

Spatial patterns of macrobenthic alpha and beta diversity at different scales in Italian transitional waters (central Mediterranean)

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Abstract

Biodiversity is a multidimensional concept encompassing many scales of variation, originally partitioned into three components: alpha, the number of species in a single sampling unit, beta, the variation in species identities from site to site, and gamma, the overall number of species within a defined geographical area. Investigations on macrobenthic assemblages in transitional waters have been traditionally focused on alpha- and gamma-diversity, largely neglecting beta-diversity. The aim of the work was to identify patterns of variation of macrobenthic invertebrates in transitional waters from 18 different Italian lagoons (central Mediterranean) at three different scales (site, lagoon and region), combining classical and multivariate measures for partitioning diversity. Classical alpha, beta and gamma diversity were calculated, together with measures considering also relative species abundances. The highest variability of macrobenthic assemblages was observed at the intermediate scale (among lagoons), with significant variations in terms of both alpha and beta diversity. At the smallest analysed scale (among sites) the variability was mainly in terms of beta diversity, whereas at the biggest scale (among regions), the variability was mainly in terms of alpha diversity. At the intermediate scale (among lagoons) alpha diversity was influenced by the regional species pool, with one exception (Grado-Marano lagoon) where the habitat heterogeneity and beta diversity played a major role. Beta diversity, measured as variability of dispersion with Jaccard resemble measure, was consistent with results obtained with the original formulation of Whittaker. Considering alpha diversity, a different pattern of variability was observed considering relative abundances, whereas considering beta diversity, no significant differences were observed in terms of relative species abundances. The patterns of macrobenthic assemblages among lagoons in terms of both alpha and beta diversity resulted from the complex interaction of different drivers acting in a framework of geographical variability. Alpha diversity was mainly influenced by salinity, but other factors (size, confinement, trophic status and sediment composition) were likely to contribute. Beta diversity was mainly influenced by habitat heterogeneity, deriving from different environmental parameters, such as trophic condition and water confinement. Our results support the usefulness of partitioning diversity in alpha, beta and gamma components, and of combining different univariate and multivariate measures of dispersion, to consider patterns of richness and relative abundances separately.

1. Introduction

Biodiversity is a multidimensional concept (Purvis and Hector 2000) and encompasses many scales of variation in biological organisation, from genes to ecosystems. Whittaker (1960) originally proposed partitioning biological diversity into alpha, beta, and gamma components to characterize different aspects or levels of diversity. Alpha diversity (α) is commonly measured as the number of species in a single sampling unit, while gamma diversity (γ) is generally defined as the overall number of species within a defined geographical area. Beta diversity (β) is a concept used to describe variation in species identities from site to site (Anderson et al., 2011) and can be measured in many different ways (Koleff et al., 2003). Beta diversity was first defined as the extent of change in community composition along gradients (Whittaker, 1960). β diversity provides a direct link between biodiversity at local scales (α diversity) and the broader regional species pool (γ diversity). Subsequently, many different measures of beta diversity have been introduced, but there was no overall consensus about which ones are most appropriate for addressing particular ecological questions. Anderson et al. (2011) proposed a roadmap for the use of different measures of beta diversity according to the aim of the study, stating that beta diversity can be conceptualized both as the change in community structure along a gradient (turnover) or the variation in community structure among sampling units within a given area without reference to a particular gradient or direction (Anderson et al., 2011). Independently of the perspective, turnover versus variation, beta-diversity patterns are determined by two basic processes: the replacement of species and richness differences (Carvalho et al., 2012). The classical measures for both alpha and beta diversity, including the original measure described by Whittaker, 1960, focused on species identities alone, while more recent measures (Jost, 2007) include also relative abundance information. In this view Anderson et al. (2006) proposed a measure of beta diversity that can easily be partitioned into a component driven by compositional differences (d_j) and a component driven by order-of-magnitude changes in abundance ($d_{MG} - d_j$). Comparing analyses of beta diversity that emphasize species identities alone (with a strong role for rare species) to those that emphasize differences in relative abundances (where common and numerically dominant species play a strong role) can yield useful insights into the specific nature of community-level changes (Olsgard et al., 1997; Anderson et al., 2006).

For both terrestrial and marine environments, investigations have been traditionally focused on α - and γ -diversity, largely neglecting β -diversity (Bevilacqua et al., 2012). Indeed, beta diversity is essential in estimating and mapping diversity, in identifying its relevant scales of change, and in understanding processes underlying the formation and evolution of biological systems (Vellend, 2010). One of the most important factors in generating and maintaining high assemblage heterogeneity is the spatial variability of habitat structure (Hewitt et al., 2005; Matias et al., 2011), and therefore quantifying the relative contribution of beta diversity in determining the global diversity in a given area or region could provide valuable information particularly useful for conservation purposes (Crist et al., 2003; Bevilacqua et al., 2012). Homogenisation is considered an early warning of habitat loss, acting when the component of alpha diversity still increase (Hewitt et al., 2010). Plans for biodiversity conservation should be designed with the aim of maintaining beta diversity (and the processes that shape it) across the full range of taxa and spatial scales, through multiscaled conservation approaches (Barton et al., 2013). Measures of beta diversity are currently receiving renewed interest in marine environment, with publications increasing worldwide, from tropical areas (e.g. De Troch et al., 2001; Harborne et al., 2006; Arias-González et al., 2008) to high latitudes (e.g. Gray, 2000; Ellingsen and Gray, 2002; Ellingsen et al., 2007), considering different taxonomic

groups, from fishes (Villéger et al., 2013; Porter et al., 2018) to microbial communities (Xu et al., 2015). Beta diversity play a central role in linking local and regional diversity (Witman et al., 2004) and exploring variations across environmental and biogeographical gradients (Ellingsen and Gray, 2002). The assessment of beta-diversity as variation could potentially unveil patterns of change in assemblages that would remain unnoticed analysing other components of diversity (Bevilacqua et al., 2012). Nevertheless, works scaling up alpha and beta diversity of macrobenthic communities in transitional environments are still scant, with few works published on few Mediterranean lagoons (Munari and Mistri, 2008; Tataranni et al., 2009) and some estuaries in different world regions (Barnes and Ellwood, 2012; Barnes, 2013; Séguin et al., 2013; Piló et al., 2015; Medeiros et al., 2016).

This paper analyses inventories of macrobenthic communities obtained through research programmes carried out on 18 lagoons, representing all main Adriatic and Tyrrhenian Italian lagoons, with different typologies, from mesohaline to hyperhaline, from oligotrophic to hypertrophic, non-tidal to microtidal lagoons (both leaky and restricted), different dimensions (from 0.4 to 160 km²), different sediment composition, and subjected to different anthropogenic pressures, and different levels of protections. Different values of the components of diversity were expected.

The aim of the present work was to explore the potential of combining classical and multivariate measures for partitioning diversity in order to identify patterns of variations of macrobenthic invertebrates in transitional waters at three different scales (site, lagoon and region). The work was performed following three steps: (i) to analyse the three component of diversity using classical measures and multivariate measures of beta diversity based on species richness alone; (ii) to weight the role of species abundances in community variability using univariate and multivariate measures at two levels corresponding to alpha and beta diversity; (iii) to test the influence of the following environmental drivers on the analysed patterns: lagoon typology (microtidal vs non tidal lagoons), water confinement (choked, leaky and restricted lagoons), lagoon dimension, salinity, trophic status and sediment composition.

2. Materials and methods

2.1 Study areas and data collection

The analysed dataset was gathered during several monitoring campaigns carried out in eighteen Italian lagoons. Samples were collected repeatedly over time, from the following Italian lagoons: Grado-Marano, Venice (Palude della Rosa), Caleri, Marinetta, Vallona, Barbamarco, Canarin, Scardovari, Goro, Comacchio, Baiona, and Lesina (Adriatic Sea), Orbetello, Caprolace, Fogliano, Feraxi, Porto Pino, and San Teodoro (Tyrrhenian Sea). A total of 107 sites, 64 of which were located in Adriatic and 43 in Tyrrhenian Sea (**Errore. L'origine riferimento non è stata trovata.**), have been chosen as representative of the different habitats found within each transitional environment. The only exception was the lagoon of Venice, where representative data from the whole lagoon were not available, but sampling was performed only in a part called Palude della Rosa. This dataset comprises different typology of transitional waters, from large to small, from microtidal to non-tidal, hyperhaline to mesohaline, oligotrophic to hypertrophic ecosystems (see Table 1).

