Macroalgal biomass and species variations in the Lagoon of Venice (Northern Adriatic Sea, Italy): 1981-1998*

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SUMMARY: Over the past hundred years, the composition of the submerged aquatic vegetation of the Lagoon of Venice has changed considerably, due to increased anthropic activities and large-scale industrialisation. Seagrasses have gradually been reduced, whereas macroalgae (*Ulva rigida*, *Enteromorpha* spp., *Cladophora* spp., *Chaetomorpha* spp.) have increased. Macroalgal overgrowths peaked between 1970 and 1990 to the extent that, in order to estimate macroalgal biomass and coverage, the Venice *Magistrato alle Acque* (the Lagoon water management authority) started a series of investigations including monthly in situ measurements and aerial photo surveys. In the present paper these data are compared with available information on the Lagoon of Venice, and the widespread phenomenon of macroalgal proliferation is described. At the end of the 1980s, in our study area (78 km^2 in the central part of the Lagoon) biomass values ranged from 10 to 25 kg wet weight (w.w.) m^{-2} (sub-areas of Lido and Sacca Sessola), with a total mean biomass of 392,000 t w.w. A slight reduction took place in 1992 and at the end of the 1990s the highest biomass values were relatively low, 5 kg w.w. m^{-2}, with a total mean biomass of 1,600 t w.w. Our qualitative research carried out in 1991 on 130 sampling stations in the study area showed that soft substrates had a greatly reduced floristic composition in the five sub-areas in comparison with the control area (from 18 to 6 taxa), with Chlorophyta (50-80%) prevailing over both Rhodophyta (14-38%) and Phaeophyta (0-14%), and a slight or reduced distribution of seagrasses. The trend in macroalgal reduction during the 1990s corresponded to seagrass recolonisation, mainly of *Zostera marina,* taking advantage of new, compacted, oxidised and stabilised sediments that were no longer covered by extensive *Ulva* beds.

Key words: Lagoon of Venice, macroalgal distribution, *Ulva*.

RESUMEN: CAMBIOS EN LA BIOMASA Y LA COMPOSICIÓN ESPECÍFICA DE MACROALGAS EN LA LAGUNA DE VENECIA (ADRIÁTICO NORTE, ITALIA): 1981-1998. – Durante los últimos cien años la composición de la vegetación acuática sumergida de la laguna de Venecia ha cambiado considerablemente a causa del incremento de actividades antrópicas y la industrialización a gran escala. Las fanerógamas marinas han reducido su extensión y las macroalgas (*Ulva rigida*, *Enteromorpha* spp., *Cladophora* spp., *Chaetomorpha* spp.) la han aumentado. El crecimiento de macroalgas alcanzó una cota máxima entre 1970 y 1990 hasta el extremo que la Agencia Veneciana del Agua inició una serie de proyectos para estimar la biomasa y el recubrimiento algal que incluían medidas mensuales en el campo y fotografías aéreas. En este trabajo estos datos se comparan con la información disponible de la laguna de Venecia, describiéndose las proliferaciones algales. A finales de los años 80, en nuestra área de estudio (78 km2 en la parte central de la laguna) las biomasas oscilaban entre 10 y 25 kg de peso húmedo por metro cuadrado (subáreas de Lido y Sacca Sessola) con una biomasa media de 392.000 Tm. Una leve disminución tuvo lugar en 1992, y, al final de los 90, las biomasas más elevadas eran relativamente bajas (5 kg m-2), con una biomasa media de 1600 Tm. Nuestras investigaciones, llevadas a cabo en 1991 a lo largo de 130 estaciones, mostraron que los substratos blandos tienen una composición florística reducida en las cinco subáreas en comparación con una área control (de 18 a 6 táxones), con las algas verdes (50-80%) predominando sobre las algas rojas (14-38%) y las pardas (0-14%), y una leve representación de las fanerógamas marinas. La tendencia observada hacia una reducción de la biomasa algal durante los años 90 se corresponde con la recolonización por parte de las fanerógamas, principalmente *Zostera marina*, que coloniza favorablemente los nuevos sedimentos estabilizados y compactados desprovistos de los prados de *Ulva*.

Palabras clave: Laguna de Venecia, distribución de macroalgas, *Ulva*.

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INTRODUCTION

Anthropic activities and heavy industrialisation after the Second World War have had a serious environmental impact on the Lagoon of Venice. Damage includes the effects of waste from the industrial zone of Porto Marghera, run-off from the drainage basin (covering about 1900 km^2, of which 1000 km^2 are under intensive agriculture), and hydrologic alterations due to dredging of navigable canals (e.g. Malamocco-Porto Marghera Canal) (Cossu *et al*., 1984, Zucchetta, 1983), which all result in more rapid drainage into the Lagoon.

