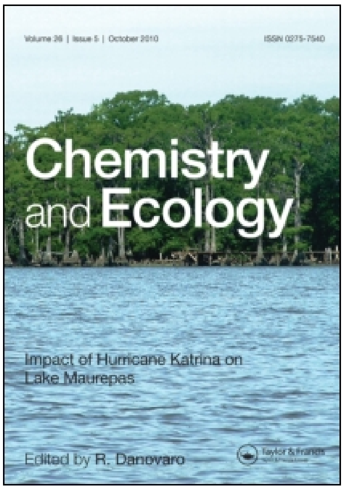

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Environmental influences on fish assemblage in the Venice Lagoon, Italy

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This study aimed to investigate the small fish assemblage in the Venice Lagoon shallow waters in relation to selected environmental variables, such as water-quality parameters, sediment grain-size variables, and habitat structure factors. Fish sampling was carried out in 68 stations, seasonally, by using a small beach seine net. The results highlighted the primary importance of habitat structure variables, such as seagrass and salt marsh coverages, with regard to fish distribution in the lagoon, in association with turbidity and salinity gradients. Two distinct fish assemblages were identified, corresponding to opposite species preferences in relation to salt marsh coverage-turbidity and seagrass coverage-salinity gradients. These results confirmed the importance of the biologically mediated influence of environmental parameters over physical parameters on small fish assemblages in dynamic systems such as the Venice Lagoon.

Keywords: Fish assemblages; Species distribution; Environmental influences; Habitat structure; Venice Lagoon

1. Introduction

Environmental variables may act as structuring forces of fish communities in estuarine and lagoon systems, where steep spatial gradients and strong temporal changes in morphological and physico-chemical parameters occur [1]. In particular, many environmental factors, such as temperature, salinity, turbidity, dissolved oxygen, vegetation, sediment characteristics, and substratum heterogeneity, are known to affect the distribution, abundance, and composition of estuarine fish assemblages [2–16]. In turn, it has been suggested that biotic factors, such as prey–predator interactions and inter- and intra-specific competition, serve to mediate community relationships within the physical framework of the environment [12, 15].

This study investigates shallow-water fish species association within the Venice Lagoon, a microtidal lagoon on the Italian coast in the Northern Adriatic Sea. Usually, fish assemblages in shallow waters of estuaries and lagoons consist of relatively small individuals, such as small resident species and juveniles of larger transient species [4, 17–23]. Atherinidae,

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Gobiidae, and Mugilidae, in particular, are the families which mainly characterize these fish assemblages in warm, temperate, and semi-tropical coastal lagoons and estuaries [19, 24, 25]. The small shallow-water fish assemblages of the Venice Lagoon have been only recently studied by Malavasi *et al.* [26] and Franco *et al.* [27]. These authors highlighted spatial and temporal variations in the lagoon fish assemblages, due to the variety of shallow habitats within the lagoon environment and to the seasonality of recruitment and migration patterns of fish species, respectively. The present study aims at evaluating the small species distribution in the lagoon shallow waters in relation to selected environmental variables, by using canonical correspondence analysis (CCA). Although CCA does not provide an insight into how the biotic interactions mediate the species relationships, which is beyond the scope of this study, it will allow the relationships between species composition and environmental factors to be directly examined [28]. Water-quality parameters, such as temperature, salinity, dissolved oxygen, and turbidity, and sediment grain-size variables, such as percentages of clay and sand, were included in the analysis. Moreover, as habitat type proved to be an important factor in determining the fish assemblage composition in the shallow waters of the Venice Lagoon, with particular regard to 'structuring' habitats such as seagrass beds and creeks in salt marshes [26, 27], factors characterizing these habitat structures were also considered.

2. Materials and methods

2.1 *Study site*

The Venice Lagoon (figure 1) is the largest lagoon in the Mediterranean basin, with an area of about 540 km^2. It is a shallow-water environment, with an average depth of around 1 m [29]. Connection with the sea is provided by three wide mouths, Lido, Malamocco, and Chioggia (figure 1), through which tidally induced flows enter the lagoon. These flows, ranging between ± 50 cm during spring tides [30], generate a high water exchange between lagoon and sea, such that the lagoon environment is well ventilated and quickly flushed [31]. Freshwater inflows are also present in the internal areas of the lagoon, although they have been reduced in past times (from the 16th century) by diverting the largest rivers outside the lagoon in order to prevent them to fill in this environment with sediments. At present, only one river, the Dese, in the northern area of the lagoon, and a number of small channels coming from the diverted rivers flow into the lagoon environment (figure 1). As found from hydrological studies, two main watersheds divide the lagoon into three sub-basins, the Northern, Central, and Southern [32, 33].

