Effect of Ecological Recovery on Macrophyte Dominance and Production in the Venice Lagoon

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In the last decade, the Venice Lagoon showed a significant environmental recovery that changed the assemblages of macroalgal and aquatic angiosperm dominant species and significantly increased the primary production. The decreasing of anthropogenic impacts, such as eutrophication and clam harvesting, favored a strong reduction of Ulvaceae, replaced by species with higher ecological value, and the recolonization of aquatic angiosperms. Consequently, hypo-anoxic conditions, once frequently occurring in the lagoon, have been considerably reduced and aquatic angiosperms have recolonized the area, covering 94.8 km^2 in comparison to the 55.9 km^2 recorded in 2003 (+70%). *Cymodocea nodosa*, *Zostera marina*, and *Zostera noltei* expanded by 37.5%, 44.6%, and 191%, respectively, with a significant increase in biomass and primary production. In late spring 2018, angiosperms showed a standing crop of approximately 372 ktonnes (+77%) and a net primary production of approximately 1189 ktonnes FW (+67%). In the meantime, *Ruppia cirrhosa*, which since the 1980s had disappeared from the lagoon areas subjected to tidal expansion, but was still present in some fishing valleys, recolonized the bottoms of the northern lagoon with meadows of over 6 km^2; this accounted for a standing crop and net primary production of 8.9 and 18.0 ktonnes, respectively. Based on surveys carried out in 2021, ecological conditions are still improving, and this is increasing both the biodiversity and the production of macroalgae and aquatic angiosperms.

Keywords: aquatic angiosperms, biomass, environmental recovery, macroalgae, primary production, Venice Lagoon

1 INTRODUCTION

The Venice Lagoon, with an area of 549 km^2, is the largest transitional water system (TWS) in the Mediterranean Sea (**Figure 1**). The number of TWS in the Mediterranean is very high; there are 209 basins with an area >0.25 km^2, for a total surface of approximately 2230 km^2. The Venice Lagoon alone occupies approximately 25% of this area and approximately 39% of the Italian TWS surface (1398 km^2) (Sfriso et al., 2017).
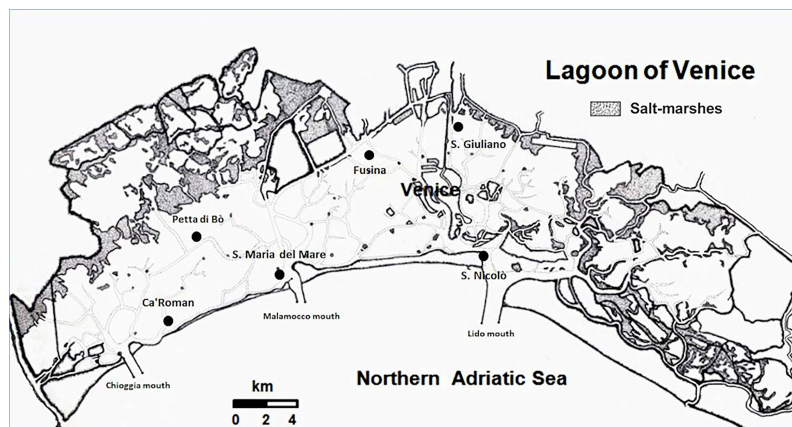
FIGURE 1 | Map of the Venice Lagoon and the 6 stations sampled bimonthly.

For its size, the extremely variable morphology [i.e., there are areas heavily influenced by seawater exchanges and choked areas where water renewal takes up to 30-40 days (Cucco and Umgiesser, 2006)] and its more than millenary mercantile history, the Venice Lagoon is a basin characterized by a very high biodiversity. Macrophytes (aquatic angiosperms and macroalgae) are among the most studied organisms. The first studies, generally extensive monographs, date back to the 18th and 19th centuries (Olivi, 1794; Naccari, 1828; Zanardini, 1847; De Toni and Levi, 1885; De Toni and Levi, 1888b; De Toni, 1889; De Toni, 1924) and continued in the 20th century (Schiffner and Vatova, 1938; Sighel, 1938; Vatova, 1940; Pignatti, 1962). These monographs are systematic studies that report lists of species along with their areas of discovery. Subsequently, in the 1980s, an abundant production of scientific papers regarding Venice Lagoon macrophyte biodiversity started. A complete review of this literature up to 2007 was reported by Sfriso and Curiel (2007), whereas information on the biomass changes and global production of macroalgae and seagrasses are shown by Sfriso and Facca (2007). In the following years, studies of macrophytes were mainly focused on their correlation with water and sediment parameters and on the discovery of new species, many of which are alien species (Sfriso et al., 2020a).

However, from the second half of the 20th century, the lagoon experienced continuous environmental changes. After the Second World War, the lagoon was affected by a pronounced chemical and organic pollution that caused replacements in the vegetation, until that period represented by aquatic angiosperms and sensitive macroalgae (Pavoni et al., 1992; Marcomini et al., 1995). Until the end of the 1980s, the lagoon was dominated by luxuriant growth of Ulvaceae (Sfriso and Facca, 2007), whose expansion declined in the 1990s (Sfriso and Marcomini, 1996). In the following years, the basin was affected by an intense fishing of the clam *Ruditapes philippinarum* Adams and Reeve, which peaked in the late 2010s with approximately 40,000 tonnes per year. This activity had a serious impact on the sediment resuspension and bottom erosion (Sfriso et al., 2005), the

macrofauna (Pranovi and Giovanardi, 1994), and the aquatic vegetation (Sfriso and Facca, 2007).

Since the beginning of the 2010s, clam fishing has significantly been reduced due to overfishing of the resource and the lagoon has started a rapid ecological recovery (Sfriso et al., 2019; Sfriso et al., 2021a; Sfriso et al., 2021b).

In 2018 and 2019, an extensive study on the macrophytes of the entire Venice Lagoon was carried out, with the goal of investigating macroalgal and aquatic angiosperm changes on time and spatial scales. The performed analyses allowed us to update biomass and net primary production (NPP) data for macroalgae and single aquatic angiosperms and to compare these data with those obtained in 2003, when the Venice Lagoon was affected by an intense clam overexploitation. Furthermore, the simultaneous sampling of the main physico-chemical parameters and of the nutrient concentrations in the water column and in the surface sediments allowed us to discriminate their correlation with the main variables of both aquatic angiosperm and macroalgae.

2 MATERIALS AND METHODS

2.1 Study Area
The lagoon of Venice is a wide shallow basin of approximately 549 km^2 (432 km^2 of water surface), located in the northern Adriatic Sea (sexagesimal coordinates: 45° 35'-11'N; 12°08'-38'E) (**Figure 1**). The mean depth is approximately 1.2 m and tidal excursion is ±31 cm on the average tidal level, although there are seasonal tidal extremes of over 2 m. The lagoon is connected to the sea through three large (400–900 m) and deep (15–50 m) mouths (Lido, Malamocco, and Chioggia), which divide the area into three hydrological basins separated by watersheds that shift according to tides and winds.

