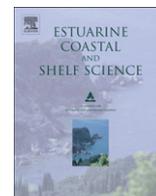




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Spatial patterns of biodiversity in the Black Sea: An assessment using benthic polychaetes

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ABSTRACT

The current study broadens the biodiversity information available for the Black Sea and neighbouring regions and improves our knowledge about the polychaete biogeographic patterns to be discerned in them. There appears to be a well-defined *zoogeocline* from the Marmara Sea and Bosphorus Strait to the inner parts of the region (Azov Sea), depicted both as a multivariate pattern and in terms of species (or taxa) numbers. The emergent multivariate pattern complies, to a certain extent, with Jakobova's (1935) views: three main sectors can be defined in the basin: (a) Prebosphoric, (b) the Black Sea and, (c) the Azov Sea, whereas the Bosphorus Strait and Marmara Sea show less faunal affinities with the aforementioned sectors. Patterns derived both from the cosmopolitan and Atlanto-Mediterranean species closely follow the one coming from the polychaete species and genera inventories. As a general trend, species numbers decrease along with the decrease in salinity towards the inner parts of the region. The trend is homologous to that seen in the benthic invertebrate inventories of all the major European semi-enclosed regional seas. Salinity and food availability appear to be the dominant abiotic factors correlated, though weakly, with the various patterns deriving from the taxonomic/zoogeographic categories. With the exception of the Anatolia, polychaete inventories from all sectors appear to be random samples of the total inventory of the region, in terms of taxonomic distinctness values. Therefore, these sectoral inventories can be used for future biodiversity/environmental impact assessment studies. A massive invasion of Mediterranean species after the opening of the Black Sea, in the lower Quaternary period, appears to be the likely biogeographic mechanism through which the old Sarmatic fauna was almost completely replaced by species of marine origin.

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1. Introduction

Biodiversity, the variety of life at all levels of biological organization and all scales of observation, is unevenly distributed on Earth. The study of the variations, or exceptions, in biodiversity patterns is proving to be a difficult task requiring a multi-disciplinary approach (e.g. Gray, 1997; Gaston, 2000). The formulation of

a single hierarchical (top–down) theory, encompassing even a single level of species diversity, its variations over space and time, and the associated environmental factors, is still a matter of contemporary research (Whittaker et al., 2001).

Biogeography, by integrating theory and practice both from ecology and taxonomy has been established as a particularly useful discipline for identifying patterns of biological diversity and potential mechanisms (e.g. vicariance vs. founder-dispersal) for their formulation on different scales and particularly on large geographical scales (Croizat, 1958; MacArthur and Wilson, 1967). Large-scale approaches are essential for managerial purposes: for example, many of the EU directives, such as the Water Framework Directive, the Common Fisheries Policy and the Habitats Directive

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are targeted at ecosystem or even larger spatial scales. This is because they also focus on the socio-economic dimension of the environmental policy and particularly on the uncertainties in ecosystem services provision.

Recent reviews highlight the pan-biogeography concept over the founder-dispersal one in the marine environment and try to interpret current taxa distributions as a function of historical (geological) processes, such as plate tectonics (Hedges, 2005). Latitude and salinity gradients are also included among the variables which have been proposed as dominant in shaping marine biodiversity patterns. Salinity gradients are well documented in enclosed or semi-enclosed brackish water bodies, in which they create systems of an economically important fauna (McLusky and Elliot, 2004; Arvanitidis et al., 2005). Such systems are represented by major European regional seas (e.g. the Baltic, Mediterranean, and Black Seas).

The Black Sea is considered to be a “*unicum hydrobiologicum*”, because of several characteristics that distinguish this sea (see Section 2.1). This regional basin has undergone major changes caused by anthropogenic activities arising from uncontrolled development: since the late 1960s, the Black Sea, especially its north-western part, has been subjected to severe anthropogenic eutrophication forced by increased delivery of nutrients by the Danube, Dnieper and Dniester rivers which resulted in critical levels of primary production (Mee, 1992; Zaitsev and Mamaev, 1997; Oguz, 2005). In the early 1970s as a result of eutrophication significant areas of summer hypoxia on the north-western shelf were observed and within five years these hypoxic areas had extended over most of the shelf, leading to the mass mortality of huge quantities of benthic organisms throughout the 1980s (Zaitsev, 1992). The macro-zoobenthos subsequently experienced loss of biodiversity and severe disturbance of the community structure and functioning (Gomoiu, 1992; Mee et al., 2005). Benthic community degradation has been further intensified by pollution, the impact of exotic invaders and unsustainable exploitation (Gomoiu, 1998, 1999, 2001; Mee et al., 2005). During the 1990s, due to the socio-economic recession in the riparian Black Sea countries and the introduction of several national and international programmes aimed at reducing eutrophication, a lowering of the nutrient input from rivers was observed, which gave the ecosystem an opportunity for recovery (Kideys, 2002; Mee et al., 2005). The recovery trend is however still not fully confirmed by the scientific results and many uncertainties need to be overcome in order to establish a sound and environmentally-benign management of the eutrophication in the future (Mee et al., 2005).

Polychaetes have traditionally been considered either as the dominant group, in terms of abundance or biomass values, or as an important contributor to the structure and functioning of the entire range of macrobenthos communities (Fauchald, 1977; Knox, 1977). For this reason the taxon has received considerable scientific attention in order to explore its potential for environmental quality monitoring studies in various habitats (e.g. Pocklington and Wells, 1992; Hutchings, 1998; Arvanitidis et al., 2005), as well as in zoogeographic studies (Musco and Giangrande, 2005; Arvanitidis et al., 2009). The species richness of the taxon as well as its dominance in the majority of the soft-bottom habitats may explain, up to a certain degree, the anticipated distribution of the biogeographic provinces and sectors along zoogeographical gradients: a considerably diverse taxon inherently has more possibilities to depict faunal responses to past geological changes which are potentially expressed through their contemporary inventories. Therefore, polychaetes may well contribute to a more natural representation of the biogeographic provinces and sectors than the entire benthic fauna. This has also been the case for the total European benthic fauna (Arvanitidis et al., 2009).

