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Microbial–meiofaunal interrelationships in coastal sediments of the Red Sea

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Abstract Population density and biomass of bacteria and meiofauna were investigated seasonally in the sediments of the north-western bank of Red Sea. Samples of sediments were collected seasonally from three different stations to determine microphytobenthic biomass (chlorophyll a), protein, lipid, carbohydrate, and total organic matter concentrations. These investigations revealed that microbial components tended to increase their dominancy, whereas sensitive meiofauna were extremely reduced during the entire study period. Thus a very low density of the total meiofauna (with an annual average of 109 ± 26 ind./10 cm2) was recorded whilst the benthic microbial population densities exhibited higher values (ranging from 0.31 ± 0.02 x 108 to 43.67 ± 18.62 x 108/g dry sediment). These changes in the relative importance analysis of benthic microbial components versus meiofaunal ones seem to be based on the impact of organic matter accumulation on the function and structure of these benthic communities. Proteins, lipids and carbohydrates showed very low concentration values, and the organic matter mostly consisted of carbohydrates, reflecting lower nutritional values for benthic fauna in general and meiofauna in particular. The distribution of microbial and meiofaunal communities seems to be dependent on the quality of the organic matter rather than on its quantity. Total organic matter concentrations varied between 5.8 and 7.6 mg/g, with organic carbon accounting for only 32% of the total organic matter. Chlorophyll a attained very low values, fluctuating between 0.11 and 0.56 µg/g, indicating the oligotrophy of the studied area. The very low concentration of chlorophyll a in the Red Sea sediment suggests that the sedimentary organic matter, heterotrophic bacteria and/or protozoa constitute an alternative resource...
1. Introduction

The health of the sedimentary ecosystem can be assessed using data concerning the structure and abundance of its biological communities (Maher et al., 1999). Since the early 1980s biologists have been increasingly interested in studying benthic meiofauna. This work presents obstacles, however, due to their small size, and the difficulties of isolating the benthic communities from the sediments and identifying species belonging to different taxa (Austen et al., 1994; Harguinteguy et al., 2012).

Meiofaunal organisms play an important ecological role in the aquatic ecosystem and are well suited for environmental impact assessment studies. Their short life spans, continuous reproduction and direct development in situ mean that meiofauna have a high potential to respond rapidly to both natural and anthropogenic environmental changes (Giere, 1993; Mirto and Danovaro, 2004; Fraschetti et al., 2006; Gyedu-Ababio and Baird, 2006; Moreno et al., 2008; Harguinteguy et al., 2012). Moreover, beaches may function as natural filters responsible for the remineralisation of substances, which then return to the sea as nutrients (Coull and Chandler, 2001). The interstitial system of beaches, in particular the system protected by muddy sediments, is formed by long and intricate food chains of bacteria, protozoa and meiofauna at the first levels. Marine biological systems are therefore dependent on the productivity of coastal areas (Higgins and Thiel, 1988; Leguerrier et al., 2003).

Measuring carbohydrate, lipid and protein contents in marine sediments is usually very important to evaluate the availability of food (Fabiano et al., 1995; Pusceddu et al., 1996). Meanwhile, benthic microbes, in the form of bacteria, play an effective role in converting this organic matter into living biomass in the sediment, which in its turn can be utilised by benthic protozoa (Fenchel, 1967; Sleigh et al., 1992; Danovaro et al., 1999; Foissner, 2012) and meiofauna (Danovaro, 1996). This allows the transfer of feeding materials and energy to the higher trophic levels (Hondeveld et al., 1994; Mirto et al., 2004). Currently, however, no study has provided quantitative information on the trophic interaction between the three important sedimentary groups (bacteria/protozoa/meiofauna) and sedimentary organic matter within the Red Sea benthic ecosystem (El-Serehy et al., 2015).

In this research, population fluctuations of meiofauna and benthic heterotrophic bacteria were studied in relation to the seasonal fluctuation of sedimentary chlorophyll a and organic matter biochemical constituents at three different sites along the northern part of the Red Sea. The present work aims to investigate the microbial–meiofaunal population dynamics with relation to chlorophyll a, the organic matter content, biochemical composition and granulometric structure of the sediment.

