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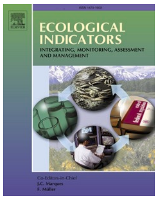

Macrophyte changes in transitional water systems: Role of water and sediment parameters, the Venice Lagoon as study case

Adriano Sfriso[a,*], Alessandro Buosi[a], Abdul-Salam Juhmani[b], Yari Tomio[a], Marion Adelheid Wolf[a], Katia Sciuto[c], Andrea Augusto Sfriso[c]

[a] Department of Environmental Sciences, Informatics and Statistics (DAIS), University Ca' Foscari Venice, Via Torino 155, 30170 Mestre (Ve), Italy
[b] Department of Biology and Biotechnology, Faculty of Science, The Hashemite University, Zarqa 13133, Jordan
[c] Department of Chemical, Pharmaceutical and Agricultural Sciences, University of Ferrara, Via Luigi Borsari 46, 44121 Ferrara, Italy

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ABSTRACT

The changes in macrophyte biodiversity and cover from the soft bottoms of 87 stations spread in the entire Venice Lagoon in 2011, 2014, 2018 and 2021 have been analyzed. Results showed a strong macrophyte resilience with an increase in the spread of sensitive macroalgae and aquatic angiosperms, especially *Z. noltei* and *R. cirrhosa,* which were not affected by the increase of non-indigenous species (NIS) introduction.

The simultaneous analysis of macrophyte variables and the main water and sediment parameters carried out in 2021 highlighted the key role of water transparency and salinity to regulate the vegetation, especially the presence/absence of aquatic angiosperms and sensitive macroalgae. Vice versa, high chlorophyll-*a*, total suspended solids, nitrogen and silicate concentrations in the water column, and high moisture, low grain-size and phosphorus concentrations in surface sediments favored the presence of opportunistic species, especially *Ulva rigida, Gracilariopsis longissima, Agardhiella subulata* and *Solieria filiformis*. The distribution of the aquatic angiosperms and the 41 most widespread macroalgae in association with the main environmental parameters allowed us to highlight their different ecological value, their possible presence/absence and abundance; indeed, their spatial and temporal changes can be excellent tools to determine and predict the ecological status of transitional water systems (TWS).

These results carried out in a polyhedric basin such as the Venice Lagoon, composed by a complex of very different microhabitats, can be considered representative of most environmental conditions present in the main TWS of the Italian coastline, and spatial and temporal macrophyte changes can be excellent tools to determine and predict their ecological status evolution.

1. Introduction

After a long period of high eutrophication level which lasted from the end of the Second World War to the end of the '90s (Marcomini et al., 1995; Morand and Briand, 2006), the trophic conditions of the Venice Lagoon changed significantly since the early 2000s, with a strong decline of nuisance macroalgae (Sfriso and Facca, 2007) and nutrient concentrations, both in the water column and surface sediments (Sfriso et al., 2005). During the '80s, macroalgae, mainly *Ulva rigida* C. Agardh, showed a massive growth (biomass: 5–20 kg FW m^{-2}; gross production: 18.6 million tonnes FW y^{-1}), followed by a rapid decline with extensive anoxic phenomena that killed benthic and fish fauna. In this period, macroalgal biodiversity reached the minimum value in history (Solazzi et al., 1991). During the '90s, the synergy of various factors, especially climatic changes (Sfriso and Marcomini, 1996), contributed to reduce the macroalgal biomass by approx. 90 % (with peaks over 95 % in the

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Abbreviations: NIS, non indigenous species; TWS, transitional water systems; ARPAV, Regional Agency for Environmental Prevention and Protection of the Veneto; ISPRA, Italian Institute for Environmental Protection and Research; MaQI, Macrophyte Quality Index; pHw, pH in water column; Ehw, redox potential in water column; DO, dissolved oxygen; Chl-*a*, chlorophyll-*a*; Phaeo-*a*, phaeophytin-*a*; RP, reactive phosphorus; DIN, Dissolved Inorganic Nitrogen; NH_4^+, ammonium; NO_2^-, nitrite; NO_3^-, nitrate; SiO_4^{4-}, silicate; TSS, total suspended solids; pHs, pH in surface sediments; Ehs, redox potential in surface sediments; Fines, sediment fraction <63 µm; Ptot, total phosphorus; Pinorg, inorganic phosphorus; Porg, organic phosphorus; PCA, principal component analysis.

[*] Corresponding author.

E-mail address: sfrisoad@unive.it (A. Sfriso).

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central basin) and reduce significantly angiosperm spread (Sfriso and Facca, 2007). In this period *Ruppia cirrhosa* survived only in the fishing valleys which are separated from the free lagoon by artificial stone reefs (Mannino et al., 2015). Contributing causes of these events were the increase of sediment resuspension by wave motion (due to the reduction/absence of biomass cover), the increase of invertebrate grazing (due to the reduction of anoxic events), and the progressive decreasing of nutrients inputs. At the end of the '90s (1995–1999), the fishing of the Manila clam *Ruditapes philippinarum* Adams & Reeve, whose harvesting with hydraulic and mechanical dredges reached 40,000 tonnes y^{-1} (Zentilin et al., 2008), represented another factor that negatively influenced macroalgal growth. Since 2010 the lagoon showed a rapid environmental recovery with the increase of aquatic angiosperms and macroalgal biodiversity (Sfriso et al., 2022).

In order to assess the ecological status of the lagoon in the framework of the European Water Directive (2000/60/EC), transposed into Italian law through Legislative Decree 152/2006, in 2011 the monitoring of the ecological status of the entire lagoon started by applying ecological indices based on macrophytes (macroalgae and aquatic angiosperms), benthic fauna and fish fauna. Macrophyte sampling on the soft substrata of 118 (2011) and 88 (2014, 2018, 2021) stations was carried out in late spring-early summer. At each station the biomass, cover, abundance, and the taxonomic list of aquatic angiosperms and macroalgae were recorded. In addition, the most common physico-chemical parameters of the water column and surface sediments were also monitored.

This study analyses the changes in macrophyte cover and biodiversity in the entire Venice Lagoon during the 4 sampling years, from 2011 to 2021, enhancing the high resilience of this basin whose environmental conditions are representative of the conditions present in most of the Italian TWS, (Sfriso et al., 2017). Moreover, the correlations/associations of aquatic angiosperm (*Cymodocea nodosa* (Ucria) Ascherson*, Zostera marina* Linnaeus*, Zostera noltei* Hornemann*, Ruppia cirrhosa* (Petagna) Grande) cover, some macroalgal variables (biomass and cover, sensitive taxa, crustose calcareous taxa, Rhodophyceae and Chlorophyceae cover), and the 41 most spread macroalgae were analyzed simultaneously with the determination of a high number (24) of water and surface sediment parameters.

The obtained results highlight the most important factors driving the presence/absence and increase/decrease of aquatic angiosperms and many macroalgae in TWS and allow to understand their ecological status. The analysis of the most common environmental parameters, in fact, allows us to predict or exclude the presence/absence of individual taxa and forecast the future evolution of the water basin considered.

2. Materials and methods

2.1. Study area

The study has been performed in 87 common stations spread throughout the entire area of the Venice Lagoon (Fig. 1). Sampling was carried out in late spring-early summer in 2011, 2014, 2018 and 2021. The studied basin represents the largest Mediterranean lagoon with a surface of approx. 549 km^2, a mean depth of approx. 1.2 m and the ecological characteristics recorded in the main Italian TWS (Sfriso et al., 2017). On average, 60 % of waters are exchanged with the sea each tidal cycle (12 h) throughout three large (400–900 m) and deep (10–16 up to 53 m) port-entrances (Lido, Malamocco, Chioggia), although in the choked areas water exchange can take up to 30–40 days (Cucco and Umgiesser, 2006).

The sampling sites that better represent all the different environmental conditions were chosen by the Regional Agency for Environmental Prevention and Protection of the Veneto (ARPAV), which also selected the ecological indices based on macrophytes (macroalgae and aquatic angiosperms) to determine the ecological status of the lagoon according to the European Water Directive (2000/60/EC). For a complete characterization of the different stations, the main water column and sediment parameters were also recorded.

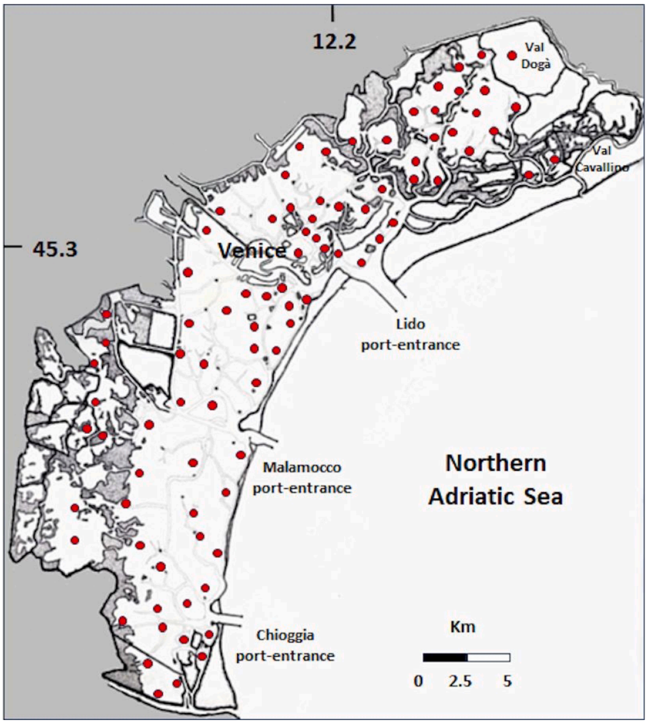


Fig. 1. Venice Lagoon and the 87 sampling stations.

