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Temporal and spatial changes of macroalgae and phytoplankton in a Mediterranean coastal area: the Venice lagoon as a case study

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Abstract

Since the late 1980s the lagoon of Venice, a shallow Mediterranean coastal area, has experienced strong environmental changes. Macroalgae, which were the predominant primary producers of the lagoon, reduced markedly, but neither phytoplankton nor seagrasses replaced them. Temporal and spatial changes in macroalgal standing crop (SC) and phytoplankton concentration were investigated between 1987 and 1998. Maps of macroalgal SC show a marked declining trend. Biomass in fresh weight decreased from: 558 ktonnes in 1987, to 85 ktonnes in 1993 and to 8.7 ktonnes in 1998. As a whole, the biomass in 1998 was only 1.6% of the biomass recorded in 1987. Similarly the macroalgal net (NPP) and gross (GPP) primary production decreased from ca. 1502 and 9721 ktonnes year^{-1} to ca. 44 and 229 ktonnes year^{-1}, respectively. In the early 1990s the clam *Tapes philippinarum* Adams & Reeve and seagrasses, especially *Zostera marina* Linnaeus, colonised the bottoms free of macroalgae, but the development of intense clam-fishing activities prevented both phytoplankton blooms and seagrass spreading. Maps of chlorophyll *a* drawn according to data collected in parallel to macroalgal standing crop show unchanged concentrations. Macroalgae changes are enhanced by comparing annual trends in four areas of the central lagoon during 1989–1992 and 1998–1999. In those areas phytoplankton also decreased significantly. Marked changes of some environmental variables strongly associated with the primary production were recorded both during the lagoon mapping and in the areas studied on a yearly basis.

Keywords: Macroalgae; Phytoplankton; Environmental variables; Shallow areas; Clam-fishing; Venice lagoon

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1. Introduction

In the second part of the twentieth century, with the increase of eutrophication, the dominant primary producers in the world's shallow coastal environments have undergone many changes. In general, seagrasses and phytoplankton were affected by excessive macroalgal growth, especially nuisance taxa (Morand & Briand, 1996; Rijstenbil & Haritonidis, 1993; Schramm & Nienhuis, 1996; Sfriso, Pavoni, Marcomini, & Orio, 1992), with serious consequences for the environment.

Industrial, agricultural and domestic waste, introduced into the lagoon environment since the 1970s, caused an increase in nutrients and pollutants, but the construction of harbours and the excavation of deep navigable canals also altered the hydrodynamic equilibrium. Both these factors favoured the proliferation of macroalgae, especially *Ulva rigida* C. Agardh. The abnormal growth of this species triggered hypertrophic–dystrophic conditions and changed the natural equilibria of the lagoon for over 20 years. Although studies on macrophyte and nutrient cycles have produced exhaustive knowledge (Marcomini, Sfriso, Pavoni, & Orio, 1995; Sfriso & Ghetti, 1998; Sfriso, Pavoni, & Marcomini, 1989; Sfriso et al., 1992; Sfriso, Pavoni, & Orio, 2000, chap. 18; Sfriso & Marcomini, 1996a, chap. 15, 1996b, 1997, 1999; Sorokin, Sorokin, Giovanardi, & Dalla Venezia, 1996) and models have been built to understand their processes (Bendoricchio, Coffaro, & De Marchi, 1993; Bendoricchio, 2000; Bocci, 2000; Coffaro, 1993; Coffaro & Sfriso, 1997; 2000; Lvov, Pastres, Sfriso, & Marcomini, 2000; Solidoro, Deiak, Franco, Pastres, & Pecenik, 1993; Zharova, Pavoni, Sfriso, & Voinov, 1996; Zharova, Sfriso, Voinov, & Pavoni, 2001), no integrated information on biomass and production changes is available.

This study aims at investigating changes in the standing crop and the production of macroalgae and phytoplankton in the central part of the Venice lagoon during the past 15 years. Changes have been recorded both on a spatial and temporal basis in the whole central lagoon by monitoring four stations where sampling campaigns were scheduled 2–3 times a month during three significant periods: The excessive *Ulva* growth (1970–1990), its decline (1990–1994) and the intense fishing of the bivalve *Tapes philippinarum* (1994–2001), which colonised the areas progressively free of macroalgal biomass.

2. Methods

2.1. Study areas

The main target of this study is the central part of the Venice lagoon which is situated from south to north, between the Malamocco-Marghera canal and the Burano and Torcello tidal lands (Fig. 1). This lagoon basin consists of a water surface of ca. 132 km^2 whose mean depth is ca. 1 m at the mean tidal level.

The spatial distribution of macroalgae (especially *Ulva rigida*) was investigated by sampling the biomass in exactly the same areas (178 stations) during the first week of June in 1987, 1993 and 1998, which is the period of the highest *Ulva* abundance

(Sfriso, Marcomini, & Pavoni, 1987; Sfriso, Pavoni, Marcomini, & Orio, 1988). Sampling sites were not selected according to a regular grid but taking into account both the lagoon morphology and the bottom visibility, because of the high water transparency (Fig. 2).

Phytoplankton and some physico-chemical variables (oxygen saturation, pH, E_h and water transparency) of the entire water column (ca. 1 m±31 cm) were also determined in 55 of the 178 stations.

The results of samples from June were integrated with samples carried out weekly/monthly during one year (from July to June of the following year) at four stations (A–D during 1989–1990; A–C during 1990–1991; D during 1991–1992; A–D during 1998–1999) placed between the mainland and the Malamocco sea inlet (Fig. 1). Three of them used to be populated by macroalgae (stations A–C) and the fourth (station D) only by phytoplankton.