2. Material and methods

Three stations were chosen along the north-western bank of the Red Sea for this study (Fig. 1). The three stations were selected based on their proximity to mangrove. Safaga (lat 26° 36’ 56”N, long 34° 00’ 43”E) and Al-Qulaan (lat 24° 21’ 28”N, long 35° 18’ 23”E) were closer to mangrove vegetation than Gabal El-Zeit (27° 48’ 10”N, long 33° 33’ 59”E). Station I (Gabal El-Zeit) is located in a triangular bay at the entrance of the Gulf of Suez, 70 km to the north of Hurghada city. This site is surrounded by an extensive oily land area used by the GABCO Company for oil production services. Sediments have a red colour and are dominated by coarse and median sand particles. In addition, vegetation consists of Padina sp. (Phaeophyceae) and Caulerpa racemosa (Chlorophyceae). Station II (Safaga) is sheltered by mangrove trees (Avicennia marina). The sediment texture is composed mainly of fine sand.
and muddy materials and is a grey colour with an odour of H2S. Fiddler crabs (*Uca inversa*), blue green algal mats and a dense population of the muddy snail, *Pirenella cailliaudi*, are the most common fauna and flora inhabiting the sediment of this site. Station III (Al-Qulaan) is characterised by a huge mangrove forest of *A. marina*. The sediment texture is dominated by muddy sediments. Calcified fragments of the Chlorophycean *Halimeda opuntia* densely cover the sediment of this location.

Sediment samples were collected to assess environmental parameters, bacteria and meiofauna from the three stations of Gabal El-Zeit, Safaga and Al-Qulaan with the help of a hand core of 4.5 cm inner diameter and 10 cm length. Carbonates were removed from the sediment samples using the method described by Buchanan and Kain (1971). The total organic matter in each sediment sample was calculated using the method given by Parker (1983). Lipids, proteins and carbohydrates were determined using the methods described by Marsh and Weinstein (1966), Hartree (1972) and Gerchacov and Hatcher (1972), respectively. Concentrations recorded for the three components were converted to carbon equivalent using the conversion factor given by Fichez (1991). Blank and three replicates were made for each biochemical analysis. Chlorophyll *a* concentrations (in µg/g sediment) were measured according to Lorenzen and Jeffrey (1980).

Bacterial cells in the sediment samples were immediately fixed in 2% buffered formaldehyde and kept at 4 °C until further analyses (Epstein and Rossel, 1995). In the laboratory, bacterial cells were stained with Acridine Orange and counted under an epifluorescence microscope (Olympus BH-2) on ten randomly selected fields. The frequency of the bacterial cell’s division was calculated according to Fry, 1988). Bacterial population density was standardised to biomass per 20 cm² of sediments according to Albertelli et al. (1999), and data on microbial biomass were expressed as mg C/g.

Meiofauna in the sediment samples were fixed in 4% buffered formaldehyde and sieved through 0.50 and 0.062 mm mesh size sieves. The fraction remaining on the 0.062 mm sieve was centrifuged three times. All meiobenthic animals were stained with Rose Bengal (0.5g/l), taxonomically classified and counted under a stereo microscope (Prior, S2000) accord

Figure 2 Concentrations of total organic matter (mg/g), chlorophyll *a* (µg/g) and organic carbon (mg C/g) in the sediment of the three sites.

Figure 3 Carbohydrate, lipid and protein contents in the sediments of the three sites of the Red Sea.

3. Results

Station I showed the highest contents of chlorophyll *a* with an annual average of 0.56 ± 0.3 µg/g, but contained the lowest values of total organic matter and organic carbon with annual values of 5.8 ± 0.4 mg/g and 1.85 ± 0.88 mg C/g, respectively. On the other hand, station III showed the lowest values of chlorophyll *a* and the highest annual values of total organic matter and organic carbon, with values of 0.11 ± 0.01 µg/g; 7.5 ± 1.1 mg/g and 2.4 ± 0.45 mg C/g, respectively (Fig. 2).
respectively (Fig. 6). Station III showed the highest meiofaunal species number followed by station II, whilst station I sustained the smallest number of meiofaunal species (Fig. 7). Nematodes were the most dominant group, contributing 67% of the total meiofaunal density, followed by harpacticoid copepods, contributing 12%. Polychaetes 10%, ostracods 4%, whilst oligochaetes and gnathostomulids contributed 3% each. Other taxa (Amphipoda, Cumacea, Isopoda and Nemertina) occurred in limited numbers and collectively averaged 1% of the total meiofauna (Fig. 8). The four major meiofaunal groups represented in the present study were dominated by nematodes with an annual average of 81.4% at station I; 49.1% at station II and 46.7% at station III (Fig. 9).

