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Environmental restoration by aquatic angiosperm transplants in transitional water systems: The Venice Lagoon as a case study

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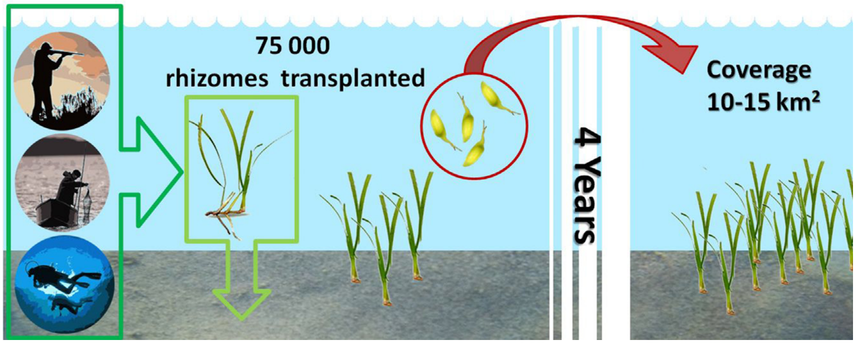
HIGHLIGHTS

- The northern Venice Lagoon was restored by aquatic angiosperm transplants.
- Areas characterized by low eutrophic status favoured aquatic angiosperm rooting.
- Small sod and rhizome transplants were efficient and cheap rooting technique.
- Fishermen and hunters actively participated in transplanting activities.
- Aquatic angiosperms are indicators of good-high ecological status.

GRAPHICAL ABSTRACT



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ABSTRACT

The paper reports the results obtained after 4 years of aquatic angiosperm transplants in areas of the Venice Lagoon (North Adriatic Sea, Mediterranean) where meadows almost disappeared due to eutrophication, pollution and overexploitation of clam resources. The project LIFE12 NAT/IT/000331-SeResto, funded by the European Union, allowed to recolonize the Habitat 1150* (coastal lagoons) in the northernmost part of the lagoon, by extensive manual transplants of small sods or single rhizomes of *Zostera marina*, *Zostera noltei*, *Ruppia cirrhosa* and, in some stations also of *Cymodocea nodosa*. Over the 4 years of the project more than 75,000 rhizomes were transplanted in 35 stations with the support of local stakeholders (fishermen, hunters and sport clubs). Plants took root in 32 stations forming extensive meadows on a surface of approx. 10 km^2 even if some failures were recorded in areas affected by outflows of freshwater rich in nutrients and suspended particulate matter. The rapid recovery of the ecological status of the involved areas was the result of this meadow restoration, which was in compliance with Water Framework Directive (WFD 2000/60/EC) objectives. Moreover, the monitoring of environmental parameters in the water column and in surface sediments allowed to identify the best conditions for successful transplants. Small, widespread interventions and the participation of local stakeholders in the environmental recovery, make this action economically cheap and easily transposable in other similar environments.

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1. Introduction

Pristine or nearly pristine transitional water systems (TWS) should be mainly colonized by aquatic angiosperms (Orfanidis et al., 2001, 2003; Sfriso et al., 2007, Sfriso et al., 2009a; Sfriso et al., 2009b; Sfriso et al., 2014a) and sensitive macroalgae (ISPRA, 2011; Sfriso et al., 2020). However, the anthropogenic pressures affecting these highly populated environments have often profoundly degraded their ecological conditions (Orth et al., 2006). Since the last decades of the twentieth century, a progressive deterioration of TWS was reported due to the increase in industrial activities, agricultural monocultures, urban sewages, fishing and aquaculture activities (Cossu and De Fraja Frangipane, 1985; Nedwell et al., 1999; Kastler and Michaelis, 1999; Schramm and Nienhuis, 1990; Wolfe, 1986) and to propagation of pathogenic parasites, such as *Labyrinthula zosterae* Porter and Muehlstein, that triggered wasting disease on *Zostera* leaves (Den Hartog et al., 1996; Ralph and Short, 2002).

The change of vegetation composition and structure, due to loss of seagrass meadows, is one of the main consequences of this environmental degradation. Seagrasses were rapidly replaced by nuisance macroalgae (Ulvaceae, Gracilariaceae and Cladophoraceae) (Morand and Briand, 1996) and, under extreme conditions, by phytoplankton and cyanobacteria blooms (Munari and Mistri, 2012; Sorokin and Zakuskina, 2010). Hence, a gradual disappearance of the aquatic angiosperms and sensitive macroalgae associated with the loss of biodiversity was usually observed (Boudouresque et al., 2009; Burkholder et al., 2007; Orth et al., 2006; Pérez-Ruzafa et al., 1989; Short and Wyllie-Echeverria, 1996, Tan et al., 2020). In the case of the Venice Lagoon, aquatic angiosperms decreased significantly (Sfriso and Facca, 2007), especially in the choked areas, where water renewal ranges from 12 to 40 days (Cucco and Umgiesser, 2006) and pollutants and nutrients stagnate affecting the flora and fauna of these basins.

In the early 2000s submerged aquatic angiosperms disappeared almost completely in the northernmost region of the northern basin due to both increasing eutrophication and clam fishing with heavy hydraulic and mechanical dredges (Pranovi and Giovanardi, 1994; Sfriso et al., 2003). In fact, in this area, *Zostera noltei* Hornemann, *Zostera marina* Linnaeus, *Ruppia cirrhosa* (Petagna) Grande and *Cymodocea nodosa* (Ucria) Asherson meadows have been completely replaced by tionitrophilic macroalgae.

A trend inversion is possible as reported for other European seagrass meadows (de los Santos et al., 2019) and in other parts of the world like in Chesapeake Bay (USA) where the measures adopted to restore water quality reduced significantly nutrient and sediment loads (Lefcheck et al., 2018). In the Venice Lagoon the decrease of clam stock harvesting observed since the 2011, led to the reduction of nutrients and macroalgal biomass (Facca et al., 2014; Sfriso et al., 2003; Sfriso et al., 2005a; Sfriso et al., 2009a). As a result, aquatic angiosperms began to recolonize the lagoon (Curiel et al., 2006; Rismondo et al., 2003; Sfriso and Facca, 2007; Sfriso et al., 2009a), but only in the areas where meadows were already present, whereas in strongly choked areas no recolonization was observed.

In the light of this new context, the Life Nature Project "Habitat 1150* (Coastal Lagoon) recovery by Seagrass Restoration". A New strategic approach to meet HD & WFD objectives" (Life12 NAT/IT/000331 – SeResto) was funded by the European Union. The aim of the project was the recolonization of the northern area of the Venice Lagoon (SCI it 3250031) by large scale transplants of aquatic angiosperms in order to restore the ecological quality status to good or high (sensu Dir. 2000/60/EC, WFD) and improve the conservation status of the coastal lagoon habitat (sensu Dir. 92/43/EEC, Habitat Directive) and the associated ecosystem services (Costanza et al., 1997).

Restoration of aquatic seagrasses is a well-studied topic although the obtained results were often contrasting depending on the different transplantation methods and ecological conditions (Boudouresque et al., 2021; Burkholder et al., 2007; Calumpong and Fonseca, 2001; de Jonge et al., 2000; Fonseca et al., 1998; Kastler and Michaelis, 1999; Orth et al., 2020; Orth and McGlathery, 2012; Phillips, 1980; van Katwijk et al., 2009, van Katwijk et al., 2016; Tan et al., 2020; Zhang et al., 2021).

Among these, Sfriso et al. (2019b) reported the results of Life12 NAT/IT/000331 – SeResto transplants obtained after the 1st year of the project. In this study we showed the analyses of the most common environmental parameters and nutrient concentrations in the various environmental matrices (water column, surface sediments, and suspended particulate matter (SPM)), the transplantation methods, and the most suitable environmental conditions to ensure the success of species rooting.

The aim of this paper is to report the analysis of the global growth and spread of the angiosperm meadows after 4 years from the first transplants, focusing on the meadow formation and the relationship with the environmental parameters and variables monitored throughout the whole period. In addition, the changes of the ecological status of the transplanting areas were determined by the application of three ecological indices based on macrophytes, benthic macrofauna and fish fauna. Finally, a cost analysis of the adopted transplant techniques was carried out.

2. Materials and methods

2.1. Study area

Transplant activities took place in the northernmost region of the northern lagoon in an area of approx. 36.6 km^2 (sexagesimal coordinates: 45° 30′ 34″ N, 12° 27′ 33″ E) (Fig. 1).

