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Article

Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss

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Summary

Background: Recent investigations suggest that biodiversity loss might impair the functioning and sustainability of ecosystems. Although deep-sea ecosystems are the most extensive on Earth, represent the largest reservoir of biomass, and host a large proportion of undiscovered biodiversity, the data needed to evaluate the consequences of biodiversity loss on the ocean floor are completely lacking.

Results: Here, we present a global-scale study based on 116 deep-sea sites that relates benthic biodiversity to several independent indicators of ecosystem functioning and efficiency. We show that deep-sea ecosystem functioning is exponentially related to deep-sea biodiversity and that ecosystem efficiency is also exponentially linked to functional biodiversity. These results suggest that a higher biodiversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed. The exponential relationships presented here, being consistent across a wide range of deep-sea ecosystems, suggest that mutually positive functional interactions (ecological facilitation) can be common in the largest biome of our biosphere.

Conclusions: Our results suggest that a biodiversity loss in deep-sea ecosystems might be associated with exponential reductions of their functions. Because the deep sea plays a key role in ecological and biogeochemical processes at a global scale, this study provides scientific evidence that the conservation of deep-sea biodiversity is a priority for a sustainable functioning of the worlds' oceans.

Introduction

The accelerating loss of biological diversity poses serious concerns, exemplified by recent predictions that species loss might impair the functioning and the sustainability of terrestrial ecosystems [1–3]. The global scale of the biodiversity crisis has stimulated investigations that explore the relationships between biodiversity (expressed as the number, identity, and relative abundance of species), productivity, stability, and services in different ecosystems of the world [1–5].

Deep-sea sediments cover 65% of the world's surface. The microbial processes occurring there provide essential services, driving the nutrient regeneration and global biogeochemical cycles that are essential to sustain primary and secondary production in the oceans [6]. Deep-sea habitats are also the largest reservoirs of biomass and nonrenewable resources (e.g., gas hydrates and minerals) [6], and although the census of deep-sea life is in its infancy, there is increasing evidence that they host a large proportion of undiscovered biodiversity on our planet (from 0.3 to 8.3×10^6 species) [5, 6]. Understanding the relationships between biodiversity and deep-sea ecosystem functioning is therefore crucial for understanding the functioning of our biosphere.

Benthic faunal diversity provides an ideal tool for exploring the relationships between biodiversity and ecosystem functioning [7], and among benthic faunal taxa, nematodes are ideal model organisms. Nematodes are, indeed, the most abundant metazoans on Earth; in terrestrial ecosystems, they account for 80% of the abundance of multicellular animals, and in the deep sea, this proportion rises to more than 90% [8]. This phylum is also characterized by (1) very high species richness (i.e., among the most diverse of marine Phyla), (2) distinct and easily recognizable feeding types, and (3) life strategies that make it possible to also identify functional diversity traits [9]. Moreover, although comparative studies are rare, deep-sea nematode diversity appears to be related to that of other benthic components, including Foraminifera [10], macrofauna [11], and the richness of higher meiofaunal taxa (a group which includes 22 of the 35 modern animal Phyla; Figure S1 available online).

Ecosystem functioning involves several processes, which can be summarized as production, consumption and transfer of organic matter to higher trophic levels, organic matter decomposition, and nutrient regeneration. Terrestrial ecologists have related biodiversity to ecosystem functioning through analyses of ecosystem processes estimated by measuring the rates of energy and

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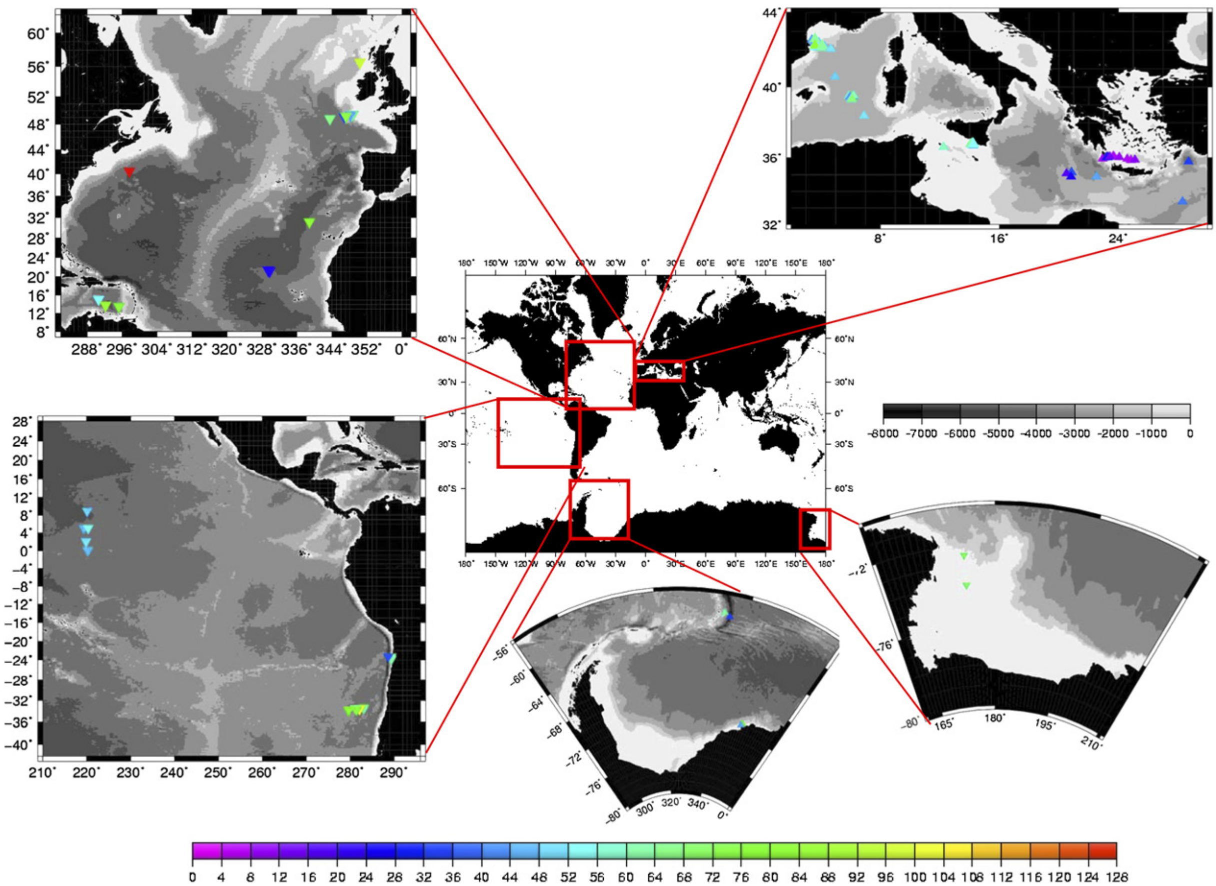

Figure 1. Sampling Areas and Deep-Sea Nematode Diversity

Maps of the sampling areas and the magnitude of deep-sea nematode species richness (a proxy for deep-sea benthic biodiversity) at the individual sampling points. Data from the Northeast and Central-East Atlantic are based on nematode genera. Nematode species richness from the deep anoxic Black Sea is not reported. Colored bars and symbols refer to species richness (and to genus richness only for the Porcupine Abyssal Plain); the black-and-white bar refers to sampling depths.

material flow between biotic and abiotic compartments (e.g., biomass production, organic matter decomposition, nutrient regeneration, or other measures of material production, transport, or loss) [2]. Applying the same approach through a series of independent and synoptic measures, we investigated the relationships between deep-sea biodiversity and ecosystem functioning. Deep-sea ecosystems lack photosynthetic primary production, and their functioning reflects the collective activities of animals, protists, and prokaryotes in exploiting and recycling the inputs of material from the photic zone. We therefore identified the following key processes: (1) benthic prokaryote production, (2) total meiofaunal biomass (a measure of the production of renewable resources by ecosystems), and (3) the rates at which organic matter is decomposed and recycled. The three independent indicators of ecosystem functioning represent key variables of deep-sea ecosystems as they regulate (1) the transfer of mobilized organic matter to higher trophic levels, (2) the ability of the ecosystem to transfer energy and material to higher trophic levels, thus providing indications of the heterotrophic production of the ecosystem, and (3) nutrient regeneration processes, which reflect the ability of ecosystems to sustain their functions over time.

Results

We report here the results of largest data set produced so far for investigating the interaction between deep-sea biodiversity and ecosystem processes. From 116 deep-sea sites, we compiled an inventory of 270 data sets, each comprising benthic faunal (nematode) biodiversity and other variables reflecting ecosystem functioning (Figure 1). This inventory integrated all relevant information from the literature with data from 83 new sites obtained with the same protocols and taxonomic references. Our database covers latitudes from 55° N to 75° S and depths from approximately 200 m to 8200 m (information for each data set is provided in Table S1) and includes quantitative data from deep-water sites spanning a bottom water temperature ranges from approximately −1.9°C (Southern Ocean) to 13.0°C (Mediterranean Sea). In total, approximately 61,000 individuals were counted, and about 25,000 of these were classified to the species level (in five data sets, nematodes were identified only to genus level).

Our analyses have revealed for the first time that ecosystem functioning is positively and exponentially related to biodiversity in all of the deep-sea regions investigated (Figure 2). This relationship applies also when

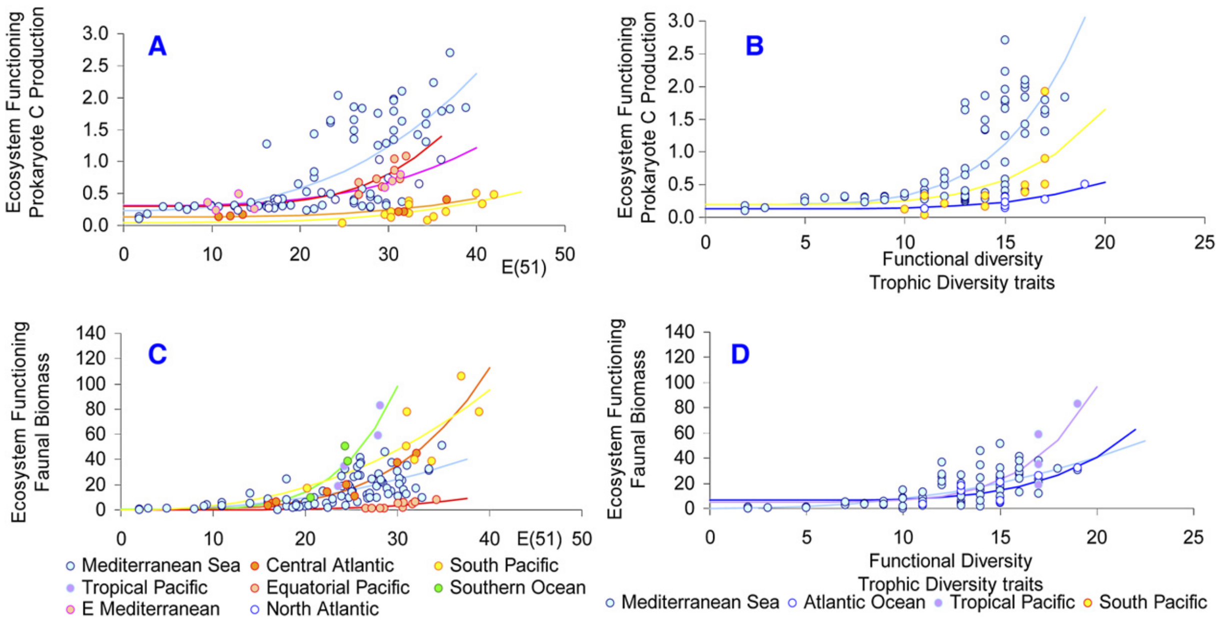

Figure 2. Relationship between Biodiversity and Ecosystem Functioning

(A) The relationship between expected species number [ES(51)] and ecosystem functioning (as prokaryote C production, expressed as $\mu g\ C\ g^{-1}\ d^{-1}$). The equations of the fitting lines are (1) $Y = 0.24 + 1.2 \times 10^{-4} \times (X^{2.6})$ for the Mediterranean Sea ($n = 75$, $R^2 = 0.52$, $p < 0.01$), (2) $Y = 0.31 + 6.7 \times 10^{-6} \times (X^{3.2})$ for the Eastern Mediterranean Sea ($n = 7$, $R^2 = 0.82$, $p < 0.05$), (3) $Y = 0.08 + 2.3 \times 10^{-3} \times (X^{1.7})$ for the North Atlantic ($n = 10$, $R^2 = 0.77$, $p < 0.05$), (4) $Y = 0.30 + 2.2 \times 10^{-7} \times (X^{4.3})$ for the Equatorial Pacific ($n = 8$, $R^2 = 0.59$, $p < 0.05$), (5) $Y = 0.05 + 1.5 \times 10^{-6} \times (X^{3.3})$ for the South Pacific ($n = 13$, $R^2 = 0.67$, $p < 0.01$), and (6) $Y = 0.1 + 9.7 \times 10^{-7} \times (X^{3.2})$ for the Central Atlantic ($n = 6$, $R^2 = 0.81$, $p < 0.05$).

(B) The relationship between functional diversity (number of trophic traits) and ecosystem functioning (as prokaryote C production, expressed as $\mu g\ C\ g^{-1}\ d^{-1}$). The equations of the fitting lines are (1) $Y = 0.41 + 9.3 \times 10^{-3} \times (X^{2.3})$ for the Mediterranean Sea ($n = 80$, $R^2 = 0.45$, $p < 0.01$), (2) $Y = 0.50 + 3.1 \times 10^{-5} \times (X^{4.1})$ for the Central Atlantic ($n = 8$, $R^2 = 0.94$, $p < 0.01$), (3) $Y = 2.1 \times 10^{-6} \times (X^{4.2})$ for the Equatorial Pacific ($n = 10$, $R^2 = 0.60$, $p < 0.05$), and (4) $Y = 1.3 \times 10^{-2} \times (X^{2.4})$ for the South Pacific ($n = 7$, $R^2 = 0.66$, $p < 0.05$).

(C) The relationship between expected species number (ES(51)) and ecosystem functioning (as faunal biomass, expressed as $mg\ C\ m^{-2}$). The equations of the fitting lines are (1) $Y = 0.19 + 2.3 \times 10^{-6} \times (X^{4.8})$ for the Mediterranean Sea ($n = 75$, $R^2 = 0.80$, $p < 0.01$), (2) $Y = 0.13 + 2.4 \times 10^{-7} \times (X^{4.8})$ for the Atlantic Ocean ($n = 7$, $R^2 = 0.80$, $p < 0.05$), and (3) $Y = 0.22 + 8.8 \times 10^{-7} \times (X^{4.8})$ for the South Pacific ($n = 11$, $R^2 = 0.43$, $p < 0.05$).

