

Analysis of 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 variations 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) a direct relationship between alpha and gamma diversity, and a negative relationship between beta and alpha/gamma diversity were observed, indicating how alpha diversity was influenced by the regional species pool, with the exception of 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 of dispersion 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, such as size and confinement, in a framework of geographical variability.

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 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). 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, non-tidal to microtidal lagoons, different dimensions (from 0.4 to 160 km²) 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), and lagoon dimension.

Materials and methods

The analysed dataset was gathered during several sampling 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). This dataset comprise different typology of transitional waters, from large to small, from microtidal to non-tidal, hyperhaline to mesohaline ecosystems (see **Errore. L'origine riferimento non è stata trovata.**). 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). 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. Comparable environmental data for all the lagoons studied were not available, therefore, the environmental information were categorized (**Errore. L'origine riferimento non è stata trovata.**). Samples were sieved on a 0.5 mm mesh-size sieve and retained benthic fauna was identified to species level whenever possible. Species abundance data were averaged for each sampling occasion and average density values per m² was calculated.

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). 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 graphs 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 resemblance 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 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 between typology (microtidal vs non tidal), size (small $\leq 5 \text{ km}^2$, $5 \text{ km}^2 < \text{medium} < 100 \text{ km}^2$, big $\geq 100 \text{ km}^2$), and the two factors combined. A crossed design with two random factors (typology, size), nested in the factor “region”, with “Permutation of residuals under a reduced model” was performed to test whether community respond to typology, and size within geographical factors. Tests for homogeneity of dispersion (PERMDISP) were performed among lagoons of different typology, different sizes, and with the two factors combined. 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 (RDevelopmentCoreTeam, 2008). A value of $p < 0.05$ was chosen as significant threshold.

Results

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 ($\alpha = 11 \pm 4 \text{ SD}$), whereas the highest were observed at CO ($\alpha = 72 \pm 17 \text{ SD}$), CA ($\alpha = 68 \pm 14 \text{ SD}$), FO ($\alpha = 61 \pm 10 \text{ SD}$) and GO ($\alpha = 56 \pm 14 \text{ SD}$) (Fig. 1). 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 (Fig. 1). 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 ($\beta_w = 4.5$; $d_j = 51 \pm 2 \text{ SE}$) and DV ($\beta_w = 4.2$; $d_j = 49 \pm 3 \text{ SE}$); the lowest at BA ($\beta_w = 1.4$; $d_j = 23 \pm 3 \text{ SE}$).

At the intermediate scale (among lagoons) there was a direct relationship between alpha and gamma diversity ($p_s = 0.883$; $p\text{-value} < 0.05$). 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) (Fig. 1). Conversely there was a negative relationship between alpha and beta diversity (β_W : $p_s = -0.642$; $p\text{-value} < 0.05$; d_j : $p_s = -0.695$; $p\text{-value} < 0.05$), 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 (Fig. 1).

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 (Fig. 2), 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 though 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 and ST, but lowest at FO (Table 4).

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 (KW, $p > 0.05$), nor among lagoons with different dimensions (KW, $p > 0.05$), but significant differences were found when typology and size of the lagoons were considered together (KW, $p < 0.05$). In particular big non-tidal lagoons showed higher alpha diversity than microtidal big and medium, and non-tidal medium lagoons. Estimated species richness showed a pattern similar to alpha diversity, but with significant differences also among microtidal and non-tidal lagoons (higher values for microtidal), lagoon with different dimensions (higher values for big lagoons), and the two factors combined (KW, $p < 0.05$). Shannon and Simpson indices differed significantly with lagoon dimension (KW, $p < 0.05$), in particular small and big size lagoons

showed higher diversity and lower dominance compared to medium ones ($W, p < 0.05$). 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. Combining the factors “dimension” and “typology” together (Fig. 3), we observed significant differences in both Shannon and Simpson indices (KW, $p < 0.05$). In particular non tidal small lagoons showed lower dominance and higher Shannon diversity compared to medium microtidal lagoon ($W, p < 0.05$).