The morphology and hydrology of the Venice Lagoon environment determine high levels of spatial heterogeneity, such that a single-direction environmental gradient cannot be identified as in most of estuarine areas. A patchy system of interconnected habitats, such as seagrass beds, sand flats, mud flats, and salt marshes, is present in the shallows of the lagoon. The spatial arrangement of these habitat 'patches' reflects the variations in hydrodynamic, physical, and chemical characteristics. Habitats with muddy bottoms, such as mud flats and salt marshes, are mostly found in the internal areas of the lagoon, further from the sea inlets, where freshwater contributions are more intense, and wave energy is low. By contrast, most seagrasses (mainly *Zostera marina* Linnaeus and *Cymodocea nodosa* (Ucria) Asher, second *Nanozostera noltii* Hornem) and sand flats are closer to the sea inlets and deeper canals, where sediments are relatively coarser. The seagrasses constitute large meadows especially in the Central and Southern sub-basins [34]. Seasonally, some presence of macroalgae (mainly *Ulva rigida* C. Agardh) could be detected in the lagoon, although they have almost completely disappeared as a result of a declining trend begun in the 1990s [35].

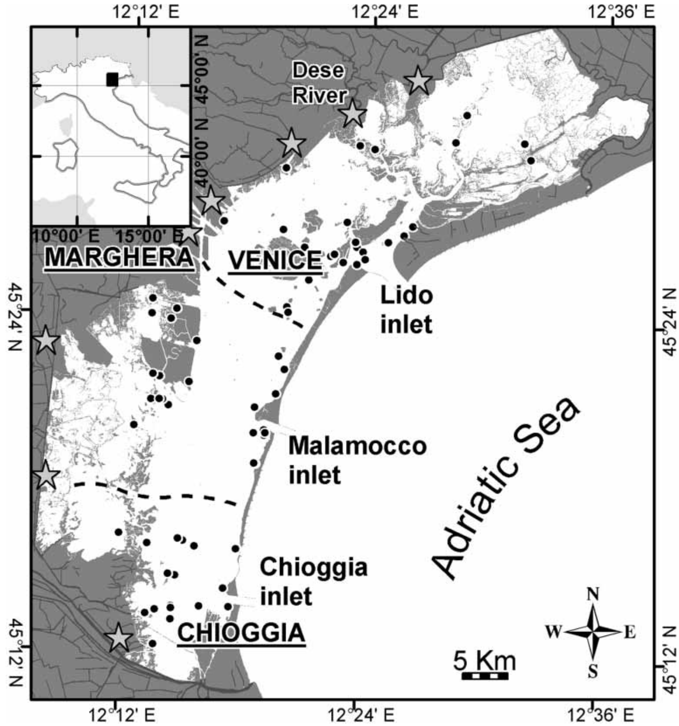

Figure 1. Sampling stations in the Venice Lagoon. The two watersheds dividing the lagoon in Northern, Central, and Southern basins are shown on the map. Stars denote the main freshwater inlets.

2.2 *Samples and data collection*

The small fish assemblages were sampled on a seasonal basis, during the spring (April–May), summer (July–August), and autumn (October–November) 2002, in 68 stations distributed in the shallow waters (depth lower than 1.5 m) of the Venice Lagoon (figure 1). Based on the distance from the nearest sea inlet (measured on the map of the stations as the linear distance of each station from the mid-point of the nearest sea inlet, by using GIS tools), sampling stations were allocated to three inlet-distance categories: (1) marine sites, with an inlet distance of less than 4.7 km (with a minimum recorded value of about 1 km); (2) intermediate sites, with an inlet distance between 4.7 and 8.5 km; (2) internal sites, with an inlet distance of more than 8.5 km (with a maximum recorded value of about 12 km).

The sampling gear used was a 10-m-long beach seine (mesh size 2 mm), which was trawled on an area of 360 m^2 in each station. The fish abundance (number of individuals) in each sample was recorded for each species and expressed as fish density (number of individuals per 100 m^2). Data on environmental variables, such as water temperature, salinity, oxygen saturation, water turbidity, and percentages of clay and sand in the superficial (0–15 cm) sediments, were collected for each sampling station. In particular, water temperature and salinity were measured before the sampling using a digital thermometer (± 0.1 °C) and a temperature-compensated refractometer (± 1, measured as PSU), respectively. They were assessed by collecting water samples from the middle of the water column, and the resulting measures were considered representative of the entire water column, due to the shallow nature of the sampling stations. As regards the other environmental variables, relative to both water quality (oxygen saturation, %; water turbidity, FTU) and sediment grain size (clay and sand, %), data for each sampling station were obtained from the interpolation, using an ordinary kriging method, of the dataset resulting from the 2002 MELa1 survey, a monitoring project carried out during 2002 in the Venice Lagoon by Consorzio Venezia Nuova, on behalf of the Magistrato alle Acque, Venezia [36]. The original data, being collected on a monthly basis and, regarding the water-quality data, every 10 cm in the water column, were averaged on a seasonal basis and on the entire water column before the analysis. Based on the same dataset and using the same methodology, habitat characteristics, in terms of salt marsh and seagrass coverages, were also assessed for each station. In particular, salt marsh coverage was measured by the percentage area covered by salt marshes around each station (within 150 m from the station). Instead, regarding seagrass coverage, sampling stations were allocated to five classes, based on the percentage area covered by seagrasses in each station, and determined as follows: 0 = 0% seagrass percentage coverage; 1 = seagrass percentage coverage from 0 to 5%; 2 = seagrass percentage coverage from 5 to 50%; 3 = seagrass percentage coverage from 50 to 75%; 4 = seagrass percentage coverage from 75 to 100%.