2.2. *Macroalgal biomass determination*

The macroalgal biomass was sampled by means of a cubic box (0.5 m^2). Macroalgae, mainly composed of the free-floating thalli of *Ulva rigida*, were cut around the box walls and collected by means of a pitchfork and a hand net. Because of the high

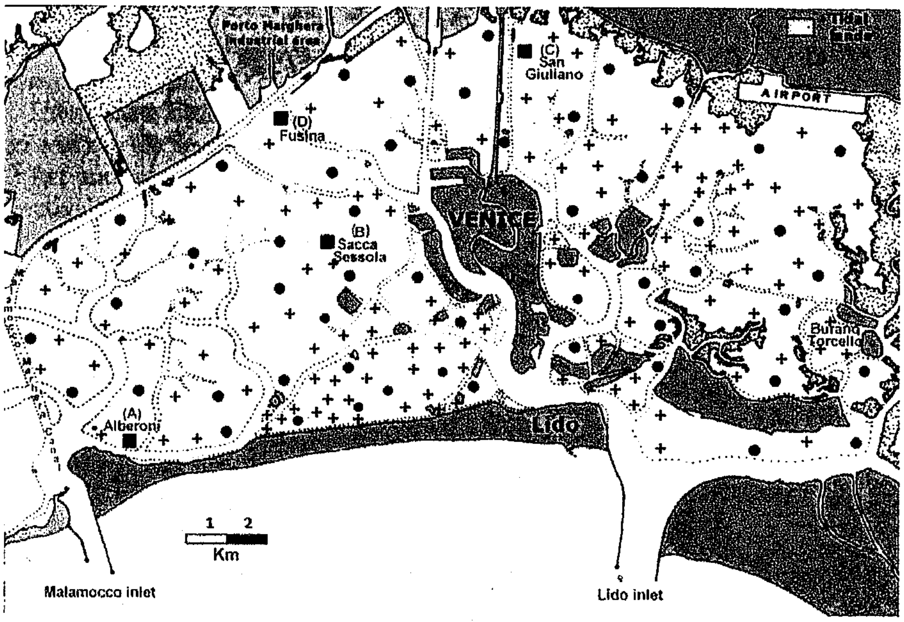

Fig. 1. Map of the Venice lagoon and 178 sampling sites. In the circled stations also phytoplankton pigments and some physico-chemical parameters were determined. The four areas sampled 2–3 times per month: station A (Alberoni) located near the Malamocco port-entrance, station B (Sacca Sessola) placed in the Lido watershed, station C (San Giuliano) located in proximity of the mainland and the urban sewage plant of the city of Mestre and station D (Fusina) located near Porto Marghera industrial area are indicated by black squares.

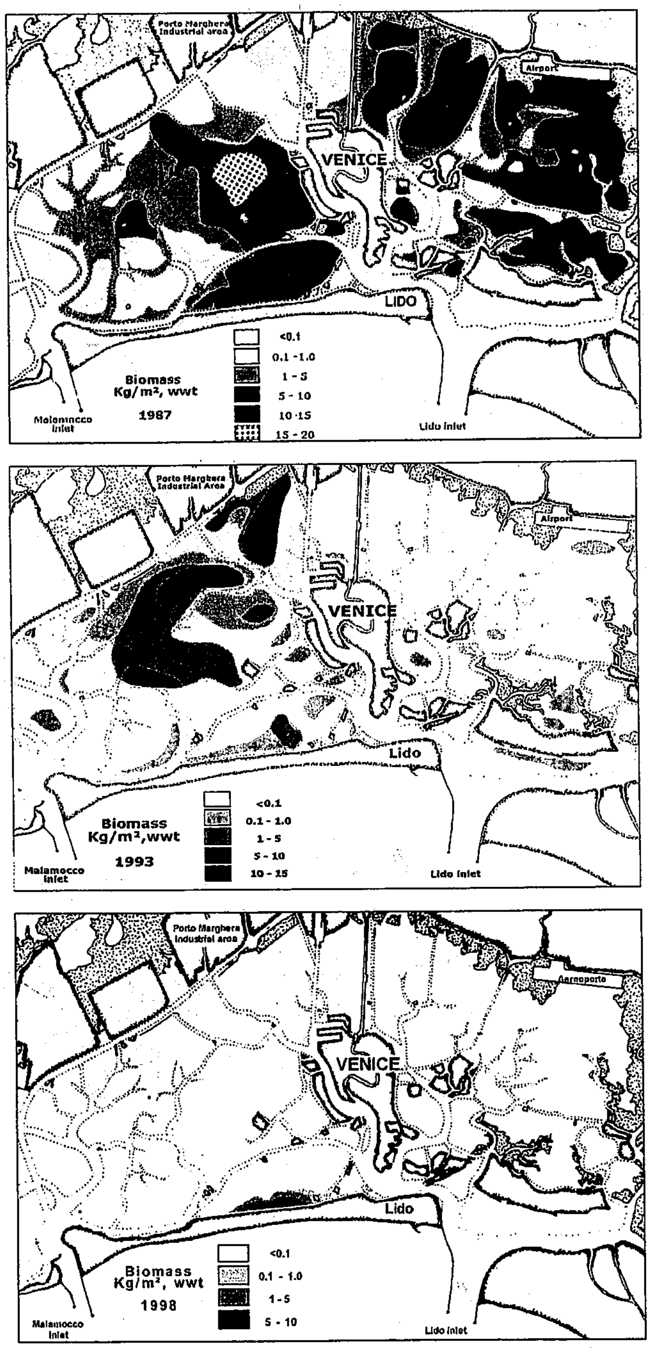

Fig. 2. Maps of the macroalgal biomass distribution on fresh weight basis during 1987, 1993 and 1998 June campaigns. Biomass distribution is drawn according to six biomass intervals, i.e.: <0.1 kg m^{-2}, 0.1–1.0 kg m^{-2}, 1–5 kg m^{-2}, 5–10 kg m^{-2}, 10–15 kg m^{-2} and 15–20 kg m^{-2}.

biomass in the sampling areas and the number of replicates, only fresh weight (fwt) was determined. However, on the basis of some ten samples collected during the June and the monthly campaigns, the dry weight biomass was found to be ca. 11% of the fresh weight. The biomass was weighed by means of a mechanical balance (precision 10 g) for weight exceeding 3 kg m^{-2} and by means of an electronic balance (precision: 1 g) for lower weights. According to the method of Sfriso, Raccanelli, Pavoni, and Marcomini (1991), three replicates collected within a pre-determined sampling grid guarantee a precision of: (a) >95% for a biomass >5 kg m^{-2}, (b) >90% for a biomass ranging from 5 to 1 kg m^{-2} and (c) >85% for a biomass <1 kg m^{-2}. That precision was considered suitable to map the biomass in six ranges (Fig. 2).