To have well-defined boundaries, the lagoon was divided into three morphological basins (northern, central, and southern basins), which are separated at the North by Burano and

Torcello tidal marshes and at the South by the deep Malamocco-Marghera artificial canal. Of the three basins, the central one (ca. 132 km^2 of water surface) is the most anthropized and, in the past, was heavily affected by the impact of industrial waste, urban sewage, and other anthropogenic pressures, such as touristic and commercial activities and the illegal fishing of Manila clam (*Ruditapes philippinarum* Adams & Reeve) carried out by disruptive fishing gears (Pranovi and Giovanardi, 1994; Sfriso et al., 2003; Sfriso et al., 2005). In the last decade, these impacts have been greatly reduced and the lagoon has begun a progressive environmental recovery (Sfriso et al., 2019; Sfriso et al., 2021a). The southern and northern basins are less artificial but have different ecological conditions due to, respectively, a greater and lesser exchange with marine waters. Therefore, the southern basin has less trophy and is abundantly colonized by seagrasses, especially *C. nodosa* and *Z. marina* which cover a large part of the shallow bottoms. Although the anthropogenic impacts are not significant, the northern basin has conditions strongly affected by the low water turnover. It is mainly colonized by *Z. noltei* and *R. cirrhosa* while *Z. marina* and *C. nodosa* are present along the edges of the canals which have a higher water turnover. Since the 1980s all these species had almost completely disappeared due to high trophy, clam fishing, and a picocyanobacteria bloom which eliminated much of the remaining prairies in the summer of 2001 (Sorokin et al., 2004). Aquatic angiosperms were reintroduced into the choked areas with the Life SeResto Project (Life12 NAT/IT/000331) by transplanting more than 75,000 rhizomes that have now colonized extensive areas of this basin (Sfriso et al., 2021b).

The present study refers to biweekly samplings at 6 stations for one year and to late spring-early summer samplings carried out in the soft bottoms of 88 stations, spread in the whole lagoon, in 2018. Samplings were performed in the framework of the project MOVECO III (ecological monitoring of the Venice Lagoon), which aimed at assessing the ecological status of the lagoon by the determination of the biological element "Macrophytes" and the application of the Index MaQI (Macrophyte Quality Index by Sfriso et al., 2009; Sfriso et al., 2014). The 6 stations were selected to study the annual growth of aquatic angiosperms and macroalgae before and after the entry into operation of the MOSE (experimental electromechanical module) gates which took place in October 2020, to counteract the exceptional high tides that affect the Venice Lagoon. Three stations were placed near the lagoon mouth: San Nicolò (SN), Santa Maria del Mare (SMM), Ca' Roman (Ca'R), and three in the innermost areas: San Giuliano (SG), Fusina (Fus), and Petta di Bò (PBò) (**Figure 1**).

2.2 Physico-Chemical Parameters

In the six stations at each sampling campaign the physico-chemical parameters of the water column [%DO, salinity, pH, Eh, Chl-*a*, phaeopigments, reactive phosphorus (RP), ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), silicate (Si)], and the 5-cm sediment top layer [fraction <63μm (Fines), density, moisture, porosity, total, inorganic and organic phosphorus (Ptot, Pinorg, Porg), total nitrogen (Ntot), total, inorganic and organic carbon (Ctot, Cinorg, Corg), sedimentation rates (SPM = Settled Particulate Matter)] where recorded. The analytical procedures have been reported in specific papers (Sfriso et al., 2017; Sfriso et al., 2019; Sfriso et al., 2021a).

2.3 Macrophyte Sampling

Following Sfriso et al. (1991), during each sampling campaigns the biomass of macroalgae was determined as the mean of 6 sub-samples using a frame of 50x50 cm. A selection of the different taxa was stored in 4% formaldehyde solution until taxonomic determination. When present, 6 samples of aquatic angiosperms were also collected by using a frame of 20x25 cm, to determine the biomass of shoots, rhizomes, and dead parts (blackened, no longer vital parts), the shoot density, the shoot height, and the number of leaves, according to Sfriso and Ghetti (1998). Each sample was collected manually by taking the plants inside the square. The rhizomes were cut with a blade along the edge of the square and the samples with sediments were collected up to 20-30 cm deep, placed in a 0.5-cm mesh basket and washed to remove sediments, shell fragments, and live organisms. Each sample was then collected in a bag and kept in the refrigerator at 4°C until the morphological analysis took place within 2-3 days. During the analyses, each sample was washed with tap water to remove salts and sediment residues and carefully dried with laboratory paper. Then each plant was divided into three parts (rhizomes+roots, leaf bundles, and dead parts), which were weighed separately for each sample with a technical balance (precision 0.01 g). The final value was the average weight of the 6 samples, whose values were then extrapolated to the square meter. The average measurement of the 20 longest leaf bundles provided the height of the prairie while the average of the number of leaves allowed us to have the average number of leaves. The dry weight of the samples was determined after sample lyophilization.

The study on spatial basis was carried out by sampling 88 stations, equally distributed throughout the lagoon, in late spring-early summer 2018. The sexagesimal coordinates are reported in **Supplementary Table S1** together with those of the 6 stations. At each station, the cover and biomass of macroalgae and the cover of aquatic angiosperms were determined by collecting samples for the taxonomic determination.

The distribution of macroalgae throughout the whole lagoon was reported in biomass ranges (0.01-0.1, 0.1-0.5, 0.5-1.0, 1.0-5.0, 5.0-10.0 kg m^{-2}) of fresh weight (FW) biomass, marking in a map the boundaries of the distribution ranges with a GPS when reference morphological structures were not available. Then the area of each biomass range was calculated in a map with a scale of 1:50,000 (1 cm^2 = 500*500 m = 250,000 m^2) by reporting the mean and maximum surface for each biomass range. The sum of the areas and biomasses of the individual ranges provides the lagoon surface covered by macroalgae and the total biomass. These calculations were made for each of the lagoon basins and then added together to obtain the total values.

The distribution of each aquatic angiosperm in the whole lagoon was obtained by drawing biomass distribution maps in the same way. For each species, the biomass was reported into 4 ranges (0-25, 25-50, 50-75, 75-100%) of cover. A biomass range was then associated with each cover range using the maximum

value obtained during the annual sampling in the 6 stations studied in this paper or those previously found in other stations (Sfriso and Facca, 2007).

2.4 Primary Production Determination
2.4.1 Aquatic Angiosperms
At each station, the NPP of the aboveground part of the aquatic angiosperms (shoots) was determined by piercing the leaf bundles above the basal meristem with a needle in accordance with Dennison (1990a) and Dennison (1990b). At each campaign, approximately 20 leaf bundles were drilled and, at the subsequent sampling, the leaf growth of 10 leaf bundles was determined. The growth of each bundle was assessed bimonthly by adding the displacement of the hole from the basal meristem of the single leaves. These data were transformed into a linear leaf production for square meter considering the mean leaf bundles per square meter (sum of the leaf increase of each shoot * number of shoots m^{-2}) and biomass production by mean fresh (FW) weight and dry weight (DW) of 10 linear meters of leaves.

