

Meiofaunal community structure in Thermaikos Gulf: Response to intense trawling pressure

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Abstract

Among the most important impacts of trawling is the disturbance of the benthic environment as well as the mortality of the larger benthic organisms, which is caused by the passage of the fishing gear. Meiofauna, which are among the smallest benthic organisms, may be more resistant to disturbance by trawling since they are likely to be re-suspended rather than killed by trawls. Their short generation times allow populations to withstand elevated mortality. In this study, we determined the effect of trawling disturbance, season and sediment type on the structure of meiofaunal communities in a commercial fishing ground in Thermaikos Gulf, north Aegean Sea, Greece. The trawling season is limited to 8 months between October and May. A grid of five nearshore stations was chosen along a north–south productivity gradient and an additional offshore station was included as a reference point. Sediment chemistry and meiofaunal community structure were studied before the trawling season started, as well as 1 and 4 months after the initiation of the fishing period. Results showed that there were no short term (30 days) trawling impacts on meiofauna in terms of abundance and community structure but that there were recognizable effects on the community structure of nematodes and the abundance of polychaetes. In contrast, most meiofaunal taxa displayed significant seasonal variability, 4 months after the initiation of the fishing period; however, other closely related factors such as temperature, sediment particle size and primary productivity are more likely to be responsible for the observed patterns.

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1. Introduction

Bottom trawling is a source of disturbance and is known to result in long-term and large-scale changes both on the seabed and the composition of benthic marine assemblages (de Groot and Lindeboom, 1994; Jennings and Kaiser, 1998;

Lindeboom and de Groot, 1998; Hall, 1999; Collie et al., 2000; Kaiser and de Groot, 2000; Kaiser et al., 2000). Investigations by means of experimental and field studies showed that the direct contact of the fishing gear with the sea bottom may have positive or negative effects on the benthos. Positive effects can be the turnover of the sediment surface, causing the oxygenation of the deeper layers and release of buried organic matter and nutrients. On shallow continental shelves, this could lead to a general increase in primary production and subsequently to

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increases in benthic biomass and densities. On the other hand, the release of buried nutrients could also lead, due to excessive eutrophication, to hypoxic or even anoxic conditions which in turn would result in a significant reduction of the benthic populations due to mortality (Kemp and Boynton, 1992; Heip, 1995). Trawling may also be beneficial for scavenging species if their increased mortality is balanced by an increasing food supply from discarded offal, by-catch and moribund animals left in trawl tracks (Lindeboom and de Groot, 1998). On the other hand, negative effects may be more important since they include the alteration of the sediment surface, the destruction of habitats and the removal or damage of the larger organisms, thus resulting in an overall reduction in production. The latter is probably a key limiting factor for demersal fish production, since benthic production is known to be the food and energy resource for most demersal fish (Rijnsdorp and van Beek, 1991; Edgar and Shaw, 1995; Rijnsdorp and van Leeuwen, 1996).

A series of papers have been published concerning the impact of this particular type of disturbance for different gear types (Eleftheriou and Robertson, 1992), intensity of trawling disturbance (Lindeboom and de Groot, 1998) and habitat type (Auster et al., 1996; Kaiser and Spencer, 1996), showing similar results regarding macrofaunal succession but large differences regarding the spatial extent of the impacts. Most of these studies have focused on impacts on larger animals, i.e. macrofauna (de Groot, 1984; Jones, 1992; Kaiser et al., 1996; Gilkinson et al., 1998; Lindegarth et al., 2000; Smith et al., 2000) and megafauna (Collie et al., 1997; Watling and Norse, 1998), primarily because reduction in their abundance and diversity are an important conservation issue.

In recent years, there has been an increase in studies worldwide which consider the use of meiofauna as potential indicators of anthropogenic disturbance in aquatic ecosystems (Coull and Chandler, 1992). However, despite the increasing interest, only a few studies of trawling impacts on meiofauna have been undertaken so far, most of them being experimental (Pranovi et al., 2000; Ernst et al., 2002; Schratzberger et al., 2002; Schratzberger and Jennings, 2002). Long-term effects of an anthropogenic disturbance on deep-sea meiobenthos were also investigated during the disturbance and recolonization experiment (DISCOL) conducted in early 1989 (Ahnert and

Schriever, 2001; Vopel and Thiel, 2001). Thus, the effects of trawling disturbance on meiofauna on real fishing grounds are almost unknown (Schratzberger et al., 2002).

Meiobenthic animals may be more resistant than the larger animals to disturbance by trawling because they are likely to be re-suspended rather than killed by trawls and because their high reproduction rates allow populations to withstand elevated mortality. Previous studies on the impacts of fishing on meiofaunal assemblages have pointed out that there were no short to medium-term trawling impacts on meiofaunal diversity or biomass, but there were mild effects on community structure and that any impacts due to trawling were minor in relation to seasonal changes in the meiofaunal communities (Schratzberger et al., 2002; Schratzberger and Jennings, 2002). In contrast, trawling had a significant impact on the composition of nematode assemblages since diversity and species richness were lower in areas subject to high levels of trawling disturbance than in areas subject to low or medium levels of disturbance (Schratzberger and Jennings, 2002).

Most field studies on the response of benthic communities to trawling have been undertaken in northern European waters (Lindeboom and de Groot, 1998). However, not all results may be relevant to the Mediterranean because the latter is markedly different since it contains some of the most extreme oligotrophic waters in the world (Dugdale and Wilkerson, 1988). It also displays high salinity, high temperatures and unique hydrographic characteristics with negligible tidal currents (Turley, 1999). Furthermore, studies on this particular type of disturbance in the eastern Mediterranean are practically non-existent (Smith et al., 2000).

In the present paper, data on the response of meiofauna to trawling are reported from real fishing grounds in Greek coastal waters. Samples were collected before and after the official initiation of the fishing period from a grid of five stations placed in a north–south productivity gradient. A reference station placed further offshore was also taken into account. In this context, the present paper provides information that could improve our understanding of processes related to anthropogenic disturbance (such as commercial trawling), as well as the response of the meiofauna to such an impact.