Sampling site location and biomass distribution have been obtained by means of triangular and GPS (Global Position System) measurements. Maps have been drawn using Corel Photo-Paint 8 (Corel Corporation Limited, 1997, Dublin, Ireland).

The total standing crop (SC) was obtained by summing the mean biomass calculated per each biomass range and lagoon surface (km^2).

The net primary production (NPP) was estimated by applying different production/biomass (P/B) ratios (Sfriso, Marcomini, Pavoni, & Orio, 1993) to the maximum biomass value per range and surface. According to the biomass variation method, P (annual production) was the sum of significant (one-way ANOVA) biomass increases (g m^{-2} day^{-1}) measured, weekly, in the period (one vegetative year) between the highest SC of two consecutive years and B (biomass) was the highest SC. The named authors found that in the presence of $SC \geqslant 10$ kg m^{-2} fwt, the P/B ratio was ca. 1.6. It was ca. 2.0 in areas characterised by SC ranging from 5 to 10 kg m^{-2} fwt and increased to ca. 3.5 and 4.5 when the SC was <5 and <1 kg m^{-2} fwt, respectively.

The GPP/NPP ratios calculated by Sfriso and Marcomini (1994) enable us to determine also the annual gross primary production (GPP) of the central lagoon. In fact, those authors noticed that in the presence of $SC > 10$ kg m^{-2} fwt, (which means a biomass so densely stratified in the water column that it affects both light transmission and water renewal) the annual GPP/NPP ratio was ca. 6.7. That ratio decreased to ca. 3.5 when the SC was <1 kg m^{-2}. In that case the GPP/NPP ratio lowered because the absence of biomass stratification and anoxic crises which prevented the grazing pressure (Balducci, Sfriso, & Pavoni, 2001).

2.3. Phytoplankton

Phytoplankton was monitored as chlorophyll-*a* (Chl. *a*) and phaeophytin-*a* (Phaeo. *a*) concentrations in order to determine both active and declining microalgal populations. Six to ten samples of the entire water column were collected by means of a home-made Plexiglas bottle (height: 150 cm, diameter 4 cm) and mixed in a tank. Water aliquots ranging from 100 to 1000 ml were immediately filtered in situ by means of a Whatman GF/F glass microfibre filter (pore 0.7 μm). Filters were stored at −20 °C till the pigment determination according to the spectrophotometric procedure (Lorenzen, 1967) as reported in Parsons, Maita, and Lalli (1984). The Chl. *a* results of the June campaigns have been plotted in a map by considering four concentrations ranges (Fig. 3).

2.4. Physico-chemical parameters

The temperature, pH and redox potential (E_h) of the water column were recorded by means of a portable pH-meter (model HD 8705, Delta OHM, Padua, Italy). The oxygen concentration was obtained by an oximeter (Oxi 196, Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) equipped with a battery stirrer BR 190. Data were transformed into % air saturation depending on water temperature and chlorinity. Chlorinity was determined by silver nitrate titration according to a modified Knudsen method (Oxner, 1962). Water transparency was monitored by the Secchi disk. The mean water depth is generally ca. 1 meter (mean tidal variation: ±31 cm), but it varied between sampling occasions, therefore transparency measurements are reported as percentages of the water column visibility: a value of 100% means that the bottom was visible; a value of 50% means that the disk disappeared at half way from the bottom.

2.5. Statistical analyses

Macroalgal and phytoplankton data sets referring to different year campaigns were statistically compared using the Friedman's test (non parametric analysis of variance). Significant differences in physico-chemical parameters were tested according to one way-ANOVA (Statistica, release 5, 1997 edition of the StatSoft, copyright Microsoft Corporation, Tulsa OK 74104).

3. Results

3.1. 1987, 1993, 1998 June campaigns in the whole central lagoon

In 1987, the mean biomass for 178 sampling sites was ca. 4.78 kg m^{-2} fwt, with peaks up to 25 kg m^{-2} fwt (Table 1). In 1993, the mean biomass decreased to 0.69 kg m^{-2} fwt and in 1998 it was ca. 0.11 kg m^{-2} fwt, only. The biomass decrease was highly significant (Friedman test, $P<1\times10^{-5}$).

The variation of Chl. *a* concentration was not significant. In fact mean and peak values ranged between 3.4 and 4.0 μg dm^{-3} and between 29 and 32 μg dm^{-3}, respectively. In contrast Phaeo. *a* showed marked changes (Friedman test, $P<1\times10^{-5}$) both in the mean (from 1.29 to 5.21 μg dm^{-3}) and maximum (from 5 to 18–22 μg dm^{-3}) values.

3.1.1. Macroalgal maps

In June 1987, the total macroalgal SC was ca. 558 ktonnes fwt (Table 2). The highest density was found in the Lido watershed and in the area north of Venice

