	**798**	**52**
Calciosolenia brasiliensis	119	23	156	30	**238**	**46**

Note: The relative importance of each taxa is compared among the three groups (%). Values > 40% are shown in bold.

abundance) have been correlated with temperature, salinity, nutrient concentration, and light (table 4). Although several correlations were statistically significant ($p < 0.05$; $p < 0.01$), the values of the correlation coefficients were generally low ($r < 0.5$). Therefore, we considered these only as a clue of the prevalent distribution of the species in relations with the main environmental variables.

The highest phytoplankton abundance was generally found in the group 1 samples (table 3). The most relevant species were *Skeletonema marinoi*, *Asterionellopsis glacialis*, *Thalassiosira* sp., and *Cerataulina pelagica*. The first three were late-winter/early-spring species: they were, indeed, inversely correlated with temperature and salinity and directly with inorganic nutrients (table 4). *Skeletonema marinoi* typically blooms in late winter in the Northern Adriatic ([38], as *S. costatum*). During the present study, between February and March 2001, it attained abundance up to 3.5×10^7 cells dm^{-3} and biomass up to $1900\,\mu\mathrm{g\,C\,dm}^{-3}$ at some coastal stations. During the bloom, the contribution of this species to total particulate organic carbon (POC) ranged between 47 and 100%.

Cerataulina pelagica is, on the contrary, a summer species: its abundance is positively correlated with temperature and inversely with salinity and nutrients. This species attained a relatively low maximum abundance ($<10^6$ cells dm^{-3}), but its contribution to total phytoplankton biomass was considerable: it ranged between 20 and 100%, with an average value of 52%.

Beside these species, a bloom of *Chaetoceros compressus* was also recorded, only at one station (E01), on September 1999: it attained the abundance of 10^7 cells dm^{-3}, contributing 30% of total phytoplankton biomass and 10% of total particulate organic carbon.

A mixed phytoplankton community characterized the second group samples: the dinoflagellates *Prorocentrum minimum* and *Scrippsiella trochoidea*, the diatoms *Cerataulina pelagica*, *Leptocylindrus danicus*, *Proboscia alata*, and the *Pseudo-nitzschia delicatissima*-group, the coccolithophorids *Rhabdosphaera clavigera* and *Syracosphaera pulchra*, and several undetermined cryptophyceans. These species were prevalently found in late spring and summer, in most of the basin but especially at the surface.They were all correlated directly with temperature and inversely with nutrients. Among these species, *Prorocentrum minimum* and the undetermined cryptophyceans attained bloom abundances (between 1 and 1.4×10^7 cell dm^{-3}) in the middle of the basin, in May 2000; their biomass comprised almost 100% of total particulate organic carbon.

Taxa belonging to group 3 were typical of summer deep waters and of the mixing period (late autumn–early winter) and showed an inverse correlation with temperature and a direct correlation with salinity: the most important were the coccolithophorids *Emiliania huxleyi*, *Calciosolenia murrayi*, and *C. brasiliensis*, the silicoflagellates *Octatis octonaria* and *Dichtyocha fibula*, and diatoms such as the *Pseudo-nitzschia seriata* group, *Nitzschia longissima*, and *Diploneis crabro*.

The average vertical distribution of the most important species was analysed considering the data from stations C10 and E06. At station E06, water-column stratification, due to vertical gradients of anomaly of density (γ_t) driven by low salinities, was detected throughout the whole study period; at station C10, pycnoclines were less marked, and the thermal stratification often prevailed (figure 4).

Most of the species belonging to groups 1 and 2 showed an average vertical distribution of abundance decreasing from surface to bottom (figure 5). On the contrary, most species of group 3 appeared more evenly distributed along the water column (e.g. the silicoflagellates *Octatis octonaria* and *Dictyocha fibula* in winter) or were preferentially located in the water layers below the pycnocline (e.g. some coccolithophorids, in particular *Emiliania huxleyi*, *Calciosolenia murrayi*, pelagic diatoms such as the *Pseudo-nitzschia seriata* group, and some benthic diatoms such as *Nitzschia longissima* and *Diploneis crabro*; figures 5 and 6). The

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Table 4. Bravais Pearson correlations among the most important species and some hydrochemical parameters, with correlation coefficients significant at $p < 0.05$ and at $p < 0.01$ shown in bold.