During the 1970s and 1990s, due to nutrient over-enrichment and trophic alterations, dense macroalgal overgrowths, mainly represented by *Ulva rigida* C. Agardh and secondarily by *Enteromorpha* spp., *Cladophora* spp. and *Chaetomorpha* spp., occurred extensively in the Lagoon, clogging fishing nets and resulting in bad odours and a fall in oxygen levels after the death of the algae. Between the early works of Schiffner and Vatova (1937) and Vatova (1940) and the 1980s little information was published on submerged plant communities in the Lagoon of Venice. However, anecdotal information indicates the gradual reduction of seagrasses such as *Zostera marina* (L.), *Z. noltii* Hornemann and *Cymodocea nodosa* (Ucria) Ascherson, and an increase in macroalgae, especially in the central part of the Lagoon. In the 1980s, studies on macroalgal proliferation (Croatto, 1982; Viglia, 1983) reported a biomass of 1,000,000 t w.w. for the whole Lagoon, with peaks of 10-25 kg w.w. m^{-2}. *Ulva rigida* C. Agardh, *Gracilariopsis longissima* (S.G. Gmelin) Steentoft, L.M. Irvine et Farnham (=*Gracilaria verrucosa* (Hudson) Papenfuss, in Furnari *et al.*, 2003), *Valonia aegagropila* C. Agardh and *Chaetomorpha linum* (O.F. Müller) Kützing were the most widespread algal species. Again during the 1980s, Solazzi *et al*. (1981) and Sfriso (1987) reported two algal distribution maps for the central Lagoon for *Ulva rigida*. By the end of the decade, the literature on seagrass and algal biomass, distribution and floristic composition on soft sediments had become extensive (Caniglia *et al*., 1992; Magistrato alle Acque, 1992; Rismondo and Scarton, 1991; Rismondo *et al*., 1995, 1997; Scarton *et al*., 1995; Sfriso, 1987; Sfriso *et al*., 1992a; Solazzi *et al*., 1991, 1994).

At the present, in our study area algal coverage is smaller than 1 km^2 and mean biomass is lower than 0.1 kg w.w. m^{-2} (Magistrato alle Acque, 2002). For this reason local water authority reduced survey and selective harvesting operations of algal masses.

Our aim in the present work is to provide a historical description of macroalgal biomass and coverage patterns between 1980 and 2000, based on our data and information in the literature. Data for 1981 (Solazzi *et al*., 1981) and 1987 (Sfriso *et al*., 1992a) referring to a total area of about 130 km^2 in the central Lagoon were re-analysed and compared with our results from a ten-year monitoring period (1989-1998) to estimate macroalgal biomass and coverage, carried out monthly from spring to autumn by both air and sea surveys over an area of 78 km^2 by the *Consorzio Venezia Nuova*, on behalf of the *Magistrato alle Acque* of Venice, the local water authority. In this work, we use maps and biomass values as a term of comparison only referring to May and June, the most representative months as regards maximum biomass extent. A specific qualitative-quantitative investigation of floristic composition at 130 stations was performed only in 1991.

STUDY AREA

The Lagoon of Venice (Fig. 1) is a coastal lagoon system covering 550 km^2 (45°20'N, 12°23'E). It is connected to the Adriatic Sea through three wide sea entrances (also called 'mouths') 10-20 m deep and 400-900 m wide, which were dredged for purposes of navigation, with a water turnover of 1.5 x 10^8/m^3 every 12 hours (Magistrato alle Acque, 1989). The Lagoon, with a network of natural and artificial channels, has an average depth of about 1 m and a tidal range of about 60 cm, which exceeds 1 m during spring tides. It is composed of shallows, tidal flats exposed during low tide, and salt marshes submerged at high tide. It is generally subdivided into three morphological basins. The northern and southern basins typically contain aquaculture farms, salt marshes and seaweed meadows (Caniglia *et al*., 1992). The central basin, in which the city of Venice is located, is subject to the heaviest environmental impact, due to great nutrient enrichment and discharge of waste from the nearby industrial zone. New algal species for the Lagoon of Venice native to other geographical areas have not been found on the soft substrata but only on hard substrata of islands and littorals (Rismondo *et al.*, 1993; Gargiulo *et al.*, 1992; Curiel *et al.*, 1996; 1999, 2001, 2002).

Mapping was carried out over an area of 78 km^2 encompassing much of the central Lagoon (Fig. 1).