The Grado-Marano lagoon (160 km²) is a large microtidal coastal lagoon, located in the Northern Adriatic between the rivers Isonzo and Tagliamento, with a shoreline of ca. 32 km. The main

freshwater inputs come from seven rivers (Stella, Turgnano, Zellina, Aussa-Corno, Natissa, Tiel and Cormor) and thirty drainage pumps. It is a complex and heterogeneous ecosystem showing a broad range of depth, salinity (meso- to euhaline), and trophic conditions (from oligotrophic to hypertrophic) depending on the sub-basins, differing for factors such as tides, freshwater inputs (higher in the western sector) and degree of confinement (Bettoso et al., 2010, Acquavita et al., 2015, and references therein). Twenty-one sites were sampled.

The Palude della Rosa (9 km²) is a shallow semi-enclosed water basin located in the northern part of the Venice Lagoon. The hydrology is determined predominantly by tidal seawater and, to a lesser extent, by freshwater coming from a branch of the Sile River (Tagliapietra et al., 2000). Nine sites were sampled.

Caleri, Marinetta, Vallona, Barbamarco, Canarin, and Scardovari lagoons, are part of the Po River Delta complex in the Veneto region (northern Adriatic Sea). Those lagoons are almost deprived of hard substrata and macrophytes, and they are influenced by semi-diurnal micro-tidal regime (till 1 m), but differ in terms of salinity, river inflow, seawater exchange and depth (Sfriso et al., 2016). Caleri lagoon (11.5 km²) is located in the northern part, it communicates with the sea through a 150-200 m long mouth. Marinetta and Vallona lagoons are part of the same basin. The Marinetta lagoon (0.8 km²) is in communication also with Caleri lagoon, it receives seawater through a channel and freshwater from Po river (Balasso, 2010). The Vallona Lagoon (11.5 km²) is a shallow basin that receives fresh water input from a series of sources, the most important one is the Po River. Two mouths, one at the north and at the south of the lagoon, have considerable influence as regards the lagoon's hydraulic system (Maggi et al., 2017). Barbamarco Lagoon is a small (7 km²), shallow, coastal lagoon. Its hydrodynamic regime is a complex interplay of water exchange with the sea through two mouths (Bocca Sud and Bocca Nord), and freshwater inputs from the Po River via the mouths and inflow channels (Spillman et al., 2009). The Sacca del Canarin (6 km²) is shallow, oval shape, elongated in the North-South direction. Its hydrology is complicated by numerous inputs of fresh and brackish water, mixing with seawater entering through two large openings in the eastern side (Bianchi and Morri, 1996). The Sacca di Scardovari is the largest embayment (32 km²) located between two branches of the Po River delta. The lagoon is connected to the Adriatic Sea through a wide mouth that is partly obstructed by sand banks. It varies in depth from 0.5 to 2.8 m. Its northern area receives nutrient-rich agricultural run-offs, while the southern area hosts extensive bivalve cultures (Munari and Mistri, 2015). In total 20 sites were sampled (4 in Caleri, 4 in Marinetta, 2 in Vallona, 2 in Barbamarco, 3 in Canarin, and 5 in Scardovari).

The Sacca di Goro is a wide (26 km²) microtidal lagoon subjected to large daily and seasonal fluctuations. Tides penetrate the lagoon through two mouths and inside the lagoon seawater mixes with fresh water, which mainly comes from the Po di Volano river and the Po di Goro river, through lock gates, and some drainage canals (Corbau et al., 2016). Three sites were sampled.

The Valli di Comacchio (100 km²) are a large complex of shallow (average depth of 1 m) choked (not influenced by the tidal regime) lagoons with an average depth of 1 m, surrounded by earthen dikes and separated from the sea by the highly modified Spina spit. The seawater exchanges are limited to two channels, and freshwater inputs come from the Reno River and a few drainage canals. Marine and freshwater inflows are regulated by sluice gates and dams (Munari and Mistri, 2015). Four sites were sampled.

The Pialassa Baiona (10 km²) is a eutrophic micro-tidal lagoon located along the northern Adriatic coast of Italy, composed of several shallow basins (60 cm deep on average) connected through channels. Seawater exchange with the Adriatic Sea is regulated by an artificial channel linked to Ravenna harbour. Salinity in the lagoon (25–35 psu) is mainly controlled by water exchange with the Adriatic Sea through this channel (Guerra et al., 2014). The lagoon receives limited freshwater inputs from five main channels that drain a watershed of 264 km², including agricultural areas. The southern channel collects also the wastewater coming from urban and industrial sewage treatment plants and from two thermal power plants (Ponti et al., 2011). Three sites were sampled.

The lagoon of Lesina (50 km²) is located in the southern Adriatic, characterised by shallow waters (0.7–1.5m) and limited exchange with the sea through two tidal channels. The lagoon is long (25 km), and narrow (maximum width 2 km) and receives freshwater from two minor rivers, and partially treated waste waters from nearby settlements and drainage waters from intensive agriculture, aquaculture and livestock (Sfriso et al., 2014 and references therein). The combination of the moderate water exchange with the sea and freshwater inflows, produce a salinity gradient in the lagoon with decreasing values from west to east (Specchiulli et al., 2009). Four sites were sampled.

The Orbetello lagoon (27 km²) is located in the eastern Tyrrhenian Sea. It is embraced within two sandbars and consists of two communicating sub-basins. It is a shallow, non-tidal environment with weak hydrodynamics, which reduces the dilution potential of organic matter and nutrients discharged from aquaculture facilities, and agriculture waste waters (Munari and Mistri, 2015). It has limited water exchange with the sea and receives modest freshwater inputs (Sfriso et al., 2014). Eleven sites were sampled.

Caprolace and Fogliano are two shallow coastal lakes located in the Circeo National Park (eastern Tyrrhenian Sea). Lake Caprolace (2.26 km²) is connected to the Tyrrhenian Sea by the ‘San Niccolò’ channel and is influenced by a microtidal regime (Table 1). The sandy bottom is almost entirely covered by the macrophyte *Cymodocea nodosa*, with patches of *Ruppia cirrhosa* and *Zostera noltii* (Signorini et al., 2008). Lake Fogliano is connected to the sea by the ‘Foce del Duca’ channel. It is larger than Lake Caprolace, and the salinity is more variable during the year (Table 1). The sandy bottom is covered by *R. cirrhosa*, with few patches of *C. nodosa* (Signorini et al., 2008). A total of 9 sites were sampled: 5 in Caprolace and 4 in Fogliano.

The Feraxi pond is a small (0.4 km²) oligotrophic coastal pond located in south eastern Sardinia (western Tyrrhenian Sea), and communicates with the sea through an open channel (Sannio et al., 1997). This site has been poorly investigated and to date information are very limited. Ten sites were sampled.

The Porto Pino lagoon is a choked lagoon located in the southwestern Sardinia, part of a system of five basins connected through pumps, and directly connected to the sea through a canal (Rossi and Cannas, 1984). Also for this site information were scant. Ten sites were sampled.

The Stagno di San Teodoro is a hypertrophic, shallow (average: 0.7 m) coastal pond located in northeastern Sardinia (western Tyrrhenian Sea). It is characterized by sandy bottoms with granitic outcrops, and is connected to the sea through a narrow (20 m wide) and shallow (0.3 m deep) mouth, which is often impounded by sand and *Posidonia oceanica* debris (Munari and Mistri, 2007). The pond receives municipal wastewaters from the town, and nutrient rich freshwater from two small rivers (Rio San Teodoro and Rio Filicani). Three sites were sampled.

At each site three replicates were collected for macrofaunal community analysis using a Van Veen grab. Those samples were sieved at 0.5 mm and preserved in 8% formalin. Taxonomic identification was carried out to the species level whenever possible, all specimens were counted and average density values per m² was calculated. For statistical analyses lagoons from Po river delta in Veneto region (Barbamarco, Caleri, Canarin, Marinetta, Scardovari and Vallona) were considered together (as DV), given the low number of sites for each lagoon (2-5).

Comparable environmental data for all the considered lagoons were not available, therefore, for the purpose of this analysis environmental information were gathered from published literature (for a total of 33 references, see table 1) and categorized as follows: two categories of typology (microtidal and non-tidal); five categories of salinity (< 5‰ oligohaline, 5-19‰ mesohaline, 20-29‰: polyhaline, 30-40‰ euryhaline, >40‰ hyperhaline); three categories of trophic status (oligotrophic, eutrophic, hypertrophic); three categories of water confinement (leaky, choked and restricted); two categories of tidal amplitude (0.3 to 1 m: large, 0.1-0.5 m: small); and six categories of sediments according to the percentage of fines (< 5% sand, 5-25% slightly muddy sand, 25-50% muddy sand, 50-75% sandy mud, 75-95% slightly sandy mud, >95% mud), following Flemming, 2000 (**Errore. L'origine riferimento non è stata trovata.**).