The NPP of the belowground part (rhizomes+roots, hereinafter referred to as rhizomes) of the plants was obtained monthly by sampling all rhizomes with the biomass variation method within dense and uniform prairies (Sfriso and Ghetti, 1998). Indeed, the drilling of the rhizomes could only be applied to *Zostera marina* Linnaeus, but not to *Zostera noltei* Hornemann and with difficulty to *Cymodocea nodosa* (Ucria) Ascherson. In fact, *Z. marina* rhizomes can be perforated above the basal meristem, but the operation is complex and subjected to a high margin of error; *Z. noltei* has rhizomes that are too thin, and the drilling could compromise their growth; *C. nodosa* has very elongated rhizomes and only the apical bundles can be pierced. Therefore, for all three species it was preferred to apply the biomass variation method. Sfriso and Ghetti (1998) showed that 6 replicated sub-samples with a frame of 20x25 (0.05 m^2) cm are sufficient to obtain an accurate biomass measurement with an error of less than 5%. The sum of the rhizome biomass increases recorded monthly for 1 year, excluding the values found not significant by one-way ANOVA, supplies the NPP of the underground part. This value added to that of shoots gives the total production of each species.

Following Sfriso and Facca (2007), the NPP of the whole lagoon was estimated based on the production/biomass ratios (P/B) (i.e., the ratios between the annual NPP and the annual maximum biomass) determined for each species, sampled during the year in the framework of different projects and characterized by different biomass intervals in accordance with the following calculation:

Standing Crop(SC) = Sum of the mean biomass*lagoon surface of each biomass range

Net Primary Production (NPP) = Sum of the maximum biomass*lagoon

surface*P/B ratio of each biomass range

2.4.2 Macroalgae
In the 6 stations macroalgae were sampled twice a month determining the cover, the biomass, the total number of taxa, the number of sensitive taxa according to ISPRA (2011), and the

parameters for the application of the index of ecological status MaQI (Macrophyte Quality Index of Sfriso et al., 2009, Sfriso et al., 2014). It was not possible to calculate the P/B ratios because macroalgae require a higher number of samplings, especially in the period of greatest growth of the dominant species. Therefore, the NPP of macroalgae was determined by using the P/B ratios reported in Sfriso and Facca (2007). They were calculated in stations characterized by different biomass ranges (0-2 kg FW m^{-2}, 5-8 kg FW m^{-2}, 8-12 kg FW m^{-2}) because the P/B ratio increased with the decreasing biomass. Indeed, macroalgae have a higher growth rate in the presence of smaller biomass as they are not self-limited.

For macroalgae, it was also possible to determine the gross primary production (GPP) by using the GPP/NPP ratios reported in Sfriso and Facca (2007) and calculated from the balance of phosphorus, an element that completes its cycle between sediments, water, and biota, in stations placed in the lagoon watershed or without water exchanges (Sfriso and Marcomini, 1994). In brief, the ratio of all phosphorus recycled annually from macroalgae to that recycled from NPP provided the GPP/PPN ratio. For the calculation we used the average value of phosphorus in the annual macroalgal biomass, the minimum winter value of phosphorus retained by the surface sediments, and the average value of the phosphorus in the particles captured annually with sedimentation traps (SPM = settled particulate matter). The system reported below:

$$\begin{cases} Ax + By = C \\ x + y = 100 \end{cases}$$

A = mean value of P in macroalgae
B = winter background of P in surface sediment
C = mean value of P in SPM
x = fraction of macroalgae in SPM
y = fraction of sediment in SPM

Taking into account the total amount of SPM collected by traps during the year made it possible to separate the contributions of phosphorus due to the degradation of macroalgae produced during 1 year from that contained in the resuspended surface sediments settling into the traps in the same period of time. Since phosphorus is a sedimentary element with negligible losses as phosphines, which occur only in the case of anoxic events, it was possible to calculate the total amount of this element recycled by macroalgae and released in the particulate collected by traps during their degradation.

2.5 Statistical Procedures
All the data of physico-chemical parameters of the water column, surface sediments, sedimentation rates (29 parameters), and some macrophyte variables (angiosperm cover, macroalgal biomass, macroalgal cover, total macroalgal taxa, number of sensitive taxa, number of calcareous taxa) collected in the 6 stations were analyzed together in a PCA analysis to highlight their associations and grouping. In addition, the analysis of the transposed matrix allowed us to see the associations between stations discriminating the stations characterized by good high ecological conditions from those of poor ecological conditions.

3 RESULTS

3.1 Environmental Parameters

In **Figure 2**, some parameters of the water column and surface sediments highlight the main differences between the 6 stations. SG and Fus showed the highest concentrations of reactive phosphorus (RP: 1.36 and 0.96 μM, respectively) and inorganic dissolved nitrogen (DIN = sum of ammonium, nitrite, and nitrate: 19.0 and 10.1 μM, respectively) in the water column. The same stations also showed the highest values of total Chl-*a* (7.73 and 3.91 μg L^{-1}, respectively) and SG the highest amount of TSS (89.2 mg L^{-1}). Similarly, the number of fines was higher at SG (90.0%) and Fus (66.7%). Consequently, SG exhibited the

highest concentrations of Porg (141 μg g^{-1}) and Corg (15.51 mg g^{-1}) followed by Ca'R (100 μg g^{-1} and 15.47 mg g^{-1}, respectively) that also had the highest concentration of Ntot (1.49 mg g^{-1}).