Overall, 35 shallow stations were identified, mostly along the border of salt marshes and tidal channels. The intervention area is divided in two main basins by San Felice and Cenesa channels. The south-eastern side is characterized by the absence of freshwater inputs and by shallow waters (approx. −0.5/−1.0 m above m.s.l.), and the north-western side by lower salinity, due to the connection with the Silone river (average flow rate approx. 5–6 $m^3\ s^{-1}$). In addition, recurring overflows from the Sile river during the rainy periods affected the northern area of Palude Ca' Zane with flow rates ranging from a few $m^3\ s^{-1}$ up to 70 $m^3\ s^{-1}$ (Sfriso et al., 2019b).

2.2. Angiosperm transplants

Angiosperm transplants (*Z. marina*, *Z. noltei*, *R. cirrhosa*, *C. nodosa*,) were carried out in 17 stations within an area of approx. 100 m^2 (10 × 10 m) in spring 2014 and in 18 stations in spring 2015 (Fig. 1). *Zostera noltei* was transplanted in the shallower waters (approx. 0.5 m deep) of all sites along the edges of the salt marshes whereas *Z. marina* mostly in slightly deeper bottoms (approx. 1.0 m deep) along the edges of tidal channels characterized by high water renewal. *Ruppia cirrhosa* was transplanted in the most chocked sites where water exchange is between 12 and 40 days (Cucco and Umgiesser, 2006). *Cymodocea nodosa* was transplanted only in two sites characterized by compact sediments and salinity generally higher than 28 psu.

Sods of approx. 30 cm in diameter were collected from the boat with a manual corer taking care to not cut the leaves and to transfer the sods in moist perforated buckets until the transplant. The single rhizomes of *Z. marina* and *C. nodosa*, were collected manually or with a rake, gathered in bundles and immersed in a tank of sea water. Sods and rhizomes were transplanted within 2–3 h from the explant.

Sods were transplanted in groups of three for a total of nine sods per station, following the scheme in Fig. S1 (supplementary material). This transplant scheme was adopted to favor the rapid formation of large patches, easy to monitor even in very turbid waters. All operations were carried out on board of local flat boats to avoid trampling and damage to the bottom. The shallow depth of the intervention area (on average < 1 m above m.s.l.) favoured all transplant activities.

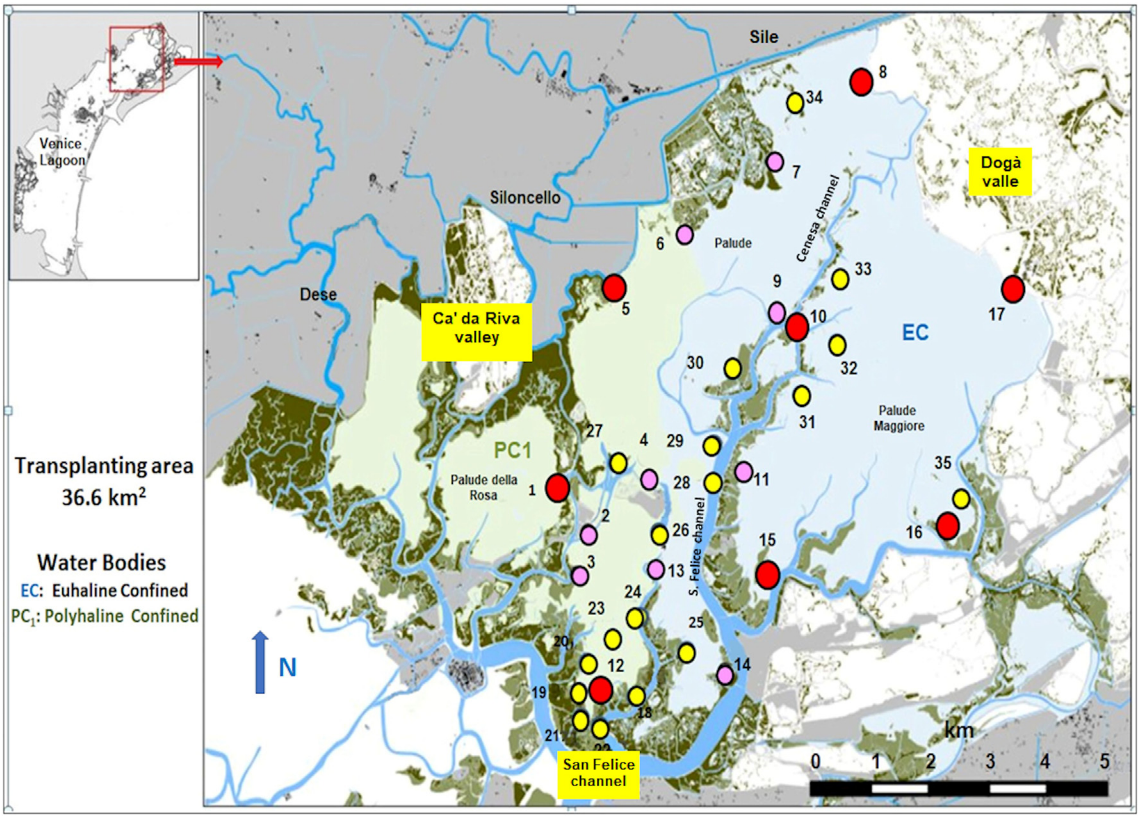


Fig. 1. Map of the sampling area with the 35 transplanting stations. In red and pink, the 17 stations transplanted in spring 2014. The stations in red were subject to intensive ecological monitoring. In yellow, the 18 stations transplanted in spring 2015. In light blue: EC = euryhaline confined water body (>30 psu); in light green: PC1 = polyhaline confined water body (18–30 psu). The donor sites are marked in yellow: Dogà valley, Ca' da Riva valley, San Felice channel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In addition, approx. 400 rhizomes, with 1–2 full-grown shoots, were transplanted individually at each station and between stations every year using pliers with a handle of approx. 1 m length.

At the beginning of the project the transplanting sods were provided by managers of surrounding fishing ponds (Dogà valley and Ca' da Riva valley, Fig. 1). These water systems are physically separated from the lagoon and are characterized by high ecological conditions and widespread aquatic angiosperm meadows.

To reduce the time of the operations and to become independent from fishing ponds, after the 1st year, aquatic angiosperms were collected from well-developed donor sites near the lagoon mouth of Lido (San Felice channel, Fig. 1) with prior authorization of the Interregional Superintendency of Public Works in Veneto – Trentino Alto Adige – Friuli Venezia Giulia (OOPP).

The results obtained during the 1st year of the project (Sfriso et al., 2019b) suggested continuing the transplants with sods for *Z. noltei* and *R. cirrhosa*, which are small in size, and single rhizomes for *Z. marina* and *C. nodosa* which are larger plants. Furthermore, the operations were preferentially carried out with a corer of 15 cm instead of 30 cm to reduce the explant/transplant efforts. Sfriso et al. (2019b) reported that the best seasons for transplanting the different species were autumn for *Z. marina*, late spring and autumn for *Z. noltei*, late spring and early summer for *C. nodosa* and summer-autumn for *R. cirrhosa*.

2.3. Angiosperm rooting and growth monitoring

The success/failure of sod transplants was assessed at each station monthly during the first 6 months after transplants (spring 2014 and spring 2015), and three times a year (early spring, early summer, autumn) until the end of the project. The average growth of angiosperm patches was recorded during each survey by measuring their number and diameter (only diameters >20 cm).

The success rate of single rhizome transplants was also assessed seasonally.

2.4. Physico-chemical parameter determination

The environmental conditions of the water column [temperature, pH, Eh, salinity, dissolved oxygen (DO), nitrites (NO_2^-), nitrates (NO_3^-), ammonium (NH_4^+), reactive phosphorus (RP), silicates $(SiO_4)^{4-}$, total suspended solids (TSS), chlorophyll-*a* (Chl-*a*), phaeophytin-*a* (Phaeo-*a*), total chlorophyll-*a* (sum of Chl-*a* and Phaeo-*a*), water transparency, light underwater transmission], surface sediments [pH, Eh, sediment fraction <63 μm (Fines), density, moisture, porosity, inorganic phosphorus (Pinorg), organic phosphorus (Porg), inorganic carbon (Cinorg), organic carbon (Corg), total nitrogen (Ntot)] and the settled particulate matter (SPM) collected by sedimentation traps placed on the bottom were monitored during all the transplanting period, from April 2014 to June 2017 (29 surveys), at eight stations (1, 5, 8, 10, 12, 15, 16, and 17), representative of the environmental conditions of the whole area. Surveys were carried out monthly for 1 year at the beginning and at the end of the project and quarterly in the intermediate period.

All analytical procedures follow Sfriso et al. (2005b) and Sfriso et al., 2019a) and in Strickland and Parsons (1984).