	Temperature	Salinity	N-NH$_3$	N-NO$_2$	N-NO$_3$	DIN	SI-SIO$_4$	P-PO$_4$
Asterionellopsis glacialis	**−0.37**			**0.34**	**0.17**	**0.17**	0.11	
Skeletonema marinoi	**−0.36**	**−0.36**	**0.17**	**0.39**	**0.32**	**0.32**	**0.26**	**0.13**
Thalassiosira sp.	**−0.11**	**−0.28**	**0.17**	**0.28**	**0.25**	**0.25**	**0.24**	**0.15**
Cylindrotheca closterium	**−0.15**			**0.13**				
Thalassionema nitzschioides							**0.10**	
Prorocentrum micans	**0.26**	**−0.17**		**−0.16**				
Bacteriastrum sp.	**0.24**			**−0.13**			**−0.10**	
Cerataulina pelagica	**0.26**	−0.12	**−0.14**	**−0.14**	−0.11	−0.12	−0.12	**−0.15**
Cyclotella sp.	**0.24**	**−0.12**		−0.12				
Leptocylindrus danicus	**0.16**		−0.12	**−0.15**				
Prorocentrum minimum	**0.17**	−0.16	−0.11	**−0.15**				
Proboscia alata	**0.12**		**−0.19**	**−0.15**		−0.10	**−0.11**	
Pseudo-nitzschia delicatissima group	**0.43**		−0.11	**−0.26**	**−0.15**	**−0.16**	−0.10	−0.10
Gymnodinium sp.	**0.17**	**0.21**	**−0.15**	**−0.20**	**−0.24**	**−0.24**	**−0.20**	**−0.13**
Protoperidinium diabolus	**0.22**							
Und. Cryptophyceae	**0.12**		**−0.17**	**−0.25**	**−0.20**	**−0.21**	**−0.17**	**−0.23**
Scrippsiella trochoidea	**0.14**			**−0.14**				
Pleurosigma sp.				**0.16**			**0.13**	
Rhabdosphaera clavigera	**0.28**			**−0.21**	**−0.10**	−0.10		
Syracosphaera pulchra	**0.18**		−0.12	−0.10	**−0.10**	−0.11	**−0.11**	**−0.17**
Ceratium furca	**0.12**							
Ceratium fusus	**0.18**							
Gyrodinium sp.	**0.14**	**0.16**	**−0.18**	**−0.21**	**−0.18**	**−0.19**	**−0.17**	**−0.16**
Ophiaster hydroideus	**−0.03**	0.10						
Lioloma pacificum	**−0.10**							
Diploneis crabro	**−0.32**	**0.23**						
Nitzschia longissima	**−0.15**							
Pseudo–nitzschia seriata complex	**−0.43**			**0.19**				
Calciosolenia brasiliensis		**0.13**	**−0.13**		−0.10			
Calciosolenia murrayi	**−0.13**	**0.13**		**0.24**				
Emiliania huxleyi	**−0.49**	**0.19**	−0.10	**0.22**				
Dictyocha fibula	**−0.38**	0.12		**0.32**				
Octactis octonaria	**−0.21**	**0.17**		**0.18**				
Chaetoceros compressus								
Chaetoceros decipiens	**−0.21**							
Coscinodiscus sp.	**−0.22**	0.12		**0.24**				
Dactyliosolen fragilissimus			**−0.15**	−0.12			**−0.14**	−0.12
Guinardia flaccida	**0.14**	**0.13**	**−0.15**	**−0.14**	**−0.15**	**−0.15**	**−0.17**	**−0.10**
Guinardia striata		**0.18**	**−0.15**		**−0.14**	**−0.14**	**−0.14**	**−0.11**
Hemiaulus hauckii	**−0.32**		**−0.17**					

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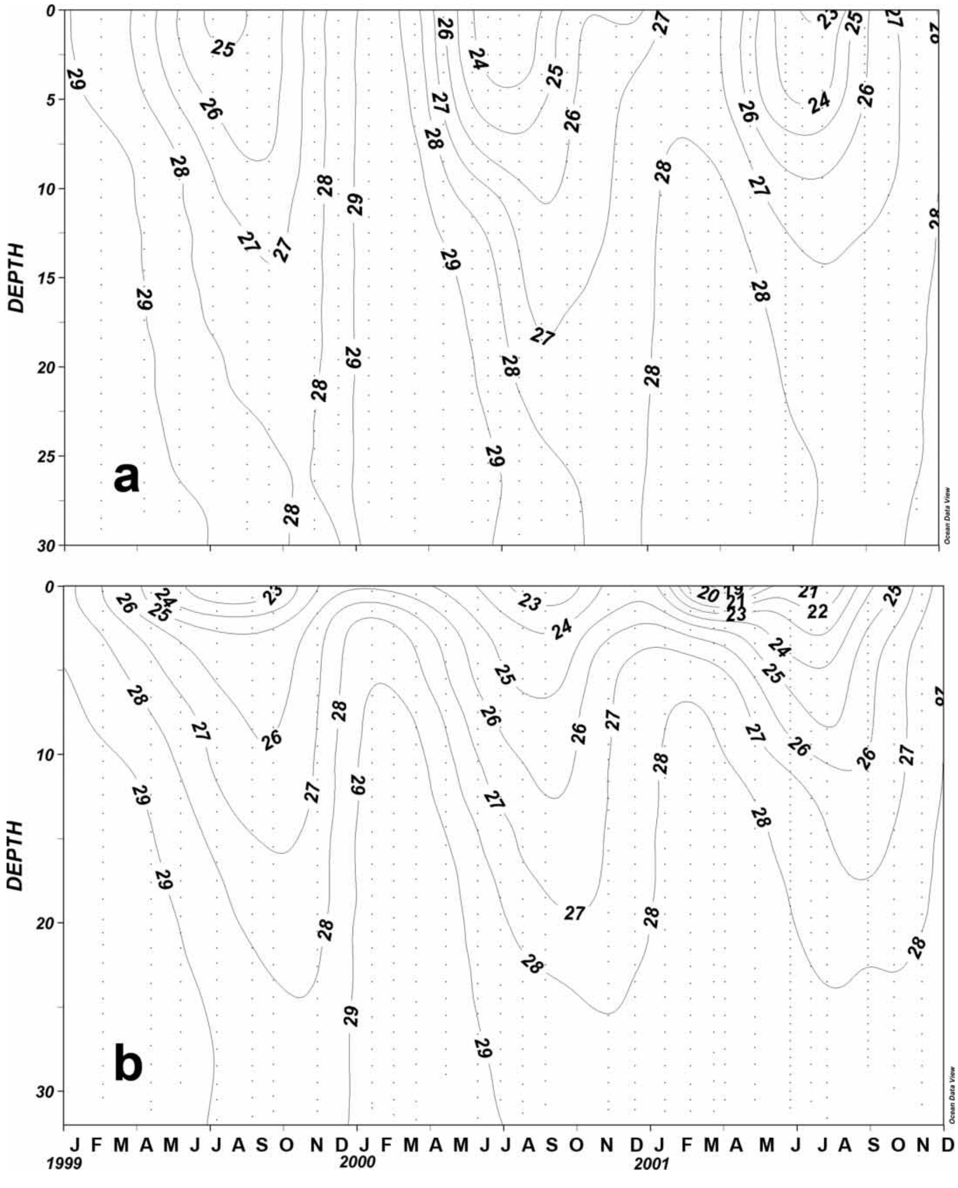