(D) The relationship between functional diversity (number of trophic traits) and ecosystem functioning (as faunal biomass expressed as $mgC\ m^{-2}$). The equations of the fitting lines are (1) $Y = 3.2 \times 10^{-2} \times (X^{2.4})$ for the Mediterranean Sea ($n = 79$, $R^2 = 0.41$, $p < 0.01$), (2) $Y = 6.6 + 6.3 \times 10^{-6} \times (X^{5.2})$ for the Atlantic Ocean ($n = 8$, $R^2 = 0.58$, $p < 0.05$), and (3) $Y = 5.0 + 2.3 \times 10^{-6} \times (X^{5.8})$ for the Tropical Pacific ($n = 4$, $R^2 = 0.60$, not significant [ns]).

Data originate from the Equatorial Pacific (bathymetric range: 4305–4994 m, mean ± standard deviation [SD]: 4606 ± 283 m), Tropical Pacific (bathymetric range: 1140–1355 m, mean ± SD: 1248 ± 152 m), South Pacific Ocean (bathymetric range: 2040–3070 m, mean ± SD: 2629 ± 440 m), Central Atlantic (bathymetric range: 3858–5411 m, mean ± SD: 4460 ± 914 m), North Atlantic (bathymetric range: 1034–4850 m, mean ± SD: 2720 ± 1547 m), Western Mediterranean (bathymetric range: 2755–3870 m, mean ± SD: 2912 ± 256 m), Eastern Mediterranean Sea (bathymetric range: 1078–1840 m, mean ± SD: 1350 ± 286 m), and Southern Ocean (bathymetric range: 228–588 m, mean ± SD: 462 ± 166 m). Data from the North Atlantic are based on nematode genera; all other data are based on nematode species.

different biodiversity measures (including the richness of all higher meiofaunal taxa) and independent measures of ecosystem functioning are used (Table S2, Figures S2 and S3). The analysis of descriptive data represents, at present, the most convenient approach for investigating the relationships between biodiversity and ecosystem functioning in remote habitats, such as the deep-sea ecosystems, at large spatial scales. However, because measures of biodiversity and ecosystem functioning can change in response to different environmental factors, these relationships could reflect the covariation of different variables rather than a causal relationship. Previous studies have related patterns of deep-sea biodiversity to a variety of factors, including (1) temperature, (2) water depth, and (3) the export of primary organic matter from the photic zone and oxygen availability [11, 12]. Although differences of temperature among different deep-sea systems can be relevant, the relationships reported in Figure 2 are presumably not affected by temperature because they were obtained by the plotting of values of biodiversity and ecosystem functioning within deep-sea regions in which temperatures were highly homogenous (e.g., all of the deep-Mediterranean samples displayed temperatures of 13.0 ± 0.2°C), and the same applies to all deep-sea regions within the bathymetric ranges considered (Table S1).

We also investigated the relationships between benthic biodiversity and deep-sea ecosystem efficiency [2], which reflects the ability of an ecosystem to exploit the available energy (food sources) and thereby maximize the biomass and its production [1, 2]. Given the specificity of deep-sea ecosystem functioning, we used three independent indicators of ecosystem efficiency: (1) the ratio of meiofaunal biomass to organic C fluxes, reflecting the ability of the system to exploit the input of primary production from the photic zone, (2) the ratio of prokaryote C production to organic C flux, representing a basic estimate of the ability of the system to convert organic detritus into bacterial biomass and thus to recycle organic matter deposited on the sea floor, and (3) the ratio of total benthic meiofaunal biomass to biopolymeric C content in the sediment as an estimate of the ability of the system to channel detritus to higher trophic levels.

We found significant and exponential relationships between benthic biodiversity and different independent measures of ecosystem efficiency (Figure 3) (Table S2, Figure S4). Moreover, species number and the diversity of functional traits were directly and positively related (Figure 4). We also carried out statistical analyses revealing that the relationships between biodiversity and ecosystem functioning are highly significant even when the effects of depth and C flux are discounted (i.e., considering depth and C fluxes as covariates), both independently and simultaneously (Table 1, Figure S5).

Biodiversity and ecosystem functioning can be affected by hypoxic or anoxic conditions. In deep-water hypoxic settings, sedimentary carbon cycling is depressed at depths where oxygen depletion is most severe and metazoan abundance and diversity are lowest. ^{13}C tracer experiments conducted in the Arabian Sea oxygen minimum zone (OMZ) suggest that Foraminifera are responsible for most organic matter processing in these stressed, but food-rich, environments [13]. At slightly higher bottom-water oxygen concentration within the OMZ, high-density, virtually monospecific populations of macrofaunal metazoans (polychaetes) are active in the short-term uptake of organic matter [13]. Moreover, in the permanently anoxic and sulphidic deep Black Sea, where conditions are even more extreme and the sediments are devoid of eukaryotic life, rates of prokaryote C production and C cycling are extremely low (Figure S6). However, all of the deep-sea sites investigated (except the deep Black Sea) display constantly high oxygen concentrations (typically > 5.0 ml O_2 L^{-1}), which are ten times higher than those potentially limiting deep-sea metazoan life [11]. As such, the effect of oxygen concentration on biodiversity is negligible in the deep-sea systems considered here.

The spatial scales at which biodiversity interacts with ecosystem functioning are also crucial for understanding the significance of these relationships. Data presented here (Figure S7) reveal that patterns of benthic biodiversity are consistent at local and larger scales (hundreds of km) and congruent over time (within ecological time scales; Figure S8, Table S3).

Discussion

Overall, our findings indicate that the exponential relationships between deep-sea biodiversity and ecosystem functioning are consistent across a wide range of bottom-water temperatures (including the warm, deep-water regime of the Mediterranean) and trophic conditions and therefore reflect interactions between organismal life and deep-sea ecosystem processes occurring on a global scale.

Taken together, the relationships between biodiversity and ecosystem functioning and efficiency suggest that a higher biodiversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed. The exponential relationship between biodiversity and ecosystem efficiency supports previous studies that hypothesized

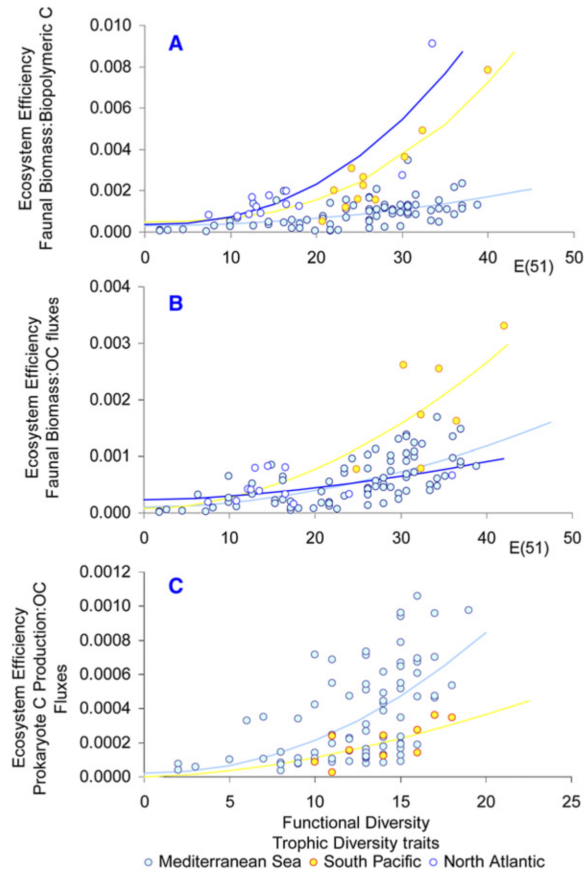

Figure 3. Relationships between Biodiversity and Ecosystem Efficiency and between Functional Diversity and Ecosystem Functioning

Relationships between biodiversity and ecosystem efficiency and between structural and functional diversity. Three independent indicators of ecosystem efficiency are plotted against expected species number [ES(51)] and functional diversity. Data origins and bathymetric ranges as detailed for Figure 2.

(A) The ratio of faunal biomass to biopolymeric C (as a measure of the bioavailable organic detritus). The y axis is adimensional. The equations of the fitting lines are (1) $Y = 3.1 \times 10^{-4} + 8.7 \times 10^{-7} \times (X^{2.0})$ for the Mediterranean Sea ($n = 78$, $R^2 = 0.29$, $p < 0.01$), (2) $Y = 3.6 \times 10^{-4} + 1.7 \times 10^{-6} \times (X^{2.4})$ for the Atlantic Ocean ($n = 11$, $R^2 = 0.77$, $p < 0.01$), and (3) $Y = 5.0 \times 10^{-4} + 3.4 \times 10^{-7} \times (X^{2.7})$ for the South Pacific ($n = 11$, $R^2 = 0.86$, $p < 0.01$).

(B) The ratio of faunal biomass to organic carbon (OC) fluxes. The unit of the y axis is d^{-1}. The equations of the fitting lines are (1) $Y = 1.0 \times 10^{-4} + 1.1 \times 10^{-6} \times (X^{1.9})$ for the Mediterranean Sea ($n = 81$, $R^2 = 0.39$, $p < 0.01$), (2) $Y = 2.3 \times 10^{-4} + 1.6 \times 10^{-6} \times (X^{1.6})$ for the Atlantic Ocean ($n = 12$, $R^2 = 0.58$, $p < 0.05$), and (3) $Y = 7.3 \times 10^{-5} + 2.5 \times 10^{-6} \times (X^{1.9})$ for the South Pacific ($n = 7$, $R^2 = 0.45$, ns).

(C) The ratio of prokaryote C production to OC fluxes. The y axis is adimensional. The equations of the fitting lines are (1) $Y = 2.2 \times 10^{-5} + 1.5 \times 10^{-6} \times (X^{2.1})$ for the Mediterranean Sea ($n = 82$, $R^2 = 0.31$, $p < 0.01$) and (2) $Y = 1.0 \times 10^{-7} + 2.3 \times 10^{-6} \times (X^{1.7})$ for the South Pacific ($n = 10$, $R^2 = 0.52$, $p < 0.05$).

the existence of mutually positive functional interactions (ecological facilitation) [14]. In addition, results reported here from all latitudes and depths suggest that interactions of this kind among species are common in the largest biome of our biosphere.

It is generally accepted that changes in species diversity are associated with changes in functional diversity [2], but the relationship between these two community

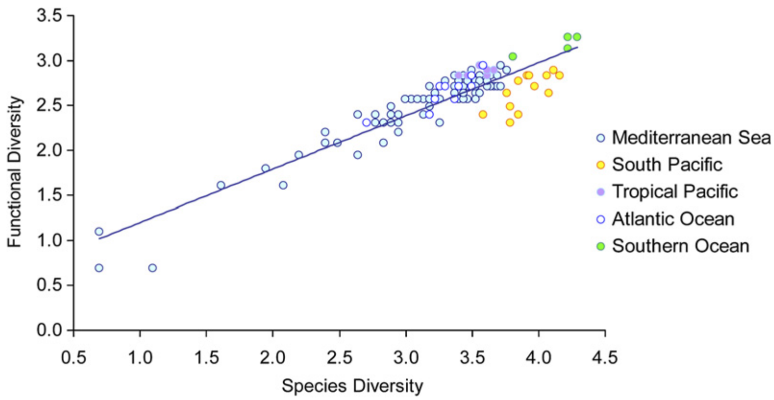

Figure 4. Relationship between Biodiversity and Functional Diversity

Relationship between species diversity (as SR) and functional diversity (as total number of trophic traits). The equation for the line fits for the full data set (log transformed) is Y = 0.59X + 0.61 (n = 115, R^2 = 0.83, $p <$ 0.01) (Mediterranean Sea: R^2 = 0.91, Atlantic Ocean: R^2 = 0.77, Southern Ocean: R^2 = 0.75, and South Pacific: R^2 = 0.47). Data origins and bathymetric ranges as detailed for Figure 2.

properties remains largely unknown, especially in deep-sea ecosystems. A low functional redundancy has been observed in coastal marine assemblages [15]. Similarly, in deep-sea sediments, species number and the diversity of functional traits are directly and positively related (Figure 4), so that a higher structural biodiversity (species richness) has a direct and positive effect on functional diversity and related ecological processes.

Recent studies have emphasized the importance of functional diversity traits that influence ecosystem functioning [1, 16] and agree that such measures require validation [17]. Understanding how species interactions influence the relationship between biodiversity and ecosystem functioning or efficiency implies a thorough knowledge of the processes regulating deep-sea benthic food webs and the ecological role of each species. In benthic ecosystems, a higher functional diversity can promote ecosystem processes in different ways [18, 19]. (1) A higher benthic diversity might increase bioturbation, with a consequent increase of benthic fluxes [20, 21] and the redistribution of food within the sediment; nematodes, together with Foraminifera, are mainly responsible for cryptobioturbation [22, 23]. (2) A higher number of nematode species stimulates prokaryote C production to a greater extent than selective grazing by a few species [24]. (3) Higher benthic species richness can also promote higher rates of detritus processing, digestion, and reworking, thus resulting in faster rates of organic matter remineralization. (4) Predatory nematodes might influence the structural and functional diversity of meio-, macro- and megafaunal assemblages by preying selectively on the larvae of organisms displaying lower mobility [23].

One case study from the deep Eastern Mediterranean enabled us to identify a clear linkage between ecosystem functioning and functional diversity. Here, an extreme climate event determined the cascading of dense and cold waters down to bathyal depths, profoundly modifying the physical and chemical characteristics of the entire water column and determining a remarkable drop of deep-water temperature. Such changes had a major impact on deep-sea fauna because nematode functional diversity decreased by approximately 35%. Such a loss in functional diversity was associated with an exponential decrease in ecosystem functioning because benthic faunal biomass decreased by 40% and prokaryote biomass decreased by more than 80% (Figure 5). Although the mechanisms causing changes in nematode biodiversity have not been completely clarified, it has been hypothesized that temperature changes had direct effects on nematode abundance and biodiversity by reducing metabolic rates and reproduction potential and favoring the nematode species with higher tolerance to the new temperature settings [19]. These results support the evidence of a linkage between deep-sea ecosystem functioning and functional biodiversity and suggest that a reduction in functional biodiversity might be associated with an exponential decline of ecosystem processes. Overall, our results suggest that a higher biodiversity can enhance the ability of deep-sea benthic systems to perform the key biological and biogeochemical processes that are crucial for their sustainable functioning.