2. Methods

2.1. Study site and sampling procedures

Bottom trawling impacts were investigated at five stations placed on a north–south productivity gradient in the Thermaikos Gulf in the northern Aegean (Fig. 1). An offshore station was also investigated. The stations were placed between the 50 and 100 m isobaths, where most of the commercial trawling takes place. The Gulf is characterized by smooth bottom topography and four major rivers (Aliakmon, Loudias, Axios and Gallikos) flow into the Gulf, with a total annual water

discharge of $10.2 \times 10^6 \text{ m}^3$. Trawling takes place from the beginning of October until the end of May (open trawling season), while for the remaining months any fishing activity in the area is prohibited. Sampling was done just before the start of the trawling season (September 2001) and 1 and 4 months after the initiation of the fishing period (October 2001 and January 2002, respectively) on board the R/V AEGEO. Samples were collected using a Bowers and Connelly multicorer that allowed for undisturbed samples (Barnett et al., 1984) and penetrated to a depth of 20–30 cm in the sediment. In all cases, three replicates were taken from different deployments of the multicorer

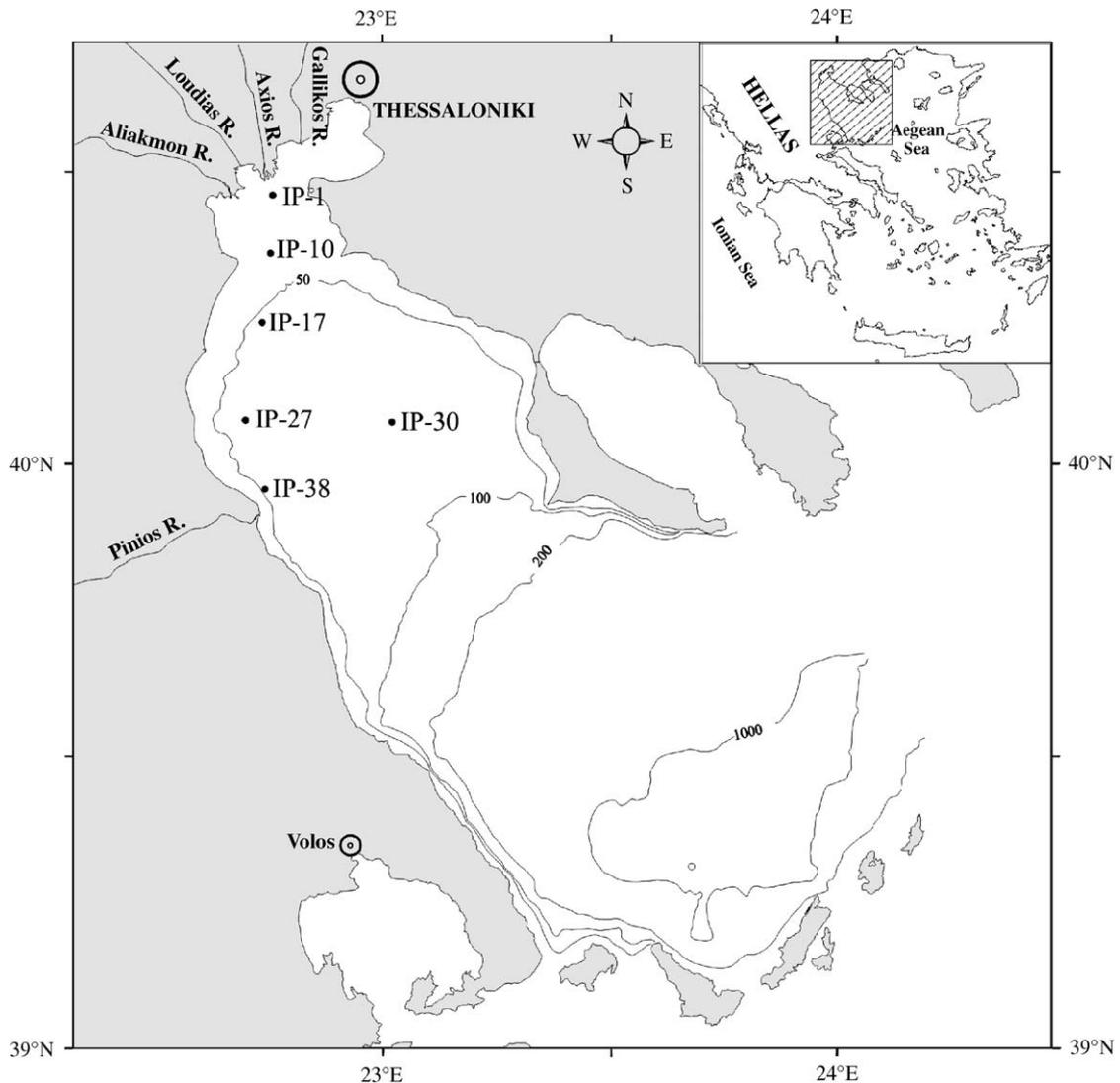


Fig. 1. Map of the investigation area including the sampling stations in the Thermaikos Gulf.

in order to avoid pseudo-replication (Hurlbert, 1984).

2.2. Determination of environmental variables

Samples were collected by sub-sampling the cores of the Multicorer using smaller 3.2 cm internal diameter cores. Samples were then sectioned into six layers (0–0.3, 0.3–1, 1–2, 2–4, 4–6 and 6–10 cm) and stored frozen under -20°C until further laboratory analysis. Chlorophyll *a* and phaeopigment concentrations were determined according to the fluorometric method of Yentsch and Menzel (1963) and Lorenzen and Jeffrey (1980), using a TURNER 112 fluorometer. A 90% acetone was used as an extractant, while phaeopigments were estimated by acidification with 0.1 N HCl. The fluorometer was calibrated using an acetone extract of pure chlorophyll *a* from the algae *Anacystis nidulans* obtained from SIGMA. Total organic carbon (TOC) measurements were undertaken according to Hedges and Stern (1984), with the use of a Perkin Elmer CHN 2400 analyser.

Redox potential (Eh) measurements were acquired at 1 cm intervals with the use of calibrated combined electrodes (Russell pH, Scotland, type no. CMPT 11/280/SA1.5), as described in Pearson and Stanley (1979). Sediment particle size analyses of the top 4 cm layer was carried out by wet sieving through a $63\ \mu\text{m}$ sieve to separate the coarse and fine fraction, while the % silt/clay was determined by pipette analysis (Buchanan, 1984).

Organic carbon mineralization was estimated according to Dauwe et al. (2001) by measuring the production of CO_2 in the headspace above sediment water slurries. Samples for CO_2 were collected using cores of 3.2 cm internal diameter to sub-sample the cores of the Multicorer and sectioned into six layers (0–0.3, 0.3–1, 1–2, 2–4, 4–6 and 6–10 cm). Slurries were flushed with CO_2 -free air and incubated in the dark at in-situ bottom water temperature until further laboratory analysis. At the end of the incubation period (60 days), samples from the headspace gas was analysed for CO_2 using a HP 5890 II gas chromatographer equipped with a thermal conductivity detector.