2.3 *Statistical analyses*

Environmental data on water quality, sediment grain size, and habitat characteristics were analysed using the principal component analysis (PCA) option within the Multi-Variate Statistical Package (MVSP) [37] in order to detect trends within the data. As the environmental variables were measured in different units, it was necessary to standardize the data before the analysis, such that each value was expressed as a percentage of the maximum value recorded for that variable. The samples were arbitrarily grouped after the analysis according to the sea inlet-distance category (three levels: marine, intermediate, and internal sites) and to the sampling season (three levels: spring, summer, and autumn) in order to relate possible environmental gradients to spatial or seasonal variations.

Structural analysis of the fish assemblage was carried out by using the canonical correspondence analysis (CCA) option within the MVSP package [37]. The analysis was performed on fish abundance ($\log_{10}$-transformed) and environmental data (standardized), for each sampling season. Rare species were down-weighted according to the parameters of the programme. The axes defined by CCA and the environmental variables were examined by Pearson's correlation analysis to assess the possibility of colinearity in the multivariate analyses.

3. Results

3.1 *Ordination of sites by environmental characteristics*

About 70% of the total observed variation in environmental data among stations was accounted for by the first three axes (over eight) determined by the principal component analysis (table 1). A spatial ordination of samples, with increasing sea inlet distance (from marine to internal sites), was observed along Axis 1, which accounted for about 39% of the observed variation by all eight axes (figure 2, table 1). Turbidity and sediment composition (measured as sand and clay percentages) were the main environmental gradients affecting this spatial ordination of samples, with increasing turbidity and decreasing sediment grain size from marine to internal sites (from negative to positive scores on the axis) (figure 2, table 1). A seasonal ordination of samples, mainly driven by increasing water temperature (from autumn to spring to summer), was observed along Axis 3, which accounted for 13% of the total observed variation (figure 2, table 1). In turn, Axis 2, which

Table 1. Principal components analysis results.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
Eigenvalues	3.092	1.29	1.037	0.751	0.642	0.602	0.446	0.139
Percentage	38.653	16.131	12.963	9.39	8.023	7.521	5.578	1.741
Cum. percentage	38.653	54.783	67.746	77.136	85.159	92.68	98.259	100
PCA variable loadings								
Temp	0.086	−0.375	0.792	−0.241	−0.152	0.376	−0.032	−0.010
Sal	−0.299	0.527	−0.055	−0.034	−0.402	0.559	0.393	0.005
OD	−0.330	−0.071	0.367	0.756	0.011	−0.253	0.333	−0.072
Turb	0.437	0.044	0.090	−0.272	−0.166	−0.422	0.691	0.207
Sand	−0.475	−0.375	−0.157	−0.117	−0.058	−0.008	0.050	0.768
Clay	0.390	0.475	0.252	0.302	0.143	0.097	−0.277	0.600
Sgr	−0.335	0.289	0.240	−0.347	0.765	−0.037	0.195	−0.025
Stm	0.336	−0.353	−0.284	0.265	0.422	0.541	0.373	0.032

Note: Temp: temperature; Sal: salinity; OD: oxygen saturation; Turb: turbidity; Sand: sand percentage; Clay: clay percentage; Sgr: seagrass coverage class; Stm: salt marsh coverage percentage.

accounted for 16% of the total variation and was influenced mainly by salinity and clay percentage (positive gradients along the axis) (table 1), did not make a clear contribution to the ordination of samples either seasonally or spatially (in terms of sea-inlet distance) (figure 2).

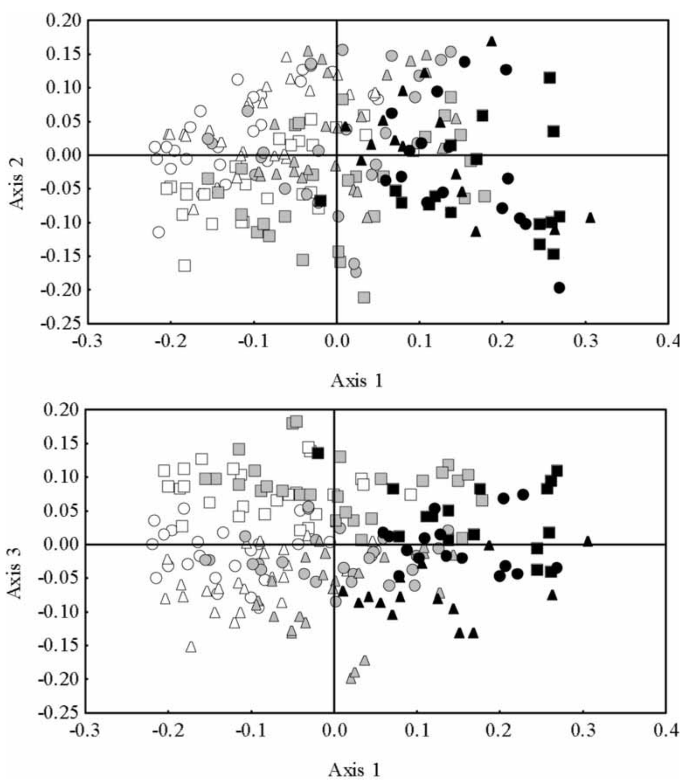

Figure 2. PCA diagrams of stations, classified by season and sea inlet-distance category. ○: spring, marine; ●: spring, intermediate; ●: spring, internal; □: summer, marine; ■: summer, intermediate; ■: summer, internal; △: autumn, marine; ▲: autumn, intermediate; ▲: autumn, internal.