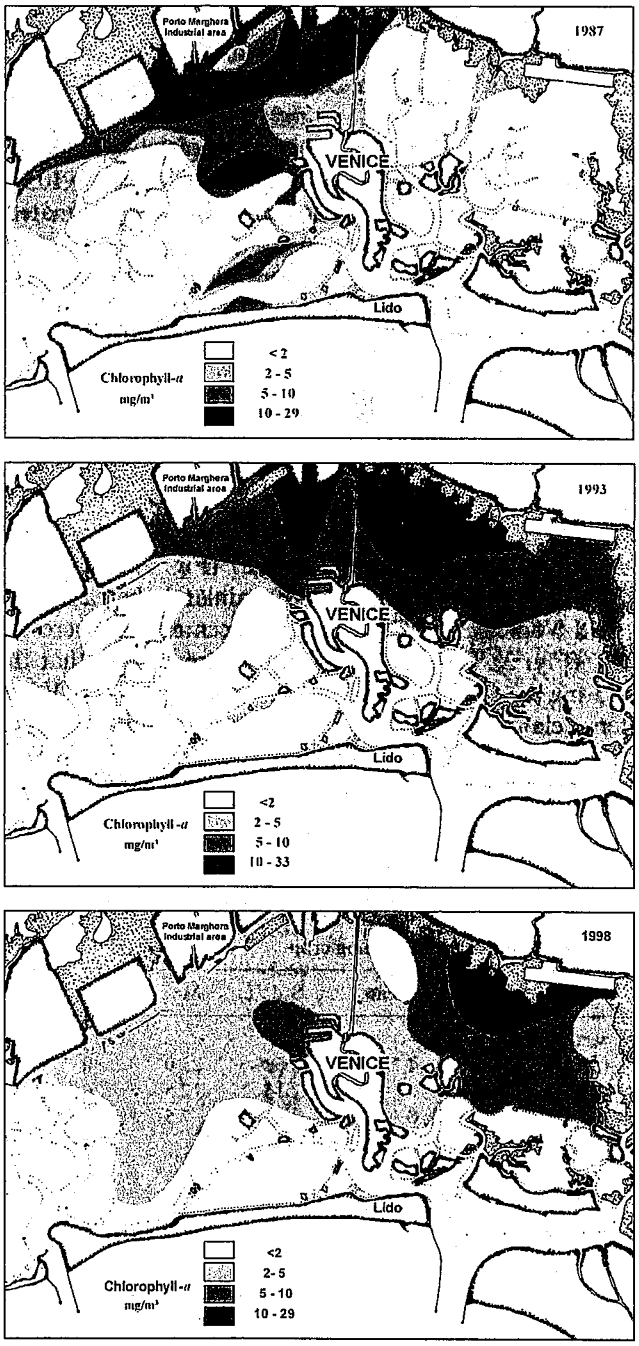

Fig. 3. Maps of the phytoplankton distribution during the 1987, 1993 and 1998 June campaigns. Biomass distribution is drawn according to 4 Chl. *a* intervals, i.e. <2 mg m^{-3}, 2–5 mg m^{-3}, 5–10 mg m^{-3} and 10–29 or 10–33 mg m^{-3}.

(Fig. 2). In 1993, the macroalgal biomass had significantly reduced and SC had dropped to ca. 85 ktonnes fwt, ca. 15.2% of the biomass recorded in 1987. Macroalgae were absent NNW of Venice and the range from 15 to 20 kg m^{-2} fwt, was missing.

Then, in 1998 the biomass disappeared almost completely. Only a small area of ca. 3×0.4 km was populated by macroalgae with a biomass up to 10 kg m^{-2}. On the whole, during the 1998 campaign, the macroalgal SC was estimated to be ca. 8.7 ktonnes fwt only, which was ca. 1.6% of the SC in 1987.

On a yearly basis, the NPP of the entire central lagoon, changed from ca. 1502 ktonnes fwt in 1987, to ca. 377 ktonnes fwt, in 1993, and to ca. 44 ktonnes fwt, in 1998. The 1998 value was equivalent to ca. 2.9% of the NPP estimated in 1987.

Similarly, the GPP dropped from ca. 9721 ktonnes in 1987, to ca. 2182 ktonnes in 1993 and to ca. 229 ktonnes in 1998, which was ca 2.4% of the GPP estimated in 1987.

3.1.2. Phytoplankton (Chl. a) maps

In the presence of a remarkable macroalgal biomass, phytoplankton was negligible in almost all the considered stations in 1987 (Fig. 3). The highest Chl. *a* concentrations (10–29 mg m^{-3}) were near the mainland, between Porto Marghera Industrial zone and Venice. In 1993, Chl. *a* concentrations were similar to those monitored in 1987 (Fig. 3, Table 1). The only difference was that the highest concentrations (10–33 mg m^{-3}) were monitored in the area NW of Venice. In 1998, in the period of intense clam-fishing activities, Chl. *a* concentrations were again similar to the previous ones but the highest values (10–29 mg m^{-3}) were found in samples from the northern part of the central basin, near Venice airport.

Table 1
Comparison of macroalgal and phytoplankton biomass in the central part of the Venice lagoon

Year	Sampling sites	Standing crop				Friedman's test
		Mean	Std	Max.	Min.	
Macroalgae (kg m^{-2}, wet wt.)						
1987	178	4.78	5.69	25.0	0	$P < 1 \times 10^{-5}$
1993	178	0.69	2.14	12.5	0	
1998	178	0.11	0.79	7.5	0	
Phytoplankton						
Chlorophyll a (µg dm^{-3})						
1987	55	3.61	5.62	29.0	0.53	n.s.
1993	55	4.01	5.43	32.0	0.43	
1998	55	3.36	4.55	29.1	0.20	
Phaeophytin a (µg dm^{-3})						
1987	55	1.29	1.11	5.4	0.28	$P < 1 \times 10^{-5}$
1993	55	2.12	3.15	22.4	0.20	
1998	55	5.21	4.65	18.2	0.50	

3.1.3. Physico-chemical variables in the water column

During the June campaigns the mean water temperature ranged between 22.8±2.1 and 25.8±1.7 °C and chlorinity between 16.4±1.6 and 17.3±1.1 g l^{-1} (Table 3). No significant differences were found. In contrast the dissolved oxygen (DO) saturation, pH, E_h and water transparency differed significantly. The mean%DO had decreased from 274±73 in 1987 to 113±23 in 1998. Peak values had decreased from 394 to 202%. Similarly, pH mean values had decreased from 8.82±0.38 to 8.01±0.12 and peaks from 9.54 to max 8.27. The same changes were observed for E_h which, at present, has never been over 367 mV (Table 3). Water transparency had also