2.2. Macrophytes

Macrophytes include macroalgae and aquatic angiosperms, and the latter include seagrasses and freshwater plants. *Cymodocea* and *Zostera* species, growing in marine waters, are considered seagrasses, while the species of the genus *Ruppia*, not being exclusively marine, are not universally accepted as seagrasses but are classified as freshwater plants, together with all the plant species that thrive in fresh or brackish waters (Short, 2003). For this reason, we use the term aquatic angiosperms when referring to all species together.

The nomenclature of macroalgae has been updated following Guiry and Guiry (2023) and the most recent specific literature. Sensitive species were selected according to the list of the Italian Institute for Environmental Protection and Research (ISPRA, 2011), whereas non-indigenous species were identified according to Sfriso et al. (2023).

Visual Census methods (Mellors, 1991) were used to estimate macrophyte cover in shallow clear waters, whereas in turbid conditions the presence/absence of macrophytes was assessed by touching 20 times the bottom with a rake in order to obtain a 5 % resolution according to Sfriso et al. (2014). The mean macroalgal biomass weight was reported within the following ranges: <0.1, 0.1–0.5, 0.5–1, 1–3, 3–5, 5–10 kg FWT m^{-2}. The dominance of Chlorophyta or Rhodophyta was determined by collecting 3–6 subsamples of macroalgae and weighting the different drained taxa. Samples were stored in a 4 % formaldehyde solution and morphologically identified by light microscopy. Taxonomically problematic taxa were determined with the DNA barcoding method (Hebert et al., 2003). The ecological status of each station was obtained by applying the Macrophyte Quality Index (MaQI, Sfriso et al., 2014) according to the Water Framework Directive (2000760/EC),

2.3. Environmental parameters

At each station, the following environmental parameters were measured: water transparency by Secchi disk; pH (pHw) and redox potential (Ehw) by a portable Hanna pHmeter (mod. HI98190, Hanna

Instruments Italia srl); dissolved oxygen (DO) by a WTW portable dissolved oxygen meter Oxi 3310 (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). Six samples of the entire water column were collected with a handmade bottle (diameter 4 cm, heigh 150 cm) and 0.25–1.0 L of the mixed subsamples were filtered with a Swinnex filter holder through Whatman GF/F glass microfiber filters (porosity 0.7 μm). Filters and 250 ml of filtered water samples were stored at −20 °C for Chlorophyll-*a* (Chl-*a*)*,* Phaeophytin-*a* (Phaeo-*a*) and nutrient (reactive phosphorus: RP, silicate: SiO_4^{4-}, DIN: sum of ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-)) determination following Strickland and Parsons (1984). Other two sub-samples (250–500 ml) were filtered through GF/F glass microfiber filters after desiccation at 130 °C for one hour, for the determination of total suspended solids (TSS). Filters were stored frozen within the laboratory analysis after washing with Milli-Q water to remove salts. Finally, subsamples of 20 ml were retained for the determination of salinity by titration method following Oxner (1962).

Surface sediments were collected with a Plexiglas corer (i.d. 10 cm) and the first 5 cm top-layers of three cores were carefully mixed in a tank. pH (pHs) and redox potential (Ehs) were immediately measured with a second portable Hanna pH-meter used only for sediment measurements. Two subsamples of 50–100 ml were frozen for the analyses of the main sediment characteristics (Fines: fraction <63 μm, density, moisture) and the concentration of total phosphorus (Ptot), inorganic phosphorus (Pinorg) and organic phosphorus (Porg).

Dry sediment density was obtained in laboratory after sediment desiccation at 110 °C in tared crucibles of approx. 30 ml. The percentage of Fines was determined by wet sieving approx. 50 g of dried sediment throughout Endecotts sieves (ENCO Scientific Equipment, Spinea, Italy). All analyses were performed in duplicate.

Total phosphorus (Ptot) was analyzed after 2 h combustion at 550 °C of 0.3–0.4 g of pulverized dried sediment, followed by 30 min sonication of the residue in 50 ml of 1 N HCl. After decantation of the sample for at least 1 h, 0.5 ml of the supernatant were taken with a graduated gas-chromatographic syringe and diluted to exactly 10 ml in volumetric flasks to have a final dilution of 1 L and the results expressed directly in μM. Phosphorus concentration was determined spectrophotometrically at the absorbance of 885 nm (Aspila et al., 1976). Inorganic phosphorus (Pinorg) was obtained with the same procedure used for Ptot but without combustion at 550 °C. The concentration of organic phosphorus (Porg) was determined by difference. All analyses were replicated in duplicate in different days and values were considered reliable when the coefficient of variation (standard deviation/mean) was <5 %.

2.4. Statistical analyses

Spearman's non-parametric coefficients ($p < 0.05$) of 12 macrophyte variables and 24 water/sediment parameters sampled in the 87 stations in late spring-early summer 2021 were determined using STATISTICA Software, release 10 (StatSoft Inc., Tulsa, USA). The coefficients between macrophyte variables and environmental variables have been ordinated in a table according to the number of significant values ($p < 0.05$, in bold).

The Principal Component Analysis (PCA) was performed with the same software and showed the multivariate patterns of the matrix after the deletion of some redundant parameters/variables (DIN, Ptot, Chl-*a* tot). The first two components were plotted in a plane to highlight the association between environmental parameters and macrophyte variables. Finally, the plot of the first two components of a PCA matrix, composed by the main 20 environmental parameters and the 41 most abundant macroalgae recorded in 2021 showed the affinity of each taxon with the single parameters.

3. Results

3.1. Macroalgae

The mean values of macroalgal biomass, macroalgal cover, total number of taxa, number of taxa per station, Rhodophyceae/Chlorophyceae ratio, total number of alien taxa, total number of sensitive taxa, number of sensitive taxa per station, number of calcareous taxa per station, total annual rainfall recorded in the 87 common stations spread in the soft bottoms of the entire lagoon in 2011, 2014, 2018, 2021 are shown in Fig. 2.

The mean macroalgal biomass ranged from 0.563 Kg FW m^{-2} in 2011 to 0.923 Kg FW m^{-2} in 2014, decreasing to 0.543 Kg FW m^{-2} in 2021, whereas the mean macroalgal cover was between 52.8 % and 74.6 %. The highest values of biomass and cover were recorded in 2014, characterized by the heaviest annual rainfall (1736 mm).

Overall, in the 4 sampling years, 186 taxa were found: 73 Chlorophyta, 91 Rhodophyta, 22 Ochrophyta, but the number recorded every year ranged from 126 to 132 taxa with averagely 18.9 taxa per station. On average, the number of Rhodophyceae (65) was higher than that of Chlorophyceae (53) accounting for a mean Rhodophyceae/Chlorophyceae ratio of 1.23. Globally, 21 NIS were found with an increasing trend ranging from 11 NIS in 2011 to 18 NIS in 2021. At the same time, according to ISPRA (2011) 40 sensitive taxa were recorded in total but every year the number was similar ranging from 25 to 29 taxa. However, the mean number of sensitive taxa per station increased from 1.93 in 2011 to 3.85 in 2021 (mean value 2.76) and that of crustose calcareous taxa per station changed from 0.87 to 1.47 (mean value 1.14). On average total rainfall was 1214 mm y^{-1}, ranging from 9.47 mm y^{-1} in 2011 to 1736 mm y^{-1} in 2014.

The mean percent presence (0–1 %, 1–5 %, 5–10 %, 10–20 %, 20–67 %) of the single taxa in the total stations and the list of species with a mean presence ≥ 20 % of the total stations are shown in Fig. 3.