MDS ordination plot based on Jaccard measure (d_j) showed differences among lagoons (Fig. 4A), 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 (Fig. 4C). Superimposed to this geographical gradient a distinction between microtidal and non-tidal lagoon (Fig. 4B), and small, medium and big lagoons (Fig. 4) could also be observed. Results of PERMANOVA confirmed the combined role of type and size of the lagoon (PERMANOVA, $p < 0.05$), showing significant differences between microtidal and non-tidal lagoon for medium and large-size Adriatic lagoons. The same result was obtained considering the general community structure (Modified Gower), whereas considering abundance component only (Manhattan) no significant differences were found (PERMANOVA, $p > 0.05$). Considering the dispersion component of variation, significant differences of beta diversity (Jaccard measure d_j) and of the more general community structure (Modified Gower measure d_{MG10}) were observed only when the two factors, typology and size, were combined (PERMDISP, $p < 0.05$) and only for Adriatic lagoons. No significant differences (PERMDISP, $p > 0.05$) were observed considering the dispersion of the abundance component only (Manhattan measure d_{Manx}).

Discussion

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 species richness 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. 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. GM was known to be characterised by a variety of hydrological conditions, leading 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, related with salinity, freshwater input, and confinement degree (Bettoso et al., 2010).

Comparison among different methods

In general alpha diversity increased with increasing expected species richness (ES), and Shannon diversity (H), and with decreasing dominance (λ). The different patterns of variability of alpha diversity among the three different scales (site, lagoon and region) were in general maintained using measures that consider also relative abundances. Diversity measured with ES, Shannon and Simpson indices varied significantly at level of lagoons and regions, but not at the smallest scale (among sites), with the only exception of Simpson index 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.

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 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).

Influence of environmental factors

A geographical gradient with a separation of lagoons between island/continental (with the exception of ST) and Tyrrhenian/Adriatic Sea was observed (MDS, Permanova). Such 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). In the present work the differences among lagoons in different geographic regions were observed only in terms of alpha diversity (position component) and not in terms of beta diversity (dispersion component). A reason could be the superimposed effect of other factors, such as the dimension and the typology of the lagoon.

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). The size of the lagoon could also affect both alpha and beta diversity in different ways. Considering 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). In the present work a different pattern was observed. The dimension of the lagoon was not directly related with alpha diversity, but with other parameters, such as expected species richness (ES), dominance (λ) and Shannon diversity (H), with higher dominance and lower diversity in medium size lagoons, pattern which was maintained also considering microtidal and non-tidal lagoon separately. 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 could be related with the size of the lagoon, but not necessarily. The highest beta diversity was observed at GM, the biggest microtidal lagoon of the present study, accounting also for the highest habitat heterogeneity, as discussed above. Conversely CO lagoon, the biggest non tidal lagoon of the present study, showed very low values of beta diversity, despite high alpha diversity, due to habitat homogeneity. The habitat homogeneity of the CO lagoon, was the consequence of different factors, among those the progressive reduction of the surface covered by seagrasses (Mistri et al., 2000; Munari et al., 2003; Pitacco et al., 2018). In general microtidal lagoons were expected to show higher values of beta diversity than non-tidal lagoons, but this was not observed in the present work probably because of the superimposed effect of other factors.

Both alpha and beta diversity were not directly related to the dimension or the typology of the lagoon alone, but they showed a differential response when the two factors were considered together. There was a differential distribution of lagoons typologies and dimensions among geographic regions. While non-tidal lagoons were present in each of the three analysed geographic regions, all microtidal lagoons were located in the Adriatic Sea. The biggest lagoons were located only in the Adriatic Sea and the smallest only in Tyrrhenian and island. This differential distribution, could explain why the response of beta diversity to dimension and typology of the lagoon was clearly detectable only at Adriatic level.

Given that each of the analysed factors alone was not sufficient to explain the observed pattern, 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, such as size and confinement in a framework of geographical variability. Our results are consistent with previous investigations highlighting the necessity to take into account the scaling of taxonomic richness with lagoon surface area in order to minimise the variability of taxonomic richness among transitional water types, which is a major reason for splitting transitional water ecosystems into ecosystem types, as required by the European Water Framework Directive - EU-WFD 60/2000 (Sabetta et al., 2007).

Conclusions

Among the scales considered in the present work the highest variability was observed at the intermediate scale (among lagoons), where macrobenthic assemblages showed 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. Our results confirmed that the use of beta diversity as variation could provide complementary information crucial to the understanding of spatial pattern of benthic assemblages at different scales.

