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RESEARCH ARTICLE

Spatio-temporal variability of macrozoobenthos size structure of a coastal lagoon: the influence of spectrum resolution

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Abstract

1 - The influence of spectrum resolution on the detection of spatio-temporal variability in macrozoobenthos size structure was investigated in a coastal lagoon located in southern Italy (Le Cesine, Puglia).

2 - In fall 2004 and spring 2005, the individual dry mass of benthic macroinvertebrates collected in box-corer samples was determined at six experimental sites. Individual data were allocated to size class scales with logarithmic bases ranging from ×1.2 to ×3.0 with a 0.1 increment; spectra with a decreasing degree of resolution were produced and tested for the effects of the two orthogonal factors “season” and “site”.

3 - Significant interaction effects between the two factors were observed independently from the scale used to produce the size spectrum. Subsequent post-hoc comparisons showed no predictable, scale-dependent patterns either in fall or in spring; nonetheless, in the two seasons the minimum and maximum number of significant inter-site post-hoc comparisons were respectively observed for an octave class (×2) spectrum.

4 - Our results indicate that evaluating the influence of scale-dependent effects on size spectra might be helpful for increasing the consistency of size-related approaches to the analysis and monitoring of macrozoobenthic assemblages.

Introduction

In coastal habitats, the linkage between the structure of macrozoobenthic communities and environmental constraints has been generally investigated assuming a taxon-based perspective; *i.e.*, expecting species (or higher groups aggregated by taxonomic or functional criteria) to vary in terms of occurrence and abundance in response to spatio-temporal changes of abiotic parameters (see, among others, Rosenberg, 1995, Mancinelli *et al*, 1998, 2002 and literature cited for specific examples; Ricciardi and Bourget, 1999 for a global-scale analysis; Pearson and Rosenberg, 1978; Snelgrove and Butman, 1994 for reviews).

In recent years, taxon-based approaches have been progressively questioned; a number of drawbacks - among others, the dependency of taxonomic resolution upon sampling effort - have been repeatedly emphasized (*e.g.*, Muillot *et al*, 2006). Moreover, the panoply of taxon-based indices that have been proposed to date (Pinto *et al*, 2008 for a recent review) and the non-univocal agreement on their appropriate use (see for example Borja *et al*, 2003, 2004 and Simboura, 2004 on BENTIX and AMBI indices) implicitly testify the lack of a sound conceptual framework univocally supporting taxon-based approaches.

Taxon-free, size-based approaches have been proposed for the analysis of aquatic macrozoobenthic communities, alternative or complementary to taxonomic analysis (Rasmussen, 1993; Muillot *et al*, 2006 and literature cited; Lampadariou *et al*, 2008). Their conceptual bases are well rooted in ecological theory, since organisms are expected to perceive and exploit the surrounding habitat (*e.g.*, in terms of spatial architecture or resource availability) in relation to their size, thus interacting with it - and in it - as functionally different ecological species (*sensu* Polis, 1984; Werner and Gilliam, 1984). Additionally, the apparent, deep connections with community-scale energetics (*e.g.*, Damuth, 1981) and, in general, with metabolic topics, as synthesized in the Metabolic Theory of Ecology (West et. al., 1997) foster the strong interest that size-based, taxon-free approaches is currently raising (*e.g.*, see Harris *et al*, 2006 for coastal habitats).

The size spectrum represents the basic operative tool of any size-based approach. Noticeably, besides the conventional distinction among micro, meio- and macrofauna, no general theory is to date available motivating the choice of the number and width of size classes (see Han and Straskraba, 1998, 1999, 2001). The only exception seems the octave (×2) class scaling, originally proposed by Hutchinson (1959) for mass-based niche partitioning. Blanco *et al*, (1994) and Vidondo *et al*, (1997) scrutinized in detail the use of the octave scale in benthic studies; yet, scant efforts have been made to assess whether alternative approaches to the construction of the biomass spectrum may provide novel, useful information on the size structure of the assemblage under analysis.

The present study was carried out to assess whether the scale unit used to build a size spectrum affects the detection of spatial-temporal multivariate variability in macrozoobenthos size structure. To this end, size spectra varying in resolution were produced from individual dry mass data relative to the macrozoobenthos collected at six sampling sites within a coastal lagoon located in southern Italy; univariate measures of central tendency and dispersion (*e.g.*, modality, percentiles, skewness, kurtosis) and in multivariate characteristics of whole spectra were analysed in order to highlight scale-dependent variation patterns.