2.3. Meiofauna and Foraminifera

All samples were collected using cores of 4.5 cm internal diameter to sub-sample the cores of the

Multicorer. Samples were sliced in 0.5 cm sections down to 2 cm, and in 1 cm sections thereafter down to 10 cm, placed in 6% magnesium chloride solution to promote tissue relaxation and preserved with 10% buffered formalin in pre-filtered seawater solution until later analysis. In the laboratory, samples were stained with Rose Bengal solution ($0.5\ \text{g l}^{-1}$) and sieved through 500 and $32\ \mu\text{m}$ mesh. The fauna from the fraction remaining on the $32\ \mu\text{m}$ sieve were extracted by triplicate centrifugation in Ludox TM [density $1.15\ \text{g cm}^{-3}$; Heip et al., 1985]. All meiobenthic animals in the supernatant and the stained foraminifera in the residual were counted and identified under a stereomicroscope.

Nematode biomass was estimated by measuring the length (excluding the filiform tail section, if present) and maximal body width of at least one hundred randomly selected individuals from each station. All measurements were made using a light microscope and a drawing tube. Individual biomass was calculated from Andrassy's (1956) formula for body weight ($\text{mg wwt} = L \times W^2 / 16 \times 10^5$) and a dry to wet weight ratio of 0.25 was assumed (Wieser, 1960).

2.4. Data analysis

For each taxon, differences in density between months and sampling stations were investigated by means of two-way analyses of variance (ANOVA). Paired a posteriori comparisons of density estimates were carried out with the Tukey test using 95% confidence limits. When the conditions for the use of parametric tests were not fulfilled, data were $\log_{10}(x + 1)$ transformed and the assumption of homoscedasticity was checked using the Cochran's test.

Multivariate analyses (cluster analysis) were performed based on the Bray–Curtis similarity index after fourth root transformation by means of the PRIMER software (Clarke and Warwick, 1994). The significance of the resulting groups was tested using the ANOSIM test (Clarke, 1993).

Differences in nematode length frequency distributions were investigated with the Kolmogorov–Smirnov two-sample test and the Spearman's rank correlation coefficient was used to correlate the faunal data with the various environmental parameters measured.

3. Results

3.1. Environmental data

All the investigated parameters obtained from the surface sediments during all three sampling events displayed a north–south productivity gradient. Bottom water temperature ranged from 16–21 °C in September–October to 9–10 °C in January. All sediments were classified as silty sediments (median grain size between 0.012 and 0.024 mm) with the exception of station IP-30 which was characterized as fine sand (Table 1). The redox potential (Table 1) attained its lowest values at stations IP-1 and IP-38 both of which receive heavy organic loading being under the riverine influence of Axios and Pinios. With the exception of the innermost station (IP-1) in September, all values were well above zero. Stations placed in the inner part of the Gulf display high chlorophyll *a* and organic carbon concentrations, which tend to decrease drastically towards the southern areas of the Gulf as well as offshore (Table 1). Carbon mineralization rates were higher in the inner part of the Gulf, displaying a slight decrease along the north–south productivity (Table 1). Markedly lower values ($<0.12 \mu\text{M CO}_2/$

d/g) were only measured at the offshore station (IP-30). SCOC measurements (unpublished data) verified the trend displayed by the carbon mineralization rates with higher consumption rates measured at stations IP-01 and IP-10 and lower at stations IP-17 and IP-38.

3.2. Faunal data

3.2.1. Metazoan

Total metazoan meiofaunal density in the top 4 cm of the sediments ranged from 1108 to 3552 ind./10 cm² before the initiation of the trawling period in September and from 927 to 3791 ind./10 cm² during the trawling period in October. During winter time in January, total metazoan density ranged from 376 to 3711 ind./10 cm². Nematodes were the most abundant taxon (Table 2) at all stations, ranging between 51% and 75% in September, 46% and 75% in October and 57% and 77% in January. Copepods together with their nauplii were the second most abundant taxon, ranging between 9% and 13% in September, 4% and 16% in October and 10% and 27% in January. From the remaining metazoan groups, only kinorhynch and polychaetes showed a relative

Table 1
Summary of sediment environmental data obtained from three sampling events in Thermaikos Gulf

	Stations	Depth (m)	Latitude (N)	Longitude (E)	MD	% S&C	Carb. min.	Chla	OC	Eh
September	IP-1	30	40° 28.92	22° 45.00			0.14	2.34	1.19	–8
	IP-10	41	40° 22.08	22° 43.50				5.62	1.04	206
	IP-17	55	40° 15.00	22° 42.50			0.09	5.95	0.86	413
	IP-27	64	40° 05.00	22° 40.50	0.013	97.9		4.46	1.02	486
	IP-38	51	39° 58.00	22° 43.20	0.012	98.0	0.18	2.94	0.99	98
	IP-30	86	40° 05.00	23° 00.00			0.09	0.50	0.32	475
October	IP-1				0.014	98.1	0.30	5.71	1.44	45
	IP-10				0.013	97.5		6.56	1.26	108
	IP-17				0.015	90.8	0.33	4.62	0.90	143
	IP-27				0.013	96.3		2.58	0.98	167
	IP-38				0.013	97.9	0.19	2.52	1.11	102
	IP-30				0.127	40.9	0.12	0.83	0.57	457
January	IP-1				0.014	99.1	0.03	10.40	1.51	274
	IP-10				0.013	92.7		6.10	1.01	112
	IP-17				0.012	94.4	0.02	4.87	0.95	388
	IP-27				0.013	94.9		4.95	0.94	88
	IP-38				0.013	97.8	0.02	3.68	1.00	83
	IP-30				0.024	71.1	0.01	1.72	0.44	328

KEY: MD—Median diameter (mm); % S&C—% of silt and clay; Carb. min.—Carbon mineralization rates in the top 1 cm of the sediment; Chla—Chlorophyll *a* ($\mu\text{g/g}$) in the top 0–0.3 mm of the sediment; OC—% of organic carbon in the top 4 cm of the sediment; and Eh—Redox potential, at 2 cm depth.