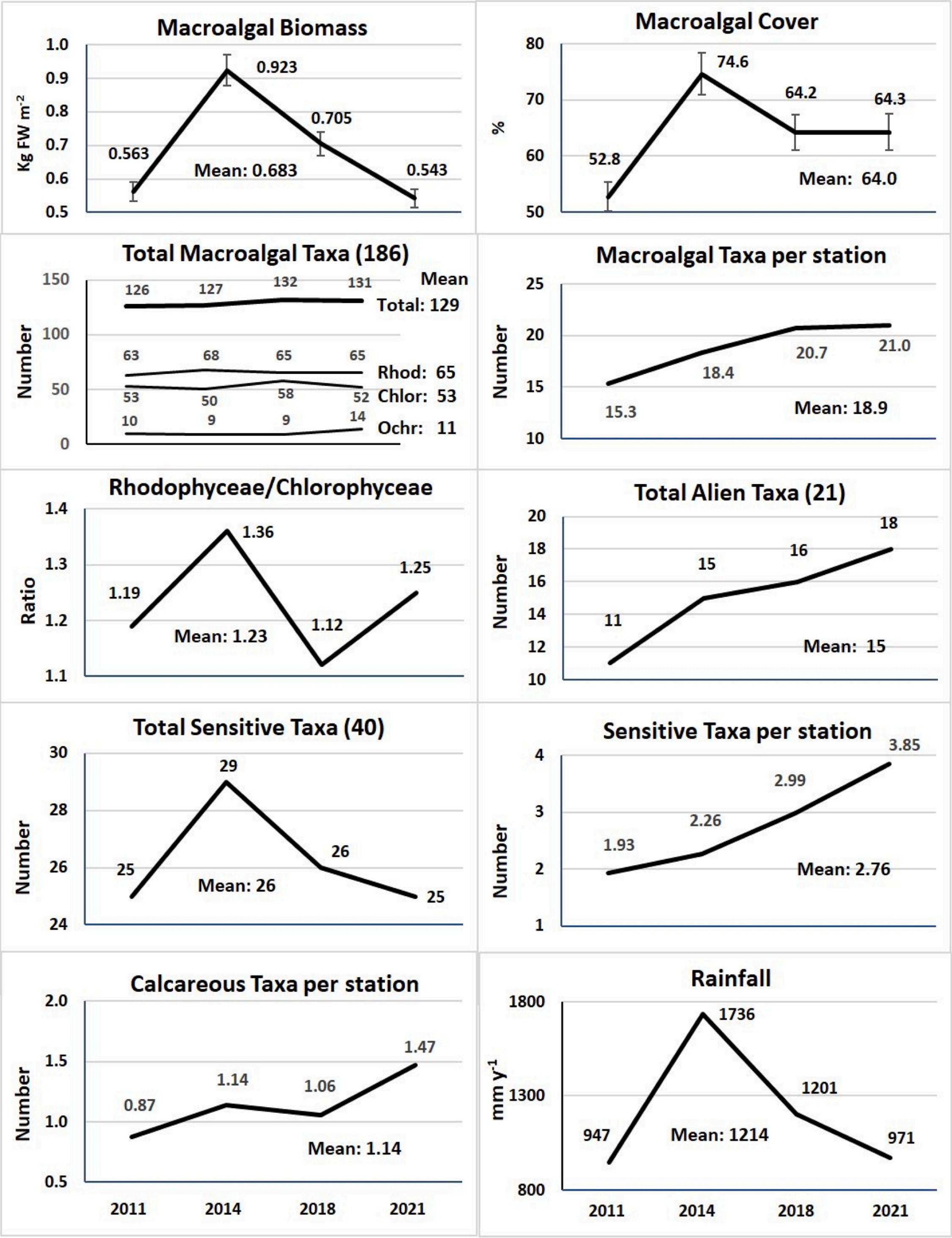
During the 4 sampling years the highest number of taxa (55) was occasionally recorded in less than 1 % of the total stations, decreasing progressively to 17 taxa in 10–20 % of the total sites, whereas 32 taxa were found in 20–67 % of the stations. The NIS *Ulva australis* Areschoug (before reported as *Ulva laetevirens* Areschoug)*,* together with the two native species, *Ulvella viridis* (Reinke) R. Nielsen, C.J. O'Kelly & B. Wysor and *Chondria capillaris* (Hudson) M.J. Wynne*,* showed the highest frequency (67.3–63.7 %). *Gracilaria gracilis* (Stackhouse) Steentoft, L.M. Irvine & Farnham followed with a lower frequency (48.8 %). The NIS *Agardhiella subulata* (C. Agardh) Kraft & M.J. Wynne (48.7 %), *Hypnea cervicornis* J. Agardh (45.3 %), *Uronema marinum* Womersley (44.4 %), and in a minor extent *Kapraunia schneideri* (Stuercke & Freshwater) Savoie & G.W. Saunders (23.2 %) and *Acanthosiphonia echinata* (Harvey) Savoie & G.W. Saunders (22.1 %), were also very frequent. Many taxa were present in one station only, although some of them were very abundant in the hard substrata or in other seasons.

3.2. Aquatic angiosperms

The percent mean frequency and cover of *Z. marina*, *Z. noltei, C. nodosa* and *R. cirrhosa* in the 87 common stations recorded during the 4 years are reported in Fig. 4**.**

All the species displayed a progressive increase; their mean frequency in the total station was 46.6 ± 14.1 %, doubling from 26.4 % in 2011 to 52.9 % in 2021, with a peak of 58.6 % in 2018, whereas their total cover was 28.5 ± 7.3 % increasing from 19.3 % in 2011 to 33.7 % in 2021, with a peak of 34.9 % in 2018.

Zostera marina was the species present in the greatest number of stations, as well as the angiosperm with the highest cover in all the 4 sampling years (Fig. 4). On average, it inhabited 28.7 % of the 87 stations, ranging from 9.20 % in 2011 to 15.9 % in 2018, with a slight decline in 2021. *Zostera noltei* followed with a mean frequency of 19.0 %; this species showed a strong increase, ranging from 5.7 % in 2011 to



Macroalgal Biomass

Macroalgal Cover

Total Macroalgal Taxa (186)

Macroalgal Taxa per station

Rhodophyceae/Chlorophyceae

Total Alien Taxa (21)

Total Sensitive Taxa (40)

Sensitive Taxa per station

Calcareous Taxa per station

Rainfall

Fig. 2. Mean values of some macroalgal variables recorded in the 87 common stations from 2011 to 2021. In all the figures the mean values are also reported. In the macroalgal taxa, alien taxa and sensitive taxa, the total number of taxa recorded in the 4 years is also reported. Abbreviations: Rhod. = Rhodophyta; Chlor. = Chlorophyta; Ochr. = Ochrophyta.

28.7 % in 2018. *Ruppia cirrhosa*, with a mean frequency of 6.9 % and a mean cover of 2.6 %, was the least widespread species; however, its frequency ranged from 3.4 % in 2011 to 12.6 % in 2021. Finally, *Cymodocea nodosa* showed the lowest changes, with an average frequency of 14.7 % and a total mean cover of 8.8 %.

3.3. *Environmental parameters*

During each late spring-early summer survey, in the 87 stations, some parameters of the water column and the 5 cm sediment top-layer were recorded. In Table 1 the values monitored in 2021 are reported.

On average, water temperature ranged from 20.6 to 31.6 °C, with a mean value of 26.6 °C. The mean salinity was 27.1 psu, with extreme values between 12.7 and 34.1 psu. The environment was averagely well

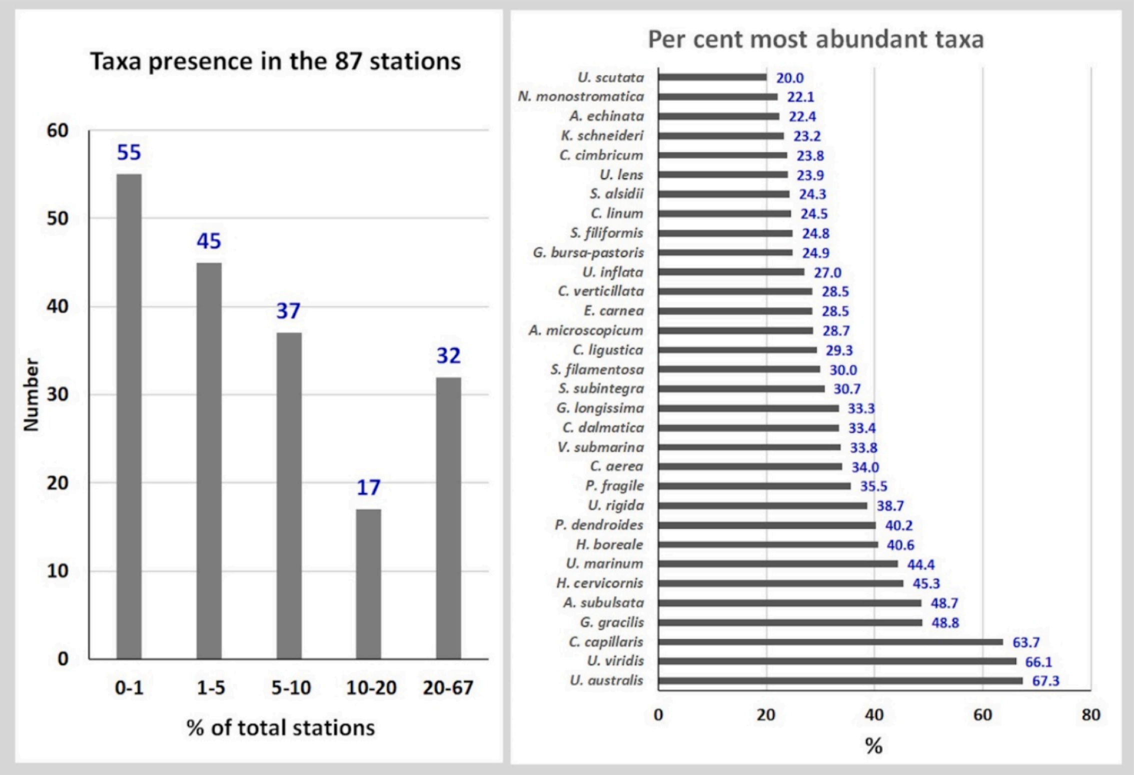


Fig. 3. On the left mean number of stations with the presence of single species in the ranges: 0–1%, 1–5%, 5–10%, 10–20%, 20–67% of total stations. On the right frequency of the most abundant taxa in the range 20–67%.