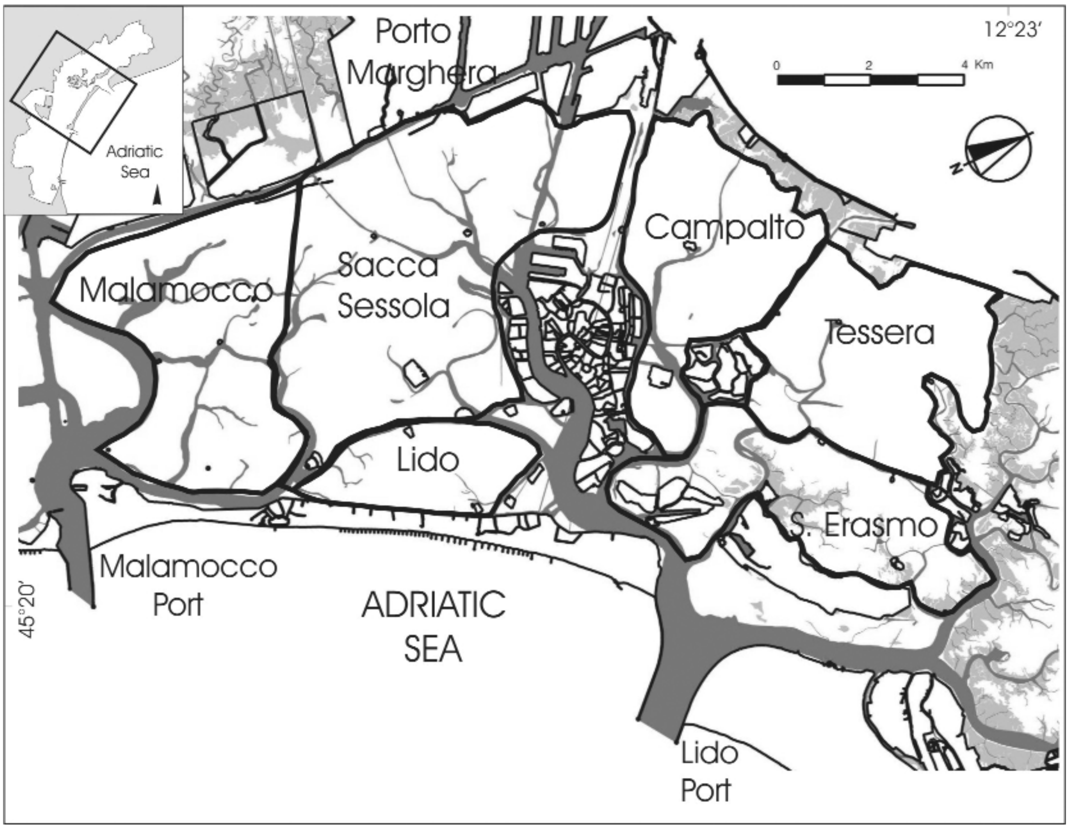

FIG. 1. – Central Lagoon of Venice and study area. Air and sea survey carried out only in Lido, Sacca Sessola, Campalto, Tessera and S. Erasmo. Floristic specific research was carried out in each sub-area including Malamocco only in 1991.

For convenience, the study area was divided into five sub-areas: Lido, Sacca Sessola, Campalto, Tessera, and S. Erasmo. Salinity in Campalto and Tessera is 10-24‰ and varies greatly due to freshwater inputs from nearby rivers and low water turnover. The other sub-areas have higher average salinity (20-35‰) because of their proximity to the mouths. The Lido and Sacca Sessola sub-areas are located between basins drained by the Lido and Malamocco mouths. Only floristic research was undertaken in Malamocco (May and June 1991) because during our project (1989-1998) this area did not show significant macroalgal overgrowths.

Sandy sediments prevail near the mouths and silt-clay in inner areas with weak currents (Barillari, 1981). Water temperature is normally 4-5°C in winter, and in the inner areas, where salinity is reduced, the water occasionally freezes, as happened in 1991. Water temperatures may reach 27-29°C in July and August, and sometimes exceed 30°C in areas with low water turnover and in the presence of macroalgae. Specific data about physico-chemical characteristics (nutrients, oxygen, turbidity, etc.) in central Lagoon stations has been reported in Sfriso (1995).

MATERIALS AND METHODS

Aerial surveys of algal coverage were carried either by helicopter (at an altitude of 300 m) or by aeroplane (3,000 m) between 1989 and 1998 over a few months each year. Macroalgal coverage was mapped using vertical aerial photos, and data were transferred to a computerised data-base from which the surface area could be calculated accurately.

Wet weight algal biomass (kg w.w. m^{-2}) was measured during surveys by boat and collected in a 1x1x1 m frame. Some of the stations were part of an already established monitoring network of 28 stations; others were chosen each time according to seasonal coverage patterns. Algae were drained of water: special care was taken to remove water completely from the thalli. Three replicates, according to Sfriso *et al*. (1991), were collected at each station in order to obtain a mean biomass value within 10% of the best estimate. Algal species were determined both in the field and in the laboratory. Macroalgal biomass maps of May or June distributions are presented for some years (1989, 1990, 1992, 1994, 1996, 1998; Fig. 4) and the complete sequence for the last ten years is shown in Table 1. Total mean biomass was estimated as average biomass values collected during boat surveys. Biomass and coverage data refer mainly to *Ulva rigida* as the presence of other species was always very low (biomass <0.1 kg/m^2). Aerial photograms and maps were processed with Autocad software. Calculation of surface coverage was carried out with the same program. To draw up biomass data for each study area (Table 1), we used biomass average values collected at the stations.

In order to compare our data with earlier information, algal distribution maps for 1981 (Fig. 2; from Solazzi *et al.*, 1981 modified) and 1987 (Fig. 3; from Sfriso *et al.*, 1992a modified), for the whole central Lagoon (about 130 km^2) in the same time period were re-analysed on our maps (78 km^2). Algal coverage and biomass data are listed in Table 1.

A more specific quantitative and qualitative research was organised in May and June 1991 by the Ecology Section of the City of Venice at 130 stations in the six sub-areas of the central Lagoon (Table 2).

In this study, the Malamocco sub-area was used as a term of comparison because during the projects it had never been severely affected by algal overgrowth. Algae collected in a 1 square metre, 1 metre high frame in three replicates were drained and conserved in plastic bags at -18°C. The laboratory procedure included defreezing and microscope observation for species determination and calculation of coverage and biomass.

Similarity indexes among the sub-areas were calculated according to the formula of Sorensen and Kulczinsky (Boudouresque, 1971). The similarity (SIMPER) routine (Clarke and Warwick, 1994) was used to analyse which species were responsible for the differences between sites.

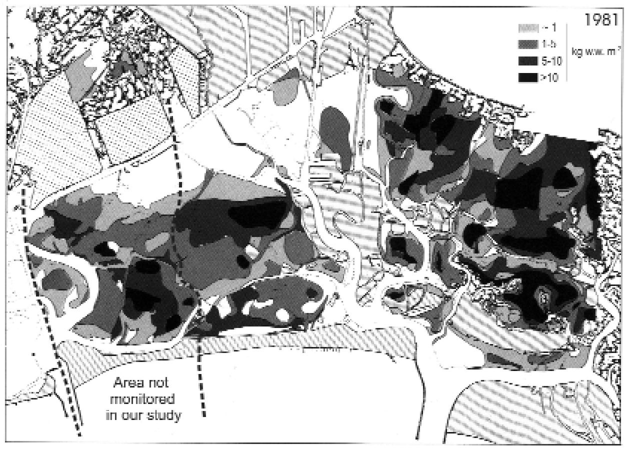

FIG. 2. – Algal distribution of *Ulva rigida* in central Lagoon of Venice in June 1981 (from Solazzi *et al.*, 1981, modified).

