Impact of offshore gas platforms on the structural and functional biodiversity of nematodes

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ABSTRACT

The Mediterranean Sea hosts hundreds of offshore gas platforms, whose activity represents a potential threat to marine ecosystems. Evidence from several studies indicates that nematodes can be highly sensitive to changes in the environmental quality. Here, we investigated the response of nematode assemblages to the presence of offshore gas platforms (located in the central Mediterranean Sea) in terms of spatial heterogeneity, structural and functional diversity. Since the effect of the investigated offshore platforms on macrofaunal assemblages were previously assessed by Terlizzi et al. (2008), the study provided also the opportunity to compare the response of different benthic compartments to the same impact related to fossil fuel extraction on marine environments. The platforms had a significant impact on nematode assemblages up to 1000 m distance from the structure. The effects were evident in term of: a) more homogeneous spatial distribution of nematode assemblages, b) increased trophic diversity of deposit feeders and c) changes in life strategies with an increase of opportunistic species in sediments closer to the platforms. Such effects seemed to be related to the dimension of the platform structures, rather than to chemical pollution or changes in food availability. These findings suggest that the platforms exert a physical alteration of the surrounding environment that is reflected by altered structural and functional traits of nematode biodiversity. The use of nematodes for monitoring the effects of the platforms only partially matched with the results obtained using macrofauna, providing further insights on potential outcomes on the functional response of marine assemblages to fossil fuel extraction.

1. Introduction

Understanding the ecological consequences of the human activities on marine environments is still a major challenge for ecologists. Available information suggests that there are no single variables, biotic components or functional traits able to detect all kinds of environmental alteration (Claudet and Fraschetti, 2010; Simboura and Zenetos, 2002; Terlizzi et al., 2005). Recently the relevance of the biological component for the evaluation of the good environmental status of marine ecosystems has been recognised in the current policy of the European Union on the protection and management of coastal marine areas (Water Framework Directive, 2000/60/EC; Marine Strategy Framework Directive, 2008/56/EC; EC, 2000; EU, 2008). The EU is specifically asking with the MSFD to move beyond the use of physical and chemical descriptors that were previously used to evaluate the Good Environmental Status (GES). Biotic components are more sensitive than physical-chemical variables in detecting changes driven by anthropogenic activities (Borja et al., 2003) and have thus a major potential in the impact assessment and monitoring programmes. Focussing directly on the structure and the functioning of biodiversity is presently considered a profitable strategy to assess the effects of human pressures.

However, the use of biological descriptors requires the development of sensitive and accurate ecological indices able to assess the environmental quality of marine ecosystems (e.g., Borja et al., 2003; Simboura and Zenetos, 2002). The main problem encountered so far is that most of classical indices are strongly affected by sample size, natural environmental variability and often lack of consistency in responses to anthropogenic disturbances (Bevilacqua et al., 2012a; Green and Chapman, 2011). The use of

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biotic assemblages has a greater possibility to show a wider sensitivity to environmental changes than a single indicator species (Terlizzi et al., 2005) or univariate index (Green and Chapman, 2011). Moreover, in order to enhance the understanding of ecosystem functioning and its relative status, the use of the biological traits of species can be critical (Hooper et al., 2005). Finally, all investigated descriptors have to identify the standardised reference conditions and multiple control locations (Claudet and Fraschetti, 2010) in order to provide reliable results. The use of univariate and multivariate approaches based on entire assemblages investigated at highest taxonomic resolution coupled with information on the functional diversity within the framework of well-designed experiments is, at present, probably, the most advanced framework to assess the impact of human activities.

Nematodes are the most abundant multicellular organisms on Earth, accounting for about 2/3 of all metazoa (Higgins and Thiel, 1988). They are ubiquitous, highly diverse and able to colonize all marine ecosystems, from the shores including vegetated and non-vegetated habitats down to the hadal trenches, from the tropics to the poles and from pristine to extremely contaminated habitats (Bianchelli et al., 2010; Danovaro et al., 2008a, b; Lambshead, 2004; Fraschetti et al., 2006; Gambi et al., 2014; Wilson and Kakouli-Duarte, 2009). The use of nematodes as a proxy for environmental health is already established for a variety of terrestrial and marine habitats (Danovaro et al., 2004; Mirto et al., 2002; Pusceddu et al., 2007) and are widely used to detect the effect of different typologies of impacts in the marine environments (Ahnert and Schriever, 2001; Danovaro et al., 1995; Fraschetti et al., 2006; Gambi et al., 2009; Goodsell et al., 2009; La Rosa et al., 2001; Mirto et al., 2002; Moreno et al., 2011; Schratzberger et al., 2000; Vincx and Heip, 1987). Their morphological features, and particularly the analysis of their functional traits, such as buccal apparatus, the characteristics of the tail, tegument and reproductive system, allow gathering important insights on their functional diversity (Danovaro et al., 2008a; Soetaert and Heip, 1995). The almost transparent nature of the nematode body, which permits the observation of the internal structures (e.g. mouth, gonads), and experimental evidence allow identifying also their life strategies (Bongers and Bongers, 1998; Ferris and Bongers, 2006). Moreover, recent findings demonstrated that their biodiversity is closely related with key ecosystem functions: a higher nematodes diversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed.

The consequence is that any biodiversity loss can be associated with the important reductions of ecosystem services (Danovaro et al., 2008a).

Offshore gas platforms represent an increasing threat for the quality of marine systems (e.g., Grant and Briggs, 2002; Kark et al., 2015; Schroeder and Love, 2004) related with the alterations of the surrounding seafloor due to the release of materials and contaminants and to the physical impact on the system (e.g., on habitat topography, grain size, sedimentation rates and hydrodynamism; Barros et al., 2001; Kennicutt et al., 1996; Olsgard and Gray, 1995).

So far, the effect of offshore platforms has been reported to determine a change in species richness and biodiversity of macrofaunal assemblages (e.g., Fiorentino et al., 2012; Manoukian et al., 2010; Olsgard and Gray, 1995; Terlizzi et al., 2008), but with different responses for each platform, according to the platform characteristics, dimensions and local biogeographic/climatic factors (Ellis et al., 1996; Wilson-Ormond et al., 2000).

Quantitative information on meiofaunal assemblages is still extremely limited, especially at temperate latitudes (Montagna and Harper, 1996; Netto et al., 2009; Peterson et al., 1996). Here, we investigated the structural (species composition and their relative abundance) and functional (trophic diversity and maturity index) response of nematode assemblages to the presence of different typologies of gas platforms in the central Mediterranean Sea, to identify the most sensitive indicators enabling the development of *ad hoc* descriptors of this kind of impacts. Since the effects of the same offshore platforms were investigated synoptically for macrofaunal assemblages (Terlizzi et al., 2008), this study also provided the opportunity to compare the response of different benthic compartments in detecting the impact due to fossil fuel extraction on marine environments. The aims of the present work can be summarised as follows: a) providing a better understanding of the ecological impacts of offshore platforms; b) providing indications of the suitability of meiofauna in monitoring studies; c) providing evidence of similarities and/or differences using meiofauna and macrofauna in assessing ecological impacts.

2. Materials and methods

2.1. Study area and experimental design

The investigated platforms are located in the North Ionian Sea (39°05′N, 17°09′E, Fig. 1). Four offshore platforms were installed in this area for gas drilling since the beginning of 1980s.