Statistical analysis (Table 2) showed that station III was the station which sustained the highest diversity indices with values of 0.92; 2.86 and 4.0 for evenness (E); Shannon-weaver index (H) and species richness (D), respectively. Also, a significant positive correlation was recorded between the median sediment particles and copepods ($r = 0.68, p < 0.05$); whilst a negative correlation was recorded between median sediment particles and nematodes ($r = -0.78, p < 0.01$).

4. Discussion

Concentrations of chlorophyll $a$ recorded on the north-western bank of the Red Sea (Fig. 2) were very low compared to other marine coastal areas, but comparable to those recorded in various aquatic oligotrophic habitats (Plante et al., 1986; Fabiano et al., 1995; Albertelli et al., 1999; Mirto et al., 2004). The very low values of chlorophyll $a$ recorded during the present study (<1.0 $\mu g/g$, Fig. 2) therefore confirm the oligotrophy of the Red Sea area, in other words suggesting a low input of fresh primary organic matter from microalgal organisms. During the present work, proteins, lipids and carbohydrates showed very low concentrations, and the organic matter was mostly composed of carbohydrates (Fig. 3), reflecting lower nutritional values for benthic fauna in general and meiofauna in particular. Concentrations of chlorophyll $a$ in the sediment are generally correlated with the biochemical classes of organic compounds in the form of proteins, lipids and carbohydrates (Fabiano and Danovaro, 1994; Albertelli et al., 1999).

According to Danovaro (1996) a high ratio of protein to carbohydrate indicates the presence of living organic matter and/or freshly generated detritus. In the present study, this ratio was very low (equal 0.31), similar to the values found in deep-sea sediment of the highly oligotrophic Ceratin Sea (Danovaro et al., 1993), and shelf areas (e.g. the Ligurian Sea, NW Mediterranean) (Albertelli et al., 1999). This also, therefore, tends to confirm the oligotrophic status of the studied area.
The distribution of benthic communities in the bottom sediment of oligotrophic environments varies in response to many variables (Albertelli et al., 1999; El-Serehy et al., 2015). Among these variables is the food quality, which plays an important role for bacteria (Deming and Yager, 1992; Bahgat et al., 2013), meiofauna (Danovaro et al., 1995; Danovaro, 1996; El-Serehy et al., 2015) and macrofauna (Rosenberg, 1995). Moreover, the sediment texture influences the structuring of meiobenthic communities. The three sampling localities chosen for the present study along the north-western bank of the Red Sea showed different sediment textures with median sediment particle diameters at station I, and a prevalence of muddy sediments in the other two stations (Table 1). The significant positive correlations recorded between the median sediment particles and copepods ($r = 0.68$, $p < 0.05$); and the negative relationships recorded between median sediment particles and nematodes ($r = -0.78$, $p < 0.01$) during the present study.

![Figure 8](image1.png)  Meiofaunal community structure in the sediment of the Red Sea.

![Figure 9](image2.png)  The percentage contribution of nematodes, polychaetes, copepods, ostracods and other taxa to the meiofaunal community at each of the Red Sea three sites.

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### Table 1  Locations and descriptive features of anthropogenic activities of the three sampling stations.