Table 2
Macroalgal standing crop and biomass production in the central lagoon

			Standing crop					Biomass production		
Biomass kg/m², fwt.			Lagoon surface[a]		Tonnes (fwt)		P/B[b]	NPP	GPP/NPP[c]	GPP
Range	Mean	Max.	km²	%	Mean	Max.		Tonnes		Tonnes
1987										
15–20	17.5	20	2.3	1.7	40,250	46,000	1.6	73,600	6.7	493,120
10–15	12.5	15	23.8	18.0	297,500	357,000	1.6	571,200	6.7	3,827,040
5–10	7.5	10	19.9	15.1	149,250	199,000	2.0	398,000	6.7	2,666,600
1–5	3.0	5	20.1	15.2	60,300	100,500	3.5	351,750	6.7	2,356,725
0.1–1	0.55	1	19.3	14.6	10,615	19,300	4.5	86,850	3.5	303,975
<0.1	0.01	0.10	46.6	35.3	466	4660	4.5	20,970	3.5	73,395
Total			132	100	558,381	726,460		1,502,370		9,720,855
1993										
10–15	12.5	15	2.9	2.2	36,250	43,500	1.6	69,600	6.7	466,320
5–10	7.5	10	1.5	1.1	11,250	15,000	2.0	30,000	6.7	201,000
1–5	3.0	5	9.7	7.3	29,100	48,500	3.5	169,750	6.7	1,137,325
0.1–1	0.55	1	13.5	10.2	7425	13,500	4.5	60,750	3.5	212,625
<0.1	0.01	0.10	104	79.1	1044	10,440	4.5	46,980	3.5	164,430
Total			132	100	85069	130,940		377,080		2,181,700
	Residual per cent				15.2			25.1		22.4
1998										
5–10	7.5	10	0.75	0.6	5625	7500	2.0	15,000	6.7	100,500
1–5	3.0	5	0.50	0.4	1500	2500	3.5	8750	6.7	58,625
0.1–1	0.55	1	0.50	0.4	275	500	4.5	2250	3.5	7875
<0.1	0.01	0.03[d]	130	98.7	1303	3908	4.5	17,584	3.5	61,543
Total			132	100	8703	14,408		43,584		228,543
	Residual per cent				1.6			2.9		2.4

[a] Lagoon surface = 132 km².

[b] P/B = Annual production/highest biomass. These values have been calculated with reference to annual field data at different biomass ranges.

[c] GPP/NPP = Gross/Net production. These values have been obtained by field data at different biomass ranges.

[d] The highest biomass used to calculate the GPP, in this case, is 0.03 kg m^{-2}, fwt because in that year the biomass was almost missing.

lowered. In 1987, when macroalgae covered most of the lagoon bottoms, water transparency was high and the mean Secchi depth was at ca. 93% of the water column. In 1998 the mean Secchi depth corresponded to ca. 75% of the water column, but in many stations the disk was visible at 15–40 cm from the surface, only.

3.2. Monthly campaigns at the four stations

3.2.1. Changes in macroalgal biomass and species composition

By analysing the biomass behaviour on a yearly basis at the four stations it is interesting to observe that the maximum biomass values had changed much more remarkably than the mean values, especially in the period of the macroalgal decrease between 1989–1990 and 1990–1991 (Table 4). Particularly, stations B and C, which during 1989–1990 exhibited a luxuriant biomass, showed a remarkable decline in 1990–1991 and resulted in very low biomass values in 1998–1999. Station B, which displayed a biomass peak of ca. 20 kg m^{-2} fwt in 1989–1990, in 1998–1999 showed the highest biomass at ca. 0.31 kg m^{-2} fwt, only. The mean value had decreased from ca. 0.98 to 0.05 kg m^{-2} fwt. Similarly, at station C the highest biomass had

Table 3
Mean, standard deviation (std), maximum (max.) and minimum (min.) values of some relevant environment variables monitored during the June campaigns in the whole central lagoon

Variables	Year	Samples	Mean	Std	Max.	Min.	ANOVA one-way $P<0.001$
Water temperature (°C)	1987	55	22.8	2.1	27.8	18.8	n.s.
	1993	55	25.8	1.7	29.6	22.7	
	1998	55	24.5	2.5	29.7	20.7	
Secchi disk (%)	1987	55	93	14	100	48	9.70E-07
	1993	55	90	13	100	40	
	1998	55	75	23	100	26	
Oxygen saturation (%)	1987	55	274	73	394	159	3.20E-37
	1993	55	135	31	226	76	
	1998	55	113	23	202	70	
Water pH	1987	55	8.82	0.38	9.54	8.18	1.10E-32
	1993	55	8.48	0.14	8.90	8.21	
	1998	55	8.01	0.12	8.27	7.65	
Water E_h (mV)	1987	55	378	46	438	153	5.90E-26
	1993	55	367	20	411	323	
	1998	55	294	27	367	238	
Chlorinity (g l^{-1})	1987	55	16.8	1.0	18.6	14.1	n.s.
	1993	55	17.3	1.1	19.3	13.7	
	1998	55	16.4	1.6	19.3	12.3	

n. s., no significance.

decreased from ca. 8.23 kg m^{-2} fwt in 1989–1990 to ca. 5 g m^{-2} fwt in 1998–1999, whereas the mean biomass had changed from ca. 1.47 kg m^{-2} fwt to 3.4 g m^{-2} fwt, only.

Station A, placed close to the Malamocco sea inlet showed a less significant biomass variation, because *Ulva* was not the only dominant species. That area, was in fact covered with several macroalgal taxa and four of them: *Ulva rigida* C. Ag., *Gracilaria longa* Gargiulo, De Masi et Tripodi, *Dictyota dichotoma* (Hudson) Lamouroux and *Porphyra leucosticta* Thuret constituted ca. 90% of the total biomass production (Sfriso et al., 1993). Therefore, the decrease of *Ulva,* monitored since 1990–1991 in the whole lagoon at station A was negligible. In 1998–1999 the mean standing crop appeared to have only halved, and the highest biomass was reduced to ca. 1/3 of the biomass monitored in 1989–1990 (Table 4).

Station D did not display any macroalgal biomass either in 1991–1992 or in 1998–1999.