Materials and Methods

The study was carried out in Le Cesine Lagoon, a coastal basin located in Puglia (SE Italy; 40°21’05”N, 18°23’05”E; Fig 1),. The lagoon is a system of several interconnected water bodies (0.9 Km^2 total area); the largest of them - the Pantano Grande basin - is 2.12 km long, with an approximate surface area of 0.68 km^2 and a mean depth of 0.80 m. The whole area is included since 1980 in a natural reserve protected by WWF.

Direct water exchange with the Adriatic Sea is prevented by a continuous sand dune; yet, due to the narrowness of the dune itself (< 10 m in some sections) the seawater front diffuse towards the lagoon throughout the year, while occasional dune breaks and direct seawater ingression occur in fall and winter due to storm episodes. Beside meteoric inputs, freshwater is provided by several ephemeral drainage ditches and underwater springs along the landward coast. The interaction of these marine and freshwater inputs together with strong summer evaporation and reduction in freshwater inputs determines strong seasonal fluctuations in lagoon water salinity: to a mean annual value of 10 - 15 PSU correspond values of 5 - 7 PSU in winter - spring and 28 - 30 PSU during storm events and at summer droughts (Menéndez *et al*, 2003; Sangiorgio *et al* 2008).

The riparian vegetation of the lagoon is dominated by the reed *Phragmites australis* (Cav.) Trin. *ex* Steudel, although spiny rush