Figure 4. Temporal distribution of γ_t along depth at (a) st. C10 and (b) st. E06 in the three years of sampling.

comparison between the two stations (figures 5 and 6) also shows that most of the taxa (with the exception of *Prorocentrum minimum*) reached higher abundances at station E06, where the river plume influence is more pronounced, while the vertical pattern of both stations seems to be quite similar.

Keeping in mind the horizontal variability encountered in the Gulf of Venice, we have attempted to define a general phytoplankton seasonal pattern (figure 7). The phytoplankton seasonal cycle showed an abrupt peak in winter 2001 (from late January to the end of March) mainly due to the diatom *Skeletonema marinoi*, which was present at the coastal stations with bloom abundances. In this period, the highest yearly abundances for the whole basin were attained. Secondary peaks were then observed in spring, mainly due to the diatoms

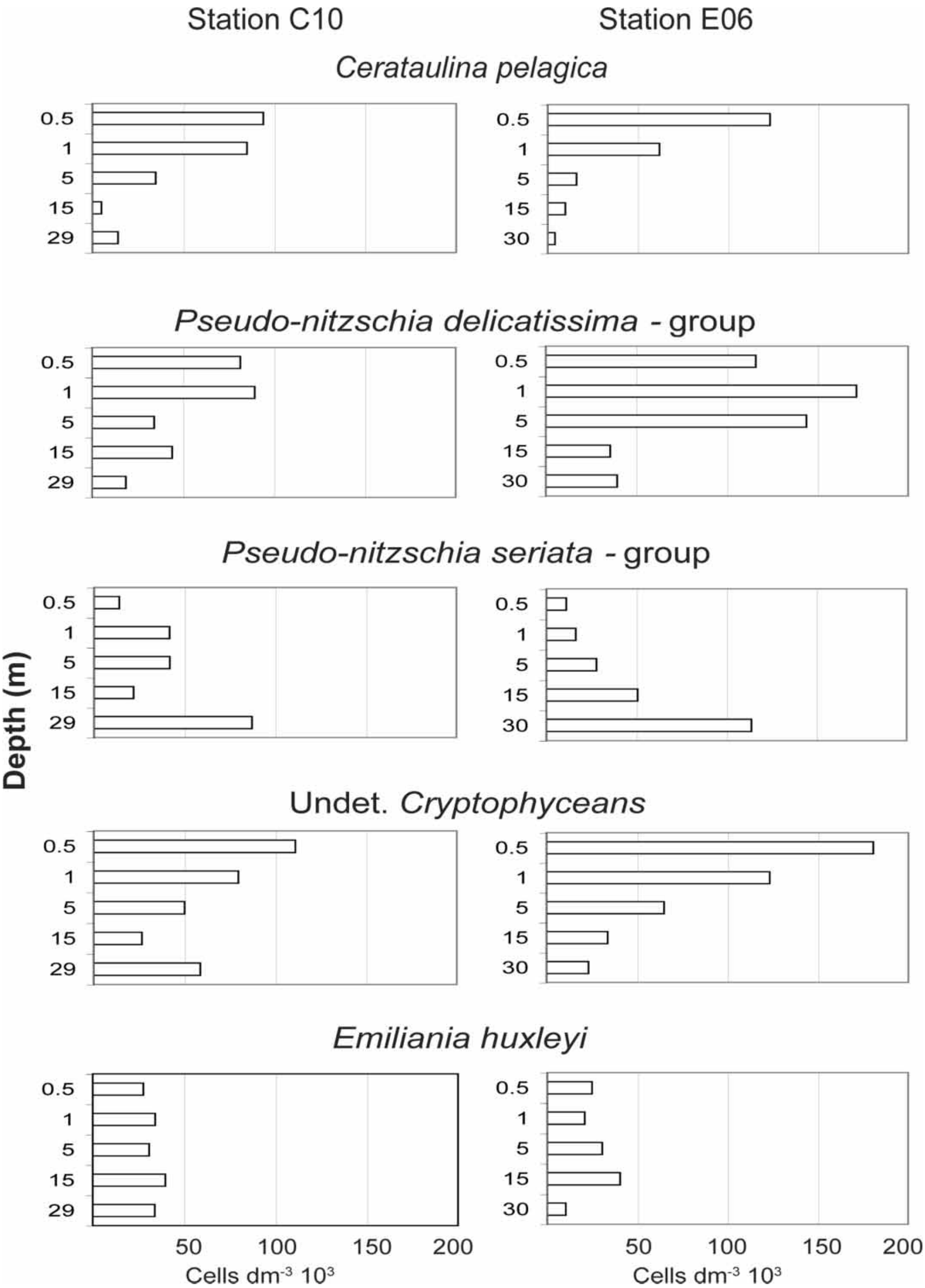

Figure 5. Vertical distributions of the abundance of selected species at stations C10 and E06. Abundance values represent the averages of the whole data set.

Pseudo-nitzschia spp. (April–May) and to small ($<$20 μm) dinoflagellates (e.g. *Gymnodinium* sp. and *Prorocentrum minimum*). During summer and early autumn (from July to October) the dominant species were *Cerataulina pelagica*, the *Pseudo-nitzschia delicatissima* group, and *Gymnodinium* spp. These species sporadically attained fairly high abundances and biomass