Table 2

Mean density (mean number of individuals per 10 cm² ± SE) of all meiobenthic taxa and mean percentage of the most abundant taxa (nematodes, foraminiferans and copepods including nauplii), for all sampling sites over the sampling periods

	Sampling stations	Mean no. of metazoans per 10 cm ²	Mean no. of foraminiferans per 10 cm ²	Mean % nematodes	Mean % foraminiferans	Mean % copepods
Before trawling (September)	1	1213 ± 283	449 ± 150	54	31	10
	10	2870 ± 203	1231 ± 147	51	29	13
	17	1486 ± 119	690 ± 115	52	31	11
	27	2609 ± 254	438 ± 46	68	14	10
	30	1562 ± 88	105 ± 7	75	6	13
	38	2799 ± 278	1175 ± 378	57	29	9
30 days of trawling (October)	1	1873 ± 128	576 ± 131	59	23	10
	10	3114 ± 309	1356 ± 238	46	30	16
	17	2045 ± 63	439 ± 69	59	17	16
	27	1198 ± 78	365 ± 44	68	23	4
	30	1464 ± 139	111 ± 15	75	7	10
	38	2175 ± 178	1350 ± 156	53	38	5
120 days of trawling (January)	1	2253 ± 246	423 ± 51	62	15	10
	10	1223 ± 85	83 ± 9	58	6	18
	17	1583 ± 127	35 ± 9	57	2	27
	27	2470 ± 365	69 ± 3	64	3	19
	30	888 ± 153	12 ± 2	77	1	14
	38	2694 ± 224	140 ± 28	70	5	18

significance, contributing on average more than 1% to the total metazoan abundance. At the central stations of the transect particularly, kinorhynchans were relatively abundant, reaching in some samples as much as 9% of the total metazoan abundance. All other groups such as molluscs (both gastropods and bivalves), nemertines, ostracodes, turbellarians and other soft-body meiofauna comprised less than 1% of the total abundance.

The densities of the most important metazoan taxa comprising on average more than 1% of the total metazoan fauna, are presented in Figs. 2–4. Although nematodes varied considerably along the transect line and between the three sampling events, there were no statistically significant interactions (two-way ANOVA, $p > 0.05$) between seasons and stations (Table 3). Between stations, total nematode abundance was significantly lower at stations IP-17 and IP-30, which were those not directly influenced by the riverine discharge of rivers Axios, Aliakmon and Pinios (Fig. 1). The observed temporal variation in nematode abundance could not be attributed

to trawling since there were no significant differences in nematode abundance before and 30 days after the initiation of the fishing period (see Table 3, post hoc comparisons). In a similar way, copepods (without their nauplii), total metazoans as well as the remaining metazoans (figures not shown here) did not show any significant differences in abundance before and 30 days after the initiation of the fishing period. The only difference from the above pattern was shown by polychaetes (Fig. 4 and Table 3, post hoc comparisons), which showed significant differences before and after the initiation of the fishing season, having in general higher abundances during the trawling period.

3.2.2. Nematode biomass

Nematode biomass differed significantly between September and October (Kolmogorov–Smirnov Test, $p < 0.05$), the only exception being station IP-30, which was characterized by coarse sediments. Differences were most obvious in the larger size classes since the peak size class shifted towards

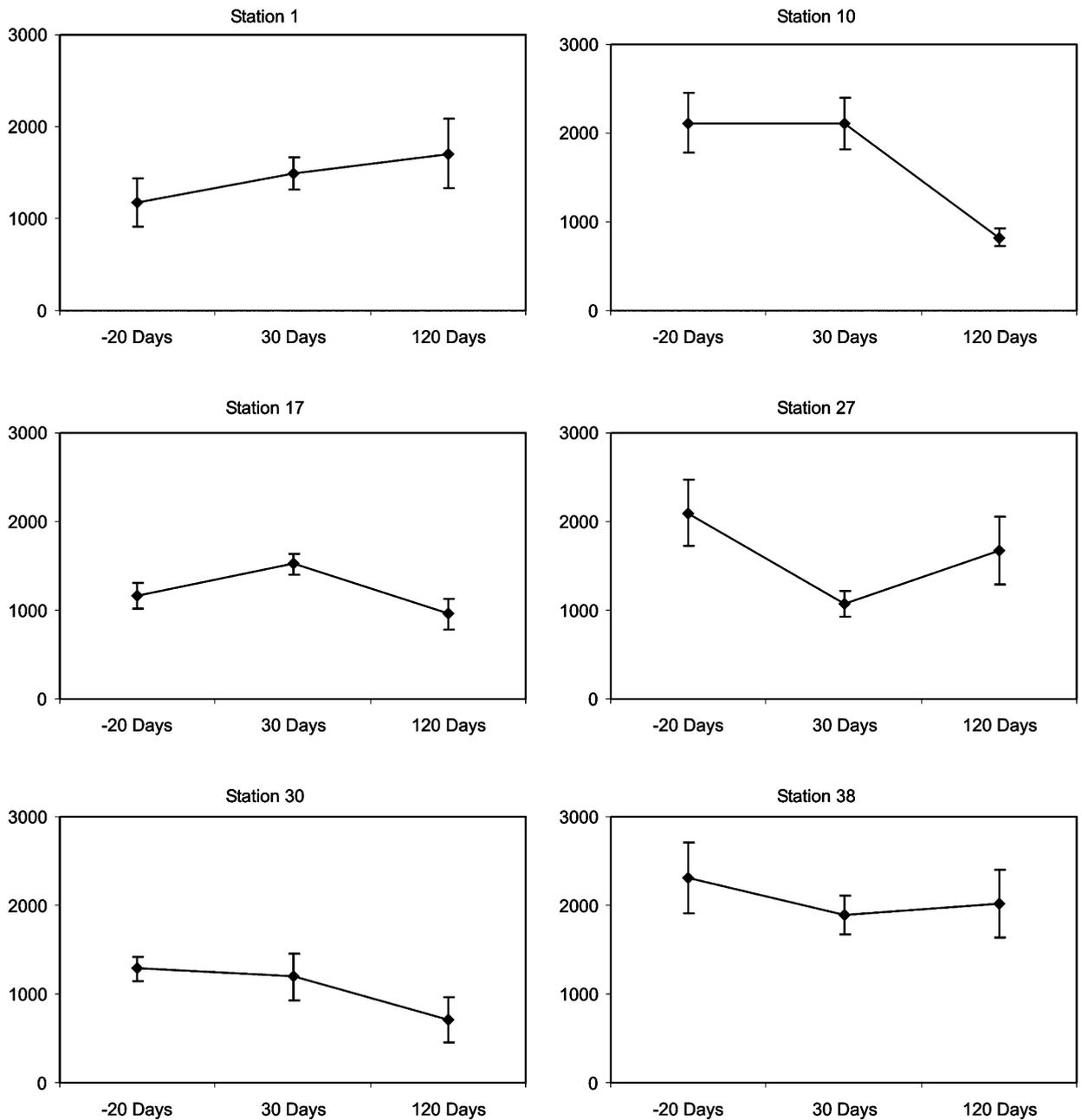


Fig. 2. Average number of nematodes per 10 cm² ± standard error before and 30 and 120 days after the initiation of the fishing period.

lower size classes (Fig. 5). The maximum individual length before the initiation of the fishing period ranged between 1833 and 2653 μm , whereas 30 days after the start of the fishing period the maximum length decreased significantly, ranging from 1326 to 1881 μm . Although the length frequency distributions at all stations and all sampling events were

strongly skewed towards the smaller sizes (Fig. 5), this pattern was more pronounced before the initiation of the fishing period.