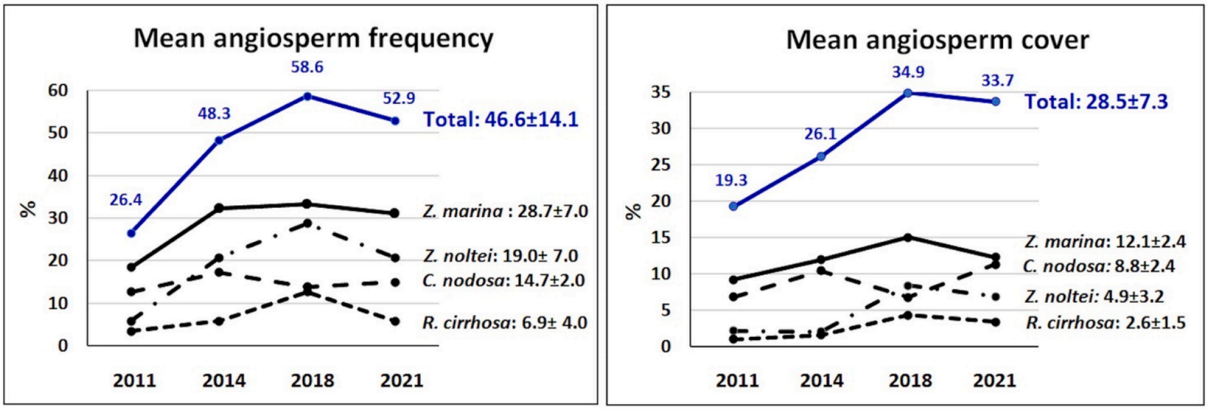


Fig. 4. Time variation of the aquatic angiosperms in the period 2011–2021. To the right of the linear trends the mean ± std values are reported.

oxygenated (8.6 mg/L), with a mean pHw of 8.33 and Ehw of 319 mV.

Water transparency was high and, on average, bottom was visible in 91 % of the station depth; the mean value of TSS was 35 mg/L. Similarly, total Chl-*a* (Chl-*a* tot) showed a mean value of 2.79 μg/L, peaking to 13.5 μg/L in a station close to the mainland. The inactive Chl-*a* (i.e. phaeopigments = Phaeo-*a*) were slightly higher than the active Chl-*a*.

Reactive phosphorus (RP), total dissolved nitrogen (DIN) and silicates (SiO_4^{4-}) showed mean values of 0.18, 5.81 and 13.1 μM, respectively, with peaks of 3.81, 43.5 and 33.3 μM. Ammonium (NH_4^+) was the most abundant nitrogen species with a mean value of 3.06 μM and a peak of 42.5 μM, whereas nitrates (NO_3^-) and nitrites (NO_2^-) showed mean values of 2.32 and 0.43 μM, respectively.

Surface sediments showed very different characteristics, presenting all the possible environmental conditions. pHs and Ehs, on average, were 7.46 and −286 mV with strong station variations. Fines ranged from 2.9 to 90.2 % (mean value: 43.4 %), sediment moisture from 21.5 to 79.8 % (mean value: 38.6 %) and dry density from 0.23 to 1.78 g DW cm^{-3} (mean value: 1.04 g DW cm^{-3}). Similarly, Ptot (mean value: 448 μg/g) ranged from 216 to 1034 μg/g and Pinorg (mean value: 313 μg/g) was averagely twice higher than Porg (mean value: 135 μg/g).

3.4. Statistical analyses

Spearman's non-parametric coefficients of macrophyte variables (12) and water/sediment parameters (26), recorded in late spring-early summer 2021, are shown in Table 2 highlighting several strong correlations. Sensitive and crustose calcareous taxa showed the highest frequency of significant correlations (14) with water and sediment parameters. In the water column, these macroalgae showed a significant positive correlation with water transparency and salinity, and negative

Table 1
Mean, standard deviation (std), minimum (Min) and maximum (Max) values of water column and surface sediment recorded in the 87 stations in late spring-early summer 2021.

Late spring-early summer 2021								
	Parameters		Mean		std	Min		Max
Water column	Temperature	°C	26.6	±	2.5	20.6	–	31.6
	Ehw	mV	319	±	41	206	–	418
	pHw	Units	8.33	±	0.09	8.05	–	8.57
	Salinity	psu	27.1	±	4.1	12.7	–	34.1
	DO	mg/L	8.6	±	1.4	5.8	–	13.2
	Transparency	%	91	±	12	44	–	100
	TSS	mg/L	35	±	14	16	–	84
	Phaeo-*a*	μg/L	1.64	±	1.92	0.15	–	11.8
	Chl-*a*	μg/L	1.30	±	0.93	0.06	–	2.99
	Chl-*a* tot	μg/L	2.79	±	2.66	0.32	–	13.5
	RP	μM	0.18	±	0.55	0.01	–	3.81
	NO_3^-	μM	2.32	±	2.61	0.02	–	11.4
	NO_2^-	μM	0.43	±	0.37	0.01	–	1.71
	NH_4^+	μM	3.06	±	5.10	0.08	–	42.5
	DIN	μM	5.81	±	6.06	0.40	–	43.5
	SiO_4^{4-}	μM	13.1	±	6.75	1.71	–	33.3
Sediment 5 cm top layer	pHs	Units	7.46	±	0.26	6.81	–	8.09
	Ehs	mV	−286	±	86	−414	–	−85
	Fines	%	43.4	±	18.0	2.9	–	90.2
	Moisture	%	38.6	±	11.3	21.5	–	79.8
	Density	g DW cm^{-3}	1.04	±	0.29	0.23	–	1.78
	Ptot	μg/g	448	±	136	216	–	1034
	Pinorg	μg/g	313	±	91	150	–	584
	Porg	μg/g	135	±	100	19	–	780

Table 2
Spearman's non-parametric coefficients of macrophyte variables and water/sediment parameters recorded in 2021. In Bold significant values ($p < 0.05$ *per* r > < 0.212). The last line and column report the number of significant values.

Parameters/ Variables	Sens. Algae	Calc. Algae	MaQI	*C. nod.* Cover	*Z. mar.* Cover	*R. cirr.* Cover	Algae number	Algae biomass	Algae Cover	*Z. nol.* Cover	Chlor. Cover	Rhod. Cover	Significant value number
Salinity	**0.39**	**0.42**	**0.47**	**0.37**	**0.28**	0.02	0.12	**0.27**	−0.01	−0.11	**0.24**	**−0.22**	8
Transparency	**0.57**	**0.54**	**0.60**	**0.32**	**0.36**	0.09	**0.26**	0.16	−0.02	0.18	0.17	−0.16	6
Chl-*a* Tot	**−0.39**	**−0.38**	**−0.42**	**−0.37**	**−0.21**	0.00	−0.17	**−0.22**	0.18	0.05	−0.20	0.16	6
Porg	**−0.23**	**−0.22**	−0.16	−0.17	**−0.22**	**0.21**	**−0.31**	−0.05	**0.29**	−0.14	0.03	−0.02	6
NH_4^+	**−0.32**	**−0.29**	**−0.30**	−0.17	−0.19	0.06	−0.09	**−0.23**	−0.17	**0.23**	−0.07	0.04	5
Phaeo-*a*	**−0.29**	**−0.34**	**−0.34**	**−0.37**	−0.15	0.01	−0.17	−0.18	0.15	0.03	−0.18	0.17	4
Chl-*a*	**−0.34**	**−0.26**	**−0.37**	**−0.30**	−0.207	0.00	−0.09	−0.17	0.17	0.06	−0.15	0.11	4
NO_3^{-}	**−0.48**	**−0.35**	**−0.37**	**−0.32**	0.04	−0.18	−0.18	−0.09	−0.02	0.05	−0.03	0.02	4
NO_2^-	**−0.47**	**−0.40**	**−0.42**	**−0.28**	−0.06	−0.09	−0.14	−0.11	−0.08	0.00	0.07	−0.08	4
DIN	**−0.46**	**−0.38**	**−0.39**	**−0.28**	−0.11	−0.08	−0.19	−0.14	−0.07	0.11	−0.01	−0.01	4
Ehs	−0.03	−0.04	0.03	−0.11	0.02	**0.33**	0.05	**−0.34**	**−0.28**	**0.30**	−0.10	0.10	4
Fines	**−0.32**	**−0.35**	**−0.33**	**−0.36**	−0.08	0.03	0.02	−0.08	0.02	0.12	−0.08	0.08	4
Moisture	**−0.21**	−0.17	−0.17	−0.14	**−0.23**	**0.25**	**−0.39**	−0.07	0.20	−0.18	0.05	−0.03	4
Density	0.20	0.15	0.17	0.12	**0.25**	**−0.24**	**0.34**	0.03	**−0.23**	0.18	−0.03	0.01	4
Ptot	−0.12	−0.09	−0.15	−0.07	**−0.22**	0.05	**−0.23**	0.10	**0.25**	**−0.27**	0.09	−0.07	4
DO	0.10	0.13	0.18	**0.22**	0.12	0.01	0.04	0.18	−0.07	0.13	**0.26**	−0.23	3
SiO_4^{4-}	**−0.27**	**−0.26**	**−0.22**	−0.20	−0.13	0.10	−0.17	−0.14	0.04	0.06	0.01	−0.02	3
Porg	−0.20	−0.15	−0.17	−0.13	**−0.21**	**0.26**	**−0.43**	−0.13	0.14	−0.15	0.09	−0.06	3
Pinorg	−0.05	−0.02	−0.13	−0.02	−0.11	**−0.22**	−0.04	**0.27**	0.18	**−0.31**	0.10	−0.08	3
pHw	0.15	0.07	**0.22**	**0.34**	0.00	0.05	−0.01	0.12	0.03	0.03	0.15	−0.13	2
TSS	**−0.21**	**−0.23**	−0.17	−0.17	−0.11	−0.01	−0.07	−0.13	0.03	0.02	0.02	−0.04	2
RP	−0.20	**−0.24**	−0.16	−0.12	**−0.25**	0.07	−0.16	−0.02	0.06	0.01	−0.11	0.07	2
pHs	−0.01	0.02	0.05	−0.20	**0.24**	0.02	−0.04	−0.14	**−0.24**	0.18	−0.03	0.02	2
Temperature	−0.10	−0.05	−0.10	0.00	**−0.28**	0.07	−0.16	−0.05	0.06	−0.02	−0.13	0.10	1
Ehw	0.06	0.06	−0.02	0.01	0.09	**−0.24**	0.11	0.02	0.11	−0.18	0.12	−0.14	1
Significant value number	14	14	12	11	11	7	6	5	5	4	2	2	