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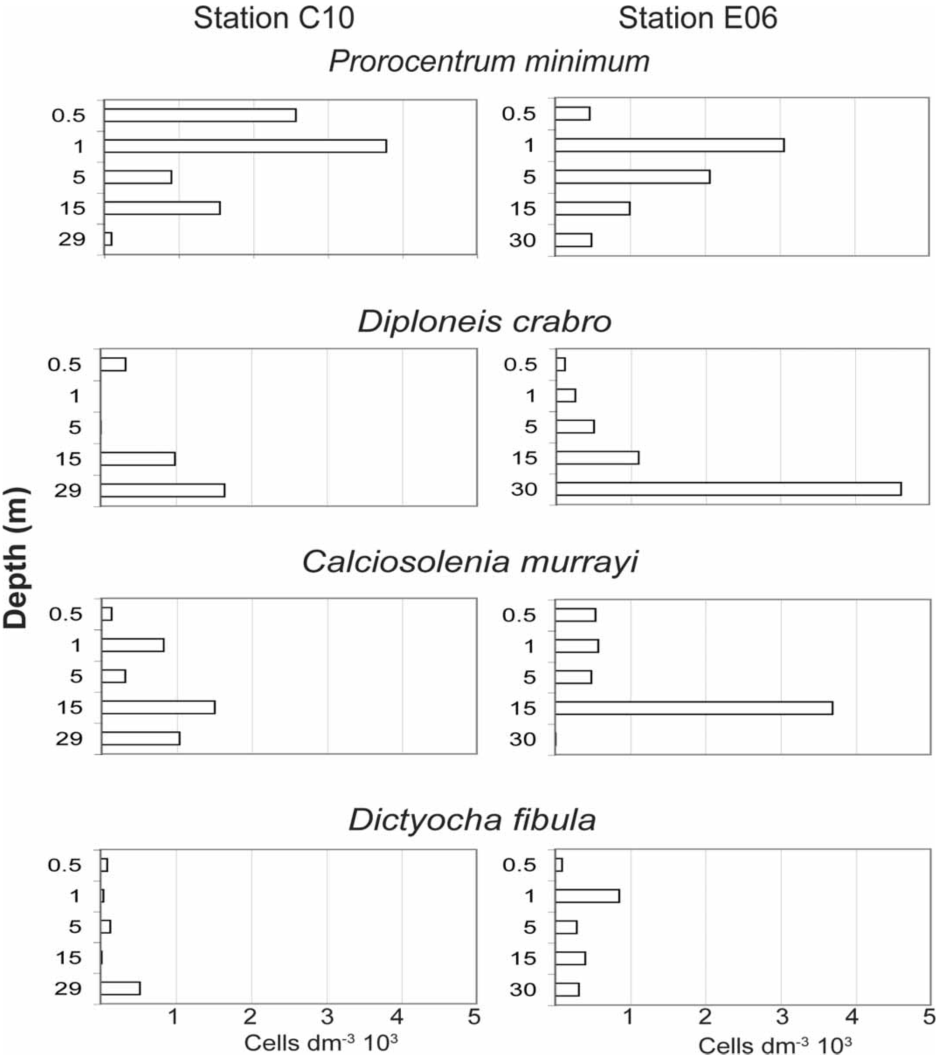

Figure 6. Vertical distributions of the abundance of selected species at stations C10 and E06. The abundance values represent the averages of the whole data set.

values. From autumn to winter, phytoplankton abundance progressively decreased down to the minimum values, generally recorded in December, when *Emiliania huxleyi* is the most important species.

The comparison among the three studied years was carried out, considering only the phytoplankton community of the surface samples of the station where the largest number of samples were gathered (st. C10, period February 1999–December 2001, 31 samples), in order to exclude the horizontal and vertical variability and to maximize the temporal variability. The statistical procedure was applied only to this station, since the number of samples from the other stations were less appropriate for a correct temporal analysis. The list of the phytoplankton species was reduced to the 40 most significant ones, and the undetermined nanoflagellates were not included, to avoid the background noise due to this heterogeneous and almost ever-present group.