Beta diversity measured as variability of dispersion with Jaccard resemble measure gave results consistent with those obtained with the original formulation. The introduction of Shannon diversity index and Simpson index of dominance, showed a different pattern of variability in terms of relative abundances compared with the pattern depicted by alpha diversity. Conversely, the introduction of measures for the partitioning of the heterogeneity of dispersion showed that the variability among

lagoons was mainly related to species richness (i.e. beta diversity), 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, both geographical (insularity and biogeography) and physical (size and typology of the lagoon). The same factors influenced indices based also on relative abundances (ES, H, λ), as well.

Our results showed how the usually neglected measures of beta diversity in terms of species composition, allow the identification of patterns of macrobenthic community that could be important for a conservation perspective, which would be unnoticed with other metrics. 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). In fact, homogenisation is considered an early warning of habitat loss, acting when the component of alpha diversity still increase (Hewitt et al., 2010).

Our results supported also the importance of introducing measures for partitioning the variability in two components: richness and relative abundances. The use of measures weighing these two components 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 are typical of population dynamics in transitional waters, but could create bias, in particular for comparison at geographic scale.

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Table 1. Characteristics of sampled lagoons and number of sampled sites.

Lagoon	Code	Coordinates	Area (km ²)	Average depth (m)	Typology	Salinity	Sites	References
Venice (Palude della Rosa)	PR	45°31'N; 12°30'E	5.5	0.3-0.8	microtidal	poly/ euhaline	9	Sabil et al., 1994
Grado-Marano	GM	45°42'N; 13°20'E	160	1.5	microtidal	meso/poly/ euhaline	21	Bettoso et al., 2010
Caleri	CL	45.09°N; 12.31°E	11.5	2	microtidal	meso/ polyhaline	4	Mistri et al., 2018
Marinetta	MA	45°04'N; 12P22'E	10	0.8	microtidal	meso/ polyhaline	4	Mistri et al., 2018
Vallona	VA	45°02'N; 12°23'E	11.5	2	microtidal	meso/ polyhaline	2	Mistri et al., 2018
Barbamarco	BR	45°00'N; 12°46'E	8	0.8	microtidal	meso/ polyhaline	2	Spillman et al., 2009
Canarin	CN	44°92'N; 12°49'E	10.0	0.8	microtidal	meso/ polyhaline	3	Bianchi and Morri, 1996
Scardovari	SC	44°86'N; 12°42'E	32	1.5-2	microtidal	meso/ polyhaline	5	Marchini et al., 2008
Goro	GO	44°82'N; 12°31'E	26	1.2-1.5	microtidal	meso/ polyhaline	3	Corbau et al., 2016
Comacchio	CO	44°61'N; 12°17'E	100	0.5-1.5	non-tidal	euhaline	4	Munari et al., 2005
Baiona	BA	44°50'N; 12°25'E	10	1	microtidal	polyhaline	3	Ponti et al., 2011
Lesina	LE	41°53'N; 15°26'E	50	0.8	non-tidal	meso/ polyhaline	4	Marchini et al., 2008
Orbetello	OR	42°26'N; 11°12'E	27	0.5-1	non-tidal	polyhaline	11	Lardicci et al., 1997
Caprolace	CA	41°20'N; 12°58'E	2.26	1.3	non-tidal	euhaline	5	Prato et al., 2009
Fogliano	FO	41°24'N; 12°54'E	4.08	0.9	non-tidal	euhaline	4	Prato et al., 2009
San Teodoro	ST	40°48'N; 09°40'E	2.2	0.7	non-tidal	polyhaline	3	Munari and Mistri, 2007
Feraxi	FE	39°20'N; 09°35'E	0.4	NA	non-tidal	euhaline	10	Sannio et al., 1997
Porto Pino	PP	38°58'N; 08°36'E	4.4	NA	non tidal	hyperhaline	10	Rossi and Cannas, 1984

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 Gower 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 Gower, and modified Manhattan (excluding double zeros).

		Jaccard		Modified Gower	
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

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). β_w =Whittaker original formulation; d_j = 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 of different typologies (MT = microtidal, NT = non tidal), dimensions (B = big, M=medium, S = small) and for the two factors combined (MTB = big microtidal, MTM = medium microtidal, NTB = big non tidal, NTM = medium non tidal, NTS = small non tidal).
- Fig. 4. Non-metric MDS plots on the basis of Jaccard resemblance measure, showing spatial pattern of analysed sites, with highlighted: lagoons (A), typology (B), geographic region (C) and size (C). For lagoon codes see Table 1. MT = microtidal, NT = non tidal, S = small, M = medium, B = big.