Although considerable scientific effort has been expended on the macro-zoobenthic communities in various parts of this fragile Black Sea environment, studies have focused almost exclusively on patterns deriving from species numbers (see extensive literature provided in the next section). Additionally, the scale of observation on which almost all of the previous studies focused was mainly local and only rarely sectoral. A few studies (e.g. Jakubova, 1935; Losovskaya, 1977; Kisseleva, 1981, 2004), however, included data from the entire basin. Others dealt with the biogeographic zonation of the Black Sea and adjacent brackish water bodies, again based on species numbers and composition, such as Jakubova (1935), Marinov (1964) and Băcescu et al. (1971). None of these studies has however tested, through the application of robust scientific techniques, the proposed biogeographic zonation, the environmental variables likely to affect these zonations and the utility of the inventories collated from the various sectors for biodiversity/ecosystem assessment and for management and conservation purposes.

The objectives, therefore, of this study are: (1) to search for biodiversity patterns along the Black Sea and its surrounding water bodies based on the polychaete inventories; (2) to examine how these patterns change as information on species distribution is aggregated to higher taxonomic and zoogeographic categories; and (3) to investigate the environmental variables associated with these patterns.

2. Methods

2.1. Study area

The Black Sea is a semi-enclosed basin connected to the Sea of Marmara and the Azov Sea by the narrow Bosphorus and Kerch Straits, respectively. Due to its semi-enclosed character, the Black Sea has almost no tidal action, with a maximum of 13 cm during spring tides (Arnoldi, 1948). Its catchment area of over 2 million km² (Zaitsev and Mamaev, 1997) is five times its own surface area (423 000 km²) covering large parts of Europe and Asia, and providing a total fresh water supply of 3×10^2 km³ per year (Stanev, 2005). Because of the large fresh water influx compared to the basin volume ($\sim 5.4 \times 10^5$ km³), the Black Sea has the hydrological and physiographical characteristics of a typical brackish water basin with a low salinity (17–18 on average). Unlike other large brackish water basins such as the Baltic Sea, the Black Sea basin is deep with a maximum depth of 2212 m (Zaitsev and Mamaev, 1997). The input of fresh waters in the upper layer and saline Mediterranean waters in the lower layer creates a distinct and permanent pycnocline between the surface waters (upper 150–200 m) and the deep waters, limiting the vertical exchange and creating a unique chemical and biological environment (Kononov et al., 2005). As much as 87% of the Black Sea is entirely anoxic and contains high levels of hydrogen sulphide (Zaitsev and Mamaev, 1997). Under undisturbed conditions, Black Sea faunal diversity is less than one third that of the Mediterranean Sea (Zaitsev et al., 2002). The abundance of individuals, total biomass and productivity of the Black Sea are however much higher than in the Mediterranean Sea (Alexandrov and Zaitsev, 1998).

Three major systems for the division of the Black Sea into biogeographic sectors have previously been proposed.

- (1) Firstly, the continental shelf of the Black Sea was divided by Jakubova (1935) into three bio-geographical sectors, based primarily on soft-bottom macrobenthos species:
 - (a) The *eastern sector*, which includes the continental shelf from Cape Khersones, along southern Crimea, the Caucasus and eastern Anatolia to Cape Bafra, characterised by

a narrow continental shelf (maximally 20 km wide) and by relatively stable salinity values due to reduced continental run-off. The benthic fauna of this sector is considered to be the most typical of the Black Sea.

- (b) The *south-western* or *Prebosphoric* sector, extending between western Anatolia and Burgas Bay and under the influence of bottom currents, which transport high-salinity (36–38) Mediterranean water masses through the Bosphorus Strait. The benthic fauna of the Prebosphoric sector appears to be dominated by stenohaline species. Half of the Mediterranean immigrants present in Prebosphoric region are not found in other parts of the Black Sea.
 - (c) The *north-western sector*, in which the extended continental shelf situated between Cape Kaliakra and the westernmost point of the Crimea Peninsula (Cape Tarkhankut) is included. This sector is characterised by low salinity (less than 15), high nutrient concentration and very low winter temperatures, caused by the increased run-offs from the large rivers such as the Danube, the Dniester, the Dnieper and Southern Bug. It is assumed that the species composition is most likely dominated by euryhaline, eurythermal and psychrophilic faunal elements. Although this sector has been considered as having the lowest species diversity of the three sectors, it is nevertheless associated with the highest productivity in the region.
- (2) Subsequently, [Marinov \(1964, 1968, 1977\)](#) proposed a different division of the Black Sea region into 7 smaller sectors: Bulgarian, Romanian, Odessa-Karkinitzky Bay (North-western Black Sea), Sevastopol (Western Crimea), Karadag (Southern Crimea), Anatolian and Prebosphoric. He also suggested that the Prebosphoric region should be restricted. Additionally, he considered the Azov Sea as a separate bio-geographical sector of the Black Sea.
 - (3) Finally, [Băcescu et al. \(1971\)](#) also restricted the Prebosphoric sector to a radius of 20 nautical miles around the mouth of Bosphorus and moved the southern limits of the north-western sector to Mangalia. They also distinguished a *western sector* comprising continental shelves off the Romanian coast to the south of Mangalia, the Bulgarian and the Rumelian (European Turkey) coasts to a distance of 20 nautical miles from the mouth of the Bosphorus.

The current study acknowledges eleven biogeographic sectors of the region, following suggestions made mainly by [Jakubova \(1935\)](#), [Vodyanitskii \(1949\)](#), [Marinov \(1977\)](#) and [Kisseleva \(2004\)](#): the Sea of Marmara, Bosphorus, Prebosphoric, Bulgaria, Romania, North-Western Black Sea, Sevastopol, Karadag, Azov Sea, Caucasus and Anatolia. Some of these areas represent, in geomorphological terms, individual sub-basins separated from each other by straits and sills (e.g. Marmara Sea, Bosphorus, and Azov Sea). Other areas are defined by the states' borders (Bulgaria, Romania) or by extensive "aquatoria" (water bodies) of the Black Sea. For the sector of Anatolia it was possible to find reliable data only in a single publication ([Çinar and Gönügür-Demirci, 2005](#)) so the southern part of the Black Sea is considerably under-studied.

