Looking for patterns in the phytoplankton community of the Mediterranean microtidal Venice Lagoon: evidence from ten years of observations

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SUMMARY: By analysing a ten-year series (1998-2007) of data on hydrochemical properties, phytoplankton abundance and species composition in the Venice Lagoon, we identified i) the average annual phytoplankton biomass cycle, mainly unimodal and fairly well tuned with the fluctuations in temperature and irradiance and (ii) the seasonal succession of the most important species, allowing us to construct a "phytoplankton calendar". Phytoplankton biomass was significantly lower in the second half of the ten-year period (2003-2007) than in the first half (1998-2002).

Keywords: phytoplankton community, multiannual variation, seasonal pattern, spatial variability, Venice Lagoon, Adriatic Sea.

RESUMEN: Búsqueda de patrones en la comunidad fitoplanctónica de una laguna micromareal (Laguna de Venecia): evidencias en diez años de observación. – A través del análisis de propiedades hidroquímicas, abundancia fitoplanctónica y composición de especies, en series de diez años (1998-2007), en la laguna de Venecia, se han identificado: i) Un promedio anual del ciclo de la biomasa prevalentemente de forma unimodal y bien sintonizada con las fluctuaciones de temperatura e irradiación; ii) Una composición cualitativa del fitoplancton que nos ha permitido realizar un "calendario del fitoplancton"; iii) Un decrecimiento en los últimos 5 años (2003-2007), de la biomasa con respecto a los 5 primeros años (1998-2003).

Palabras clave: comunidad fitoplanctónica, variación multi-anual, patrón estacional, variabilidad espacial, laguna de Venecia, Adriatico.

INTRODUCTION

The study of the seasonal phytoplankton cycle is crucial for identifying temporal shifts related to climate variability or local impacts. The annual phytoplankton cycle differs across aquatic ecosystems and patterns of biomass variation often do not closely follow annual climate change (Winder and Cloern 2010). A variety of phytoplankton seasonal cycles are found in transitional and coastal ecosystems (Cloern and Jassby 2008), so recognition of recurring spatial and temporal patterns often represents a challenging task. Some traits of these ecosystems, such as shallowness, close benthic-pelagic coupling and connectivity to both land and sea, affect phytoplankton composition and distribution on both spatial and temporal scales (Cloern and Jassby 2010). The complexity of these areas and the exposure of phytoplankton to the climate cycle and a range of local drivers explain the heterogeneity of annual fluctuations (Winder and Cloern 2010).

On the mesoscale at least, a small number of climatic factors may be recognized as the main drivers of the seasonal phytoplankton cycle in aquatic ecosystems such as open seas and large lakes. Here, the seasonal succession of phytoplankton species and biomass variation shows some regularities, which can be

more easily assessed than in transitional environments and even predicted in some cases. The phytoplankton community of transitional waters appears to be characterized by a pronounced degree of unpredictability, making it harder to define "baselines" against which to evaluate local vs large-scale changes as well as multi-annual trends (Edwards *et al.* 2010). The high noise-to-signal ratio and the multiple-process and multiple-scale regulation of phytoplankton complicates the task of detecting climate-driven trends. In this respect, the availability of multiannual ecological series, gathered with appropriate methods and on suitable scales of investigation, is a unique and invaluable tool.

The intrinsically high variability of phytoplankton communities in transitional environments should be taken into account not only because of phytoplankton ecological importance, the definition of community patterns being a critical question in ecology, but also because of the implications for environmental management. Indeed, phytoplankton is the only planktonic element included as a water quality indicator in the European Water Framework Directive (WFD 2000/60/EC). Some phytoplankton-related variables (composition, abundance, biomass, frequency and intensity of blooms) are essential for the definition and the classification of water quality.

The Venice Lagoon (Fig. 1) is the largest Italian lagoon and is included in the Italian Long Term Ecosystem Research network (LTER-Italy). Data on phytoplankton composition in the Lagoon date back to the 1970s (Voltolina 1975, Socal *et al.* 1985, Socal *et al.* 1987, Tolomio *et al.* 1999, Bernardi Aubry and Acri 2004, Acri *et al.* 2004, Socal *et al.* 2006). The phytoplankton assemblage is dominated by diatoms: neritic species, adapted to survival over large salinity ranges, and tychopelagic species, suspended due to hydrodynamics (Socal *et al.* 1985; Tolomio and Bullo 2001). Neritic species (dinoflagellates or coccolithophorids) are often introduced by saline waters at flood tide, whereas at ebb tide we find oligohaline species (chlorophyceans, euglenophyceans) in the inner areas of the Lagoon (Socal *et al.* 1987). Most studies have considered restricted areas of the Lagoon and only one-year cycles; repeated long-term observations only started in 1998. In transitional water ecosystems, primary producers are usually highly diversified, involving several functional levels and types (phytoplankton, benthic microalgae, aquatic angiosperms and macroalgae). At present, considering the whole basin, the bed of the Venice Lagoon appears to be dominated by seagrasses, particularly *Cymodocea nodosa* (Sfriso *et al.* 2005, Sfriso and Facca 2007). However, in some areas, phytoplankton is the main primary producer (Acri *et al.* 2004, Sfriso *et al.* 2005). The focus of the present paper is the analysis of a ten-year series (1998-2007) of monthly data on the phytoplankton community and the main related abiotic factors. Our main aim is to identify mesoscale phytoplankton patterns and trends in the Lagoon of Venice by considering: i) spatial variability, ii) seasonal dynamics, and iii) multiannual series.
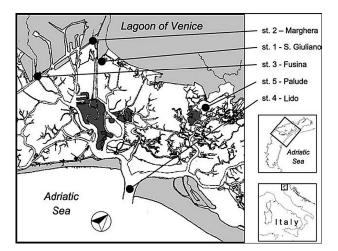

Fig. 1. – Venice Lagoon and five sampling stations.

MATERIALS AND METHODS

Study area and sampling strategy

The Lagoon of Venice (Fig. 1) is a large Mediterranean lagoon (550 km^2) in the northern Adriatic Sea. It is delimited by densely inhabited shores and industrial areas and is affected by high tourist flows, fisheries and aquaculture. It has an average depth of 1 m and is morphologically characterized by the presence of large shallow areas and a network of deeper (5-10 m) channels. It is separated from the Adriatic Sea by sandbars, which are interrupted by three inlets. Water turnover in the Lagoon is maintained by the tidal cycle through the inlets. Water circulation results from the interactions of tide, wind and topography (Solidoro *et al.* 2004, Gačić *et al.* 2005); water renewal ranges from a few days, close to the inlets, to one month in the inner areas (Solidoro *et al.* 2004, Cucco and Umgiesser 2006). The tidal amplitude is 100 cm, with maxima of 150 cm. The Lagoon can be classified as polyhaline. Twelve main tributaries discharge an annual average of about 35 m^3 s^{-1} of freshwater into the Lagoon with seasonal peaks in spring and autumn (ARPAV 2009) and the monthly maximum in November (55.5 m^3 s^{-1}; Zuliani *et al.* 2005). Nitrogen and phosphorus loading is of the order of 4000 t year^{-1} and 230 t year^{-1}, respectively (Collavini *et al.* 2005). The Venice Lagoon presents marked habitat heterogeneity and habitat classification is still a matter of debate (Tagliapietra *et al.* 2009).