3.2.3. Protozoa

Foraminifera contributed significantly to the total meiofauna, comprising in some samples almost half

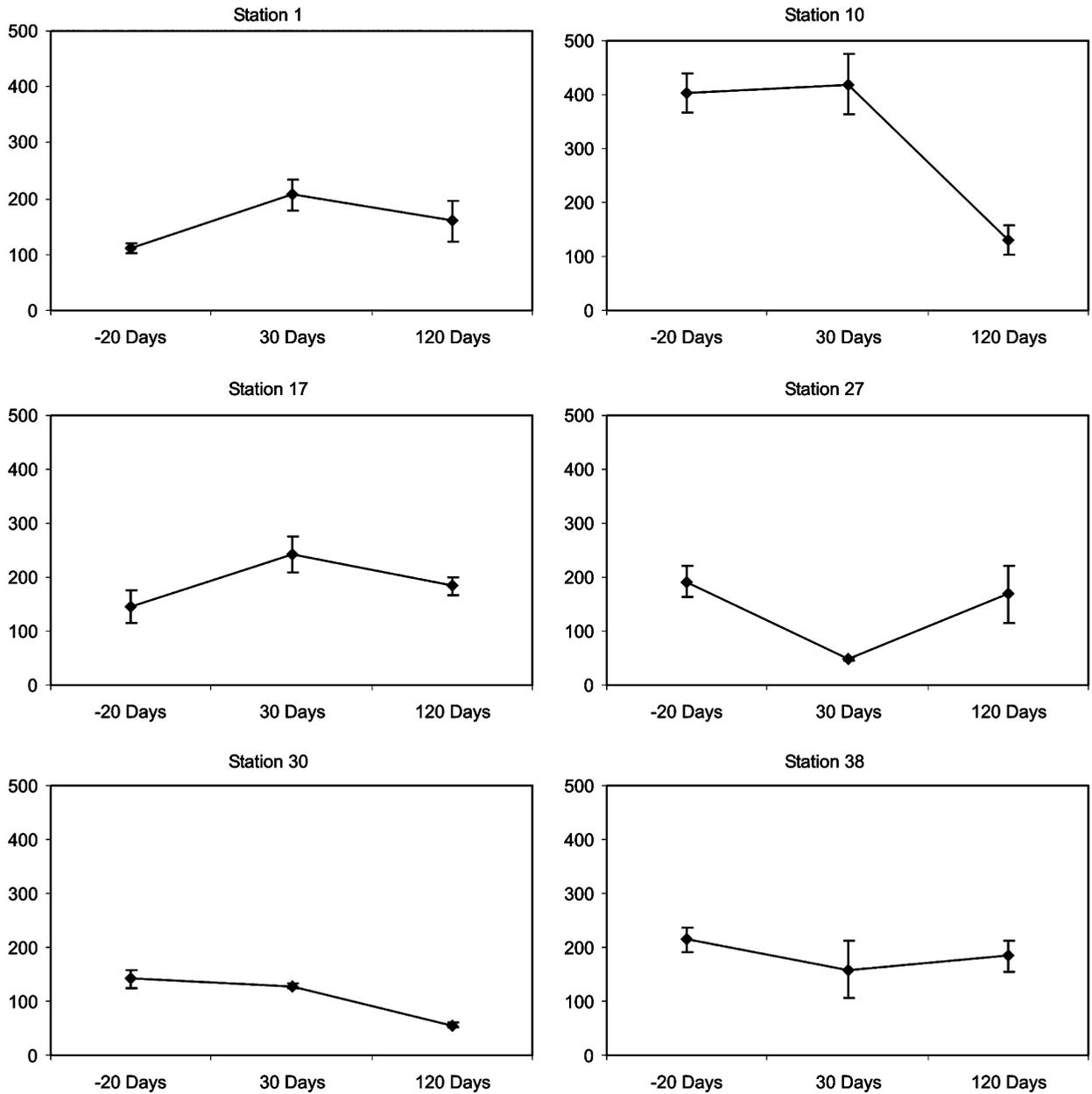


Fig. 3. Average number of adult copepods per 10 cm² ± standard error before and 30 and 120 days after the initiation of the fishing period.

of the total abundance. Before the trawling period (September 2001), their abundance ranged from 80 to 2477 ind./10 cm², whereas after the initiation of the fishing season their abundance ranged from 70 to 2027 ind./10 cm² in October and from 7 to 517 ind./10 cm² in January. During September 2001, foraminifera comprised 14–31% of the total meiofauna at stations 1, 10, 17, 27 and 38, whereas at station 30 they comprise 6% of the total abundance.

During October 2001, foraminifera comprised 7–38% of the total community, whereas in January their abundance dropped significantly, comprising on average only 6% of the total abundance (range 1–15%).

Similar to nematodes and metazoan meiofauna in general, foraminifera varied considerably along the transect line and between the three sampling events. However there were no statistically significant