3.2 Macrophyte Variables

The macrophytes variables recorded in the 6 stations [San Nicolò (SN), Santa Maria del Mare (SMM), Ca' Roman (Ca'R), San Giuliano (SG), Fusina (Fus), Petta di Bò (PBò)] in 2019 are reported in **Table 1**. The number of total taxa was 130 (44 Chlorophyceae, 67 Rhodophyceae, 19 Phaeophyceae). The highest biodiversity was recorded at SN (86 taxa) and the lowest at Fus (17). Out of them, 25 were sensitive taxa and 3 crustose calcareous taxa. The highest number of sensitive taxa
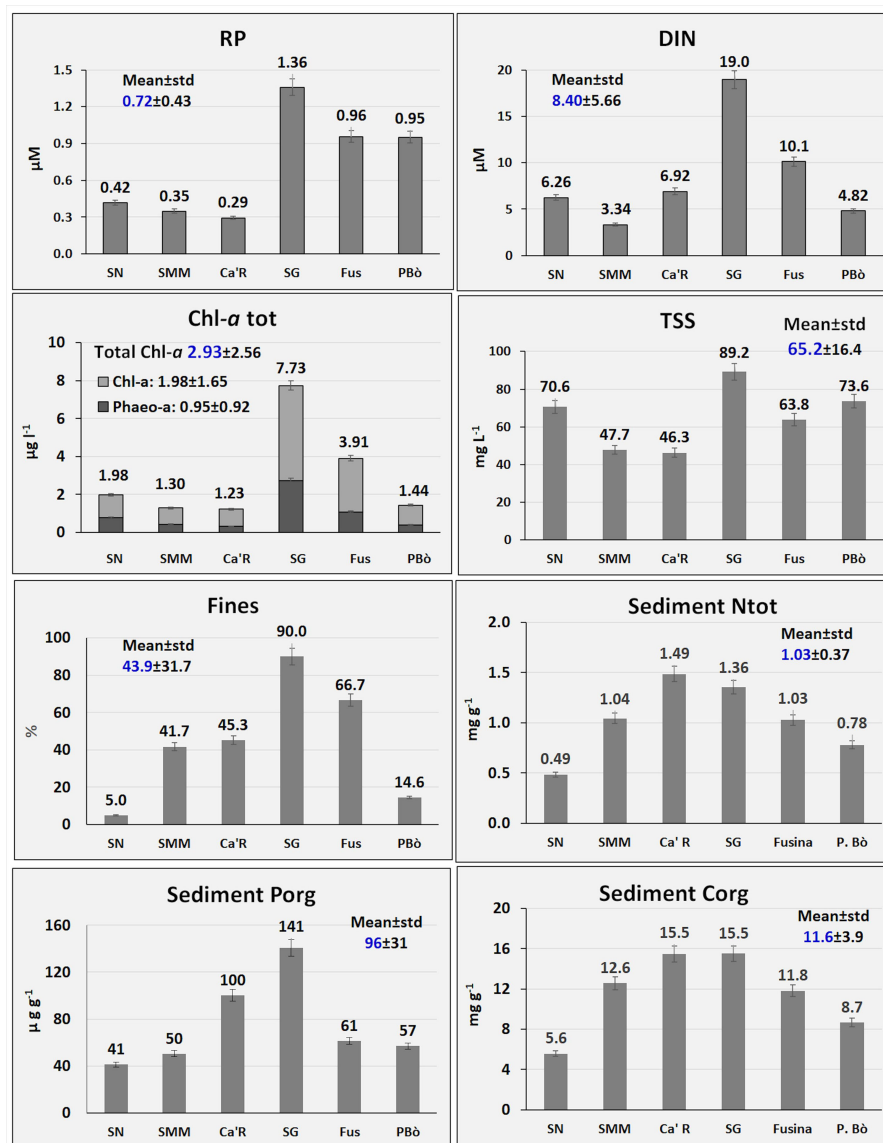

FIGURE 2 | Main ecological parameters.

TABLE 1 | Macrophyte variables.

Macrophyte variables	Ca' R	SMM	SN	PBò	Fus	SG
N° of Samples	24	24	24	24	24	24
N° Taxa (max)	73	71	86	56	17	25
N° Sensitive taxa (tot)	10	15	12	8	0	0
% Sensitive taxa	13.7	21.1	14	14.3	0	0
N° Calcareus taxa	2	3	2	3	0	0
Chlorophyta N°	22	20	24	21	7	10
Rhodophyta N°	41	40	51	30	7	12
Ochrophyta N°	10	11	11	5	3	3
Rhodophyta/Chlorophyta (R/C)	1.9	2	2.1	1.4	1	1.2
Cover %	78	66	53	30	82	45
Chlorophyta %	68	70	38	38	33	27
Rhodophyta %	32	30	62	62	67	73
Mean Macroalgal Biomass (g FW m^{-2})	593	415	146	161	2422	397
Max Macroalgal Biomass (g FW m^{-2})	3448	1546	505	1383	4650	2525
Macroalgae NPP (g FW m^{-2} y^{-1})*	12068	5411	2273	4841	16275	8838
C. nodosa cover %	0	100	100	+	0	0
C. nodosa NPP (g FW m^{-2} y^{-1})	0	12554	12274	+	0	0
Z. marina cover %	90	0	0	+	0	0
Z. marina NPP (g FW m^{-2} y^{-1})	12981	0	0	+	0	0
Z. noltei cover %	+	0	0	90	0	0
Z. noltei NPP (g FW m^{-2} y^{-1})	+	0	0	6647	0	0
Total Macrophyte NPP (g FW m^{-2} y^{-1})	25049	17955	14547	11488	16275	8838
MaQI	0.85	1	0.85	0.85	0.35	0.35

According to Sfriso and Facca (2007), the P/B value for macroalgal biomass ranging from 1 to 5 Kg FW m^{-2} is 3.5. For lower biomass the P/B ratio is 4.5.

was recorded at SMM (15, i.e., 21.1%) whereas at SG and at Fus sensitive taxa were missing.

The Rhodophyta/Chlorophyta (R/C) ratio ranged from 1.0 at Fus to 2.1 at SN. The mean macroalgal cover range was 30–82% with the highest value at Fus and the lowest at PBò.

The NPP recorded by applying the P/B reported by Sfriso and Facca (2007) for different levels of biomass ranged from 2273 g FW m^{-2} y^{-1} at SN to 16,275 g FW m^{-2} y^{-1} at Fus.

The mean annual macroalgal biomass was the highest at Fus (2422 g FW m^{-2}) where no aquatic angiosperms were present. In the same station, the highest biomass (4650 g FW m^{-2}) was also recorded.

By considering the total NPP of macroalgae and aquatic angiosperms, the highest production was recorded at Ca'R (25049 g FW m^{-2} y^{-1}) where macroalgae and *Z. marina* contributed with a quite similar biomass (**Table 1**). The lowest NPP was recorded at SG (8838 g m^{-2} y^{-1}) where no angiosperms were recorded. The other stations showed intermediate values with different macrophyte contributions. However, at Fus, where only macroalgae were present, the NPP was higher than at PBò colonized by the angiosperm *Z. noltei*.

The application of the Macrophyte Ecological Index (MaQI) assessed SMM, Ca'R, PBò, and SNN as "High" quality and Fus and SG as "Poor" quality.

Aquatic angiosperms were represented by the species *Cymodocea nodosa* at SMM and SN (cover 100%), *Zostera marina* at Ca'R (cover 90%), and *Zostera noltei* at PBò (cover 90%). The annual biomass variation of these plants is reported in **Figure 3**.

C. nodosa was recorded at SMM in a shallow area (ca. 0.6 m depth) and at SN near the border of Lido port entrance at the same depth. At SMM *C. nodosa* showed both the highest mean

biomass (3095 g FW m^{-2}) and the biomass peak (7067 g FW m^{-2}) in July. On average, rhizomes contributed with 1920 g FW m^{-2} (62% of the total), whereas shoots reached 1032 g FW m^{-2} only. The presence of dead parts was lower than 5% 143 g FW m^{-2}. This species started to grow in May and sharply declined in September. At SN the mean biomass was lower (2816 g FW m^{-2}) as well as the biomass peak (4474 g FW m^{-2}).