Our findings suggest that the shape of the relationship between biodiversity and the functioning of natural deep-sea ecosystems is different from that typically

Table 1. Species Diversity

	Prokaryote C Production[a]			Faunal Biomass[b]		
	df	SS	MS	df	SS	MS
Covariables	2	0.00077		2	635132.88	
Regression	1	0.00087	0.00087	1	1536282.84	1536282.84
Residual	87	0.01212	0.00014	131	5247823.93	40059.72
Total	90	0.01376		134	7419239.65	

Effects of biodiversity, measured as ES(51), on ecosystem functioning. In the regression analyses, all tests were based on Euclidean distances calculated among observations from untransformed data. The following abbreviations are used: degrees of freedom (df), sum of squares (SS), and mean squares (MS). Regression SS, residual SS, and residual df were calculated after the removal of SS and df because of covariables: depth and organic carbon fluxes.

[a] Pseudo-F = 6.25. Permutation p = 0.01.

[b] Pseudo-F = 38.35. Permutation p = 0.00020.

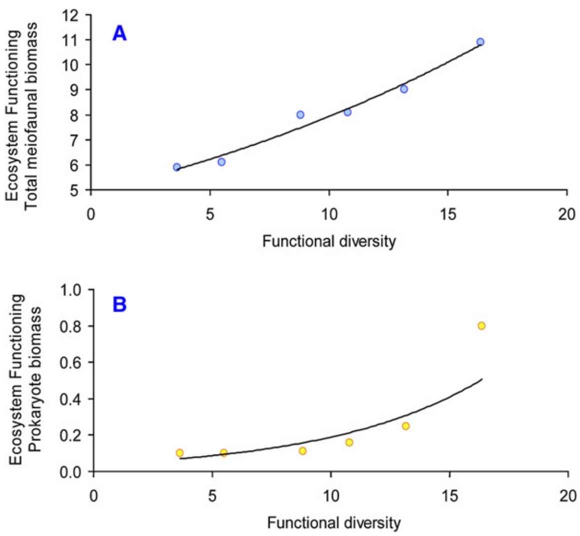

Figure 5. Relationship between Functional Diversity and Ecosystem Functioning

Relationship between functional biodiversity and ecosystem functioning based on a study carried out in the deep Eastern Mediterranean before and after an extreme climate event, which changed the deep-sea water characteristics. Data referred to sediment samples collected at approximately 1600 m depth before the event in 1989 and after the event in 1995 (twice a year), 1996 (twice a year), and 1998.

(A) Relationship between functional diversity (number of trophic traits) and ecosystem functioning (as total meiofaunal biomass, mg C m^{-2}; $R^2 = 0.939$, $p < 0.01$).

(B) Relationship between functional diversity (number of trophic traits) and ecosystem functioning (as prokaryote biomass, μg C g^{-1}; $R^2 = 0.898$, $p < 0.01$).

observed in manipulative experiments conducted in other ecosystems (i.e., null, positive, or idiosyncratic, [25–27]). An exponential relationship might reflect several factors, including the characteristics of deep-sea ecosystems and the nature of the relationship between structural and functional biodiversity, as well as the functional role and identity of the species involved [28]. Notably, our results suggest that the effect of deep-sea benthic biodiversity on ecosystem functioning becomes more evident when biodiversity values are high. Results presented here, demonstrating exponential relationships in all deep-sea ecosystems, provide valuable pointers to the mechanisms that might cause the observed patterns and point to the need for new experiments capable of reflecting conditions occurring in deep-sea ecosystems.

Over the geological past, the fossil record preserved in deep-sea sediments reveals substantial fluctuations in the diversity of important benthic taxa, notably the Foraminifera [29] and Ostracoda [30]. Changes in deep-sea foraminiferal diversity are often accompanied by changes in functional types (e.g., infaunal versus epifaunal). Some periods—for example, the Paleocene-Eocene Thermal Maximum—witnessed a sharp decrease in deep-sea benthic foraminiferal diversity [31]. If such shifts are representative of the wider benthic community, then these events must have had a profound effect on ecosystem functioning.

Deep-sea ecosystems are highly vulnerable and susceptible to biodiversity losses [5, 6, 11]. In modern oceans, deep-sea ecosystems are already being threatened by man through trawling, dumping, oil, gas and mineral extraction, and other pollution sources [32]. Moreover, impacts due to changes in thermohaline circulation linked to global climate change [33] are expected to be extremely severe [19]. Empirical and theoretical studies increasingly argue that biodiversity regulates the ecosystem functions that are responsible for the production of these goods and services [2, 4, 16, 17, 28]. If the mechanisms that have been widely demonstrated in a number of studies [2, 4, 12, 16] can be applied in the deep sea, then reductions of biodiversity might be associated with exponential reductions of ecosystem functions. Deep-sea ecosystems provide goods (including biomass, bioactive molecules, oil, gas, and minerals) and services (climate regulation, nutrient regeneration and supply to the photic zone, and food) and, for their profound involvement in global biogeochemical and ecological processes, are essential for the sustainable functioning of our biosphere and for human wellbeing. Our results suggest that the conservation of deep-sea biodiversity can be crucial for the sustainability of the functions of the largest ecosystem of our biosphere.

Experimental Procedures

Sampling Sites

Sampling was carried out in the North and Central Atlantic Ocean (20 sites), the Equatorial and South Pacific (26 sites), the Western and Eastern Mediterranean Sea (57 sites), the Southern Ocean (the Ross and Weddell Seas; five sites), and the Black Sea (eight sites). The investigated areas included only open-ocean sites and continental-margin systems and excluded specific hot-spot ecosystems (i.e., deep-water coral sites, canyons, cold seeps, and hydrothermal vents) and minimum oxygen zones, with the exception of the permanently anoxic deep Black Sea, an area with extremely low biodiversity. Except for those in the deep Black Sea, all sites are overlain by fully oxic bottom water. The sampling design allowed for the comparison of similar systems covering more than 96% of the deep-sea surface. Overall, approximately 30% of the sampling sites were located at depths between 200 m and 1000 m, approximately 15% between 1000 m and 2000 m, approximately 30% between 2000 m and 3000 m, and approximately 25% from 3000 m to over 8000 m.

Benthic Biodiversity

At all of the sites, samples were collected for the analysis of richness of higher meiofaunal taxa and nematode diversity. Synoptic samples for macrofaunal diversity were collected at 18 selected sites (Western, Central, and Eastern Mediterranean) (Figures S1A and S1B); the biodiversity values from the Equatorial Pacific and Atlantic Ocean were obtained from literature (see References for Data Sources in the Supplemental Data). All meiofaunal taxa were counted and identified under a stereomicroscope. All of the nematodes have been identified to the species level, except in the Northeast and Central-East Atlantic, where identification was conducted to genus level (see Table S1). Macrofaunal samples were identified to the species level.

Because most indices of species diversity are sample-size dependent, the rarefaction method was applied so that all samples could be reduced to the same size, with ES(51) as the expected number of species in a hypothetical random sample of 51 individuals. Previous studies have shown that this approach enables the provision of robust data on species richness in the deep sea and the expected species number is the best density-independent index for the comparison of areas with a nonstandardized sample size [34].

All indexes of biodiversity were calculated with the PRIMER 6 statistical package (www.primer-e.com). The results are also presented as the number of species present in a sample (species richness [SR]) or with widely accepted biodiversity indices. Shannon-Wiener diversity (H') was calculated as $H' = -p_i \Sigma \log_2 p_i$, where $p_i = n_i/N$, n_i is the number of individuals of the i species, and N is the total number of individuals.

Functional Diversity

Functional diversity is the range of functions that are performed by organisms in a system [18]. In the present study, we used the number of different functional (trophic) traits based on the analysis of the feeding types according to the classical literature [35] and updated to the most recent approaches [36]. The diversity of morphofunctional traits has been measured with the assumption that different morphologies, buccal sizes, and other traits reflect a diverse ecological role (e.g., selection of food items within the same feeding guild). The number of predator species is another measure of functional diversity that depends upon the assumption that the number of species at the top of the benthic food web reflects a higher functional diversity of the entire benthic assemblage [37] (Table S4).

Ecosystem Functioning

Three independent indicators of ecosystem functioning were considered: (1) prokaryote biomass and production, (2) total faunal biomass, and (3) organic-matter decomposition. Prokaryotic biomass was estimated after cell counting, carried out by epifluorescence microscopy (EM).

Biovolumes were calculated after intercalibration with measurements conducted with EM and scanning electron microscopy (SEM) and converted into C content, with 310 fg C μm^{-3} assumed as a conversion factor. Benthic prokaryotic production was measured by [^{3}H]-leucine incorporation [38]. So that the effect of decompression on prokaryotic production could be determined, additional experiments were conducted under in situ pressure and at 1 atmosphere on samples collected at the sediment-water interface at approximately 2500 and 3500 m depth. Our results indicated that there were no significant differences between samples collected under in situ pressure and samples analyzed at 1 atmosphere (at approximately 2500 m depth: 0.068 ± 0.02 ngC ml^{-1} h^{-1} both at in situ pressure and at 1 atmosphere; at 3500 m depth: 0.056 ± 0.03 and 0.048 ± 0.01 ngC ml^{-1} h^{-1} in situ pressure and at 1 atmosphere, respectively). These results apply to all the samples collected above 3500 m depth (i.e., more than 70% of all samples).

For the determination of faunal biomass, we calculated the individual biomass of all animals belonging to different taxa. Nematode biomass was calculated from biovolume (n = 100 per replicate) with Andrassy's formula ($V = L \times W^2 \times 0.063 \times 10^{-5}$; body length L in μm and width W in μm). For all of the other taxa, the biovolume was measured for all of the specimens encountered. Body volume was derived from measurements of body length (L; in mm) and width (W; in mm) with the formula $V = L \times W^2 \times C$, where C is the approximate conversion factor for each meiofaunal taxon [39]. The body volume was multiplied by an average density (1.13 g cm^{-3}) to obtain the biomass (μg DW) assuming that the dry:wet weight ratio was 20%–25%, and the C content was considered as 40% of the dry weight.

For the measurement of organic matter decomposition, we determined extracellular enzymatic activities (as aminopeptidase) on surface sediments in triplicate by adding L-leucine-4-methylcoumarinyl-7-amide. This method has been widely used on sediments, including deep-sea systems [40].

Ecosystem Efficiency

Three independent indicators of ecosystem efficiency have been utilized: (1) the ratio of benthic faunal biomass to organic C fluxes, (2) the ratio of prokaryote C production to organic C flux, and (3) the ratio of benthic faunal biomass to biopolymeric C content in the sediment. For the determination of organic C fluxes data, originated from sediment traps deployed in the Equatorial Pacific, North Atlantic, and the Mediterranean at 50–150 mab (see Supplemental Data). Organic C concentrations were determined via standard protocols with a carbon hydrogen nitrogen (CHN) analyzer. The determination of the biopolymeric C in the sediment was estimated through the analysis of the biochemical composition of sediment organic matter [9]

Spatial and Temporal Variability of Deep-Sea Biodiversity

Analyses for the effect of spatial variability were conducted in the Western and Eastern Mediterranean Sea with samples collected in two bathyal plains within an extremely narrow bathymetric range at 3000 m depth (approximately 1%). Spatial patterns were investigated with a hierarchical sampling design, as illustrated in Figure S7B (Table S1). The two regions are at a distance of more than 1000 km, allowing a comparison a large spatial scale. Within each of the two regions, a triangle of approximately 30 km along each side was identified. Three stations were located at approximately 7 km apart at the corner of each triangle. Finally, at each station, three independent deployments were performed. For the analysis of temporal variability, sediment samples were collected in three main areas: (1) the Porcupine Abyssal Plain (seasonal sediment sampling conducted at depth of 4850 m), (2) the Western Mediterranean, and (3) the Eastern Mediterranean (in both cases, biannual sampling conducted at 3000 m depth).

Statistical Analyses

The relationships between biodiversity and ecosystem functioning and ecosystem efficiency in the different deep-sea sites were assessed by nonlinear-regression analyses. The following equation was used for the fitting of the experimental data: $Y = a + m \times (X^b)$. A multivariate multiple regression analysis was also used for the investigation of the relationships between individual indexes of biodiversity and measures of ecosystem functioning and efficiency. All the analyses were done with the routine distance-based multivariate analysis for a linear model (DISTLM) forward [41], and the effects of depth and C fluxes were included as covariates in the analyses. p values were obtained with 4999 permutations of residuals under the reduced model [42].

Supplemental Data

Experimental Procedures, eight figures, four tables, and references for data sources are available at http://www.current-biology.com/cgi/content/full/18/1/1/DC1/.

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References

1. Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., et al. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science *294*, 804–808.
2. Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., and Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. Nature *368*, 734–736.
3. Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., et al. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. *75*, 3–35.
4. Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. Science *314*, 787–790.
5. Grassle, J.F., and Maciolek, N.J. (1992). Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. Am. Nat. *139*, 313–341.
6. Gage, J.D., and Tyler, P.A. (1991). Deep-Sea Biology: A Natural History of Organisms at the Deep Sea Floor (Cambridge: Cambridge University Press).