2.2 Data analysis

Classical measures of alpha, beta and gamma diversity, based on species identities only, were calculated at three different levels: site, lagoon, and region (island, continental/Adriatic and continental/Tyrrhenian). Alpha diversity (α) was calculated as the average number of species per individual sample (following Gray, 2000), and gamma diversity (γ) was calculated as the total number of species per level (site, lagoon, region) merging all individual samples (following Ellingsen and Gray, 2002). Beta diversity (β), was here intended as the non-directional variation in community structure among a set of sample units within a given spatial extent, or habitat type (according to the definition of Anderson et al., 2011). Measures of beta diversity were calculated in two different ways: (i) following Whittaker original formulations: $\beta_w = \gamma/\alpha - 1$ (Whittaker, 1960), and (ii) following Anderson et al. (2006), considering beta diversity (d_J) as the dispersion of sample units in multivariate space, using the average distance-to-centroid of the points (i.e. sample units) in the space defined by the Jaccard similarity as resemblance measure (calculated on presence/absence data). The differences in beta diversity (measured as dispersion with d_J) among groups at the three levels were tested using a test of homogeneity of dispersions (PERMDISP). Permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008) was run in order to determine if there was significant variability in multivariate position/dispersion at different scales, and which scale accounted for the highest variability. The differences of alpha diversity among groups at the three levels were tested using Chi-square test applied to Kruskal-Wallis (KW) ranks (Wallis Kruskal and Wallis, 1952). The response of the different metrics used to calculate alpha, beta and gamma diversity were compared with Spearman rank correlation coefficient (r_s) (Spearman, 1907).

Subsequently, analyses considering also species abundances were calculated, in order to weight the relative importance of this component of biological diversity (relative abundances), in determining the variability of macrobenthic communities among and within different lagoons. In correspondence of calculation for alpha diversity, the following indices were added: expected taxa richness (ES) calculated with rarefaction method (for number of individuals $n=10000$), Shannon index of diversity based on $\log_e(H)$, and Simpson index of dominance (λ). Those analyses were chosen in order limited

as much as possible potential bias related with uneven sampling design (Clarke and Warwick, 2001). Mean values and standard deviations of each index were calculated for each lagoon. Chi-square test applied to Kruskal-Wallis (KW) ranks (Wallis Kruskal and Wallis, 1952) was run to check for significant differences among sites, lagoons and regions (island, continental/Adriatic and continental/Tyrrhenian). When significant differences were encountered, a Wilcoxon rank sum test (W) post hoc comparison test was also carried out.

In order to partition multivariate dispersion into a component driven by compositional differences and a component driven by changes in abundance the following measures, representing a spectrum in the amount of emphasis placed on species composition vs. relative abundance, were used: (i) the Jaccard (1900) similarity measures (d_J), calculated on presence/absence data, representing the proportion of shared species out of the total number of species recorded in two units, (ii) the modified Gower dissimilarity measure (d_{MG}) proposed by Anderson et al. (2006), interpretable as the average change in orders of magnitude per species between two sampling units, and (iii) Manhattan (or Czekanowski) dissimilarity measure (d_{Manx}), modified with weights to exclude double zeros (Legendre and Legendre, 1998). MDS graph were built to show the outputs graphically. Permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008) was run in order to determine if there was significant variability in position/dispersion related with different scales. A nested design with three random factors (corresponding to scales: regions, lagoons, and sites), with “Permutation of residuals under a reduced model” was performed to test variability among scales. Tests for homogeneity of dispersion (PERMDISP) were performed among sites, among lagoons and among regions. For lagoons and regions the analysis was performed on resemble matrices among centroids for sites and lagoons, respectively, according to Anderson et al. (2008).

In order to test the influence of the environmental drivers on the analysed patterns of alpha and beta diversity the following analyses were performed. Spearman rank correlation coefficient (r_s) (Spearman, 1907) was used to test the relationship between the different components of diversity and the size of the lagoon. Chi-square test applied to Kruskal-Wallis (KW) ranks (Wallis Kruskal and Wallis, 1952), and eventual Wilcoxon rank sum test (W) post hoc comparison test were used to test for differences in alpha diversity and related measures between typology (microtidal vs non tidal), size (small $\leq 10 \text{ km}^2$, $10 \text{ km}^2 < \text{medium} < 100 \text{ km}^2$, big $\geq 100 \text{ km}^2$), confinement (leaky, choked and restricted), tidal amplitude, salinity (oligohaline, mesohaline, polyhaline, euryhaline, hyperhaline), trophic status (oligotrophic, eutrophic, hypertrophic) and sediments (predominantly sandy, predominantly muddy and variable). Tests for homogeneity of dispersion (PERMDISP) were performed in order to test for differences in beta diversity among lagoons of different typology, sizes, salinity, trophic status, sediment types, confinement and tidal amplitude. The analyses were performed on resemble matrices among centroids, according to Anderson et al. (2008), and was repeated considering geographical regions separately.

Calculations were performed with PRIMER v6 + PERMANOVA software package (Anderson et al., 2008; Clarke and Gorley, 2006), and R software package v3.5.0 (R Development Core Team, 2008). A value of $p < 0.05$ was chosen as significant threshold.

3. Results

3.1. Diversity measured based on species richness

No significant differences between sites were observed for alpha diversity (KW, $p > 0.05$), whereas marked significant differences were observed among lagoons (KW, $p < 0.05$). Lowest values were observed at PP ($\alpha = 11 \pm 4$ SD), whereas the highest were observed at CO ($\alpha = 72 \pm 17$ SD), CA ($\alpha = 68 \pm 14$ SD), FO ($\alpha = 61 \pm 10$ SD) and GO ($\alpha = 56 \pm 14$ SD) (**Errore. L'origine riferimento non è stata trovata.**). Alpha diversity showed significant differences also at level of region (KW, $p < 0.05$), between Adriatic and Tyrrhenian (W, $p < 0.05$), and between continental (Adriatic/Tyrrhenian) and island (W, $p < 0.05$).

There was a general agreement in the rank order of measures of beta diversity, using Whittaker formulation (β_w) and using distance to centroid on the basis of the Jaccard measure (d_j). The only difference was that with β_w OR showed higher values than LE and PP, while with d_j the opposite trend was observed (**Errore. L'origine riferimento non è stata trovata.**). The relationship between β_w and d_j was very high ($r_s = 0.9$, $p < 0.05$). Considering resemblance matrix based on Jaccard measure (d_j) significant differences were found among regions, among lagoons and among sites (PERMANOVA, $p < 0.05$). The greatest variation in species composition occurred within the smallest spatial scale (residual component), which may share only around 51% of their species, followed by lagoons, with additional 34% of species dissimilarity, and then region and site (Table 2). Conversely, beta diversity (d_j) significantly differed among both sites and lagoons (PERMDISP, $p < 0.05$), but not among regions (Adriatic/Tyrrhenian/island) (PERMDISP, $p > 0.05$). The highest values of beta diversity were observed at GM ($\beta_w = 4.5$; $d_j = 51 \pm 2$ SE) and DV ($\beta_w = 4.2$; $d_j = 49 \pm 3$ SE); the lowest at BA ($\beta_w = 1.4$; $d_j = 23 \pm 3$ SE).

At the intermediate scale (among lagoons) there was a direct relationship between alpha and gamma diversity ($p_s = 0.883$; p -value < 0.05). The highest values of alpha and gamma diversity were found at CA ($\gamma = 130$), and CO ($\gamma = 122$), the lowest at PP ($\gamma = 26$), ST ($\gamma = 32$), and FE ($\gamma = 39$). GM represented an exception, since the high value of gamma diversity ($\gamma = 111$) correspond to a rather low alpha diversity ($\alpha = 26 \pm 14$ SD) (**Errore. L'origine riferimento non è stata trovata.**). Conversely there was a negative relationship between alpha and beta diversity (β_w : $p_s = -0.642$; p -value < 0.05 ; d_j : $p_s = -0.695$; p -value < 0.05), with lagoons characterized by high values of alpha diversity (e.g. CO and CA), showing low values of beta diversity and lagoons showing low values of alpha diversity (e.g. DV) with high values of beta diversity (**Errore. L'origine riferimento non è stata trovata.**).

3.2. Diversity measured considering abundances

Alpha diversity was positively correlated with estimated species richness calculated with rarefaction method ($r_s = 0.724$; $p < 0.05$), and Shannon diversity ($r_s = 0.601$; $p < 0.05$), but negatively related with Simpson dominance ($r_s = -0.446$; $p < 0.05$). Estimated species richness (ES), Shannon diversity (H) and Simpson (λ) index of dominance showed no significant differences between sites (KW, $p > 0.05$), but significant differences among lagoons (KW, $p < 0.05$). DV and ST in particular showed high and variable dominance (**Errore. L'origine riferimento non è stata trovata.**), with Simpson index at DV, significantly higher than at CA, FE, GM, and PR (W, $p < 0.05$). As a result, Shannon diversity index (H) at DV was significantly lower than at CA, FE, GM, and PR (W, $p < 0.05$). Significant differences of diversity indices were observed among regions (KW, $p < 0.05$). Expected species richness (ES) showed a significant difference among regions, but only between island and

continental/Adriatic ($W, p < 0.05$), Shannon diversity (H) significantly differed only between Adriatic and Tyrrhenian ($W, p < 0.05$). Simpson index (λ) did not varied significantly among regions ($KW, p > 0.05$).