| Sampling sites               | Coordinates of sampling sites | General features of anthropogenic activities |
|-----------------------------|-------------------------------|---------------------------------------------|
| Gabal El-Zeit (Station I)   | 27° 48’ 10''N-33° 33’ 59''E | – Extensive oily land areas for GABCO Company  |
|                             |                               | – Sediments have red colour                 |
|                             |                               | – Sediment texture are dominated by median sand |
|                             |                               | Vegetation: Padina sp. (Phaeophyceae)       |
|                             |                               | Caulerpa racemosa (Chlorophyceae)           |
|                             |                               | – Macrofaunal abundance: Low abundance      |
| Safaga (Station II)         | 26° 36’ 56''N-34° 00’ 43’E   | – Phosphate Abu Tartour Company             |
|                             |                               | – Sediments have grey colour                |
|                             |                               | – Sediments have an H2S odour               |
|                             |                               | – Sediment texture are dominated by silt and clay |
|                             |                               | Vegetation: Mangrove forest                 |
|                             |                               | Blue green algal mats                       |
|                             |                               | – Macrofaunal abundance: High abundance      |
| Al-Qulaan (Station III)     | 24° 21’ 28’N-35° 18’ 23’E   | – Wadi El Gemale Protectorate               |
|                             |                               | – Sediments have grey colour                |
|                             |                               | – Sediments are dominated by silt and clay  |
|                             |                               | Vegetation: Mangrove forest                 |
|                             |                               | Algal calcified fragments                   |
|                             |                               | – Macrofaunal abundance: High abundance      |
might suggest that sediment texture has a strong effect on the structuring of meiofaunal communities along the northwestern bank of the Red Sea. Copepods showed their highest population density, 21% of the total meiofaunal densities, at station I (Fig. 9). Nematodes showed the opposite pattern, however; displaying their lowest population density at this station: only 42% of the total meiofaunal density. Station I was characterised by the dominance of median sand particles (Table 1). In stations II and III, however, there was a predominance of muddy sediments and it is in these stations that nematodes recorded their highest population densities (84% and 75% of the total meiofauna, respectively). The distributional patterns of meiofaunal communities which this study describes in the marine sediment of the Red Sea are similar to those described in most other marine environments, with an increasing nematode dominance but decreasing copepod dominance in muddy sediments (Heip et al., 1985; Higgins and Thiel, 1988; Brown and McLachlan, 1990; Villora-Moreno et al., 1991).

Bacterial population density and biomass recorded in the sediment collected from the Red Sea coasts during the present study were higher than those found in other oligotrophic environments (Albertelli et al., 1999; La Rosa et al., 2001). In oligotrophic areas, the distributional pattern of bacterial bacteria varies in response to food quality rather than food quantity (Deming and Yager, 1992). Thus, the quality of feeding particles available for bacteria in the Red Sea sediments seems to be the main factor for the higher bacterial population density recorded in this study. On average, the benthic bacterial biomass accounted for just 15% of the sedimentary carbon, which suggests that the microbial loop strongly dominates the sedimentary compartments in the Red Sea.

On the other hand, meiofaunal population densities were very low, ranging between 41 and 167 ind./10 cm², and fluctuating seasonally with a peak of 192.52 ind./10 cm² during summer at station II (Fig. 6). These low values of meiofaunal population densities suggest that the organic matter accumulated in the Red Sea sediments is not able to support a higher meiofaunal density, which may be due to, the lower nutritional values of organic matter. Food quality usually controls population density and spatial distribution of meiofauna in the sediment (Lee et al., 1977; Pusceddu et al., 2009, 2014).

Despite the extremely low density of the total meiofauna, the benthic microbial population densities exhibited higher values, ranging from $0.26 \pm 0.02 \times 10^8$ to $102.67 \pm 18.62 \times 10^5$ g dry sediment (Fig. 4). Moreover, a higher ratio of benthic microbial biomass to total meiofaunal biomass was recorded in the Red Sea during the present study (Fig. 5). This high ratio clearly indicates that the benthic community in the Red Sea sediments is strongly dominated by microbial components in the form of bacteria, whilst also showing that a large proportion of the benthic microbes (bacteria) are not converted into meiofaunal biomass. This high ratio of bacterial/meiofaunal biomass can provide important information on the energy transfer pathways in the benthic food web of the Red Sea, whereby bacteria in the sediment of the Red Sea clearly play a primary role as a trophic reservoir for higher trophic levels by converting refractory compounds into available food in the form of bacterial biomass. A large quantity of organic carbon (derived from bacterial biomass) is not channelled towards higher trophic levels (meiofauna) in the Red Sea marine ecosystem, however. Thus, there is a missing link in the bacterial–meiofaunal interaction in this ecosystem. Data from the literature indicates that whilst the meiofauna can consume bacteria, protozoa are a more likely and more attractive meiofaunal food source. On this basis, protozoa, as the primary bacterivores in most aquatic systems, can be postulated to be the missing link in bacterial–meiofaunal interaction in the Red Sea marine ecosystem. Bacterivory by meiofauna is undetectable in most aquatic sediments (Montagna et al., 1982; Bott, 1999; Bott and Borchardt, 1999; Mirto et al., 2004; Pascal et al., 2009), but meiofaunal consumption of protozoa is detectable in different marine sediments (Bott and Borchardt, 1999; Epstein and Gallagher, 1992; Walters and Moriarty, 1993), whilst, protozoa are the primary bacterivores in most aquatic ecosystems (Fenchel, 1968, 1978; Schönborn, 1982, 1984; Sleight et al., 1992; Bott and Borchardt, 1999; Foissner, 2012).