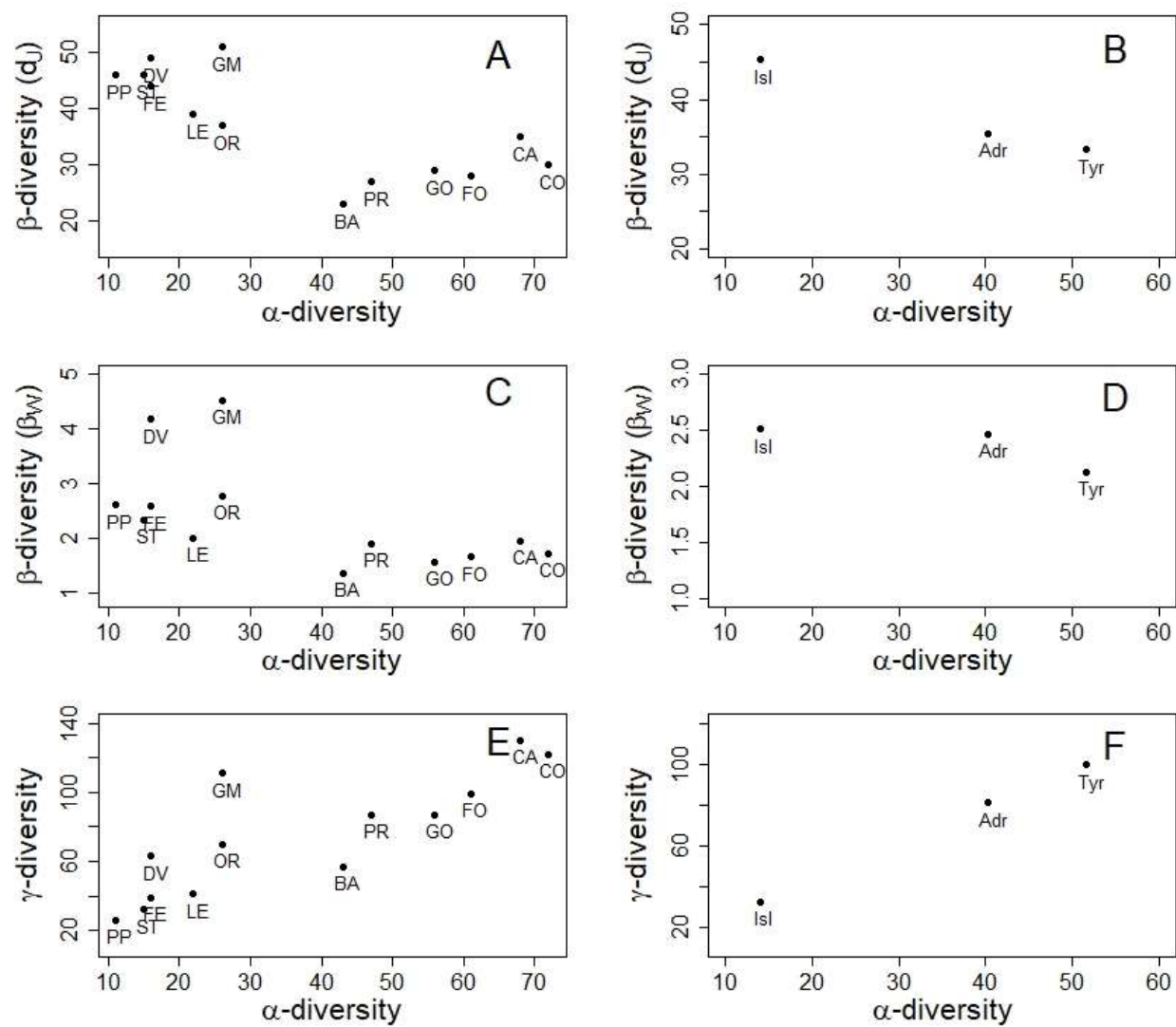


Fig.1