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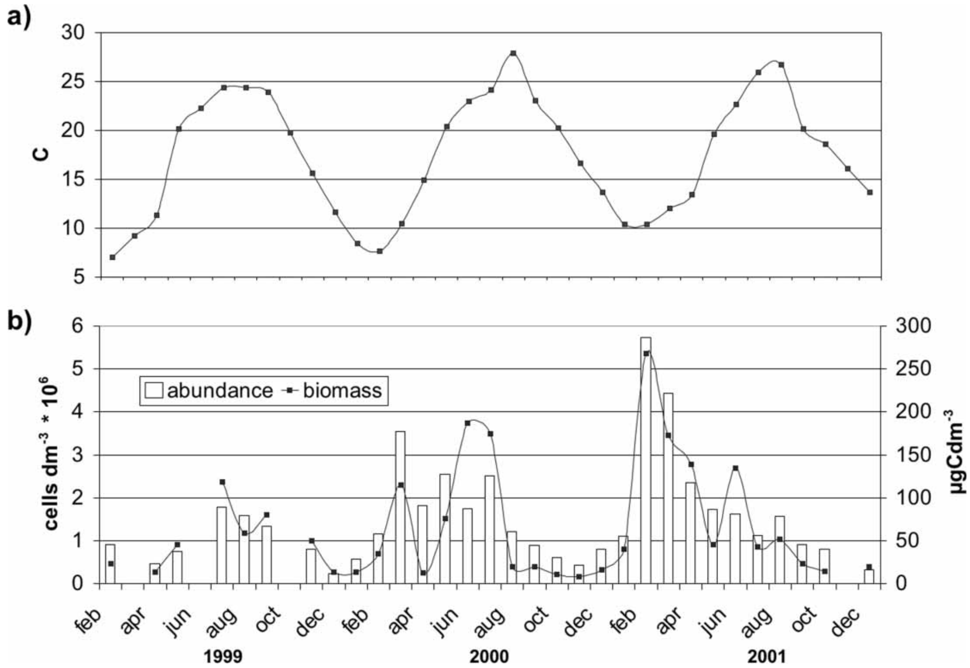

Figure 7. Temporal trend of (a) surface temperature and (b) total phytoplankton abundance and biomass: values represent the averages for the whole sampling area.

The cluster analysis (figure 8), obtained according to the Bray–Curtis similarity matrix (Q mode), evidenced five groups of samples, corresponding to seasonal periods common to the three years [39].

The Hellinger distance among the species abundance was then calculated [37], and hierarchical agglomerative clustering (R mode) was carried out. Six groups of taxa were singled out from the analysis of the dendrogram (figure 9). The species and the seasonal periods were then combined. The seasonal pattern that could be evidenced basically confirmed the average species succession described for the whole basin (see above). Based on this analysis, the phytoplankton composition and seasonal pattern did not change over the three years. However, some discrepancies between the univariate statistical analyses and the taxa dendrogram were found. For example, the spring taxa *P. minimum* and *Gymnodinium* spp. belonged to different clusters, as did the summer–autumn taxa *Cerataulina pelagica* and the *Pseudo-nitzschia delicatissima* group. This was probably a consequence of the different size of the set analysed; in fact most of the surface samples of station C10 ($n = 31$) belong to group 2 and represent a small fraction of the whole data set (441).

Comparing summer 2000, when large mucilage aggregates occurred, with summers 1999 and 2001, when only marine snow and microflocs were observed, no significant differences in the phytoplankton community structure could be found. A rich diatom community, mainly made up by the *Pseudo-nitzschia delicatissima* group, *Chaetoceros compressus*, and *Cerataulina pelagica*, characterized the phytoplankton composition during all three summers.

Instead, some differences in species composition were found following the Po River flood that occurred in October 2000: diatoms (in particular *Hemiaulus hauckii* and the *Pseudo-nitzschia seriata* group) displayed higher abundances in November and December 2000, after the Po river flood, in comparison with the same months of 1999 and 2001 (data not shown).