2.2. Data

The distribution of the benthic polychaetes in the Black Sea is based on a considerable body of literature. Some literature resources cover the whole basin and both hard and soft substrates, such as that published by [Kisseleva \(1981, 2004\)](#) but most focus on a restricted sector or are on an even narrower scale. Polychaete species distribution information is, however, well summarized in the following representative publications: [Vorobjov \(1949\)](#),

[Mordukhai-Boltovskoi \(1960\)](#), [Kisseleva \(1985\)](#) for the Azov Sea; [Marinov \(1959, 1964, 1968, 1977, 1990\)](#), for the Bulgarian coast; [Surugiu \(2005\)](#), for the Romanian coast; [Marcusen \(1867\)](#); [Vinogradov and Losovskaya \(1963\)](#); [Vinogradov et al. \(1967\)](#), [Losovskaya \(1977\)](#); [Kisseleva \(1992\)](#), for the North-Western part of the sea; [Bobretzky \(1868, 1870, 1881\)](#); [Perejaslavzeva \(1891\)](#); [Jakubova \(1930\)](#); [Kisseleva and Slavina \(1964\)](#); [Revkov \(2003\)](#), for the Bay of Sevastopol and its surroundings (Western Crimea); [Vinogradov \(1948, 1949\)](#); [Kisseleva and Slavina \(1963\)](#), [Kisseleva \(1964\)](#); [Murina et al. \(2004\)](#), for the Karadag region (Southern Crimea); [Czerniavsky \(1880, 1881, 1882\)](#); [Annenkova \(1929\)](#); [Komakhidze and Mazmanidi \(1998\)](#), for the Caucasian coast; [Jakubova \(1948\)](#); [La Greca \(1949\)](#); [Dumitrescu \(1960, 1962\)](#), [Rullier \(1963\)](#); [Gillet and Ünsal \(2000\)](#), for the Prebosphoric region. Classification and coding of the higher taxa follow that suggested by [Fauchald and Rouse \(1997\)](#); [Rouse and Fauchald \(1997\)](#) and [Rouse and Pleijel \(2001\)](#).

Polychaete species were assigned to zoogeographical categories according to their distribution, as suggested by [Arvanitidis et al. \(2002\)](#):

- (1) Species distributed only in the Mediterranean and the Black Seas are considered as endemic (E); some of these are exclusively endemic elements of the region (mentioned in the discussion section);
- (2) Species distributed in the Mediterranean, Black Sea and the eastern Atlantic are considered as Atlanto-Mediterranean (AM);
- (3) Species distributed in the Atlantic, the Mediterranean and Black Seas and the Indo-Pacific are considered as cosmopolitan (C). All the faunal matrices can be downloaded from <http://www.medobis.org/Districtsv2.xls>.

Three categories of environmental variables were considered during the study: geographic, climatic and trophic. The geographic variables include: (1) shelf surface; (2) distance of the area from the Bosphorus Strait; and (3) distance from the Dardanelles Strait. These geographic variables were calculated using distance and area calculation functions in a geographic information system (GIS). Data were referenced under a common geo-reference system (geographic projection in decimal degrees) and converted to regular grids. The climatic variables include: (1) precipitation ([Adler et al., 2003](#)); (2) sea-surface temperature ([EOWEB, 2004](#)); (3) salinity ([Boyer et al., 2005](#)); (4) Photosynthetically Active Radiation; (5) water column Dissolved Oxygen; (6) Alkalinity. Climatic records describe the average physical and chemical parameter levels for the last 8–50 years (depending on dataset) and cover the Black Sea continental shelf (0–200 m). The trophic variables include: (1) chlorophyll-*a* concentration ([McClain et al., 1998](#)); Phosphate (2), Silicate (3), Ammonium (4), Nitrate (5) and Nitrite (6) concentration in the water column; (7) Hydrogen sulphide; (8) pH. The trophic variables (apart from chlorophyll-*a* concentration) were obtained from the same source ([The MEDAR Group, 2005](#)). For these variables no data were available for three sectors (Marmara Sea, Bosphorus, and Azov Sea).

Summary statistics (minimum, mean, maximum and range) were computed for the climatic and trophic variables of the eleven regions using ESRI's Arc/Info GRID GIS ([ESRI, 1994](#)).

2.3. Analyses

An initial binary matrix was constructed where species' presence/absence in the Black Sea sectors was denoted as 1 or 0, respectively. The information included in the initial matrix was subsequently aggregated into the generic and family levels. Three

additional matrices were also constructed in which the distribution of the three zoogeographical categories (endemics, Atlanto-Mediterranean, cosmopolitan) in the Black Sea sectors was recorded.

To derive similarity patterns from the above matrices, the Jaccard coefficient was utilized (Legendre and Legendre, 1998). The overall multivariate biodiversity pattern was obtained from the initial matrix by using the non-metric multidimensional scaling (nMDS) (Clarke and Green, 1988; Warwick and Clarke, 1991).

The resulting multivariate patterns from the zoogeographic and taxonomic categories were compared to each other by using the second-stage MDS ordination method, described by Somerfield and Clarke (1995). According to the mathematical procedure they describe, a rank correlation using the harmonic rank correlation coefficient (Clarke and Ainsworth, 1993) was computed between each pair of the six similarity matrices. A final triangular matrix was constructed with fifteen cells, containing the resulting values of the harmonic rank correlation coefficient. These correlation values were first ranked and then subjected to the second-stage MDS (Olsford et al., 1997).

The correlation between the multivariate patterns derived from the similarity matrices and the various combinations of the environmental variables was examined using the BIO-ENV analysis (Clarke and Ainsworth, 1993).