3.2.2. Changes in phytoplankton pigment values

The largest phytoplankton (Chl. *a* and Phaeo. *a*) differences, on an annual basis, where found at stations C and D near the mainland (Table 5). In those stations the annual mean Chl. *a* concentrations decreased from 10.3 to 1.5 μg dm^{-3} (st. C) and from 9.1 to 1.7 μg dm^{-3} (st. D), which means ca. 6.7 and 5.4 times, respectively. When considering the Chl. *a* peak concentrations, the differences were again very pronounced with values decreasing by ca. 10–20 times. At stations A and B the mean Chl. *a* concentrations had diminished by only 27–36% and the peak values were also lower.

Table 4
Comparison of annual macroalgal biomass in four stations of the central lagoon placed close to the mainland (sts. C,D), in the middle lagoon (st. B) and near the Malamocco mouth (st. A)

Station	Year	N^a	Mean	Std	Min.	Max.
			g m^{-2} fwt			
A	1989–1990	36	597	742	0	2855
(Alberoni)	1990–1991	36	334	422	17	1436
	1998–1999	24	354	297	37	1072
B	1989–1990	36	982	2022	0	19638
(Sacca Sessola)	1990–1991	36	954	2561	0	10692
	1998–1999	24	54	70	5	311
C	1989–1990	36	1467	2517	0	8228
(San Giuliano)	1990–1991	36	433	777	0	3178
	1998–1999	24	3.4	4.9	0	5.0
D	1989–1990	34	0	0	0	0
(Fusina)	1991–1992	34	0	0	0	0
	1998–1999	24	0	0	0	0

[a] Samples in 1989–1990, 1990–1991, 1991–1992 were taken three times per month. In 1998–1999 samples were taken twice per month.

In contrast Phaeo-*a* showed different behaviours. It halved at stations C and D but doubled at stations A and B, where the increase of the sediment re-suspension was more pronounced (Sfriso, 2000).

3.2.3. *Physico-chemical variable changes*

The environmental variables monitored in the central lagoon during the June campaigns have also been monitored in stations A–D during one whole year (Table 6). On average, all the considered variables showed the lowest mean values in 1998–1999. The differences appear to be more marked when the extreme values are considered. In fact in the past the minimum and maximum values depended on the alternations of periods affected either by biomass production or decomposition. In particular, in 1990–1991 (92) the DO saturation ranged from 0 (anoxic crises) to values higher than 250% and even up to 400% in other areas (Sfriso et al., 1997). In 1998–1999 only weak hypoxic conditions were found and maximum values were usually lower than 200%.

Table 5
Comparison of annual changes of phytoplankton (Chl. a and Phaeo. a) concentrations in four stations of the central lagoon placed in proximity of the mainland (sts. C-D), in the middle lagoon (st. B) and near the lagoon mouth (st. A)

Station	Year	*N*[a]	Mean	Std	Min.	Max.
			μg dm^{-3}			
Chlorophyll a						
A	1990–1991	36	1.60	2.43	0.09	11.4
(Alberoni)	1998–1999	24	1.17	0.57	0.40	2.40
B	1990–1991	36	2.04	2.34	2.04	7.35
(Sacca Sessola)	1998–1999	24	1.31	1.15	0.16	4.81
C	1990–1991	36	10.3	19.3	0.19	86.0
(San Giuliano)	1998–1999	24	1.53	1.03	0.32	4.01
D	1991–1992	34	9.13	13.1	0.43	57.8
(Fusina)	1998–1999	24	1.69	1.45	0.32	6.14
Phaeophytin a						
A	1990–1991	36	1.16	1.70	0.03	9.87
(Alberoni)	1998–1999	24	3.21	3.13	0.08	10.0
B	1990–1991	36	1.61	1.68	1.61	5.61
(Sacca Sessola)	1998–1999	24	2.67	3.19	0.01	15.1
C	1990–1991	36	11.5	24.1	0.28	109.8
(San Giuliano)	1998–1999	24	5.73	9.14	0.03	42.1
D	1991–1992	34	16.5	11.5	2.00	47.5
(Fusina)	1998–1999	24	7.92	16.6	0.00	54.1

[a] Samples in 1990–1991 and 1991–1992 were taken three times per month. In 1998–1999 samples were taken twice per month.

Table 6
Comparison of annual values of some physico-chemical variables strictly associated to algal cycles in the considered areas

Variables	Year	Samples	Mean	Std	Min	Max
Secchi disk (%)						
A	1990–1991	36	100	0	100	100
	1998–1999	24	100	0	100	100
B	1990–1991	36	100	0	100	100
	1998–1999	24	87	26	25	100
C	1990–1991	36	84	23	30	100
	1998–1999	24	70	35	35	100
D	1991–1992	34	82	17	50	100
	1998–1999	24	66	24	35	100
Oxygen saturation (%)						
A	1990–1991	36	157	42	96	281
	1998–1999	24	140	28	113	205
B	1990–1991	36	144	42	60	254
	1998–1999	24	138	26	102	180
C	1990–1991	36	131	44	0	243
	1998–1999	24	117	19	85	149
D	1991–1992	34	139	47	86	274
	1998–1999	24	125	24	82	180
Water pH						
A	1990–1991	36	8.46	0.30	7.98	9.26
	1998–1999	24	8.20	0.14	8.03	8.57
B	1990–1991	36	8.44	0.33	7.60	9.56
	1998–1999	24	8.16	0.19	7.94	8.57
C	1990–1991	36	8.40	0.36	7.28	9.35
	1998–1999	24	8.14	0.31	7.58	8.68
D	1991–1992	34	8.28	0.38	7.48	8.95
	1998–1999	24	7.98	0.26	7.44	8.50
Water E_h (mV)						
A	1990–1991	36	379	25	312	445
	1998–1999	24	309	31	271	370
B	1990–1991	36	358	39	250	432
	1998–1999	12	307	31	272	367
C	1990–1991	36	356	85	−110	419
	1998–1999	24	321	44	273	403
D	1991–1992	34	293	78	31	397
	1998–1999	24	306	32	260	371

Samples in 1990–1991, 1991–1992 were taken 3 times per month. In 1998–1999 samples were taken twice per month

Similarly, during the high biomass production monitored in the past, maximum pH values were above 9.00 with peaks up to 9.56. But in 1998–1999 maximum pH never exceeded 8.68.