7. Snelgrove, P.V.R. (1999). Getting to the bottom of marine biodiversity: Sedimentary habitats. Bioscience *49*, 129–138.
8. Lambshead, P.J.D. (2004). Marine nematode biodiversity. In Nematology: Advances and Perspectives Volume 1: Nematode Morphology, Physiology and Ecology, Z.X. Chen, S.Y. Chen, and D.W. Dickson, eds. (London: CABI Publishing), pp. 436–467.
9. Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A., and Tselepides, A. (2001). Deep-sea ecosystem response to climate changes: The eastern Mediterranean case study. Trends Ecol. Evol. *16*, 505–510.
10. Gooday, A.J., Bett, B.J., Shires, R., and Lambshead, P.J.D. (1998). Deep-sea benthic foraminiferal diversity in the NE Atlantic and NW Arabian sea: A synthesis. Deep Sea Res. *45*(Part II), 165–201.
11. Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., and Pawson, D. (2001). Environmental influences on regional deep sea species diversity. Annu. Rev. Ecol. Syst. *32*, 51–93.
12. Stuart, C.T., Rex, M.A., and Etter, R.J. (2003). Large-scale spatial and temporal patterns of deep-sea benthic species diversity. In Ecosystems of the Deep Sea. Ecosystems of the World 28, P.A. Tyler, ed. (Amsterdam: Elsevier), pp. 295–311.
13. Woulds, W., Cowie, G.L., Levin, L.A., Andersson, J.H., Middelburg, J.J., Vandewiele, S., Lamont, P.A., Larkin, K., Gooday, A., Schumacher, S., et al. (2007). Oxygen as a control on sea floor faunal communities and their roles in sedimentary organic matter cycling. Limnol. Oceanogr. *52*, 1698–1709.
14. Cardinale, B.J., Palmer, M.A., and Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. Nature *415*, 426–429.
15. Micheli, F., and Halpern, B.S. (2005). Low functional redundancy in coastal marine assemblages. Ecol. Lett. *8*, 391–400.
16. Heemsbergen, D.A., Berg, M.P., Loreau, M., van Hal, J.R., Faber, J.H., and Verhoef, H.A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science *306*, 1019–1020.
17. Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., and Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. Science *294*, 843–845.
18. Petchey, O.L., and Gaston, K.J. (2006). Functional diversity: Back to basics and looking forward. Ecol. Lett. *9*, 741–758.
19. Danovaro, R., Dell'Anno, A., and Pusceddu, A. (2004). Biodiversity response to climate change in a warm deep sea. Ecol. Lett. *7*, 821–828.
20. Lohrer, A.M., Thrush, S.F., and Gibbs, M.M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature *431*, 1092–1095.
21. Meysman, J.R.F., Middelburg, J.J., and Heip, C.H.R. (2006). Bioturbation: A fresh look at Darwin's last idea. Trends Ecol. Evol. *21*, 688–695.
22. Pike, J., Bernhard, J.M., Moreton, S.G., and Butler, I.B. (2001). Microbioirrigation of marine sediments in dysoxic environments: Implications for early sediment fabric formation and diagenetic processes. Geology *29*, 923–926.
23. Giere, O. (1993). Meiobenthology. The Microscopic Fauna in Aquatic Sediments (Berlin: Springer).
24. De Mesel, I., Derycke, S., Moens, T., Van der Gucht, K., Vincx, M., and Swings, J. (2004). Top-down impact of bacterivorous nematodes on the bacterial community structure: A microcosm study. Environ. Microbiol. *6*, 733–744.
25. Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M., and Raffaelli, D. (2001). Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature *411*, 73–77.
26. Bolam, S., Fernandes, T., and Huxham, M. (2002). Diversity, biomass, and ecosystem processes in the marine benthos. Ecol. Monogr. *72*, 599–615.
27. Connor, N.E., and Crowe, T.P. (2005). Biodiversity loss and ecosystem functioning: Distinguishing between number and identity of species. Ecology *86*, 1783–1796.
28. Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., and Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature *443*, 989–992.
29. Gooday, A.J. (2003). Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: Environmental influences on faunal characteristics. Adv. Mar. Biol. *46*, 1–90.
30. Cronin, T.M., and Raymo, M.E. (1997). Orbital forcing of deep-sea benthic species diversity. Nature *385*, 624–627.
31. Thomas, E. (1998). The biogeography of the late Paleocene benthic foraminiferal extinction. In Late Paleocene-Early Eocene Biotic and Climatic Events in the Marine and Terrestrial Records, M.P. Aubry, S. Lucas, and W.A. Berggren, eds. (New York: Columbia University Press), pp. 214–243.
32. Glover, A.G., and Smith, C.R. (2003). The deep-sea floor ecosystem: Current status and prospects of anthropogenic change by the year 2025. Environ. Conserv. *30*, 219–241.
33. Bryden, H.L., Longworth, H.R., and Cunningham, S.A. (2005). Slowing of the Atlantic meridional overturning circulation at 25 N. Nature *438*, 655–657.
34. Soetaert, K., and Heip, C. (1990). Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. Mar. Ecol. Prog. Ser. *59*, 305–307.
35. Heip, C., Vincx, M., and Vranken, G. (1985). The ecology of marine nematodes. Oceanogr. Mar. Biol. Annu. Rev. *23*, 399–489.
36. Moens, T., and Vincx, M. (1997). Observations on the feeding ecology of estuarine nematodes. J. Mar. Biolog. Assoc. U. K. *77*, 211–227.
37. Ngai, J.T., and Srivastava, D.S. (2006). Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. Science *314*, 963.
38. Danovaro, R., Manini, E., and Dell'Anno, A. (2002). Higher abundance of bacteria than of viruses in deep Mediterranean sediments. Appl. Environ. Microbiol. *68*, 1468–1472.
39. Feller, R.J., and Warwick, R.M. (1988). Energetics. In Introduction to the Study of Meiofauna R, P. Higgins and H. Thiel, eds. (London: Smithsonian Institution Press), pp. 181–196.
40. Dell'Anno, A., and Danovaro, R. (2005). Extracellular DNA plays a key role in deep-sea ecosystem functioning. Science *309*, 2179.
41. Anderson, M.J. (2004). Dros. Inf. Serv.TLM version 5: A FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model (Auckland, New Zealand: Department of Statistics, University of Auckland).
42. Anderson, M.J. (2001). Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. *58*, 626–639.

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Supplemental Data

Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss

Roberto Danovaro, Cristina Gambi, Antonio Dell'Anno, Cinzia Corinaldesi, Simonetta Fraschetti, Ann Vanreusel, Magda Vincx, and Andrew J. Gooday

Supplemental Experimental Procedures

Sample Collection and Processing

At all of the sampling sites, the sediments were collected with a multiple corer (Mod. Maxicorer; i.d., 9.0 cm; depth penetration, > 20 cm, or alternatively with a single mono corer or piston corer) or a box corer (details in Table S1). Chemical and microbiological analyses were carried out from replicate sediment cores (n = 3–10) collected from different deployments. Replicate sediment samples were also used for meiofaunal and macrofaunal extraction and analysis. At each sampling time and station, the nematode diversity was analyzed from three to ten independent sediment cores, whereas macrofaunal diversity was analyzed from at least three independent deployments. The extraction of deep-sea macrofauna (sensu stricto) was performed by the sieving of the sediment immediately after collection through a 0.5 mm mesh net. Material retained on the sieve (organisms, shell fragments, vegetal debris, coarse sediment, and any other matter) was transferred to a 4% buffered formalin solution in seawater and stained with Rose Bengal. No nematodes (nor other taxa belonging to the permanent meiofauna) were encountered in the macrofaunal fraction. For deep-sea meiofaunal extraction, the sediment samples (top 15 cm of the sediment cores) were passed through a 500 μm mesh, and a 20 μm mesh was used so that the smallest organisms could be retained. The fraction remaining on the latter sieve was resuspended and centrifuged three times with Ludox HS40 (density arranged to 1.18 g cm^{-3}). Immediately after collection, all of the meiofaunal samples were stained with Rose Bengal (0.5 g L^{-1}). Because the analysis of soft-body organisms can be difficult in formalin-preserved samples, some fresh samples were analyzed immediately after the sampling for the identification of the characteristics of the different meiofaunal taxa when viewed at 1000× magnification.

Macrofaunal Diversity

Taxonomic identifications of macrofauna were performed with a dissecting stereomicroscope, together with a compound microscope when observation of fine details was required. The organisms were separated according to their main taxonomic groups (i.e., polychaetes, oligochaetes, nemerteans, bivalves, gastropods, amphipods and other crustaceans, cnidarians, sponges, and others) and always identified to the species level.

Meiofaunal Diversity: Higher Taxa

All of the meiobenthic animals were counted and classified per taxon. The following taxa were identified: nematodes, copepods (and naupliar stages), polychaetes, oligochaetes, isopods, cumaceans, tardigrades, amphipods, acari, ostracods, oligochaetes, tanaidaceans, cnidarians, kinorhynchs, turbellarians, gastrotrichs, nemerteans, bivalves, priapulids, cladocerans, decapod (larvae), and loricifera.

Nematode Diversity

At least 300 nematode specimens were identified at each station (more than 100 per sediment core from three independent replicates per station). Nematodes were randomly withdrawn and mounted on slides, according to the formalin-ethanol-glycerol technique (so that dehydration could be prevented). All of the nematodes were identified to the species level according to the recent literature dealing with descriptions of new nematode species. Undescribed species were assigned to a genus followed by sp 1, sp 2, etc.

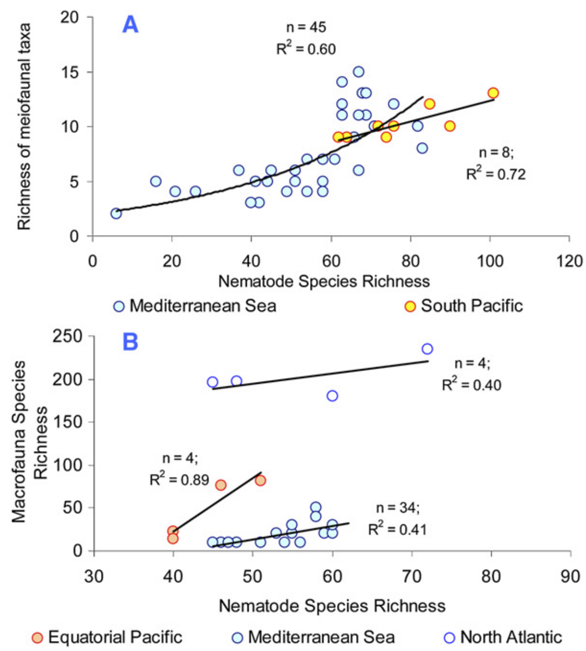

Figure S1. Relationship between Nematode Diversity and Meio- and Macrofaunal Diversity

Relationship between species richness of nematodes and total number of meiofaunal taxa (A) and species richness of macrofauna in deep-sea samples collected synoptically (B). Data originate from the Mediterranean Sea (600–3055 m, mean ± SD: 2117 ± 945 m) and South Pacific Ocean (2040–3070 m, mean ± SD: 2629 ± 440 m) (Figure 1A) and from the North Atlantic (1034–4850 m, mean ± SD: 2720 ± 1547 m) Equatorial Pacific Ocean (4305–4994 m, mean ± SD: 4606 ± 283 m), and Mediterranean Sea (Figure 1B). Data from the North Atlantic refer to nematode genus richness.

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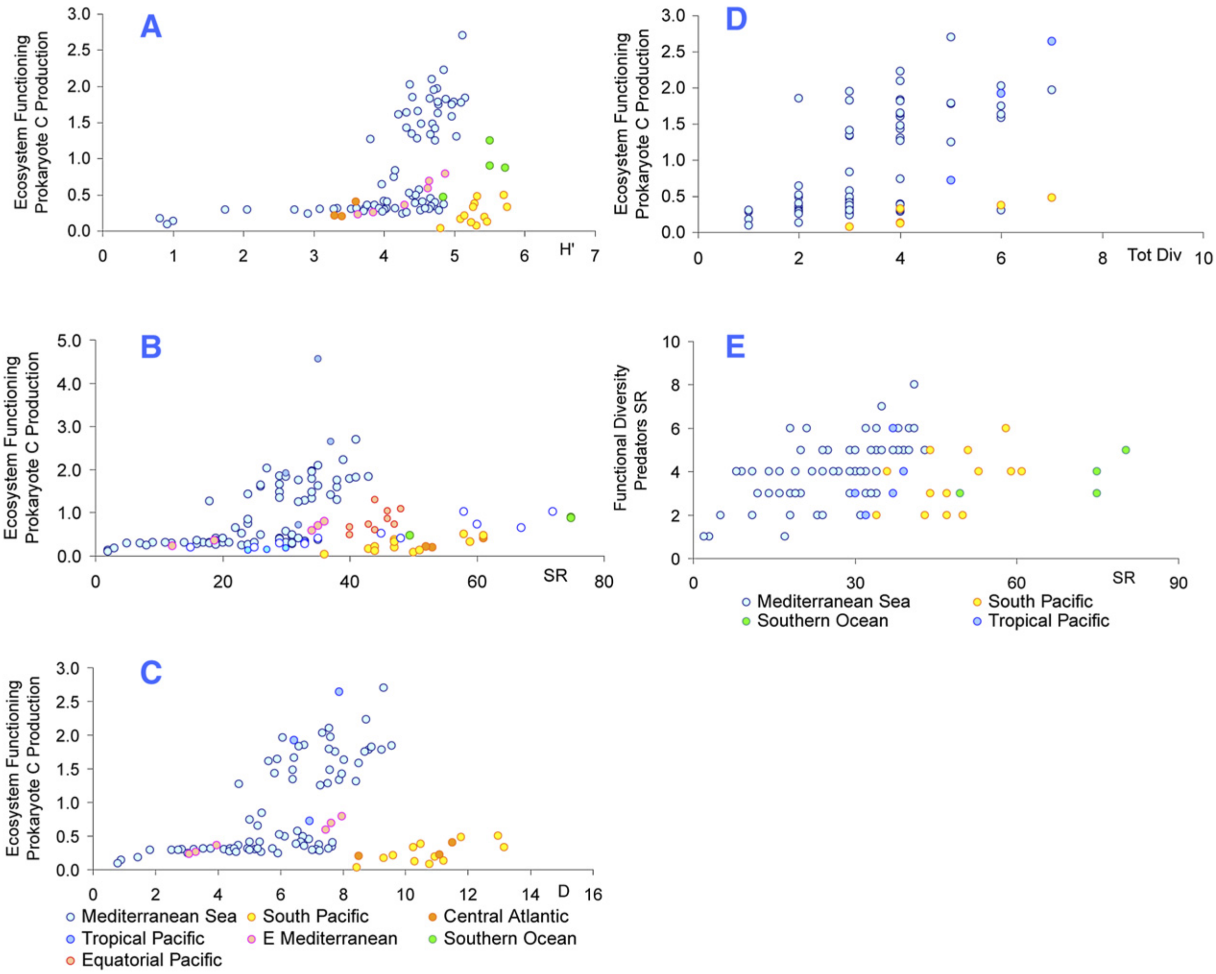


Figure S2. Relationship between Biodiversity and Ecosystem Functioning and between Biodiversity and Functional Diversity

Relationships between biodiversity and ecosystem functioning (measured as prokaryote C production, expressed as μg C g^{-1} d^{-1}) and between total nematode biodiversity and predator species richness (E) in deep-sea sediments. Biodiversity is reported as Shannon-Wiener ("H'") (A), (B) species richness ("SR") (B), Margalef diversity index ("D") (C), total number of taxa ("Tot DIV") (D), and predator species richness ("Predators SR") (E). Data originate from the Western and Eastern Mediterranean Sea, North and Central Atlantic, Equatorial, Tropical, and South Pacific Ocean, and Southern Ocean. Data from the North and Central Atlantic refer to nematode genus richness.
(A) Mediterranean Sea (R^2 = 0.41), Eastern Mediterranean Sea (R^2 = 0.96), South Pacific (R^2 = 0.41), and Southern Ocean (R^2 = 0.68).
(B) Mediterranean Sea (R^2 = 0.52), Eastern Mediterranean Sea (R^2 = 0.81), North Atlantic (R^2 = 0.91), South Pacific (R^2 = 0.67), Equatorial Pacific (R^2 = 0.58), and Central Atlantic (R^2 = 0.82).
(C) Mediterranean Sea (R^2 = 0.52), Eastern Mediterranean Sea (R^2 = 0.94), and South Pacific (R^2 = 0.43).
(D) Mediterranean Sea (R^2 = 0.38), Tropical Pacific (R^2 = 0.70), and South Pacific (R^2 = 0.73).
(E) Mediterranean Sea (R^2 = 0.41), Tropical Pacific (R^2 = 0.31), South Pacific (R^2 = 0.21), and Southern Ocean (R^2 = 0.42).
Depth ranges are 2755–3870 m (mean ± SD: 2919 ± 256 m) for the Western Mediterranean Sea, 1078–1840 m (mean ± SD: 1350 ± 286 m) for the Eastern Mediterranean Sea, 2040–3070 m (mean ± SD: 2629 ± 440 m) for the South Pacific Ocean, 1140–1355 m (mean ± SD: 1248 ± 152 m) for the Tropical Pacific, and 228–588 m (mean ± SD: 462 ± 166 m) for the Southern Ocean.