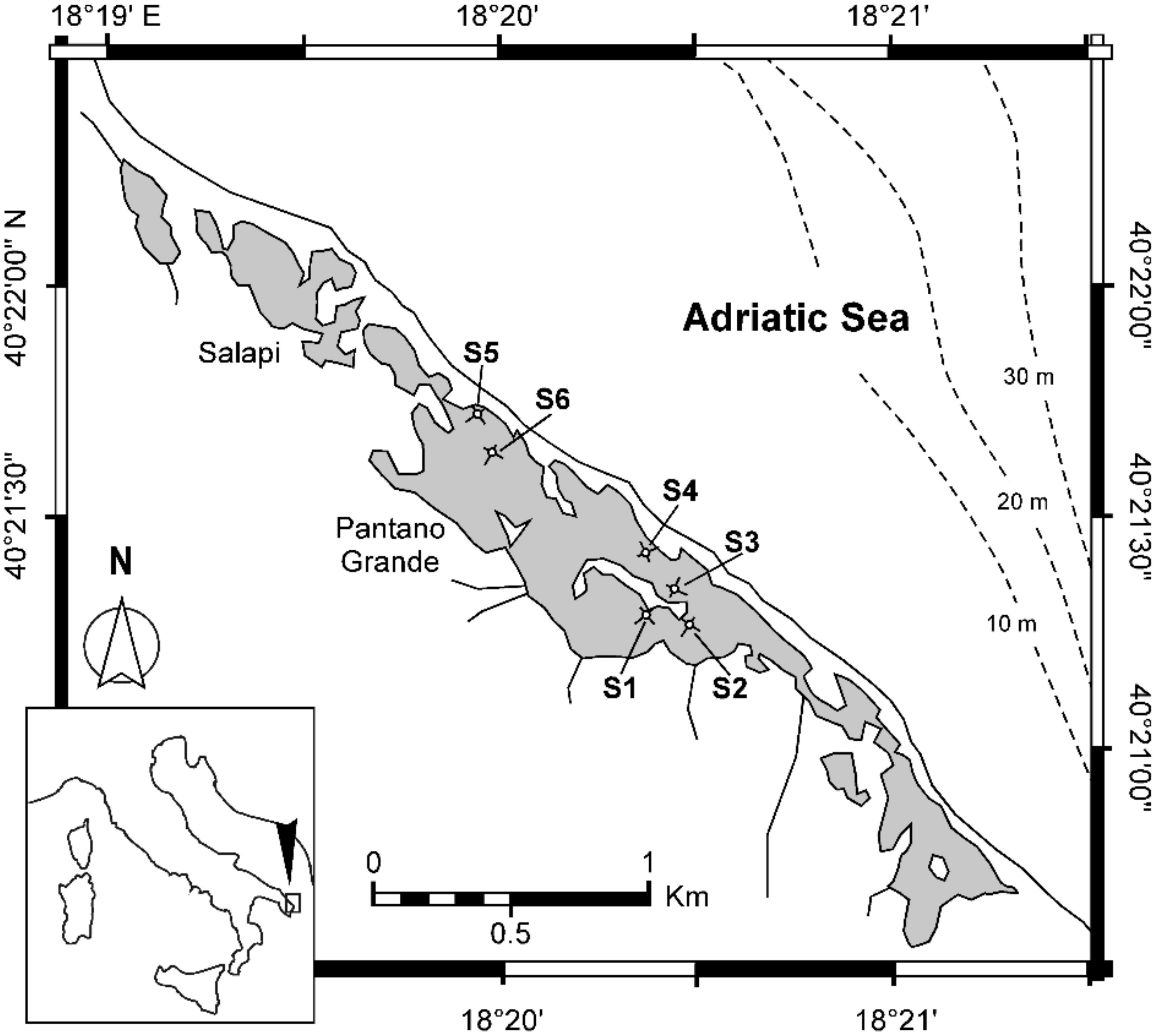

Figure 1. Le Cesine Lagoon; sampling sites are indicated.

[*Juncus acutus* (L.)], brown-headed club-rush [*Holoschoenus australis* (L.)], and black bog-rush [*Schoenus nigricans* (L.)] can be locally abundant. *Ruppia cirrhosa* (L.) is widely distributed in the lagoon and dominates the submerged vegetation.

In late spring 2004 a pilot survey of the Pantano Grande benthic habitats was carried out by boat. Six stations (S1 to S6 in Fig. 1) were identified for further sampling activities. The choice was done order to maximize among-station differences in emerged and submerged vegetation occurrence, sediment type and organic content (Tab. 1).

In September 2004 five sediment cores were randomly taken from each sampling site to a depth of 10 cm with a hand-held Reineck box-corer (289 cm^2 sampling area). In the laboratory, core samples were wet-sieved (0.5 mm mesh size); macroinvertebrates retained by the sieve were separated from inorganic particles, identified to the lowest taxonomic level according to the available literature, enumerated, and dried (60°C for at least 72h). An identical sampling procedure was replicated in April 2005. On both sampling occasions, dried specimens were individually weighed to the nearest 0.001 mg.

Individual dry mass data were allocated to a series of 19 size frequency distributions

Table 1. Depth, vegetation type (E = emerged; S = submerged; + = dominant) sediment granulometry (expressed as % sediment dry mass in the < 0.0063 mm size class, corresponding to clays) and organic matter content (expressed as % loss on ignition at 450°C for 6 h) determined at the six sampling sites in Le Cesine Lagoon during the pilot study. Data are means ± 1 SE (*n* = 3).

Site	Depth (cm)	Vegetation type	Sediment[a] (% Clay)	Organic content[b] (%)
S1	120	E+	6.52 (0.35)	36.49 (1.17)
S2	110	E+	9.34 (0.42)	43.71 (2.24)
S3	150	E / S+	4.45 (0.31)	11.08 (1.07)
S4	140	S+	3.61 (0.34)	5.46 (1.18)
S5	60	S	3.00 (0.71)	3.07 (0.60)
S6	50	S+	2.11 (0.07)	2.15 (0.04)

[a] 1-way ANOVA on arc-sin transformed data: $F_{5,12} = 28.78$, $P < 0.0001$; further pairwise comparisons confirmed significant differences with the exception of the comparison S5 vs. S4 and S5 vs. S6 ($P < 0.05$ for both comparisons);

[b] 1-way ANOVA on arc-sin transformed data: $F_{5,12} = 102.31$, $P < 0.0001$; further pairwise comparisons confirmed significant differences with the exception of the comparison S5 vs. S4 and S5 vs. S6 ($P < 0.05$ for both comparisons).

with logarithmic bases ranging from ×1.2 to ×3.0 with a 0.1 increment to produce an array of mass spectra characterised by a different number of bins, varying in size. Standard descriptive parameters (*i.e.*, mean, median, mode, maximum and minimum, 10th and 90th percentiles) were eventually calculated on the size frequency distributions characterizing each spectrum.

A distance-based permutational multivariate ANOVA (Anderson, 2001) was used for multivariate analysis of the macrozoobenthos size structure in relation to spatial and seasonal sources of variability. In particular, the general model consisted of the two orthogonal factors Season [(Se), two levels, fixed] and Site [(St), two levels, fixed] with five replicates. Multivariate analyses were performed using the FORTRAN program PERMANOVA (Anderson 2001).