correlations with nitrites, nitrates, ammonium, DIN, Chl-*a*, Phaeo-*a*, silicates and TSS. By considering surface sediments, sensitive and crustose calcareous taxa were negatively correlated especially with Fines and, in a minor extent, with moisture and Porg concentration. The Macrophyte Quality Index (MaQI) showed 12 significant values with almost the same parameters. The cover of the angiosperms *C. nodosa* and *Z. marina* had 11 significant values, but with different parameters. *C. nodosa* was correlated with the same parameters found for sensitive and crustose calcareous taxa. *Z. marina,* besides, showed positive correlations with water transparency, salinity, sediment density, pHs and negative correlations with temperature, RP, moisture, Chl-*a,* Ptot and Porg. The other macrophyte variables showed only 2–6 significant correlations; the lowest number was found with Chlorophyta and Rhodophyta, both correlated in an opposite way with salinity and DO.

Salinity, water transparency (positive values), Chl-*a* tot (negative value) and Porg were the water column parameters most correlated (6–8 significant correlations) with macrophyte variables, especially with the presence of taxa of high ecological value, MaQI, *C. nodosa* cover and

Z. marina cover. In the water column, nitrogen compounds (i.e. nitrite, nitrate, ammonium and DIN) showed 4–5 negative correlations, whereas Ehs, Fines, moisture, density and Ptot had 4 significant values, followed by 2–3 correlations for the other parameters.

After the deletion of the redundant values, the PCA analysis between 33 environmental parameter/macrophyte variables, recorded in the soft substrata of the 87 stations spread throughout the lagoon, showed 10 components explaining 74.2 % of the total variance. Fig. 5 shows the results of the first two components. The parameters/variables are split into two groups correlated to good-high and poor-bad environmental conditions. Water transparency and salinity were the parameters characterizing the best environmental conditions, which favored the presence of calcareous taxa and more generally of species of high ecological value, but also led to a higher number of taxa, the presence of aquatic angiosperms and a lower chlorophycean biomass and cover. Other parameters linked to good ecological conditions were sediment density, pHw, pHs, DO and Ehw. Among the aquatic angiosperms, *C. nodosa* and *Z. marina* were better correlated to higher environmental conditions, whereas *Z. noltei* and *R. cirrhosa* characterized environments slightly more deteriorated.

At the opposite plot side (Fig. 5), the other group was characterized by parameters associated to the worse conditions (i.e. nitrites, nitrates, ammonium, silicates, Fines, TSS, temperature), but also by a high sediment moisture and concentration of Porg and Pinorg. Reactive phosphorus (RP) was intermediate and strictly associated to *R. cirrhosa.*

Fig. 6 shows the associations between environmental parameters, total aquatic angiosperms and the 41 macroalgae present in more than 20 % of the 87 stations: 24 Rhodophyta, 15 Chlorophyta and 2 Ochrophyta. The latter, except for *Gongolaria barbata* (Stackhouse) Kuntze and *Vaucheria submarina* (Lyngbye) Berkeley, were recorded in a limited number of stations.

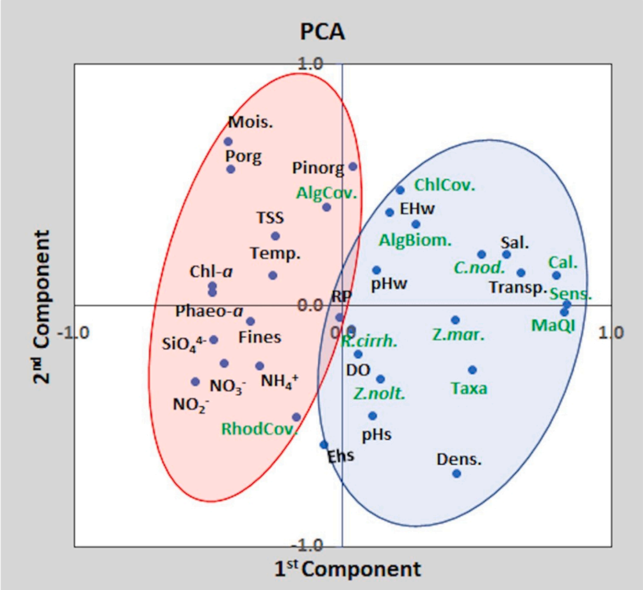


Fig. 5. Plot of PCA analysis between environmental parameters (in black) and macrophyte variables (in green) sampled in 2021. They are clustered into groups characterizing high (blue circle) and low (red circle) environmental conditions. Macrophyte variable abbreviations: AlgBiom. = Algal Biomass; Algcov. = algal cover; Calc. = Calcareous macroalgae; ChlCov. = Chlorophyta cover; *C.nod.* = *Cymodocea nodosa* cover; *R.cirrh.* = *Ruppia cirrhosa* cover; RhodCov. = Rhodophyta cover; Sens. = sensitive macroalgae; Taxa = number of macroalgae; *Z.mar.* = *Zostera marina* cover; *Z.nolt.* = *Zostera noltei* cover. Environmental parameter abbreviations: Chl-*a* = chlorophyll-*a* concentration; Dens. = sediment density; DO = dissolved oxygen; Ehw = water redox potential; Ehs = sediment redox potential; Moist. = sediment moisture; Phaeo-*a* = phaeophytin-*a* concentration; Pinorg = inorganic phosphorus; Porg = organic phosphorus; P = reactive phosphorus; pHw = water pH; pHs = sediment pH; Sal. = salinity; Temp. = temperature; Transp. = water transparency; TSS = total suspended solids. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Water transparency and salinity were strongly associated with *Chaetomorpha linum* (O.F. Müller) Kützing, *Sahlingia subintegra* (Rosenvinge) Kornmann*,* the small calcareous taxa (i.e. *Pneophyllum fragile* Kützing, *Hydrolithon boreale* (Foslie) Y.M. Chamberlain, *H. cruciatum* (Bressan) Y.M. Chamberlain and *Melobesia membranacea* (Esper) J.V. Lamouroux), and the four aquatic angiosperms. On the opposite side of the plot (Fig. 6) nitrogen species (i.e. NH_4^+, NO_2^- and NO_3^-), SiO_4^{4-}, total Chl-*a*, Fines, TSS, temperature, Porg and moisture favored the presence of *A. subulata, U. rigida, Gracilariopsis longissima* (S.G. Gmelin) Steentoft, L.M. Irvine & Farnham and *Solieria filiformis* (Kützing) Gabrielson. All the other species showed intermediate associations and were plotted closer either to one or the other group according to their ecological value.

4. Discussion

The analysis of the vegetation of soft bottoms in the entire Venice Lagoon in 2011, 2014, 2018 and 2021 highlights the high resilience of TWS when anthropogenic pressures decrease (Solidoro et al., 2010) and the close correlation/association between ecological conditions and different macrophytes in TWS. A high number (26) of waters and surface sediment parameters, some macrophyte variables (12) and many taxa (4 angiosperms and 41 macroalgae) have been analyzed together in a high number of stations showing the progressive vegetation replacement and the different ecological value of each taxon whose presence is only possible under determinate ecological conditions.

In particular, macrophyte biomass, between 2011 and 2021, decreased significantly (from 0.56 to 0.92 Kg FW m^{-2}) confirming the negative trend (ca. −90 %) recorded between the ‘80s and 2003 (Sfriso and Facca, 2007), also depending on the meteorological conditions of the considered year. In 2014, higher rainfall (Fig. 2) increased significantly both the macroalgal biomass and cover, although the highest biomass value found in a single station was only approx. 7.5 kg FW m^{-2}, whereas in the ‘80s biomasses up to 15–20 kg FW m^{-2} were common in many areas of the central and northern lagoon.

The number of macroalgae recorded in the soft substrata of the entire lagoon was approx. 58 % of the total taxa recorded by considering also hard substrata (i.e. 186 out of 323 taxa, Sfriso et al., 2020a) and Rhodophyceae were more numerous than Chlorophyceae (R/C ratio: 1.12–1.36). The number of NIS increased markedly (from 11 in 2011 to 18 in 2021) accounting for approx. 1/3 of the total macroalgal biomass estimated by Sfriso et al., (2020a). However, after the synonymization (Guiry and Guiry, 2023, last access 22 August 2023) of *Ulva laetevirens* with *Ulva australis* proposed by Womersley (1984), currently this species is the most abundant NIS present in the lagoon (Sfriso et al., 2023), accounting for approx. 50 % of the total NIS biomass, which now exceeds that of all native species. However, the total number of macroalgae was not affected by the high presence of NIS, in fact, also considering the hard substrata, the number of macroalgae present in the lagoon exceeds 320 taxa (Sfriso et al., 2020a) and new species, that had disappeared in the past or were never recorded before, are continually being added to this list.