The same consideration can be made for E_h values. In 1990–1991 (92) they ranged from −110 to 445 mV, whereas in 1998–1999 they varied between 31 and 403 mV.

As for water transparency, the data of the Secchi disk show a general increase of the water turbidity, although at station A, the bottom was always visible. At station B, in the presence of significant macroalgal biomass, water was very clear and the bottom was always visible in 1990–1991. But in 1998–1999 the bottom visibility was often affected by the high sediment re-suspension and on an average the disk was visible at a distance corresponding to 87% of the water depth, but sometimes only at 25%. Water transparency decreased similarly also at stations C and D (Table 6).

4. Discussion

As a result of the increase of nutrient inputs and strong hydrological alterations between the 1970s and the 1980s, macroalgae replaced seagrasses in the whole central lagoon. On about half (ca. 66 km^2) of the basin SC ranged between 5 and 20 kg m^{-2} fwt. The abnormal growth (in situ RGRs up to 30% day^{-1}) and production (GPP: up to 130 kg m^{-2} $year^{-1}$ fwt) of *Ulva rigida* (ca. 90% of the total biomass) showed values among the highest in the world. *Ulva* production and degradation cycles were repeated over a period of ca. 20 years (Sfriso & Marcomini, 1996a, chap. 15; Sfriso et al., 1992) and their effect was a strong alteration of the lagoon environment.

Then, in the 1990s *Ulva* rapidly declined. In 1993, the highest macroalgal SC reduced to 15.2% only and in 1998 the SC, NPP and GPP lowered to 1.6, 2.9, 2.4% of the values monitored in 1987. Literature (Sfriso & Marcomini, 1996b) shows that at first, macroalgal variations were mainly due to the climatic changes recorded on a global scale, and particularly in the Po Delta. But then, the biomass reduced because of other cofactors such as the increase in sedimentation fluxes (Sfriso & Marcomini, 1996b) and the grazing impact of invertebrate herbivores (Balducci et al., 2001; Sfriso & Pavoni, 1994) which, in the absence of anoxic crises, enhanced their role as "biomass controllers". In particular, between 1989 and 1991, unfavourable weather conditions in May–June, the period of highest *Ulva* biomass increase, caused a marked reduction of the macroalgal growth. In 1991 peak values corresponded to 30–50% of the values recorded in the 1970s and the 1980s and the lagoon coverage reduced significantly. In the mean time the lack of a marked biomass coverage (laminar free-floating thalli of *Ulva* were densely stratified in the water column) favoured the tidal or wind induced re-suspension of surface sediment. Sediment fluxes (g m^{-2} $year^{-1}$) increased up to 4.2 times. The increase in water turbidity and the settling of fine material on *Ulva* thalli significantly affected the macroalgal growth (Sfriso & Marcomini, 1996b) leading to a reduction of the dramatic anoxic crises which had occurred annually in June–July. These anoxic crises had caused the death of fish and macrofauna in the central lagoon. As a consequence of the decline in anoxic events during the 1990s macrofauna survived the summer and the impact of invertebrate herbivores on the macroalgal biomass increased significantly. Balducci et al. (2001) found that the amphipod *Gammarus aequicauda* Martinov and other organisms fed on *Ulva* thalli at a rate close to, and even over (up to +165% a day), the daily biomass production in July–August. Those results suggested the possibility that grazers, in the absence of anoxic crises, could act as controllers of the *Ulva* production in the lagoon.

Other factors, such as the biomass harvesting and the decrease of nutrient inputs played a minor role in the initial biomass decrease (Sfriso & Marcomini, 1996b). Biomass harvesting, in fact, accounted for a maximum of ca. 50,000 m^3 $year^{-1}$ (CVN, 1994), only ca. 0.5% of the total macroalgal GPP. Moreover, the biomass harvesting by means of reaping machines usually started in April–May when *Ulva* exhibited the highest growth. Under those conditions a SC reduction favoured the increase of the biomass growth rate and/or promoted phytoplankton blooms by re-suspending nutrients trapped in surface sediments.

Similarly, the reduction of nutrient inputs in the lagoon did not significantly affect the macroalgal growth in the central lagoon because of the high seawater exchange (ca. 60% of the entire volume at any semidiurnal tidal cycle: 12 h) which provided the necessary amounts of nutrients (Sfriso & Marcomini, 1994, 1996a, chap. 15). In fact the total amount of nutrient inputs (direct and indirect sources) in the central lagoon (Andreottola, Cossu, & Ragazzi, 1990) accounted only for 42% of the nutrients annually stored in the macroalgal standing crop and temporarily trapped in the surface sediments during the summer. Moreover, an amount equivalent to ca. 4.3 times the total nitrogen introduced yearly into the central lagoon was lost to the atmosphere by denitrification as N_2O and N_2 (Sfriso & Marcomini, 1994).

Finally, since 1994 the direct impact of hundreds of clam-fishing devices has contributed to the further reduction of macroalgal biomass as well as seagrass colonisation in areas free of macroalgae. This has primarily been due to the disturbance of the lagoon bottom and the re-suspension of large amounts of fine sediments with a significant reduction of light transmission. For example, *Zostera marina* which had started to colonise bottoms between the Malamocco-Marghera canal and Venice since 1990, disappeared in 1994 when the intense clam-fishing began, with the exception of a small area along the southern coast of the Lido Island.

Results presented in Tables 3 and 5, show the way some physico-chemical variables changed according to the variation of the macroalgal production and degradation cycles. In the absence of biomass, they showed values remarkably reduced, both in the mean and the maximum values.