Table 2. List of fish species caught in the shallows of the Venice Lagoon with beach seine net.

Species	Family	Sp.	Tot. Ab.	Species	Family	Sp. code	Tot. Ab.
Pomatoschistus marmoratus	Gobiidae	Pma	11011	*Symphodus* sp.	Labridae	Symp	11
Atherina boyeri	Atherinidae	Abo	6938	*Syngnathus acus*	Syngnathidae	Sac	10
Knipowitschia panizzae	Gobiidae	Kpa	4599	*Sprattus sprattus*	Clupeidae	Ssp	10
Syngnathus abaster	Syngnathidae	Sab	3960	*Hippocampus guttulatus*	Syngnathidae	Hgu	9
Syngnathus typhle	Syngnathidae	Sty	3016	*Symphodus roissali*	Labridae	Sro	9
Liza saliens	Mugilidae	Lsa	2179	*Gambusia holbrooki*	Poeciliidae	Gho	8
Pomatoschistus minutus	Gobiidae	Pmi	1776	*Syngnathus tenuirostris*	Syngnathidae	Ste	8
Zosterisessor ophiocephalus	Gobiidae	Zop	1674	*Carassius carassius*	Cyprinidae	Cca	7
Engraulis encrasicolus	Engraulidae	Een	912	*Sciaena umbra*	Sciaenidae	Sum	7
Aphanius fasciatus	Cyprinodontidae	Apfa	906	*Chelon labrosus*	Mugilidae	Cla	6
Pomatoschistus canestrinii	Gobiidae	Pca	856	Juvenile not identified	Sparidae	SparJ	5
Liza ramado	Mugilidae	Lra	573	*Diplodus puntazzo*	Sparidae	Dpu	4
Nerophis ophidion	Syngnathidae	Nop	429	*Parablennius tentacularis*	Blennidae	Pte	4
Salaria pavo	Blennidae	Spa	213	*Echiichthys vipera*	Trachinidae	Evi	3
Platichthys flesus	Pleuronectidae	Pfl	195	*Lithognathus mormyrus*	Sparidae	Lmo	3
Solea vulgaris	Soleidae	Svu	193	*Arnoglossus laterna*	Bothidae	Ala	2
Gobius niger	Gobiidae	Gni	177	*Dicentrarchus labrax*	Moronidae	Dla	2
Liza aurata	Mugilidae	Lau	91	*Diplodus sargus*	Sparidae	Dsa	2
Syngnathus taenionotus	Syngnathidae	Sta	56	*Hippocampus hippocampus*	Syngnathidae	Hhi	2
Gobius cobitis	Gobiidae	Gco	53	*Sparus aurata*	Sparidae	Sau	2
Mullus surmuletus	Mullidae	Msu	52	*Solea impar*	Soleidae	Sim	2
Belone belone	Belonidae	Bbe	37	*Symphodus cinereus*	Labridae	Sci	2
Parablennius sanguinolentus	Blennidae	Psa	32	*Mugil cephalus*	Mugilidae	Mce	1
Callionymus risso	Callionymidae	Cri	20	*Merlangius merlangus*	Gadidae	Mme	1
Boops boops	Sparidae	Bbo	17	*Sardina pilchardus*	Clupeidae	Spi	1
Chelidonichthys lucernus	Triglidae	Tlu	16	*Scophthalmus rhombus*	Scophthalmidae	Srh	1
Diplodus annularis	Sparidae	Dan	13				

Note: Species are listed by decreasing abundance (Tot. Ab., total number of individuals) in the fish assemblage. The family and code name (Sp.) are reported for each species.