Considering resemblance matrix based on untransformed data and Modified Gower measure (d_{MG10}) the results were similar to results obtained with Jaccard measure (d_j), with significant differences among regions, among lagoons and among sites (PERMANOVA, $p < 0.05$). The greatest variation in species composition occurred within the smallest spatial scale (residual component), followed by lagoons, and then region and site (Table 2). PERMDISP analysis showed a difference in dispersion among sites and lagoons, but not among regions (Table 3). Considering resemblance matrix based on untransformed data and Manhattan (or Czekanowski) dissimilarity measure (d_{Manx}) significant differences were not found among regions, among lagoons nor among sites (PERMANOVA, $p > 0.05$). PERMDISP analysis did not showed a difference in dispersion among sites, among lagoons, nor among regions (Table 3), as well. The rank order among lagoons obtained with the two methods, showed some differences. Beta diversity calculated in terms of multivariate dispersion through Jaccard measure (d_j), indicated that the highest values were at GM and DV and the lowest at BA (Table 4). The analyses based on the modified Gower measure (d_{MG}), showed a similar pattern, with highest values at DV an ST, but lowest at FO (Table 4).

3.3. Influence of environmental variables

No significant relationship was observed between α and β diversity and the size of the lagoons ($p > 0.05$). No significant differences of α diversity were observed between microtidal and non-tidal lagoons, nor among lagoons with different dimensions, different level of confinement, different sediment composition, nor different tidal range of the area ($KW, p > 0.05$). Conversely significant differences were found among lagoons with different salinity ($KW, p < 0.05$). In particular ($W, p < 0.05$) poly/euhaline lagoon showed different alpha diversity than others, and meso/polyhaline showed lower alpha values than euhaline and higher than hyperhaline lagoons (Fig. 3). Estimated species richness showed a pattern similar to alpha diversity, but with significant differences ($KW, p < 0.05$) also among microtidal and non-tidal lagoons (higher values for microtidal), lagoon with different dimensions (higher values for big lagoons), different salinity (lower values for hyperhaline than euhaline and poly/euhaline, and lower for polyhaline than poly/euhaline), trophic status (higher values for oli/hypertrophic than oligo/eutrophic, lower values for oligo/eutrophic than eutrophic lagoons), sediment composition (higher and more variable values in lagoons with predominantly muddy bottom compared to predominantly sandy ones) and confinement (higher values for leaky than choked lagoons) and tidal range (higher and more variable values for lagoons located in areas with large tides) ($KW, p < 0.05$; Fig. 3). Shannon and Simpson indices differed significantly with lagoon dimension, salinity, trophic status, and sediment composition ($KW, p < 0.05$), in particular ($W, p < 0.05$) small and big size lagoons showed higher diversity and lower dominance compared to medium ones; poly/euhaline showed higher diversity and lower dominance than polyhaline, lower diversity than euhaline lagoons, and lower dominance than meso/poly lagoons; eutrophic lagoons showed lower diversity and higher dominance than oligotrophic lagoons; lagoons with predominantly muddy or sandy bottom showed higher diversity and lower dominance than lagoons were both typology were present ($W, p < 0.05$; Fig. 3). Barely significant differences of Shannon diversity ($KW, p = 0.05$), but not of Simpson index ($KW, p > 0.05$) were observed among microtidal and non-tidal lagoons. No

significant differences were observed for both indices among lagoons with different levels of confinement non tidal amplitude (KW, $p > 0.05$).

MDS ordination plot based on Jaccard measure (d_J) showed differences among lagoons (**Errore. L'origine riferimento non è stata trovata.A**), related to both position and dispersion of sites (Table 2, Table 3). A biogeographical gradient could be identify with island on the right (with the exception of ST), Adriatic on the bottom left and Tyrrhenian on the upper left (**Errore. L'origine riferimento non è stata trovata.B**). Superimposed to this geographical gradient a distinction between microtidal and non-tidal lagoon (**Errore. L'origine riferimento non è stata trovata.C**), and small, medium and big lagoons (**Errore. L'origine riferimento non è stata trovata.D**), trophic status (Fig. 4E) and sediment composition (Fig. 4F) could also be observed.

Considering the dispersion component of variation, significant differences of beta diversity (Jaccard measure d_J) were observed among lagoons with different trophic status, in particular eutrophic lagoons showed higher beta diversity than oligotrophic ones. Considering the more general community structure (Modified Gower measure d_{MG10}) this differences were barely significant (PERMDISP, $p = 0.05$). When only Adriatic lagoons were considered, differences of beta diversity were observed also among lagoons with different level of confinement, with higher beta diversity in restricted lagoons compared with choked ones (PERMDISP, $p < 0.05$). No significant differences (PERMDISP, $p > 0.05$) were observed considering the dispersion of the abundance component only (Manhattan measure d_{Manx}).

4. Discussion

4.1. Partitioning diversity in alpha, beta and gamma diversity

Species composition varied significantly within macrobenthic communities at all three analysed scales: site, lagoon and region (PERMANOVA on presence/absence data and Jaccard measure, d_J). Nevertheless, diversity partitioning showed that macrobenthic assemblages varied significantly in terms of both alpha and beta diversity only at the intermediate scale (among lagoons). At the smallest analysed scale (among sites) the communities varied only in terms of beta diversity, whereas at the biggest scale (among regions), there was significant variability only in terms of alpha diversity. The highest variability of macrobenthic assemblages (in terms of both position and dispersion, PERMANOVA) was within the smallest scale, at level of residuals within each site, consistently with results reported for macrobenthic invertebrates from other marine habitat types, such as kelp holdfast assemblages and soft bottom Norwegian continental shelf (Anderson et al., 2005), and in line with the environmental instability typical of transitional waters. The variability at the smallest scale could depend on a number of different factors, for instance stochastic occupancy, species interactions, resource specificity, or niche requirements (Barton et al., 2013), and a detailed analysis was beyond the aim of the present work. Among the three scales considered, the highest variability was observed at the intermediate scale (among lagoons). The variation in alpha diversity among lagoons probably reflects colonization stochasticity, which itself is a function of immigration and regional species richness (Munari and Mistri, 2008). The observed pattern of beta diversity is consistent with conceptual approaches to the spatial scaling of beta diversity described by Barton et al. (2013). According to this approach beta diversity might be expected to follow a concave parabolic scaling relationship, wherein dissimilarity among sampling units is higher at the smallest and biggest scales,

but lower at intermediate scales (when based on differentiation measure with varying grain and extent).

Alpha, beta, and gamma diversity are, by definition, interplaying related variables. In cases of habitat homogeneity, when beta diversity will be low, alpha and gamma diversity tended to converge; conversely, in case of habitat heterogeneity, when patches will show different species composition, beta diversity will be high and the limit to gamma diversity will be set by the number of habitat patches (Cornell and Lawton, 1992). At the intermediate scale (among lagoons) the observed direct relationship between α and γ diversity, corresponded to a Type I relationship (straight line) according to Cornell and Lawton (1992) and indicates that in general the number of species that coexist at level of site is affected by the size of the lagoonal species pool, consistently with previously published works on other Italian lagoons (Munari and Mistri, 2008). The opposite trend of beta diversity compared to alpha and gamma diversity observed in the present work, indicated that lagoons with higher alpha diversity showed also lower beta diversity, and therefore lower habitat heterogeneity, that in transitional waters could be related with change in confinement, salinity, sedimentary organic matter, or presence of phanerogams (see 4.3.). GM, the biggest microtidal lagoon analysed, represented a deviation from this trend, showing medium-low values of alpha diversity and high values of gamma and beta diversity, indicating that in this lagoon gamma diversity was strongly influenced also by beta diversity.

4.2. Comparison with pattern of relative abundances

In general alpha diversity showed the same pattern of expected species richness (ES), and Shannon diversity (H), but the opposite of Simpson dominance (λ), indicating that lagoons with low alpha diversity showed also high dominance of the most abundant species. The different patterns of variability of alpha diversity among the three different scales (significant only at scale of lagoon and region) were in general maintained using measures that consider also relative abundances (ES and H), with the only exception of Simpson index (no significant variation at regional level). Nevertheless, the rank order vary depending on the index considered, indicating that the patterns of variability in terms of relative abundances within the intermediate (among lagoons) and higher scales (among regions) differed from patterns described by alpha diversity. Those differences influenced their response to environmental drivers (see 4.3.).