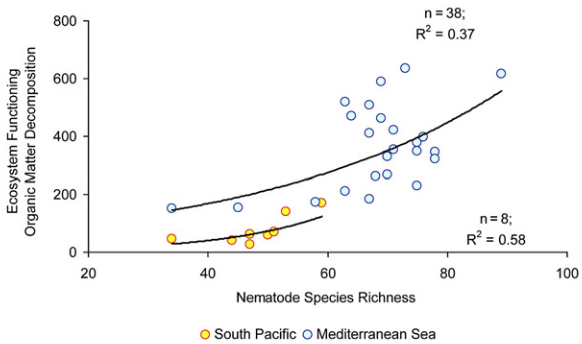


Figure S3. Relationship between Biodiversity and Ecosystem Functioning

Relationship between biodiversity (as nematode species richness) and ecosystem functioning (as aminopeptidase activities, used here as a measure of the rates of decomposition of the protein pool, expressed as nmol g^{-1} h^{-1}). Synoptic data originate from the South Pacific Ocean and the Mediterranean Sea. Data from the South Pacific are multiplied by a factor ten to fit within the same y axis. Depth ranges are 600–3055 m (mean ± SD: 2117 ± 945 m) for the Mediterranean Sea and 2040–3070 m (mean ± SD: 2629 ± 440 m) for the South Pacific Ocean.

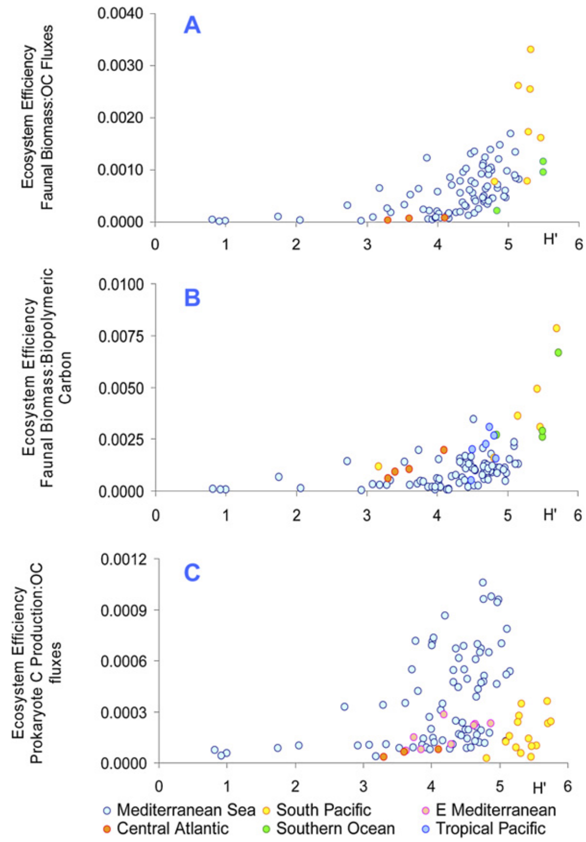


Figure S4. Relationship between Deep-Sea Biodiversity and Ecosystem Efficiency

Relationship between deep-sea biodiversity (reported as H') and ecosystem efficiency determined as the ratio of faunal biomass to organic carbon flux (OC Flux, expressed as d^{-1}) (A), the ratio of faunal biomass to biopolymeric carbon concentration in the sediment (y axis adimensional) (B), and the ratio of prokaryote C production to OC fluxes (y axis adimensional) (C).

(A) Mediterranean Sea (R^2 = 0.55), Central Atlantic (R^2 = 0.84), South Pacific (R^2 = 0.27), and Southern Ocean (R^2 = 0.98).

(B) Mediterranean Sea (R^2 = 0.34), Central Atlantic (R^2 = 0.94), Tropical Pacific (R^2 = 0.35), South Pacific (R^2 = 0.59), and Southern Ocean (R^2 = 0.34).

(C) Mediterranean Sea (R^2 = 0.30), Eastern Mediterranean Sea (R^2 = 0.52), Central Atlantic (R^2 = 0.84), and South Pacific (R^2 = 0.24).

Depth ranges are 1078–3870 m (mean ± SD: 2912 ± 256 m) for the Mediterranean Sea, 3858–5411 m (mean ± SD: 4460 ± 914 m) for the Central Atlantic, 2040–3070 m (mean ± SD: 2629 ± 440 m) for the South Pacific, and 228–588 m (mean ± SD: 462 ± 166 m) for the Southern Ocean.

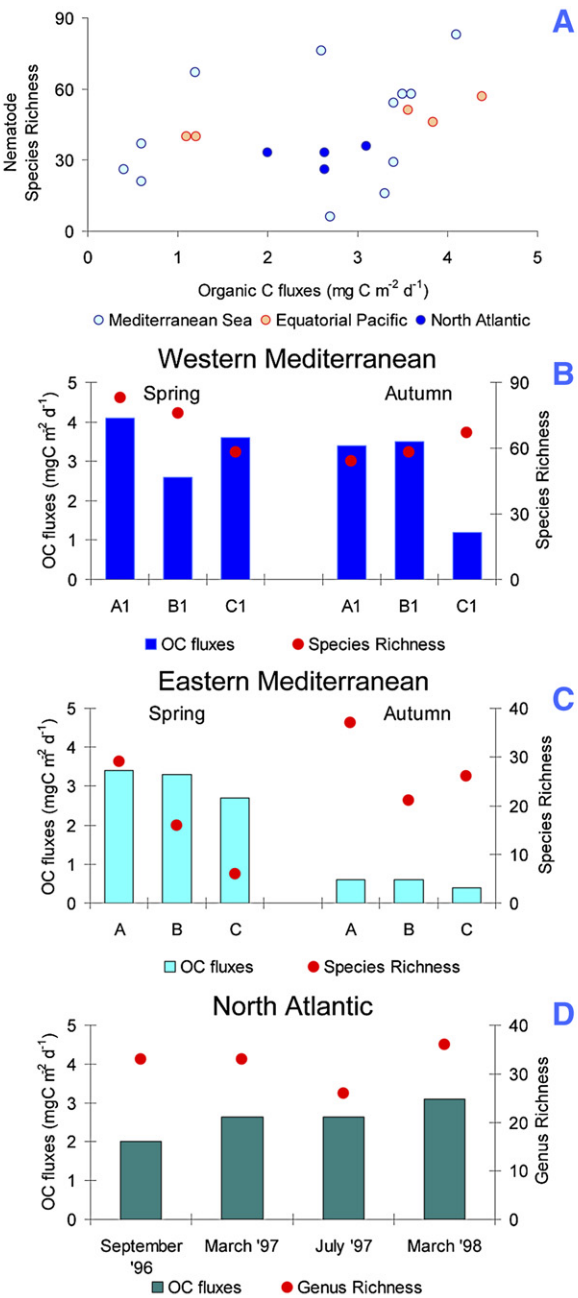


Figure S5. Relationship between Organic Carbon Fluxes and Biodiversity

Patterns of organic C fluxes (expressed as mg C m^{-2} d^{-1}) versus biodiversity (as nematode species richness) in different deep-sea areas (A) and comparison of organic C fluxes versus biodiversity in different periods and in different deep-sea sites (B, C, and D). Data for (A) originate from the Western and Eastern Mediterranean Sea, the North Atlantic (these data refer to genus richness), and the Equatorial Pacific Ocean. The data on downward fluxes used for the Western and Eastern Mediterranean Sea refer to samples collected from March 2001 to May 2002 in traps placed at 50 meters above the bottom (mab). The data on downward fluxes used for North Atlantic refer to annual integrated flux collected from 1994 to 1998 in traps placed at 150 m above the bottom of the Porcupine Abyssal Plain. The data on downward fluxes used for Equatorial Pacific refer to average OC flux collected in 1992 at 700 m depth above the bottom. Measures of organic C flux and benthic diversity from the Mediterranean Sea and the North Atlantic are based on synoptic samplings. Data for (B) and (C) originate from the Western and Eastern Mediterranean Sea, respectively. Data for (D) originate from the North Atlantic Ocean. Depth ranges are 2850–2854 m (mean ± SD: 2852 ± 2 m) for the Western Mediterranean Sea, 2760–2810 m (mean ± SD: 2786 ± 25 m) for the Eastern Mediterranean Sea, 4850 m for the North Atlantic, and 4305–4994 m (mean ± SD: 4606 ± 283 m) for the Equatorial Pacific.

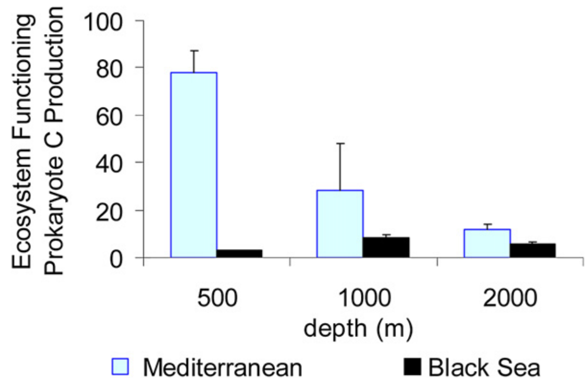
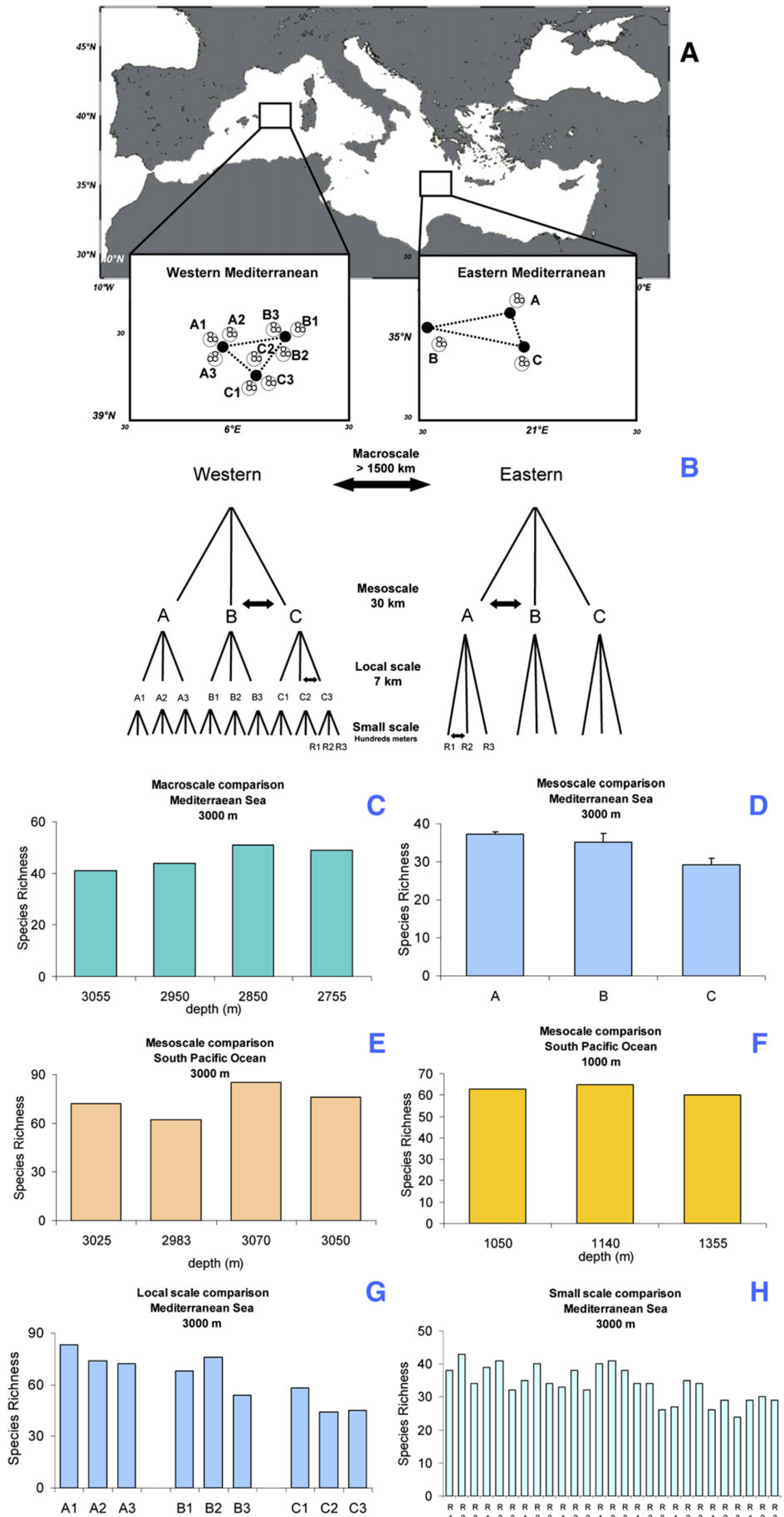


Figure S6. Ecosystem Functioning in the Permanent Anoxic Deep Black Sea and in the Deep Western Mediterranean

Comparison between species richness and ecosystem functioning in the permanent anoxic deep Black Sea and in the deep Western Mediterranean. Selected stations range from 500 m to 2000 m depth. Ecosystem functioning is reported here as benthic prokaryote C production, as ng C ml^{-1} h^{-1}.