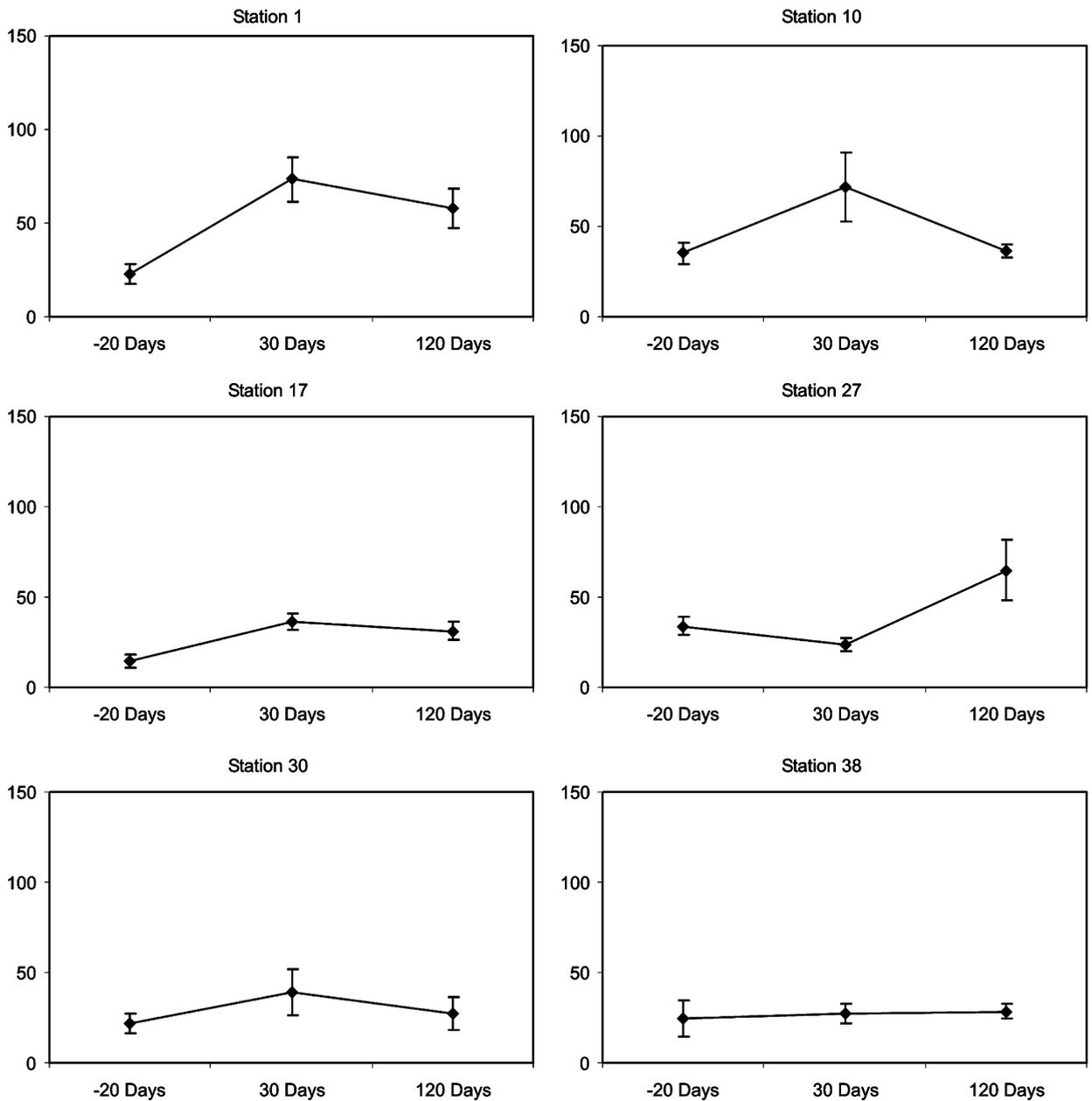


Fig. 4. Average number of polychaetes per 10 cm² ± standard error before and 30 and 120 days after the initiation of the fishing period.

interactions at a 5% significant level (Table 3). On a spatial scale, and with the exception of station IP-1 (where the lowest redox levels were measured), foraminiferal abundance was significantly higher at stations directly influenced by the river outflows (stations IP-10 and IP-38). Temporally, the observed variation again could not be attributed to trawling since there were no significant differences in abundances before and 30 days after the

initiation of the fishing period (see Table 3, post hoc comparisons).

3.2.4. Structural analysis

Multivariate analysis with the use of all three replicates indicated that replication was reasonably good. For reasons of simplicity and in order to present the data in a more comprehensive way further analysis was carried out with combined

Table 3
Results from two-way ANOVA

Group	ANOVA-two way		Tukey a posteriori test		
	F	P	Sep	Oct	Jan
<i>Nematoda</i>					
Season	5.45	0.010*	—————		
Station	6.72	<0.001**	—————		
Season × Station	2.24	0.052			
<i>Copepoda</i>					
Season	7.12	0.03*	—————		
Station	18.32	<0.001**	—————		
Season × Station	7.17	<0.001**			
<i>Polychaeta</i>					
Season	3.33	0.049*	—	—————	
Station	3.26	0.025*			
Season × Station	2.57	0.029*			
<i>Total Metazoa</i>					
Season	2.58	0.093			
Station	6.65	<0.001**			
Season × Station	3.57	0.005*			
<i>Foraminifera</i>					
Season	101.94	<0.001**	—————		
Station	30.36	<0.001**	—————		
Season × Station	1.03	0.439			
<i>Total Protozoa</i>					
Season	71.97	<0.001**	—————		
Station	36.52	<0.001**	—————		
Season × Station	0.97	0.479			

Copepoda, Foraminifera and Total Protozoa were $\log_{10}(x + 1)$ transformed, to normalize the data.

* $p < 0.05$.

** $p < 0.01$.

replicates. Cluster analysis using square root transformed data of meiofaunal density, clearly separated samples from station IP-30 as this was the station with the coarsest sediments as well as the lowest chlorophyll *a* and organic carbon values (Fig. 6). For the remaining samples, a similar pattern was produced with the ANOVA (Table 3), since samples before and 30 days after the initiation of the trawling period could not be separated. In contrast, all samples from January, with the exception of station IP-1, were grouped together forming a separate cluster. This was confirmed from the pairwise ANOSIM tests which showed that the

structure of meiofauna were different at station IP-30 ($R = 0.79$, $p < 0.01$) and in January ($R = 0.71$, $p < 0.01$).

The non-parametric correlation between the biological abundances and the measured environmental variables are presented in Table 4. Most meiobenthic groups were positively correlated with chlorophyll *a* and the organic carbon, whereas foraminifera were positively correlated with the median diameter of the sediment and negatively with the percentage of silt and clay.

4. Discussion

Side scan sonar imaging before and about 1 month after the initiation of the trawling period clearly showed that almost 80% of the trawling area is intensively disturbed by the trawl gear. However, despite the conclusive evidence, sediment grain size analysis before and after trawling showed no change in the physical characteristics of the sediment, a result consistent with previous studies (Caddy, 1973; Eleftheriou and Robertson, 1992; Pranovi and Giovanardi, 1994; Kaiser and Spencer, 1996; Tuck et al., 1998). The effects on the sediment chemistry were also not evident since chloroplastic pigments as well as other parameters, such as organic carbon and phaeopigments, were similar before and after trawling.

Our results showed that trawling did not have a drastic effect on the nematode community structure, both in terms of biomass and size frequency distribution. With the exception of station IP-30, biomass was significantly lower 30 days after trawling at all stations, mainly because of the disappearance of individuals belonging to the larger size classes. Body length distributions of nematodes have been discussed in a number of different papers (Soetaert and Heip, 1989; Vanhove et al., 1995; Soltwedel et al., 1996). Size frequency distributions of nematodes are typically skewed towards the smaller size classes with a longer tail extending into the larger size classes. The reason for this is mainly because of the large contribution of juveniles to the smaller size classes and the deceleration of their growth as they reach adulthood in a certain class (Soetaert et al., 2002). In Thermaikos Gulf, the size frequency distribution of nematodes showed the typical skewed distribution. However, 30 days after trawling most of the larger individuals were absent, indicating thus an alteration of the nematode community due to the impact from trawling. A