For ten years monthly samplings were taken at five stations (120 monthly surveys in total from 1998 to 2007). These were selected so as to be representative of the natural and anthropogenic environmental variability of the northern and central basins of the Lagoon (Fig. 1), which are characterized by a complex interplay between freshwater and marine inputs (Cucco and Umgiesser 2006; Solidoro *et al.* 2004) and by anthropogenic impacts (Bianchi *et al.* 2003). The stations are located in areas where the presence of macrophytes is negligible

and most primary production is by phytoplankton (Acri *et al.* 2004, Sfriso *et al.* 2005). Station 1, S. Giuliano (depth 2 m), is an area of intense maritime traffic (Bianchi *et al.* 1996, Socal *et al.* 1999); it collects urban waste from the town of Mestre, and receives freshwater inputs from a small channel. Station 2, Marghera (depth 9.5 m), receives both seawater inputs, during the tide, from the Lido inlet, and fresh waters from a channel; it is also affected by pollutants of industrial origin (Perin 1975, Guerzoni *et al.* 2007). Station 3, Fusina (depth 3.5 m), is affected by both freshwater and marine inputs and by heat emissions from the Porto Marghera power station (Alberighi *et al.* 1992, Socal *et al.* 1999). Station 4, Lido (depth 7 m), is located in the northernmost inlet of the Lagoon under the direct influence of Adriatic coastal waters. Station 5, Palude (depth 2.7 m), is in an inland marshy area, a typical lagoon environment, influenced both by fresh waters entering from a channel and, to a lesser extent, by sea water carried by the tide (Bianchi *et al.* 1999). At every station measurements and samplings were performed at neap tide. Only the surface water layer was sampled, vertical phytoplankton distribution and the abiotic structure of the water column lying outside the scope of this study. The water column was assumed to be well mixed, irregular measurements carried out along the water column indicating negligible salinity and temperature differences between surface and bottom.

Measured variables

During each survey we measured transparency with Secchi disks; temperature, with a bucket thermometer; salinity, with a Guildline Autosal 8400B laboratory salinometer; dissolved oxygen, in accordance with Winkler's method (Strickland and Parsons 1972); dissolved nutrients including nitrogen as ammonium ($N-NH_4$), nitrites ($N-NO_2$) and nitrates ($N-NO_3$), phosphorus as orthophosphates ($P-PO_4$) and silica as orthosilicates ($Si-SiO_4$), all measured after filtering through Whatman GF/F glass fibre filters and analysed with a Systea-Alliance auto-analyser (Strickland and Parsons1972; Hansen and Koroleff 1999); chlorophyll *a* (chl *a*; Holm-Hansen *et al.* 1965), after filtering with Whatman GF/F filters and measurement of the acetone extract by Perkin Elmer LS5B spectrofluorometer before and after acidification; and phytoplankton, fixed in neutralized formalin with hexamethylentetramine, recognized and counted with an invertoscope (Uthermöhl 1958, Zingone *et al.* 2010). Species composition was mainly defined in accordance with Tomas (1997). Determinations for specific algal groups were also carried out with reference to Peragallo (1897-1908), Hustedt (1930-1966), Sournia (1986) and Hendey (1964) for diatoms; Schiller (1931-1937), Rampi and Bernhard (1980) and Sournia (1986) for dinoflagellates; Throndsen (1993) for dictyophyceans; Rampi and Bernhard (1981) and Heimdal (1993) for coccolithophorids; Throndsen (1993) for euglenohyceans; and Pascher (1915) for chlorophyceans.

Phytoplankton analysis was confined only to those forms that were detectable by light microscopy, so the phytoplankton fraction <3 μm (picophytoplankton) was not considered. The 'nanoflagellates' group included all the undetermined organisms whose sizes varied between 3 and 4 μm, consisting of cryptophyceans, chrysophyceans, prymnesiophyceans (except coccolithophorids), prasinophyceans, and chlorophyceans. Incident irradiance was obtained from the ISMAR–CNR meteorological archive.

Statistical analyses

Statistical analyses (ANOVA, Kruskall-Wallis, Mann-Whitney test and correlation analysis) were performed using Statistica by Statsoft Kernel release 5.5, after log-transformation of biological data (Cassie, 1962) to account for non-normal data distributions (Sokal and Rohlf 1981). We used a matrix composed of 216 taxa and 600 samples for describing spatial differences among stations and temporal (both seasonal and interannual) dynamics. We used the Shannon index (Shannon and Weaver 1949) to estimate phytoplankton biodiversity. This index increases with the number of species (with the above-mentioned qualifications regarding microscopic determination) and the evenness of their distribution. In order to analyse the spatial and temporal pattern of community structure, the original phytoplankton abundance data were used to produce data matrices and perform multivariate analyses using PRIMER 5.2.2 software. The multi-dimensional scaling (MDS) ordination method was used on the species-samples matrix, after a double square root transformation of abundance data (Clarke and Warwick 1994; Carr 1996).

Redundancy analysis (RDA; CANOCO 4.53 software) was used to identify relations between phytoplankton taxa and environmental variables. RDA is an extension of multiple regression and it is used when there is more than one response variable (here, the taxa). RDA was used to analyse the environmental and biological data together, with taxa ordination related to a combination of environmental variables (Legendre and Legendre 1998). Within this analysis, the relative proximity of samples, or averaged groups of samples, reflects relative similarity in species composition. The environmental variables are represented by vectors: their length indicates the magnitude of the correlation between the environmental variables and the phytoplankton species. The most characteristic species or species assemblages of each group of samples (stations, seasons, years or samplings) were considered to be "indicator species". These were identified using INDVal 2.0 software (http://biodiversite.wallonie.be/outils/indval/), considering those species or assemblages that were found mostly in a single group or at the majority of the sites belonging to that group (Dufrêne and Legendre 1997). For each species *i* in each group of sites *j*, we derived IndVal$_{ij}$ from A$_{ij}$ (the mean

abundance of species i in the sites of group j) and B_{ij} (the relative frequency of occurrence of species i in the sites of group j) as follows:

$$A_{ij} = \text{N individuals}_{ij}/\text{N individuals}_i;$$
$$B_{ij} = \text{Nsites}_{ij}/\text{Nsites}_j;$$
$$\text{IndVal}_{ij} = A_{ij} \, B_{ij} \times 100$$

where IndVal is the Indicator Value of species i in site cluster j. The statistical significance of the species indicator values was assessed using a randomization procedure. The species that best characterize each group are those with the highest IndVal.

Spatial variability

In order to provide a clearer picture of the study area, the sampling sites were aggregated into Zones of Similar Influence (ZSIs; Boyer *et al.* 1997) based on cluster analysis of the main hydrochemical parameters: temperature, salinity, DIN as a sum of $N-NH_4$, $N-NO_2$ and $N-NO_3$, $P-PO_4$, $Si-SiO_4$ and chl *a*. MDS analysis was then used to define spatial differences dependent on the qualitative composition of phytoplankton populations in the different sampling sites. The various ZSIs were compared using the Kruskall-Wallis non-parametric test, the key result of which is a *p* value that indicates whether groups of samples have the same median.