During the 4 years of survey many species were common to numerous stations, while many others colonized restricted areas. On average, 32 macroalgae were common to a high number of stations, but 55 taxa were only present in 1–2 stations. *Ulva australis*, which replaced *U. rigida* in the less eutrophicated areas (Sfriso, 2010), was the most abundant species whereas the spread of *U. rigida* decreased from 54.0 % of the stations in 2011 to 33.0 % in 2021; this species is currently present only in areas characterized by high concentrations of nitrogenous species (i.e. ammonium, nitrite, nitrate), silicates, Chl-*a* and Fines.

Similarly, the number of sensitive and calcareous taxa per station is increasing doubling between 2011 and 2018. The presence of many

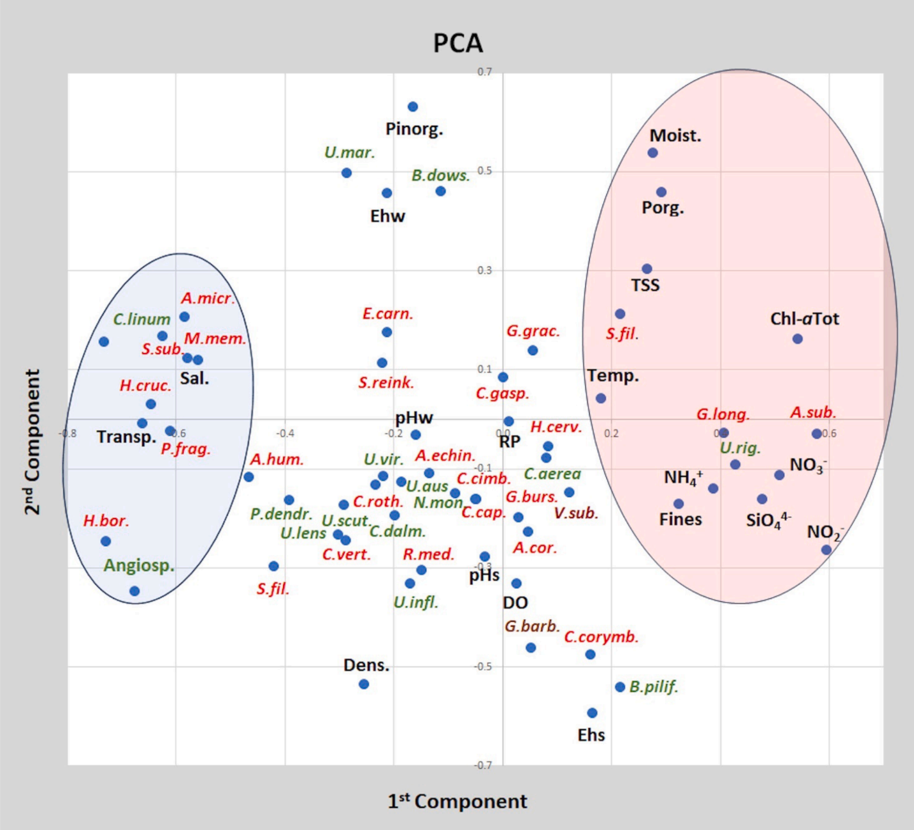


Fig. 6. Plot of PCA analysis between the main environmental parameters (in black) and the more common macroalgae present in the 87 stations sampled in 2021. They are clustered into groups characterizing high (blue circle) and low (red circle) environmental conditions. In red = Rhodophyta; in green: Chlorophyta; in brown = Ochrophyta. Environmental parameter abbreviations: see Fig. 5. Macrophyte abbreviations: *A. cor.* = *Alsidium corallinum*; Ang. = angiosperms; *A. echin.* = *Acanthosiphonia echinata*; *A. hum.* = *Acrochaetium humile*; *A. micr.* = *Acrochaetium microscopicum*; *A. sub.* = *Agardhiella subulata*; *B. dows.* = *Blidingia dowsonii*; *B. pil.* = *Bolbocoleum piliferum; C. corymb.* = *Callithamnion corymbosum*; *C. gasp.* = *Centroceras gasparrinii*; *C. cim.* = *Ceramium cimbricum*; *C. roth.* = *Ceramium rothianum*; *C. aer.* = *Chaetomorpha aerea*; *C. linum* = *Chaetomorpha linum*; *C. dalm.* = *Cladophora dalmatica*; *C. cap.* = *Chondria capillaris*; *C. vert.* = *Chylocladia verticillata*; *E. carn.* = *Erythrotrichia carnea*; *G. barb.* = *Gongolaria barbata*; *G. burs.* = *Gracilaria bursa-pastoris*; *G. grac.* = *Gracilaria gracilis*; *G. long.* = *Gracilariopsis longissima*; *H. cerv.* = *Hypnea cervicornis*; *H. bor.*= *Hydrolithon boreale*; *H. cruc.* = *Hydrolithon cruciatum*; *M. membr.* = *Melobesia membranacea*; *N. mon.* = *Neostromatella monostromatica*; *P. dendr.* = *Phaeophyla dendroides*; *P. frag.* = *Pneophyllum fragile*; *R. med.* = *Radicilingua mediterranea*; *S. sub.* = *Sahlingia subintegra*; *S. fil.* = *Solieria filiformis*; *S. filam.* = *Spyridia filamentosa*; *S. reink.* = *Syncoryne reinkei*; *U. rig.* = *Ulva rigida*; *U. aust.* = *Ulva australis*; *U. infl.* = *Ulvella inflata*; *U. lens* = *Ulvella lens*; *U. scut.* = *Ulvella scutata*; *U. vir.* = *Ulvella viridis*; *U. mar.* = *Uronema marinum*; *V. sub.* = *Vaucheria submarina.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sensitive taxa (i.e. *C. linum* and crustose calcareous species belonging to the genera *Pneophyllum*, *Hydrolithon* and *Melobesia*) is particularly significant, because they anticipate the possible colonization by aquatic angiosperms. Vice versa, the absence of these species is an excellent indicator of environmental conditions not suitable for plant rooting.

Seagrass beds are among the most threatened ecosystems on the planet, with global loss rates rising from 0.9 % in the 1940s to 7.0 % in the late 20th century (Waycott et al., 2009); in particular, in Europe Duarte et al. (2013) reported that, between 1869 and 2016, about one third of the area occupied by aquatic plants was lost due to eutrophication. Conversely, in the last decade, the cover and production of aquatic angiosperms are increasing in the Venice Lagoon, with their presence ranging from 26.4 % of the stations in 2011 to 52.9 % in 2018, accounting for a total cover of 19.3 % and 34.9 %, respectively, with a slight decrease in 2021 (Fig. 4). The highest changes were found for the species that preferentially colonize the inner and choked areas, due to the progressive reduction of the trophic status and clam harvesting (Sfriso et al., 2021a). Indeed, *Z. noltei*, which in 2011 colonized only 5.7 % of the stations, in 2018 almost quadrupled its frequency increasing to 28.7 %. *Ruppia cirrhosa*, that since the ‘80s disappeared from the lagoon open to water exchange with the sea, surviving only in fishing valleys (Val Dogà and Val Cavallino), in 2014 has recolonized some areas of the northern lagoon, reaching 12.6 % of the total stations in 2018, accounting for a total cover of 4.33 %. In the same time frame, *Z. marina* and *C. nodosa* almost doubled their frequency and cover, the first one colonizing preferentially marinized areas with salinities >20 psu, and the second one areas with high water renewal and temperatures <26–28 °C.

Overall, the obtained results indicated water transparency and salinity as the two main parameters that, directly or indirectly, have driven the colonization of aquatic angiosperms and sensitive species. Vice versa, their presence was hampered by parameters such as Chl-*a*, nitrogen compounds (NO_2^-, NO_3^-, NH_4^+,), SiO_4^{4-}, TSS in the water column and Porg, Fines, moisture in surface sediments.

The key role of water transparency and light availability in driving the presence of aquatic angiosperms was recorded also by Ralph et al. (2007), Silva et al. (2013), Statton et al. (2018). According to Duarte (1991), almost all the aquatic angiosperms require a minimum quantity of light, which is attested at about 10–20 % of the incident surface radiation. Similarly, Barnet et al. (2014) found that light requirements for the seagrasses *Halophila engelmannii* Ascherson and *Halodule wrightii* Ascherson were 8–10 % and 25–27 % of surface irradiance, respectively. Hemminga and Duarte (2000) concluded that nutrient and Chl-*a* concentrations in waters must be relatively low (Ptot: 0.55–1.13 μM, Ntot: 30.4–34.3 μM; Chl-*a*: 3.1–6.6 μg/L) for seagrass colonization, confirming the results of the present paper.

Similarly, Gillet and Holt (2023) reported that water turbidity and shading are the most pervasive threats to seagrasses, due to their dependence on light as photosynthesizers. Increased turbidity, nutrient-driven blooms of phytoplankton and epiphytic micro-macroalgae growing on the plant surfaces are factors that decrease water transparency and light availability, negatively affecting plant health (Fitzpatrick and Kirkman, 1995; McGlathery, 2001; Moore et al., 2014; Short et al., 1995). In addition, high biomasses of nuisance macroalgae, which grow more rapidly (Liu et al., 2013; Setthamongkol et al., 2015; Xie et al., 2020) than aquatic angiosperms (Sfriso and Ghetti, 1998), can obscure and kill the plants; this was reported, for example, by Hauxwell et al. (2001) in two estuaries of Waquoit Bay, Massachusetts, USA and it happened also during transplants carried out in the Venice Lagoon, as part of the project Life Seresto (LIFE 12 NAT/IT/000331), in two stations colonized by high algal biomass (Sfriso et al., 2021b).