Two out of four of the selected platforms (hereafter LA and LB) had a eight-legs structure and were located about 7 km off the coast, on mud flats at about 90 m depth. Two additional platforms (hereafter HL and HL14) had a smaller structure being HL a monopod while HL14 is a four-legs platform closer to the coastline (about 2 km) on a sandy-detritic bottom at approximately 30 m depth. Sampling activities were carried out in July 2005, following the same design of Terlizzi et al. (2008).

For each of the four platforms, four sampling sites (100 s m apart one from each other) were randomly selected at increasing distance from the platform: i.e., 300, 1000 and 3000 m (Fig. 1). At each site, three sediment samples were collected by independent deployment of Van Veen grab (0.1 m^2). One subsample was taken from each grab using Plexiglas corer, (3.6 cm-inner diameter, down to 5 cm depth into the sediment). All samples were preserved in a buffered 4% formalin solution and stained with Rose Bengal (0.5 g l^{-1}) until extraction in the laboratory.

2.2. Structural and functional diversity of nematode assemblages

Sediment samples were sieved through a 1000 μm mesh to extract meiofauna, and a 32 μm mesh was used to retain the smallest organisms (Danovaro, 2010). The fraction remaining on the 32 μm-mesh sieve was re-suspended with Ludox HS40 (density arranged to 1.18 g cm^{-3}) and centrifuged three times. For the analysis of nematode diversity, at least 100 specimens were randomly picked from each of the three independent replicates at each sampling site (for a total of >300 nematodes identified per site). Nematodes were mounted on slides (following the formalin-ethanol-glycerol technique to prevent dehydration). They were identified to species level or morphotypes (indicated as sp1, sp2, sp3, etc., due to the presence of several unknown species) according to Platt and Warwick (1983, 1988), Warwick et al. (1998) and the recent literature dealing with new nematode genera and species (NeMys database, Vanaverbeke et al., 2015).

To provide an indication on the functional diversity of nematode assemblages, the index of trophic diversity ITD (Ferris and Bongers, 2009; Heip et al., 1985) was calculated. Nematodes were classified by feeding groups, according to Wieser (1953), in selective (1A) and non-selective (1B) deposit feeders, epigrowth (diatoms) feeders (2A) and predators/omnivores (2B). The ITD was calculated as $\Sigma\theta 2$, where θ is the percentage contribution of each feeding type. For the purposes of this study, we used 1-ITD values ranging from 0 (lowest

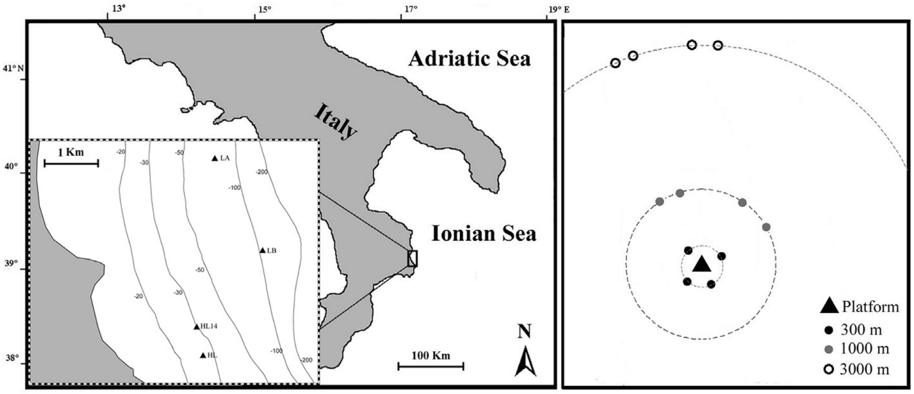


Fig. 1. Study area and position of the four investigated platforms. On the right side, an example of sampling site positioning around platforms (modified after Terlizzi et al., 2008).

trophic diversity; i.e., one trophic guild accounts for 100% of nematode density) to 0.75 (highest trophic diversity; i.e., the four trophic guilds account for 25% each).

The effects of offshore platforms on nematode life-history traits were also investigated (Bongers, 1990). Each nematode was classified into one of the five c-p (colonizer-persister) classes for the calculation of Maturity Index (MI; Bongers, 1990; Bongers et al., 1991). The colonizer-persister scale is composed of five classes: 1–5; the colonizers, characterised by a high reproduction receive a low value, the persisters, which reproduce slowly, are allocated to c-p $= 5$. The MI was calculated as the weighted average of the individual colonizer-persistent values: $MI = \Sigma\, \nu(i)\, f(i)$, where ν is the c-p value (colonisers-persisters) of genus i as given in the Appendix of Bongers et al. (1991) and $f(i)$ is the frequency of that genus. The contribution of nematode groups based either on life-history traits and on feeding types to the total nematode assemblage was also calculated.

2.3. *Statistical analyses*

The number of species (SR), Pielou's evenness (J), trophic diversity (1-ITD) and the maturity index (MI) were calculated for each sample. All metrics referred to the same sample size (i.e. 50.8 cm^3). A distance based permutational ANOVA (Anderson, 2001; Anderson et al., 2008) was carried out to test, in a univariate context, the effect of platforms, depth and distance on all the investigated variables. Analyses were based on Euclidean distance and each term in the analysis was tested using 4999 permutations. This procedure is distribution-free (Anderson, 2001), and robust to variance heterogeneity when experimental designs are balanced (Anderson and Walsh, 2013), as in our case. Significant terms relevant to hypotheses were investigated through post hoc pairwise comparisons using a t-test and 999 permutations (Anderson, 2001).

The experimental design included 4 factors: Depth (De), 2 levels, fixed; Distance (Di), 3 levels, fixed and orthogonal; Platform (P), 2 level, random and nested in De (since there were two platforms lying on soft bottoms at 30 m depth and another two at 90 m depth); Site (Si), 4 levels, random and nested in Di × P(De) interaction (since there were four sites at each distance from each platform), with $n = 3$ replicates for each combination of factors.

Distance-based permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used to test for differences amongst nematode assemblages at increasing distance from platforms. The analysis was based on Bray–Curtis dissimilarities and was performed on untransformed data (144 samples × 292 species) using 4999 random permutations. Post hoc pair-wise comparisons were done if appropriate using the PERMANOVA t-test and 999 random permutations.

For each platform multivariate patterns of variation among distances were visualised by using non-metric multidimensional scaling (nMDS) of sites centroids. The SIMPER analysis (Clarke, 1993) was conducted to quantify the percentage contribution of each variable (untransformed data) to the Bray–Curtis dissimilarities among distances for each platform, allowing identifying species most contributing to patterns of assemblages' variation among distances. Only variables whose contribution exceeded an arbitrarily chosen threshold value of dissimilarity >2% were selected.

Finally, to investigate the effects of platforms on spatial heterogeneity of nematode distribution at different spatial scales (amongst replicates and among sites), permutational analysis of multivariate dispersion (PERMDISP, Anderson et al., 2006) was carried out for the factor Di. The analysis was conducted separately for each of the four platforms on the basis of Bray–Curtis dissimilarities (untransformed data) and each term was tested using 999 random permutations. Pair-wise comparisons were made to analyse patterns of variation of replicate and site heterogeneity among distances. All analyses were performed using the computer program PRIMER v6, including the add-on package PERMANOVA+ (Anderson et al., 2008).

3. Results

Overall more than 10,000 individuals were analysed and identified, belonging to 30 families and 114 genera for a total of 291 species identified (see Appendix 1 in Supplementary material). The total number of species identified in HL 14 was 162, 147 species in HL, 141 species in LA and 185 species in LB, respectively. All gas platforms displayed the presence of exclusive species: 29 species (most abundant: *Halichoanolaimus* sp3) in LB, 20 species (most abundant: *Pierrickia* sp*1*) in LA, 23 species (most abundant: *Cyatholaimus* sp*1*) in HL 14 and 18 species (most abundant: *Sabatieria* sp3) in HL respectively, while 59 nematode species were common among all gas platforms.