Z. marina showed a slightly smaller mean biomass (2399 g FW m^{-2}) with a peak of 4830 g FW m^{-2} in June. This species, which grows all year round, had a minimum biomass in September. The mean biomass of shoots (975 g FW m^{-2}) was slightly greater than that of rhizomes (950 g FW m^{-2}) but in this species the dead parts reached almost 20% of the total biomass (474 g FW m^{-2}).

Z. noltei biomass was significantly lower (1991 g FW m^{-2}). The mean biomass peak value was recorded in July (3628 g FW m^{-2}), whereas the minimum was in March. Rhizomes of this species, as for *C. nodosa*, showed the maximum contribution reaching even 70% of the total biomass.

The number of shoots per square meter is reported in **Figure 4A**. *Z. noltei*, the smallest species, and *Z. marina* showed the highest (5502 m^{-2}) and the lowest (696 m^{-2}) mean number of shoots, respectively. Both these species peaked in June with 13,021 and 1327 shoots m^{-2}. *C. nodosa* showed almost twice as many shoots as *Z. marina* with a mean value ranging from 1273 m^{-2} at SMM to 1373 m^{-2} at SN. The highest values were recorded in June both at SMM and SN (2747 and 2333 shoots m^{-2}, respectively).

On average shoot height was the highest for *C. nodosa* at SMM with a peak in August (86.6 cm, **Figure 4B**) whereas at SN the mean value was slightly smaller (36.4 cm) but with a peak of 89.4 cm in July. *Z. marina* showed an intermediate mean value (37.7 cm), and the peak was 53.1 cm only. *Z. noltei* peaked in August (29.3 cm) with a mean value of 19.1 cm.
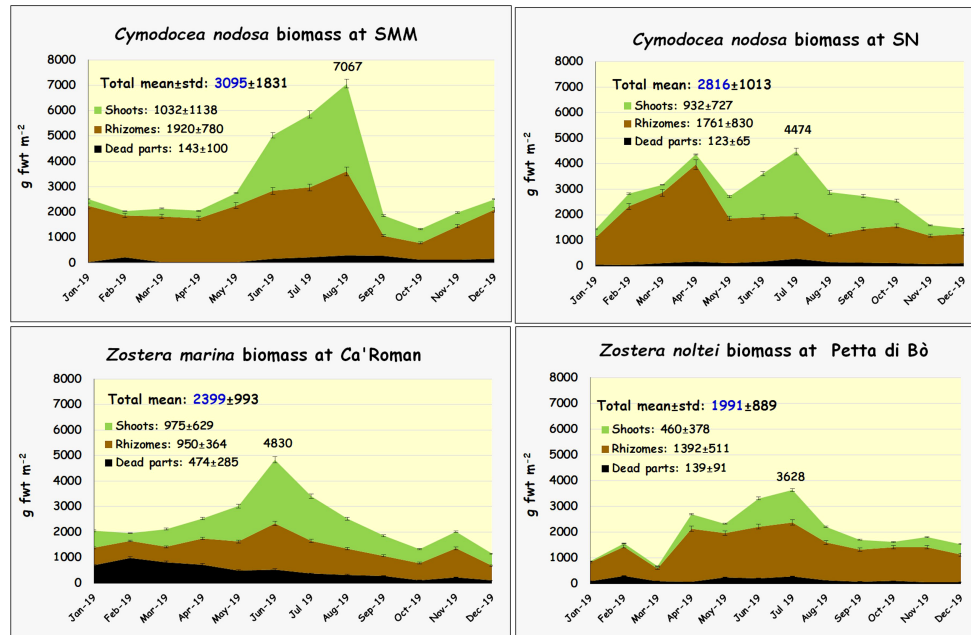
FIGURE 3 | Biomass changes of *C. nodosa*, *Z. marina*, and *Z. noltei* during the year.

The number of leaves was average between 2.45 for *C. nodosa* at SMM and 3.35 for *Z. marina* at Ca'R. (**Figure 4C**). In autumn and winter *C. nodosa* showed 1-2 small sleeping leaves that started to grow only in May.

The growth of shoots was measured about twice a month and scaled monthly (**Figure 4D**). *Z. marina* showed a mean value (2.73 cm d^{-1}) almost double than that of *C. nodosa* (1.26-1.39 cm d^{-1}) and over three times higher than that of *Z. noltei* (0.82 cm d^{-1}). The highest shoot increase was recorded at Ca'R for *Z. marina* in the last two weeks of May (6.88 cm d^{-1}, i.e., 5.69 cm d^{-1} monthly) and at SN in the first week of July for *C. nodosa* (6.18 cm d^{-1}, i.e., 5.47 cm d^{-1} monthly).

The NPP of the aquatic angiosperms in 2018 is reported in **Table 2**. It is sorted in the production of shoots and rhizomes. The NPP of *C. nodosa* and *Z. marina* in the three stations was very similar ranging from 12,274 to 12,981 g FW m^{-2} y^{-1}, whereas that of *Z. noltei* was about half (6647 g FW m^{-2} y^{-1}).

On average, the production of shoots was significantly higher than that of rhizomes ranging from 61.3% in *Z. noltei* to (83.7%) in *Z. marina*. The percentage of shoot production in *C. nodosa* in both stations was very similar ranging from 73.2 to 73.9%.

By considering these values and the highest biomass of the single species recorded during the year it was possible to calculate the P/B ratios. They were 1.78 and 2.74 for *C. nodosa* (mean value: 2.26), 2.69 for *Z. marina*, and 1.83 for *Z. noltei*.

3.3 Biomass Maps and Total Macrophyte NPP
3.3.1 Aquatic Angiosperms
The data of macrophyte biomass of the entire lagoon, collected as part of the MOVECO III project, allowed us to

calculate the cover, standing crop (SC), and NPP throughout the lagoon and draw the biomass distribution. For macroalgae it was also possible to determine the GPP. An example of the procedure used to define these variables is shown in **Supplementary Table S2**. The three basins were analyzed separately and globally.

Maps report the biomass of each angiosperm species in the three Venice basins (southern, central, northern, **Supplementary Figures S1** and **S2**) in 4 cover ranges with the corresponding biomass (**Supplementary Figure S1**).

Overall, the angiosperms *C. nodosa*, *Z. marina*, and *Z. noltei* together with the rarer species *Ruppia cirrhosa* that was present only in the northern basin (**Supplementary Figure S2**), colonized approximately 94.8 km^2 (**Table 3**), although in many cases they overlapped. The southern basin presented the highest cover (63.5 km^2) followed by the central basin (18.4 km^2) and the northern basin (12.9 km^2). The total standing crop (SC) was 372 ktonnes FW, of which 298 (ca. 80%) were in the southern basin.