Temporal variability

RDA analysis was used to define temporal differences between phytoplankton populations in the different years or groups of years and to relate them to the main environmental parameters; values for phytoplankton species abundance and environmental variables were averaged for the stations sampled. We defined the seasonal categories as follows: winter (January-March), spring (April-June), summer (July-September) and autumn (October-December). For the interannual trends, we applied seasonal Kendall-τ non-parametric analysis to the whole data set using WQ2 software (release 2.0 by EQMetric, LLC and Virginia Tech Intellectual

Properties Inc.). This analysis determines the direction of trends (+ or −), goodness of fit (τ) and the statistical significance of fit (Boyer *et al.* 1999, Hirsch *et al.* 1991). The rate of change of each variable is quantified by the seasonal Kendall slope: the median (over all pairs of years for each month) of the change-per-year of each parameter (Theil 1950, Sen 1968). To compare different groups of samples (years), we performed the Mann-Whitney non-parametric test, the key result of which is a *p* value that indicates whether two groups of samples have the same median.

Bloom definition

"Blooms" were defined as cases dominated by a single species (abundance >50%) and chl *a* >10 µg l^{-1} (see also Sin *et al.* 1999, Gameiro *et al.* 2007), the latter corresponding to mean abundance of 23×10^6 cells l^{-1} (standard deviation 17×10^6 cells l^{-1}). The bloom frequency at each station, in each season and throughout the period was simply calculated as the ratio between the number of bloom samples and the total.

RESULTS

From a total of 600 phytoplankton samples we identified 216 distinct taxa belonging to 10 divisions: diatoms (141), dinoflagellates (40), chlorophyceans (21), coccolithophorids (10), chrysophyceans and euglenohyceans (4). Identifiable dictyophyceans, chlorophyceans, chryptophyceans, and prasinophyceans accounted for less than 4 taxa each; bearing in mind that most of the individuals from these divisions were unidentifiable at species level, in this study they were included in the group 'nanoflagellates'.

Diatoms and nanoflagellates dominated the community, accounting for 61% and 32% of abundance, respectively, while cryptophyceans, dinoflagellates, chlorophyceans and euglenophyceans accounted for 1% to 3%. All other taxa (coccolithophorids, dictiochophyceans, prymnesiophyceans) accounted for less than 1%, although they were abundant in some individual samples. A small number of species dominated the community: the "top ten" accounted for 88% of

TABLE 1. – List of "top ten" phytoplankton taxa recorded throughout study period at all stations, with average (whole dataset) abundance, standard deviations and relative and cumulative percentage of each taxon. Cumulative abundance is the sum of relative contribution of abundance of a single species.

	Species	Author	Abundance (cells l^{-1})	Standard deviation (cells l^{-1})	Abundance contribution (%)	Cumulative abundance contribution (%)
Diatoms	*Thalassiosira* sp.		897756	4412277	29.0	29.0
Diatoms	*Nitzschia frustulum*	Grunow 1862	505596	3690909	16.4	45.4
Diatoms	*Skeletonema marinoi*	Sarno and Zingone 2005	468276	1993843	15.1	60.6
Diatoms	*Cyclotella* sp.		259555	1795480	8.4	68.9
Diatoms	*Cylindrotheca closterium*	(Ehrenberg) Lewin and Reimann 1964	189563	1219608	6.1	75.1
Cryptophyceans	Und. Cryptophyceae		143521	388876	4.6	79.7
Diatoms	*Chaetoceros* sp.		92319	504805	3.0	82.7
Diatoms	*Navicula* sp.		68147	160299	2.2	84.9
Diatoms	*Chaetoceros compressus*	Lauder 1864	54183	570080	1.8	86.7
Diatoms	*Navicula cryptocephala*	(Kützing) Kützing 1844	35585	107255	1.2	87.8

TABLE 2. – Averages (AVG) and standard deviations (SD) for whole study period of main abiotic parameters Shannon index and phytoplankton biomass and abundance at each station.
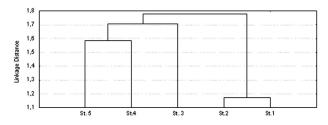
	Station 1 San Giuliano		Station 2 Marghera		Station 3 Fusina		Station 4 Lido		Station 5 Palude	
	AVG	SD	AVG	SD	AVG	SD	AVG	SD	AVG	SD
Temperature (°C)	16.2	7.9	18.0	6.8	22.4	5.4	16.4	7.0	15.5	8.1
Salinity	23.77	5.51	30.03	2.26	29.60	2.87	33.76	2.29	26.91	4.55
N-NH$_4$ (µM)	18.01	12.80	16.74	12.55	13.70	7.80	4.08	3.79	9.32	6.48
N-NO$_2$ (µM)	2.12	1.35	1.80	0.97	1.48	0.68	0.70	0.66	1.43	0.82
N-NO$_3$ (µM)	41.93	33.51	32.53	22.00	37.66	21.16	16.21	12.73	38.55	34.60
DIN (µM)	62.06	41.35	51.07	31.60	52.84	23.92	20.99	14.15	49.30	37.64
SI-SIO$_4$ (µM)	51.84	34.52	30.09	31.05	32.75	24.47	21.81	32.62	48.85	44.25
P-PO$_4$ (µM)	1.52	1.00	1.09	0.96	1.02	0.48	0.13	0.12	0.36	0.47
Shannon (bit)	0.72	0.27	0.61	0.28	0.76	0.26	0.79	0.22	0.82	0.22
Chlorophyll a (µg l^{-1})	12.66	19.68	9.47	14.48	3.38	4.56	2.28	4.59	4.37	9.34
Total phytoplankton Abundance (cells l^{-1})	8444779	14821876	7475161	11818155	2671208	4060586	1618115	2280961	3060024	5178748
Diatoms (cells l^{-1})	5855717	12070027	4513282	9494444	1384491	2385960	640005	1113899	1748657	4012019
Dinoflagellates (cells l^{-1})	97637	336745	146527	738125	37127	95888	50754	117055	26982	55700
Coccolitophorids (cells l^{-1})	2576	8037	3104	13676	5618	33161	23424	68486	4019	11990
Cryptophyceae (cells l^{-1})	122576	281929	226174	415833	55694	95190	181320	611632	149205	371411
Chrysophyceae (cells l^{-1})	326	3510	4408	46405	0	0	339	1759	0	0
Chlorophyceae (cells l^{-1})	42113	209973	25465	131144	113243	649804	2239	16083	16372	59112
Euglenophyceae (cells l^{-1})	122769	971318	38793	93201	3759	16170	3412	20183	5147	30968
Prasinophyceae (cells l^{-1}))	3819	23470	10880	49614	1039	6781	2170	8972	3530	20956
Prymnesiophyceae (cells l^{-1})	141	1517	831	9023	0	0	465	5005	0	0
Dictyochophyceae (cells l^{-1})	0	0	91	992	431	4659	79	483	0	0
Nanoflagellates (cells l^{-1})	2141949	4244353	2505606	5586118	1069809	2188504	713910	933176	1105607	1564852
Cyanophyceae (cells l^{-1})	55157	581651	0	0	0	0	0	0	506	3917

FIG. 2. – Cladogram identifying three Zones of Similar Influence (ZSI) based on environmental parameters (temperature, salinity, nutrients) and chl a.

cumulative abundance (Table 1), while fewer than 60 species accounted for 99%.