Results obtained measuring beta diversity as variability of dispersion with Jaccard resemble measure (d_j) were consistent with results obtained with the original formulation (β_w) of Whittaker (1960), as it was reported also for different habitat types (Anderson et al., 2006). The advantages of the use of multivariate methods for the calculation of β diversity are that they allow statistical comparisons of β diversity between two or more areas with more flexibility, testing rigorously for differences in beta diversity (i.e. dispersion of species composition data) among groups of multivariate samples (Anderson et al., 2006). This method respond also to the requirement of independence from values of alpha diversity (Wilson and Shmida, 1984; Barton et al., 2013), which is fundamental to compare beta diversities of regions with different alpha diversities (which are likely to change also at different scales).

The pattern of variability obtained with Jaccard measure (d_j) among the three scales (site, lagoon, and region) was consistent with the pattern resulting from modified Gower measure (d_{MG10}), which explicitly weights a compositional change equal to an order-of-magnitude change, showing significant differences at the three scales (PERMANOVA), and differences in dispersion at the two

scales: among sites and among lagoons (PERMDISP). Conversely, using Manhattan dissimilarity measure (d_{Manx}), focusing only on the abundance component, no differences were detected, nor in terms of dispersion nor of position, at neither of the three different scales. This indicates that the variability of macrobenthic assemblages in terms of dispersion at the two lowest scales (site and lagoon) was mainly driven by species composition. Our results were consistent with previous works, showing that Italian lagoons shared relatively few common species and each lagoon has its peculiar biological features (Sabetta et al., 2007; Munari and Mistri, 2008). Those results could be important from a conservation point of view, since Italian transitional waters are known to exhibit remarkably high species richness, notwithstanding the generalized anthropogenic disturbances to which they are subjected (Naldi and Viaroli, 2002; Munari and Mistri, 2008).

4.3. Influence of environmental factors

In the present work the highest variability was observed among lagoons in terms of both alpha and beta diversity. This variability was likely the results of combined effect of different factors, such as the geomorphology of the systems (here considered in terms of dimension, typology, and confinement) and the trophic status of the lagoon. Alpha diversity measured in terms of species richness (α) responded only to salinity and trophic status, while alpha diversity measured in terms of ES responded to all factors analyses (typology, dimension, salinity, trophic status, confinement tidal range and sediment composition). Conversely, beta diversity (Jaccard measure d_j) responded to different trophic status and, when only Adriatic lagoons were considered, level of confinement. Moreover, a geographical gradient with a separation of lagoons between island/continental (with the exception of ST) and Tyrrhenian/Adriatic Sea was observed (MDS, Permanova), but only in terms of alpha diversity (position component) and not in terms of beta diversity (dispersion component).

Considering alpha diversity, such a geographical gradients have already been observed for macrobenthic invertebrates in Mediterranean lagoons. The existence of a biogeographical boundary between the eastern and western part influencing the faunal distribution of the Mediterranean Sea was first proposed by Pérès and Picard (1964) and is now widely accepted by most biogeographers. Moreover, Munari and Mistri (2008) advanced the hypothesis that a series of north–south gradients also plays a major role in determining the faunal distribution in Italian transitional waters. A geographical clustering of Italian transitional waters was reported also by Sabetta et al. (2007). A similar bioclimatic gradient was proposed also for specific taxonomic groups in other Mediterranean marine habitat types (i.e. syllids, Musco and Giangrande, 2005; corals and gastropods, Bianchi, 2007). The effect of other factors superimposed to this geographical gradient changed with the type of analysis. Alpha diversity measured in terms of species richness, responded only to differences in salinity. The decrease of richness with decreasing salinity was a common pattern already observed from many transitional areas (e.g. Jorcin, 1999; Telesh and Khlebovich, 2010), although the relationship was not necessarily strong and linear. Conversely, if we considered alpha diversity measured as ES, different factors seemed to contribute to the observed pattern, together with salinity: typology, dimension, trophic status, confinement, tidal range and sediment composition. None of those factors alone explained completely the pattern, therefore alpha diversity is likely the result of a combination of those factors, which are all known to influence richness in transitional environments. Different levels of confinement, depending on the marine influence, is known to be very influential on alpha diversity of macrobenthic assemblages, because it is linked to biotic (such as larval transport) and hydrodynamic determinants (Munari and Mistri, 2008). Differences of alpha diversity (in terms

of ES) were also related to the influence of the sea, with higher values where the influence of the sea was strongest (microtidal, leaky lagoons, located in areas with large tidal amplitude). The size of the lagoon is also known to affect alpha diversity. The species-area relationship, proposed by Arrhenius (1921) and subsequently implemented, describes the pattern in which the species richness increases with the increasing sampling area, and is among the best known and most studied paradigms in ecology (Rosenzweig, 1995). The efficiency of this theory was proved also for macroinvertebrates of Mediterranean transitional waters (Sabetta et al., 2007), emphasising the insularity of lagoonal ecosystem in the coastal landscapes, despite their peculiarity of being patches surrounded by a space which is a suitable habitat rather than an unsuitable habitat, as the definition of island specifies (MacArthur, 1972). Sediments grain size is also usually correlated with faunal distributions (Giménez et al., 2014), even if some investigation (Lardicci et al., 1993; Snelgrove and Butman, 1994; Carvalho et al., 2005) pointed out that within brackish habitats, macrobenthic zonation cannot be explained by a single major factor, such as grain size, but also by other factors associated with this parameter (e.g. the organic matter content). As most of the environmental parameters are closely related to each other, it is difficult to segregate the effect of each parameter analysed on the spatial distribution of macrobenthic fauna. Alpha diversity is likely to be influenced by different interplaying factors, and according to our data it is not possible to disentangle their effect.

Considering beta diversity, one of the most important factors in generating and maintaining this component of diversity is the spatial variability of habitat structure (Hewitt et al., 2005; Matias et al., 2011). Habitat heterogeneity in lagoons could be related with the different factors. In the present work beta diversity responded to the trophic status of lagoons: oligotrophic lagoons showed a general higher beta diversity than eutrophic lagoons. Oligotrophic lagoons are usually in nearly pristine condition, such as CA and FO, where the presence of macrophytes provided multi-niche habitats for aquatic organisms, with both trophic and nursery functions (Signorini et al., 2008; Prato et al., 2014), whereas eutrophic lagoons such as those located at the Po river delta are usually deprived of vegetation (Marchini et al., 2008), with consequent reduced habitat heterogeneity for benthic animals. The level of isolation from the sea and freshwater inputs are also known to influence heterogeneity of condition for benthic animals in transitional areas. In the present work, when considering only Adriatic lagoons higher beta diversity was observed in restricted compared with choked lagoons. There was a differential distribution of lagoons typologies among geographic regions. In Tyrrhenian Sea the marine influence is scarce, because tidal amplitude is small (50 cm maximum) and considered lagoons were all non-tidal, choked. Conversely in the Adriatic Sea tidal amplitude is larger (1 m maximum), both micro- and non-tidal lagoons were present, and microtidal lagoons were both leaky and restricted, therefore differing for the degree of marine influence. The same happened with lagoons dimensions: the biggest lagoons were located only in the Adriatic Sea and in island only small ones were present. This differential distribution explains why the response of beta diversity to the confinement of the lagoon was clearly detectable only at Adriatic level. The absence of a clear response to lagoon dimension could also be related with the superimposition of this geographic distribution and other factors (trophic status and confinement). Therefore it is likely that also beta diversity responded to a combination of different factors. The highest beta diversity was observed at GM, the biggest microtidal lagoon of the present study, accounting also for the highest habitat heterogeneity, followed by DV, accounting for the second biggest total area and high levels of heterogeneity. GM was characterised by a variety of hydrological conditions, related with freshwater input, and confinement degree, and consequent changes in salinity, and trophic status. Those

differences lead to a decreasing gradient of biodiversity from the eastern to the western part of the lagoon, and from the inlets to the inner bank of the lagoon (Bettoso et al., 2010). Conversely CO lagoon, the biggest non tidal lagoon of the present study, showed very low values of beta diversity, despite high alpha diversity, likely due to habitat homogeneity. The habitat homogeneity of the CO lagoon, was the consequence of different factors, among those the scarce water exchange with the sea and the progressive reduction of the surface covered by seagrasses (Munari et al., 2005; Pitacco et al., 2018).