Beside the main result of the test, which was always significant for both the factor "Site" and "Season" (see results) further analyses were carried out on bivariate comparisons; in particular, the number of non-significant bivariate comparisons were calculated for the factor "Site" in both seasons, and plotted against the scale base used to build the mass spectra. We followed this procedure to investigate the effects of variations in the scale base on the detection of inter-site differences. To assess the occurrence of thresholds or breaks in the observed patterns, the piecewise linear model with a single breakpoint c:

$$y_1 = a_1 + b_1 * x \text{ for } x \leq c \text{ and}$$
$$y_2 = a_1 + c*(b_1 - b_2) + b_2 * x \text{ for } x > c,$$

was fitted by least squares using a Levenberg-Marquardt estimation method.

Results

In total, 3288 individuals belonging to 13 macrofaunal taxa were found in core samples (Tab. 2). In fall, the macroinvertebrate assemblage (761 individuals in total) was numerically dominated by *Chironomus plumosus*, followed by the polychaetes *Nereis diversicolor* and the amphipod *Gammarus*

Table 2. List of macroinvertebrate taxa collected at the six sampling sites in fall and spring. Relative abundance is expressed as the percentage of the total number and total dry mass of macroinvertebrates sampled at each sampling occasion, respectively.

Taxon	Abundance (%)			
	fall		Spring	
	Numerical	Mass	Numerical	Mass
Mollusca				
Cerastoderma glaucum (Poiret)	5.26	68.50	0.36	8.24
Hydrobia ventrosa (Montagu)	---	---	1.62	4.46
Annelida				
Nereis diversicolor (Müller)	16.43	13.53	2.69	28.84
Ficopomatus enigmaticus (Fauvel)	5.52	0.64	13.42	9.69
Crustacea				
Gammarus aequicauda (Martynov)	6.70	2.80	15.95	8.56
Lekanesphaera hookeri (Leach)	1.97	2.19	2.53	9.22
Insecta				
Psychomyidae (larval stage)	---	---	0.24	0.29
Stratiomyidae (larval stage)	2.63	1.25	---	---
Tabanidae (larval stage)	0.26	1.28	---	---
Chironomidae - Tanypodinae undet.	---	---	0.36	0.13
Chironomidae undet. (Pupal stage)	---	---	0.51	0.56
Chironomus plumosus (L.)	61.24	9.81	62.29	30.01
Chironomidae – Diamesinae undet.[a]	---	---	0.04	---

[a] single specimen

aequicauda. On the other hand, The infaunal bivalve *Cerastoderma glaucum* contributed more than 68% to total dry mass, followed by *N. diversicolor* and *C. plumosus*. In spring, the total macroinvertebrate abundance was higher - 2527 sampled specimens - with *C. plumosus* representing the most abundant taxon, followed by *G. aequicauda* and the tubicolous sabellidae *Ficopomatus enigmaticus*. In contrast to fall, dry mass was more homogeneously distributed among *C. plumosus*, *N. diversicolor*, *C. glaucum* and *G. aequicauda*, with *C. plumosus* and *N. diversicolor* contributing for approx. 30% and 29% to total dry mass, respectively.

In both seasons, the whole assemblage spanned in individual mass more than five orders of magnitude; in particular, in spring, dry masses ranged from 0.01 to 49.36 mg (49.35 mg min-max absolute difference), with a median value of 0.21 mg and an average value of 0.55 ± 0.04 mg. In Fall, individual mass variation resulted slightly lower compared to Spring, ranging from 0.01 to 44.14 mg (44.13 mg absolute difference, with 0.30 mg and 1.15 ± 0.13 as a median and mean value, respectively. At a species-specific scale, all taxa were characterized by a high variation in size that reflected on a high degree of overlap, hence contributing significantly to the size distribution of the whole assemblage (Fig. 2).

In figure 3 the effect of changing the resolution of the size spectrum is shown. In general,