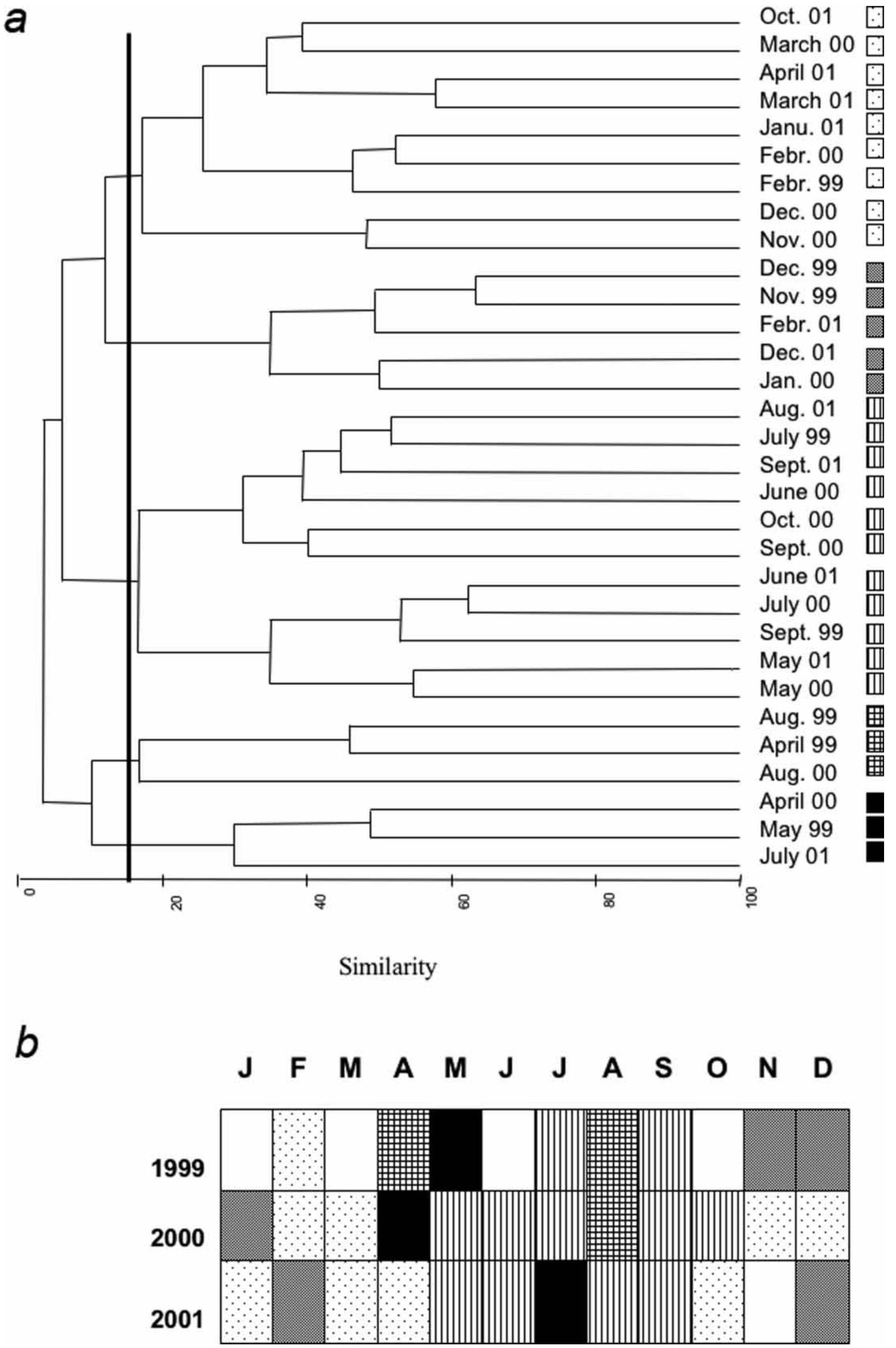

Figure 8. Station C10: dendrogram of 31 surface samples, obtained from a Bray–Curtis similarity matrix. At a cutoff value of 18, five distinct clusters were obtained, each assigned a different pattern; distribution of the five clusters of samples obtained from the dendrogram over the three years of sampling (b). The five patterns correspond to the five clusters of the dendrogramm. Missing samples are shown in white.

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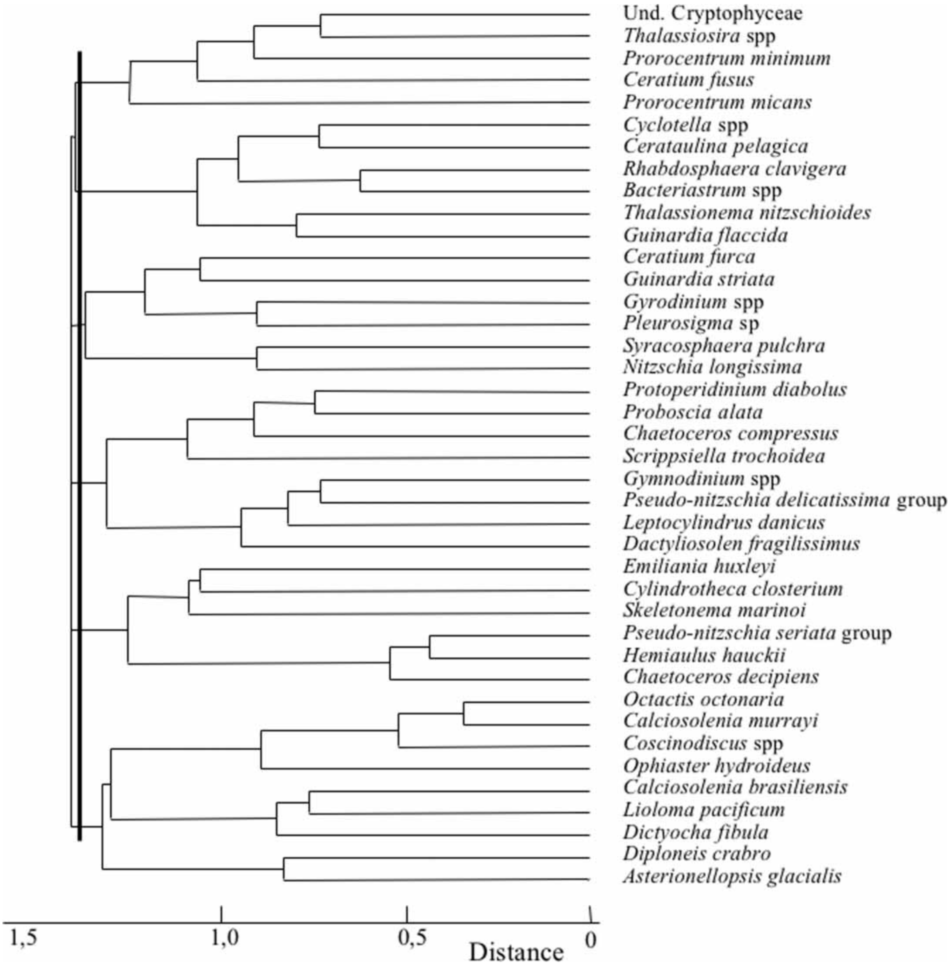

Figure 9. Dendrogram of 40 taxa (station C10, surface) obtained using the Hellinger distance.