PERMANOVA carried out on the whole dataset showed significant differences in assemblage structures among platforms and depths [P(De) and De]. Apparently, no effect of distance from platforms were detected for nematode assemblages, although the Di × P(De) interaction showed a P-value at the limit of significance (Table 1). PERMANOVAs carried out separately for each depth revealed the lack of significant differences of nematode assemblages at shallow depth among distances for platforms HL and HL14 (Table 1). Conversely, at 90 m depth, the multivariate analysis showed that platforms LA and LB were characterised by significant

Table 1
PERMANOVA analysing differences among assemblages at increasing distance from platforms based on Bray–Curtis dissimilarities of untransformed data (144 samples × 292 taxa). Each test was performed using 4999 permutations of appropriate units. P-values given in italics were obtained using 4999 Monte Carlo samples from the asymptotic permutation distribution. Significant results are given in bold.The term used for the denominator mean square in each case is given in column MSDEN. Results of pair-wise tests for the significant term Di × P(De) were reported down in the table after PERMANOVAs conducted separately for each depth (see the text for further details).

Source of variability	d.f.	MS	*F*	*P*	MS_{DEN}
Depth = De	1	95863	12.11	***0.0002***	P(De)
Distance = Di	2	6890.1	1.5032	0.2444	Di × P(De)
Platforms = P(De)	2	7915.3	2.6396	**0.0098**	Si(Di × P(De))
De × Di	2	5594.3	1.2204	0.3282	Di × P(De)
Di × P(De)	4	4583.9	1.5286	0.0508	Si(Di × P(De))
Site = Si(Di × P(De))	36	2998.7	2.1048	**0.0002**	Res
Residual = Res	96	1424.7			

Source of variability	d.f.	Depth = 30 m			Depth = 90 m			MS_{DEN}
		MS	*F*	*P*	MS	*F*	*P*	
Platforms = P	1	6315	1.82	0.061	9515	3.74	**0.000**	Si(Di × P)
Distance = Di	2	5172	1.50	0.149	7313	1.28	0.253	Di × P
Di × P	2	3442	0.99	0.451	5726	2.25	**0.002**	Si(Di × P)
Site = Si(Di × P)	18	3454	2.39	**0.000**	2543	1.18	**0.000**	Res
Residual = Res	48	1446			1374			

Pair-wise tests for term Di × P at 90 m depth.
LA 300 m = 1000 m ≠ 3000 m LB 300 m ≠ 1000 m ≠ 3000 m.

differences in terms of the structure of nematode assemblages at different distances from the platform. More specifically, pair-wise tests revealed that, for platform LA, nematode assemblages at 3000 m distance from the platform significantly differed from those at 300 m and 1000 m, which, in turn, did not differ between themselves. For LB, nematode assemblages significantly differed among all distances. PERMANOVA also revealed a significant variability at the scale of site and platforms (Table 1). The same pattern of differences in assemblages at increasing distance from the platforms was observed on macrofauna (Terlizzi et al., 2008).

Multivariate patterns of differences among distances were clearly illustrated in the nMDS ordinations of site centroids (Fig. 2). For HL 14 (Fig. 2a) and HL (Fig. 2b), ordination plots showed a distribution of centroids independent from the distance from the platforms. In contrast, sampling sites at 3000 m distance from the platforms were generally separated from those closer to the platform (i.e., at 300 and 1000-m distance) for LA (Fig. 2c), whereas for LB centroids for all distances were separated (Fig. 2d).

SIMPER analysis revealed that 20 and 15 species out of 292 were important in determining these differences among distances in LA and LB, respectively (Table 2). Among these species, *Dorylaimopsis* sp1, *Hopperia* sp1, *Metalinhomoeus* sp3, *Paramonhystera* sp4, *Sabatieria* sp1, *Sabatieria* sp5, *Sabatieria* sp8, *Setosabatieria* sp1 were able to discriminate the assemblages at different distances from the platform. However, only *Sabatieria* sp5 and *Setosabatieria* sp1 showed a consistent pattern, with the abundances of *Sabatieria* sp5 increasing at increasing distance from the platforms, while those of *Setosabatieria* sp1 decreased (Table 2).

Results of PERMDISP showed significant differences in multivariate dispersion of replicates and sites among distances for all platforms except for LA (Fig. 3). This suggests an effect of platforms in modifying assemblage heterogeneity at both the investigated spatial scales. In general, pair-wise comparisons showed significant differences in the variability among sites between 3000 m and the other two distances that, in turn, did not differ. This was also evident in nMDS plots, which showed for all platforms except LA, a generally higher scattering of sites' centroids at 3000 m than at 1000 m and 300 m (Fig. 2). Moreover, a clear trend of increase in the multivariate dispersion with increasing distance from platforms can be observed in HL and HL14 (Fig. 3). Such patterns were comparable to those observed in the study by Terlizzi et al. (2008) on macrofauna, but limited to the scale of sites.

Results of ANOVA revealed significant differences in nematode species richness (SR), evenness (*J*), functional diversity (1-ITD) and

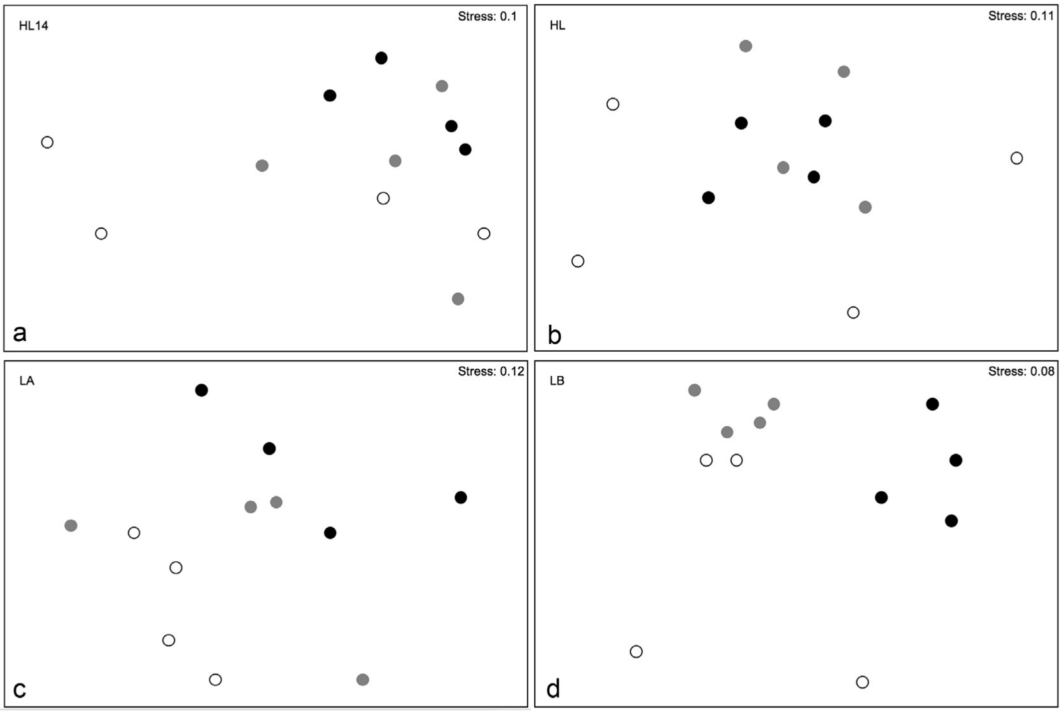
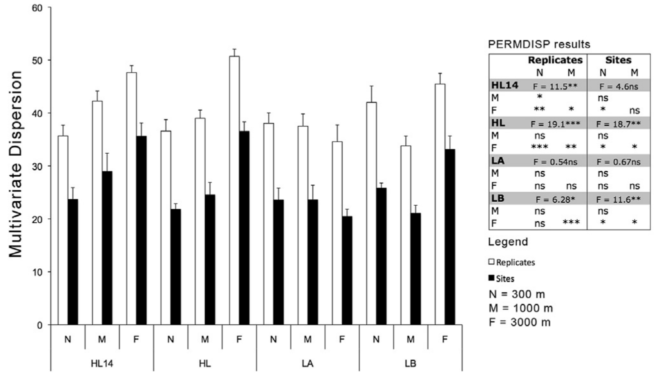