We conclude that the patterns of macrobenthic community observed among lagoons, in terms of both alpha and beta diversity, resulted from the complex interaction of different drivers. To minimise the variability of taxonomic richness among transitional water types, is a major reason for splitting transitional water ecosystems into ecosystem types, as required by the European Water Framework Directive - EU-WFD 60/2000. Previous investigations highlighted the necessity to take into account the scaling of taxonomic richness with lagoon surface area (Sabetta et al., 2007). Our results suggested that the analysis of beta diversity could be helpful to scale the degree of habitat heterogeneity influencing benthic diversity, that in transitional water bodies comes from different interplaying factors.

4.4. Comparison and usefulness of the different methods

From the methodological point of view, our results suggest to combined classical univariate measures deriving from alpha diversity (ES, H, λ) to multivariate measures of beta diversity, to obtain complementary information crucial to the understanding of spatial pattern of benthic assemblages at different scales.

Considering univariate measures, the introduction of ES, H, and λ , beside classical α values, enable to detect also pattern of variation of the community in terms of relative abundances. Observed richness is known to be heavily dependent on sample size and effort, which is a potential problem for comparison at geographical scale, when heterogeneous datasets are analysed (Clarke and Warwick, 2001). The use of ES as a measure of alpha diversity, could be useful to limit the potential bias related in case of different or unknown sampling size and effort. Notwithstanding the limitation of the method, i.e. the strict assumption that individuals arrive in the sample independently (Clarke and Warwick, 2001), ES had the advantage to respond better to environmental variables, providing a more complex picture of driving factors influencing alpha diversity. λ gives information on the degree of dominance of the most abundant species, it demonstrated lack of bias related with sample size/effort (Clarke and Warwick, 2001), therefore is suitable for comparison at geographical scale.

Beta diversity measured as variability of dispersion with Jaccard resemble measure (d_j) gave results consistent with those obtained with the original formulation (β_w), but it has the advantage to be more suitable for rigorous and flexible statistical comparison. Moreover, our results supported also the importance of introducing measures for partitioning the multivariate variability in two components: richness and relative abundances. This partitioning is a common routine for univariate measures, but rarely considered for multivariate measures. The use of measures weighing these two components (d_j , d_{MG10} , d_{Max}), compared with the most commonly used measures (e.g. Bray-Curtis), provides additional information on macrobenthic community, without covering differences related with the presence of less abundant and rare species. This could be particularly important in transitional

environments, where benthic communities are subjected to high rate of fluctuations in abundances, with picks of few species accounting for a high number of individuals. Those fluctuations of abundances, which are typical of population dynamics in transitional waters, could create bias, in particular for comparisons at geographic scale, when the available dataset is usually heterogeneous.

5. Conclusions

In the present work, the highest variability of macrobenthic assemblages was observed at the intermediate scale (among lagoons), where those variations were significant in terms of both alpha and beta diversity. Conversely at the smallest analysed scale (among sites) the variability was mainly in terms of beta diversity, whereas at the biggest scale (among regions), the variability was mainly in terms of alpha diversity. At the intermediate scale (among lagoons) the number of species at level of site (alpha diversity) is affected by the size of the lagoonal species pool (gamma diversity), whereas beta diversity showed an opposite trend.

The introduction of ES, H, and λ , indicated the existence of a pattern of variability of the community in terms of relative abundances that was opposite of the pattern depicted by alpha diversity. Conversely, the introduction of measures for the partitioning of the heterogeneity of dispersion showed that the variability of beta diversity among sites and lagoons was mainly related to species richness, with no significant differences in terms of relative abundances.

Differences between lagoons in terms of both alpha and beta diversity were most probably a result of a complex combined effect of different factors. Alpha diversity responded both to geographical (insularity and biogeography) and chemico-physical factors (salinity and typology of the lagoon). The measures of beta diversity, allowed the identification of additional patterns of macrobenthic community related with habitat heterogeneity (mainly related with trophic status and level of confinement). The detection of those patterns were particularly important at the smallest scale (among sites), where variability was unnoticed with other metrics (alpha diversity).

Our results support the usefulness of portioning diversity in alpha, beta and gamma components, and of combining different univariate (α , ES, λ) and multivariate measures of dispersion (d_J , d_{MG10} , d_{Manx}), in order to analyse separately patterns of richness and relative abundances.

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Figure legends

Fig. 1. Relationship between the different component of diversity considering species composition. Comparison of alpha (α), beta (β), and gamma (γ) diversity among the studied lagoons (A, C, E), and among regions (B, D, F). βW =Whittaker original formulation; dJ= Jaccard similarity measure; Isl =island; Adr =Adriatic; Tyr = Tyrrhenian.

Fig. 2. Average (\pm SD) diversity indices for each lagoon (A-C) and region (D-E). ES = expected species richness, H = Shannon diversity, Lambda = Simpson index.

Fig. 3. Average alpha diversity (α), estimated species richness (ES), Shannon index (H) and Simpson index (λ), for lagoon with different confinemeny (choked, leaky, restricted), dimensions (big, medium, small), salinity (euH = eurihaline, hyH = hyperhaline, me/poH = meso-/polyhaline, po/euH = poly-/eurihaline, poH = polyhaline), trophic status (eu/hyT = euri-/hypertrophic, euT = eutrophic, me/euT = meso-/eutrophic, ol/euT = oligo-/eutrophic, ol/hyT = oligo-/hypertrophic, olT = oligotrophic), and sediment composition (mud = predominantly muddy, sand= predominantly sandy, mix =both types present).

Fig. 4. Non-metric MDS plots on the basis of Jaccard resemblance measure, showing spatial pattern of analysed sites, with highlighted: lagoons (A), geographic region (B), confinement (C), size (D), trophic status (E) and sediments (F). For lagoon codes see Table 1. S = small, M = medium, B = big, hyp = hypertrophic, eu = eutrophic, oli = oligotrophic, mes =mesotrophic, Sa = predominatly sandy, Mu = predominantly Muddy, Mi = both sediment typologies, NA = no data available.

Table 1. Characteristics of sampled lagoons (information gathered from cited literature) and number of sampled sites.

Lagoon	Code	Area (km ²)	Average depth (m)	Typology	Tidal range	Confinement	Salinity	Trophic status	Residence time (d)	Sediments	References
Valli di Comacchio	CO	100	0.5-1.5	non-tidal	large	choked	euhaline	hyper/eutrophic	115	sandy mud	Mistri et al. (2000); Mistri and Munari (2015); Pitacco et al. (2018)
Sacca di Goro	GO	26	1.2-1.5	microtidal	large	leaky	meso/polyhaline	eu/mesotrophic	4	slightly sandy mud	Corbau et al. (2016); Mistri et al. (2001); Munari and Mistri (2008)
Sacca di Scardovari	SC	32	1.5-2	microtidal	large	leaky	meso/polyhaline	eutrophic	NA	sandy mud	Marchini et al. (2008); Sfriso et al. (2016)
Lesina Lagoon	LE	50	0.8	non-tidal	small	choked	meso/polyhaline	eutrophic	30 to 300	muddy sand to sandy mud	Pusceddu et al. (2007); Roselli et al. (2009); Specchiulli et al. (2010)
Orbetello Lagoon	OR	27	0.5-1	non-tidal	small	choked	poly/hyperhaline	eu/oligotrophic	NA	muddy sand	Lardicci et al. (2001); Marchini et al. (2008); Munari and Mistri (2007, 2008); Munari et al. (2009)
Caprolace Lake	CA	2.26	1.3	non-tidal	small	choked	eu/hyperhaline	oligotrophic	90	sand	Prato et al. (2009, 2014); Signorini et al. (2008)
Fogliano Lake	FO	4.08	0.9	non-tidal	small	choked	eu/hyperhaline	oligotrophic	60	sand	Prato et al. (2008, 2014); Signorini et al. (2008)
Grado-Marano Lagoon	GM	160	1.5	microtidal	large	restricted	poly/euhaline	oligo/hypertrophic	2 to 20	slightly sandy mud	Bettoso et al. (2010), Reizopoulou et al. (2014), Acquavita et al. (2014, 2015)