Habitat heterogeneity and phytoplankton spatial variability

Phytoplankton was sampled across a wide range of environmental conditions (Table 2), as demonstrated by the variability of temperature (0.6°C to 29.9°C), salinity (8.6-37.1) and nutrients (DIN 1.2-243.9 µM; Si-SiO$_4$ 1.7-294.2 µM; P-PO$_4$ 0.01-7.9 µM).

TABLE 3. – Kruskall-Wallis test of abiotic parameters and chl a, highlighting differences among three ZSIs (N, number of samples).

	St. 1-2	St. 3	St. 4-5	p level
Salinity	28.35	30.12	31.36	0.01
Temperature (°C)	18.35	24.15	16.55	0.01
DIN (µM)	47.73	49.43	27.37	0.01
Si-SiO$_4$ (µM)	31.8	23.63	21.05	0.01
P-PO$_4$ (µM)	1.1	0.91	0.14	0.01
Chl a (µg l^{-1})	3.81	1.75	1.49	0.01
N	240	120	240	

Based on the main abiotic parameters (temperature, salinity, DIN as a sum of N-NH$_4$, N-NO$_2$ and N-NO$_3$, P-PO$_4$, and Si-SiO$_4$) and chl a, the five sampling sites were aggregated into three ZSIs (Fig. 2).

The highest phytoplankton biomass and the lowest salinity were found at stations 1 and 2, station 3 had the highest temperature, and stations 4 and 5 relatively low nutrient concentrations (Si-SiO$_4$, P-PO$_4$ and DIN, Table 3). In contrast, phytoplankton species composition at the five stations did not exhibit significant differences (Fig. 3). From the qualitative point of view, the most abundant species appear to be largely shared by all stations. Indeed, as indicated by IndVal analysis (Table 4), the differences between the stations are mainly due to: 1) marked dissimilarities in the abundance and frequency of a pool of taxa common to all stations (see "top ten", Table 1 and Table 4); and 2) the presence of specific taxa that are associated, albeit to different degrees, with individual stations (Table 4). Considering this last group, station 4 is mainly typified by a marine community, with species that are also found in the coastal waters of the northern Adriatic Sea (Bernardi Aubry et al. 2004) but are usually infrequent inside the Lagoon: the diatoms *Proboscia alata, Pseudo-nitzschia delicatissima* and *Cerataulina pelagica,* the dinoflagellates *Gyrodinium* sp. and the coccolithophorid *Emiliania huxleyi.* Even rarer and exclusive or nearly exclusive to this station are the dinoflagellates *Neoceratium furca,* the diatom *Guinardia striata* and the coccolitophorids *Rhabdosphaera claviger, Syracosphaera pulcra* and *Calciosolenia murrayi.* Station 2 is characterized by a few flagellate species (nanoflagellates and dinoflagellates such as *Gymnodinium* sp.), the diatom *Skeletonema marinoi* and some species, such as *Eutreptia lanowii,* that typically inhabit fresh waters but

TABLE 4. – IndVal for "top ten" taxa (A) and other taxa (B): significant IndVal values are highlighted for each station.

	Station 1	Station 2	Station 3	Station 4	Station 5	p level
A)						
Thalassiosira spp.	**42.0**	30.0	9.0	1.2	2.7	0.003
Cylindrotheca closterium	**33.3**	3.6	5.8	2.1	7.3	0.007
Nitzschia frustulum	**17.7**	0.5	1.3	0.06	12.5	0.011
Skeletonema marinoi	5.6	**46.1**	6.6	0.8	0.2	0.000
Chaetoceros sp.	2.6	**11.1**	1.1	4.3	2.9	0.046
Und. Cryptophyceae	12.7	**27.1**	6.3	23.0	16.7	0.050
Cyclotella sp.	7.0	7.6	3.3	1.8	1.0	0.7
Chaetoceros compressus	0.02	3.1	0.2	4.1	0.04	0.127
Navicula sp.	33.7	3.9	11.7	2.9	**34.7**	0.000
Navicula cryptocephala	30.8	1.4	3.6	0.6	**35.5**	0.000
B)						
Und. Pennatae	**21.6**	0.9	4.1	0.7	5.6	0.001
Gyrosigma fasciola	**17.3**	0.01	0.09	0.02	1.6	0.000
Cocconeis sp.	**12.0**	0.5	4.1	2.4	8.8	0.014
Nitzschia conscricta	**9.9**	0.5	1.5	0.01	2.2	0.003
Gomphonema olivaceum	**6.7**	0.3	1.1	0.003	0.005	0.001
Gomphonema parvulum	**5.9**	0.02	1.5	0.04	0.1	0.003
Skeletonema marinoi	5.6	**46.1**	6.6	0.9	0.2	0.000
Nanoflagellates	28.1	**32.7**	13.9	9.6	14.5	0.002
Gymnodinium sp.	9.4	**20.8**	3.6	12.5	4.4	0.002
Eutreptia lanowii	12.8	**14.4**	0.1	0.06	0.05	0.000
Scenedesmus quadricauda	0.9	0	**8.2**	0.002	0.03	0.000
Aulacoseira granulata	0.03	0	**6.8**	0	0.2	0.000
Hermesinum adriaticum	0	0	**2.5**	0	0	0.005
Emiliania huxleyi	0.7	1.4	3.3	**33.3**	1.9	0.000
Cerataulina pelagica	0.005	0.2	0.5	**24.6**	0.1	0.000
Pseudo-nitzschia delicatissima	0.4	0.8	1.0	**23.8**	1.4	0.000
Proboscia alata	0	0.05	0.02	**14.2**	0.07	0.000
Syracosphaera pulchra	0	0	0.006	**11.3**	0.6	0.000
Und. Coccolitophorids	0.4	0.7	0.3	**9.7**	0.1	0.000
Leptocylindrus danicus	0.07	0.9	0.03	**9.6**	0.1	0.000
Asterionellopsis glacialis	0.01	0.03	0.03	**9.0**	0.09	0.000
Prorocentrum micans	0.008	2.0	0.05	**7.9**	0.03	0.000
Chaetoceros decipiens	0	1.0	0.02	**6.5**	0.07	0.001
Gyrodinium sp.	0.9	0.01	0.4	**5.2**	0.06	0.008
Guinardia striata	0.09	0	0	**5.1**	0	0.001
Neoceratium furca	0	0	0	**4.1**	0	0.000
Rhabdosphaera claviger	0	0	0	**3.2**	0	0.005
Calciosolenia murrayi	0	0	0.03	**3.1**	0	0.006
Amphora sp.	21.8	2.7	8.1	2.4	**37.0**	0.000
Amphora exigua	12.2	1.7	2.0	1.1	**24.2**	0.000
Amphora coffaeformis	9.9	0.3	1.1	1.1	**20.3**	0.000
Cocconeis scutellum	16.7	1.5	6.3	0.9	**17.1**	0.003
Psammodictyon panduriforme	1.4	0.6	2.6	0.03	**15.5**	0.000
Halamphora veneta	2.5	0.8	1.4	0.8	**14.2**	0.000
Amphora hyalina	0.05	0	0	0	**12.7**	0.000
Licmophora gracilis	0.01	0	1.5	0.03	**7.4**	0.000
Amphora lineolata	0.01	0	0.04	0	**7.1**	0.000
Amphora laevissima	0	0	0	0	**5.7**	0.000

are also fairly widespread in coastal waters. Freshwater species (the diatom *Aulacoseira granulata* and the chlorophycean *Scenedesmus quadricauda*) characterize station 3. Benthic-resuspended diatoms (e.g. *Halamphora exigua*, *Amphora coffaeformis*, *Cocconeis scutellum*, *Cocconeis* sp., *Cylindrotheca closterium*, *Navicula* spp., *N. cryptocephala*, *Nitzschia frustulum*, *Psammodictyon panduriforme*) are mainly found at stations 1 and 5, probably as a result of their shallow depth, which allows close benthic-pelagic coupling.