Fig. 2. Non-metric multidimensional scaling ordinations (nMDS) on the basis of the Bray–Curtis dissimilarity measure of sites' centroids for each of the three distances from (a) HL, (b) HL14, (c) LA and (d) LB. Black circles = 300 m; grey circles = 1000 m; white circles = 3000 m.

Table 2
Summary of SIMPER analysis for platforms LA and LB. For each species are given the average abundance (Avg. ab.) at each of the three distances (N = 300 m, M = 1000 m, F = 3000 m) from the platform and its contribution (Contr.%) to differences between pair of distances. The average dissimilarity between each pair of distances was reported in parentheses. Only species whose contribution was at least in one case ≥2% are reported.

LA	N	M	F	N vs M	N vs F	M vs F
	300 m	1000 m	3000 m	(57.93)	(59.90)	(56.44)
Species	Avg. ab.	Avg. ab.	Avg. ab.	Contr.%	Contr.%	Contr.%
Dorylaimopsis sp1	17.25	13.58	12.33	12.19	13.23	11.00
Setosabatiera sp1	7.67	6.67	6.50	8.63	8.94	7.35
Sabatiera sp5	1.50	5.75	7.75	6.77	9.29	9.49
Hopperia sp1	0.83	4.83	2.67	6.63	3.59	6.96
Paramonhystera sp4	4.33	3.75	1.08	5.08	5.58	4.96
Sabatiera sp8	2.75	1.83	7.50	4.19	8.41	9.97
Sabatiera sp1	0.92	1.92	1.50	2.84	1.81	3.31
Sphaerolaimus sp1	1.58	0.58	0.92	2.24	2.48	1.67
Metalinhomoeus sp3	0.08	1.50	0.58	2.20	0.85	2.21
Parasphaerolaimus sp1	1.00	0.92	0.75	2.17	2.00	1.88
Dolicholaimus sp	0.83	0.08	1.08	1.31	2.77	1.94
Vasostoma sp2	0.25	0.33	1.83	0.68	2.45	2.64

LB	N	M	F	N vs M	N vs F	M vs F
	300 m	1000 m	3000 m	(68.64)	(74.56)	(65.45)
Species	Avg. ab.	Avg. ab.	Avg. ab.	Contr.%	Contr.%	Contr.%
Dorylaimopsis sp1	8.42	15.92	7.83	13.17	7.30	14.38
Setosabatiera sp1	9.58	5.25	2.33	8.60	8.94	5.55
Hopperia sp1	0.67	6.08	7.83	7.30	8.56	6.04
Sabatiera sp8	0.25	4.67	1.25	6.02	1.49	5.51
Marylinnia sp3	2.83	0.83	0.42	3.45	3.01	1.23
Sabatiera sp1	1.17	2.33	2.42	2.73	2.61	3.27
Rhabdodemania sp1	2.17	0.00	0.42	2.73	2.23	0.53
Metalinhomoeus sp3	0.00	1.92	0.33	2.68	0.40	2.44
Odontophora sp1	2.00	0.00	0.17	2.48	2.22	0.23
Sabatiera sp5	1.83	2.08	4.75	2.46	4.47	4.81
Cervonema sp1	1.92	0.42	1.58	2.45	2.56	2.35
Setosabatiera sp2	1.83	0.75	0.08	2.45	2.04	1.02
Actinonema sp1	1.92	0.08	0.50	2.43	2.15	0.67
Paramonhystera sp4	0.25	1.33	1.00	1.74	1.23	2.17
Sabatiera sp4	0.00	0.17	1.75	0.25	2.13	2.34



	Replicates		Sites	
	N	M	N	M
HL14	F = 11.5**		F = 4.6ns	
M	*		ns	
F	**	*	*	ns
HL	F = 19.1***		F = 18.7**	
M	ns		ns	
F	***	**	*	*
LA	F = 0.54ns		F = 0.67ns	
M	ns		ns	
F	ns	ns	ns	ns
LB	F = 6.28*		F = 11.6**	
M	ns		ns	
F	ns	***	*	*

Fig. 3. Summary of PERMDISP analyses investigating differences in multivariate dispersion (i.e. average distance to centroids and standard errors) of replicates (group size = 12) and sites (group size = 4) at the three distances from platforms. Details on the outcomes of the analyses (i.e. F-ratio given for deviation from centroids for each platform, and pair-wise comparisons [t-test] among distances) are also reported. ns = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.01$.

life strategy (MI) among distances. However, such differences were not consistent among platforms as shown by the significant interaction Di × P(De) (Table 3). Results of ANOVA also showed a high variability at the scale of sites for all the investigated variables (Table 3). In particular, pair-wise comparisons revealed no significant differences among distances for all investigated variables in HL, while *J* and MI significantly increased and decreased respectively, at increasing distance from the platform HL14 (Fig 4). For platforms at 90 m depth, significant differences among distances for all variables, except *J*, were observed in LB, although not compatible with a gradient effect. For platform LA, analyses showed clear spatial patterns with increasing distance from the platform for SR (decreasing) and 1-ITD (increasing) (Fig. 4).

The functional traits of biodiversity were investigated in terms of trophic composition of nematode assemblages and life strategies (i.e., the relative importance of colonisers *vs* persisters) at increasing distance from each platform (Fig. 5a and b). None of the trophic groups showed a clear spatial pattern with increasing distance from the platforms. Epigrowth feeders (2A) were the dominant feeding group, representing up to 60% of all individuals in both platforms HL14 and HL (Fig. 5a). In platforms LA and LB both selective and no-selective deposit feeders were the most abundant feeding types, followed by epi-growth feeders. The contribution of predators was low at all sites and in all platforms.

Nematode life-history traits displayed a clear spatial pattern among distances (Fig 5b). The relative contribution of colonizers (c-p: 2) to nematode assemblages generally decreased with increasing distance from platform in HL14, HL and LA. The contribution of these nematode colonizers (c-p: 2) was higher in platforms at 90 m (LA and LB) than in those at 30 m (HL and HL14).

4. Discussion

Marine nematodes have a huge potential in detecting environmental alterations and have been used to investigate the impact of

Table 3
Summary of ANOVAs investigating differences among assemblages at increasing distance from platforms in the mean number of species (SR), Pielou evenness (J), Trophic diversity index (1-ITD) and Maturity index (MI). ns = not significant; *P < 0.05; **P < 0.01; ***P < 0.001.