In conclusion, the very low values of chlorophyll a recorded during the present study confirm the oligotrophy of the investigated area and can suggest that sedimentary organic matter, heterotrophic bacteria and/or protozoa constitute an alternative resource that is consumed by meiofauna. Despite the extremely low density of the total meiofauna, the benthic microbial population densities exhibited higher values in the Red Sea sediments. Changes in the relative importance analysis of benthic microbial components versus meiofaunal ones seem to be based on the impact of organic matter accumulation on the function and structure of these benthic communities. The distributional patterns of microbial communities seems to be organic matter quality dependent, and protozoa are postulated to be the missing link in bacterial–meiofaunal interaction in the Red Sea.

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References

Albertelli, G., Covazzi, A., Danovaro, R., Fabiano, M.M., Fraschetti, S., Pusceddu, A., 1999. Differential responses of bacteria, meiofauna and macrofauna in a shelf area (Ligurian Sea, NW Mediterranean): role of food availability. J. Sea Res. 42, 11–26.
Fenchel, T., 1968. The ecology of marine microbenthos. II. The food of marine benthic ciliates. Ophelia 5, 73–121.

Fenchel, T., 1978. The ecology of micro- and meiobenthos. Annu. Rev. Ecol. Syst. 9, 99–121.

Fichez, R., 1991. Suspended particulate organic matter in a Mediterranean submarine cave. Mar. Biol. 108, 167–174.

Foissner, W., 2012. Protist diversity and distribution: some basic considerations. 2nd European Workshop on the Evolutionary Ecology of Terrestrial Isopods. Salzburg, Austria.

Fraschetti, S., Gambi, C., Giacosa, A., Musco, L., Terlizzi, A., Danovaro, R., 2006. Structural and functional responses of meiofauna rocky assemblages to sewage pollution. Mar. Pollut. Bull. 52, 540–548.

Fry, J.C., 1988. Determination of biomass. In: Austin, B. (Ed.), Methods in Aquatic Bacteriology. Wiley, London, pp. 27–72.

Gerchakov, S.M., Hatcher, P.G., 1972. Improved technique for analysis of carbohydrates in sediments. Limnol. Oceanogr. 17, 938–943.

Giere, O., 1993. Meiobenthology. Springer, Berlin, 328 pp.

Gyedu-Ababio, T., Baird, D., 2006. Response of meiofauna and nematode communities to increased levels of contaminants in a laboratory microcosm experiment. Ecotox. Environ. Safe. 63, 443–450.

Harguinteguy, C.A., Cofré, M.N., De Ward, C.T.P., 2012. Change in the meiofauna community structure of sandy beaches of the Nuevo Gulf (Chubut, Argentina). Papeis Avulsos de Zoologia (SAO Paulo) 52 (34), 411–422.

Hartree, E.F., 1972. Determination of proteins: a modification of the Lowry method that give a linear photometric response. Anal. Biochem. 48, 422–427.

Heip, C., Vinex, M., Vranken, G., 1985. The ecology of marine nematodes. Oceanogr. Mar. Biol. Annu. Rev. 23, 399–489.

Higgins, P.P., Thiel, H., 1988. Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, D.C., p. 488.

Hondeveld, P.-G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the meiofauna community structure of sandy beaches of the Nuevo Gulf (Chubut, Argentina). Papeis Avulsos de Zoologia (SAO Paulo) 52 (34), 411–422.

Lee, J.J., Tietjen, J.H., Mastropaolo, C., Rubin, H., 1977. Food quality and heterogeneous spatial distribution of meiofauna. Helgoländer Meeresunters 30, 272–279.

Leguerrier, D., Niquil, N., Boileau, N., Rzeznik, J., Pierreguy Sauriau, P.-G., Le Moine, O., Bacher, C., 2003. Numerical analysis of the food web of an intertidal mudflat ecosystem on the Atlantic coast of France. Mar. Ecol. Prog. Ser. 246, 17–37.