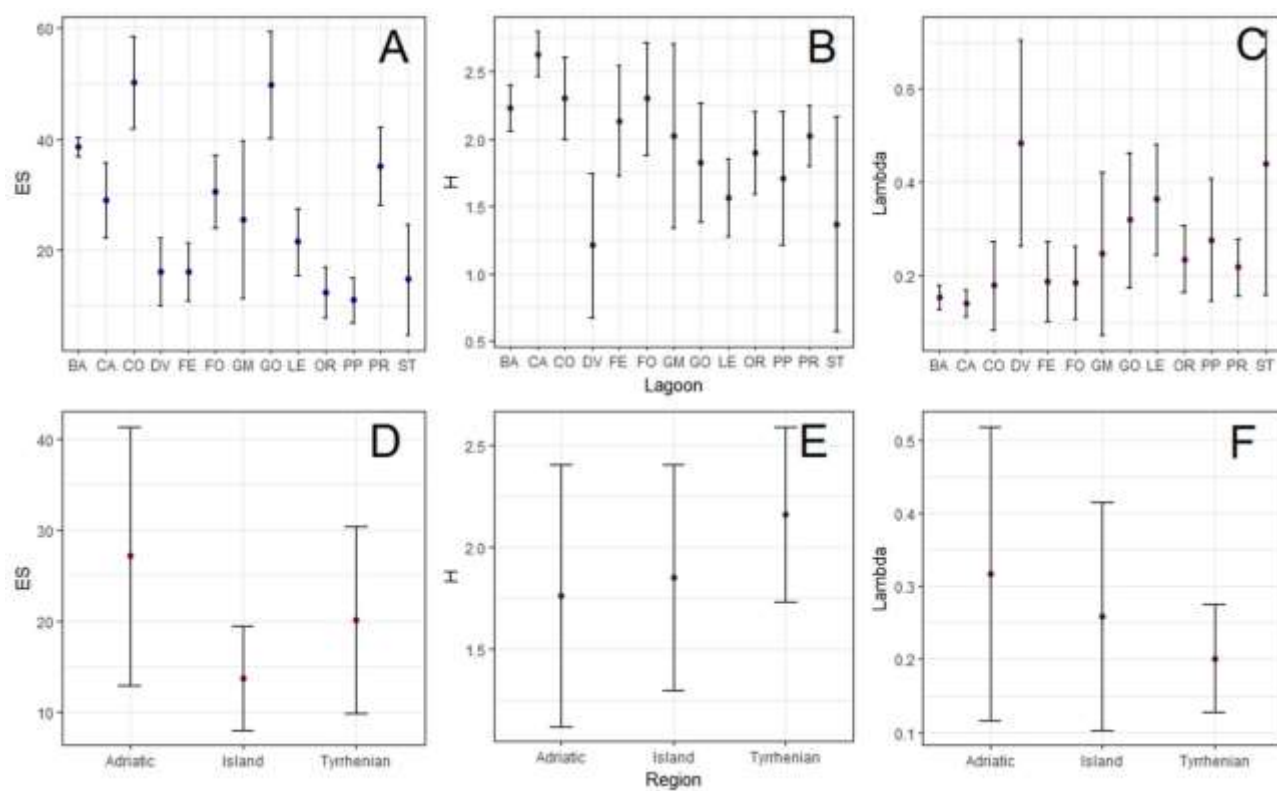


Fig.2

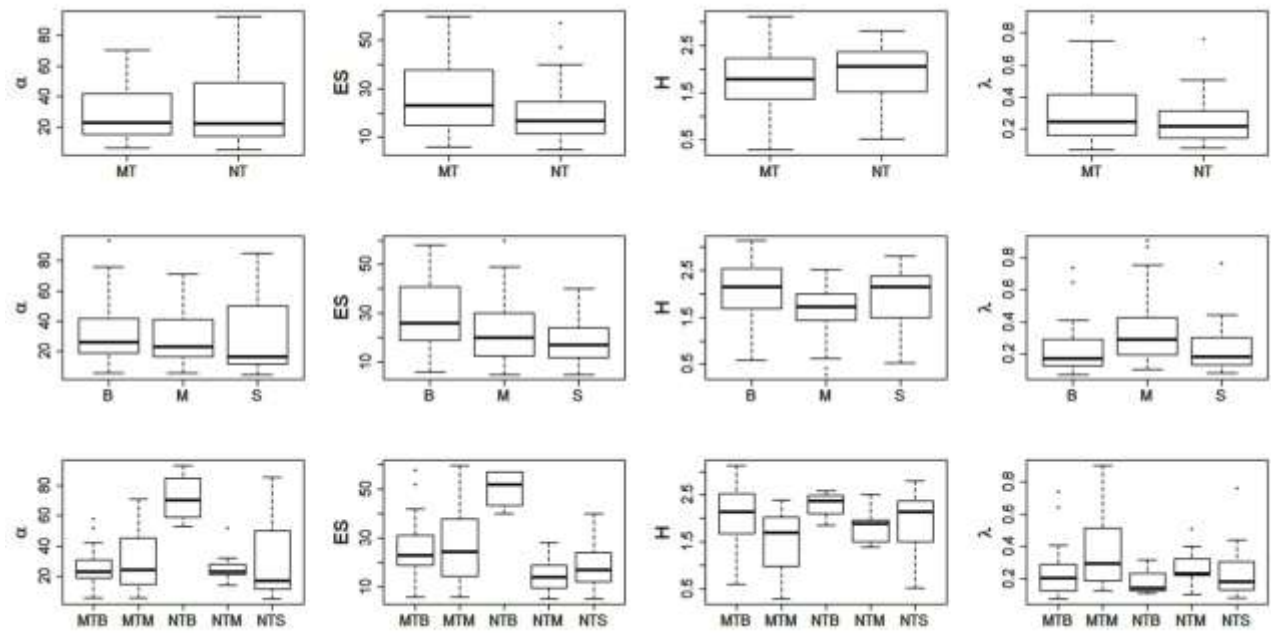