2.5. Ecological status determination

The changes of the ecological status in the transplanting area were determined at all sites using the Italian system for Transitional Waters, i.e. MaQI (Macrophyte Quality Index, Sfriso et al., 2007, Sfriso et al., 2019a, 2019b), HFBI (Habitat Fish Bioindicator index, ISPRA, 2017) and M-AMBI (*Multivariate-Azti* Marine Biotic Index, Muxika et al., 2007). MaQI and HFBI are typical indices used in Italy, while M-AMBI is used on a wider scale. Nevertheless, the Italian, French and Greek systems have been intercalibrated within the Mediterranean eco-region in the framework of the European Water Directive (2000/60/EC) (European Commission, 2018; Orfanidis et al., 2012). Furthermore, the MaQI index was validated considering the main physical-chemical parameters and environmental variables both in degraded environments and in environments of high ecological quality (Sfriso et al., 2009a), so it responds very well to any environmental change.

Macrophyte assemblages (seaweed species number, sensitive species number, seaweed and plant cover, seaweed biomass) were sampled twice a year according to the protocol used for the application of the Macrophyte Quality Index (MaQI) (Sfriso et al., 2007, Sfriso et al., 2019a, 2019b).

The sampling of the macrophyte variables in the first 17 stations took place from 2013, during the selection of the stations, to 2017. In the other 18 stations macrophytes were sampled from 2014 to 2017.

In addition, benthic macrofauna (once a year) and fish fauna (twice a year) were also monitored for the determination of M-AMBI (Muxika et al., 2007) and HFBI (ISPRA, 2017) at 8 stations, representative of the entire transplant area.

2.6. Statistical analyses

The average values of a) thirty two physico-chemical parameters determined in the water column, surface sediments and SPM, b) ten aquatic angiosperm and seaweed variables and (c) the results of the application of three indices of ecological status (MaQI, HFBI, M-AMBI), assessed at the end of the project, were analysed. The correlation between the macrophyte variables (angiosperms and seaweeds), water and sediment parameters and ecological indices (MaQI, HBFI, M-AMBI) was investigated. Shapiro–Wilk test differentiated non-normal data and the non-parametric Spearman's correlation coefficients were calculated.

The analysis of variance (one-way ANOVA) was applied to assess the significant differences between the parameters at the 8 stations. The normal distribution of experimental errors by residuals vs fitted and normal Q-Q plots was tested applying a logarithmic transformation to our data and/or outlier. The homoscedasticity of variances was tested using Bartlett test ($p > 0.05$). In addition, the post hoc test was applied to see differences between the paired station parameters with the relative significance p-value.

The principal component analysis (PCA), was applied to the same log-transformed data, after removing redundancies, to investigate the variance and associations between environmental parameters, aquatic angiosperm variables and ecological indices at the 8 stations. Data were processed by Statistica software, release 10 (StatSoft Inc. Tulsa, OK, USA).

3. Results

3.1. Aquatic angiosperm spreading

At the end of the 4 years of the project the total number of rhizomes with 1–2 shoots, transplanted by sods or single rhizomes was 75,121, mainly of *Z. marina* and *Z. noltei*, but also of *R. cirrhosa* and *C. nodosa*.

Among these, the number of rhizomes contained in the sods (9 sods × 35 stations) was approx. 9450. *Cymodocea nodosa* sods were transplanted in two stations (4, 7) characterized by compact sediments. In all the stations, *Z. noltei* was preferentially transplanted in shallower areas (<0.5 m) near the edges of salt marshes and *Z. marina* in areas approx. 1 m deep. *Ruppia cirrhosa* was transplanted in the most choked stations (6, 8, 9, 16, 17, 30, 34, 35).

After the first year, approx. Other 65,511 rhizomes were transplanted both as smaller sods (15 cm) for *Z. noltei* and *R. cirrhosa* and as single rhizomes for *Z. marina* and *C. nodosa* (Table S1, Supplementary material).

The impact of the explants from the donor sites, was less than 25 m^2 during the 1st year, and less than half in the successive years when only *Z. noltei* and *R. cirrhosa* were transplanted by sods. The removal of single rhizomes of *Z. marina* from donor sites did not damage the angiosperm meadows. In total, 51,260 rhizomes were transplanted by stakeholders (fishermen, hunters, members of sport clubs) and 14,451 by the researchers of the University of Venice (DAIS-UNIVE) (Table S1, Supplementary material).

The initial cover of the 9 sods (diameter: 30 cm) at each station (10×10 m = 100 m^2) was 0.64 m^2. After the 1st year the mean cover of the patches formed by the grown sods and single rhizomes was 8.59 m^2 (i.e. 8.59%, Fig. 2) with high differences among the single stations. This mean value increased to 57.4% at the end of the 2nd year and to 67.8% and 68.4% after 3 and 4 years, respectively. After 3 years, 21 stations out of 35, were completely colonized by the aquatic angiosperms (Fig. 2). At the end of the 4th year, the stations completely covered by angiosperms were 22, whereas no plants were recorded in 3 stations (1, 2, 5). In other 5 stations the cover was negligible (<3.0%) and in the remaining 5 stations the values were intermediate.

Moreover, the high number of seeds produced by the transplanted angiosperms colonized the surrounding edges of the salt marshes and tidal channels in the whole area of the project. In autumn 2017, almost 3.5 years after the first transplants, aquatic angiosperm patches colonized a lagoon surface of approx. 10 km^2 with an average cover of 40%. An increase of approx. 5 km^2 at the end of 2018 was observed, due to an extensive spread of *R. cirrhosa* in Ca' Zane valley during the 4th year (Fig. 3).

3.2. Cost-effectiveness of seagrass transplanting

In this project, the transplants of aquatic angiosperms were done manually. A few manual transplants are enough to rapidly develop new meadows in the presence of suitable environmental conditions. Further transplant efforts are useless as long as the environmental conditions do not change. The costs of these manual transplants were almost negligible. In the project Life SeResto the daily cost to transplant 18 sods of aquatic angiosperms with a diameter of approx. 30 cm was 300 €. This quote included the use of a flat boat with two operators. The total budget invested in 4 years to colonize the edges of salt marshes and channels in a lagoon area of approx. 15 km^2 (35 stations) was about 42,000 €. However, the transplants carried out during the last 2 years of the project were necessary only in the stations where the first ones were not successful. Therefore, the transplants essential for the angiosperm recolonization were those conducted during the first 2 years. In this way the budget could be reduced by 50%.

3.3. Main environmental parameters and aquatic angiosperm spread relationships

The average values of reactive phosphorus (RP) and dissolved inorganic nitrogen (DIN = nitrite + nitrate + ammonium) recorded in the water column (29 surveys), and total nitrogen (Ntot), organic phosphorus (Porg) and organic carbon (Corg) present in surface sediments (8 surveys) together with the angiosperm cover were reported for 8 stations from April 2014 to September 2017 (Fig. 4**)**.

The highest nutrient concentrations were found at stations 5 and 1, located in the polyhaline confined (PC1) water body, close to the river outflows (Fig. 1). The difference of DIN, Porg, Ntot and Corg concentrations between stations 5, 1 and station 12 placed in the same water body, but far from river outflows, and the other stations placed in the euryhaline confined (EC) water body was particularly significant (one-way ANOVA: $p < 0.001$, Table S2, Supplementary material). In this table the differences between the paired station parameters with the relative significance p-value were reported. The stations 1, 5 and 12 showed the highest difference compared to the other stations.