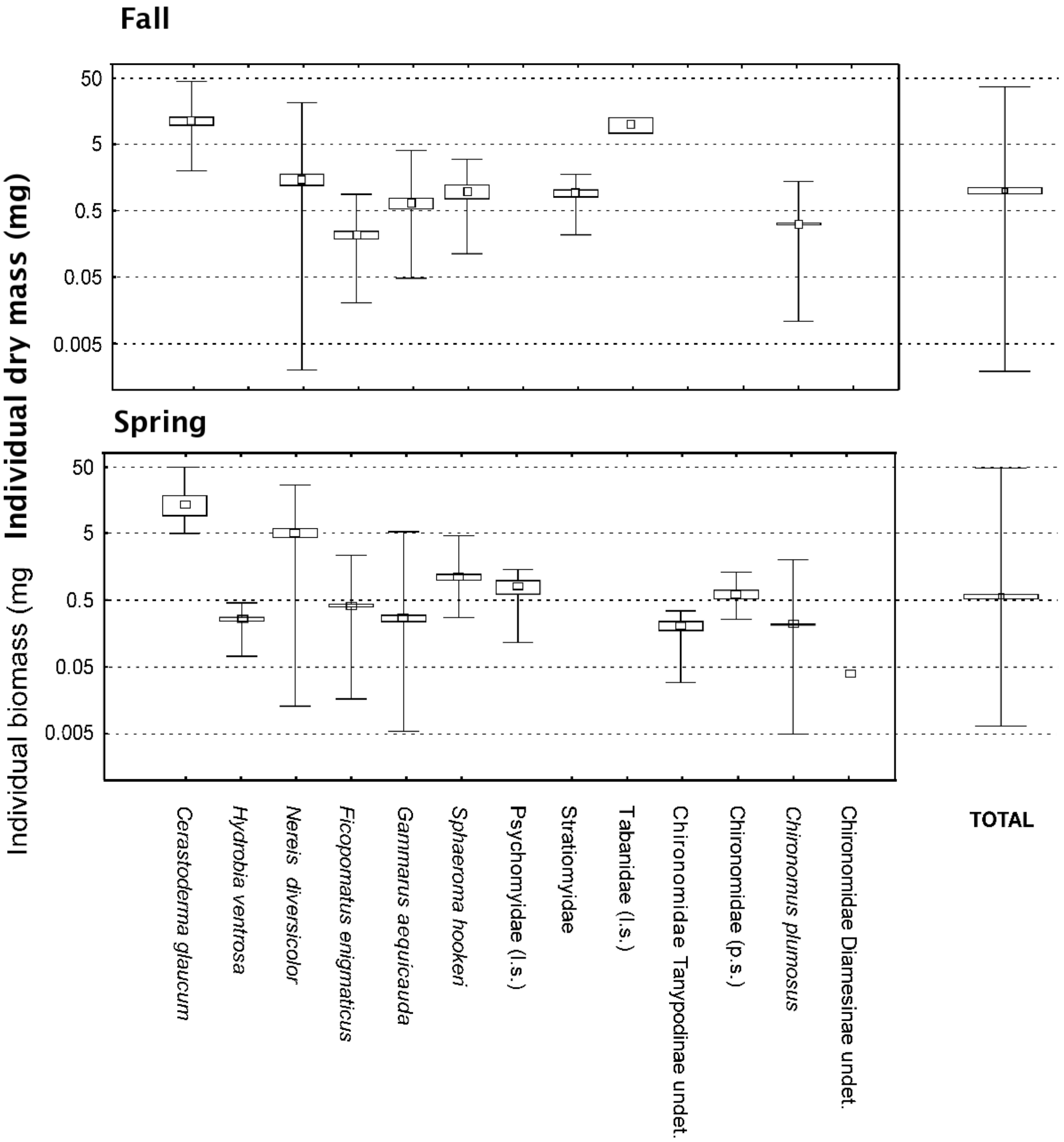

Figure 2. Mass of dominant macroinvertebrate taxa sampled in fall and spring; square = mean, box = ± 1 SE, whisker = minimum, maximum value. Cumulative values are also reported.

changes in the class scale used to allocate individual mass data corresponded to strong variations in central tendency and dispersion measures of size spectra. Passing from a ×1.2 to a ×3.0 basis, skewness and kurtosis decreased considerably, levelling at the ×2.0 class scale (Fig. 4a) while the median, the 10% and 90% percentiles increased steadily (Fig. 4b). In addition, the modes decreased from a maximum of 4 for a ×1.2 class scale to 2 for a ×1.5 scale to unimodality for increments > ×1.5 - ×2.0 (Fig. 4b).

Significant interaction effects between the main factors were observed independently from the scale used to produce size spectra (PERMANOVA, *P* always < 0.05 for the