Source of variability	d.f.	SR		*J*		1-ITD		MI	
		MS	F	MS	F	MS	F	MS	F
Depth = De	1	21.01	0.106ns	0.036	2.246ns	0.002	0.047ns	5.72	31.782ns
Distance = Di	2	45.65	0.305ns	0.006	0.479ns	0.022	1.015ns	0.24	2.851ns
Platform = P(De)	2	197.87	6.952**	0.016	3.300*	0.046	6.423**	0.18	6.689**
De × Di	2	25.05	0.167ns	0.001	0.102ns	0.015	0.723ns	0.13	1.565ns
Di × P(De)	4	149.56	5.255**	0.012	2.521*	0.021	2.963*	0.08	3.105*
Site = Si(Di × P(De))	36	28.46	1.594*	0.005	2.039**	0.007	2.356***	0.03	2.501***
Residual	96	17.85		0.002		0.003		0.01	
Total	143								

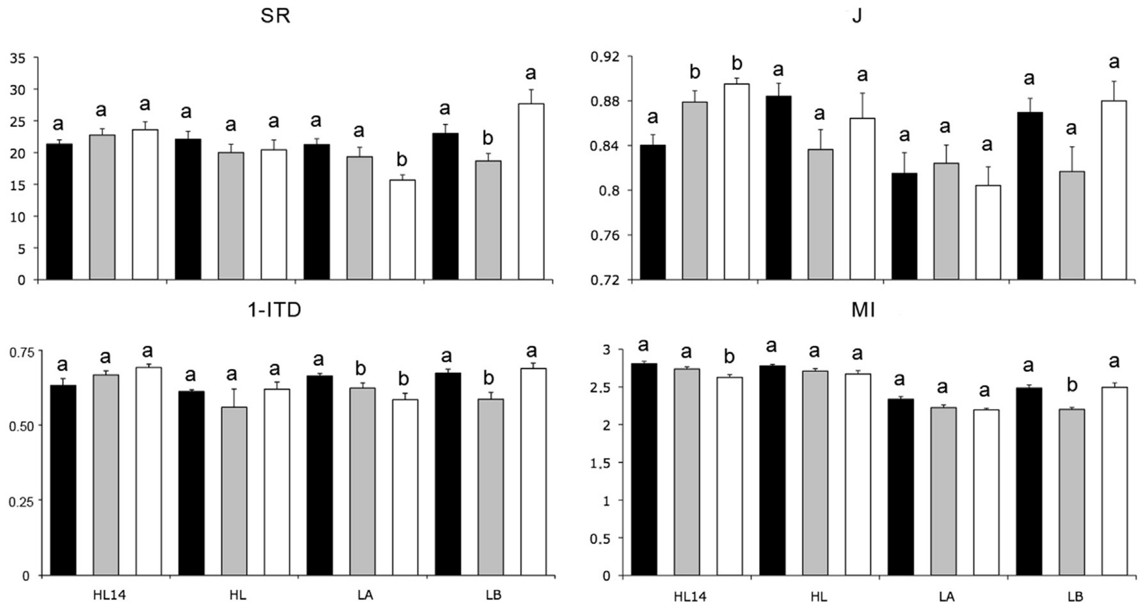


Fig. 4. Mean values (±SE, n = 12) of species richness (SR), evenness (Pielou's index − J), trophic diversity (calculated through 1 − ITD) and life-history diversity (calculated as Maturity Index − MI) across distances for each platform. Letters above columns illustrate the outcome of t tests; different letters indicate significant differences at P < 0.05. Black bars = 300 m; grey bars = 1000 m; white bars = 3000 m.

aquaculture, sewage discharge, organic enrichment and chemical contamination (Danovaro et al., 2004; Losi et al., 2013; Mirto et al., 2002; Pusceddu et al., 2007). Our results indicate that offshore gas platforms significantly altered the structure, spatial heterogeneity, functional diversity and life-history traits of nematode assemblages. The impact of the platforms changed depending on depth, platform features and location, and decreased at increasing distances from the platforms. These effects were particularly evident from the multivariate analysis of the structure of nematode assemblages for the platforms located at 90 m, where significant differences amongst all distances from the platform were observed. For all platforms investigated, such differences appeared evident within a distance of 1000 m from the structure indicating a direct association between alteration of the assemblages and presence of the platforms. Patterns of change in the multivariate structure of nematode assemblages at increasing distance from the offshore structures largely overlapped those found conisdering macrofauna (Terlizzi et al., 2008), indicating a generalized effect of platforms on the whole benthic systems, affecting both macro- and meiofauna.

The effect of homogenization of the spatial distribution of benthic assemblages has been already reported for different kinds of disturbance (Balata et al., 2007; Bevilacqua et al., 2012b; Guarnieri et al., 2012; Warwick and Clarke, 1993). Accordingly, the heterogeneity (in terms of multivariate dispersion) of nematode assemblages generally decreased moving closer to the platforms, independently from platforms' depths. Such patterns, consistent with those observed at the smallest spatial scale (i.e., among replicates), suggest an effect of the structures in reducing both small-scale patchiness and among-sites spatial variability. Data providing evidence of a “biotic homogenization” of the assemblages closer to the investigated platforms have been already reported from the analysis of macrofauna (Terlizzi et al., 2008): our findings thus reinforce the idea that a decrease of the spatial heterogeneity of benthic assemblages is a general response of marine biota to anthropogenic impacts (Warwick and Clarke, 1993; Balata et al., 2007; Bevilacqua et al., 2012b; Guarnieri et al., 2012). Such findings are counterintuitive, as the deployment of a new structure on soft bottoms is expected to increase habitat heterogeneity with a potential positive effect on biodiversity at local scale, and indicate that the deployment of platforms should be considered only as an additional source of human impacts on offshore benthic habitats. Halpern et al. (2007) included “benthic structures” among the major anthropogenic threats at regional and global scale, even though the score for soft substrate vulnerability to this threat did not rank particularly high. Data reported here indicate that the impact of large “benthic structures” cannot be ignored when

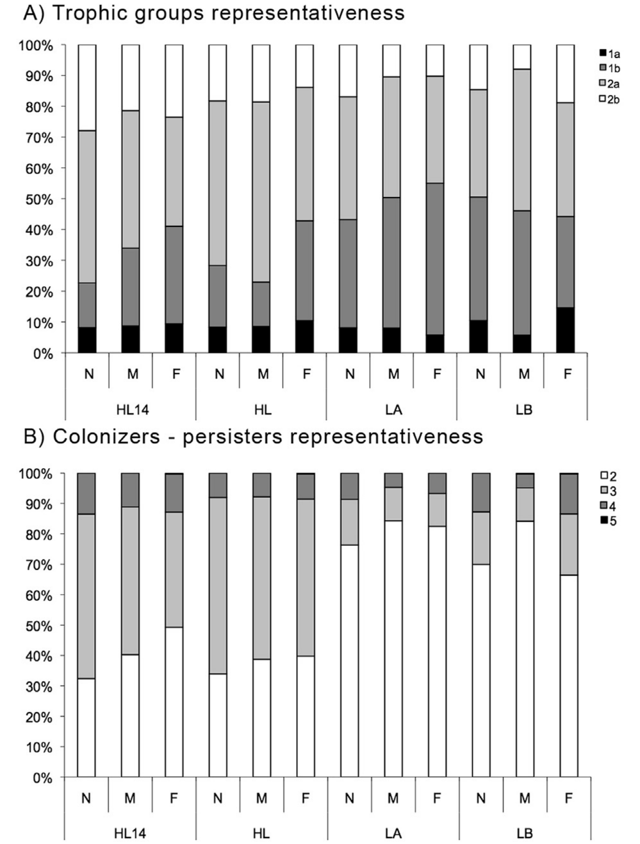


Fig. 5. A) Trophic structure and B) life-history characteristics of nematode assemblages at the different distances from each platform (see explanation in the text for further details). 1A (selective deposit feeders); 1B (non selective deposit feeders); 2A (epigrowth feeders); 2B (predators/omnivores). 2–5 = c-p values (colonizers-persisters scale). N = 300 m; M = 1000 m; F = 3000 m.

assessing the outcomes of multiple sources of impact in marine ecosystems.