The NPP reached 1189 ktonnes FW with 954 ktonnes produced in the southern lagoon whereas 157 and 77 ktonnes FW were produced in the central and northern lagoons, respectively.

The highest cover was displayed by *Z. marina* (38.2 km^2, 40%), whereas *C. nodosa* covered 32.4 km^2 (34%). *Z. noltei* and *R. cirrhosa* covered 18.1 km^2 (19%) and 6.0 km^2 (6.4%), respectively.

Conversely, the highest SC was that of *C. nodosa* (181 ktonnes, 49%) followed by *Z. marina* (145 ktonnes, 39%), and *Z. noltei* and *R. cirrhosa* showed 37 ktonnes (10%) and 8.9 ktonnes (2.4%), respectively.

The NPP of *C. nodosa* and *Z. marina* were quite similar: 539 and 545 ktonnes, respectively, accounting for 45% and 46% of
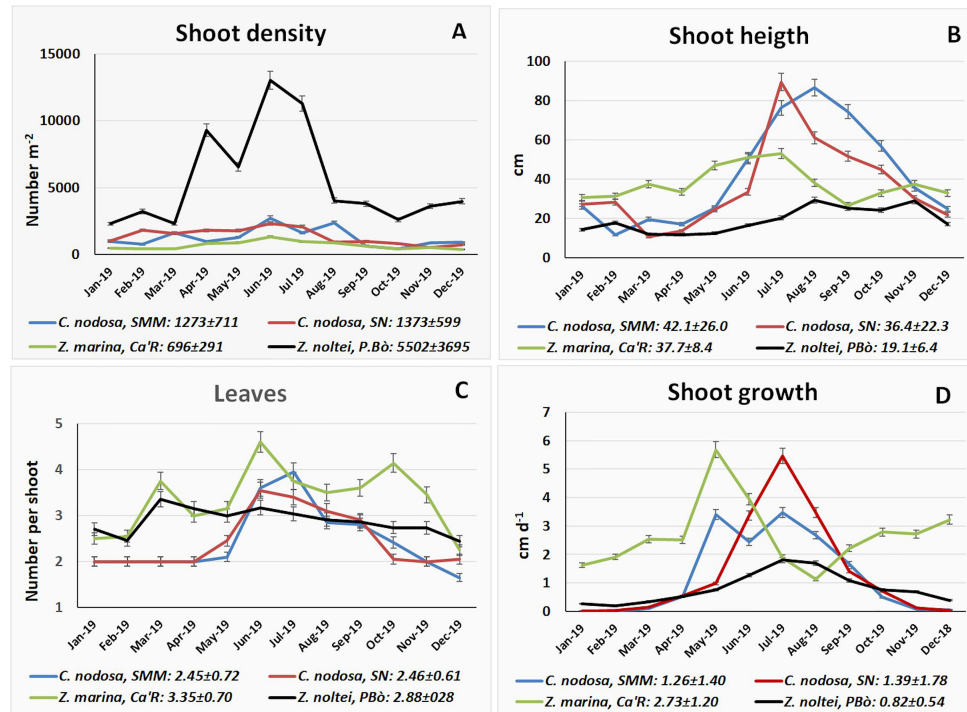
FIGURE 4 | **(A)** Shoot density, **(B)** shoot height, **(C)** leaf number, and **(D)** shoot growth of aquatic angiosperms monthly for 1 year.

the total. *Z. noltei* and *R. cirrhosa* contributed with 86 ktonnes (7.3%) and 18 ktonnes (1.5%), respectively.

3.3.2 Macroalgae
Total macroalgal species covered approximately 133 km^2 with a biomass ranging from 0.01 to 10.0 kg FW m^{-2} and 214 km^2 with a biomass >0.001 kg FW m^{-2}. The highest cover (ca. 100.3 km^2) was recorded in the southern lagoon where the SC reached 59.5 ktonnes FW, that is, approximately 57% of the biomass recorded in the whole lagoon (104 ktonnes FW) (**Table 3**; **Supplementary Figure S3**).

However, in the southern basin the SC reached a maximum of 5 kg FW m^{-2} (**Supplementary Figure S3**), whereas in the central

lagoon SC up to 10 kg FW m^{-2}, composed mainly by Gracilariaceae, was also recorded.

The macroalgal NPP reached 648 ktonnes FW and 369 (57%) of them were produced in the southern lagoon. The total GPP reached approximately 3014 ktonnes FW of which 1705 ktonnes were produced in the southern lagoon (**Supplementary Table S2**).

3.4 Statistical Analyses
The PCA (principal component analysis) between the main environmental parameters and macrophyte variables (36 in total) is plotted in **Figure 5**. The first two components explain 76.5% of the total variance. This value increases to 87.9% and

TABLE 2 | Angiosperm production.

	Net Primary Production (NPP) of aquatic angiosperms							
	C. nodosa				*Z. marina*		*Z. noltei*	
	SMM		SN		Ca'R		PBò	
	g FW m^{-2} y^{-1}	%	g FW m^{-2} y^{-1}	%	g FW m^{-2} y^{-1}	%	g FW m^{-2} y^{-1}	%
Shoots	9278	73.9	8984	73.2	10864	83.7	4073	61.3
Rhizomes	3276	26.1	3290	26.8	2117	16.3	2574	38.7
Total	12554		12274		12981		6647	
Max Biom	7067		4474		4830		3628	
P/B	1.78		2.74		2.69		1.83	

TABLE 3 | Macrophyte cover, SC and NPP .

	Total macrophytes 2018.					
Species	**Cover**					
	Basins			**Total**		
	South	**Central**	**North**			
		km²			km²	%
C. nodosa	30.1	1.28	1.07		32.4	34
Z. marina	22.6	12.7	2.91		38.2	40
Z. noltei	10.8	4.36	2.86		18.1	19
R. cirrhosa	0.0	0.0	6.03		6.03	6.4
Total angiosperms	63.5	18.4	12.9		94.8	100
Total macroalgae	100.3	82.0	31.9		214	
Species	**Standing Crop**					
	Basins			**Total**		
	Southern	**Central**	**Northern**			
		ktonnes FW			ktonnes FW	%
C. nodosa	171	5.5	4.2		181	49
Z. marina	105	33	7.4		145	39
Z. noltei	22	6.7	7.5		37	10
R. cirrhosa	0.0	0.0	8.9		8.9	2.4
Total angiosperms	298	45.2	28.1		372	100
Total macroalgae	59.5	29.2	15.7		104	
Total macrophytes	358	74	44		476	
Species	**Net Primary Production**					
	Basins			**Total**		
	Southern	**Central**	**Northern**			
		ktonnes FW			ktonnes FW	%
C. nodosa	504	20.3	15.2		539	45
Z. marina	398	119	28.4		545	46
Z. noltei	53	17.1	16.2		86	7.3
R. cirrhosa	0.0	0.0	17.2		18	1.5
Total angiosperms	954	157	77		1189	100
Total macroalgae	369	178	101		648	
Total macrophytes	1323	335	178		1837	