A
45°N
40°N
35°N
30°N
10°W
Western Mediterranean
A1
A2
A3
B1
B2
B3
C1
C2
C3
39°N
6°E
Eastern Mediterranean
A
B
C
35°N
21°E
B
Macroscale
> 1500 km
Western
Eastern
Mesoscale
30 km
A
B
C
Local scale
7 km
Small scale
Hundreds meters
R1 R2 R3
C
Macroscale comparison
Mediterraean Sea
3000 m
Species Richness
depth (m)
3055
2950
2850
2755
D
Mesoscale comparison
Mediterranean Sea
3000 m
Species Richness
E
Mesoscale comparison
South Pacific Ocean
3000 m
Species Richness
3025
2983
3070
3050
depth (m)
F
Mesocale comparison
South Pacific Ocean
1000 m
Species Richness
1050
1140
1355
depth (m)
G
Local scale comparison
Mediterranean Sea
3000 m
Species Richness
H
Small scale comparison
Mediterranean Sea
3000 m
Species Richness

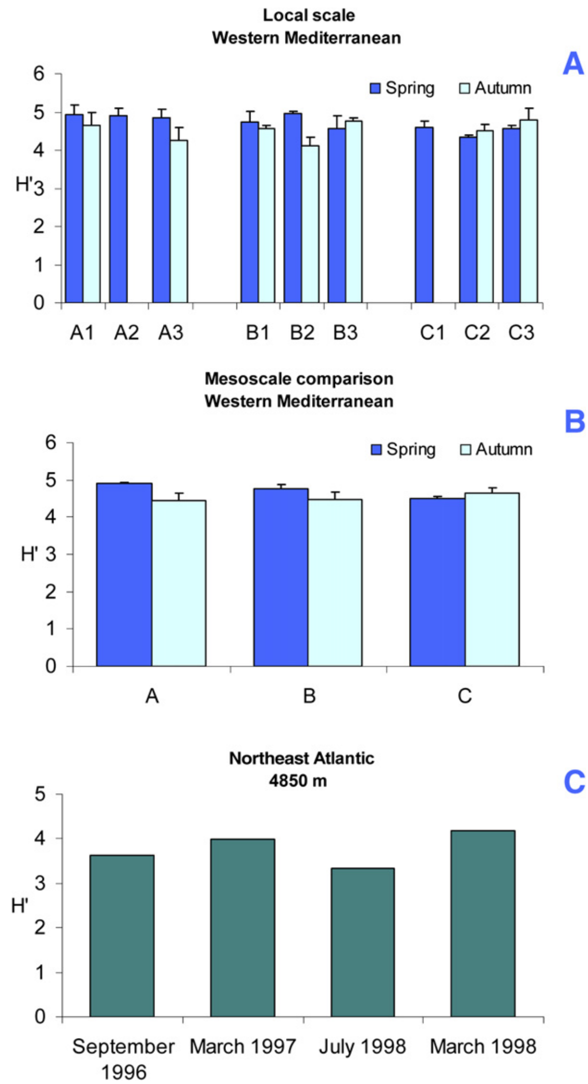


Figure S8. Seasonal Variability of the Deep-Sea Biodiversity

Short-term (seasonal) variability of deep-sea biodiversity. Temporal changes were investigated in the Western Mediterranean (two cruises, in March 2001 and November 2001, at 3000 m depth) at local (A) and mesoscale (B) and in the Northeast Atlantic Ocean (Porcupine Abyssal Plain, four cruises, from September 1996 to March 1998) (C). Data from the Northeast Atlantic are based on nematode genera. Depth ranges are 2850–2854 m (mean ± SD: 2852 ± 2 m) for the local variability analysis and the analysis of mesoscale variability and 4850 m for the Northeast Atlantic.

Figure S7. Variability of Benthic Biodiversity at Different Spatial Scales

(A) Sampling area and station locations used for comparison at the macroscale (two boxes), mesoscale (•), locale scale (O), and micro scale (°). (B–H) Schematic representation of the hierarchical sampling design adopted in the deep Mediterranean Sea (B). Spatial variability of biodiversity was determined at the following spatial scales: macroscale (1000 km) in the Mediterranean Sea (C), mesoscale (~50 km) in the Mediterranean Sea (D), mesoscale (~50 km) at 3000 m depth in the South Pacific (E), mesoscale (~50 km) at 1000 m depth in the South Pacific (F), local scale (~7 km) at 3000 m depth in the Mediterranean Sea (G), and microscale (<1 m) (H). The results of the analysis of biodiversity distribution carried out at different spatial scales (from cm to about 1000 of km) revealed that the patterns seen at the regional scale reflected those seen at the local scale. Patterns of biodiversity distribution in the Mediterranean were also formally analyzed with a permutational multivariate analysis of variance (MANOVA) so that spatial differences in the structure of assemblages at scales of site and locations could be tested for. The analysis consisted of three factors: time (two levels, random), location (three levels, random), and site (three levels, random, nested in location). Thus, with n = 3 sampling units, there were a total of 48 observation units in the data set, with 520 taxa of nematodes (variables) recorded in the study that were included in the multivariate analysis. Results indicate that the structure of assemblages varies between sites differently in time, but a lack of other relevant sources of variability was also observed from this analysis. Depth ranges are: 2755–3870 m (mean ± SD: 2192 ± 256 m) for the Western Mediterranean Sea, 1078–1840 m (mean ± SD: 1350 ± 286 m) for the Eastern Mediterranean Sea, 2983–3070 m (mean ± SD: 3032 ± 38 m) for the South Pacific (E), and 1050–1355 m (mean ± SD: 1182 ± 156 m) for the South Pacific (F).

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Supplemental Data

Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss

Roberto Danovaro, Cristina Gambi, Antonio Dell'Anno, Cinzia Corinaldesi, Simonetta Fraschetti, Ann Vanreusel, Magda Vincx, and Andrew J. Gooday

Table S1. Sampling Area and Details of All of the Investigated Deep-Sea Samples
Reported are: sampling location and period, latitude and longitude, bottom depth (m), sampling equipment (multicorer, MC; single piston corers, PC; Box corer, BC), genus richness (GR), species richness (SR), predator species richness (PSR), Functional diversity (as trophic diversity TD), Shannon-Wiener (‘H log_2), Expected species number (ES(51)), Margalef diversity index (D), Evenness (Pielou index J). n.a.: data not available.