To explore any significant relationship between the species richness and the salinity gradient, the scale of the study was enlarged to include all European regional seas from the White and Barents Seas to the Mediterranean, Black and Azov Seas. The percentages of species hosted in each of the regional seas (approximation of species richness) were then plotted against the salinity gradient, as suggested by Zenkevich (1959). Percentages of polychaetes hosted in the Mediterranean, Black and Azov Seas were superimposed on the former plot. The non-parametric ANOVA or Kruskal–Wallis statistic (Kruskal and Wallis, 1952) was applied to test for any significant difference in the percentages of the benthic species hosted in the European regional seas along salinity gradients.

To compare the polychaete diversity of the Black Sea sectors two diversity indices were applied: the average taxonomic distinctness (AvTD) and the variation in taxonomic distinctness (VarTD). Departures from expectation were determined by the corresponding simulation funnels, constructed from random subsets of species from the regional species pool (Warwick and Clarke, 1998; Clarke and Warwick, 2001).

The area-diversity formula of MacArthur and Wilson (1963, 1967) $S = C \times A^z$, (where S : the number of units, A : the geographic variables, C : intercept, z : the slope) was applied to test any significant relationship between the number of units included in each taxonomic/zoogeographic level and geographic variable. The first of the geographic variables (shelf surface) is indicative of the size of the area. The next two variables (distance of the area from the Bosphorus and Dardanelles Straits) are indicative of the distance of the areas from the source region. Values of each pair of S and A were first transformed to logarithms (base 10) and a linear regression was subsequently performed (Zar, 1999).

3. Results

3.1. Faunal composition pattern

A total of 301 polychaete species has been reported from the eight Black Sea sectors and their three adjacent water bodies (Marmara Sea, Bosphorus, Azov Sea), belonging to 182 genera and 48 families. From these, 174 species were characterised as cosmopolitan, 104 as Atlanto-Mediterranean and 23 as endemic. The total number of species and the number of species for every zoogeographical category in all the Black Sea sectors are shown in Fig. 1.

The highest number of species (105) was recorded in the Bulgaria sector and the lowest in the Azov Sea (40).

The multivariate analyses provided additional information on the similarity pattern: nMDS based on Jaccard coefficient and performed on the total species list for the eight Black Sea and their three adjacent sectors, revealed a clear gradient along the diagonal of the plot (Fig. 2). Sea of Marmara, Bosphorus Strait, and Prebosphoric sectors are placed in the most distant places; all the remainder Black Sea sectors are grouped together and Azov Sea is placed on the upper right side of the plot. When the Anatolian sector is included, it is placed on the lower right side at a large distance from all the remainder sectors.

When the geographical scale was enlarged to include all European regional seas, a clear trend in species numbers appeared: polychaete species richness, expressed as percentages hosted by the Mediterranean (1036), Black (220) and Azov Seas (40), now appears to be a function of the salinity gradient. This trend, a “zoogeocline” according to Arvanitidis et al. (2002), has also been suggested by Zenkevich (1959) for all European regional seas and is depicted in Fig. 3. Here, the distribution of the percentages of benthic species against the salinity values is provided for the North – Baltic Seas (line I), for Mediterranean – Caspian Seas (line II), for Barents and White Seas (line III) and for the Mediterranean – Azov Seas for polychaete species only (line IV). The Kruskal–Wallis statistic showed that there are no significant differences ($H_3 = 3.78$; $p = 0.23$) in the distribution of these percentages along the salinity regimes, a fact which supports Zenkevich’s (1959) view.

3.2. Taxonomic vs zoogeographic multivariate pattern

Each matrix deriving from taxonomic/zoogeographic categories was also subjected to the Jaccard similarity coefficient. Rather than comparing the resulting six clustering dendrograms and their corresponding MDS plots, the “second-stage” MDS procedure was adopted. The output plot of the latter analysis where similarity matrices with similar configuration are plotted close to each other is provided in Fig. 4. When polychaete species information is aggregated to the genus level, the resulting pattern is identical to that of the species. Patterns deriving from the cosmopolitan and Atlanto-Mediterranean species are closely related to the former ones. Conversely, patterns stemming from the endemics and families are almost unrelated to the former ones and, therefore, these categories are placed distantly from the remainder patterns on the second-stage MDS plot.

3.3. Associated environmental variables

The BIO-ENV analysis was performed twice for all the similarity matrices. In the first series of analyses, all the existing data on the environmental variables were included (Table 1a). However, three sectors (Marmara Sea, Bosphorus and Azov Sea) were not included in the analyses at this stage because of the lack of some of the environmental variables (Table 1b). Conversely, in the second run all the sectors were included but there were fewer environmental data, since there was no information on the entire set of the environmental data from all the sectors taken into account. The BIO-ENV analysis showed positively correlated ($\rho_w > 0$) variables for each of the two combinations in the data sets (Table 1). The rank correlations between environmental variables and presence/absence faunal data were weak and ranged from 0.12 to 0.58 (Table 1). Minimum chlorophyll-*a* concentration in the water column gave the maximal correlation value (0.58) with the pattern derived by the Atlanto-Mediterranean species whereas the same variable gave a much lower correlation value (0.38) with the entire polychaete inventory pattern.