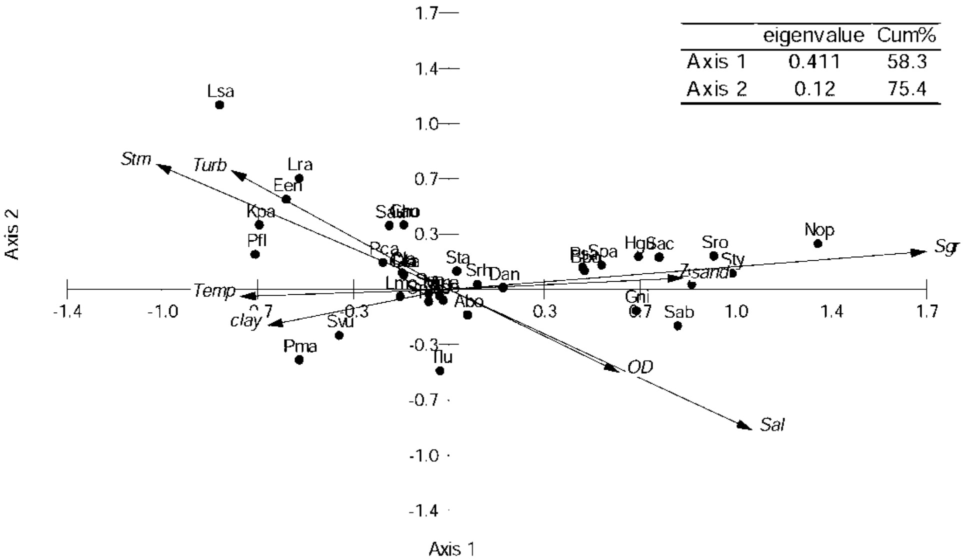

Figure 3. CCA ordination diagram of species abundance data in spring, with environmental factors represented by vectors. Eigenvalues and the cumulative percentage of explained variance (%CUM) are reported for each axis.

3.2 *Environmental influences on species distribution*

A total of 40 116 individuals, from 53 taxa (52 species + juvenile not identified sparids) were collected in the shallows of the Venice Lagoon (table 2).

The relative importance of the collected environmental parameters to the seasonal distributions of species abundance is represented in figures 3–5, as determined by CCA analyses. Each seasonal analysis determined eight canonical axes, which explained a percentage of the

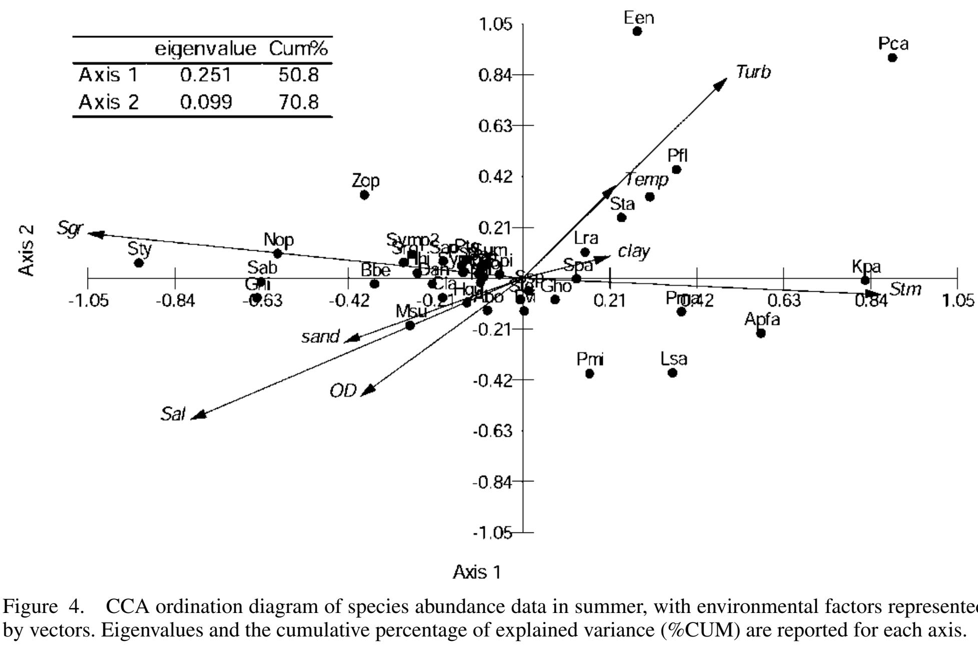

Figure 4. CCA ordination diagram of species abundance data in summer, with environmental factors represented by vectors. Eigenvalues and the cumulative percentage of explained variance (%CUM) are reported for each axis.

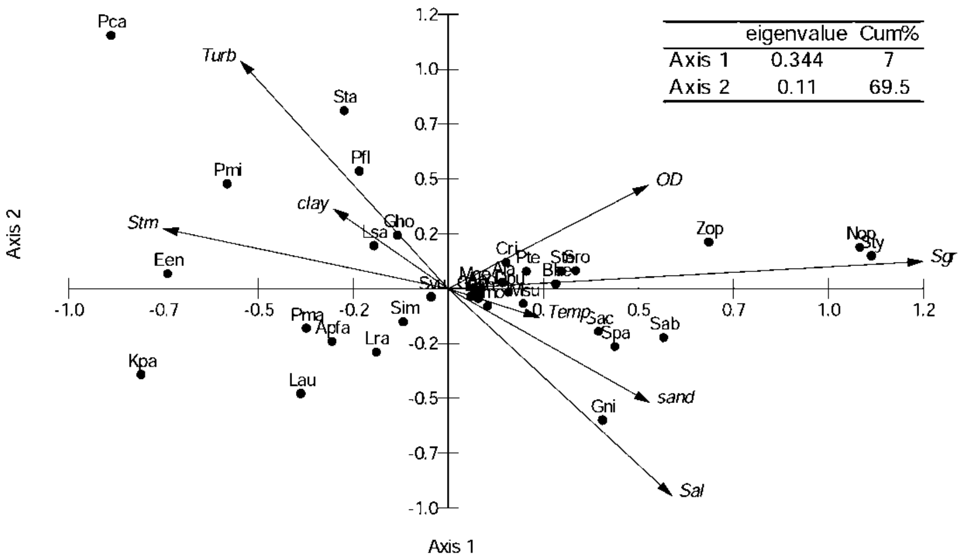

Figure 5. CCA ordination diagram of species abundance data in autumn, with environmental factors represented by vectors. Eigenvalues and the cumulative percentage of explained variance (%CUM) are reported for each axis.

total species variation of 31.2% in spring, 41% in summer, and 37.4% in autumn. However, only axes 1 and 2 were plotted, as they always accounted for more than 69% of the variability explained by all canonical axes (tables in figures 3–5).