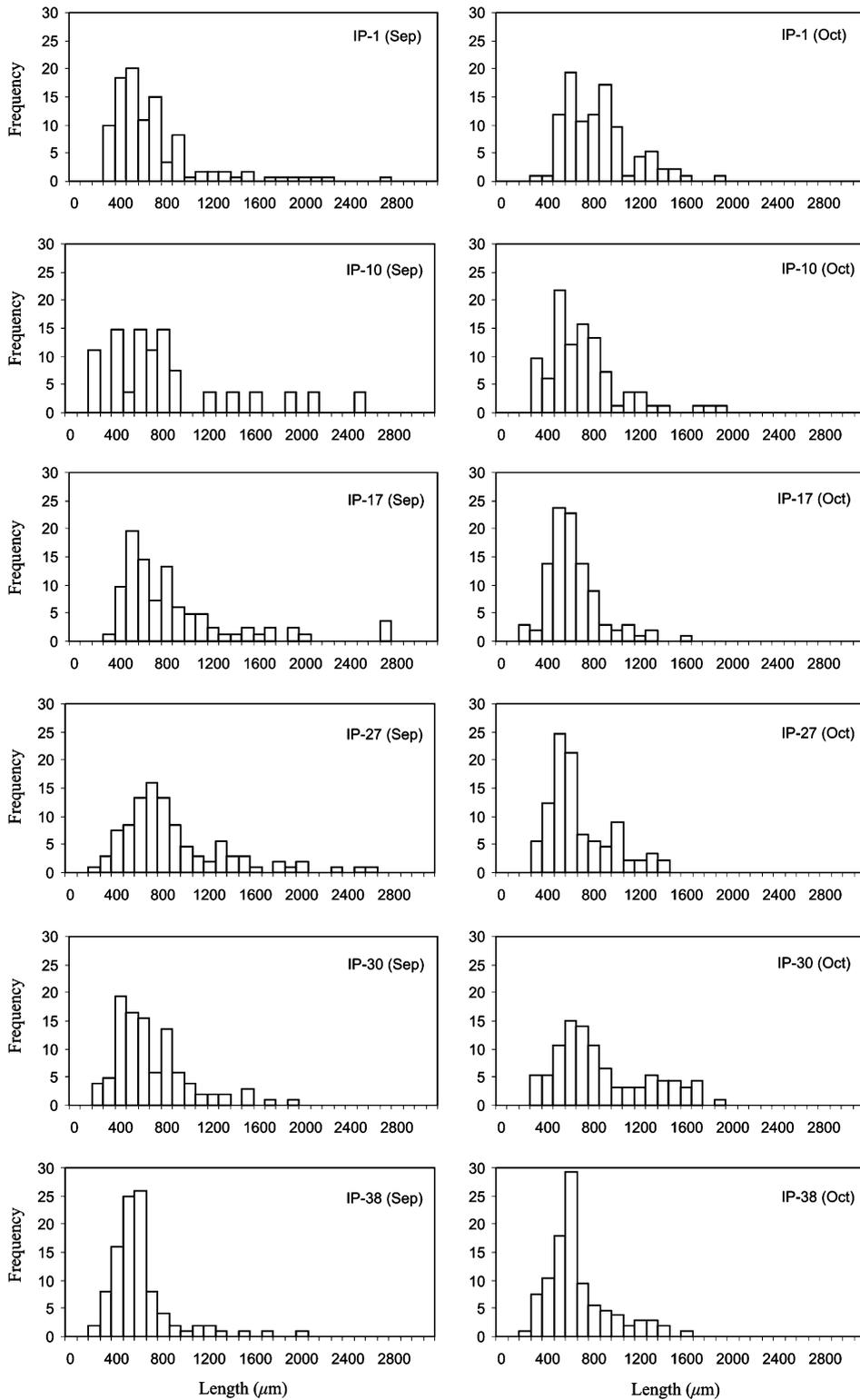


Fig. 5. Length–frequency distribution of nematodes before and 30 days after the initiation of the fishing period. Size classes were selected at increasing intervals of 100 µm.

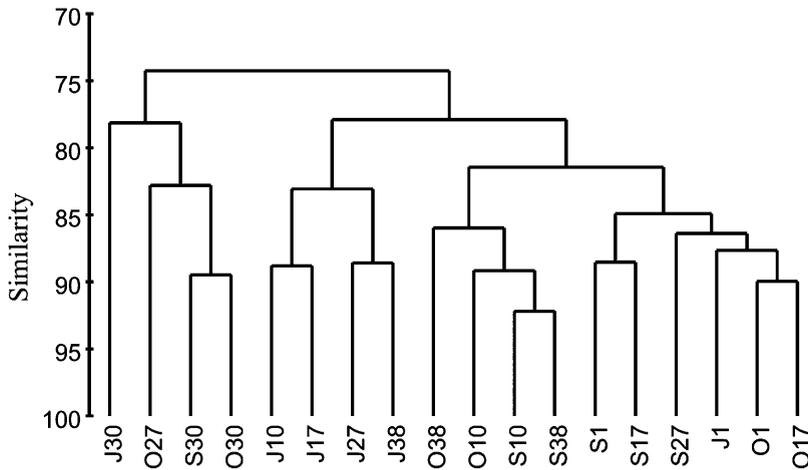


Fig. 6. Bray–Curtis similarity dendrogram on square root transformed abundance data. Letters refer to sampling events (S: September; O: October; J: January) and numbers to stations.

Table 4

Spearman correlation coefficient between sediment environmental variables and those meiobenthic groups comprising, on average, more than 1% of the total abundance

	Nematoda	Copepoda	Polychaeta	Ostracoda	Gastrotricha	Kinorhyncha	Turbellaria	Ciliophora	Foraminifera
Depth (m)	—	—	−0.70*	—	—	—	—	—	—
MD	—	—	—	—	—	—	—	—	0.88**
% S&C	—	—	—	—	—	—	—	—	−0.76*
Carb. min.	—	—	—	—	—	—	—	—	—
Chla	—	—	0.67*	—	0.91**	—	0.74*	0.76*	—
OC	—	—	0.77*	—	0.67*	−0.68*	—	—	—
Eh	—	—	—	—	—	—	—	—	—

Key: MD—Median diameter; % S&C—% of silt and clay; Carb. min.—Carbon mineralization rates in the top 1 cm of the sediment; Chla—Chlorophyll *a* (µg/g), in the top 0–0.3 mm of the sediment; OC—% of organic carbon in the top 4 cm of the sediment; and Eh—Redox potential, at 2 cm depth.

**p* < 0.05.
 ***p* < 0.01.

possible explanation for this could be the higher resilience shown by smaller individuals to sediment removal, re-suspension and re-layering of the sediment. However, it is difficult to explain the exception observed at station IP-30, which is probably due to the fact that this particular station had much coarser sediments.