Of the taxa common to all stations, some, mainly diatoms, give rise to recurrent phytoplankton blooms. The blooming species are prevalently small, often colonial, and include *Chaetoceros compressus*, *Chaetoceros* spp., *Cylindrotheca closterium*, *Nitzschia frustulum*, *Skeletonema marinoi* and *Thalassiosira* spp. Blooms
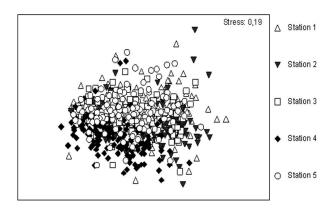

FIG. 3. – MDS plot from the matrix of 216 species and 600 phytoplankton samples; five stations are indicated by different symbols.

TABLE 5. – A) Common species among seasonal groups; species with highest IndVal values, although not significant (n.s.), are highlighted; B) Indicator species recorded in the seasonal groups. Significant IndVal values are highlighted;

	Autumn	Winter	Spring	Summer	p level
A)					
Dactyliosolen fragilissimus	**1.225**	0.008	0.964	0.216	n.s
Diploneis crabro	**1.599**	0.535	1.527	0.007	n.s
Psammodictyon panduriforme	**4.659**	0.953	3.469	3.217	n.s
Nitzschia sigma	**2.222**	0.555	0.583	1.576	n.s
Thalassionema nitzschioides	**7.659**	2.556	2.842	4.475	n.s
Syracosphaera pulchra	**3.364**	0.346	0.191	1.002	n.s
Asterionellopsis glacialis	1.806	**1.946**	0.094	0.266	n.s
Chaetoceros decipiens	1.171	**1.732**	0.443	0.162	n.s
Gomphonema olivaceum	0.749	**2.325**	1.772	0.08	n.s
Gomphonema parvulum	1.15	**1.486**	0.402	0.748	n.s
Fallacia forcipata	0.347	**2.596**	0.121	0.077	n.s
Luticola mutica	0.829	**3.838**	2.649	0.036	n.s
Pleurosigma normanii	2.878	**7.743**	2.323	4.731	n.s
Pseudo-nitzschia delicatissima	0.567	**7.070**	3.265	6.609	n.s
Skeletonema marinoi	0.417	**16.630**	15.404	14.126	n.s
Synedra affinis	0.678	**2.199**	0.126	0.939	n.s
Emiliania huxleyi	7.905	**13.505**	2.513	3.658	n.s
Nitzschia conscricta	2.594	**2.788**	0.778	2.781	n.s
Nitzschia longissima	0.096	**2.210**	1.016	0.587	n.s
Amphora coffaeformis	6.542	4.414	**10.251**	2.518	n.s
Amphora exigua	6.025	7.243	**11.136**	6.347	n.s
Cerataulina pelagica	0.044	0.178	**7.066**	3.544	n.s
Cocconeis placentula	1.238	1.294	**4.343**	0.284	n.s
Cocconeis scutellum	10.758	6.367	**14.201**	4.447	n.s
Licmophora gracilis	0.698	0.911	**2.671**	0.098	n.s
Nitzchia longissima f. parva	0.32	0.13	**3.815**	0.042	n.s
Rhoicosphenia abbreviata	0.784	1.615	**4.565**	0.044	n.s
Nitzschia palea	0.01	0.035	**1.389**	0.618	n.s
Leptocylindrus danicus	1.047	1.747	0.236	**2.346**	n.s
Leptocylindrus minimus	0.122	0.111	0.245	**0.335**	n.s
B)					
Halamphora veneta	**10.891**	1.879	2.925	1.663	0.01
Calciosolenia murrayi	**3.378**	0	0	0	0.01
Melosira nummuloides	0.148	**9.707**	0.18	0.012	0.01
Pseudo-nitzschia fraudolenta	0.084	**7.819**	0.123	0.093	0.01
Pseudosolenia calcaravis	0	**0.704**	0	0	0.01
Navicula cryptocephala	2.884	20.716	**22.377**	9.374	0.05
Prorocentrum minimum	0.047	2.654	**16.394**	2.765	0.01
Eutreptia lanowii	1.251	0.705	**13.558**	1.44	0.01
Chaetoceros tenuissimus	0.211	0.017	**6.460**	0.81	0.01
Prorocentrum micans	0.492	0.004	**6.433**	0.89	0.01
Entomoneis paludosa	0.019	0.031	**2.845**	0	0.01
Cylindrotheca closterium	0.265	0.891	7.259	**58.209**	0.01
Nitzschia frustulum	0.351	0.015	2.923	**41.034**	0.01
Chaetoceros compressus	0.002	0.302	0.62	**7.123**	0.01
Proboscia alata	0.006	0.003	0.897	**7.025**	0.01
Scrippsiella trochoidea	0.466	0.553	4.313	**6.637**	0.05
Protoperidinium bipes	0.006	0.146	0.112	**6.298**	0.01
Scenedesmus quadricauda	0.027	0.054	1.617	**3.703**	0.05
Guinardia flaccida	0.012	0	0	**1.889**	0.05

occur throughout late winter and summer (93% from March to September). From March onwards, diatoms bloom most frequently at stations 1 and 2. At station 2 *Skeletonema marinoi* was the main blooming species throughout the period. At station 1 the late winter *S. marinoi* bloom is followed by other blooms of species such as *Cylindrotheca closterium, Thalassiosira* spp. and *Nitzschia frustulum* in spring and summer. The blooms at stations 3 and 5 are much less frequent and intense. They are observed only in summer and are associated with nanoflagellates (undetermined forms) at station 3 and the tychopelagic diatom *Nitzschia frustulum* at station 5. At least by our definition, blooms are not recorded at station 4.

The highest average Shannon index values (Fig. 4) are seen in ZSI 4-5. Indeed, at station 5 the community is the richest in benthic taxa (46%), and at station 4 the phytoplankton community is characterized by the lowest frequency of a single dominant species.

Seasonal phytoplankton patterns (Table 5)

The seasonal chl *a* pattern appears fairly uniform across all stations (Fig. 4), differing in the maximum values attained rather than in timing. The highest biomass was always recorded from May to September, with the maximum in July and a decrease in winter. The highest chl *a* values (with a peak of 124.6 µg l^{-1} in
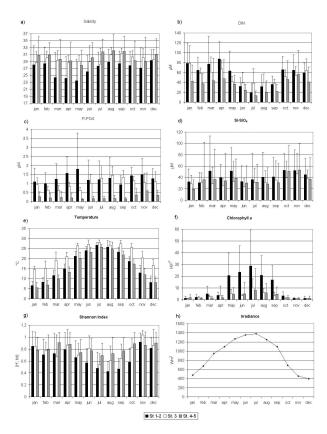
FIG. 4. – Average (bars) temporal variation and standard deviations (whiskers) at three ZSIs, of a) salinity, b) DIN, c) P-PO$_4$, d) Si-SiO$_4$, e) temperature, f) chl *a*, g) Shannon index; h) incident irradiance at the common measurement point.