4. Discussion

Plankton abundance and species composition in coastal and shelf waters are characterized by a high degree of spatial and temporal variability. The Northern Adriatic basin is a highly complex system in which the spatial distribution and the seasonal variations of the phytoplankton community are mainly driven by the river discharge and by the alternation of the stratification/mixing regime [1, 4]. High N/P ratios are typically found in the Northern Adriatic [4, 19, 40]; moreover, rapid variations of nutrient availability may occur, in relation to abrupt changes in the Po River discharge [3, 41].

In the present work, we have analysed the spatial (from the coastal belt up to 40 nautical miles offshore), seasonal and interannual variations of the phytoplankton community in the Gulf of Venice over a 3 year period. In this northwestern area of the Northern Adriatic Sea, the hydrological and trophic variability is particularly noticeable. A long-term study carried out only in the coastal belt of the Gulf of Venice [15] evidenced the complex interactions among hydrological, meteorological, and biological factors that may affect the temporal phytoplankton sequence. The ranges of abundance and biomass of phytoplankton varied about three orders of magnitude throughout this study (table 1). This high variability is typically reported for coastal and shelf waters [42]. Moreover, the high nutrient inputs in the Gulf of Venice enhance phytoplankton abundance which, as an average, are the highest among those reported for the Northern and Central Adriatic (figure 10).

The hydrological and trophic variability of the Gulf of Venice seems to affect mainly the phytoplankton abundance and biomass rather than the community composition. As already reported by other authors [9, 11, 15, 38, 45–47], the most abundant taxa are common both to the coastal and to the offshore area, and they only differ in their relative importance. However, several differences in the community composition along the trophic gradient were observed. Relatively small species, with a high S/V ratio, were typically found in areas influenced, permanently or sporadically, by the river inputs, where most of these species were nanoflagellates ($S/V = 2$), small diatoms (*Skeletonema marinoi* $S/V = 0.9$, *Thalassiosira* spp., and *Cyclotella* sp.) whose abundances showed negative linear relationships with salinity and positive relationships with nutrients, along with colonial species (*Asterionellopsis glacialis, Pseudo-nitzschia* spp., and *Cerataulina pelagica*) despite their large linear dimension. All these taxa can efficiently exploit nutrients and are characterized by inherently high grow rates [48].

In those periods and in those areas not or rarely affected by diluted riverine waters, relatively large-sized species (more than 1000 μm^3), having low S/V and/or low growth rates may be of considerable importance. Among these are the diatoms *Proboscia alata* ($S/V = 0.5$), *Lioloma pacificum*, the dinoflagellates *Prorocentrum minimum* ($S/V = 0.4$), *Ceratium fusus*, and the silicoflagellates *Dictyocha fibula* and *Octatis octonaria.* Some small coccolithophorids, e.g.

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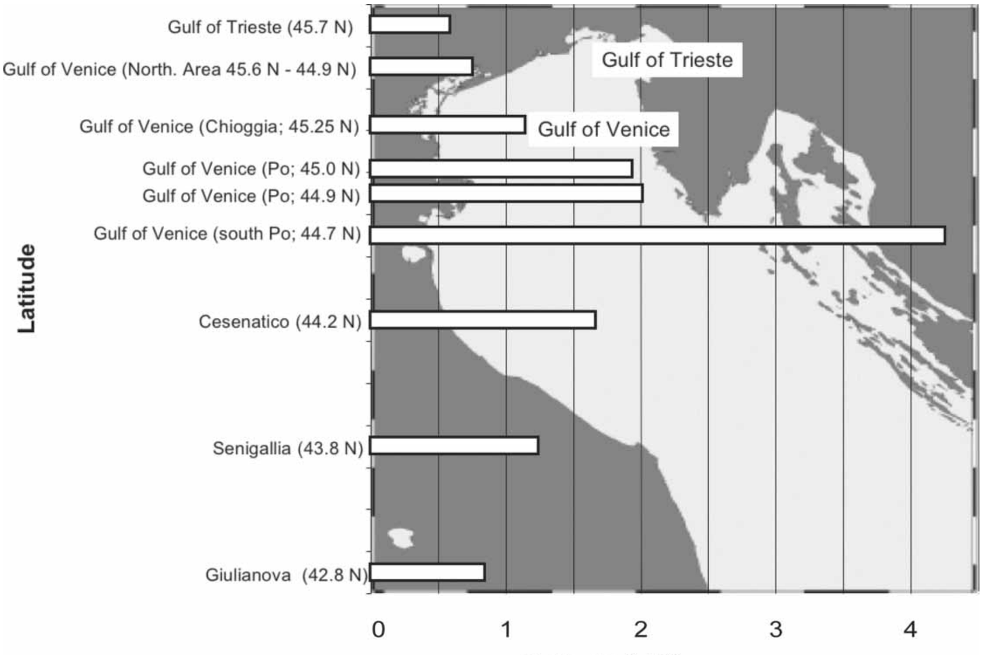