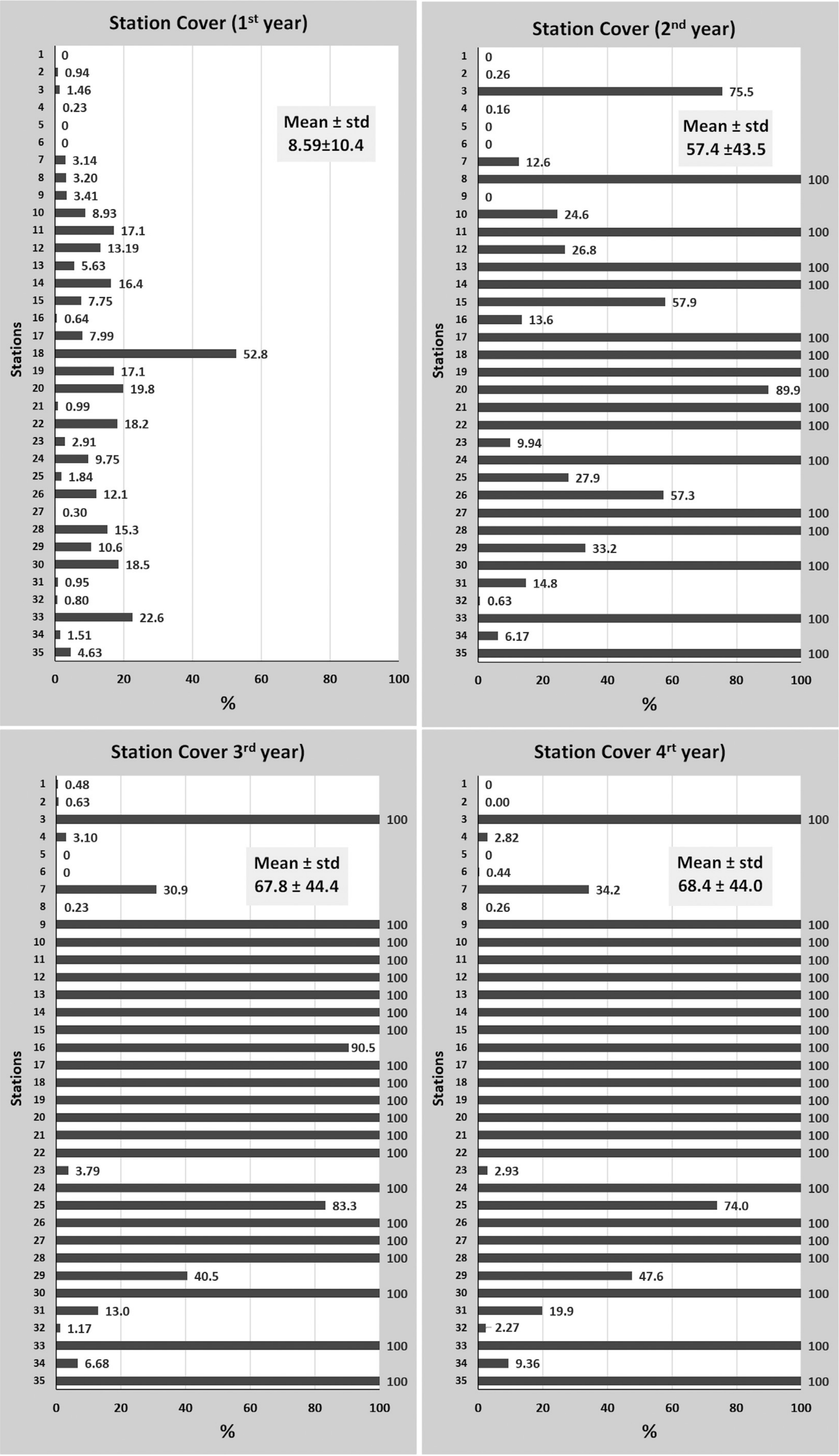


Fig. 2. Mean cover of the aquatic angiosperms in the single 35 stations at the end of each year.

However, in all the 8 stations, both the average values of RP and DIN were lower than the threshold established by the Environment Ministry Decree 260/2010 for good ecological status (euryhaline water bodies (>30 psu): DIN <18 μM, RP <0.48 μM; polyhaline water bodies (18–30 psu): DIN <30 μM; RP value not yet defined, LD, 2010).

In surface sediments the concentrations of Porg, TN and Corg were higher at station 1 and especially at station 5, whereas the lower concentrations of nutrients were recorded at stations 8, 12, 15 and 16, the furthest from the freshwater inputs. These values were comparable to those found in the same areas in 2011, 2014, 2018 (Buosi et al., 2020; Facca et al., 2014). Angiosperm cover was null at stations 1 and 5, high at stations 10, 12, 15, 16 and 17 and very low at station 8. The last station was completely colonized by *R. cirrhosa* during the 2nd year whereas during the 3rd and 4th years *Ruppia* disappeared almost completely to colonize again the station during the following years.

The non-parametric Spearman's correlation coefficients between macrophyte variables (angiosperms and seaweeds), ecological indices (MaQI, HBFI, M-AMBI) and the water and sediment parameters are shown in Table 1. In the water column the highest number of significant correlations (six) was recorded between the number of sensitive seaweeds (Table S3, supplementary material) and some physico-chemical parameters. The correlation was negative with the nitrogen compounds (NO_2^-, NO_3^-, NH_4^+, DIN) and silicate $(SiO_4)^{4-}$, and positive with pH. Similarly, five significant correlations were recorded between the total plant cover and some parameters: negative with NO_2^-, NO_3^-, NH_4^+, DIN and positive with Eh. Among the single angiosperm species, the highest number of significant negative correlations was recorded between the cover of *R. cirrhosa* and the nitrogen compounds. *Cymodocea nodosa*, transplanted only in two stations, did not show any significant correlation, whereas *Z. marina* and *Z. noltei* showed significant inverse correlations with Chl-*a* and Phaeo-*a*. The indices MaQI and HFBI showed inverse significant correlations with the concentrations of ammonium and nitrite whereas M-AMBI did not show any significant correlation.

In surface sediments, *Z. noltei* cover showed the highest number of correlations (seven), followed by total plant cover. *Zostera noltei* was negatively correlated with moisture, porosity and with the concentrations of Ptot, Porg, Corg and Ntot and positively with density. *Cymodocea nodosa* and *R. cirrhosa* did not show significant correlations. *Zostera marina* was positively correlated with Fines (fraction <63 μm). Total plant cover showed five significant correlations. It was negatively correlated with moisture, the concentration of Porg, Ntot and positively with density and the concentration of Cinorg. A lower number of significant values was recorded for other variables and parameter correlations (Table 1).

Among the ecological indices MaQI showed a highly significant inverse correlation with the concentration of Pinorg, whereas HFBI was positively correlated with pH. Finally, M-AMBI showed two positive correlations with Eh and Fines.

The Principal Component Analysis (PCA) between the mean values of all the considered parameters, variables and indices (38) after the elimination of redundant parameters is shown in Table S4 (supplementary material). The first two components showed a cumulative variance of 68.8% whereas that of five components was 93.7%. The number of significant loadings ($p > 0.7$) was very high, however the association between the various parameters and variables was much more important (Fig. 5). Indeed, by plotting the values of the first two components, two main groups were highlighted, one that included all the parameters and variables associated with bad environmental conditions (nutrient concentrations in the water column and surface sediments, pigment concentrations, sediment moisture and porosity, total suspended solids) and the other that was associated with good environmental conditions (pH, Eh of water and sediments, salinity, light availability at bottom (Light-B), sediment density (Dens), inorganic carbon (Cinorg), aquatic angiosperms, sensitive seaweeds (Sens) and calcareous seaweeds (S.calc.)). The orthogonal projections of each parameter/variable on the line that connects the two extreme ecological conditions showed that NO_2^-, NO_3^-, NH_4^+ and $(SiO_4)^{4-}$, were the parameters mainly associated with bad environmental conditions whereas pHw and Ehw of the water column, salinity, sediment density and water transparency at the bottom of the stations (Light-B), were associated with high ecological conditions.

The number of total seaweeds and sensitive seaweeds were highly associated with good-high ecological conditions, followed by the presence of *C. nodosa*, *R. cirrhosa*, *Z. noltei* and *Z. marina*. Among the ecological indices, MaQI (macrophytes) and HFBI (fish fauna) were associated with high ecological conditions whereas M-AMBI (benthic macrofauna) was still far from the group of parameters and variables associated with high ecological conditions.

An annual analysis of these index changes during the 4 years after the first angiosperm transplants carried out at the 8 stations is shown in Table 2.

All the three indices showed an average ecological improvement from poor (HFBI) -moderate (MaQI, M-AMBI) to moderate (HFBI), good (MaQI, M-AMBI) ecological conditions, with marked differences among the stations.

The ecological changes that occurred in all 35 stations were monitored by applying the Macrophyte Quality Index (MAQI) (Fig. S2, supplementary material).

4. Discussion

4.1. Aquatic angiosperm spreading

The role of aquatic angiosperms in the environmental health and ecosystem services is well known (Costanza et al., 1997; Cullen-Unsworth and Unsworth, 2013; Den Hartog, 1970; Duarte et al., 2013; Nordlund et al., 2016; Orth et al., 2006; Waycott et al., 2009) They are the most important primary producers of pristine or near to pristine transitional water systems (TWS), guarantee the ecosystem functionality and sustainability and are an indicator of high environmental quality (Orfanidis et al., 2003; Sfriso et al., 2007). Aquatic angiosperm meadows are a shelter and food area for juvenile fish (Hannan and Williams, 1998; Moussa et al., 2020; Scapin et al., 2019a, 2019b), oxygenate the surrounding environment and the surficial sediments (Borum et al., 2007) favoring the colonization of the benthic macrofauna (Leopardas et al., 2014; Lewis and Stoner, 1983; Lin et al., 2018). The good environmental oxygenation maintains water and sediment pH high and allows the engraftment and growth of calcareous epiphytic algae trapping high amounts of CO_2 (Barron et al., 2006; Canals and Ballesteros, 1997; Romero, 1988; Sfriso et al., 2020). In addition, aquatic angiosperm rhizomes avoid the sediment erosion trapping the suspended particles (de Boer, 2007; Potouroglou et al., 2017; Sfriso et al., 2005b).