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log_2				
W-Med	Oct 05	42°34.44' (N)	03°24.04' (E)	434	MC/BC	29	36	7	14	4.7	25.8	7.6	0.901	present study
W-Med	Oct 05	42°34.44' (N)	03°24.04' (E)	434	MC/BC	26	33	3	13	4.5	23.3	6.9	0.883	present study
W-Med	Oct 05	42°34.44' (N)	03°24.04' (E)	434	MC/BC	33	40	5	16	5.0	28.4	8.4	0.931	present study
W-Med	Oct 05	42°34.13' (N)	03°39.19' (E)	334	MC/BC	34	45	2	17	5.1	29.7	9.4	0.921	present study
W-Med	Oct 05	42°34.13' (N)	03°39.19' (E)	334	MC/BC	29	44	6	15	5.1	29.5	9.2	0.925	present study
W-Med	Oct 05	42°34.13' (N)	03°39.19' (E)	334	MC/BC	34	47	9	15	5.2	31.5	9.9	0.939	present study
W-Med	Oct 05	42°26.56' (N)	03°31.83' (E)	990	MC/BC	29	42	6	15	4.9	28.0	8.8	0.907	present study
W-Med	Oct 05	42°26.56' (N)	03°31.83' (E)	990	MC/BC	31	37	7	15	4.6	24.5	7.7	0.873	present study
W-Med	Oct 05	42°26.56' (N)	03°31.83' (E)	990	MC/BC	29	37	5	14	4.6	25.2	7.8	0.878	present study
W-Med	Oct 05	42°26.49' (N)	03°51.32' (E)	1,022	MC/BC	29	40	4	13	5.0	29.0	8.4	0.935	present study
W-Med	Oct 05	42°26.49' (N)	03°51.32' (E)	1,022	MC/BC	31	41	4	14	5.1	30.1	8.7	0.947	present study
W-Med	Oct 05	42°26.49' (N)	03°51.32' (E)	1,022	MC/BC	25	33	5	11	4.6	25.8	7.2	0.921	present study
W-Med	Oct 05	42°21.96' (N)	03°49.41' (E)	1,497	MC/BC	31	43	4	16	5.0	29.5	9.2	0.921	present study
W-Med	Oct 05	42°21.96' (N)	03°49.41' (E)	1,497	MC/BC	13	15	0	8	3.7	15.0	4.5	0.946	present study
W-Med	Oct 05	42°21.96' (N)	03°49.41' (E)	1,497	MC/BC	26	35	4	15	4.4	24.2	7.4	0.863	present study
W-Med	Oct 05	42°12.88' (N)	04°15.43' (E)	1,874	MC/BC	35	44	6	17	5.0	28.8	9.2	0.909	present study
W-Med	Oct 05	42°12.88' (N)	04°15.43' (E)	1,874	MC/BC	33	47	8	18	5.0	30.6	10.0	0.909	present study
W-Med	Oct 05	42°12.88' (N)	04°15.43' (E)	1,874	MC/BC	34	51	6	17	5.2	31.5	10.5	0.916	present study
W-Med	Oct 05	42°12.64' (N)	03°49.22' (E)	1,434	MC/BC	20	25	0	12	4.4	25.0	6.6	0.953	present study
W-Med	Oct 05	42°12.64' (N)	03°49.22' (E)	1,434	MC/BC	21	27	2	13	4.4	25.5	6.4	0.931	present study
W-Med	Oct 05	42°12.64' (N)	03°49.22' (E)	1,434	MC/BC	25	35	4	13	4.7	26.2	7.6	0.909	present study
W-Med	Oct 05	42°08.85' (N)	03°35.06' (E)	398	MC/BC	22	33	3	14	4.4	24.0	6.9	0.880	present study
W-Med	Oct 05	42°08.85' (N)	03°35.06' (E)	398	MC/BC	30	35	4	16	4.4	23.3	7.4	0.852	present study
W-Med	Oct 05	42°08.85' (N)	03°35.06' (E)	398	MC/BC	27	42	1	12	4.9	28.1	8.8	0.903	present study
W-Med	Oct 05	42°07.72' (N)	03°46.63' (E)	985	MC/BC	32	41	4	17	5.0	28.8	8.7	0.927	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
W-Med	Oct 05	42°07.72' (N)	03°46.63' (E)	985	MC/BC	24	32	3	14	4.3	23.4	6.8	0.866	present study
W-Med	Oct 05	42°07.72' (N)	03°46.63' (E)	985	MC/BC	32	38	5	16	4.9	27.5	8.0	0.925	present study
W-Med	Oct 05	42°07.05' (N)	04°02.74' (E)	1,887	MC/BC	34	46	5	17	5.2	31.8	9.6	0.950	present study
W-Med	Oct 05	42°07.05' (N)	04°02.74' (E)	1,887	MC/BC	26	38	7	15	4.6	25.4	8.0	0.876	present study
W-Med	Oct 05	42°07.05' (N)	04°02.74' (E)	1,887	MC/BC	28	41	7	15	4.6	27.3	8.8	0.866	present study
W-Med	Oct 05	42°04.78' (N)	04°40.90' (E)	2,342	MC/BC	36	48	3	18	5.3	32.8	10.2	0.943	present study
W-Med	Oct 05	42°04.78' (N)	04°40.90' (E)	2,342	MC/BC	36	53	1	16	5.4	34.0	11.1	0.947	present study
W-Med	Oct 05	42°04.78' (N)	04°40.90' (E)	2,342	MC/BC	36	47	5	16	5.2	31.5	9.9	0.931	present study
W-Med	Jul 99	40°33.99' (N)	04°57.14' (E)	2,755	MC/BC	29	31	4	14	4.5	25.7	7.0	0.913	present study
W-Med	Jul 99	40°33.99' (N)	04°57.14' (E)	2,755	MC/BC	29	33	3	15	4.6	27.0	7.5	0.908	present study
W-Med	Jul 99	40°33.99' (N)	04°57.14' (E)	2,755	MC/BC	18	19	4	9	4.0	19.0	4.6	0.936	present study
W-Med	Mar 01	39°31.37' (N)	05°54.11' (E)	2,850	MC	29	38	5	17	5.0	30.5	8.5	0.945	present study
W-Med	Mar 01	39°31.37' (N)	05°54.11' (E)	2,850	MC	35	43	5	18	5.2	33.4	9.6	0.950	present study
W-Med	Mar 01	39°31.37' (N)	05°54.11' (E)	2,850	MC	27	34	3	14	4.7	29.3	7.9	0.915	present study
W-Med	Nov 01	39°31.37' (N)	05°54.11' (E)	2,850	BC	30	33	3	18	4.7	30.0	7.6	0.933	present study
W-Med	Nov 01	39°31.37' (N)	05°54.11' (E)	2,850	BC	32	37	6	15	4.9	30.7	8.4	0.948	present study
W-Med	Nov 01	39°31.37' (N)	05°54.11' (E)	2,850	BC	23	23	2	13	4.3	23.0	5.9	0.943	present study
W-Med	Mar 01	39°31.12' (N)	06°12.37' (E)	2,852	MC	31	33	5	16	4.5	26.0	7.5	0.886	present study
W-Med	Mar 01	39°31.12' (N)	06°12.37' (E)	2,852	MC	33	38	6	17	5.0	31.0	8.4	0.959	present study
W-Med	Mar 01	39°31.12' (N)	06°12.37' (E)	2,852	MC	25	32	4	15	4.7	27.8	7.3	0.945	present study
W-Med	Nov 01	39°31.12' (N)	06°12.37' (E)	2,852	BC	28	31	4	17	4.7	26.7	6.9	0.941	present study
W-Med	Nov 01	39°31.12' (N)	06°12.37' (E)	2,852	BC	29	31	7	15	4.5	25.1	6.7	0.899	present study
W-Med	Nov 01	39°31.12' (N)	06°12.37' (E)	2,852	BC	28	29	4	15	4.5	26.8	6.6	0.935	present study
W-Med	Mar 01	39°31.07' (N)	06°10.54' (E)	2,853	MC	27	34	3	15	4.8	28.4	7.6	0.936	present study
W-Med	Mar 01	39°31.07' (N)	06°10.54' (E)	2,853	MC	31	34	2	16	4.8	28.0	7.6	0.934	present study
W-Med	Mar 01	39°31.07' (N)	06°10.54' (E)	2,853	MC	25	26	1	10	4.2	22.0	5.6	0.894	present study
W-Med	Nov 01	39°31.07' (N)	06°10.54' (E)	2,853	BC	27	35	5	14	4.9	28.9	7.2	0.946	present study
W-Med	Nov 01	39°31.07' (N)	06°10.54' (E)	2,853	BC	31	32	6	16	4.7	28.2	7.7	0.946	present study
W-Med	Nov 01	39°31.07' (N)	06°10.54' (E)	2,853	BC	25	29	3	13	4.7	27.8	6.8	0.961	present study
W-Med	Mar 01	39°30.07' (N)	05°58.58' (E)	2,850	MC	27	39	5	15	4.8	30.2	8.7	0.917	present study
W-Med	Mar 01	39°30.07' (N)	05°58.58' (E)	2,850	MC	33	41	6	15	5.1	33.4	9.3	0.954	present study
W-Med	Mar 01	39°30.07' (N)	05°58.58' (E)	2,850	MC	27	32	4	13	4.8	32.0	7.7	0.955	present study
W-Med	Mar 01	39°29.54' (N)	06°10.85' (E)	2,854	MC	33	40	6	17	5.0	30.2	8.8	0.937	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
W-Med	Mar 01	39°29.54' (N)	06°10.85' (E)	2,854	MC	35	41	8	19	4.9	30.0	8.9	0.911	present study
W-Med	Mar 01	39°29.54' (N)	06°10.85' (E)	2,854	MC	31	38	5	15	5.0	32.7	8.7	0.946	present study
W-Med	Nov 01	39°29.54' (N)	06°10.85' (E)	2,854	BC	16	19	3	11	4.0	19.0	5.3	0.941	present study
W-Med	Nov 01	39°29.54' (N)	06°10.85' (E)	2,854	BC	21	23	2	11	4.4	23.0	6.0	0.963	present study
W-Med	Nov 01	39°29.54' (N)	06°10.85' (E)	2,854	BC	15	17	1	8	4.0	17.0	5.0	0.984	present study
W-Med	Mar 01	39°28.30' (N)	05°57.37' (E)	2,850	MC	31	35	7	17	4.8	29.4	8.0	0.930	present study
W-Med	Mar 01	39°28.30' (N)	05°57.37' (E)	2,850	MC	32	40	5	15	5.1	34.9	9.2	0.958	present study
W-Med	Mar 01	39°28.30' (N)	05°57.37' (E)	2,850	MC	29	34	5	14	4.7	27.3	7.6	0.921	present study
W-Med	Nov 01	39°28.30' (N)	05°57.37' (E)	2,850	BC	26	26	4	15	4.4	24.8	6.1	0.937	present study
W-Med	Nov 01	39°28.30' (N)	05°57.37' (E)	2,850	BC	27	30	4	15	4.5	24.9	6.5	0.917	present study
W-Med	Nov 01	39°28.30' (N)	05°57.37' (E)	2,850	BC	16	17	1	10	3.9	17.0	4.5	0.950	present study
W-Med	Mar 01	39°21.27' (N)	06°05.94' (E)	2,854	MC	28	29	5	15	4.5	25.3	6.4	0.922	present study
W-Med	Mar 01	39°21.27' (N)	06°05.94' (E)	2,854	MC	29	30	5	16	4.6	26.0	6.6	0.947	present study
W-Med	Mar 01	39°21.27' (N)	06°05.94' (E)	2,854	MC	27	29	4	14	4.5	25.2	6.4	0.932	present study
W-Med	Nov 01	39°21.27' (N)	06°05.94' (E)	2,854	BC	30	41	6	15	5.1	32.4	7.5	0.951	present study
W-Med	Nov 01	39°21.27' (N)	06°05.94' (E)	2,854	BC	34	34	6	13	4.5	25.4	9.2	0.888	present study
W-Med	Nov 01	39°21.27' (N)	06°05.94' (E)	2,854	BC	28	31	2	13	4.8	31.0	7.3	0.966	present study
W-Med	Mar 01	39°21.18' (N)	06°02.30' (E)	2,854	MC	25	26	4	13	4.3	23.9	5.9	0.920	present study
W-Med	Mar 01	39°21.18' (N)	06°02.30' (E)	2,854	MC	27	29	4	14	4.4	25.7	6.8	0.906	present study
W-Med	Mar 01	39°21.18' (N)	06°02.30' (E)	2,854	MC	22	24	2	12	4.3	24.0	5.8	0.943	present study
W-Med	Nov 01	39°21.18' (N)	06°02.30' (E)	2,854	BC	26	30	3	13	4.6	29.0	7.2	0.946	present study
W-Med	Nov 01	39°21.18' (N)	06°02.30' (E)	2,854	BC	27	32	3	13	4.5	24.7	6.8	0.906	present study
W-Med	Nov 01	39°21.18' (N)	06°02.30' (E)	2,854	BC	21	24	2	13	4.3	22.3	5.4	0.942	present study
W-Med	Mar 01	39°18.81' (N)	06°04.24' (E)	2,854	MC	30	27	4	16	4.4	24.3	7.4	0.917	present study
W-Med	Mar 01	39°18.81' (N)	06°04.24' (E)	2,854	MC	30	35	5	16	4.7	26.0	7.6	0.912	present study
W-Med	Mar 01	39°18.81' (N)	06°04.24' (E)	2,854	MC	26	34	4	15	4.7	28.3	6.1	0.925	present study
W-Med	Jul 99	38°24.05' (N)	06°53.72' (E)	2,850	MC/BC	27	29	3	14	4.4	23.9	6.4	0.904	present study
W-Med	Jul 99	38°24.05' (N)	06°53.72' (E)	2,850	MC/BC	32	37	5	16	4.7	27.0	8.0	0.907	present study
W-Med	Jul 99	38°24.05' (N)	06°53.72' (E)	2,850	MC/BC	17	18	2	10	3.8	18.0	4.7	0.913	present study
W-Med	Oct 05	43°18.47' (N)	03°36.60' (E)	960	MC/BC	23	28	2	14	4.3	25.8	6.7	0.906	present study
W-Med	Oct 05	43°18.47' (N)	03°36.60' (E)	960	MC/BC	28	31	4	15	4.5	26.2	7.1	0.912	present study
W-Med	Oct 05	43°18.47' (N)	03°36.60' (E)	960	MC/BC	22	26	2	13	4.3	24.9	6.2	0.900	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
Centr-Med	Aug 05	36°88.98' (N)	14°18.91' (E)	183	BC	27	46	6	15	5.1	31.5	9.9	0.924	present study
Centr-Med	Aug 05	36°88.98' (N)	14°18.91' (E)	183	BC	24	40	5	13	4.9	29.2	8.7	0.919	present study
Centr-Med	Aug 05	36°88.98' (N)	14°18.91' (E)	183	BC	21	37	3	14	4.5	24.4	7.9	0.855	present study
Centr-Med	Aug 05	36°86.43' (N)	14°16.05' (E)	392	BC	21	43	7	16	5.1	31.3	9.4	0.935	present study
Centr-Med	Aug 05	36°86.43' (N)	14°16.05' (E)	392	BC	25	45	7	17	5.1	31.9	9.7	0.929	present study
Centr-Med	Aug 05	36°86.43' (N)	14°16.05' (E)	392	BC	19	33	7	15	4.4	25.3	7.3	0.869	present study
Centr-Med	Aug 05	36°84.40' (N)	14°22.64' (E)	217	BC	24	45	6	13	5.2	32.6	9.8	0.945	present study
Centr-Med	Aug 05	36°84.40' (N)	14°22.64' (E)	217	BC	24	44	7	17	4.8	29.0	9.3	0.884	present study
Centr-Med	Aug 05	36°84.40' (N)	14°22.64' (E)	217	BC	25	42	10	16	4.8	27.6	8.8	0.895	present study
Centr-Med	Aug 05	36°83.58' (N)	14°21.80' (E)	381	BC	26	41	5	13	5.0	29.3	8.7	0.934	present study
Centr-Med	Aug 05	36°83.58' (N)	14°21.80' (E)	381	BC	22	39	9	14	4.8	27.3	8.3	0.906	present study
Centr-Med	Aug 05	36°83.58' (N)	14°21.80' (E)	381	BC	21	37	7	13	4.6	25.1	7.8	0.877	present study
Centr-Med	Aug 05	36°83.02' (N)	14°12.07' (E)	589	BC	19	37	4	15	4.8	27.2	7.9	0.914	present study
Centr-Med	Aug 05	36°83.02' (N)	14°12.07' (E)	589	BC	19	35	5	16	4.3	24.3	7.5	0.840	present study
Centr-Med	Aug 05	36°83.02' (N)	14°12.07' (E)	589	BC	18	37	6	15	4.4	25.7	8.0	0.850	present study
Centr-Med	Aug 05	36°82.88' (N)	14°26.19' (E)	222	BC	19	33	7	12	4.7	26.1	7.2	0.923	present study
Centr-Med	Aug 05	36°82.88' (N)	14°26.19' (E)	222	BC	22	36	6	15	4.5	26.1	7.8	0.880	present study
Centr-Med	Aug 05	36°82.88' (N)	14°26.19' (E)	222	BC	26	46	7	17	4.9	30.2	9.9	0.892	present study
Centr-Med	Aug 05	36°81.68' (N)	14°19.77' (E)	543	BC	32	47	6	17	5.3	34.5	10.4	0.952	present study
Centr-Med	Aug 05	36°81.68' (N)	14°19.77' (E)	543	BC	21	38	6	13	4.7	27.9	8.3	0.900	present study
Centr-Med	Aug 05	36°81.68' (N)	14°19.77' (E)	543	BC	24	39	6	16	4.8	28.1	8.4	0.905	present study
Centr-Med	Aug 05	36°80.56' (N)	14°18.49' (E)	584	BC	22	38	7	14	4.9	28.1	8.2	0.928	present study
Centr-Med	Aug 05	36°80.56' (N)	14°18.49' (E)	584	BC	24	45	5	16	4.8	27.9	9.3	0.879	present study
Centr-Med	Aug 05	36°80.56' (N)	14°18.49' (E)	584	BC	19	34	6	13	4.2	23.3	7.2	0.821	present study
Centr-Med	Aug 05	36°80.53' (N)	14°23.42' (E)	448	BC	25	40	4	14	5.0	30.8	8.8	0.946	present study
Centr-Med	Aug 05	36°80.53' (N)	14°23.42' (E)	448	BC	16	30	3	10	4.2	22.9	6.6	0.856	present study
Centr-Med	Aug 05	36°80.53' (N)	14°23.42' (E)	448	BC	20	36	7	16	4.2	23.3	7.5	0.810	present study
Centr-Med	Aug 05	36°79.32' (N)	14°27.73' (E)	220	BC	19	31	3	15	4.3	24.1	6.9	0.875	present study
Centr-Med	Aug 05	36°79.32' (N)	14°27.73' (E)	220	BC	22	44	5	16	4.7	29.3	9.4	0.870	present study
Centr-Med	Aug 05	36°79.32' (N)	14°27.73' (E)	220	BC	18	34	3	13	4.3	22.9	7.1	0.855	present study
Centr-Med	Aug 05	36°79.31' (N)	14°17.13' (E)	621	BC	20	33	8	11	4.5	24.4	7.0	0.900	present study
Centr-Med	Aug 05	36°79.31' (N)	14°17.13' (E)	621	BC	18	33	5	14	3.9	22.1	7.0	0.775	present study
Centr-Med	Aug 05	36°79.31' (N)	14°17.13' (E)	621	BC	21	33	7	14	4.3	21.9	6.9	0.846	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
Centr-Med	Aug 05	36°78.37' (N)	14°20.73' (E)	606	BC	26	41	3	15	4.9	28.4	8.8	0.914	present study
Centr-Med	Aug 05	36°78.37' (N)	14°20.73' (E)	606	BC	17	37	6	15	4.4	25.0	7.9	0.839	present study
Centr-Med	Aug 05	36°78.37' (N)	14°20.73' (E)	606	BC	17	31	3	11	4.4	24.7	7.0	0.886	present study
Centr-Med	Aug 05	36°78.15' (N)	14°25.98' (E)	500	BC	27	47	11	18	5.1	30.2	9.8	0.916	present study
Centr-Med	Aug 05	36°78.15' (N)	14°25.98' (E)	500	BC	17	38	7	15	4.7	27.3	8.1	0.893	present study
Centr-Med	Aug 05	36°78.15' (N)	14°25.98' (E)	500	BC	19	39	8	16	4.9	28.9	8.5	0.918	present study