Villazán et al. (2015) found that low salinity had an overall negative effect on *Z. marina* pigment concentration, photosynthesis and growth, thus increasing plant mortality; moreover, concomitant exposure to high NH_4^+ concentrations showed a strong, negative synergistic effect. van Katwijk et al. (1999) reported different responses of *Z. marina* to nutrient concentrations at low or high salinities: at salinities of 26–30 psu, a high nutrient load had no detectable effect on plants, whereas, at 23–26 psu, plants were positively influenced by high nutrient loads. In our experience, low salinity affects the presence of aquatic angiosperms mostly because it is strongly correlated to high nutrient concentrations and TSS amounts; in fact, nutrients and TSS are conveyed by river flows into the lagoon (Collavini et al., 2005; Zonta et al., 2005) favoring phytoplankton growth (recorded as Chl-*a* concentrations) and increasing water turbidity.

According to Alexandre et al. (2017), seagrasses dominate shallow coastal environments, where nitrogen availability in the water column is often sporadic and mainly in the form of pulses. This is in agreement also with the results of the present research work, where aquatic angiosperms showed a highly significant inverse correlation with nitrite, nitrate and ammonium and their sum (DIN = Dissolved Inorganic Nitrogen). In contrast, the water column nitrogen compounds were significantly correlated with *U. rigida, G. longissima, A. subulata* and *S. filiformis*; Ulvaceae, in particular, are nitrophilic taxa known for their high nitrogen absorption capacity (Björnsäter and Wheeler, 1990; Li et al., 2016). In addition, ammonium can be toxic to seagrasses because its accumulation can increase protein breakdown (Brun et al., 2002; Van Katwijk et al., 1997) or produce synergic effects with low light availability (Villazán et al., 2013).

Finally, sensitive macroalgae can show higher correlations with water transparency, salinity and low nutrient concentrations than aquatic angiosperms. This is the case of many small crustose and calcareous epiphytic macroalgae of the genera *Pneophyllum*, *Hydrolithon*, *Melobesia*, which appear and/or disappear more quickly than aquatic angiosperms (Sfriso et al., 2020b) when ecological conditions change. Indeed, their rapid diffusion is probably due to the small gametes (2–12 μm in size) and spores (40–80 μm in size), which are easily spread by currents and tides, while angiosperm seeds are larger and, thus, more difficult to transport.

5. Conclusions

This paper analyzes the distribution and time changes of the aquatic vegetation in the soft bottoms of 87 stations spread in the entire Venice Lagoon in 2011, 2014, 2018, 2021. In 2021, macrophytes were also analyzed considering the main physico-chemical parameters of water column and surface sediments. In literature, several papers are focused on the responses of single macrophytes to the variation of given environmental parameters. Instead, this study has simultaneously analyzed a large number of environmental parameters and their impact on several macrophyte variables; moreover, data for 41 dominant macroalgae, present in over 20 % of the 87 stations spread in the entire Venice Lagoon in late spring-early summer, have been reported and discussed. The species changes provide immediate information on the environment improvement/worsening and makes it possible to predict the next environment evolution. The Venice Lagoon high heterogeneity makes this basin representative of the ecological conditions and macrophyte presence in the 78 % (1088 km^2 on a total area of 1398 km^2) of Italian TWS water surface (Sfriso et al., 2017). So, the obtained results, reasonably extensible also to these environments, highlight the key role of high-water transparency and salinity, as the most important drivers for favouring the presence of aquatic angiosperms and sensitive macroalgae. Vice versa, high nutrient concentrations hamper their presence, promoting the dominance of opportunistic species.

CRediT authorship contribution statement

Adriano Sfriso: Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alessandro Buosi:** Writing – review & editing, Validation, Investigation, Formal analysis. **Abdul-Salam Juhmani:** Writing – review & editing, Validation, Formal analysis. **Yari Tomio:** Writing – review & editing, Validation, Formal analysis. **Marion Adelheid Wolf:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Katia Sciuto:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis. **Andrea Augusto Sfriso:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Alexandre, A., Baeta, A., Engelen, A.H., Santos, R., 2017. Interactions between seagrasses and seaweeds during surge nitrogen acquisition determine interspecific competition. Sci. Rep. 7, 13651. https://doi.org/10.1038/s41598-017-13962-4.

Aspila, K., Agemian, H., Chair, A.S.J., 1976. A semi-automated method for the determination of inorganic, organic and total phosphorus in sediments. Analyst 101, 187–197.

Barnet, Z.C., Choice, D., Frazer, T.K., Jacoby, C.A., 2014. Light requirements of seagrasses determined from historical records of light attenuation along the gulf coast of peninsular Florida. Mar. Poll. Bull. 81, 94–102. https://doi.org/10.1016/j.marpolbul.2014.02.015.

Björnsäter, B.R., Wheeler, P.A., 1990. Effect of nitrogen and phosphorus supply on growth and tissue composition of *Ulva fenestrata* and *Enteromorpha intestinalis* (Ulvales, Chlorophyta). J. Phycol. 26, 603–611. https://doi.org/10.1111/j.0022-3646.1990.00603.x.

Brun, F.G., Hernández, I., Vergara, J.J., Peralta, G., Pérez-Lloérnz, J.L., 2002. Assessing the toxicity of ammonium pulses to the survival and growth of *Zostera noltii*. Mar. Ecol. Prog. Ser. 225, 177–187. https://doi.org/10.3354/meps225177.

Collavini, F., Bettiol, C., Zaggia, L., Zonta, R., 2005. Pollutant loads from the drainage basin to the Venice Lagoon (Italy). Environ. Int. 31 (7), 939–947. https://doi.org/10.1016/j.envint.2005.05.003.

Cucco, A., Umgiesser, G., 2006. Modeling the Venice Lagoon residence time. Ecol. Model. 193 (1), 34–51. https://doi.org/10.1016/j.ecolmodel.2005.07.043.

Duarte, C., 1991. Seagrass depth limits. Aquat. Bot. 40 (4), 363–377. https://doi.org/10.1016/0304-3770(91)90081-F.

Duarte, C., Losada, I., Hendriks, I., Mazarrasa, I., Marbà, N., 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat. Clim. Chang. 3 (11), 961–968. https://doi.org/10.1038/nclimate1970.

Fitzpatrick, J., Kirkman, H., 1995. Effects of prolonged shading stress on growth and survival of seagrass *Posidonia australis* in Jervis Bay, New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 127, 279–289. https://doi.org/10.3354/meps127279.

Gillet, D.J., Holt, A., 2023. Options, Impediments, and Supports for the Development of an Eelgrass (*Zostera marina*) Habitat Occupancy Model in the Embayments of Southern California. Southern California Coastal Water Research Project, Technical Report 1334. 38 pp.

Guiry, M., Guiry, G., 2023. www.algaebase.org. Accessed on August 22, 2023.

Hauxwell, J., Cebrián, J., Furlong, C., Valiela, I., 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology 82, 1007–1022. https://doi.org/10.1890/0012-9658.

Hebert, P.D., Cywinska, A., Ball, S.L., de Waard, J.R., 2003. Biological identifications through DNA barcodes. Proc. Biol. Sci. 270, 313–321. https://doi.org/10.1098/rspb.2002.2218.

Hemminga, M.A., Duarte, C.M., 2000. Seagrass Ecology. Cambridge University Press, New York.

ISPRA, 2011. Protocolli per il campionamento e la determinazione degli elementi di qualità biologica e fisico-chimica nell'ambito dei programmi di monitoraggio ex 2000/60/CE delle acque di transizione. El-Pr-TW-Protocolli Monitoraggio - 03.06. ISPRA.

Li, H., Zhang, Y., Han, X., Shi, X., Rivkin, R.B., Legendre, L., 2016. Growth responses of *Ulva prolifera* to inorganic and organic nutrients: implications for macroalgal blooms in the southern yellow Sea. Sci. Rep. 6, 26498. https://doi.org/10.1038/srep26498.

Liu, D., Keesing, J.K., He, P., Wang, Z., Shi, Y., Wan, Y., 2013. The world's largest macroalgal bloom in the Yellow Sea, China: formation and implications. Estuar. Coast. Shelf Sci. 129, 2–10. https://doi.org/10.1016/j.ecss.2013.05.021.

Mannino, A.M., Menéndez, M., Obrador, B., Sfriso, A., Triest, L., 2015. The genus Ruppia L. (Ruppiaceae) in the Mediterranean region: an overview. Aquat. Bot. 124, 1–9. https://doi.org/10.1016/j.aquabot.2015.02.005.

Marcomini, A., Sfriso, A., Pavoni, B., Orio, A.A., 1995. Eutrophication of the lagoon of Venice: nutrient loads and exchanges. In: Mc Comb, A.J. (Ed.), Eutrophic Shallow Estuaries and Lagoons. CRC Press, Boca Raton, Fl, U.S.A., pp. 59–80

McGlathery, K.J., 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. J. Phycol. 37, 453–456. https://doi.org/10.1046/j.1529-8817.2001.037004453.x.