Lorenzen, C., Jeffrey, J., 1980. Determination of chlorophyll in sea water. Unesco Tech. Pap. Mar. Sci. 35, 1–20.

Maher, W., Batley, G.E., Lawrence, I., 1999. Assessing the health of sediment ecosystems: use of chemical measurements. Freshwater Biol. 41, 361–372.

Margalef, D.R., 1968. Perspectives in Ecological Theory. The University of Chicago Press, Chicago, pp. 111.

Marsh, J.B., Weinstein, D.B., 1966. A simple charring method for determination of lipids. J. Lipid Res. 7, 574–576.

Mirtó, S., Danovaro, R., 2004. Meiofaunal colonization on artificial substrates: a tool for biomonitoring the environmental quality on coastal marine systems. Mar. Pollut. Bull. 48, 919–926.

Mirtó, S., La Rosa, T., Mocciaro, G., Costa, K., Sara, G., Mazzola, A., 2004. Meiofauna and benthic microbial biomass in semi-enclosed Mediterranean marine system (Stagnone of Marsala, Italy. Chem. Ecol. 20 (1), 387–396.

Montagna, P.A., Coull, B.C., Herring, T.L., Dudley, B.W., 1982. The relationship between abundances of meiofauna and their suspected microbial food (diatoms and bacteria). Estuar. Coast. Shelf Sci. 17, 381–394.
Moreno, M., Ferrero, T.J., Gallizia, I., Vezzulli, L., Albertelli, G., Fabiano, M., 2008. An assessment of the spatial heterogeneity of environmental disturbance within an enclosed harbor through analysis of meiofauna and nematode assemblages. Estuar. Coastl Shelf Sci. 77, 565–576.
Parker, J.G., 1983. A comparison of methods used for the measurement of organic matter in marine sediment. Chem. Ecol. 1, 201–210.
Pascal, P.Y., Dupuy, C., Richard, P., Mallet, C., Chatelat, E.A., Niquil, N., 2009. Seasonal variation in consumption of benthic bacteria by meio- and macrofauna in an intertidal mudflat. Limnol. Oceanogr. 54 (4), 1048–1059.
Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144.
Plante, R., Plante-Cuny, M.R., Reys, J.P., 1986. Photosynthetic pigments of sandy sediments on the north Mediterranean coast: their spatial distribution and its effects on sampling strategies. Mar. Ecol. Prog. Ser. 34, 133–141.
Pusceddu, A., Serra, E., Sanna, O., Fabiano, M., 1996. Seasonal fluctuations in the nutritional value of particulate organic matter in a lagoon. Chem. Ecol. 13, 21–37.
Pusceddu, A., Dell’Anno, A., Fabiano, M., Danovaro, R., 2009. Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. Mar. Ecol. Progr. Ser. 375, 41–52.
Pusceddu, A., Gambi, C., Corinaldesi, C., Scopa, M., Danovaro, R., 2014. Relationships between meiofaunal biodiversity and prokaryotic heterotrophic production in different tropical habitats and oceanic regions. PLoS ONE 9 (3), 1–17.
Rosenberg, R., 1995. Benthic marine fauna structured by dy- namic processes and food availability. Neth. J. Sea Res. 34, 303–317.
Scho¨ nborn, W., 1982. Die Ziliatenproduktion in der mittleren Saale. Limnologica (Berlin) 14, 329–346.
Scho¨ nborn, W., 1984. The annual energy transfer from the communities of Ciliota to the population of Chaetogaster diastrophus (Gruithuisen, 1828) in the River Saale. Limnologica (Berlin) 16, 15–23.
Shannon, C.E., Weaver, W., 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, 111 pp.
Sleigh, M.A., Baldock, B.M., Baker, J.H., 1992. Protozoan communities in chalk streams. Hydrobiologia 248, 53–64.
Villora-Moreno, S., Capaccioni Azzati, R., Garcia Carrascosa, A.M., 1991. Meiobenthos of sandy beaches from the Gulf of Valencia (Western Mediterranean): ecology of interstitial polychaetes. Bull. Mar. Sci. 48, 376–385.
Walters, K., Moriarty, D.J.W., 1993. The effects of complex trophic interactions on marine microbenthic community. Ecology 74, 1475–1489.