Platform size and the characteristics of the seafloor could explain why different effects on the structure and functional diversity of nematode assemblages were observed when comparing the platforms at 90 m and at 30 m depth. Platforms at 90 m (eight-legs structures) occupy a larger seafloor surface and thus were likely to produce larger amounts of hard substrate, sessile fauna and falling biofoulers compared to the smaller structures characterizing platforms at 30 m (four legs or monopod structures). Fouling dislodgment can determine organic nutrient enrichment and increase substrate heterogeneity in proximity of offshore structures (e.g., Barros et al., 2001; Stachowitsch et al., 2002), which in turn may affect nematode distribution patterns (Vanaverbeke et al., 2011). In our case, soft bottoms around platforms at higher depth consisted of mud flats, whereas those surrounding platforms at lower depth were characterized by sandy/detritic substrates (pers. observ.). Such differences in the nature of substrates between depths seem to suggest that the effects of the fouling rainfall could have been more severe on the seafloor around platforms LA and LB, which likely had higher substrate homogeneity than those around platforms HL and HL14. In addition, nematodes can show a significant increase of deposit-feeders as a result of such organic inputs up to 100–200 m distance from the platform (Montagna and Harper, 1996; Peterson et al., 1996). However, since in the present study the effects are evident at 300 and 1000 m from the structures we can exclude that the effect on nematodes was due to the input of fouling. Previous investigations based on macrofauna also allowed to exclude an impact related to the chemical contamination of sediments due to the lack of any significant response to the ecotoxicological tests (see Terlizzi et al., 2008). Thus, the observed differences in nematode assemblages in proximity of the platforms are possibly related to the presence of the physical structures of the platforms.

We did not find a consistent pattern of change in trophic structure of nematode assemblages with increasing distance from platforms. Only two nematode species, belonging to genera *Setosabatieria* and *Sabatieria,* displayed a clear response in both platforms located at 90 m. *Setosabatieria* is a genus typically sensitive to the presence of hydrocarbons (Danovaro et al., 1995; Heip et al., 1982) its high presence in sediments close to the platform confirms the lack of significant levels of toxicity as a consequence of platform activities. The genus *Sabatieria* is generally considered an indicator of organic enrichment. It is often dominant in hypoxic sediments (Gambi et al., 2009; Mirto et al., 2002; Schratzberger et al., 2007; Vincx et al., 1990), but its abundance increased at increasing distance from platforms, leading to exclude that changes observed were related to organic enrichment.

Assemblages far from platforms were characterised by lower trophic diversity and an increase of the importance of opportunistic species ("colonizers" characterised by a short life-cycle, higher colonization ability and tolerance to disturbances; Bongers et al., 1991; Bongers and Ferris, 1999), which accounted for up to 85% of the nematode species present. These findings are compatible with hypothesis of physical alteration of the seafloor driven, for instance, by trawling activities (Liu et al., 2011; Tuck et al., 1998). At the same time, sediments close to platforms at lower depth showed an increase of persister species (characterised by a long life-cycle, and low tolerance to disturbances; Bongers et al., 1991; Bongers and Ferris, 1999).

Our results suggest that the meiofauna is a sensitive descriptor of the environmental alterations associated to the presence of off shore platforms. In addition, the comparative analysis between the results obtained by using meiofauna and macrofauna (Terlizzi et al., 2008), indicate that these structures exert a similar impact, even though limited, on different components of benthic assemblages. The high taxonomic resolution used in both studies and the analysis of the functional traits of nematode assemblages provided some additional interesting insight on the response of the benthic biota, enabling us to shed light on the causes underlying the observed patterns. The analyses of nematode feeding traits and life strategies, for instance, indicate that changes observed for meiofaunal assemblages, and particularly for nematodes, are evident in both structural and functional terms and suggest that meiofaunal functional biodiversity is a valid indicator of human-driven changes in marine ecosystems (e.g., Moreno et al., 2011; Netto et al., 2009; Steyaert et al., 2007). Past attempts to combine or compare the effects of environmental disturbance gradients on meiofauna and macrofauna showed that the responses of these benthic compartments are not necessarily consistent (e.g., Attrill, 2002; Bick and Arlt, 2005; Flach et al., 2002; Netto and Gallucci, 2003; Patrício et al., 2012; Schratzberger et al., 2004; Somerfield et al., 2006) due to the different life strategies (presence vs absence of meroplanktonic larvae), different feeding habits and modalities of dispersal which can result in a different sensitivity to environmental changes (Attrill and Depledge, 1997). The response of meiofauna (nematodes) outlined in the present study suggests that nematodes have the potential to capture effects that are less evident from the analysis of the macrofaunal component (Terlizzi et al., 2008). In addition, the analysis of the cost-effectiveness or the typology and duration of an impact could further support the choice of meiofauna as a good alternative to macrofauna for the routine monitoring of offshore gas platforms.

The occurrence of multiple human threats to marine biodiversity is typically concentrated in coastal areas, but it is increasing also the impact on open sea systems (Doney, 2010). The increasing demand for energy production will likely lead to an increasing spread of man-made structures in offshore areas (Skladany et al., 2007; Wilson et al., 2010). Solid baseline information on the potential consequences of multiple pressures is needed for an appropriate the definition of the adequate mitigation and management strategies.

Recently, large-scale scale studies identified the Mediterranean areas where the interaction between marine biodiversity and anthropogenic threats are more pronounced (Coll et al., 2012; http://globalmarine.nceas.ucsb.edu/mediterranean/). Our results indicate that the investigated area in the northern Ionian Sea is exposed to multiple stressors and the presence of offshore platforms contribute to exacerbate the effects of these multiple stressors on offshore habitats. Thus appropriate measures of ecological compensation should be envisaged in the future in order to make more compatible industrial development and conservation of the biodiversity-mediated ecosystem functions.

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References

Ahnert, A., Schriever, G., 2001. Response of abyssal *Copepoda Harpacticoida* (Crustacea) and other meiobenthos to an artificial disturbance and its bearing on future mining for polymetallic nodules. Deep Sea Res. II 48, 3779–3794.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Anderson, M.J., Walsh, C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83, 557–574.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9 (6), 683–693.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Attrill, M.J., 2002. A testable linear model for diversity trends in estuaries. J. Anim. Ecol. 71, 262–269.

Attrill, M.J., Depledge, M.H., 1997. Community and population indicators of ecosystem health: targeting links between levels of biological organisation. Aquat. Toxicol. 38, 183–197.

Balata, D., Piazzi, L., Cinelli, F., 2007. Increase of sedimentation in a subtidal system: effects on the structure and diversity of macroalgal assemblages. J. Exp. Mar. Biol. Ecol. 351, 73–82.

Barros, F., Underwood, A.J., Lindegarth, M., 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. Estuar. Coast. Shelf Sci. 52, 191–199.