The reduction or disappearance of angiosperm meadows has further led to environmental degradation (Orth et al., 2006) with the loss of all the ecosystem benefits provided by these plants and had a significant impact on the fishing sector (Unsworth et al., 2019). To reverse this trend, between the ‘90s and the beginning of the 2000s, efforts were made to reduce the effects of anthropogenic impacts with numerous regulations both at European (CD, 1991a, 1991b, 1992, 2000) and national level (LD, 2006; LD, 2010). In particular, the European Water Framework Directive (2000/60/EC) prescribed indications for the assessment of the ecological status and the improvement of the quality of both marine and freshwater systems and all Member States began to work together to achieve this goal. The results of these efforts led to a progressive environmental improvement (Sfriso et al., 2019a; Solidoro et al., 2010) by re-establishing suitable conditions for a natural recolonization of aquatic angiosperms as reported, for example, for Portuguese and other European seagrass meadows (Cardoso et al., 2010; de los Santos et al., 2019).

However, a natural recolonization is not always possible. In fact, in the Venice Lagoon aquatic angiosperms re-colonized many areas close to already existing meadows, while in choked areas, where the aquatic angiosperms had almost completely disappeared, there was no natural

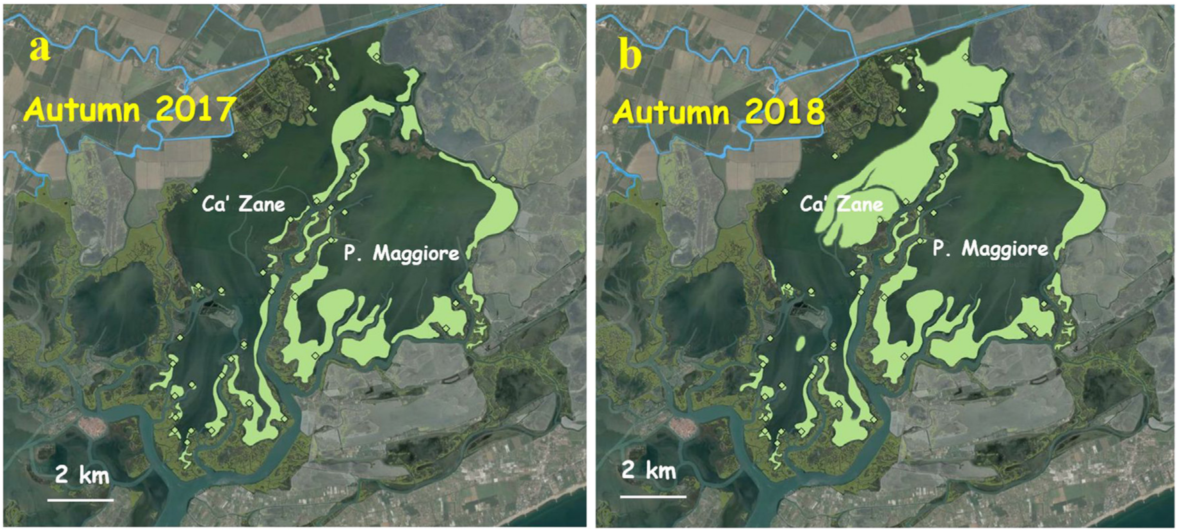


Fig. 3. Map of the angiosperm colonization covered by aquatic angiosperms (light green): a) autumn 2017 ca. 10 km^2; b) autumn 2018, ca. 15 km^2. The mean cover of the colonized areas was on average 40%. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

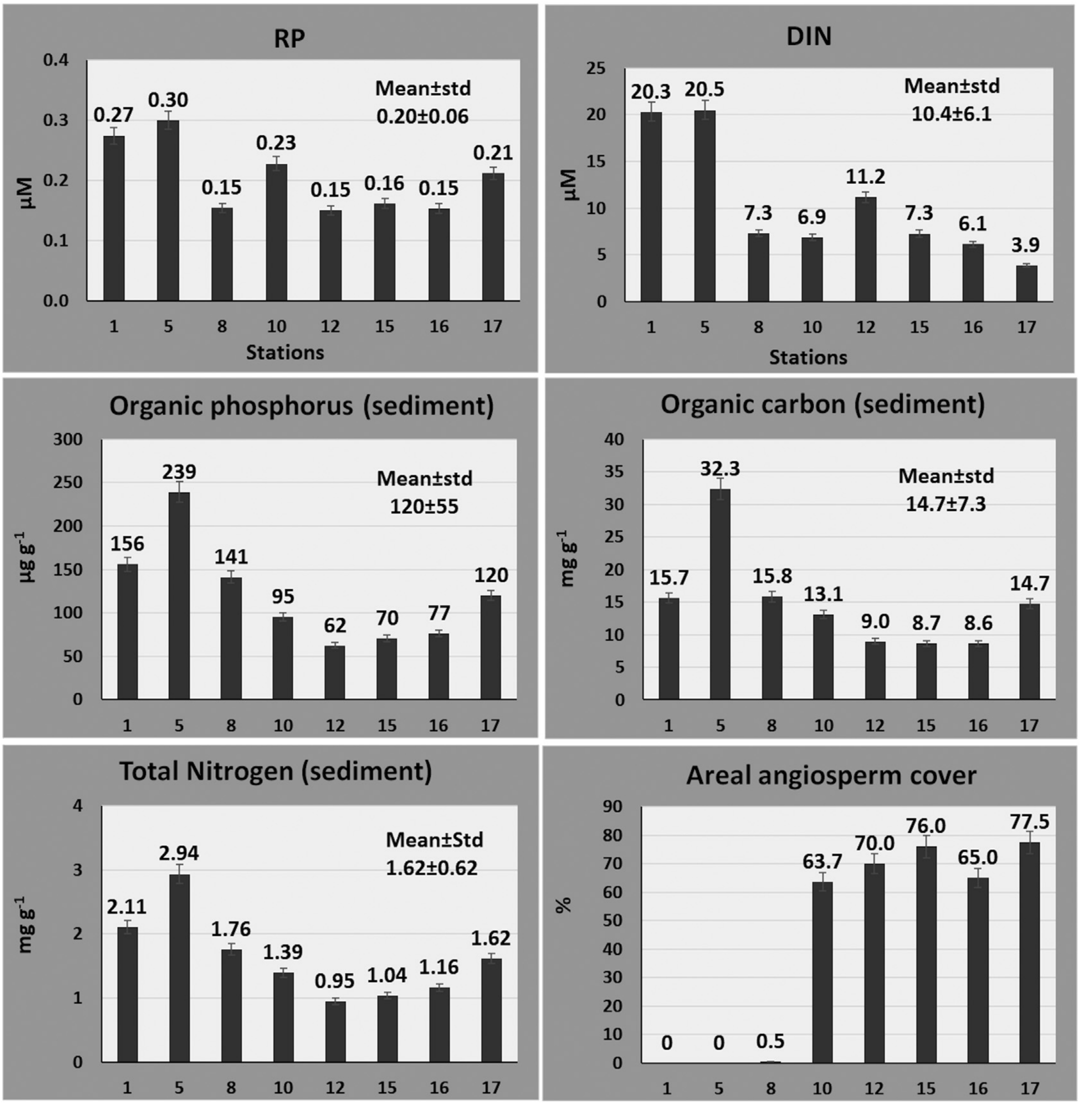


Fig. 4. Mean concentrations of the main nitrogen, phosphorus and carbon species in the water column (reactive phosphorus = RP; dissolved inorganic nitrogen = DIN), surface sediments (organic phosphorus = Porg; total nitrogen = Ntot; organic carbon = Corg) and mean angiosperm cover at the end of the project.

Table 1

Non-parametric Spearman's coefficients between biological variables and: a) water parameters and b) sediment parameters. Significant values ($p < 0.05$) are marked in red.