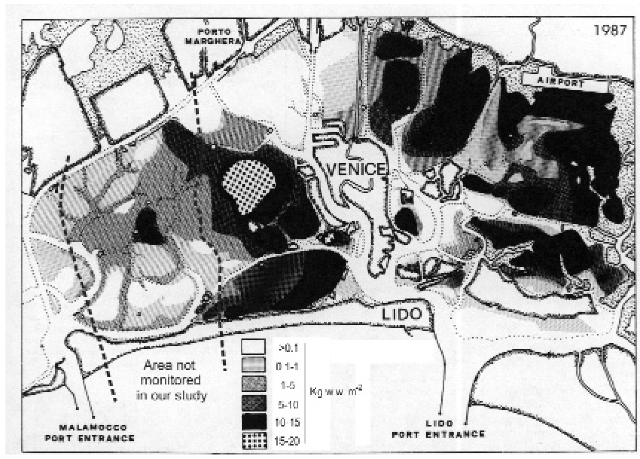

FIG. 3. – Macroalgal distribution in central Lagoon of Venice in June 1987 (from Sfriso *et al.*, 1992a, modified).

RESULTS

Distribution of algal proliferation

Processing of the map of Solazzi *et al.* (1981; Fig. 2), concerning only *Ulva rigida*, indicated an algal coverage of 53 km^2, or 68% of the study area, maximum biomass values being more than 10 kg w.w. m^{-2}. Only the area between the city of Venice and the Porto Marghera industrial zone had no algae. For the whole central basin, Solazzi *et al*. (1981) had reported an average total biomass of 600,000 t w.w., with a peak of 25 kg w.w. m^{-2}. According to our processed analysis, the average total biomass was 276,000 t w.w. (Table 1).

For the 1987 survey from Sfriso *et al*. (1992a; Fig. 3) we calculated an algal coverage of 44 km^2, or

TABLE 1. – Sequence of biomass and algal coverage from 1981 to 1998. Data of 1981 (Solazzi *et al*., 1981) and 1987 (Sfriso *et al*., 1992a) were re-analysed for present study area of 78 km^2.

Year	Algal coverage (km^2)	%	Mean total biomass t (w.w.)	Mean biomass for station kg w.w. m^{-2}
1981	53.1	68.1	276.000	—
1987	43.7	56.0	392.000	—
1989	22.9	29.6	135.700	5.8
1990	25.4	32.8	66.100	3.6
1991	14.9	19.3	28.300	2.8
1992	20.1	26.0	43.700	3.3
1993	9.3	11.9	15.900	2.9
1994	10.4	13.5	16.600	1.9
1995	10.1	13.1	3.400	0.9
1996	4.0	5.2	250	0.4
1997	3.4	4.4	550	0.6
1998	4.3	5.5	1.300	0.7