Mellors, J.E., 1991. An evaluation of a rapid visual technique for estimating seagrass biomass. Aquat. Bot. 42, 67–73. https://doi.org/10.1016/0304-3770(91)90106-F.

Moore, K.A., Shields, E.C., Parrish, D.B., 2014. Impacts of Varying Estuarine Temperature and Light Conditions on Zostera marina (Eelgrass) and its Interactions with Ruppia maritima (Widgeongrass). Estuaries Coast 37, 20–30. https://doi.org/10.1007/s12237-013-9667-3.

Morand, P., Briand, X., 2006. Excessive growth of macroalgae, a symptom of environmental disturbance. Bot. Mar. 39, 491–516. https://doi.org/10.1515/botm.1996.39.1-6.491.

Oxner, M., 1962. The Determination of Chlorinity by the Knudsen Method and Hydrographical Tables. G. M. Manufactoring Co., New York.

Ralph, P.J., Durako, M.J., Enriquez, S., Collier, C.J., Doblin, M.A., 2007. Impact of light limitation on seagrasses. J. Exp. Mar. Biol. Ecol. 350, 176–193. https://doi.org/10.1016/j.jembe.2007.06.017.

Setthamongkol, P., Tunkijjanukij, S., Satapornvanit, K., Salaenoi, J., 2015. Growth and nutrients analysis in marine macroalgae. Witthayasan Kasetsat 49 (2), 211–218.

Sfriso, A., 2010. Coexistence of *Ulva rigida* C. Agardh and *Ulva laetevirens* Areschoug (Ulvales, Chlorophyta) in Venice Lagoon and other Italian transitional and marine environments. Bot. Mar. 53, 9–18. https://doi.org/10.1515/BOT.2010.009.

Sfriso, A., Facca, C., 2007. Distribution and production of macrophytes in the lagoon of Venice. Comparison of actual and past abundance. Hydrobiologia 577, 71–85. https://doi.org/10.1007/s10750-006-0418-3.

Sfriso, A., Ghetti, P.F., 1998. Seasonal variation in the biomass, morphometric parameters and production of rhizophytes in the lagoon of Venice. Aquat. Bot. 61, 207–223. https://doi.org/10.1016/S0304-3770(98)00064-3.

Sfriso, A., Marcomini, A., 1996. Decline of *Ulva* growth in the lagoon of Venice. Bioresour. Technol. 58, 299–307. https://doi.org/10.1016/S0960-8524(96)00120-4.

Sfriso, A., Facca, C., Ceoldo, S., Marcomini, A., 2005. Recording the occurrence of trophic level changes in the lagoon of Venice over the '90s. Environ. Int. 31 (7), 993–1001. https://doi.org/10.1016/j.envint.2005.05.009.

Sfriso, A., Facca, C., Bonometto, A., Boscolo, R., 2014. Compliance of the Macrophyte Quality index (MaQI) with the WFD (2000/60/EC) and ecological status assessment in transitional areas: The Venice lagoon as study case. Ecol. Indic. 46, 536–547. https://doi.org/10.1016/j.ecolind.2014.07.012.

Sfriso, A., Buosi, A., Facca, C., Sfriso, A.A., 2017. Role of environmental factors in affecting macrophyte dominance in transitional environments: the Italian Lagoons as a study case. Mar. Ecol. 38 (2), e12414.

Sfriso, A., Buosi, A., Wolf, M.A., Sfriso, A.A., 2020a. Invasion of alien macroalgae in the Venice Lagoon, a pest or a resource? Aquat. Invasions 15 (2), 245–270. https://doi.org/10.3391/ai.2020.15.2.03.

Sfriso, A., Buosi, A., Wolf, M.A., Sciuto, K., Molinaroli, E., Mistri, M., Munari, C., Moro, I., Sfriso, A.A., 2020b. Microcalcareus seaweeds a sentinel of trophic changes and CO_2 trapping in transitional waters. Ecol. Indic. 118, 1–10. https://doi.org/10.1016/j.ecolind.2020.106692.

Sfriso, A., Buosi, A., Tomio, Y., Juhmani, A.-S., Mistri, M., Munari, C., Sfriso, A.A., 2021a. Trend of Nitrogen and Phosphorus in surface sediments, a litmus paper of anthropogenic impacts. The lagoons of the northern Adriatic Sea as a study case. Water 13, 2914. https://doi.org/10.3390/w13202914.

Sfriso, A., Buosi, A., Tomio, Y., Juhmani, A.-S., Facca, C., Wolf, M., Sfriso, A.A., Franzoi, P., Scapin, L., Bonometto, A., Ponis, E., Rampazzo, F., Berto, D., Gion, C., Oselladore, F., Boscolo Brusà, R., 2021b. Environmental restoration by aquatic angiosperm transplants in transitional water systems: The Venice Lagoon as a case study. Sci. Tot. Environ. 795, 148859 https://doi.org/10.1016/j.scitotenv.2021.148859.

Sfriso, A., Buosi, A., Wolf, M.A., Sciuto, K., Sfriso, A.A., 2023. Alien macroalgal rearrangement in the soft substrata of the Venice Lagoon. Impacts, threats, time and future trends. Sustainability 15, 8256. https://doi.org/10.3390/su15108256.

Sfriso, A., Buosi, A., Sciuto, K., Wolf, M., Tomio, Y., Juhmani, A.-S., Sfriso, A.A., 2022. Effect of ecological recovery on macrophyte dominance and production in the Venice Lagoon. Front. Mar. Sci. 9, 882463 https://doi.org/10.3389/fmars.2022.882463.

Short, F., 2003. World Atlas of Seagrasses. University of California Press.

Short, F.T., Burdick, D.M., Kaldy, J.E., 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnol. Oceanogr. 40, 740–749.

Silva, J., Barrote, I., Costa, M.M., Albano, S., Santos, R., 2013. Physiological responses of *Zostera marina* and *Cymodocea nodosa* to light-limitation stress. PLoS One 8, e81058.

Solazzi, A., Orel, G., Chiozzotto, E., Scattolin, M., Curiel, D., Grim, F., Aleffi, F., Del Piero, D., Vatta, P., 1991. Le alghe della Laguna di Venezia, Arsenale Editrice, Venezia.

Solidoro, C., Bandelj, V., Bernardi, F. A., Camatti, E., Ciavatta, S., Cossarini, G., Facca, C., Franzoi, P., Libralato, S., Melaku Canu, D., Pastres, R., Pranovi, F., Raicevich, S., Socal, G., Sfriso, A., Sigovini, M., Tagliapietra, D., Torricelli, P., 2010. Response of the Venice Lagoon Ecosystem to Natural and Anthropogenic Pressures over the last 50 years, in: Kennish, M. J. Paerl, H. W. (Eds), Coastal Lagoons – Critical Habitats of Environmental Change. CRC Press. Boca Raton Fl., U.S.A. Chapter 19, pp. 483-511.

Statton, J., McMahon, K., Lavery, P., Kendrick, G.A., 2018. Determining light stress response for a tropical multi-species seagrass assemblage. Mar. Pollut. Bull. 128, 508–518. https://doi.org/10.1016/j.marpolbul.2018.01.060.

Strickland, D., Parsons, T.R., 1984. Practical Handbook of Seawater analysis, 2nd ed. Fisheries Research Board of Canada, Ottawa, Canada.

Van Katwijk, Vergeer, L.H.T., Schmitz, G.H.W., Roelofd, J.G.M., 1997. Ammonium toxicity in eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 157, 159–173. https://doi.org/10.3354/meps157159.

Van Katwijk, M.M., Schmitz, G.H.W., Gasseling, A.P., van Avesaath, P.H., 1999. Effects of salinity and nutrient load and their interaction on *Zostera marina*. Mar. Ecol. Prog. Ser. 190, 155–165. https://doi.org/10.3354/meps190155.

Villazán, B., Pedersen, M.F., Brun, F.G., Vergara, J.J., 2013. Elevated ammonium concentrations and low light from a dangerous synergy for eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 493, 141–154. https://doi.org/10.3354/meps10517.

Villazán, B., Salo, T., Brun, F.G., Vergara, J., Pedersen, M.F., 2015. High ammonium availability amplifies the adverse effect of low salinity on eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 536, 149–162. https://doi.org/10.3354/meps11435.

Waycott, M., Duarte, C., Carruthers, T., Orth, R., Dennison, W., Olyarnik, S., Calladine, A., Fourqurean, J., Heck Jr, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. PNAS 106 (30), 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Womersley, H.B.S., 1984. The Marine Benthic Flora of Southern Australia. Part I. South Australian Government Printing Division, Adelaide.

Xie, E., Xu, R., Zhang, J., Jianjun, C., 2020. Growth characteristics of hybrids produced by closely related *Ulva* species. Aquaculture 519, 734902. https://doi.org/10.1016/j.aquaculture.2019.734902.

Zentilin, A., Pellizzato, M., Rossetti, E., Turolla, E., 2008. La venericoltura in Italia a 25 anni dal suo esordio. Pesce 3, 31–50.

Zonta, R., Collvini, F., Zaggia, L., Zuliani, A., 2005. The effect of floods on the transport of suspended sediments and contaminants: a case study from the estuary of the Dese River (Venice Lagoon, Italy). Environ. Int. 31 (7), 948–958. https://doi.org/10.1016/j.envint.2005.05.005.