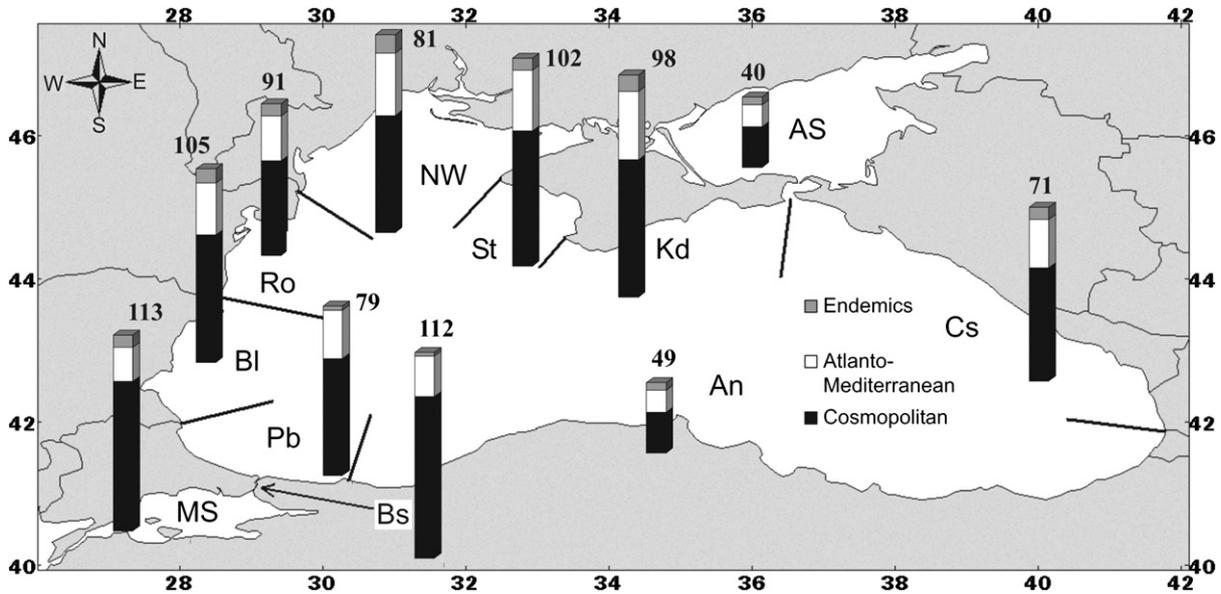


Fig. 1. Map of the study sites in the Black Sea along with the distribution of polychaete species in these sectors. The size of each column represents the total species number indicated on the top; the three zoogeographical categories are represented by the portions of the different patterns in each of the columns (cosmopolitan, Atlanto-Mediterranean and endemic). MS: Marmara Sea; Bs: Bosphorus; Pb: Prebosphoric; Bl: Bulgaria; Ro: Romania; NW: North Western Black Sea; St: Sevastopol; Kd: Karadag; AS: Azov Sea; Cs: Caucasus; An: Anatolia.

When all the environmental variables (Table 1a) are included in the analysis, the corresponding faunal matrices are best correlated with two of the three categories of the environmental variables (geographic and trophic). Distance from the Bosphorus Strait and range of ammonium concentration values are the main factors associated with the different taxonomic and zoogeographic categories of the polychaete fauna. In the case of the endemic species the highest correlation value was obtained by the distance from the Bosphorus Strait and the range of the ammonium concentration (0.33).

When all sectors were included (Table 1b) in the analysis, the corresponding similarity matrices are more often correlated with the climatic and trophic variables. The range of salinity and the minimum chlorophyll-*a* concentration are best correlated with the polychaete sectoral inventories. In the case of the cosmopolitan species geographic (shelf surface), and climatic factors (range of precipitation, range of salinity) seem to be the best correlated variables.

3.4. Biodiversity of the Black Sea benthic polychaetes

Taxonomic Distinctness Indices were calculated based on the species distributions of the various Black Sea sectors. The resulting distribution funnels of the average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) are presented in Fig. 5. Only the area of the Anatolian sector falls outside the expected ranges of both Δ^+ and Λ^+ (lower and higher than expected values, respectively). Also, Λ^+ values calculated from the Azov Sea and Sea of Marmara are placed borderline on the upper limit of the funnel.

Spearman's rank correlation coefficient for sets of calculated Δ^+ and Λ^+ values however gave negative significant results ($\rho = -0.95$; $p < 0.005$). These results show that the taxonomic distinctness indices are monotonically related, and thus should not be used simultaneously for biodiversity assessment purposes in the region.

3.5. Application of the area-diversity formula to the Black Sea sectors

Results derived from the application of the area-diversity formula are displayed in Table 2. Significant results are derived in

two cases, in which *S* represents the number of endemic species and *A* is considered as the shelf surface on the former occasion and the distance from Bosphorus on the latter.

It should be kept in mind, however, that in both cases the coefficient of determination is low, especially on the former occasion. This simply indicates that there is a weak relation between the above-mentioned variables, and does not allow for safe interpretation.

4. Discussion

4.1. The multivariate pattern

Although a clear geographic pattern appears along the diagonal of the MDS plots (from near the Aegean Sea sectors to the Azov Sea), this pattern is not associated with the number of species hosted by the various sectors. This is at odds with the well-defined zoogeocline, observed by Arvanitidis et al. (2002) along the

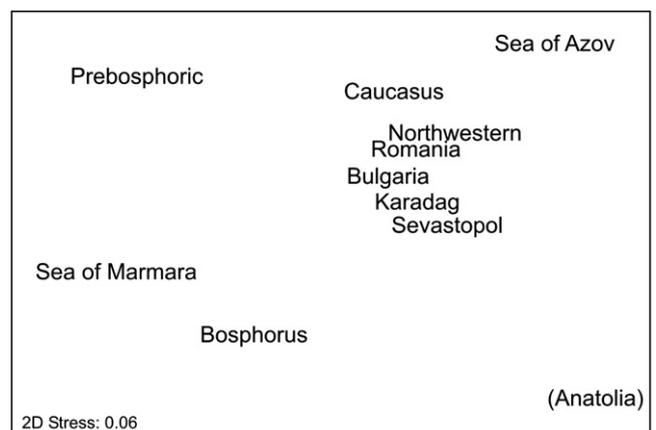


Fig. 2. Non-metric MDS plot resulting from the application of Jaccard's similarity coefficient, on the Black Sea polychaete species.