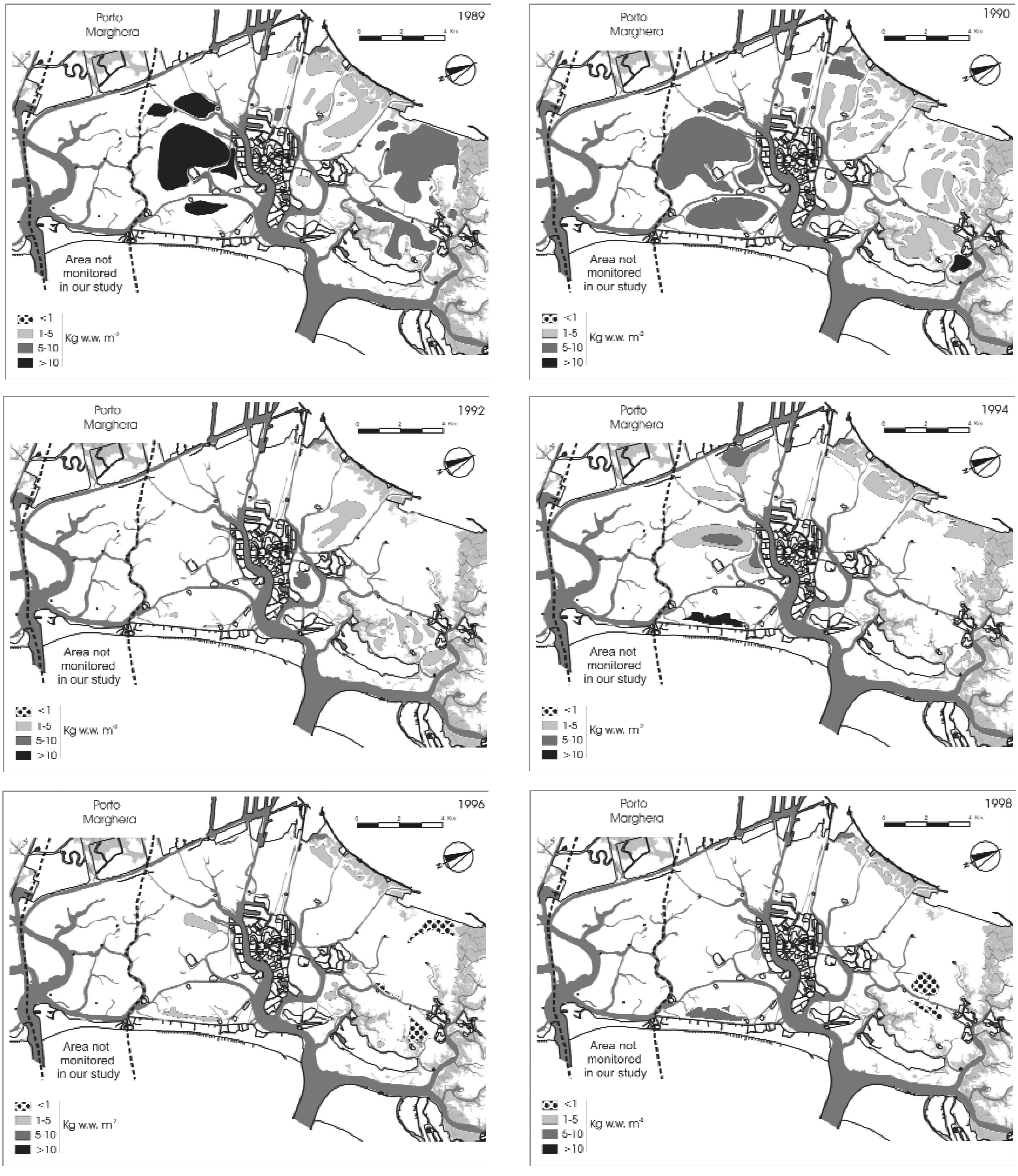

FIG. 4. – Macroalgal distribution in central Lagoon of Venice in May or June in 1989-1998.

56% of our study area. The area between Venice and Porto Marghera was without coverage, as in 1981. For the whole central basin, Sfriso *et al*. (1992a) reported an average total biomass of 558,880 t w.w., with a peak of 25 kg w.w. m^{-2}. Our re-analysis of the 1981 data for our study area indicates an average total biomass of 392,000 t w.w. (Table 1).

For both these algal maps (1981 and 1987), the highest density occurred throughout the study area, showing that the overgrowth was not local but spread over the whole central basin during different years.

For the period 1989-1992 (Figs. 4, Table 1), there was a reduction in algal coverage, total biomass (more than 50%, maximum 135,700 t w.w., minimum 43,700 t w.w.) and average biomass per station (from 5.8 to 2.8 kg w.w. m^{-2}).

Between 1993 and 1995 (Fig. 4; Table 1), there was a further reduction in macroalgal overgrowth, with coverage values of 11.9-13.5% in the study area and an average total biomass of 3,400-15,900 t w.w. (biomass 0.9-2.9 kg w.w. m^{-2}). Compared with the 1981-1987 period, this represented reductions of about 80% of coverage and 90% of biomass. In the Lido sub-area, macroalgae was only found close inshore. East of Venice, there was a shift in maximum growth towards Porto Marghera, with a corresponding reduction in Sacca Sessola, historically an area with high biomass and coverage. In the northern sub-areas, reductions were recorded in Campalto and Tessera, with coverage limited to more sheltered, shallow sites close to the mainland.

Between 1996 and 1998 (Figs. 4; Table 1), the mean algal biomass was further reduced, with coverage of the study area of 3.4-4.3 km^2 (4.4-5.5%) and a mean total biomass varying between 250 and 1,300 t w.w. Comparisons with data for 1981-1987 show coverage and biomass reductions of more than 90%.

Between the late 1980s and early 1990s, the *Magistrato alle Acque* carried out large-scale algae harvests from April to July, using collecting boats adapted for navigation in shallow waters. In 1989 and 1990, about 50,000 m^3 of seaweeds (especially *Ulva rigida*) were collected. This biomass was partly confined in special areas and partly re-used for paper production (Monegato et al., 1992)

In the following years, collections decreased, from 34,500 m^3 in 1991 to 3,500 m^3 in 1996. Over the following few years, harvesting was carried out sporadically and limited to the Lido sub-area, due to the reduced quantity and coverage of algae.

Composition of algal proliferation

During the years of greatest macroalgal overgrowth (1989-1990), *U. rigida* was the dominant species for most of the year. Only in some limited areas until the end of the 1980s were *Gracilariopsis longissima* and *Gracilaria armata* (C. Agardh) Greville recorded in significant quantities (5-10 kg w.w. m^{-2}). *G. longissima* in particular was once so common and widespread in the Lagoon that it was harvested (about 10,000 t w.w. in the 1980s) for industrial purposes (Provincia di Venezia, 1998).

In spring and summer, other Chlorophyta taxa made up less of the macroalgal coverage. Included are several species of the genera *Enteromorpha* (*E. intestinalis* (L.) Nees, *E. clathrata* (Roth) Grev., *E. flexuosa* (Wulfen) J. Agardh, *E. prolifera* (O.F. Müller) J. Agardh), *Chaetomorpha* (*C. linum* (O.F. Müller) Kützing and *C. aerea* (Dillwyn) Kützing), and *Cladophora* (*C. albida* (Nees) Kützing, *C. sericea* (Hudson) Kützing, *C. rupestris* (L.) Kützing, *C. dalmatica* Kützing). In these algal mats *Rhizoclonium tortuosum* (Dillwyn) Kützing and *Rhizoclonium lubricum* Setchell et Hamel often occurred. In winter, when algal coverage was low, colonial benthic diatoms (*Navicula* and *Melosira*) and many Phaeophyta (particularly *Punctaria latifolia* Greville, *Ectocarpus siliculosus* var. *siliculosus* (Dillwyn) Lyngbye, and *Scytosiphon lomentaria* (Lyngbye) Link were recorded. Rhodophyta, with the exception of *Gracilariopsis longissima* until the end of the 1980s, always had moderate coverage and biomass on soft substrates. Shells and gravel may become essential for the development of *Ceramium virgatum* Roth (= *Ceramium rubrum* auctorum, in Furnari *et al.*, 2003), *C. diaphanum* (Lightfoot) Roth, *Nitophyllum punctatum* (Stackhouse) Greville, *Porphyra leucosticta* Thuret in Le Jolis, and *Dasya baillouviana* (Gmelin) Montagne. *Valonia aegagropila* C. Agardh, once very frequent, is now recorded only along the northern shores of the Lagoon and in aquaculture farms. From the 1990s, *U. rigida* was partially replaced by *Gayralia oxysperma* (Kützing) Vinogradova *ex* Scagel *et al*.