Bevilacqua, S., Sandulli, R., Plicanti, A., Terlizzi, A., 2012a. Taxonomic distinctness in Mediterranean marine nematodes and its relevance for environmental impact assessment. Mar. Pollut. Bull. 64, 1409–1416.

Bevilacqua, S., Plicanti, A., Sandulli, R., Terlizzi, A., 2012b. Measuring more of β-diversity: quantifying patterns of variation in assemblage heterogeneity. An insight from marine benthic assemblages. Ecol. Indic. 18, 140–148.

Bianchelli, S., Gambi, C., Zeppilli, D., Danovaro, R., 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on the rare taxa. Deep Sea Res. Part I Oceanogr. Res. Pap. 57, 420–433.

Bick, A., Arlt, G., 2005. Intertidal and subtidal soft-bottom macro- and meiofauna of the Kongsfjord (Spitsbergen). Polar Biol. 28, 550–557.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228.

Bongers, T., Alkemade, R., Yeates, G.W., 1991. Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by mean of the Maturity Index. Mar. Ecol. Prog. Ser. 76, 135–142.

Borja, A., Muxika, I., Franco, J., 2003. The application of a marine biotic index to different impact sources affecting soft-bottom benthic communities along European coasts. Mar. Pollut. Bull. 46, 835–845.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. Biol. Conserv. 143, 2195–2206.

Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W.W.L., Christensen, V., Karpouzi, V.S., Guilhaumon, F., Mouillot, D., Paleczny, M., Lourdes Palomares, M., Steenbeek, J., Trujillo, P., Watson, R., Pauly, D., 2012. The Mediterranean under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Glob. Ecol. Biogeogr. 21, 465–481.

Danovaro, R., 2010. Methods for the Study of Deep-sea Sediments, Their Functioning and Biodiversity. CRC Press, Boca Raton, 428 pp.

Danovaro, R., Fabiano, M., Vincx, M., 1995. Meiofauna response to the Agip Abruzzo oil spill in subtidal sediments of the Ligurian Sea. Mar. Pollut. Bull. 30, 133–145.

Danovaro, R., Gambi, C., Luna, G.M., Mirto, S., 2004. Sustainable impact of mussel farming in the Adriatic Sea (Mediterranean Sea): evidence from biochemical, microbial and meiofaunal indicators. Mar. Pollut. Bull. 49, 325–333.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008a. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr. Biol. 18, 1–8.

Danovaro, R., Gambi, C., Lampadariou, N., Tselepides, A., 2008b. Deep-sea nematode biodiversity in the Mediterranean basin: testing for longitudinal, bathymetric and energetic gradients. Ecography 31, 231–244.

Doney, S.C., 2010. The growing human footprint on coastal and open-ocean biogeochemistry. Science 328, 1512–1516.

EC, 2000. Directive of the European Parliament and of the Council 2000/60/EC Establishing a Framework for Community Action in the Field of Water Policy. Available at: http://europa.eu/eur-lex/pri/en/oj/dat/2000/l 327/l 32720001222en00010072.pdf.

Ellis, M.S., Wilson-Ormond, E.A., Powell, E.N., 1996. Effects of gas producing platforms on continental shelf macro-epifauna in the northwestern Gulf of Mexico: abundance and size structure. Can. J. Fish. Aquat. Sci. 53, 2589–2605.

EU, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official J. Eur. Union L164, 19–40.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3–12.

Ferris, H., Bongers, T., 2009. Indices developed specifically for nematode assemblages. In: Wilson, M.J., Kakouli-Duarte, T. (Eds.), Nematodes as Environmental Indicators. CABI Publishing, Oxfordshire, UK, pp. 124–145.

Fiorentino, D., Caruso, T., Terlizzi, A., 2012. Spatial autocorrelation in the response of soft-bottom marine benthos to gas extraction activities: the case of amphipods in the Ionian Sea. Mar. Environ. Res. 79, 79–85.

Flach, E., Muthumbi, A., Heip, C., 2002. Meiofauna and macrofauna community structure in relation to sediment composition at the Iberian margin compared to Goban Spur (NE Atlantic). Prog. Oceanogr. 52, 433–457.

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

Gambi, C., Bianchelli, S., Pérez, M., Invers, O., Ruiz, J., Danovaro, R., 2009. Biodiversity response to experimental induced anoxia in seagrass sediments. Biodivers. Conserv. 18, 33–54.

Gambi, C., Pusceddu, A., Benedetti-Cecchi, L., Danovaro, R., 2014. Species richness, species turnover, and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. Glob. Ecol. Biogeogr. 23, 24–39.

Goodsell, P.J., Underwood, A.J., Chapman, M.G., 2009. Evidence necessary for taxa to be reliable indicators of environmental conditions or impacts. Mar. Pollut. Bull. 58, 323–331.

Grant, A., Briggs, A.D., 2002. Toxicity of sediments from around a North Sea oil platform: are metals or hydrocarbons responsible for ecological impacts? Mar. Environ. Res. 53, 95–116.

Green, R., Chapman, P.M., 2011. The problem with indices. Mar. Pollut. Bull. 62, 1377–1380.

Guarnieri, G., Terlizzi, A., Bevilacqua, S., Fraschetti, S., 2012. Increasing heterogeneity of sensitive assemblages as a consequence of human impact in submarine caves. Mar. Biol. 159, 1155–1164.

Halpern, B.S., Selkoe, K.A., Micheli, F., Kappel, K., 2007. Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. Conserv. Biol. 21, 1301–1315.

Heip, C., Vincx, M., Smol, N., Vranken, G., 1982. The systematic ecology of free-living marine nematodes. Helminthol. Abstr. Ser. B Plant Nematol. 51, 1–31.

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

Higgins, R.P., Thiel, H., 1988. Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr 75, 3–35.

Kark, S., Brokovich, E., Mazor, T., Levin, N., 2015. Emerging conservation challenges and prospects in an era of offshore hydrocarbon exploration and exploitation. Conserv. Biol. 1–13.

Kennicutt, M.C., Green, R.H., Montagna, P., Roscigno, P.F., 1996. Gulf of Mexico offshore operations monitoring experiment (GOOMEX), phase I: sublethal responses to contaminant exposure–introduction and overwie. Can. J. Fish. Aquat. Sci. 53, 2540–2553.

La Rosa, T., Mirto, S., Mazzola, A., Danovaro, R., 2001. Differential responses of benthic microbes and meiofauna to fish-farm disturbance in coastal sediments. Environ. Pollut. 112, 427–434.

Lambshead, P.J.D., 2004. Marine nematode biodiversity. In: Chen, Z.X., Chen, S.Y., Dickson, D.W. (Eds.), Nematology: Advances and Perspectives Volume 1: Nematode Morphology, Physiology and Ecology. CABI Publishing, London, pp. 436–467.

Liu, X.S., Xu, W.Z., Cheung, S.G., Shin, P.K.S., 2011. Response of meiofaunal community with special reference to nematodes upon deployment of artificial reefs and cessation of bottom trawling in subtropical waters, Hong Kong. Mar. Pollut. Bull. 63, 376–384.

Losi, V., Moreno, M., Gaozza, L., Vezzulli, L., Fabiano, M., Albertelli, G., 2013. Nematode biomass and allometric attributes as indicators of environmental quality in a Mediterranean harbour (Ligurian Sea, Italy). Ecol. Indic. 30, 80–89.

Manoukian, S., Spagnolo, A., Scarcella, G., Punzo, E., Angelini, R., Fabi, G., 2010. Effects of two offshore gas platforms on soft-bottom benthic communities (northwestern Adriatic Sea, Italy). Mar. Environ. Res. 70, 402–410.