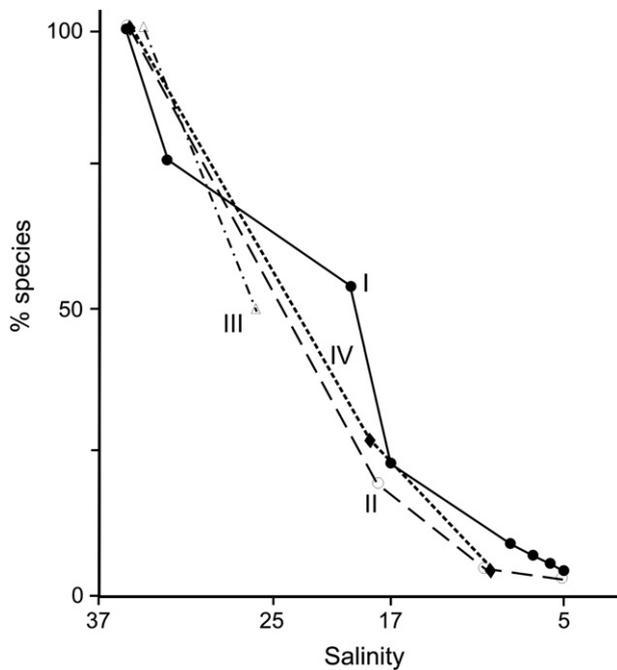


Fig. 3. Percentages of benthic species hosted by the European regional seas, as a function of the salinity gradient (redrawn from Zenkevich (1959) and modified). Lines: I (solid circles): North and Baltic Seas; II (open circles) Mediterranean, Black, Azov and Caspian Seas; III (open triangles): Barents and White Seas; IV (solid rhombi) Mediterranean, Black and Azov Seas (polychaete species only).

Mediterranean and the Black Sea region. However, when the focus of the study moves to the regional (basin) scale, then the percentages of the polychaete species hosted in each basin – Mediterranean, Black, and Azov Seas – closely follow those deriving from the benthic species as suggested by Caspers (1957) and Zenkevich (1959). This *zoogeocline*, associated with the salinity gradient, emerges from all European regional seas under a rather homogenous pattern, as depicted by Zenkevich (1959). A similar diversity pattern has been proposed for animals populating the estuarine environments by Remane and Schlieper (1958) and those populating the brackish water systems (McLusky and Elliot, 2004).

Prebosphoric, Bosphorus and Marmara Sea, being in the vicinity of the Aegean, share a number of species in common with the latter sea. However, although the species numbers reported from them

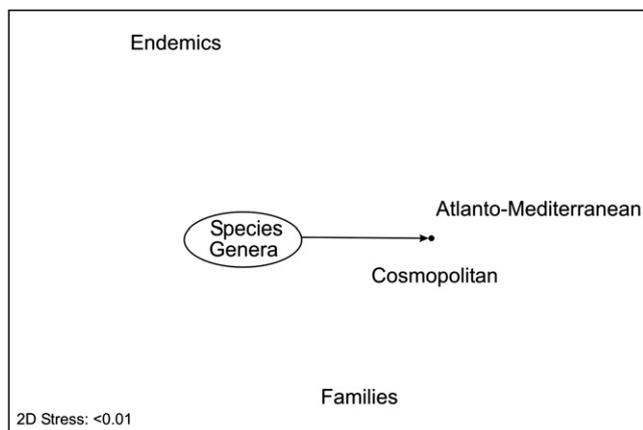


Fig. 4. Second stage ordination nMDS comparing patterns deriving from the taxonomic/zoogeographic polychaete datasets.

(79, 112, 113, correspondingly) are comparable to those reported from the Black Sea sectors, their polychaete faunas appear to be substantially divergent. This is also attested by the fact that they are more distant from the Black Sea sectors and from each other than from the remaining sectors. The Azov Sea hosts an almost exclusively brackish/fresh water fauna. Its distant place on the MDS plot is indicative of the location of the area: a semi-enclosed sea located farthest from the Bosphorus Strait and having the lowest salinity values. The remaining sectors (Bulgaria, Romania, NW Black Sea, Sevastopol, Karadag, and Caucasus) have the most species in common and, consequently, they should be considered as the most representative sectors of the region. Anatolia has received the least scientific effort and when enters in the analysis it appears far from the remainder sectors.

The multivariate analyses of the information deriving from the taxonomic (species and genus) as well as from the zoogeographic (cosmopolitan, Atlanto-Mediterranean species) categories show convergent similarity patterns. This also implies that these categories should be used in future diversity studies of the taxon in the region. High percentages of cosmopolitan polychaete faunas have been reported not only from the Mediterranean and the Black Seas (e.g. Arvanitidis et al., 2002) but also from many parts of the world (e.g. Fauvel, 1923; Bellan, 1964). The life cycles of the cosmopolitan species include often traits such as the opportunism, the ability of their populations to colonize different types of habitats and to tolerate variable environmental conditions (Grassle and Grassle, 1974; Pearson and Rosenberg, 1978). Taking into account the special environmental conditions prevailing in the Black Sea it is not surprising that this category provides a pattern closely related to the one deriving from the total polychaete inventory. The issue of the widely distributed polychaete species has been thoroughly discussed in a number of studies (e.g. Fauchald, 1984; Williams, 1984; Mackie and Hartley, 1990; Dauvin and Thiébaud, 1994) in which it was suggested that, at least for a number of names used to classify certain species (e.g. *Terebellides stroemi*, *Prionospio ehlersi*, *Spio filicornis*), several different species had been included. Hutchings (1998) demonstrated that most of the Australian terbellids suffered from the cosmopolitan “syndrome”. It is anticipated that future studies will bring a degree of evidence that the situation with the cosmopolitan species holds true also for the Black Sea. The long period of acclimatization the species have to spend in the pre-Bosphoric sector before they move towards the inner parts of the Black Sea (e.g. Ozturk, 2002) may well account for their genetic differentiation in comparison to their populations in the Aegean and the adjacent seas. Similar arguments can support the convergent multivariate pattern of the Atlanto-Mediterranean category.

However, for families and endemic species, the similarities with the other sources of information are much lower. For the family level, this result might be expected since the species and genera are unevenly distributed in families. However, for the endemic elements different multivariate patterns must be caused by different agents (see below).