Many species were located in the diagrams around the origin (figures 3–5), meaning that they either did not show a strong relationship to any of the variables considered or were found at average values for each environmental variable (reported in table 3). However, some species separated from this group in all seasons. This separation was mainly along axis 1, which was always highly correlated with seagrass coverage (positively in spring and autumn, negatively in summer) (table 4). According to the relative lengths of the vectors in the CCA diagrams, seagrass coverage was the most important environmental factor with regard to fish distribution in the lagoon, followed by another habitat variable, salt marsh coverage, and by turbidity and salinity (figures 3–5). These factors were shown to act along opposite directions in affecting species distribution in the lagoon environment, with positive seagrass coverage and salinity gradients being associated with negative salt marsh coverage and turbidity gradients (table 4; figures 3–5). The relative positions of the measured environmental vectors did not show any

Table 3. Average value and standard deviation (S.D.) of the environmental variables measured in spring ($n = 67$), summer ($n = 68$), and autumn ($n = 63$).

	Spring		Summer		Autumn	
	Average	S.D.	Average	S.D.	Average	S.D.
Temp (°C)	18.6	2.2	26.2	1.3	16.7	1.2
Sal (PSU)	29.3	6.1	27.2	3.8	29.1	5.6
OD (%)	95.2	3.4	93.4	5.6	90.9	2.0
Turb (FTU)	19.3	7.6	16.8	8.3	14.2	8.9
Sand (%)	34.1	20.1	33.9	20.0	33.8	20.1
Clay (%)	17.1	7.0	17.1	6.9	17.1	7.0
Stm (%)	10.6	18.6	10.4	18.5	10.5	18.5
Sgr	1.1	1.6	1.1	1.6	1.2	1.7

Table 4. Seasonal Pearson correlation coefficients for the scores on each of the environmental axes against the environmental variables, and correlations between all of the environmental parameters.

	Axis 1	Axis 2	Temp	Sal	OD	Turb	Sand	Clay	Sgr
Spring									
Temp	−0.31 **	−0.07 n.s.							
Sal	0.52 ***	−0.46 ***	−0.44 ***						
OD	0.29 *	−0.19 n.s.	−0.33 **	0.22 n.s.					
Turb	−0.36 **	0.30 *	0.34 **	−0.30 *	−0.89 ***				
Sand	0.32 **	0.10 n.s.	−0.23 n.s.	0.24 *	0.73 ***	−0.63 ***			
Clay	−0.24 n.s.	−0.16 n.s.	0.20 n.s.	−0.09 n.s.	−0.51 ***	0.41 ***	−0.82 ***		
Sgr	0.96 ***	0.25 *	−0.25 *	0.37 **	0.38 **	−0.39 ***	0.32 **	−0.20 n.s.	
Stm	−0.53 ***	0.40 ***	0.44 ***	−0.46 ***	−0.30 *	0.36 **	−0.31 **	0.21 n.s.	−0.38 **
Summer									
Temp	0.08 n.s.	0.33 **							
Sal	−0.65 ***	−0.45 ***	−0.03 n.s.						
OD	−0.34 **	−0.41 ***	−0.22 n.s.	0.21 n.s.					
Turb	0.45 ***	0.67 ***	0.18 n.s.	−0.45 ***	−0.84 ***				
Sand	−0.32 **	−0.24 *	−0.05 n.s.	0.30 *	0.56 ***	−0.66 ***			
Clay	0.16 n.s.	0.07 n.s.	−0.04 n.s.	−0.19 n.s.	−0.33 **	0.48 ***	−0.82 ***		
Sgr	−0.90 ***	0.17 n.s.	−0.14 n.s.	0.42 ***	0.29 *	−0.38 **	0.30 *	−0.20 n.s.	
Stm	0.70 ***	−0.04 n.s.	0.02 n.s.	−0.44 ***	−0.40 ***	0.33 **	−0.30 *	0.20 n.s.	−0.39 **
Autumn									
Temp	0.17 n.s.	−0.02 n.s.							
Sal	0.39 **	−0.52 ***	0.38 **						
OD	0.41 ***	0.46 ***	0.51 ***	0.36 **					
Turb	−0.33 **	0.72 ***	0.21 n.s.	−0.41 ***	0.42 ***				
Sand	0.26 *	−0.43 ***	−0.06 n.s.	0.15 n.s.	−0.32 *	−0.60 ***			
Clay	−0.09 n.s.	0.29 *	0.10 n.s.	−0.10 n.s.	0.28 *	0.38 **	−0.81 ***		
Sgr	0.96 ***	0.24 n.s.	0.09 n.s.	0.25 n.s.	0.23 n.s.	−0.32 *	0.32 **	−0.20 n.s.	
Stm	−0.55 ***	0.25 *	−0.21 n.s.	−0.36 **	−0.26 *	0.20 n.s.	−0.30 *	0.19 n.s.	−0.40 ***