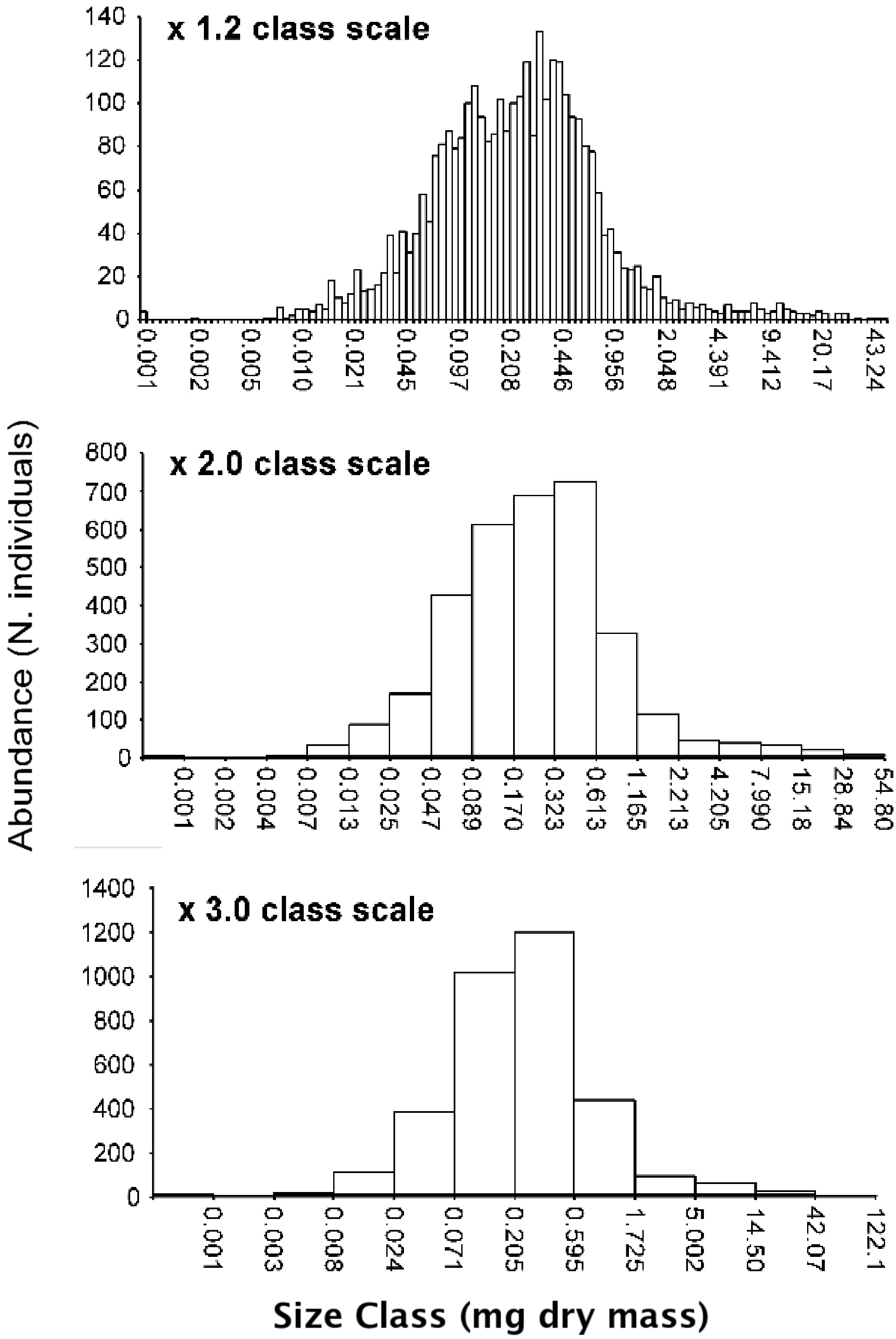

Figure 3. Size spectra of individual dry mass cumulated over the two seasons. Three examples are reported for three (i.e., ×1.2, ×2, and ×3) class bases. Note the variation in the number of modes.