During the 1980s, in the presence of macroalgal beds, water transparency was high during most of the year and the bottom was visible almost everywhere in the central lagoon. The only exceptions were the inner part of the Malamocco-Marghera canal, which is characterised by intense naval traffic, and the period of biomass decomposition when bacterial (Sorokin et al., 1996) or phytoplankton blooms and the sediment release of colloidal sulphur, which turns the water column white, took place (Sfriso et al., 1987). In contrast, water transparency was markedly reduced in the 1990s and the bottom was visible only near the sea inlets and in the areas populated by macroalgae such as the one close to the Lido island (Fig. 2). Everywhere else water transparency was <0.5 m. Sometimes visibility was difficult at 0.2 m and the bottom was not visible at low tide either. Sfriso and Marcomini (1996b), Orel et al. (2000), Sfriso (2000) have noticed that the amount of sediment re-suspension has increased significantly in the past decade. At first, this was due to the lack of macroalgal coverage, which in the past reduced the effect of water turbulence on the surface bottom, but more recently it was a consequence of the intensive fishing of the bivalve *Tapes philippinarum*. This species is caught by means of ca. 700–800 hydraulic and mechanical dredges which disrupt the sediment texture down to a depth of ca. 20 cm (Orel et al., 1998; Pranovi & Giovanardi, 1994; Sfriso, 2000).

The decrease of macroalgal biomass also significantly affected some environmental variables such as DO, pH and E_h which are strongly influenced by the alternation of macroalgal production and decomposition periods. The mean DO was more than halved in the period 1987–1998 and during this period there have been no records of the high values ($>300\%$) frequently monitored before 1990 or of the extraordinary releases of oxygen bubbles. Moreover the frequent hypoxic–anoxic crises monitored in the past have disappeared almost completely and pH and E_h have compressed their fluctuations around the mean values.

As far as phytoplankton is concerned, literature shows that microalgae played a minor role in the primary production of the lagoon (Marcomini et al., 1995; Pavoni, Marcomini, Sfriso, Donazzolo, & Orio, 1992; Sfriso & Marcomini, 1996a, chap. 15; Sfriso et al., 1992) because of the dominance of macroalgae. Before 1990, significant phytoplankton blooms were only recorded in areas where either macroalgae were absent or they had collapsed following anoxic crises (Sfriso et al., 1987, 1988). In particular phytoplankton bloomed in June–July after the decomposition of the macroalgal biomass. Under those conditions Chl. *a* peaked above 100 $\mu g\ dm^{-3}$ for 1–2 weeks. Then phytoplankton bloomed again but with decreasing intensities for 1–2 months and the values were $<5\ \mu g\ dm^{-3}$ in August–September when macroalgae started to grow again (Sfriso et al., 1987).

Figs. 3 shows that phytoplankton was low and negligible (Chl. *a* up to 29 mg m^{-3}) in comparison with the macroalgae which covered the same area (biomass up to 20 kg fwt m^{-2}, Fig. 2). When macroalgal distribution and production decreased markedly, an increase of phytoplankton might be the expected consequence, but this was not the case. Phytoplankton displayed more or less the same concentrations as those previously found in the presence of the macroalgal biomass. During early 1990s the lagoon was colonised by the bivalve *Tapes philippinarum* (on average from 0.2 to 1 kg m^{-2}) and its filter-feeding behaviour probably accounted for the removal of the microalgae from the water column in 1993. Then, in 1998, when fishing practices changed from hand to hydraulic and mechanical catch, the re-suspension of fine particles (silt and clay) increased by about one order of magnitude (from 65 to

759 kg m^{-2}, dwt at Sacca Sessola) diminishing light penetration and therefore inhibiting phytoplankton blooms (Sfriso, 2000). The only difference compared to the past was a further shifting of the highest Chl. *a* concentrations towards the northern part of the central basin where the bivalve fishing was low.

Such changes have become more evident since the significant phytoplankton decrease recorded in the four stations between 1990–1992 and 1998–1999. The greatest declines (both mean and peak concentrations) were monitored mostly at stations D and C (Table 5), but also in many other areas of the lagoon where phytoplankton bloomed frequently above 100 μg dm^{-3} (Sfriso & Pavoni, 1994; Sfriso et al., 1987; 1988). In 1998–1999 the highest Chl. *a* concentration monitored in the study areas was only 6.1 μg dm^{3}. Such data are in agreement with the decrease in phytoplankton abundance (cells dm^{-3}) recorded in the same period (Facca, Sfriso, & Socal, 2002a).

Furthermore, whereas Chl. *a* concentrations from the 1987, 1993 and 1998 campaigns were quite similar, with significant declines at the four stations, the concentration of Phaeo. *a* followed the opposite trend. It increased significantly during the June campaigns, doubled at stations A and B, but halved at stations C and D. Probably the disruptive effect of the fishing devices on the microphytobenthos communities (Facca et al., 2002b) and their re-suspension in the water column could account for the increase of that pigment, especially at station B where clam fishing activities were more intense and at station A where tidal current conveys the fine material re-suspended in the inner lagoon areas.

5. Conclusions

This study focuses on macroalgal and phytoplankton changes recorded in the central part of the Venice lagoon since late 1980s. It is a coastal environment highly modified and affected by hypertrophic-dystrophic conditions which led to an uncontrollable production of nuisance macroalgae similar to most Mediterranean's shallow areas, but it is possibly the only case witnessing the natural recovery to new mesotrophic conditions. At present macroalgal biomass and production in the central lagoon have decreased strongly and SC, NPP and GPP in 1998 are respectively ca. 1.6, 2.9 and 2.4% of the values monitored in 1987. However, in spite of the almost complete disappearance of macroalgae, phytoplankton did not increase, but showed low variations or decreasing trends. Filter-feeding effects of bivalves which colonised the bottom free of macroalgae and the high sediment re-suspension due to hundreds of clam-fishing devices which reduced water transparency account for these changes. In parallel with the macroalgal biomass reduction some physico-chemical variables which were strongly related to the biomass production and degradation (such as the DO saturation, the pH and E_h of the water column) show a marked reduction in extreme values whereas water turbidity increased significantly as a result of both the absence of a macroalgal coverage and intense clam-fishing activities. Studies carried out during the preparation of this paper show that the macroalgal biomass and water transparency are still continuing to decline.

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