Mirto, S., La Rosa, T., Gambi, C., Danovaro, R., Mazzola, A., 2002. Nematode community response to fish-farm impact in the western Mediterranean. Environ. Pollut. 116, 203–214.

Montagna, P.A., Harper, D.E., 1996. Benthic infaunal long-term response to offshore production platforms in the Gulf of Mexico. Can. J. Fish. Aquat. Sci. 53, 2567–2588.

Moreno, M., Semprucci, F., Vezzulli, L., Balsamo, M., Fabiano, M., Albertelli, G., 2011. The use of nematodes in assessing ecological quality status in the Mediterranean coastal ecosystems. Ecol. Indic. 11, 328–336.

Netto, S.A., Gallucci, F., 2003. Meiofauna and macrofauna communities in a mangrove from the Island of Santa Catarina, South Brazil. Hydrobiologia 505, 159–170.

Netto, S.A., Gallucci, F., Fonseca, G., 2009. Deep-sea meiofauna response to synthetic-based drilling mud discharge off SE Brazil. Deep-Sea Res. II 56, 41–49.

Olsgard, F., Gray, J., 1995. A comprehensive analysis of the effects of offshore oil and gas exploration and production on the benthic communities of the Norwegian continental shelf. Mar. Ecol. Prog. Ser. 122, 277–306.

Patrício, J., Adão, H., Neto, J.M., Alves, A.S., Traunspurger, W., Marques, H.C., 2012. Do nematode and macrofauna assemblages provide similar ecological assessment information? Ecol. Indic. 14, 124–137.

Peterson, C.H., Kennicutt II, M.C., Green, R.H., Montagna, P., Harper Jr., D.E., Powell Jr., E.N., Roscigno, P.F., 1996. Ecological consequences of environmental perturbations associated with offshore hydrocarbon production: a perspective on long-term exposures in Gulf of Mexico. Can. J. Fish. Acquat. Sci. 53, 2637–2654.

Platt, H.M., Warwick, R.M., 1983. Free-living Marine nematodes. Part I. British Enoplids. In: Synopses of the British Fauna (New Series), vol. 28. Cambridge University Press, Cambridge.

Platt, H.M., Warwick, R.M., 1988. Free-living Marine nematodes. Part II. British Chromadorids. In: Synopses of the British Fauna (New Series), vol. 38. Brill, Leiden.

Pusceddu, A., Fraschetti, S., Mirto, S., Holmer, M., Danovaro, R., 2007. Effects of intensive mariculture on sediment biochemistry. Ecol. Appl. 17, 1366–1378.

Schratzberger, M., Gee, J.M., Rees, H.L., Boyd, S.E., Wall, C.M., 2000. The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of the marine environment. J. Mar. Biol. Assoc. U. K. 80, 969–980.

Schratzberger, M., Whomersley, P., Kilbride, R., Rees, H.L., 2004. Structure and taxonomic composition of subtidal nematode and macrofauna assemblages at four stations around the UK coast. J. Mar. Biol. Assoc. U. K. 84, 315–322.

Schratzberger, M., Warr, K., Rogers, S.I., 2007. Functional diversity of nematode communities in the southwestern North Sea. Mar. Environ. Res. 63, 368–389.

Schroeder, D.M., Love, M.S., 2004. Ecological and political issues surrounding decommissioning of offshore oil facilities in the Southern California Bight. Ocean Coast. Manag. 47, 21–48.

Simboura, N., Zenetos, A., 2002. Benthic indicators to use in ecological quality classification of Mediterranean soft bottom marine ecosystems, including a new biotic index. Mediterr. Mar. Sci. 3, 77–111.

Skladany, M., Clausen, R., Belton, B., 2007. Offshore aquaculture: the frontier of redefining oceanic property. Soc. Nat. Resour. 20, 169–176.

Soetaert, K., Heip, C., 1995. Nematode assemblages of deep sea and shelf break sites in the North Atlantic and Mediterranean Sea. Mar. Ecol. Prog. Ser. 125, 171–183.

Somerfield, P.J., Cochrane, S.J., Dahle, S., Pearson, T.H., 2006. Free-living nematodes and macrobenthos in a high-latitude glacial fjord. J. Exp. Mar. Biol. Ecol. 330, 284–296.

Stachowitsch, M., Kikinger, R., Herler, J., Zolda, P., Geutebrück, E., 2002. Offshore oil platforms and fouling communities in the southern Arabian Gulf (Abu Dhabi). Mar. Pollut. Bull. 44, 853–860.

Steyaert, M., Moodley, L., Nadong, T., Moens, T., Soetaert, K., Vincx, M., 2007. Responses of intertidal nematodes to short-term anoxic events. J. Exp. Mar. Biol. Ecol. 345, 175–184.

Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P., Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. Mar. Ecol. Prog. Ser. 289, 27–42.

Terlizzi, A., Bevilacqua, S., Scuderi, D., Fiorentino, D., Guarnieri, G., Giangrande, A., Licciano, M., Felline, S., Fraschetti, S., 2008. Effects of offshore platforms on soft bottom macro-benthic assemblages: a case study in a Mediterranean gas field. Mar. Pollut. Bull. 56, 1303–1309.

Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E., Basford, D.J., 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Mar. Ecol. Prog. Ser. 162, 227–242.

Vanaverbeke, J., Merckx, B., Degraer, S., Vincx, M., 2011. Sediment-related distribution patterns of nematodes and macrofauna: two sides of the benthic coin? Mar. Environ. Res. 71, 31–40.

Vanaverbeke, J., Bezerra, T.N., Braeckman, U., De Groote, A., De Meester, N., Deprez, T., Derycke, S., Guilini, K., Hauquier, F., Lins, L., Maria, T., Moens, T., Pape, E., Smol, N., Taheri, M., Van Campenhout, J., Vanreusel, A., Wu, X., Vincx, M., 2015. NeMys: World Database of Free-living Marine Nematodes. Accessed at. http://nemys.ugent.be.

Vincx, M., Heip, C., 1987. The use of meiobenthos in pollution monitoring studies: a review. In: ICES, CM E33L, 1166, pp. 1–18.

Vincx, M., Meire, P., Heip, C., 1990. The distribution of nematode communities in the southern bight of the North Sea. Cah. Biol. Mar. 31, 107–129.

Warwick, R.M., Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. J. Exp. Mar. Ecol. Biol. 172, 215–226.

Warwick, R.M., Platt, H.M., Somerfield, P.J., 1998. Free-living marine nematodes. Part III. British monhysterids. In: Synopses of the British Fauna (New Series), vol. 53. Field Studies Council, Shrewsbury, UK.

Wieser, W., 1953. Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen nematoden. Eine ökologisch-morphologische Studie. Ark. för Zool. 4, 439–484.

Wilson, M.J., Kakouli-Duarte, T., 2009. Nematodes as Environmental Indicators. CABI Publishing, Oxfordshire, UK.

Wilson, J.C., Elliott, M., Cutts, N.D., Mander, L., Mendao, V., Perez-Dominguez, R., Phelps, A., 2010. Coastal and offshore wind energy generation: is it environmentally benign? Energies 3, 1383–1422.

Wilson-Ormond, E.A., Ellis, M.S., Powell, E.N., Kim, Y., Li, S., 2000. Effects of gas producing platforms on continental shelf megafauna in the northwest Gulf of Mexico: reproductive status and health. Int. Rev. Hydrobiol. 85, 293–323.