Our research carried out in May and June 1991 at 130 stations of our five sub-areas showed greatly reduced floristic compositions with respect to the sixth sub-area (control area), Malamocco (Table 2). In the five sub-areas, Chlorophyta varied between 50 and 80%, Rhodophyta between 14 and 38% and Phaeophyta between 0 and 14%; the number of algal species varied between 6 and 17 (including one Chrysophyta) and only one seagrass was found (*Zostera noltii*). *Ulva rigida* was the prevailing species (70-90% of stations) as regards mean coverage (30-70%) and mean biomass (0.4-2.3 kg w.w. m^{-2}). Other species such as *Gracilariopsis longissima*, *Gayralia oxysperma*, *Enteromorpha* spp. and *Cladophora* spp. sometimes reached high occurrence levels (up to 70% of stations), but not as regards mean coverage (< 10%) and mean biomass (< 0.3 kg w.w. m^{-2}) for all stations.

In the Malamocco control sub-area (Table 2), where water turnover is higher, the floristic composition was more balanced, with 44% Chlorophyta, 32% Rhodophyta and 9% Phaeophyta, for a total of 20 taxa (included one Chrysophyta) and the two seagrasses *Zostera marina* and *Z. noltii*. *Gracilariopsis*

TABLE 2. – Data collected from May to June during 1991 in six sub-areas in central Lagoon of Venice.

Taxa	Occurrence (%)	Mean coverage (%)	Mean biomass kg w.w. m^{-2}
Sub-area Campalto			
Ulva rigida	90	43.7	1.6
Gracilariopsis longissima	70	4.1	0.3
Ceramium rubrum	<10	< 0.1	-
Bryopsis plumosa	<10	< 0.1	-
Enteromorpha intestinalis	<10	< 0.1	-
Gayralia oxysperma	<10	1.0	-
Shannon diversity index = 1.3			
Sub-area S. Erasmo			
Ulva rigida	70	28.6	0.4
Gracilariopsis longissima	70	5.8	0.1
Gayralia oxysperma	70	3.6	-
Cladophora albida	60	0.2	-
Ceramium rubrum	10	0.2	-
Enteromorpha intestinalis	10	0.2	-
Chaetomorpha aerea	10	0.1	-
Vaucheria dichotoma f. marina	10	< 0.1	-
Bangia atropurpurea	<10	< 0.1	-
Cladophora hutchinsiae	<10	0.1	-
Cladophora laetevirens	<10	0.1	-
Cladophora rupestris	<10	0.1	-
Cladophora sericea	<10	0.1	-
Enteromorpha ralfisii	<10	0.1	-
Rhizoclonium lubricum	<10	< 0.1	-
Scytosiphon lomentaria	<10	0.1	-
Ulotrix flacca	<10	< 0.1	-
Zostera noltii	<10	0.1	-
Shannon diversity index = 2.1			
Sub-area Lido			
Ulva rigida	90	70.0	1.3
Gayralia oxysperma	50	5.0	-
Enteromorpha intestinalis	30	1.0	-
Cladophora hutchinsiae	10	< 0.1	-
Gracilariopsis longissima	10	5.0	-
Ceramium rubrum	5	< 0.1	-
Callithamnion corymbosum	3	< 0.1	-
Dictyota dichotoma v. dichotoma	3	< 0.1	-
Shannon diversity index = 1.5			
Sub-area Tessera			
Ulva rigida	90	40.0	1.4
Gracilariopsis longissima	70	0.9	-
Ceramium rubrum	30	0.2	-
Gayralia oxysperma	10	2.5	-
Sub-area Tessera (cont.)			
Enteromorpha intestinalis	10	0.3	-
Bryopsis plumosa	<10	< 0.1	-
Chaetomorpha linum	<10	< 0.1	-
Cladophora lehmanniana	<10	< 0.1	-
Cladophora rupestris	<10	< 0.1	-
Cladophora sericea	<10	< 0.1	-
Shannon diversity index = 1.8			
Sub-area Malamocco			
Gracilariopsis longissima	90	10.9	0.4
Ulva rigida	70	6.4	0.1
Gayralia oxysperma	70	13.9	-
Dictyota dichotoma v. dichotoma	70	2.3	-
Chaetomorpha linum	50	4.7	-
Enteromorpha intestinalis	50	2.7	-
Cladophora sericea	30	< 0.1	-
Acrosorium venulosum	<10	< 0.1	-
Bryopsis duplex	<10	< 0.1	-
Ceramium diaphanum	<10	< 0.1	-
Ceramium rubrum	<10	0.2	-
Cladophora albida	<10	0.1	-
Cladophora hutchinsiae	<10	< 0.1	-
Cladophora rupestris	<10	0.1	-
Codium fragile sub. tomentosoides	<10	0.1	-
Ectocarpus siliculosus var. siliculosus	<10	0.2	-
Lomentaria clavellosa	<10	< 0.1	-
Polysiphonia sanguinea	<10	< 0.1	-
Polysiphonia spinulosa	<10	0.1	-
Vaucheria dichotoma f. marina	<10	0.1	-
Zostera marina	<10	1.0	-
Zostera noltii	<10	1.0	-
Shannon diversity index = 2.9			
Sub-area Sacca sessola			
Ulva rigida	90	60.0	2.3
Gayralia oxysperma	50	10.0	-
Enteromorpha intestinalis	60	5.0	-
Cladophora sericea	60	1.0	-
Cladophora rupestris	50	1.0	-
Gracilariopsis longissima	30	4.0	-
Scytosiphon lomentaria	5	< 0.1	-
Shannon diversity index = 1.8			

longissima was dominant for frequency (90% of stations) and mean biomass (0.4 kg w.w. m^{-2}) and *Gayralia oxysperma* for mean coverage (14% of stations). In this sub-area occurrence and mean coverage of taxa were more balanced and *Ulva rigida* was no longer the dominant species.