Apart from the differences in the biomass spectra of nematodes, no other differences were observed before and after trawling in terms of the meiofaunal community structure. Nematodes, which were the dominant group, were not affected in terms of abundance by trawling, 30 days after the initiation of the fishing period. In a similar way, no other group showed any clear sign of disturbance. The only exception to the above general rule was the

pattern observed for polychaetes, which displayed higher abundances during the trawling period. This is considered to be a rather unexpected observation since the polychaete fauna of the Greek shelf areas consist mostly of soft fragile forms (Eleftheriou and Smith, 1993), and therefore is expected to be impacted from trawling. However, most species were omnivorous feeding at the sediment surface and as such they may be favoured by the disturbance caused by trawling since the latter can create a significant food resource (moribund benthos) for opportunistic species (Kaiser and Spencer, 1994; Smith et al., 2000). Similar to the univariate analysis, multivariate analyses could not reveal any impact of trawling 30 days after the initiation of the fishing period.

The main effect of trawling on the fauna is the mortality of target and by-catch species but also the mortality of benthic species that are not caught in the nets but damaged by passing gear (Bergman and van Santbrink, 1994, 2000). Besides that, the gear disturbs the surface of the sediment and indeed Sediment Profile Imagery (Rhoads and Germano, 1982) and acoustic techniques have shown that trawling has also physical effects on the seabed, decreasing the roughness of the sea bottom and increasing compaction (Schwinghamer et al., 1996, 1998; Lindeboom and de Groot, 1998; Smith et al., 2003). Jennings et al. (2001) reported that trawling reduces the complexity of both the surface and internal structure of soft-sediment habitats. Furthermore, Mayer et al. (1991), showed that the passage of the trawl can be responsible for disturbing and relayering of the sediment, causing changes in grain size and altering its chemical composition. However, since meiofauna are among the smallest animals in benthic ecosystems and since they have very fast turnover times (Schwinghamer et al., 1986), they are expected to show little or no response to trawling. Furthermore, the passage of the fishing gear could be beneficial to those organisms that remain intact since it can have some potential positive effects such as the turn-over of the sediment and the release of buried organic matter and nutrients (Duplisea et al., 2001).

To date, the only studies on the effects of trawling on meiofauna have been experimental and the results were contradictory. Pranovi et al. (2000), showed that experimental trawling induced a change in the meiobenthic community structure (at the taxon level) which was most obvious 1 week after the impact. In this study, some of the taxa decreased whereas others increased in abundance, and thus the authors pointed out that indirect effect of disturbance, mediated through reworking and disturbance of the sediment might be more important than the direct effects for these organisms. Schratzberger et al. (2002) on the other hand, showed that there were no short- to medium-term (1–392 days after experimental trawling) impacts on meiofauna diversity or biomass but that there were mild effects on the community structure of nematodes, which were however attributed mostly to seasonal impacts on the assemblage structure rather than to trawling. In contrast, in a large-scale experimental study, the comparison of nematode assemblages in areas subject to different levels of trawling showed that trawling had a significant

impact on nematode diversity (Schratzberger and Jennings, 2002). Furthermore, Ernst et al. (2002) studying the distribution of benthic foraminifera after microhabitat destruction in a microcosm experiment, showed that a number of taxa displayed rapid migration presumably to find more favourable conditions whereas other taxa were more capable of tolerating the re-established conditions and thus did not feel an immediate stimulus to migrate. They remained in their position and expanded their populations. All of the above results indicate that the effects of trawling on the smaller component of the benthos such as the metazoan or protozoan meiofauna may be more subtle than those on the larger macrofauna.

Nematodes, as well as most of the other major meiofauna taxa, displayed significant seasonal variability 4 months after the initiation of the fishing period, showing in general lower abundances in January, although there were significant fluctuations for the different meiobenthic taxa. Recently, a growing number of studies investigating the effects of fishing disturbance on the benthic habitat, have used a Before After Control Impact (BACI) experimental design (Underwood, 1992). However, in areas with high fishing pressure, such as the Thermaikos Gulf, finding a suitable control site is extremely difficult if not impossible. We thus consider the 4-month period during which fishing is prohibited, not to be long enough to allow full recovery to pre-season levels. As a consequence, our sampling design may not allow to clearly separate between trawling and seasonal impacts. For this reason, it is unlikely that trawling alone is responsible for the above-mentioned pattern of lower abundances observed during January. It is more likely that other closely related factors such as temperature, sediment particle size and primary productivity may have an important influence on meiofauna community structure. In shallow areas, there is a tight coupling between benthic organisms and the fluctuation of food among the different seasons (Graf, 1992). This in turn results in a series of events that changes the entire dynamics of the system. Thus, an increase in temperature during spring is followed by a phytoplankton bloom resulting in an increase in the microbial biomass and the depletion of oxygen (Meyer-Reil, 1983; Graf, 1992). During winter, when the temperature decreases and the primary production is much lower, a reversal of the situation is expected. In the Eastern Mediterranean and specifically in the

Aegean Sea, studies on the seasonal variation of the meiobenthos are almost absent. In the only comprehensive seasonal study on meiofauna from the Aegean Sea, Lampadariou (2001) showed that nematode abundance as well as most other major meiobenthic taxa decreased significantly during winter following the very low concentrations of chloroplastic pigments in the sediments during that period. This could partly explain the observed differences in meiofaunal abundance between January and the September–October sampling periods. However, the south Aegean is characterized as one of the most oligotrophic areas in the world (Berman et al., 1984; Azov, 1986; Psarra et al., 2000), which is reflected both in the concentrations of phytopigments in the sediment and the abundance of meiofauna. On the contrary, the north Aegean Sea is a much more productive area, as shown by the concentrations of chlorophyll *a* in January, which remained high and comparable to those observed during September and October, thus reflecting the complicating dynamics of the shallow continental shelf ecosystem of Thermaikos Gulf. Furthermore, the strong correlations found in our study between chlorophyll *a* or organic carbon and most of the faunal indices indicate a clear connection between meiofauna and food availability, a relationship which has been reported from a few seasonal studies in shallow areas (Soyer, 1971; de Bovée and Soyer, 1974; Faubel et al., 1983; de Bovée et al., 1990; Ólafsson and Elmgren, 1997), although others have failed to detect any clear relationship (Warwick and Buchanan, 1971; Juario, 1975; Boucher, 1980).

The analysis of the impacts of trawling on the meiobenthic assemblages in Thermaikos Gulf indicate that there is a lack of response at the major taxon level and that in contrast, trawling has a mild effect on the nematode community structure. However, this lack of response on the major taxon level may be misleading if individual species within the taxon react differently, something that has been shown to apply very well for nematodes (Schratzberger and Jennings, 2002) as well as for foraminifera (Ernst et al., 2002).

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