FIG. 5. – Multiannual variations of: a), temperature b) salinity, c) DIN, d) Si-SiO$_4$, e), P-PO$_4$ f) chl *a*, g) phytoplankton abundance, h) transparency. All the data are considered. In each graph the moving average and the trend are shown.

July 2001, at station 1) were attained in the ZSI with the highest nutrients (stations 1 and 2). However, at all stations the seasonal pattern of phytoplankton growth appears to be more closely related to temperature and solar irradiance than to nutrients (Fig. 4). Among nutrients we detected a clear seasonality only for DIN, with the lowest concentration in summer at every station (Fig. 4). In consideration of these general features and the common distribution of the most important taxa, described above, in this section we analyse an average seasonal cycle of the main abiotic factors, phytoplankton biomass (Fig. 4) and phytoplankton composition (IndVal analisys, Table 5).

Winter is characterized by lower temperatures, relatively low phytoplankton biomass and fairly high DIN concentrations. Phytoplankton is represented mainly by diatoms (59% of total abundance), both benthic (*Nitzschia* spp. *Gomphonema* spp., *Fallacia forcipata, Luticola mutica, Pleurosigma normanii*) and planktonic (*Pseudo-nitzschia* spp., *Skeletonema marinoi*), followed by nanoflagellates (32%); coccolithophorids attain their peak (1%) mainly with *Emiliania huxleyi*. At the end of the winter, increased daylight hours and temperatures enhance phytoplankton growth. In March diatoms grow rapidly, with *Skeletonema marinoi* (on average 1.2×10^6 cells l^{-1}, 48% of total abundances) typically blooming from
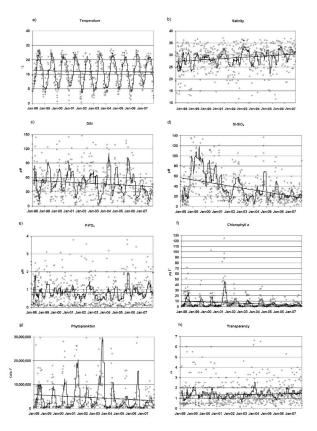
February to March not just in the Lagoon but also in the adjacent waters of the Adriatic Sea (Mozetič *et al.* 1998; Bastianini *et al.* 2004; Bernardi Aubry *et al.* 2006). Spring is characterized by fairly low salinity due to increased river discharge and precipitations (ARPAV 2009). A mixed community of flagellates (nanoflagellates, cryptophyceans, the dinoflagellates *Prorocentrum micans and P. minimus*) and euglenophyceans (e.g. *Eutreptia lanowii*) dominates (54%), together with diatoms (44%), both pelagic (e.g. *Cerataulina pelagica)* and benthic (e.g. *Navicula* spp. or *Amphora* spp., *Cocconeis* spp.). Summer sees the highest temperature and salinity and the lowest nutrient levels due to low river discharge (ARPAV 2009) and high phytoplankton uptake. In this period phytoplankton biomass peaks (average chl *a*: 12.6 µg l^{-1}). Diatoms prevail (73%), often giving rise to blooms, mainly with *Thalassiosira* spp., *Cylindrotheca closterium* and *Nitzschia frustulum*. Dinoflagellates are more frequent and abundant (2%) than in the other seasons, with *Scrippsiella trochoidea*, *Gymnodinium* spp. and *Protoperidinium bipes*. A drop in phytoplankton abundance and biomass accompanies the lower temperature and irradiance in autumn, despite increased nutrient availability. A mixed assemblage of flagellates (46%) and diatoms (40%), mainly benthic species such as *Halamphora veneta*, undeter-

TABLE 6. – Seasonal Kendall test of the main abiotic parameters and phytoplankton biomass and abundance at three ZSIs: τ values, significance of trend (*p*) and seasonal Kendall slope estimates (S.E.) in units yr^{-1} are shown. Statistically significant τ values are in bold.

	Station 1-2			Station 3			Station 4-5		
	τ	*p*	S. E.	τ	*p*	S. E.	τ	*p*	S. E.
Temperature (°C)	–0.04	0.53	–0.05	0.07	0.29	0.10	–0.02	0.66	–0.02
Salinity (PSU)	**0.19**	0.04	0.19	**0.32**	0.01	0.31	**0.32**	0.01	0.37
DIN (µM)	–0.19	0.10	–1.75	**–0.31**	0.02	–2.42	**–0.26**	0.03	–1.90
P-PO$_4$ (µM)	–0.02	0.85	–0.01	0.02	0.83	0.00	–0.08	0.17	0.00
Si-SiO$_4$ (µM)	**–0.33**	0.03	–3.43	**–0.37**	0.02	–2.15	**–0.47**	0.01	–4.04
Chlorophyll *a* (µg l^{-1})	–0.21	0.06	–0.22	–0.26	0.10	–0.07	–0.20	0.15	–0.07
Phytoplankton (cells l^{-1})	–0.15	0.31	–56656	–0.25	0.11	–58953	–0.18	0.20	–63054

FIG. 6. – Ordination of phytoplankton data (yearly average for each station), showing differences between the periods 1998-2002 (open circles) and 2003-2007 (full squares).

FIG. 7. – Yearly averages of chlorophyll peaks in "bloom samples".

2007), mainly related to higher nutrient concentrations, lower salinity and chl *a* peaks in "bloom samples" in the more recent period (Fig. 7).

The medians of the two periods (Mann-Whitney test) were found to be significantly different for phytoplankton abundance, chl *a* and the main abiotic parameters (Table 7). The significantly lower chl *a* in

TABLE 7. – Mann-Witney test. Medians of "top ten" taxa abundance, chl *a*, diatoms, dinoflagellates, total abundance and main abiotic parameters and nutrient ratios in periods 1998-2002 (I) and 2003-2007 (II); (n.s., not significant).