Baiona	BA	10	0.5-1	microtidal	large	restricted	polyhaline	eutrophic	3	slightly muddy sand to sandy mud	Ponti et al. (2011); Guerra et al. (2014)
Palude della Rosa	PR	9	1	microtidal	large	restricted	poly/euhaline	eutrophic	NA	slightly sandy mud	Ravera et al. (2000); Favero et al. (1996)
Porto Pino	PP	3.14	0.7	non tidal	small	choked	hypersaline	oligotrophic	NA	NA	Rossi and Cannas (1984)
San Teodoro	ST	2.2	0.7	non-tidal	small	choked	polyhaline	hypertrophic	NA	sand	Munari and Mistri (2007)
Feraxi	FE	0.4	NA	non-tidal	small	choked	euhaline	oligotrophic	NA	NA	Sannio et al. (1997)
Canarin	CN	10.0	0.8	microtidal	large	restricted	meso/polyhaline	eutrophic	NA	slightly sandy mud	Balasso (2010); Bianchi and Morri (1996); Sfriso et al. (2016)
Barbamarco	BR	8	0.8	microtidal	large	restricted	meso/polyhaline	eutrophic	2 to 6	slightly sandy mud/mud	Spillman et al. (2009); Balasso (2010); Sfriso et al. (2016)
Vallona	VA	11.5	2	microtidal	large	restricted	meso/polyhaline	eutrophic	NA	sandy mud	Cacciatore et al. (2008); Maggi et al. (2017); Sfriso et al. (2016)
Marinetta	MA	10	0.8	microtidal	large	restricted	meso/polyhaline	eutrophic	NA	slightly muddy sand	Balasso (2010); Mistri et al. (2018); Sfriso et al. (2016)
Caleri	CL	11.5	2	microtidal	large	restricted	meso/polyhaline	eutrophic	NA	muddy sand/sandy mud	Balasso (2010); Mistri et al. (2018); Sfriso et al. (2016)

Table 2. Estimates of components of variation resulted from PERMANOVA calculation explained by regions, lagoons, sites, and residuals

PERMANOVA - Estimates of components of variation					
Jaccard (d_J)			Modified Gower base 10 (d_{MG10})		
Source	Estimate	Square root	Source	Estimate	Square root
Region	364.5	19.1	Region	0.43	0.7
Lagoon	1184.7	34.4	Lagoon	0.57	0.8
Site	162.6	12.8	Site	0.13	0.4
Residual	2624.9	51.2	Residual	1.70	1.3

Table 3. Results of PERMDISP analysis at levels of sites, lagoons and regions, using according to Jaccard (d_J), Modified Gowler base 10 (d_{MG10}), and modified Manhattan (excluding double zeros) measures (d_{Manx}).

PERMDISP - deviation from centroid						
	Site		Lagoon		Region	
	F	P	F	p	F	p
d_J	34.03	0.0001	42.03	0.0001	0.04	0.859
d_{MG10}	36.93	0.0001	61.80	0.001	0.43	0.629
d_{Manx}	1.09	0.392	4.57	0.167	2.81	0.147

Table 4 Average and SE homogeneity of multivariate dispersion according to Jaccard, modified Gowler, and modified Manhattan (excluding double zeros).

		Jaccard		Modified Gowler	
Lagoon	Area (km²)	Average	SE	Average	SE
FE	0.4	43.6	3.0	1.24	0.07
ST	2.2	46.2	4.0	1.41	0.06
CA	2.26	34.9	1.4	0.61	0.04
FO	4.08	27.8	2.6	0.49	0.04
PP	4.4	46.4	2.5	1.36	0.07
PR	9	27.4	0.8	0.60	0.03
BA	10	23.1	1.6	0.72	0.04
GO	26	28.5	2.2	0.72	0.04
OR	27	37.4	2.1	0.67	0.04
LE	50	38.8	2.7	1.10	0.08
DV	51	49.2	1.4	1.47	0.04
CO	100	29.8	2.4	0.60	0.02
GM	160	51.0	1.1	1.25	0.03