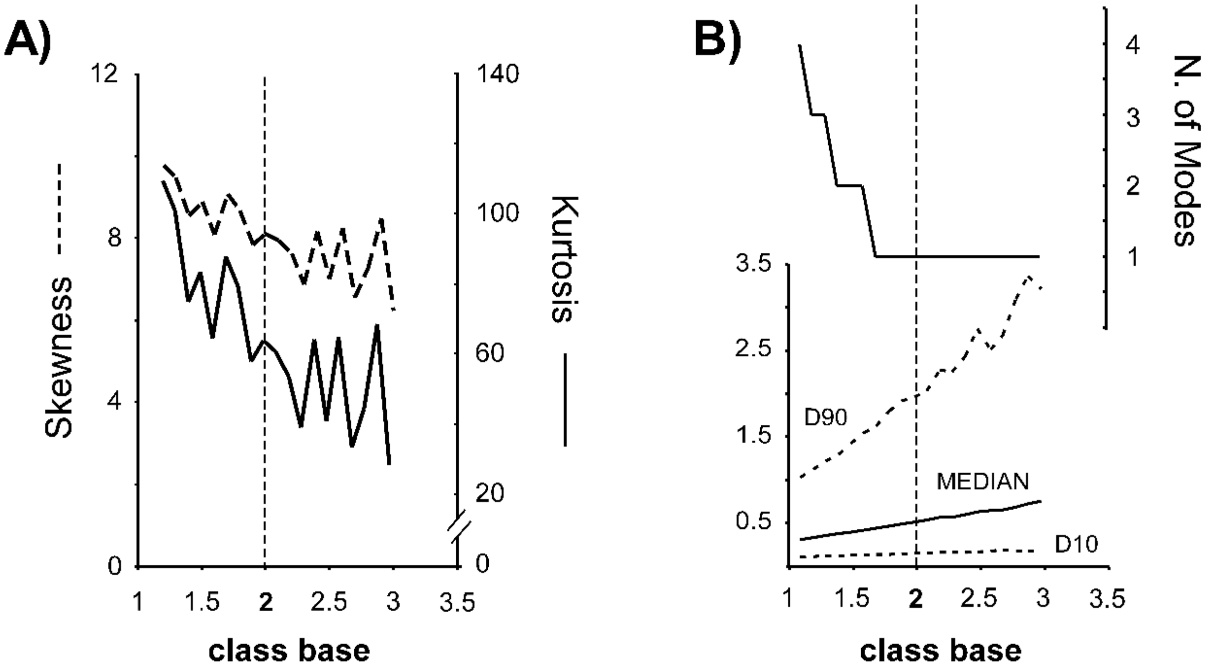

Figure 4. A): variation in skewness and kurtosis of the size frequency distributions in relation to changes in the class bases; B): changes in the number of modes, and in the values of the median, 10th and 90th percentiles.

(Si)×(St) interaction effect). Subsequent post-hoc comparisons showed no general scale-dependent patterns either in fall or in spring, as the number of non-significant inter-site comparisons showed opposite patterns in relation to class scale variations (Fig. 5a). Yet, in both seasons the minimum and maximum number of non-significant comparisons were observed for a size spectrum based on an octave (×2) increment basis. In both case, stepwise regression analysis indicate the occurrence of a significant breakpoint at a scale base of 2 (fall: 1.93 ± 0.16; spring: 2.09 ± 0.11). On the other hand, no clear patterns were observed for site-specific inter-season comparisons (Fig. 5b).

Discussion

Our study indicates that the detection of site- or season-specific multivariate effects on size spectra is strongly dependent upon the resolution of the spectrum itself. In other words, the arbitrary decision made by researchers concerning the number of size classes into which the macrozoobenthos should be parted is crucial, since size-related characteristics of the assemblage are not invariant, but totally dependent upon spectrum resolution.

In constructing a size spectrum, independently from the choice of an arithmetic (linear) or geometric (logarithmic) increment rule for the bin size, two contrasting phenomena necessarily follow from the choice of the number and size of bins. With a large number - and a corresponding small size - of bins, an increase in the noise of the abundance signal is determined: the number of individuals comprised in each bin decreases, and their occurrence in a bin or in the adjacent may be strongly affected by chance. On the other hand, reducing the number of bins and increasing their size, individuals quite far in size are grouped within the same bin. Thus, as bin size increases, specimens included in two contiguous bins might result less different in size than two others belonging to the same bin, but respectively located close