	I	II	p level
Thalassiosira sp. (*10^6; cells l^{-1})	51.694	32.438	n.s.
Nitzschia frustulum (*10^6; cells l^{-1})	15.265	10.659	n.s.
Skeletonema marinoi (*10^6; cells l^{-1})	32.107	11.533	0.01
Cyclotella sp. (*10^6; cells l^{-1})	16.557	13.983	n.s.
Cylindrotheca closterium (*10^6; cells l^{-1})	36.058	17.699	n.s.
Und. Cryptophyceae (*10^6; cells l^{-1})	56.108	28.967	0.01
Chaetoceros sp. (*10^6; cells l^{-1})	16.639	5.869	0.05
Navicula sp.(*10^6; cells l^{-1})	48.809	28.831	0.01
Chaetoceros compressus (*10^6; cells l^{-1})	4.773	0.501	0.01
Navicula cryptocephala (*10^6; cells l^{-1})	39.302	15.885	0.01
Chlorophyll a (µg l^{-1})	2.62	1.46	0.01
Diatoms (*10^6; cells l^{-1})	0.60	0.30	0.01
Dinoflagellates (*10^6; cells l^{-1})	0.01	0.02	n.s.
Total Phytoplankton (*10^6; cells l^{-1})	1.64	0.98	0.01
Dinoflagellates/Diatoms	0.02	0.04	0.01
Salinity	28.86	30.66	0.01
Temperature (°C)	18.80	18.5	n.s.
Transparency (m)	1.0	1.2	0.01
N-NH$_4$ (µM)	12.09	7.8	0.01
N-NO$_3$ (µM)	28.11	24.81	0.05
N-NO$_2$ (µM)	1.55	1.12	0.01
DIN (µM)	43.87	36.6	0.01
P-PO$_4$ (µM)	0.60	0.63	n.s.
Si-SiO$_4$ (µM)	37.9	19.55	0.01
N/P	76.80	69.00	0.05
Si/N	0.80	0.50	0.01
Si/P	61.70	34.00	0.01

mined pennate diatoms or *Psammodictyon panduriforme*, prevails. This period is also characterized by coccolithophorids (e.g. *Calciosolenia murrayi* and *Syracosphaera pulcra*), always with low abundance but high frequency.

The highest Shannon index (Fig. 4) is seen in autumn, as a result of a relatively high amount of species with similar low abundance, and the lowest in summer when monospecific phytoplankton blooms occur.

Multiannual trends and interannual variability

We applied the Kendall-τ test to the abiotic parameters and chl *a* of each ZSI over the ten years. Statistically significant trends were detected only for salinity, which increased, and Si-SiO$_4$, which decreased, in each ZSI (Table 6). Decreasing trends of DIN, chl *a* and to a lesser extent phytoplankton abundance are apparent, albeit not statistically significant (Fig. 5 and Table 6).

The ordination of averaged samples (months for each year, Fig. 6) highlighted a separation between the cluster of samples belonging to the first five years (1998-2002) and that of the following five years (2003-
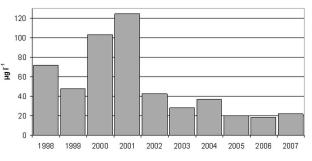
the more recent period appears mainly associated with the decrease in nutrients (DIN and Si-SiO$_4$,) and the increased salinity (Fig. 5 and Table 7). The increased salinity and transparency may be linked to decreased river discharge into the Lagoon and the nearby coastal belt over the last few years (Cozzi and Giani 2011). However, despite the greater availability of light, we observed no increase in phytoplankton biomass.

While the concentrations of P-PO$_4$ did not seem to fluctuate over the ten years, DIN shows a moderate decrease and Si-SiO$_4$ a marked one (Fig. 5). Moreover, significant changes in the ratios between nutrients were observed. The N/P ratios, which in the Venice Lagoon and Adriatic Sea are usually much higher than the canonical 16:1 (Bianchi *et al.* 1999, Justić *et al.* 1995), were lower in the second half of the ten-year period. Because of the large fall in silicate levels, the Si/N and Si/P ratios diminished significantly over the decade (Table 7).

The significant fall in Si-SiO$_4$ and the Si/N and Si/ P ratios was accompanied by a decrease in the abundance of diatoms, which was significantly lower in the second half of the period, and an increase in the abundance of dinoflagellates (Table 7). However, the most abundant species (the "top ten"), including the bloom-forming ones, were always present and dominant, although with falling abundances (Table 7).

DISCUSSION

The phytoplankton of the Venice Lagoon includes taxa that are representative of the complex and open system of the Lagoon itself, from the coastal sea to the rivers and the benthic-pelagic system. Key phytoplankton species (e.g. *Skeletonema marinoi*, small *Thalassiosira* sp., *Chaetoceros compressus*) also bloom in the adjacent Adriatic coastal waters; others (e.g. *Nitzschia frustulum*, *N.* spp, *Amphora* spp) are typical lagoon inhabitants. Many of them are of benthic origin, indicating the influence of the exchange between the sediments and the water column. Finally, some species, mostly rare, are of allochthonous origin, their presence being a result of freshwater (*Eutreptia lanowii*, *Scenedesmus quadricauda*) or tidal inputs (e.g. coccolitophorids such as *Syracosphaera pulchra*, *Rhabdosphaera claviger*, *Calciosolenia murrayi*).

The number of phytoplankton taxa identified in this study was comparable to that recorded by Facca and Sfriso (2009) in a study with a limited time span but very large spatial coverage across the Lagoon, with diatoms and nanoflagellates as the dominant groups. The most significant species observed here were also reported by Bandelj *et al.* (2008) in a one-year study of six stations distributed across the whole lagoon area.

The spatial differences between the areas considered in the present study are mainly the result of the varying degrees of impact of the interactions between the adjacent marine waters, riverine inputs and benthic-pelagic coupling. Indeed, the main dissimilarities among the ZSIs (Table 3) were due to salinity and

nutrients. The degree of benthic-pelagic coupling also determines phytoplankton composition in the different areas and seems to be mainly influenced by depth: the diatom composition (Table 4) at stations 1 and 5 (smallest depths) differs significantly in terms of the proportion of benthic species from that at stations 2 and 4 (greatest depths).

Diatoms appear to be the most representative group of the Venice Lagoon phytoplankton. They are the prevalent group in terms of abundance in most seasons and stations, and they are also representative of the riverine, coastal, benthic and pelagic influences on the system: they include species from all these systems and are also responsible for most of the blooms in the Lagoon. Indeed, diatoms dominate the nano- and microphytoplankton in other Mediterranean lagoons, such as Fusaro (Sarno *et al.* 1993), Varano (Caroppo 2000), Orbetello (Nuccio *et al.* 2003) and Stella Maris (Fanuko and Valcic 2009).

The contribution of other classes, characterizing specific periods of the year and/or sampling sites directly influenced by marine input, is rather negligible. According to Margalef's Mandala (Margalef 1978), a central paradigm of phytoplankton community ecology, the prevalence of diatoms is characteristic of permanently fertile and turbulent environments. Furthermore, the open nature of the pelagic system of many lagoons makes immigration from different systems (land, sea and sediments) an intrinsic part of their phytoplankton community structure (Cloern and Jassby 2008 and citations therein). Over the ten-year period in the Venice Lagoon, some taxa were prevalent and common (albeit with different abundances) to every station. By focusing on them, the average seasonal variation of phytoplankton composition was established, and a "phytoplankton calendar" was drawn up for the Lagoon (Fig. 8). This "calendar" may be a useful tool to evaluate alterations in the future resulting from local or global impacts that affect the timing of these key species and/or favour the dominance of new ones.

Species imported to the water column from the benthic community (benthic diatoms: *Halamphora veneta*, *Gomphonema olivaceum*, *G. parvulum*, *Navicula cryptocephala*) and from the coastal sea (coccolithophorids: *Emiliania huxleyi*, *Syracosphaera pulcra*) typify the period of lowest abundance (late autumn and winter). Planktonic diatoms mainly characterize the late winter-spring start of the growing phase (*Skeletonema marinoi*). Moving towards the summer peaks, the species composition changes again, becoming characterized by a mixed assemblage of diatoms, which remain dominant, together with cryptophyceans, dinoflagellates and euglenophyceans. Throughout the summer period, blooms may occur, mainly of *Chaetoceros compressus*, small *Chaetoceros* spp., *Cylindrotheca closterium*, *Nitzschia frustulum* and *Thalassiosira* spp.