Water column (a)

	Temperature (°C)	Salinity (psu)	pH	Eh (mV)	DO (mg/L)	NO_2^- (µM)	NO_3^- (µM)	NH_4^+ (µM)	DIN (µM)	RP (µM)	SI (µM)	TSS (mg/L)	Phaeo-*a* (µg/L)	Chl-*a* (µg/L)	Chl-*a* tot (µg/L)	Secchi disk	Light at surface	Light at bottom	Sedimentation rates	Significant correlation number
***Cymodocea nodosa* cover (%)**	0.25	-0.25	0.41	0.41	-0.41	-0.58	-0.58	-0.58	-0.58	0.08	-0.58	0.58	0.25	0.58	0.25	0.22	0.41	-0.41	0.25	0
***Zostera marina* cover (%)**	-0.22	0.35	0.11	0.16	0.14	-0.14	-0.33	-0.52	-0.46	-0.22	0.11	-0.60	-0.46	-0.76	-0.55	0.05	0.19	0.44	-0.46	1
***Zostera noltei* cover (%)**	-0.34	0.81	0.10	0.29	-0.46	-0.12	-0.34	-0.37	-0.41	-0.59	-0.20	-0.24	-0.90	-0.63	-0.83	0.08	0.07	0.54	0.37	2
***Ruppia cirrhosa* cover (%)**	0.08	-0.22	0.68	0.11	-0.52	-0.85	-0.79	-0.71	-0.71	-0.33	-0.63	0.11	0.19	0.14	0.08	0.43	0.30	-0.46	-0.03	4
Total angiosperm cover (%)	-0.37	0.47	0.42	0.79	-0.71	-0.56	-0.63	-0.80	-0.73	-0.54	-0.73	-0.16	-0.51	-0.25	-0.61	0.48	0.32	0.32	0.06	5
Seaweed number (N°)	0.10	0.47	0.69	0.55	-0.63	-0.64	-0.54	-0.36	-0.48	-0.28	-0.77	0.14	-0.31	0.33	-0.15	0.34	0.70	0.27	0.69	1
Sensitive seaweed number (N°)	-0.26	0.31	0.77	0.57	-0.62	-0.85	-0.77	-0.85	-0.77	-0.62	-0.77	-0.51	-0.31	-0.36	-0.46	0.57	0.44	0.21	-0.21	6
Calcareus seaweed number (N°)	-0.11	0.67	0.38	0.41	-0.01	-0.29	-0.38	-0.40	-0.48	-0.19	-0.19	-0.49	-0.59	-0.41	-0.49	0.19	0.67	0.77	0.04	1
Seaweed biomass (g DW m^{-2})	-0.15	-0.36	-0.26	-0.37	0.51	0.10	-0.12	-0.25	-0.25	0.19	0.42	-0.09	0.26	-0.28	0.10	0.13	-0.09	-0.15	-0.74	1
Seaweed cover (%)	-0.17	-0.43	-0.43	-0.24	0.43	0.24	0.02	-0.24	-0.12	0.19	0.45	-0.05	0.24	-0.33	0.02	-0.05	-0.36	-0.26	-0.79	1
MaQI	-0.35	0.37	0.64	0.67	-0.52	-0.70	-0.64	-0.80	-0.69	-0.57	-0.69	-0.62	-0.37	-0.44	-0.54	0.55	0.41	0.37	-0.32	1
HFBI	-0.14	0.00	0.67	0.50	-0.33	-0.76	-0.67	-0.71	-0.69	-0.24	-0.69	-0.24	0.10	0.07	-0.05	0.65	0.60	0.10	-0.31	2
M-AMBI	-0.40	0.38	-0.19	-0.10	0.33	0.26	0.17	0.21	0.07	-0.05	0.21	-0.38	-0.24	-0.29	-0.21	0.33	0.19	0.69	-0.21	0

Surface Sediments (b)

	pH	Eh (mV)	Fines (%)	Density (g cm^{-3})	Moisture (%)	Porosity (%)	Ptot (µg/g)	Pinorg (µg/g)	Porg (µg/g)	Ctot (mg/g)	Cinorg (mg/g)	Corg (mg/g)	Ntot (mg/g)	Significant correlation number
***Cymodocea nodosa* cover (%)**	0.08	-0.25	-0.25	0.08	-0.08	0.08	0.25	-0.08	0.08	0.08	0.25	0.08	0.08	0
***Zostera marina* cover (%)**	0.30	0.33	0.74	0.46	-0.46	-0.63	-0.68	-0.38	-0.55	0.19	0.60	-0.76	-0.55	2
***Zostera noltei* cover (%)**	-0.32	0.49	0.46	0.81	-0.81	-0.85	-0.76	-0.10	-0.88	-0.27	0.49	-0.78	-0.88	7
***Ruppia cirrhosa* cover (%)**	0.22	-0.52	-0.35	0.11	-0.11	-0.19	0.08	-0.52	0.03	0.14	0.38	-0.11	0.03	0
Total angiosperm cover (%)	0.23	0.36	0.28	0.83	-0.83	-0.66	-0.63	-0.51	-0.73	0.02	0.73	-0.65	-0.73	5
Seaweed number (N°)	0.26	-0.12	0.54	0.02	-0.02	-0.22	-0.09	0.10	-0.02	0.56	0.59	-0.47	-0.02	0
Sensitive seaweed number (N°)	0.05	-0.26	0.31	0.05	-0.05	-0.19	-0.07	0.07	-0.02	0.83	0.52	-0.40	-0.02	1
Calcareus seaweed number (N°)	0.20	0.36	0.00	0.31	-0.31	-0.12	-0.15	-0.25	-0.26	-0.71	0.04	0.00	-0.26	1
Seaweed biomass (g DW m^{-2})	0.57	0.08	0.10	0.54	-0.54	-0.54	-0.54	-0.93	-0.46	0.00	0.59	-0.49	-0.46	1
Seaweed cover (%)	0.48	0.77	0.87	0.48	-0.48	-0.48	-0.67	-0.30	-0.58	-0.48	0.38	-0.58	-0.58	2
MaQI	0.64	0.26	0.27	0.61	-0.61	-0.56	-0.65	-0.91	-0.54	0.05	0.63	-0.56	-0.54	1
HFBI	0.81	0.12	0.21	0.29	-0.29	-0.19	-0.24	-0.67	-0.17	0.00	0.55	-0.26	-0.17	1
M-AMBI	0.43	0.76	0.88	0.26	-0.26	-0.26	-0.43	0.17	-0.36	-0.36	0.31	-0.43	-0.36	2