Note: Temp: water temperature; Sal: salinity; OD: dissolved oxygen; Turb: turbidity; Sand: percentage of sand in the superficial sediments; Clay: percentage of clay in the superficial sediments; Sgr: seagrass coverage; Stm: salt marsh percentage coverage; n.s.: not significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

substantial changes between seasons, except for temperature. This factor, in fact, was shown to increase with increasing salt marsh coverage and turbidity and with decreasing seagrass coverage and salinity by spring and summer (figures 3 and 4), whereas it showed an opposite trend by autumn (figure 5).

Most of the pipefish species (*Nerophis ophidion* (Linnaeus, 1758), *Syngnathus typhle* Linnaeus, 1758 and *Syngnathus abaster* Risso, 1827), and larger gobies (*Zosterisessor ophiocephalus* (Pallas, 1814) and *Gobius niger* Linnaeus, 1758) were always found with higher abundances at above-average levels of seagrass coverage and salinity, and below-average levels of salt marsh coverage and turbidity (figures 3–5). In particular, as highlighted by the closeness of the species points to the environmental vector, *N. ophidion* and *S. typhle* showed strong relationships with seagrass coverage, in spring and autumn, and in summer and autumn (respectively, figures 3–5). By contrast, other species were found with high abundances at above-average salt marsh coverage and turbidity and below-average seagrass coverage and salinity, such as *Engraulis encrasicolus* (Linnaeus, 1758) and *Knipowitschia panizzae* (Verga, 1814) for all seasons, *Liza saliens* (Risso, 1810) and *Liza ramado* (Risso, 1810) for spring, *Platichthys flesus* (Linnaeus, 1758) for spring and summer, *Pomatoschistus canestrinii* (Ninni, 1883) for summer and autumn (this species was not caught in spring), and *Pomatoschistus minutus* (Pallas, 1770) and *Syngnathus taenionotus* Canestrini, 1871 for autumn (figures 3–5).

4. Discussion

4.1 *Influence of environmental factors*

The species composition of the small fish assemblage in the shallow waters of the Venice Lagoon was shown to be influenced primarily by the habitat's morphological characteristics in terms of seagrass and salt marsh coverage, followed by several water-quality variables, such as turbidity and salinity.

Although seagrass and salt marsh coverage gradients in the lagoon were not found to be important in distinguishing sampling stations from an environmental point of view (according to the principal component analysis), they proved to be important factors in affecting the fish assemblage spatial distribution in the lagoon environment. Seagrass and salt marsh coverages may be considered as indicators of a certain habitat complexity and structure, due either to the three-dimensional structure afforded by the presence of the seagrass leaf canopy or to the complex topography of the creeks systems within salt marshes. Usually, habitat complexity indirectly influences the fish assemblage composition by affecting prey availability and protection from predators, and by determining a large number of available ecological niches for the fish fauna, in seagrass habitats as well as in salt marsh areas [38–41].

Blaber [42] and Whitfield [14] reported that usually the main factors determining the distribution and the abundance of fish fauna are not independent. Accordingly, two environmental factors, turbidity and salinity, are associated with the habitat structure in affecting the spatial distribution of lagoon fish assemblages. In particular, a positive association was found between salt marsh coverage and turbidity, the opposite of that between seagrass coverage and salinity in the Venice Lagoon. However, in contrast with the habitat factors, turbidity and salinity resulted in important environmental gradients distinguishing the sampling stations in the shallows of the lagoon. Salinity is considered the primary factor affecting fish fauna variability in estuarine environments by many authors [14, 43–45]. It usually influences fish species distribution in relation to their tolerances [12], affecting particularly the distribution of those species which are less tolerant to the salinity fluctuations in the estuarine environment [14]. In turn, turbidity strongly affects the fish species distribution by providing both protection from visual predators and a higher food availability [4, 8]. Turbidity, at high levels (higher than $14\ \mathrm{g\ l^{-1}}$, corresponding to about 2800 FTU), may also induce physiological sublethal effects on fishes, due to the gills obstruction by suspended solids [7], but this condition is unlikely to be found in the Venice Lagoon, where the maximum measured turbidity was far lower than 2800 FTU. Besides, turbidity variation in the Venice Lagoon was shown to match a confinement gradient (increasing with the distance of the stations from the main sea inflows), confirming the significant contribution of this factor in defining the fish assemblage composition [46, 47].

Neither the sediment grain size nor the water temperature, which both resulted in important environmental gradients in the lagoon environment, showed a significant influence on the lagoon fish assemblage structure. However, sediment grain size composition, which proved to vary along a confinement gradient (decreasing with the distance of the stations from the main sea inflows), might influence the fish fauna distribution indirectly by influencing the distribution of other more relevant parameters, such as turbidity and the seagrass coverage. Water temperature, in turn, proved to be important in determining temporal changes in the lagoon environment, as confirmed also by its variability among seasons with respect to the other variables considered, whereas it appeared not to affect the spatial distribution of the fish fauna, in contrast with many other authors' findings [12, 48–52].