By using Anova analysis no differences were detected among the six areas for occurrence, mean coverage and biomass. The Shannon diversity index, calculated for coverage percentage, was higher in the Malamocco area than in the others (Table 2).

Hierarchical clusterings, carried out using Sorensen's formula (Fig. 5A), show two main sub-area groups: the first closer to the mouths (S. Erasmo, Malamocco) and the other closer to the mainland following a gradient (Lido, Sacca Sessola, Campalto, Tessera).

Kulczinsky's formula (Fig. 5B) applied to the mean coverage taxa for each sub-area highlights a clearcut difference between Malamocco and the

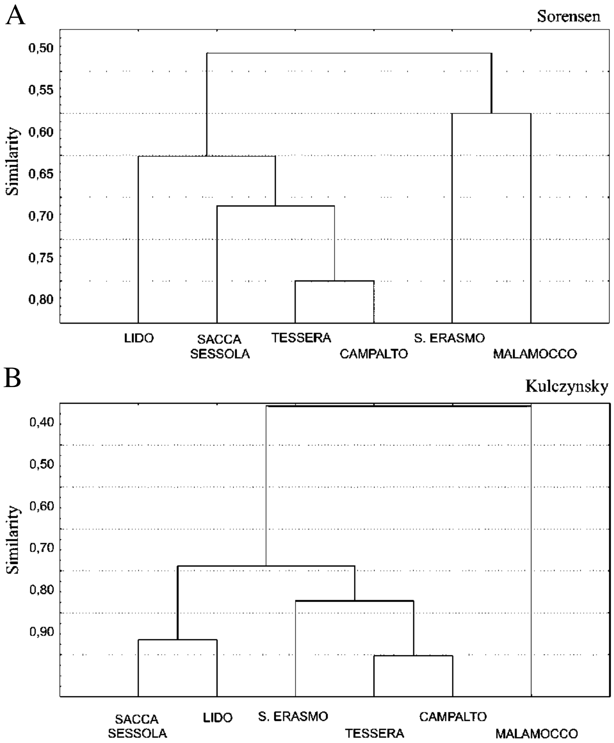

FIG. 5. – Floristic similarity dendrograms among sub-areas, from Sorensen (A) and Kulczinsky (B) formulas (WPGMA linkage).

other sub-areas; these five fall into two groups: one to the north of Venice (Tessera, Campalto, S. Erasmo) and the other to the south of the city (Sacca Sessola, Lido). Results of SIMPER analyses indicate that *Ulva rigida* is the species most responsible for similarity in the Campalto and Tessera areas (95%) and *U. rigida* and *G. oxysperma* are the most responsible species in the Lido and Sacca Sessola areas (85% and 7% respectively). *U. rigida*, *G. longissima* and *G. oxysperma* are the most responsible in Malamocco and S. Erasmo areas (38, 34 and 21% respectively).

During 1996-1998, when macroalgal biomass was almost completely missing, patchy recolonisation by *Zostera noltii* and *Z. marina* occurred in Lido, Malamocco and Sacca Sessola (Curiel *et al*., 1995; Sfriso 1996). Recolonisation of marine seagrasses, which had begun to restore the macrophyte communities present in the Lagoon before the 1970s, may have been arrested and reversed by illegal fishing for clams [*Tapes philippinarum* (Adams and Reeve, 1850)], during which sediments are churned up by boat engines and the clams are collected in dredges. The beginning of the 1990s marked a progressive increase in production of short-naked clam carried out with unauthorised dredging equipment. This activity is performed on a massive scale in the central Lagoon and involves more than 2000 fisherman with an annual turnover of 100 million USD (Sorokin *et al.,* 1999). At present this intensive fishing activity causes a serious environmental impact, mainly due to coarsening of the grain-size distribution of surface sediments, contributing to the acceleration of erosive processes (Consorzio Venezia Nuova, 1993) and alteration of the benthic biocenosis over large areas (Pranovi and Giovanardi, 1994).

DISCUSSION AND CONCLUSIONS

The study shows the history of diminishing macroalgae (mostly *Ulva rigida*) in the central Lagoon of Venice from the 1980s to the 1990s, in coverage (from 53 to 4.3 km^2), in total biomass (from a range varying between 276,000 and 392,000 t w.w. to a diminished range varying between 250 and 1,300 t w.w., and in mean biomass for station (from 5.8 to 0.4-0.7 kg w.w. m^{-2}).

The study indicates that higher macroalgae biomass is related to lower specific diversity. Diversity is generally low in more sheltered areas closer to the mainland (Campalto, Tessera) and in the proximity of watershed areas (Lido, Sacca Sessola), with species numbers varying between 6 and 10 (prevailing Chlorophyta and limited presence of Phaeophyta and Rhodophyta). Where water turnover is higher, as in the S. Erasmo and Malamocco areas, species diversity varies from 18 to 22 taxa, the ratios between Chlorophyta, Rhodophyta and Phaeophyta are more balanced both in number and coverage, and the Shannon diversity index is higher.

Cluster analysis highlights differences between Malamocco and the other five sub-areas, both for species diversity and taxa coverage. Kulczinsky's formula shows significant diversity for coverage between Campalto and Tessera, north of Venice, and Lido and Sacca Sessola, south and along the watershed.