4.2. Synergy of the environmental variables

The low values of the harmonic rank correlation coefficient do not allow for safe analyses and explanations for the environmental variables associated with the distribution of polychaetes in the Black Sea. Distance from the Bosphorus Strait along with ammonium concentrations, seem to affect the polychaete multivariate pattern, which appears to be the dominant trend in the case where only sectors for which values for all environmental variables considered were available. It is worth mentioning that these environmental variables are almost identical when correlated with the

Table 1

Environmental variables best correlated with the similarity patterns of the polychaete inventories of the Black Sea (a) for only those sectors for which values on all environmental variables were available; (b) for all the Black Sea sectors for which values on less environmental variables were available; dBs: distance from the Bosphorus Strait, rPre: range of precipitation, rSal: range of salinity, minChl-*a*: minimum of chlorophyll-*a* concentration, maxNH₄: maximum of ammonium concentration, rNH₄: range of ammonium concentration, maxNO₃: maximum of nitrates concentration, ρ_w: harmonic rank coefficient.

	Environmental variables								ρ _w
	Geographic		Climatic		Trophic				
	Shelf surface	dBs	rPre	rSal	minChl- <i>a</i>	maxNH ₄	rNH ₄	maxNO ₃	
(a)									
Species		+					+		0.14
Genera		+					+		0.12
Families		+				+			0.28
Cosmopolitan		+					+		0.12
Atlanto-Mediterranean		+				+		+	0.16
Endemic		+					+		0.33
(b)									
Species					+				0.38
Genera				+	+				0.37
Families				+	+				0.33
Cosmopolitan	+		+	+	+				0.24
Atlanto-Mediterranean					+				0.58
Endemic					+				0.26

pattern derived from similarity matrices produced by the species, genera, and families, cosmopolitan and endemic species.

When all Black Sea sectors followed by the limited data set of the environmental factors for which values were available are taken into account, a different pattern from the previous one appears: the polychaete similarity matrices seem to be affected mainly by the minimum values of chlorophyll-*a* concentration. The higher – but still weak – values of the harmonic rank coefficient for the second group of data sets indicate the dependence of the polychaete categories on food availability, primarily expressed by chlorophyll-*a* concentration. The gradient of decreasing salinity from the Sea of Marmara to the Azov Sea is weakly correlated with the polychaete species diversity pattern at the family and genus taxonomic levels and with the cosmopolitan polychaetes.

4.3. Polychaete biodiversity of the Black Sea

Both taxonomic distinctness indices show that almost all Black Sea sectors provide taxonomic distinctness values, which fall within the expected range of variability. The only exceptions occur in Δ⁺ for the Azov Sea polychaete inventory and in both Δ⁺ and Λ⁺ for the Anatolian one. A potential explanation would be that the former sector is the most isolated and it is itself a semi-enclosed basin with restricted communication capacity with the adjacent Black Sea sectors. However, Warwick and Clarke (2001) report that lower than expected Δ⁺ values, associated with higher than expected Λ⁺ values are indicators of severely degraded ecosystems. In the absence of reliable data (Δ⁺ value near to the expected average for the Azov Sea inventory), the degree to which severe anthropogenic impact, superimposed on the hyposaline regime, has resulted in a polychaete impoverished inventory in the Azov Sea, remains to be tested. The placement of the Anatolia outside the funnels for both TD indices results from the impoverished inventory of this sector, caused by the limited scientific effort spent.

The above results may be interpreted as indicative of the fact that almost all sectoral Black Sea and adjacent inventories may be considered as random samplings of the regional polychaete inventory. Consequently, their polychaete inventories may be used as a reference base for future biodiversity/environmental assessment studies.

In the Crimean sectors (Sevastopol, Karadag) numbers of recorded species are higher, but the higher taxa also include more

species than in the other sectors. This difference in the distribution of the species to the higher categories may be the result of the greater scientific effort spent in this area (e.g. Bobretzky, 1868; Zernov, 1913; Jakubova, 1930; Procludina, 1952; Kisseleva and Slavina, 1963, 1964; Kisseleva, 1981, 2004; Zaika, 1992; Mazlumyan et al., 2003 Revkov, 2003; Murina et al., 2004). The

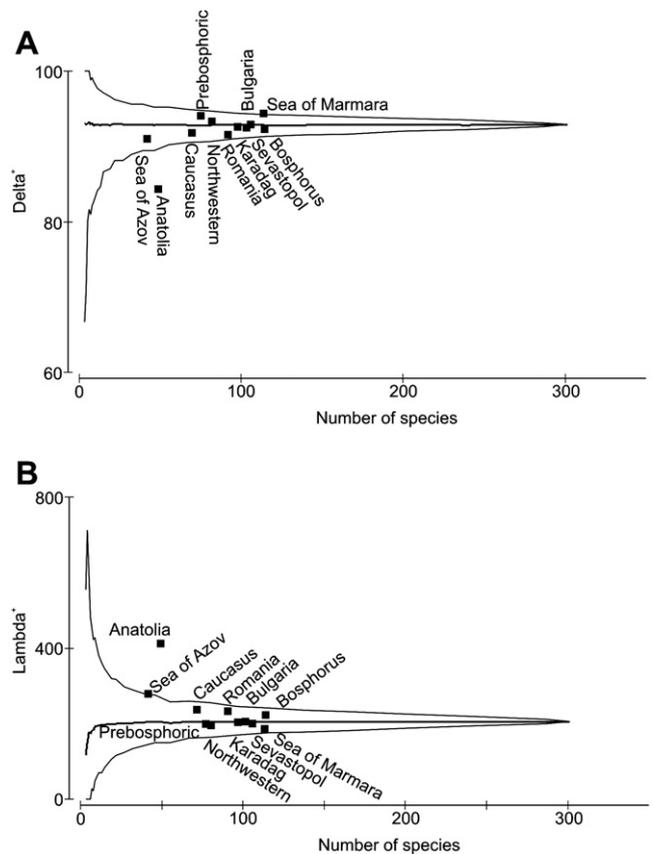


Fig. 5. The 95% probability funnels of (A) the Average Taxonomic Distinctness values (Δ⁺) and of (B) the variation in Taxonomic Distinctness values (Λ⁺), as calculated by the Black Sea polychaete inventories. Expected average indicated by the line in the middle of the funnel.