96.9% by considering three and four components, respectively. All parameters/variables are mainly plotted in two main groups associated to bad or high ecological conditions. The ecological value of each parameter/variable is shown by the orthogonal projection on the line that connects the extreme conditions. By **Figure 5A**, the parameters/variables associated with the highest ecological conditions are the pH of the water column (pHw) and the index MaQI followed by the number of sensitive taxa (Sens), the angiosperm cover (AngCOV), the total number of taxa (Taxa), water transparency (Trans), the water redox potential (Ehw), and the number of calcareous macroalgae. On the other side, the parameters/variables associated with the worst conditions are silicates (Si) and nitrites (NO_2^-) followed by all the nutrients in the water column, total suspended solids (TSS), Chl-*a*, and phaeopigments (Phaeo-*a*). All the other parameters/variables are placed in intermediate positions.

The transposed matrix (**Figure 5B**) with two components explains 86.6% of the total variance highlighting two groups of stations, associated to high (SMM, PBò, Ca'R, SN) or bad (Fus, SG) ecological conditions, respectively. The first group groups the stations colonized by seagrasses. Out of them, SMM showed the highest conditions. The second group had no seagrasses or sensitive macroalgae and Fus showed the worst conditions.

4 DISCUSSION

There is a conspicuous literature on the degradation of transitional environments both from the point of view of pollution and of the trophic status (Smith, 2003; Viaroli and Christian, 2003; Gamito et al., 2005; Howarth et al., 2011; Pérez-Ruzafa et al., 2012; Vybernaite-Lubiene et al., 2017;
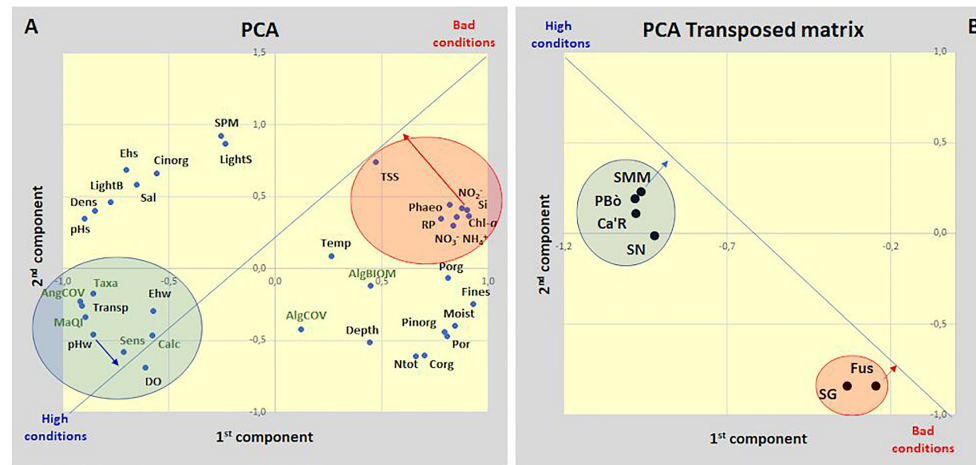
FIGURE 5 | PCA analysis of **(A)** plot of environmental parameters and macrophyte variables; **(B)** plot of the 6 stations in the transposed matrix.

Hsieh et al., 2021) but relatively fewer articles are about the possibility of a reversal of this trend and on the consequent environmental recovery (Carstensen et al., 2006; Rodrigo et al., 2013; Kralj et al., 2016; McCrackin et al., 2016). Recent studies reported that the Venice Lagoon can be taken as an example of quick environmental recovery due to a marked nutrient decrease (Sfriso et al., 2019; Sfriso et al., 2021a; Sfriso et al., 2021b) with a significant impact on the aquatic vegetation. Indeed, the decrease of the macroalgal biomass and production which occurred in the 1980s allowed the recovery of aquatic angiosperms whose biomasses increased markedly. This was the effect of several policies that were adopted in the framework of EU legislation to prevent or attenuate the impacts of nutrient pollution and its consequences on the aquatic ecosystems. Among them, the Nitrates Directive (ND, 91/676/EEC), dealing with diffuse pollution of nitrogen from agriculture, the Urban Wastewater Treatment Directive (UWWT, 91/271/EEC), addressed to the major point sources, and the Water Framework Directive (2000/60/EC) (European Commission, 2000) that prompted Member States of the European Union to enact new laws to reduce major pollutant resources because the impacts on the biota were of particular importance.

The result of these new policies on the vegetation of the Venice Lagoon was relevant. Data comparison of the cover, SC, and NPP values recorded in 2018 with those found in 2003 for macroalgae and aquatic angiosperms is reported in **Table 4** (macroalgae data from 1980 are also available).

In 1980 macroalgae, mainly represented by *Ulva rigida* C. Agardh and *Ulva australis* Areschoug ex *U. laetevirens* Areschoug (>90%) showed a luxuriant growth colonizing 202 km^2 with an SC and an NPP of approximately 841 and 2912 ktonnes FW, respectively (**Table 4**). Macroalgae reduced significantly in 2003 (Sfriso and Facca, 2007) due to the synergistic effect of many factors including climatic changes (Sfriso and Marcomini, 1996). Indeed, in this period the total SC and NPP were approximately 10 and 6 times lower than in

1980, respectively. Moreover, the dominant species changed from Ulvaceae to Gracilariaceae or other Rhodophyceae. At present Ulvaceae, mainly *U. rigida* and *U. australis* Areschoug, are frequent but usually have a negligible biomass whereas *Gracilaria gracilis* (Stackhouse) Steentoft et al., *Gracilaria bursa-pastoris* (S.G. Gmelin) P.C. Silva, *Gracilariopsis longissima* (S. G. Gmelin) Steentoft et al., *Gracilariopsis vermiculophylla* Ohmi, *Hypnea cervicornis* J. Agardh are absolutely dominant.

The result of the decrease of macroalgal biomass and production was significant growth of all aquatic angiosperms. In fact, their cover increased from 55.9 to 94.8 km^2, the SC from 209 to 372 ktonnes FW and NPP from 714 to 1189 ktonnes FW. *Ruppia cirrhosa* was the species that in the past suffered most the effects of eutrophication and anthropogenic impacts, such as clam fishing (Pranovi and Giovanardi, 1994; Sfriso et al., 2005). However, after its disappearance in the 1980s (Mannino et al., 2015) the species recolonized the northern lagoon covering 6.0 km^2 with a SC of 8.9 ktonnes FW and an NPP of 18 ktonnes FW. *Zostera noltei*, that in 2003 covered about 6.2 km^2 with an SC of 9.8 ktonnes FW and an NPP of 25 ktonnes FW, in 2018 increased its growing values even by 191% (cover), 272% (SC), and 249% (NPP) (**Table 4**). *Zostera marina* cover increased by 12.2 km^2 (+46.6%) from 26.1 to 38.2 km^2 whereas the SC and NPP increased by 61 and 59%, respectively. Finally, *C. nodosa* from 2003 to 2018 increased its cover from 23.6 to 32.4 km^2 (+37.5%).