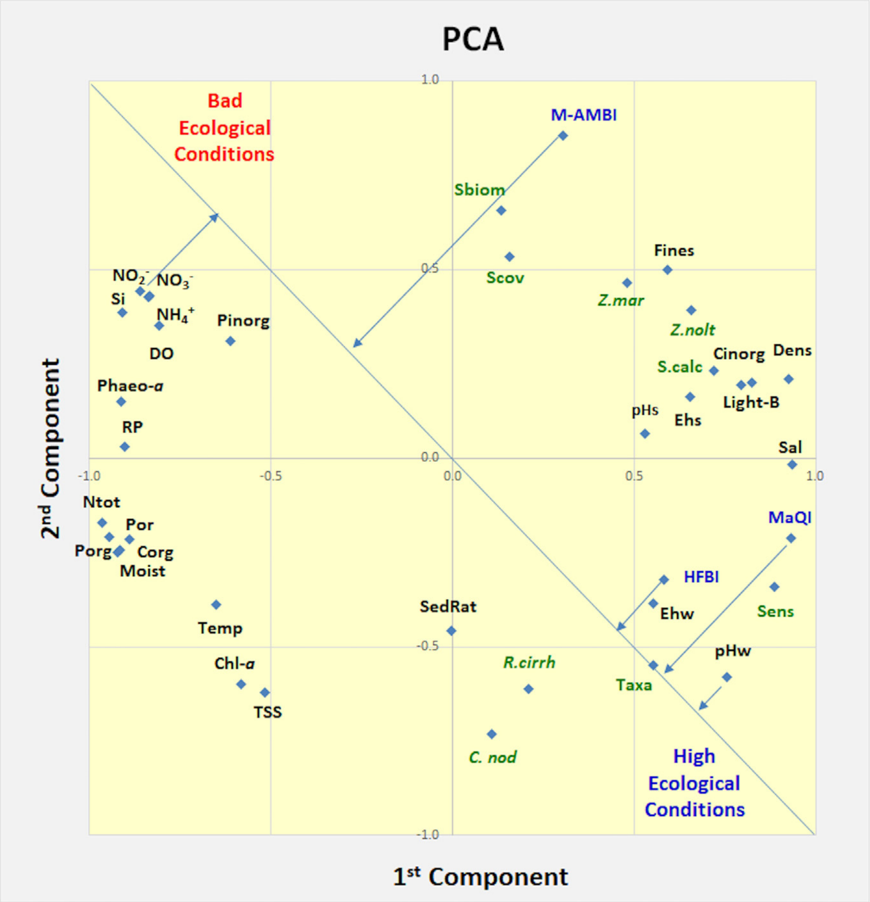


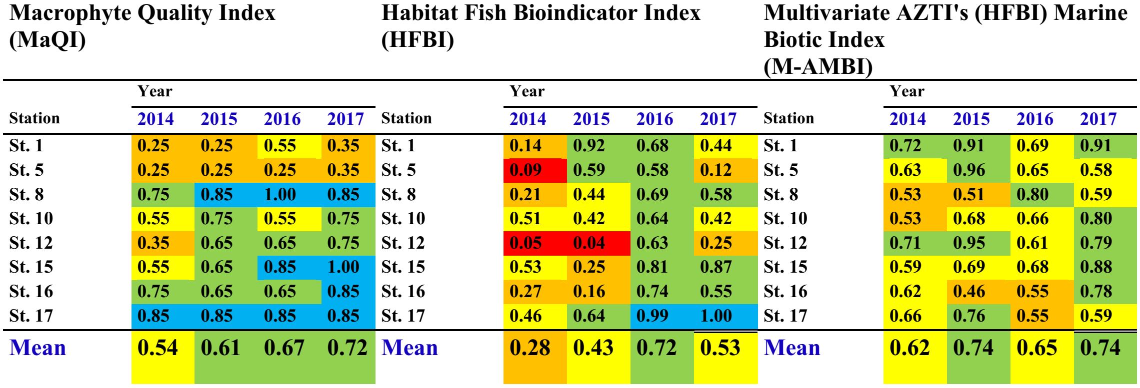
Fig. 5. Principal Component Analysis between all the considered water and sediment parameters (black colour), biological variables (green colour) and ecological indices (blue colour). Legenda: Sbiom = seaweed biomass; Scov = seaweed cover; S.calc = calcareous seaweeds; Sens = sensitive seaweeds; Taxa = number of seaweeds; *Z. mar* = *Zostera marina*; *Z. nolt* = *Zostera noltei*; *R. cirrh* = *Ruppia cirrhosa*; *C. nod* = *Cymodocea nodosa*; DO = dissolved oxygen; Sal = salinity; Transp = water transparency; TSS = total suspended solids; Chl-*a* = Chlorophyll-*a*; Phaeo-*a* = Phaeophytin-*a*; Fines = sediment fraction <63 μm; Moist = sediment moisture; Por = sediment porosity; Dens = sediment density; SedRat = Sedimentation rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recolonization due to lack of seeds. For this reason, it was necessary to adopt transplant methods to accelerate the recolonization process. In this context the transplants with small sods or single rhizomes were very efficient and low-cost techniques, especially for *Z. marina*, *Z. noltei* and *R. cirrhosa*. In fact, each shoot of *Z. marina* and *Z. noltei* produced 1 to 10 ears, each with 5–15 seeds and millions of new plants were then naturally produced with the development of a large number of patches.

The most successful species was *Zostera noltei*. It was transplanted in all stations and colonized almost all the edges of the saltmarshes and channels far from freshwater inputs. *Zostera marina*, has taken root only at the edges of the channels or in the areas with a great water turnover. The limited colonization of this species was the consequence of the excessively high summer temperatures (<30 °C) of the choked areas. Indeed, the highest optimum temperature for this cold species is <26–28 °C (Höffle et al., 2011; Sfriso et al., 2019b). *Ruppia cirrhosa*

Table 2

– Values of the three ecological indices during the 4 years of the project. EQR = Ecological Quality Ratio ranging from 0 to 1.



Macrophyte Quality Index (MaQI)					**Habitat Fish Bioindicator Index (HFBI)**					**Multivariate AZTI's (HFBI) Marine Biotic Index (M-AMBI)**				
	Year					**Year**					**Year**			
Station	**2014**	**2015**	**2016**	**2017**	**Station**	**2014**	**2015**	**2016**	**2017**	**Station**	**2014**	**2015**	**2016**	**2017**
St. 1	0.25	0.25	0.55	0.35	**St. 1**	0.14	0.92	0.68	0.44	**St. 1**	0.72	0.91	0.69	0.91
St. 5	0.25	0.25	0.25	0.35	**St. 5**	0.09	0.59	0.58	0.12	**St. 5**	0.63	0.96	0.65	0.58
St. 8	0.75	0.85	1.00	0.85	**St. 8**	0.21	0.44	0.69	0.58	**St. 8**	0.53	0.51	0.80	0.59
St. 10	0.55	0.75	0.55	0.75	**St. 10**	0.51	0.42	0.64	0.42	**St. 10**	0.53	0.68	0.66	0.80
St. 12	0.35	0.65	0.65	0.75	**St. 12**	0.05	0.04	0.63	0.25	**St. 12**	0.71	0.95	0.61	0.79
St. 15	0.55	0.65	0.85	1.00	**St. 15**	0.53	0.25	0.81	0.87	**St. 15**	0.59	0.69	0.68	0.88
St. 16	0.75	0.65	0.65	0.85	**St. 16**	0.27	0.16	0.74	0.55	**St. 16**	0.62	0.46	0.55	0.78
St. 17	0.85	0.85	0.85	0.85	**St. 17**	0.46	0.64	0.99	1.00	**St. 17**	0.66	0.76	0.55	0.59
Mean	**0.54**	**0.61**	**0.67**	**0.72**	**Mean**	**0.28**	**0.43**	**0.72**	**0.53**	**Mean**	**0.62**	**0.74**	**0.65**	**0.74**

was successfully transplanted only in the most choked stations where water turnover exceeds 12–15 days. This species produced a lower number of seeds per shoot than *Zostera* spp. but, it showed an even greater spreading capacity due to the higher number of shoots per square meter which in late summer can exceed 30,000 units as recorded by Cagnoni (1997). In these areas it quickly became the dominant species.

Finally, *C. nodosa* was the least suitable species due to the presence of too fine sediments and took roots only in one station. It produces only few seeds in the Venice Lagoon, therefore its dispersion can occur mainly by transplanting a high number of rhizomes.

In areas with high water transparency for most of the year and the low concentration of nutrients, that did not allow an excessive growth of tionitrophilic algae, aquatic angiosperms took root and spread rapidly with a significant general improvement of the conservation degree of habitat 1150* (Coastal lagoons) and its ecological status sensu WFD 2000/60/EC.

Furthermore, the rooting and spreading of these angiosperms was greatly affected by the weather conditions: 2014 showed the highest number of rainy days (105) and rainfall (1184 mm), winter 2015–2016 showed particularly intense cold conditions and freezing waters and 2016 and 2017 were particularly windy (http://www.arpa.veneto.it).

The success of the Project SeResto can be explained by the high number of rhizome transplants (>75,000) as reported also by van Katwijk et al. (2016). These authors found that the transplant success requires a minimum threshold, ranging from 1000 and 10,000 shoots/seeds of reintroduced individuals. Furthermore, mechanical transplants have generally shown less success than manual methods, although initial survival can be greater (Paling et al., 2001). Indeed, manual transplants of small sods or single rhizomes have a lower environmental impact and, in areas of shallow water, can also be done directly from the boat. They also guarantee a greater dispersion of transplants and a higher chance of success as recorded by Sfriso et al. (2019b) and Zhang et al. (2021). In addition, the transplants of single rhizomes formed patches with a mean growth higher than that of sods (rhizomes: 0.19 cm day^{-1}, sods 0.14 cm day^{-1}). The higher number of single transplants, in the presence of suitable ecological conditions, can form wide angiosperm meadows already after one year.

4.2. Cost-effectiveness of seagrass transplanting

The use of small transplants that act as a trigger for the natural development of the angiosperm meadows is a technique that was successfully adopted to transplant *Z. noltei* in Provence (Bernard et al., 2013), *C. nodosa* in the Canary Islands (de la Rosa et al., 2006) and *Z. marina* in Portugal (Paulo et al., 2019). The costs for the transplants of aquatic angiosperms in the Venice Lagoon in the framework of the project Life Seresto were considerably lower in comparison to the quote proposed by the "Morphological Plan for the Venice Lagoon Restoration" (Boato, 2017). This plan estimated a cost of 3.6–9.5 million euros to transplants 6–15 ha of lagoon bottoms (60 euros per m^2). Similar high costs were reported by Bayraktarov et al. (2016) and Tan et al. (2020), who estimated a median cost of 106,782 US$/ha. The substantial difference concerns the philosophy of transplants. In fact, the recolonization of the lagoon areas was not planned with extensive transplants and the use of mechanical means, but using simple manual techniques and focusing on the potential spreading of the transplanted species, especially for *Zostera* spp. and *R. cirrhosa* which produce millions of seeds. In the presence of suitable ecological conditions, plant recolonization will be exponential, and small triggers will be enough to ensure good coverage in just 3–4 years.