Fig.3

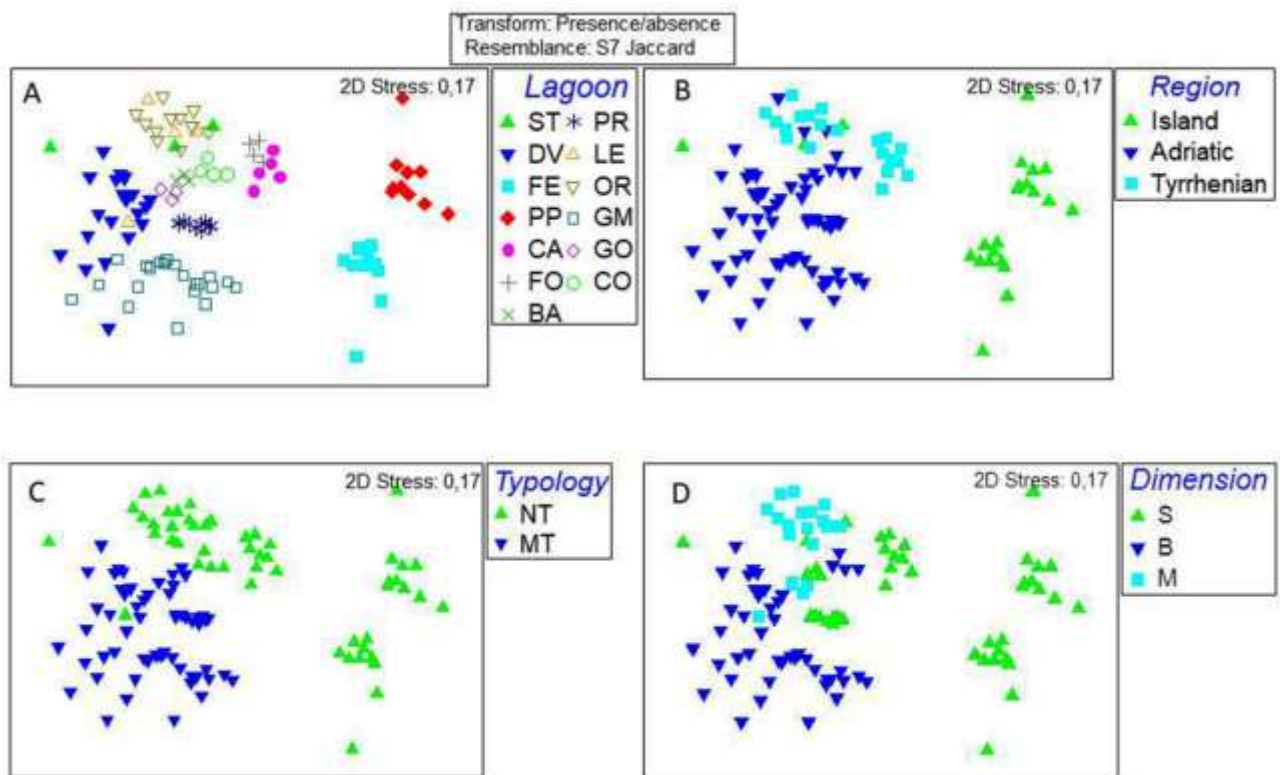


Fig.4