Also, dissolved oxygen in the water is reported among those environmental factors affecting the fish assemblage distribution in estuarine areas [9]. In contrast, this did not result in the shallows of the Venice Lagoon, probably due to the relatively high oxygen saturation of the water in this environment (80–104%). The effect of this factor on the fish assemblages, in fact, is usually present at low values of dissolved oxygen [14], with stressful effects reported for many marine species at oxygen levels lower than 4.5 mg l^{-1} [53] and lethal effects to many estuarine fish species at oxygen levels lower than 1 mg l^{-1} [54].

4.2 *Fish assemblage distribution*

The resulting importance of the habitat factors (seagrass and salt marsh coverage) to fish assemblages in the shallows of the Venice Lagoon confirms the findings of previous studies on the fish assemblages and their association with certain habitat types in the lagoon [26, 27]. According to these authors, in fact, shallow seagrass beds and salt marsh creeks are important 'structuring' habitats, where abundant specialized and characteristic fish assemblages are found, in contrast with other 'transition' habitats, such as sand flats and sparsely vegetated habitats, for example, where fish assemblages are highly variable and influenced by the contribution of the adjacent habitats. Thus, two distinct fish assemblages may be identified, corresponding to the opposite species preferences in relation to salt marsh coverage–turbidity and seagrass coverage–salinity gradients. One is mainly composed of syngnathid and larger goby species (*N. ophidion*, *S. typhle*, *S. abaster*, *Z. ophiocephalus*, and *G. niger*), which proved to be strongly associated with a higher seagrass coverage and salinity and, in turn, to lower salt marsh coverage and turbidity levels. These species were described as characteristics of seagrass meadows in the lagoon [26, 27], their strong association with seagrasses being mainly due to specific morphological and behavioural adaptations and reproductive requirements [55–57]. This strong association with seagrasses is probably the main factor determining the relative temporal stability of this fish assemblage, suggested by its constant composition over the sampling seasons. In contrast, a higher variability has been observed in the composition of the fish assemblage associated with a higher salt marsh coverage and turbidity, and, in turn, to lower seagrass coverage and salinity levels. In fact, apart from the species *K. panizzae* and *E. encrasicolus*, which were relatively abundant in the more internal salt marsh-turbid lagoon areas for all seasons, the other species constituting this fish assemblage alternated over the sampling seasons: mullets (*L. ramada*, *L. saliens*) for spring, flounder (*P. flesus*) by spring and summer, black-spotted goby (*P. canestrinii*) for summer and autumn, and sand goby (*P. minutus*) and *S. taenionotus* for autumn. This higher temporal variability of the fish assemblage composition in salt marsh areas than in seagrasses might be attributed to the higher environmental variability of the further habitat. It promotes the higher presence in the creeks of more eurytopic and mobile species, such as the marine migrants, whereas in seagrass beds, most of species are sedentary and consequently closely associated with this habitat [58]. The migrant species are represented in the salt marsh lagoon fish assemblages for example by *P. minutus*, *L. ramada*, and *E. encrasicolus*, as confirmed also by Malavasi *et al.* [26] and Franco *et al.* [27]. However, the marked recruitment patterns of resident species, such as *K. panizzae*, also may contribute significantly to the seasonal variation of salt marsh fish assemblages.

On the whole, the results of the present study highlighted the presence of a complex environmental background affecting the distribution of small fish assemblages in the Venice Lagoon. Among the environmental variables measured, the most important were those influencing species composition indirectly through biological processes such as those assisting in predator avoidance and increasing food availability, so that their effects are likely to be dependent on the presence and absence of other species. Kupschus and Tremain [15] defined this type of variable biological environmental factor, in contrast with the physical environmental factors, which in turn interact directly with the physiology of a species, such that their effects are constant, irrespective of the presence or absence of other species. The primary influence of biological environmental variables on small fish assemblages in dynamic systems, such as estuaries and lagoons, has been hypothesized by Kupschus and Tremain [15], in accordance with Menge and Sutherland [59]. These authors, in fact, predicted that physical environmental variables are more likely to control large mobile fish communities in estuaries and lagoons, as confirmed also by many studies on estuarine areas [12, 14, 15, 45]. This is mainly linked to the different mobility between larger and smaller fishes [60], leading to a different balance between the cost of migration and that of adapting to the locally variable conditions, in terms of metabolism and of survival reduction [61].

A biological influence on small fish assemblages in the shallows of the Venice Lagoon is partly suggested also by the fact that the variability of the eight considered environmental factors accounts for only 30–40% of the total species variability. Thus, the remainder of species variability is likely to be accounted for by other factors, which may be not only environmental variables other than those measured in the present study, but also biotic factors, such as prey–predator interactions and prey distributions. These biological variables will superimpose, in the definition of the fish assemblage specific composition, to the initial structure defined by the environmental characteristics in the area studied [12].

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