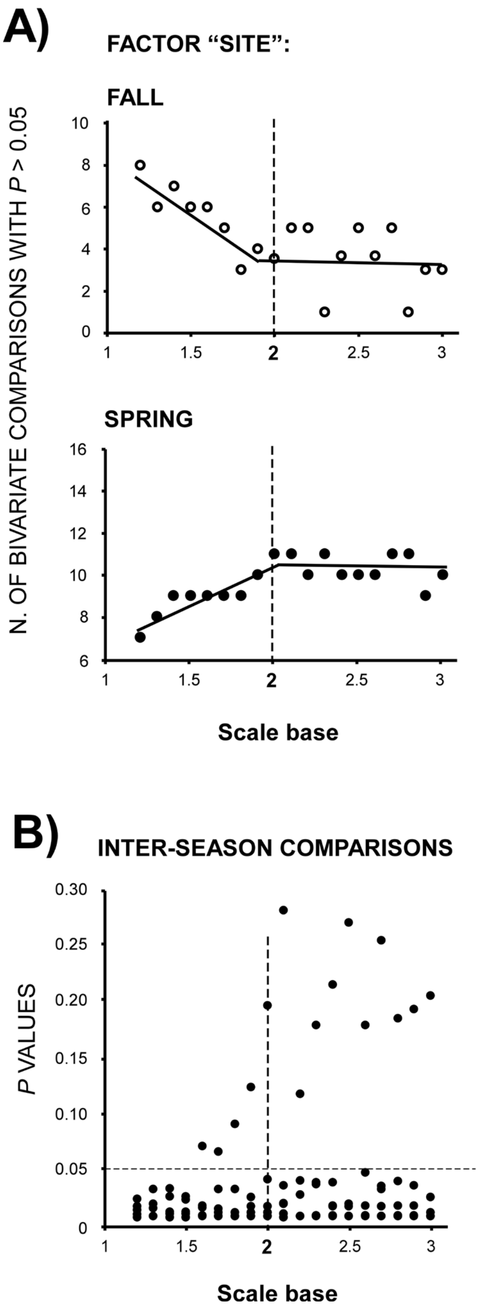

Figure 5. A): variation in the number of non-significant (P > 0.05) bivariate comparisons for the Factor "Site" in fall and spring in relation to changes in the class bases; data are fitted by a piecewise regression curve with one breakpoint; in both seasons, only regression lines for class bases < of the breakpoint were characterised by slopes significantly ≠ 0 (parallelism test, P always < 0.05); B) variation in P values for the Factor "Site×Season" in relation to changes in the class bases.

to the lower and upper limit of it. This bias might reach its maximal negative effect for size spectra built on geometric increments, regardless of the base of choice. Ultimately, such increase in within-bin dimensional heterogeneity may determine a false size structure of the community, and this effect is apparent in Fig. 3 and 4b. Increasing the bin size, the size distribution shifts from a condition of multi-modality to a strict mono-modality. In this perspective, the size structure originally present in the data is lost in response to an increase in bin size.

The possible artefact highlighted by our investigation might result particularly important when the shape of the size distribution is to be scrutinized, *i.e.*, the scope is to detect so-called "troughs" or "clumps" or "bumps" reflecting habitat- or biotic-induced discontinuities in the distribution of sizes within a species assemblage (*e.g.*, Holling, 1992; Warwick and Clarke, 1996; Manly 1996, Raffaelli *et al*, 2000). Our results indicate that, whereas strong discontinuities in a size distribution characterised by a huge size range might be preserved regardless of the size bin chosen to construct the size spectrum (see Schwinghamer, 1981, 1988 for classical examples on marine bacteria, meio- and macrofauna), an inappropriate choice of the bin size and number might induce considerable artefacts on size spectra encompassing a narrower size scale (Raffaelli *et al*, 2000).

Our results actually reflect the juxtaposition of this two counteracting effects on the structure of the size spectrum: at low bin size, in fall, small variations in the size of the bin itself obscure any site-specific variations in the spectrum structure, ultimately reflecting on a high number of non-significant pairwise comparisons. This effect reduces in intensity as bin size increases, levelling off at an octave (×2) bin size. Similarly, in spring the levelling off corresponds with the octave scale, yet the number of non-significant pairwise comparisons followed an opposite, decreasing pattern compared to fall. This discrepancy might be ascribed to season-specific differences in the size structure: in fall, at low size bins the noise in the abundance signal might have been overcome by site-specific effects, while in spring some kind of underlying, strong size structuring might have been revealed at low bin sizes (due to *e.g.*, the occurrence of juveniles in the smallest size classes) which is lost as the bin size increases.

In the present paper, to provide a mechanistic explanation regarding the effectiveness of the octave bin size in the construction of a size spectrum as suggested by the breakpoint observed both in spring and fall in the number of non-significant pairwise comparisons is beyond the actual scope of the present study. Anyway, beside straightforward, mathematical explanations - i.e., pure coincidence, or an effect due to the interplay of the size of the data base, the number of bins and their size (Blanco *et al*, 1994; Vidondo *et al*, 1997; Han and Straskraba, 1999, 2001), the hypothesis that the observed patterns might have been determined by some underlying ecological processes is appealing and finds its theoretical roots in the ×2 mass ratio, originally proposed by Hutchinson (1959) for mass-based niche partitioning of coexisting species. Further investigations, integrating taxon-based and size-based approaches to the analysis of macrobenthic communities together with information on the abiotic environment, will provide a more consistent and conclusive groundwork for discriminating among the causes of the observed patterns.

In conclusion, our study suggests that evaluating the influence of scale-dependent effects on the resolution of size spectra might be helpful for increasing the consistency of size-related approaches to the analysis and monitoring of macrobenthic communities.

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