4.3. Relationship between aquatic angiosperms, environmental parameters and seaweeds

Another aspect concerns the values of the parameters that favor the rooting and spread of aquatic angiosperms. It is difficult to give ranges for each parameter because they are very variable and act synergistically, especially in eutrophic or polluted environments like that of Transitional Water Systems (TWS). Indeed, eutrophic environments are not only characterized by high values of nutrients but also by the presence of high biomasses of macroalgae and high concentrations of particulate matter. High biomasses of tionitrophilic macroalgae (>3 kg FW m^{-2}) such as Ulvaceae, Cladophoraceae, Gracilariaceae or other fast-growing species can limit the rooting and growth of aquatic angiosperms whereas sensitive slow-growing macroalgae often coexist with seagrass meadows. In fact, these species of macroalgae (e.g. *Chaetomorpha linum* (O.F. Müller) Kützing, *Valonia aegagropila* or other species) hardly create serious overshadowing effects or conditions of hypo-anoxia, even if the biomass is very high.

In the presence of high fast-growing macroalgal biomasses nutrient concentrations can be low in the water column also in eutrophic areas because for the most part they were absorbed by the seaweeds and retained in their tissues (Sfriso and Marcomini, 1999; Sfriso et al., 1994). In addition, the trophic conditions of the different areas of the lagoon environment depend especially on the water renewal which can significantly reduce or increase the concentrations of nutrients and pollutants changing their synergies with primary producers. For example, a highly polluted area such as the industrial area of Porto Marghera, which is affected by a high number of anthropogenic pressures, due to the constant water renewal of the large and deep Malamocco-Marghera canal, presents better ecological conditions than areas affected by a lower number of pressures such as some choked areas where water renewal is negligible (Sfriso et al., 2008).

Finally, water transparency does not depend only on phytoplankton concentrations but also on sediment resuspension created by the input of freshwater from various sources (i.e. rivers, urban waste, tidal currents, etc.) or by anthropogenic activities such as clam harvesting. Occasional events of resuspension are also sufficient to significantly or completely limit the growth of aquatic angiosperms (Brodersen et al., 2017; Zabarte-Maeztu et al., 2020). Therefore, providing a fixed range of values for parameters such as nutrients or water turbidity can be hazardous or misleading as there are always exceptions or other parameters that can change the situation.

For this reason, it is easier and more reliable to use an ecological indicator that summarizes these different aspects. A good candidate is the presence/absence of macroalgal species of high ecological value, in particular, the small calcareous macroalgae of the genus *Hydrolithon*, *Pneophyllum* and *Melobesia* which are ubiquitous epiphytes on the leaves of aquatic angiosperms and on the thalli of other macroalgae (Sfriso et al., 2020). These small calcareous macroalgae, ca. 100–200 μm wide and 20–30 μm thick, are more sensitive than aquatic angiosperms to trophic changes. So, their presence on macroalgal thalli indicate that the ecological status of a given area is sufficiently good for angiosperm rooting. Conversely, if they disappear from the leaves of aquatic angiosperms or are completely missing, it means that the environment is degrading and that the aquatic angiosperms will also disappear.

The results obtained during the 4 years of the project Life SeResto showed that the fastest angiosperm recolonization was achieved in areas characterized by low trophic conditions (reactive phosphorus = RP < 0.2 μM; dissolved inorganic nitrogen = DIN < 15 μM) and far from the turbid, polluted and highly eutrophic river outflows (Collavini et al., 2005; Zonta et al., 2005). Higher concentrations of DIN, RP and low water transparency (<0.6–1.0 m) can reduce or completely hinder the rooting of aquatic angiosperms, as evidenced by the negative Spearman's correlations, the PCA analysis and the results obtained by Sfriso et al. (2019b) during the first year after transplants. On the contrary, high pH (>8.15) and Eh (>242 mV) values in the water column, high water transparency (>1.0 m) and salinities generally >27 psu favoured plant rooting and spreading. In fact, high values of pH and Eh are associated with the absence of hypo-anoxic conditions whereas salinity, in the Venice Lagoon, is an indicator of freshwater inputs because it is a lagoon strongly affected by high sea water exchanges. The separation between euryhaline (water body EC) and polyhaline (water body PC1) areas did not discriminate the angiosperm rooting although lower salinities in some stations near the mouths of rivers (1, 5, 6) were associated to higher nutrient concentrations and water turbidity that hampered or reduced angiosperm colonization.

4.4. Ecological conditions assessment

Another important aspect of angiosperm meadow formation concerns the improvement of the ecological conditions sensu European Water Framework Directive (WFD) 2000/60/EC. WFD objectives to achieve “good status” of water bodies had to be met by 2015. In case the targets were not met, Member States will have to achieve all WFD environmental targets by the end of the 2nd (2021) or 3rd (2027) management cycle (European Commission, 2012; Voulvoulis et al., 2017). The Regional Agencies for the Protection of the Environment of the Italian Regions (ARPAs) were involved in the monitoring of the ecological conditions of the Italian TWS.

In the Venice Lagoon the monitoring of ecological conditions was carried out in 11 water bodies by sampling macrophytes (MaQI), the benthic macrofauna (M-AMBI) and fish fauna (HFBI) in 2011, 2014, 2018, and the results indicated that the WFD objectives are not yet met in all water bodies. The monitoring of macrophytes (MaQI index, Sfriso et al., 2007, Sfriso et al., 2019a, 2019b), benthic macrofauna (M-AMBI index, Muxika et al., 2007) and fish fauna (HFBI index, ISPRA, 2017) carried out in the framework of the project Life SeResto showed a marked improvement in the ecological conditions of the areas where the angiosperms have taken root. Indeed, the presence of wide angiosperm meadows favoured the growth of seaweeds of high ecological status such as the microcalcareous taxa, previously very rare or completely absent in these areas (Sfriso, 2018), the increase of conservation and commercial fish species (Scapin et al., 2019a) and the improvement of the benthic macrofauna (Bonometto et al., 2018).

By analyzing the results of the three index application during the 4 years of transplants (Table 2), MaQI showed a mean progressive improvement increasing the Ecological Quality Ratio (EQR) in all the 8 stations whereas the other two indices showed mixed results even if the meadow formation at the end of the project was widespread in most of the stations.

The results of the application of the index MaQI to all the all 35 stations sampled from 2013 to 2017 (Fig. S2, Supplementary material) highlighted that, among the first 17 stations, three of them (2, 5, 6) showed no ecological improvement. In these stations, despite the fact that the transplants continued every year until the end of the project, aquatic angiosperms did not take root. All the other stations showed more or less marked improvements and 8 stations reached high conditions at the end of transplant activities. In the 18 stations transplanted the following year, on average, results were similar even if data refer to only 3 years (2015–2017). In this case all stations showed a significant improvement, but only 4 reached high conditions. However, considering only the biological quality element (EQB) “macrophytes”, a total of 28 out of 35 stations met the WFD (2000/60/EC) requirement reaching good-high conditions.

The obtained results confirmed that the MaQI index, based on the presence/absence and type of macrophytes, responds to changes in the ecological status already after a few months (Sfriso et al., 2019b). HFBI responses are close to those of MaQI but with a delay of 2–3 years, the time it takes for prairies to form and for fish to colonize the meadows. Finally, the response of M-AMBI requires a longer time before improvements can be observed also in the superficial sediments where the benthic macrofauna lives.

5. Conclusions

There was an improvement in water and sediment quality (reduction of nutrient loading and decrease of clam stock harvesting) which already had caused a reduction of nutrients and macroalgal biomass in the lagoon before the transplantations started.

A spontaneous recovery of aquatic angiosperms occurred in the lagoon but only close to already existing macrophyte vegetation. In the choked areas of the northernmost region of the northern basin, no recolonization was observed. Therefore, transplants were necessary to re-establish macrophyte vegetation and in the areas where the angiosperms have taken root they contributed significantly to the ecological status recovery sensu WFD 2000/60/EC aligning itself with the environmental directives issued at regional or national level for an ecological recovery of water bodies EC and PC1 object of the transplants in the framework of the project life SeResto. Indeed, the water bodies of this area showed a more significant improvement in comparison to the other water bodies of the lagoon where angiosperms spread only spontaneously (Sfriso, 2018).

These results were obtained with negligible costs (approx. 42.000 €) through small transplants performed by local stakeholders and are replicable in other environments. Indeed, the success of the project Life SeResto made it possible to promote the replication of transplant techniques also in other TWS: Po Delta lagoons (Italy), Mar Menor (Spain) and lagoons of Amvrakikos (Greece). In 2019 the European Union has just financed the project Life Transfer (Life19 NAT/IT/000264) to replicate the results obtained in the Venice Lagoon in other European lagoons where aquatic angiosperms have been dramatically reduced or have completely disappeared.

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CRediT authorship contribution statement

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.148859.

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