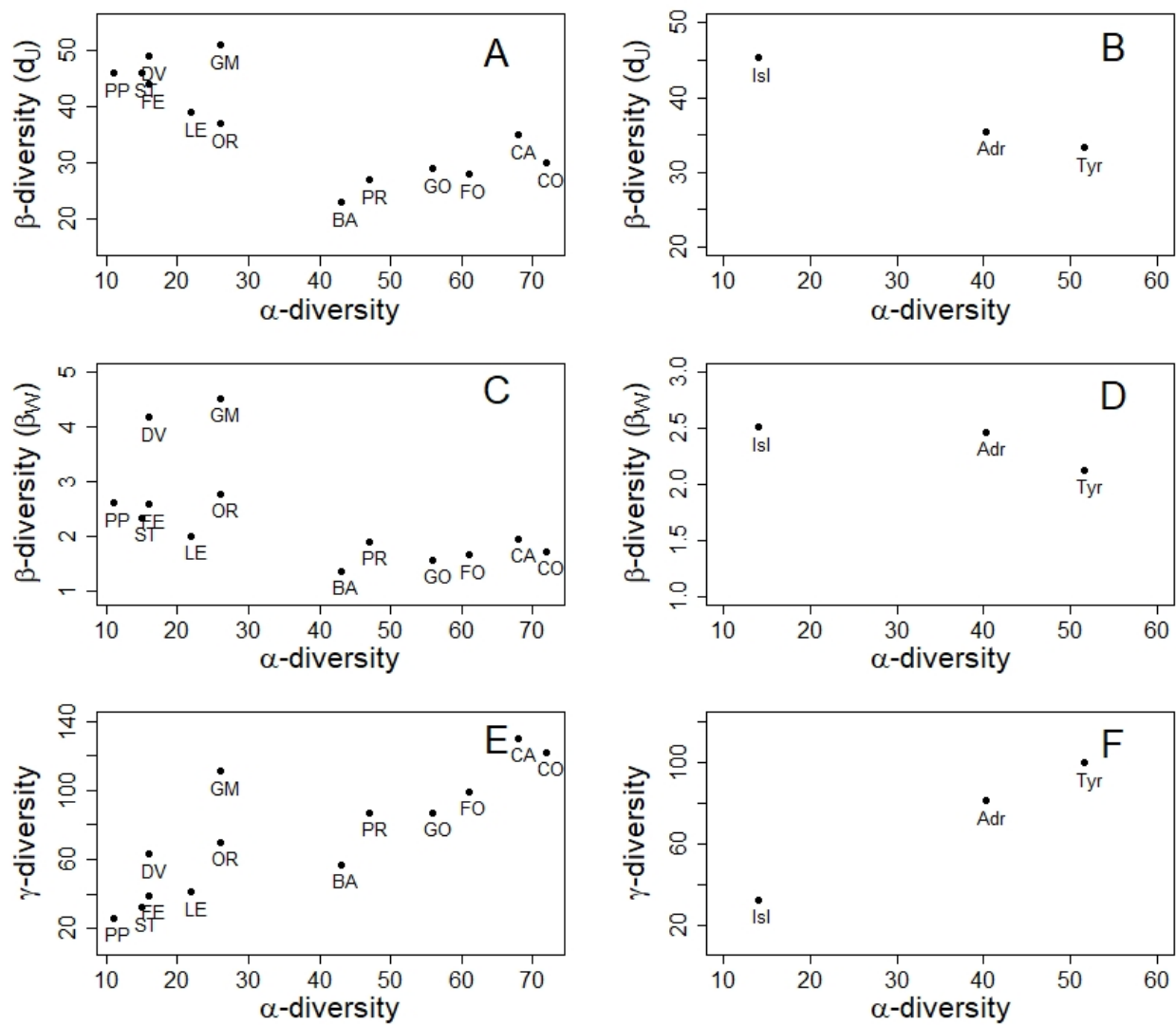


Fig.1

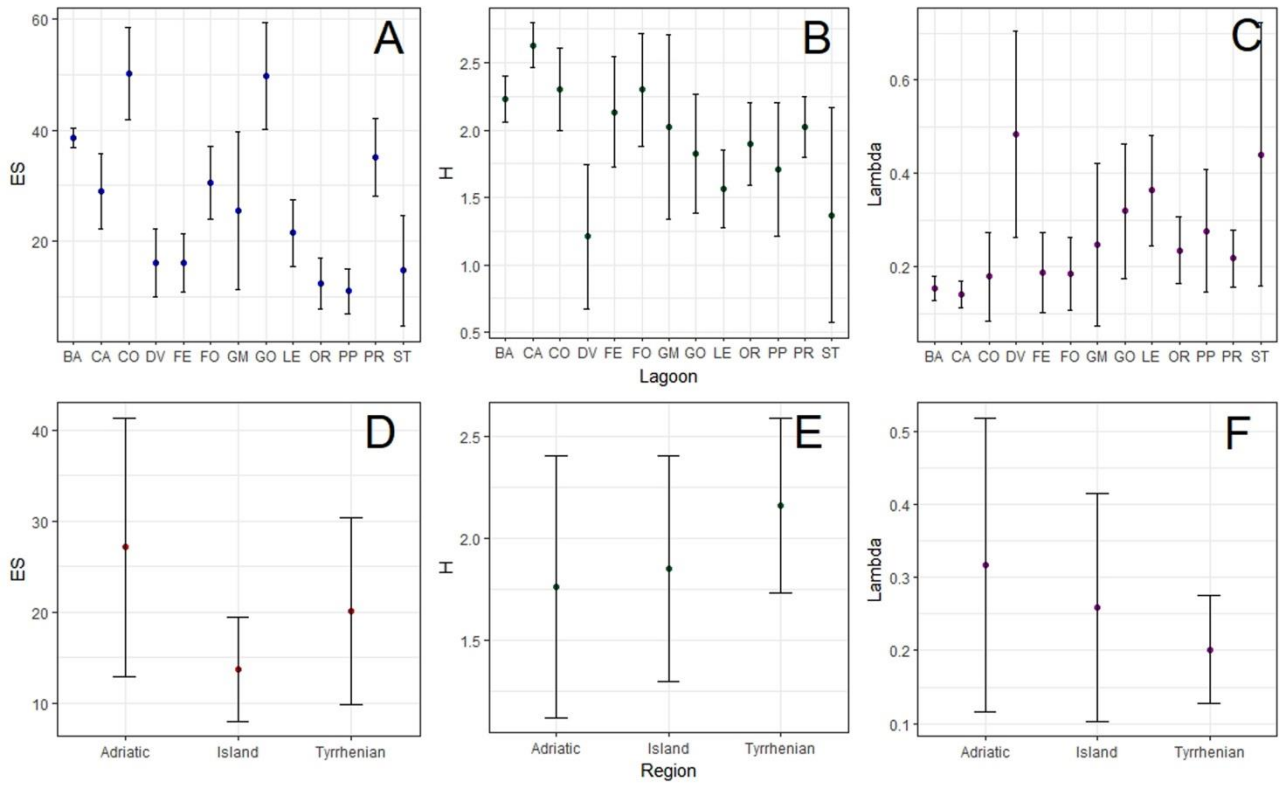


Fig.2

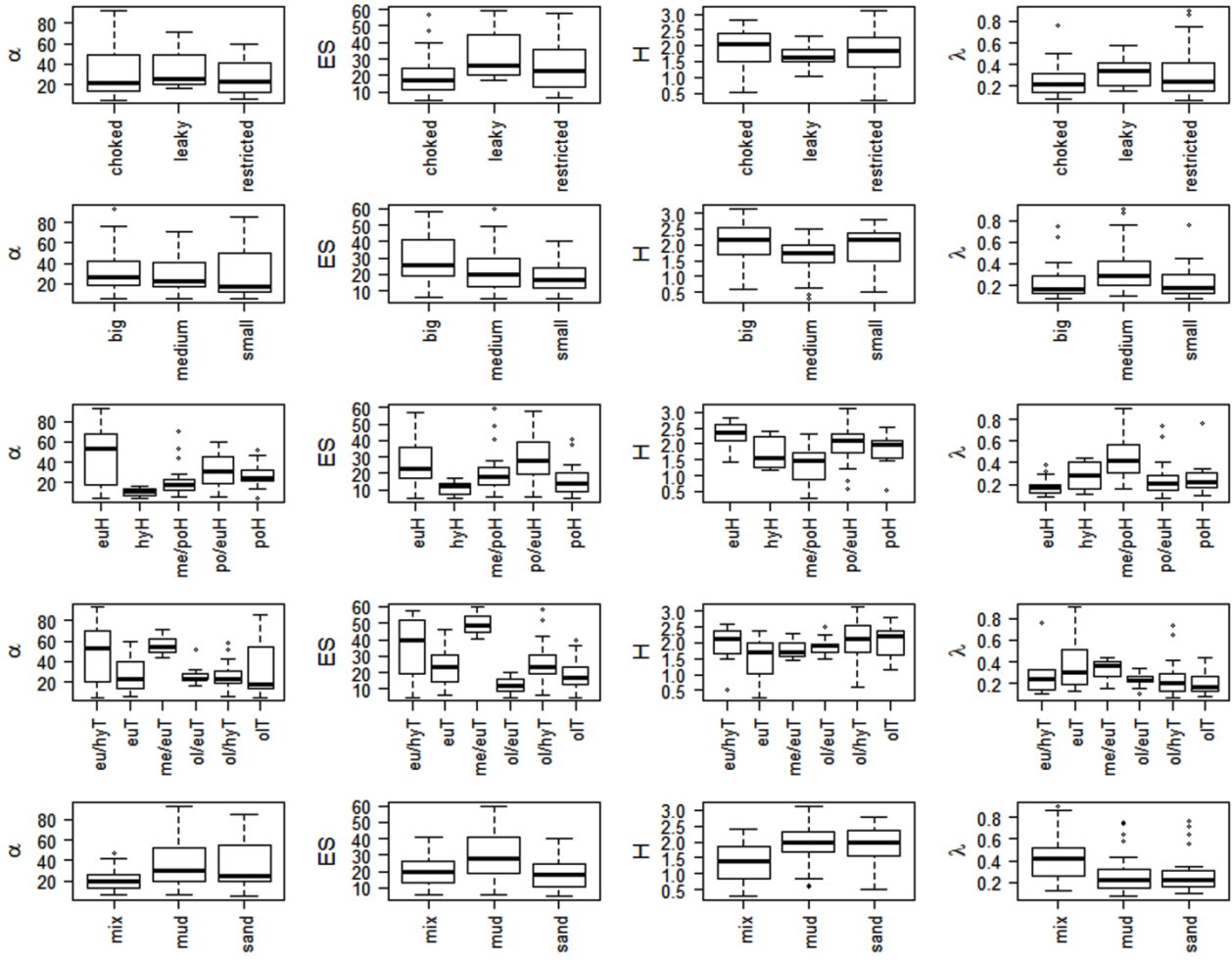


Fig.3

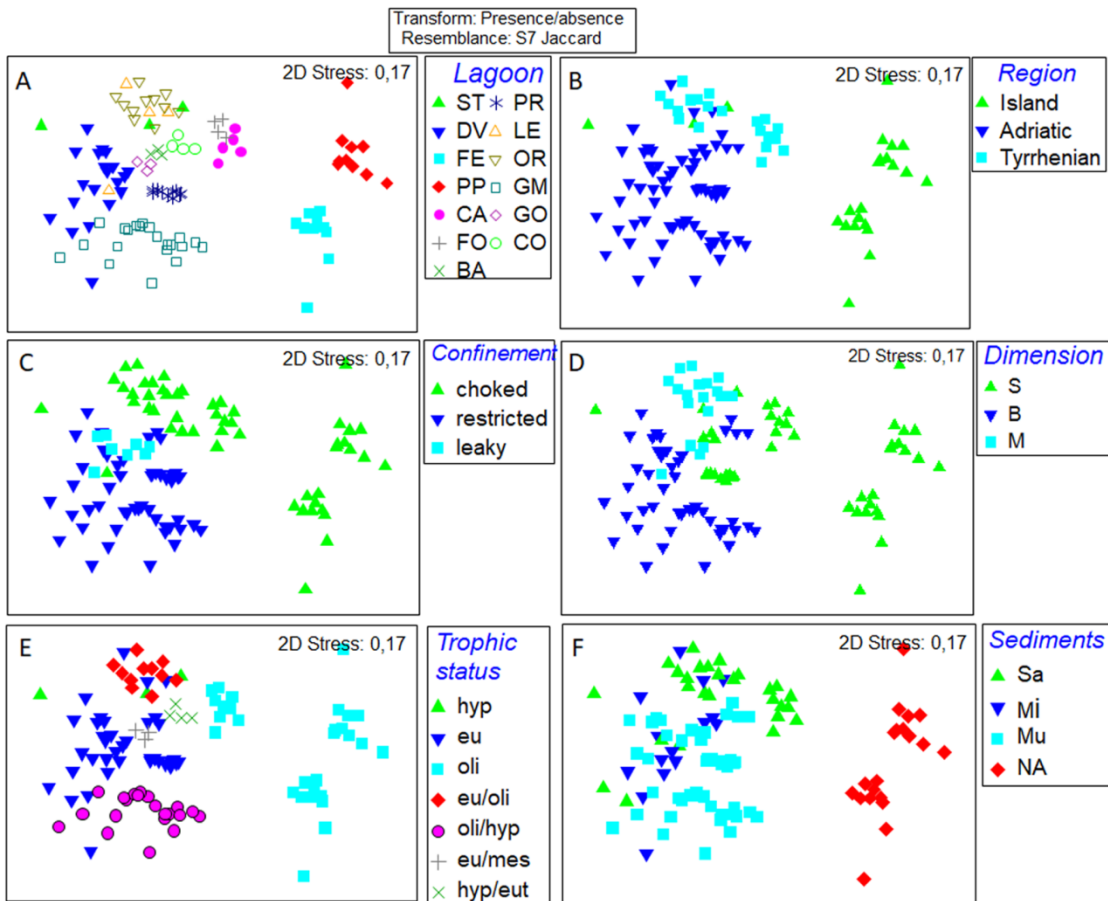


Fig.4