Table 2
Summary of the regression results of the formula applied: $S = C \times A^2$; where S represents the number of taxonomic/zoogeographic units and A represents the value of the indicated geographic variables (shelf surface, distance from Bosphorus and distance from Dardanelles Straits). Bold numbers represent significant results at the level of 0.05.

	Species	Genera	Families	Cosmopolitan	Atlanto-Mediterranean	Endemics
Shelf surface						
r^2	0.10	0.12	0.02	0.27	0.00	0.39
p -value	0.32	0.27	0.69	0.08	0.88	0.03
Intercept	2.20	2.06	1.51	2.13	1.35	0.10
Slope	-0.06	-0.06	-0.02	-0.11	0.01	0.18
Distance from Bosphorus						
r^2	0.02	0.03	0.00	0.12	0.07	0.56
p -value	0.70	0.60	0.10	0.27	0.42	0.01
Intercept	2.05	1.93	1.44	1.91	1.23	0.27
Slope	-0.02	-0.03	0.00	-0.07	0.05	0.22
Distance from Dardanelles Strait						
r^2	0.01	0.02	0.01	0.07	0.09	0.31
p -value	0.80	0.68	0.77	0.42	0.34	0.06
Intercept	2.09	2.01	1.53	2.08	1.05	-0.28
Slope	-0.04	-0.05	-0.04	-0.13	0.13	0.40

opposite occurs for the sectors of Romania and North-Western Black Sea when combined (not shown). This sectoral combination into a single larger area (NW + Romania) results in a less diverse sector, in terms of taxonomic distinctness, due to the fact that the former sectors receive the maximum influence of the Danube river waters. The shelf in the north-western part of the sea, which accounts for over half of the surface area of the entire shelf of the Black Sea, is considered to be a sector of a special nature. In this sector, flows from the major rivers of the Black Sea (Danube, Dniester, Dnieper and Southern Bug), whose average total annual discharge is approximately 261 km³ per year, account for more than 77% of the total river discharge to the sea (Reshetnikov, 1992 cited by Zaitsev and Mamaev, 1997). As a result salinity in this sector is below 15. Increased nutrient loads in the north-western part also produce frequent algal blooms which lead to hypoxia and occasional anoxia with subsequent mass mortality of bottom and near bottom organisms (Zaitsev, 1991). In addition, the north-western part of the sea is characterised by low winter temperatures which in combination with low salinity can lead to freezing water and formation of ice near the shoreline (Bondar et al., 1973). Consequently, fauna inhabiting the north-western part will probably include the most euryhaline, euryoxybiotic and eurythermic elements. The smaller number of reported species from the Caucasus as well as from the Prebosphoric area may be correlated with the smaller amount of scientific effort carried out in these areas.

4.4. Alternative biogeographic paradigm

“Endemic species” was the only category in which the area-diversity model was found to be positively related with the shelf surface and distance from the Bosphorus. MacArthur and Wilson (1963) state that the equilibrium model predicts that the logarithm of the species number is a function of immigration against extinction rates. This equilibrium model originated from the Darwin-Wallace paradigm or the founder-dispersal from a centre of origin, with area-diversity model being one of the major expressions of this paradigm. The results of the current study, however, do not support the area-diversity equation (low coefficient of determination values).

The eventful history of the formation of the Black Sea and its surrounding brackish water bodies (Ekman, 1967) suggests the existence of another biogeographic mechanism: a massive invasion of Mediterranean species after its opening in the lower Quaternary period.

In the Eocene and Oligocene periods the Tethys Sea not only occupied the Mediterranean basin but also extended over vast

areas of central and south-eastern Europe, North Africa and West Asia. In the upper Miocene a regression occurred, leading to a shallow western sector and a brackish eastern one which caused an impoverishment of the species. The eastern part finally became separated from the Mediterranean to form the Sarmatic Inland Sea. A second regression occurred in the lower Pliocene. This resulted in more brackish waters with the connection with the Mediterranean finally opening during the lower Quaternary period. Consequently, the Sarmatic fauna most probably was a rich brackish water one, mixed with fresh water species. Relics of this fauna can still be found in the Black and Azov Seas, and include: *Hypania invalida* (Grube, 1860), *Hypaniola kowalewskii* (Grimm in Grube, 1877), and *Manayunkia caspica* Annenkova, 1929. That brackish water Sarmatic fauna was destroyed by massive flooding from the salt waters of the Mediterranean. The results from the current study may support such a mechanism involving massive invasions, filtered by strong environmental gradients (primarily salinity), which are ultimately mirrored in the faunas hosted in each of the sectors along these gradients. The latter is in accordance with the *zoogeocline* observed by the multivariate techniques.

In the latter case, the Mediterranean species, hitherto “xenobiotic” to the brackish water species did not respond to the environmental factors in the same way as the native species of Sarmatic origin: their life-cycle attributes included characteristics which, in combination with the possible absence of native predator species, provided them with advantages over the brackish water species. The latter mechanism is a substantial difference from the founder-dispersal model, in which non-native species populations are founded at random and the only characteristic accounting for their establishment is their ability to disperse (Heads, 2005). Similar examples of massively invading species have also occurred in recent times (Kideys, 2002).

5. Future perspectives

Based on the results of the current study, future efforts should focus on: (a) the collection, storage and availability of high quality biodiversity datasets, including genetic diversity, from the region and particularly from the Anatolian coasts; (b) the integration of the information deposited in the various international systems, such as the IOBIS (International Ocean Biogeographic Information System, <http://www.iobis.org/>) and the GenBank (<http://www.psc.edu/general/software/packages/genbank/genbank.html>); (c) exploring the impact of the various anthropogenic pressures especially in the most vulnerable sectors such as the Northwest Black Sea and the Azov Sea.

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