With exception of *C. nodosa*, a significant growth of the angiosperm species was also favored by transplant activities carried out in the northern basin of the Venice Lagoon in the framework of the project Life SERESTO (LIFE12 NAT/IT/000331) (Project LIFE12 NAT/IT/000331, 2012; Sfriso et al., 2021b). Indeed, between 2014 and 2018 more than 75,000 rhizomes were transplanted forming wide meadows of *Z. noltei*, *Z. marina*, and *R. cirrhosa* that colonized approximately 15 km^2 of lagoon bottoms with a mean density of 40%. This contributed significantly to explain the increase of these species in the northern

TABLE 4 | Macrophyte comparison in different years.

Species	Year	Area	SC	NPP
		km²	ktonnes	
C. nodosa	2003	23.6	109	346
	2018	32.4	181	539
Increase		8.8	72	193
	%	37.5	66	56
Z. marina	2003	26.1	91	343
	2018	38.2	145	545
Increase		12.2	55	203
	%	46.6	61	59
Z. noltei	2003	6.2	9.8	25
	2018	18.1	36.5	86
Increase		11.8	27	62
	%	191	272	249
R. cirrhosa	2003	0	0	0
	2018	6.0	8.9	18.0
Total angiosperms	2003	55.9	209	714
	2018	94.8	372	1189
Increase		39	162	475
	%	70	77	67
Total macroalgae	1980	202	841	2912
	2003	97	89	472
	2018	134	104	647
Increase		37	15	175
2003-18	%	38	17	37

basin where they had almost completely disappeared. But a strong natural recruitment was also recorded in the central and southern lagoon, mainly due to the almost total disappearance of clam fishing activities caused by overexploitation. Therefore, transplantation activities in areas where the nutrient reduction hinders the bloom of thionitrophilic macroalgae or phytoplankton and there are no other significant anthropogenic impacts are an excellent tool to accelerate a quick recovery of ecological conditions. Widespread manual transplants of small sods or single rhizomes of aquatic angiosperms are the simplest, rapid, and least expensive tool to favor the formation of prairies and the recolonization of sensitive macroalgae with a strong reduction of Ulvaceae. Indeed, at present the Venice Lagoon is dominated by angiosperms and macroalgae less dangerous than Ulvaceae for the environment because they withstand higher water temperatures

and are unlikely to trigger hypo-anoxic conditions (Sfriso and Sfriso, 2017).

The strong inverse relationships between nutrient concentrations and aquatic angiosperms and sensitive macroalgae is well highlighted by the results recorded in the 6 stations sampled in the lagoon in 2019 on an annual basis. The stations characterized by a higher trophic level (SG and FUS) were only colonized by macroalgae of low ecological value and no sensitive species or aquatic angiosperm were present. Conversely, the areas characterized by a lower concentration of nutrients both in the water column and in the surface sediments (SMM, PBò, Ca'R, SN) had dense seagrass meadows and many sensitive macroalgae, especially the small calcareous macroalgae of the genus *Hydrolithon*, *Pneophyllum*, and *Melobesia* (Sfriso et al., 2020b). The latter are more sensitive than seagrasses to respond

TABLE 5 | Comparison of angiosperm biomass and Net Primary Production (NPP).

	Highest biomass		NPP		References
	g DW m⁻²		g DW m⁻² d⁻¹		
	shoots	rhizomes	shoots	rhizomes	
Mean of 30 Seagrasses	224	237	3.84	1.21	Duarte and Chiscano (1999).
C. nodosa	147	280	1.3	0.17	Duarte and Chiscano (1999).
	674	694	4.94	1.88	SMM, this paper
	594	355	5.79	1.92	SN, this paper
Z. marina	298	150	5.2	1.7	Duarte and Chiscano (1999).
	425	265	5.08	0.85	Ca'R, this paper
Z. noltei	83	66	1.1	ND	Duarte and Chiscano (1999).
	296	305	2.64	1.02	PBò, this paper

ND, Not Determined.

to an improvement in ecological conditions and their discovery is an excellent indicator to predict the possibility of a recolonization of angiosperms or the success of transplant activities.

Extensive literature is available on the biomass and production of the angiosperms treated in this paper, but an exhaustive summary has been made by Duarte and Chiscano (1999) who reported information on the highest biomass and production of 30 different species of seagrasses (**Table 5**). On average, the mean values of the above- and belowground highest biomass and production were 224 ± 18 and 237 ± 28 g DW m^{-2}, respectively. In addition, these authors also reported the values of *C. nodosa*, *Z. marina*, and *Z. noltei*. In general, the highest biomass and the production recorded in the Venice Lagoon were higher both for the above- and belowground of all three species. Shoots and rhizomes were 2-4 times higher for *C. nodosa* and *Z. noltei*, and 2 times for *Z. marina*. The production was 3-4 times higher for shoots of *C. nodosa*, 2 times for *Z. noltei*, and very similar for *Z. marina*. The production of rhizomes was markedly higher for *C. nodosa* whereas for *Z. marina* it was almost half. No information for the rhizomes of *Z. noltei* is available. The greater biomass recorded in the Venice Lagoon probably depends on the choice to study compact prairies to obtain information under optimal growth conditions. However, higher biomass and production data were also recorded by Sfriso and Ghetti (1998) who studied the annual growth of the same species in different areas of the Venice Lagoon. In addition, studies in progress show that in 2021 angiosperm biomass and production increased further.

Moreover, the recovery of angiosperm meadows contributed to a further environmental recovery accelerating the recolonization of fish species both of commercial and conservation interest (Jackson et al., 2001; Blandon and Zu Ermgassen, 2014; Bonometto et al., 2018; Scapin et al., 2018; Scapin et al., 2019) and is changing the composition of the benthic macrofauna (Orth et al., 1984; Sfriso et al., 2001; Leopardas et al., 2014; Lin et al., 2018; Mariño et al., 2018) living in these underwater forests.

These results confirm that the recovery of highly degraded TWS, such as the Venice Lagoon was up to the early 2000s, is easily achievable provided there is low trophy and clear waters. Indeed, even small reductions in anthropogenic impacts, especially in basins with high tidal exchange, can favor a rapid or progressive environmental recovery thanks to the high resilience of these environments.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AS: funding acquisition, conceptualization, methodology, formal analysis, writing–original draft; AB, AAS: methodology, formal analysis, writing–review and editing; KS, MW, YT, A-SJ: formal analysis, writing–review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.882463/full#supplementary-material

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