There is now a wealth of literature on factors affecting macroalgal distribution (e.g. Morand and Briand 1996). Several lagoons, estuaries and coastal basins like the Lagoon of Venice are highly sensitive to pollution and eutrophic conditions. Anthropic activities, together with dumping of industrial, agricultural and urban wastes, greatly disturb the natural balance of algal communities living in such environments. As a result, those species with the highest environmental requirements (i.e. *Fucus virsoides* J. Agardh, *Cystoseira barbata* C. Agardh, *Zostera* spp., *Cymodocea nodosa*) have gradually reduced their distribution, coverage and biomass since the 1940s (Schiffner and Vatova, 1937; Sighel, 1938; Vatova, 1940).

Several works have quantified pollutants reaching the Lagoon of Venice from the drainage network via rivers and from the sea through the three mouths, and the amounts taken up by algae and surface sediments (Sfriso, 1996; Sfriso *et al*., 1992a, 1992b, 1994). Several papers present mathematical models of the life-cycle of *Ulva* (Bendoricchio *et al*., 1993; Coffaro and Bocci, 1997; Coffaro and Sfriso, 1997). However, no definitive conclusions have been reached about recent macroalgal biomass trends in the Lagoon and the complex series of interrelated environmental factors which govern them.

As regards the causes of reduced macroalgal overgrowth which began around 1990, several works suggest a combination of particular climatic conditions (Curiel *et al*., 1995; Sfriso, 1996; Sfriso and Marcomini, 1996) and lower nutrient inputs to the Lagoon (Pavoni *et al*., 1992; Sfriso *et al*., 1994). In the early 1990s, precipitation in unusual periods, the strong and frequent north-east wind (*bora*), spring frosts with the formation of ice and long-lasting low temperatures hampered macroalgal overgrowths in April and May.

Frisoni and Cejpa (1989) report that wind contributes greatly to re-oxygenation of the Lagoon, and calm conditions are thought to be one of the factors contributing to the occurrence of dystrophic episodes. Data show that if cold winds and low temperatures persist through the April-May period, when macroalgal growth and photosynthetic activity are usually at their highest (Brinkhuis, 1977; Duke *et al*., 1989; Fillit, 1995), then lower biomass levels persist for the rest of the season. Lavery *et al*. (1991), in the eutrophic estuary of Peel-Havery (Western Australia), suggest that combinations of events are of major significance in explaining changes in macroalgae.

It is quite interesting to note that two other shallow coastal basins of the Northern Adriatic, within 100-200 km of the Lagoon of Venice (Grado-Marano Lagoon and Po Delta) showed similar macroalgal overgrowth pattern in the 1980s and 1990s, followed by reductions (Piccoli, 1993; Viaroli *et al*., 1996; Curiel *et al*., 1998b). At present macroalgal overgrowth no longer represents a serious problem at a large scale but occurs only at very confined sites. The repetition on a large geographic scale of the same phenomenon in the same years, suggests a factor—such as climate—acting extensively, in addition to local decreased eutrophication affecting algal growth. Unpublished data from meteorological stations in the Venice area show that 1983, 1986, 1988 and 1989 were the least rainy of the last 50 years, whereas rainfall increased by 10-20% in the 1990s (Magistrato alle Acque, 1998). Available statistical processing of average monthly water temperatures for the two periods 1985-1990 and 1992-1997 (Magistrato alle Acque, 1998) indicates lower values for the latter period, resulting in conditions less favourable to the growth and proliferation of *Ulva rigida*.

The gradual reduction in algal coverage has led to increased oxygenation of sediments, and the same sediments have changed from soft and black to firm and pale in colour. Further colonisation by marine seagrasses favoured bottom stabilisation, enhancing oxygenated conditions both in water and surface sediments. As observed by Sfriso *et al*. (1999), the lack of anoxic crises, which had earlier killed macrofauna and herbivores feeding on seaweeds, has restored the natural grazing pressure, thus limiting algal biomass production.

Macroalgal overgrowth in the Lagoon of Venice is the same as that recorded in other places of the world (Morand and Briand, 1996). In this phenomenon *Ulva rigida* represents the dominant species for coverage and biomass, and is associated with the genera *Enteromorpha*, *Cladophora*, *Gracilariopsis* and *Chaetomorpha*, which reach significant biomass values only at very few stations. These species colonise the intertidal zone, are ubiquitous, opportunistic, and efficient in taking up nutrients, and also increase their numbers efficiently by both sexual reproduction and vegetative propagation (Morand and Briand, 1996; Rosenberg and Ramus, 1984).

Moreover, like Lavery *et al*. (1991), also in other areas of the Lagoon, we observed that, after the decline in *Ulva* biomass, *Chaetomorpha linum* resumed dominance.

Monitoring carried out since the early 1990s shows that algal species from other geographic areas, such as *Undaria pinnatifida* (Harvey) Suringar (Rismondo *et al*., 1993), *Sargassum muticum* (Yendo) Fensholt (Gargiulo *et al*., 1992), *Antithamnion pectinatum* (Curiel *et al*., 1996), *Sorocarpus* sp. (Curiel *et al*., 1999), *Desmarestia viridis* (O.F. Müller) Lamouroux (Bellemo *et al*., 2001) *Polysiphonia morrowii* Harvey (Curiel *et al*., 2002), *Lomentaria hakodatensis* Yendo and *Prasiola crispa* (Lightfoot) Kützing (Curiel *et al.*, in press) do not affect the floristic composition of soft substrates, but only of hard rocky ones, with rapid colonisation and competition with local species (Curiel *et al.*, 1998a, 2001).

The importance of a regular monitoring of submerged aquatic vegetation as an important indicator of water and sediment quality has been well understood by local authorities (Magistrato alle Acque di Venezia). At present a vegetation mapping programme and the calibration of a satellite mapping programme is ongoing.

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