Figure 10. Mean phytoplankton abundance in different areas of the Northern Adriatic Sea. Comparison among the Gulf of Trieste (years 1999–2001 [43]), a northern area of the Gulf of Venice (from [36]; year 1989), Gulf of Venice (this study, transects C, E, and 2E, years 1999–2001); Northern Adriatic and Central Adriatic (transect Cesenatico-Capo Promontore; transect Senigallia-Sansego; years 1999–2002 [7]); Central Adriatic (transect Giuliano-Sebenic [44]).

Calciosolenia murrayi and *Emiliania huxleyi*, can also be found in association with these species.

The vertical distribution of the phytoplankton was analysed at two stations that can be considered as representative of the prevailing hydrological conditions of the area [18–20]. In the stratified period, the species composition in the surface layer was representative of the most productive and abundant population, with the deeper layer populations being either very similar to the surface populations or scarce. On the contrary, during periods of decreasing the thermocline, mainly occurring in August–September, deep populations might become segregated and show a different composition and/or a higher abundance compared with surface populations. Taxa linked to highly saline waters, such as *Emiliania huxleyi* and silicoflagellates [15, 49], or diatoms with a prevalent benthic life history (e.g. *Nitzschia longissima* and *Diploneis crabro* [50]) typically show this kind of distribution. The deep communities are used to survive at low irradiance, which however supplies sufficient energy especially in summer, when the river plume is scarce, and light attenuation in the water column is low. It is reasonable that these taxa may have specialized pigment adjustments, leading to an increase in intracellular chlorophyll concentration, as a physiological response to low irradiance [51, 52].

The average annual cycle of phytoplankton in the Gulf of Venice started with a winter bloom of *Skeletonema marinoi* that characterized mainly the stations close to the coast, although its presence could be detected in the whole study area, with a gradient of abundance decreasing from west to east. This diatom shows a marked seasonal behaviour in the Northern Adriatic [15, 47] and is usually responsible for the first and major annual bloom in the basin. A temporary vertical stratification, due to a freshwater surface layer over a mixed water column, in conditions of calm and sunny weather, and the increase in day length are the main environmental factors driving the temporal and spatial extension of this bloom. The winter bloom is also common to other seas, and it has been defined as the unifying feature for coastal phytoplankton in the Mediterranean [16].

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Minor phytoplankton peaks, with highly variable temporal and spatial extension, characterized the phytoplankton community from spring to summer in the Gulf of Venice. In this period, some blooms may occur sporadically, in relation to peculiar hydrological conditions and in restricted areas.

The seasonal dynamic of the phytoplankton in the spring–summer period is quite different from the late phases of the classical phytoplankton succession [53–56], which is known to require stable hydrological conditions: the mature stage of the community, characterized by the presence of large diatoms and dinoflagellates, is rarely attained in the Gulf of Venice, with this area being largely under frequent disturbance from nutrient inputs.

After the summer, the phytoplankton community in the Gulf of Venice shows a progressive decline until the winter minima are attained. In autumn, phytoplankton peaks are quite variable and do not appear related to the deepening of the thermocline, as typically observed at temperate latitudes [57, 58] but, rather, to the extent of the river inputs. In autumn 2000, the Po river flood was followed by a significant surface bloom of large pelagic diatoms, accompanied by a general increase in nutrients and primary production [19, 59].

One of the aims of this work was the evaluation of the inter-annual variability of phytoplankton seasonal pattern. The station considered for this analysis is located in the boundary area between the coastal zone and the offshore, and is sporadically influenced by the river inputs. With an acceptable approximation, it can be considered representative of the whole Gulf, because the phytoplankton seasonal pattern recorded here was similar to the average phytoplankton cycle detected in the whole area. The seasonal variations observed over the entire sampling period at this site did not reveal any significant differences among years. In particular, the taxonomic composition in summer was very similar among periods when large mucilage aggregates appeared and those in which the phenomenon was observed only at its early stage. The main recurrent taxa that are typical of the summer assemblages in the last 15 years [15, 47], such as *Cerataulina pelagica*, *Chaetoceros* spp., the *Pseudo-nitzschia delicatissima* group, and *Prorocentrum micans*, were also found in summer 2000, when the mucilage phenomenon occurred. Similar observations have also been reported for a southern area of the Northern Adriatic Sea, in the same period [7].

With the present study, although limited to three years, it was possible to recognize a seasonal cycle of the phytoplankton in the Gulf of Venice that is in good accordance with the results from other researches carried out in the past and in other areas of the Northern Adriatic Sea.

The Gulf of Venice is a site of intense oceanographic research: the phytoplankton community is still under study, and this time series will, therefore, be continued, giving the chance to improve the interpretation of the results presented here. It is in fact well known that long-term studies are necessary in order to detect regularities and trends in the phytoplankton succession and to evaluate their relations with large-scale processes and/or to local variability.

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