Some of these dominant species are also common to the adjacent coastal waters of the Northern Adriatic, in particular from winter to late spring: coccolithophorids
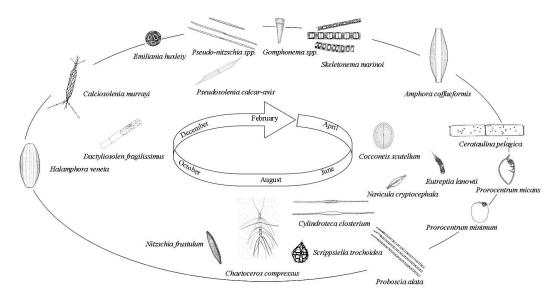
Fig. 8. – Phytoplankton calendar of Venice Lagoon; see also the text and Table 5.

and *Pseudonitzscia* spp in winter, *Skeletonema marinoi* in early spring, *Cerataulina pelagica*, *Proboscia alata*, *Chaetoceros* spp and small tecate dinoflagellates in late spring. Subsequently, from summer to autumn, the two communities clearly differ, with prevalence of large dinoflagellates and planktonic diatoms in the northern Adriatic (Bernardi Aubry *et al.* 2004).

The prevalent annual pattern of phytoplankton biomass in the Venice Lagoon is unimodal, with a summer peak, and this was seen recurrently in the ten years of study and at the five stations. This pattern appears specific to temperate enclosed coastal ecosystems, with shallow depths and permanently high nutrient concentrations (Cebrian and Valiela 1999). In contrast, the bimodal cycle of phytoplankton biomass seen in some temperate coastal ecosystems is characterized by spring blooms caused by increased light, temperature and stratification, a collapse in summer due to nutrient depletion and grazing, and autumn blooms caused by water mixing and nutrient regeneration. If nutrient availability remains high in summer, phytoplankton growth is enhanced throughout summer and is mainly linked to temperature and light.

As an ecosystem, the Venice Lagoon is constantly nutrient-enriched, apparently weakening the tight constraint on phytoplankton seasonal growth determined by nutrient limitation so that the seasonal climate cycle becomes the most recognizable driver of phytoplankton biomass. Indeed, biomass increases from spring to summer, and the maxima are generally attained in July. Within this unimodal annual cycle, which appears fairly well tuned to the seasonal cycle of temperature and irradiance, monthly fluctuations are present, highlighting the additional effect of climatic and local events occurring on shorter time scales.

A similar unimodal seasonal phytoplankton cycle is also observed in the western coastal area of the north-

ern Adriatic Sea (Bernardi Aubry *et al.* 2004), where nutrients are lower (on average DIN from 8.0-21.6 µM; Si-SiO$_4$ 4.8-12.0 µM; P-PO$_4$ 0.10-0.24 µM) than in lagoon waters and the chl *a* values are on average (1.8-4.3 µg l^{-1}) close to those measured at station 4. The phytoplankton cycle becomes much more irregular in offshore areas, with alternating minor peaks in spring and summer due to the combination of nutrient depletion and sporadic nutrient inputs (Bernardi Aubry *et al.* 2012): here actually both nutrients (DIN 2.8-10.9 µM; Si-SiO$_4$ 3.1-7.3 µM; P-PO$_4$ 0.05-0.12 µM) and chl *a* (0.8-1.7 µg l^{-1}) are much lower than in the Lagoon (Bernardi Aubry *et al.* 2006, Socal *et al.* 2008).

Comparing the first half of the study period (1998-2002) with the second (2003-2007), a significant decrease in biomass was observed. This fall was mainly determined by a reduction in the height of the peaks and the frequency of blooms throughout the year, and was not accompanied by significant changes in species community composition or the general seasonal biomass pattern. Indeed, the same dominant species in the first five years were still among the top ten in the second five, albeit with significant reductions in abundance and biomass. Specifically, we recorded a significant decrease in diatom abundance, which could be related to the fall in silicates.

Other authors have described progressive oligotrophication over the last few years in both the Venice Lagoon (Solidoro *et al.* 2010) and the adjacent Adriatic Sea (Mozetič *et al.* 2009). In the northern Adriatic Sea a recent decrease in chlorophyll has paralleled a reduction in freshwater discharge from both the Po (Zanchettin *et al.* 2008) and other smaller rivers such as the Isonzo (Comici and Bussani 2007).

This trend cannot easily be interpreted in the context of other long-term studies on phytoplankton in marine coastal ecosystems. Two recent analyses of long-term

phytoplankton trends in marine costal systems (*Journal of Sea Research*, 61, 2009; CIESM workshop monographs, 2010) examine time series (from one to four decades) of inshore phytoplankton and chlorophyll in relation to environmental data: these datasets do not contain significant signals that can be clearly identified and generally described and an overall conclusion is that the variability and complexity of these environments hinders the recognition of unambiguous signals.

CONCLUSIONS

Time series provide a unique tool for obtaining a reliable representation of the annual cycle of phytoplankton communities, for evaluating the existence of shifts and trends related to global or local impacts, and for testing hypotheses about phytoplankton ecology. The data series analysed in this study is only ten years long, a fairly short time span in comparison with the longest observations of phytoplankton in aquatic ecosystems, which extend over some decades, with the earliest records starting in the 1930s (Winder and Cloern 2010). Ten years are not sufficient to determine shifts and trends in annual cycles. However, they can at least provide a reliable reconstruction of annual phytoplankton variations, from both a qualitative and a quantitative viewpoint, an issue that appears particularly important for transitional areas.

Conceptualization, generalization and paradigms about the functioning of the plankton compartment are mostly available for open marine ecosystems (Margalef 1978, Longhurst 1998, Reynolds and Smayda 1998), while no wide-ranging rules have been defined for the seasonal phytoplankton cycle of coastal and transitional waters, characterized by higher overall complexity (Cloern and Jassby 2008). Our analysis of ten years of phytoplankton data in the Venice Lagoon allowed us to characterize the main features of the community. Specifically, our study revealed the following:

(i) A prevalent unimodal annual cycle of phytoplankton biomass was observed; notwithstanding some year-to-year variability and monthly fluctuations, phytoplankton biomass maxima are typically attained in summer. Annual climate fluctuations (mainly temperature and irradiance) are therefore the most recognizable driver of seasonal trends in phytoplankton biomass.

(ii) The most abundant phytoplankton taxa are common to all stations, regardless of the distinctive features of each area. It seems, therefore, that the most general ecological characteristics of the lagoon ecosystem itself (i.e. a turbulent, nutrient-enriched environment, open to other connected systems including land, sea and sediments), play a more important role in shaping phytoplankton communities than the specific attributes of each single area.

(iii) A significant decrease in biomass was observed in the second half of the period, without changes in community composition, hard to relate to a specific factor, but also seen in the adjacent Adriatic Sea. Only observations made in the next few years will allow a thorough evaluation of these changes (i.e. whether they are down to a real trend of oligotrophication or merely fluctuations).

Finally, the main results and evidence arising from the analysis of this ten-year series can be regarded as a kind of heritage for the future: a reference line against which to evaluate future changes in the phytoplankton community of the Venice Lagoon.

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