Centr-Med	Aug 05	36°77.80' (N)	14°05.73' (E)	786	BC	14	33	4	12	4.7	26.3	7.2	0.930	present study
Centr-Med	Aug 05	36°77.80' (N)	14°05.73' (E)	786	BC	17	32	6	12	4.0	23.0	7.0	0.796	present study
Centr-Med	Aug 05	36°77.80' (N)	14°05.73' (E)	786	BC	21	39	4	16	4.5	26.9	8.4	0.859	present study
Centr-Med	Aug 05	36°77.73' (N)	14°15.37' (E)	672	BC	18	31	4	13	4.5	25.9	7.0	0.911	present study
Centr-Med	Aug 05	36°77.73' (N)	14°15.37' (E)	672	BC	22	41	5	15	4.7	26.8	8.6	0.880	present study
Centr-Med	Aug 05	36°77.73' (N)	14°15.37' (E)	672	BC	22	42	6	16	4.6	26.1	8.8	0.858	present study
Centr-Med	Aug 05	36°76.90' (N)	14°31.75' (E)	183	BC	24	48	2	18	5.1	31.6	10.3	0.921	present study
Centr-Med	Aug 05	36°76.90' (N)	14°31.75' (E)	183	BC	15	27	5	14	3.3	18.4	5.7	0.684	present study
Centr-Med	Aug 05	36°76.90' (N)	14°31.75' (E)	183	BC	23	33	4	14	4.1	23.2	7.0	0.816	present study
Centr-Med	Aug 05	36°76.38' (N)	14°23.29' (E)	620	BC	25	40	6	15	4.8	27.6	8.6	0.896	present study
Centr-Med	Aug 05	36°76.38' (N)	14°23.29' (E)	620	BC	17	33	4	12	4.1	22.6	7.0	0.816	present study
Centr-Med	Aug 05	36°76.38' (N)	14°23.29' (E)	620	BC	23	37	3	13	4.7	27.9	8.1	0.912	present study
Centr-Med	Aug 05	36°75.50' (N)	14°30.16' (E)	337	BC	29	47	6	20	5.2	32.0	10.1	0.930	present study
Centr-Med	Aug 05	36°75.50' (N)	14°30.16' (E)	337	BC	21	35	7	15	4.7	27.4	7.7	0.917	present study
Centr-Med	Aug 05	36°75.50' (N)	14°30.16' (E)	337	BC	27	41	6	10	4.9	30.4	9.0	0.914	present study
Centr-Med	Aug 05	36°74.46' (N)	14°20.94' (E)	720	BC	25	38	5	15	4.8	27.0	8.0	0.922	present study
Centr-Med	Aug 05	36°74.46' (N)	14°20.94' (E)	720	BC	21	37	5	13	4.8	28.3	8.1	0.915	present study
Centr-Med	Aug 05	36°74.46' (N)	14°20.94' (E)	720	BC	24	41	4	15	4.9	29.3	8.9	0.920	present study
Centr-Med	Aug 05	36°74.21' (N)	14°15.69' (E)	807	BC	21	37	6	13	4.8	28.7	8.2	0.922	present study
Centr-Med	Aug 05	36°74.21' (N)	14°15.69' (E)	807	BC	23	40	7	14	4.7	28.4	8.8	0.885	present study
Centr-Med	Aug 05	36°74.21' (N)	14°15.69' (E)	807	BC	23	39	7	16	4.5	25.4	8.2	0.849	present study
Centr-Med	Aug 05	36°73.51' (N)	14°27.75' (E)	603	BC	22	40	4	15	4.8	27.6	8.5	0.905	present study
Centr-Med	Aug 05	36°73.51' (N)	14°27.75' (E)	603	BC	18	34	3	14	4.5	25.2	7.4	0.875	present study
Centr-Med	Aug 05	36°73.51' (N)	14°27.75' (E)	603	BC	17	37	4	15	4.7	27.2	8.0	0.901	present study
Centr-Med	Aug 05	36°69.43' (N)	14°22.92' (E)	760	BC	20	41	5	17	4.9	29.3	8.9	0.911	present study
Centr-Med	Aug 05	36°69.43' (N)	14°22.92' (E)	760	BC	17	37	5	14	4.5	25.8	8.0	0.868	present study
Centr-Med	Aug 05	36°69.43' (N)	14°22.92' (E)	760	BC	18	35	5	13	4.5	25.0	7.5	0.875	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
Centr-Med	Jul 99	36°36.66' (N)	12°14.74' (E)	1,290	MC/BC	31	35	6	12	4.6	26.0	7.6	0.905	present study
Centr-Med	Jul 99	36°36.66' (N)	12°14.74' (E)	1,290	MC/BC	32	36	6	14	4.9	28.6	8.0	0.942	present study
Centr-Med	Jul 99	36°36.66' (N)	12°14.74' (E)	1,290	MC/BC	31	34	6	12	4.6	25.8	7.4	0.909	present study
E-Med	Sep 89	36°02.81' (N)	23°25.80 (E)	1,215	MC/BC	17	19	1	9	4.3	17.6	4	0.97	present study
E-Med	Sep 89	36°01.66' (N)	24°03.63' (E)	1,147	MC/BC	12	13	3	8	3.9	13.2	3.3	0.98	present study
E-Med	Sep 89	35°55.15' (N)	24°36.06' (E)	1,078	MC/BC	11	12	3	10	3.6	12.1	3.1	0.94	present study
E-Med	Sep 89	35°52.22' (N)	25°07.35' (E)	1,840	MC/BC	15	17	3	12	4.2	16.5	4.2	0.98	present study
E-Med	Sep 89	35°51.25' (N)	24°50.78' (E)	1,531	MC/BC	11	12	3	8	3.7	12.1	2.6	0.98	present study
E-Med	Jul 99	35°46.29' (N)	28°43.15' (E)	3,870	MC/BC	19	19	3	11	3.9	19.0	4.6	0.910	present study
E-Med	Jul 99	35°46.29' (N)	28°43.15' (E)	3,870	MC/BC	20	20	3	13	4.0	20.0	5.0	0.936	present study
E-Med	Jul 99	35°46.29' (N)	28°43.15' (E)	3,870	MC/BC	19	19	3	10	3.9	18.7	4.5	0.925	present study
E-Med	May 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	14	14	4	11	3.5	14.0	4.2	0.928	present study
E-Med	May 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	16	18	6	12	3.7	18.0	4.4	0.896	present study
E-Med	May 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	12	12	3	8	1.7	9.3	2.5	0.487	present study
E-Med	Oct 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	18	20	5	13	4.0	20.0	5.2	0.930	present study
E-Med	Oct 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	18	21	6	13	4.0	21.0	5.3	0.918	present study
E-Med	Oct 01	35°08.32' (N)	20°50.90' (E)	2,788	BC	15	18	3	11	4.0	18.0	5.0	0.960	present study
E-Med	May 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	9	9	4	7	3.1	9.0	3.2	0.973	present study
E-Med	May 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	10	11	4	9	3.3	11.0	3.5	0.965	present study
E-Med	May 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	5	5	2	5	2.1	5.0	1.8	0.887	present study
E-Med	Oct 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	11	11	2	9	3.3	11.0	2.8	0.950	present study
E-Med	Oct 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	14	14	3	7	3.6	14.0	3.8	0.949	present study
E-Med	Oct 01	35°04.09' (N)	20°30.45' (E)	2,810	BC	7	7	0	6	2.7	7.0	2.7	0.971	present study
E-Med	Jul 99	34°52.91' (N)	22°31.97' (E)	2,950	MC/BC	22	24	4	13	4.1	20.4	5.0	0.890	present study
E-Med	Jul 99	34°52.91' (N)	22°31.97' (E)	2,950	MC/BC	23	24	5	15	4.2	21.0	5.4	0.908	present study
E-Med	Jul 99	34°52.91' (N)	22°31.97' (E)	2,950	MC/BC	21	22	4	13	4.0	19.4	5.3	0.903	present study
E-Med	May 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	2	2	1	3	1.0	2.0	0.9	1.000	present study
E-Med	May 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	3	3	1	2	0.8	3.0	1.4	0.515	present study
E-Med	May 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	2	2	1	2	0.9	2.0	0.8	0.918	present study
E-Med	Oct 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	14	16	3	11	3.7	16.0	4.4	0.929	present study
E-Med	Oct 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	15	16	4	10	3.8	16.0	4.7	0.941	present study
E-Med	Oct 01	34°52.71' (N)	20°49.14' (E)	2,760	BC	10	11	2	8	3.2	11.0	3.1	0.920	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
E-Med	Jul 99	33°23.18' (N)	28°19.04' (E)	3,055	MC/BC	23	25	5	14	4.2	22.5	5.7	0.896	present study
E-Med	Jul 99	33°23.18' (N)	28°19.04' (E)	3,055	MC/BC	27	29	0	17	4.4	24.4	6.5	0.914	present study
E-Med	Jul 99	33°23.18' (N)	28°19.04' (E)	3,055	MC/BC	8	8	4	5	2.9	8.0	3.0	0.974	present study
Black Sea	Sep 06	44°32.15' (N)	31°07.10' (E)	175	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	44°27.39' (N)	31°12.50' (E)	509	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	44°10.11' (N)	31°26.11' (E)	991	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	43°35.46' (N)	29°30.30' (E)	261	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	43°34.04' (N)	29°38.23' (E)	540	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	43°28.20' (N)	29°56.35' (E)	975	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	43°15.08' (N)	31°55.52' (E)	2,005	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Black Sea	Sep 06	42°58.60' (N)	30°41.18' (E)	2,025	MC	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	present study
Centr-Atlantic	Oct 93	21°18.00' (N)	30°32.00' (W)	4,650	MC	24	n.a.	n.a.	11	n.a.	n.a.	n.a.	n.a.	present study
Centr-Atlantic	Oct 93	21°12.00' (N)	30°18.00' (W)	4,650	MC	30	n.a.	n.a.	15	n.a.	n.a.	n.a.	n.a.	present study
Centr-Atlantic	Oct 93	21°10.00' (N)	30°15.00' (W)	4,650	MC	27	n.a.	n.a.	15	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	May 91	48°50.20' (N)	16°29.90' (W)	4,850	MC	25	n.a.	n.a.	13	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	May 91	48°50.20' (N)	16°29.90' (W)	4,850	MC	29	n.a.	n.a.	13	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	May 91	48°50.20' (N)	16°29.90' (W)	4,850	MC	15	n.a.	n.a.	10	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	Sep 96	48°50.20' (N)	16°29.90' (W)	4,850	MC	33	n.a.	n.a.	15	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	Mar 97	48°50.20' (N)	16°29.90' (W)	4,850	MC	33	n.a.	n.a.	17	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	Jul 97	48°50.20' (N)	16°29.90' (W)	4,850	MC	26	n.a.	n.a.	15	n.a.	n.a.	n.a.	n.a.	present study
NE Atlantic	Mar 98	48°50.20' (N)	16°29.90' (W)	4,850	MC	36	n.a.	n.a.	19	n.a.	n.a.	n.a.	n.a.	present study
NW Atlantic	n.a.	40°27.00' (N)	62°20.00' (W)	4,626	BC	n.a.	133	n.a.	n.a.	n.a.	24.9	n.a.	n.a.	Thistle & Sherman 1985
NW Atlantic	n.a.	40°27.00' (N)	62°20.00' (W)	4,626	BC	n.a.	124	n.a.	n.a.	n.a.	25.3	n.a.	n.a.	Thistle & Sherman 1985
NE Atlantic	Oct 93	49°28.00' (N)	11°12.00' (W)	206	BC	67	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
NE Atlantic	Oct 93	49°24.00' (N)	11°31.00 (W)	670	BC	60	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
NE Atlantic	Oct 93	49°21.00' (N)	11°48.00' (W)	1,034	BC	45	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
NE Atlantic	Oct 93	49°11.00' (N)	12°49.00' (W)	1,425	BC	72	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
NE Atlantic	Oct 93	49°09.00' (N)	12°59.00' (W)	1,961	BC	58	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
NE Atlantic	Oct 93	49°09.00' (N)	13°05.00' (W)	2,182	BC	48	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
NE Atlantic	Oct 93	49°07.00' (N)	13°10.00' (W)	2,760	BC	35	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanaverbeke et al 1997
Centr-Atlantic	1984	32°29.60' (N)	70°21.00' (E)	5,411	BC	n.a.	116	n.a.	n.a.	4.1	30.0	19.1	0.870	Tietjen 1989
Centr-Atlantic	1984	31°10.00' (N)	21°10.00' (W)	4,950	MC	n.a.	78	n.a.	n.a.	n.a.	25.4	n.a.	n.a.	Lambshead & Hodda 1994
Centr-Atlantic	1986	19°35.70' (N)	66°11.20' (E)	8,189	BC	n.a.	52	n.a.	n.a.	3.3	22.4	11.1	0.920	Tietjen 1989
Centr-Atlantic	1985	19°08.70' (N)	66°14.30' (E)	7,460	BC	n.a.	61	n.a.	n.a.	3.6	25.4	11.5	0.870	Tietjen 1989
Centr-Atlantic	n.a.	15°07.60' (N)	69°24.10' (W)	3,858	BC	n.a.	53	n.a.	n.a.	3.4	27.2	8.5	0.930	Tietjen 1984
Centr-Atlantic	n.a.	13°47.90' (N)	67°47.60' (W)	5,054	BC	n.a.	85	n.a.	n.a.	4.0	31.8	12.6	0.950	Tietjen 1984
Centr-Atlantic	n.a.	13°33.40' (N)	64°43.30' (W)	3,517	BC	n.a.	75	n.a.	n.a.	3.6	32.1	10.0	0.850	Tietjen 1984
Pacific Ocean	Jul 92	22°54.95' (N)	157°49.93' (W)	4,871	MC	n.a.	43	n.a.	n.a.	n.a.	28.2	n.a.	n.a.	Lambshead et al 2002
Pacific Ocean	Jul 92	22°54.74' (N)	157°50.21' (W)	4,880	MC	n.a.	40	n.a.	n.a.	n.a.	27.3	n.a.	n.a.	Lambshead et al 2002
Pacific Ocean	Jul 92	22°54.69' (N)	157°49.74' (W)	4,880	MC	n.a.	44	n.a.	n.a.	n.a.	28.6	n.a.	n.a.	Lambshead et al 2002
Tropical Pacific	Sep 97	23°15.00' (S)	70°40.00' (W)	1,355	BC	34	39	4	18	4.8	27.8	7.9	0.914	present study
Tropical Pacific	Sep 97	23°15.00' (S)	70°40.00' (W)	1,355	BC	35	37	3	18	4.7	26.7	8.3	0.913	present study
Tropical Pacific	Sep 97	23°15.00' (S)	70°40.00' (W)	1,355	BC	28	30	3	17	4.5	23.5	6.4	0.900	present study
Tropical Pacific	Sep 97	23°30.5' (S)	70°42.8' (W)	1,050	BC	33	33	4	17	4.6	24.8	7.0	0.907	present study
Tropical Pacific	Sep 97	23°30.5' (S)	70°42.8' (W)	1,050	BC	37	38	9	23	4.8	27.4	8.1	0.923	present study
Tropical Pacific	Sep 97	23°30.5' (S)	70°42.8' (W)	1,050	BC	21	24	2	16	3.8	22.9	5.7	0.830	present study
Tropical Pacific	Sep 97	23°46.60' (S)	70°37.40' (W)	1,140	BC	32	37	6	17	4.8	27.9	7.9	0.923	present study
Tropical Pacific	Sep 97	23°46.60' (S)	70°37.40' (W)	1,140	BC	34	35	0	19	4.7	28.1	8.1	0.924	present study
Tropical Pacific	Sep 97	23°46.60' (S)	70°37.40' (W)	1,140	BC	32	32	2	17	4.5	24.2	6.9	0.899	present study
South Pacific	Feb 02	33°18.40' (S)	76° 55.80' (W)	3,025	PC	38	47	2	16	5.4	38.9	10.9	0.976	present study
South Pacific	Feb 02	33°18.40' (S)	76° 55.80' (W)	3,025	PC	35	43	2	14	5.1	31.0	9.3	0.938	present study
South Pacific	Feb 02	33°28.50' (S)	78°52.00' (W)	2,040	PC	35	47	2	16	5.3	35.1	10.5	0.952	present study
South Pacific	Feb 02	33°28.50' (S)	78°52.00' (W)	2,040	PC	26	34	2	16	3.2	20.3	7.2	0.622	present study
South Pacific	Feb 02	33°29.00' (S)	77°45.00' (W)	2,233	PC	42	61	4	18	5.3	31.0	11.8	0.897	present study
South Pacific	Feb 02	33°29.00' (S)	77°45.00' (W)	2,233	PC	42	50	2	17	5.3	33.7	10.8	0.941	present study
South Pacific	Feb 02	33°33.10' (S)	76°54.30' (W)	2,983	PC	30	44	5	12	5.1	31.9	9.6	0.942	present study
South Pacific	Feb 02	33°33.10' (S)	76°54.30' (W)	2,983	PC	29	36	4	11	4.8	31.2	8.4	0.930	present study
South Pacific	Feb 02	33°39.30' (S)	77°51.40' (W)	2,350	PC	32	74	4	20	5.7	34.8	14.4	0.919	present study
South Pacific	Feb 02	33°39.30' (S)	77°51.40' (W)	2,350	PC	27	64	3	17	5.5	34.4	12.9	0.924	present study

Location	Period	Latitude	Longitude	Depth	Equip	GR	SR	PSR	TD	H'	ES(51)	D	J	Source
				m						log2				
South Pacific	Feb 02	33°42.40' (S)	80°20.00' (W)	3,070	PC	42	58	6	17	5.7	40.9	13.0	0.973	present study
South Pacific	Feb 02	33°42.40' (S)	80°20.00' (W)	3,070	PC	36	53	4	15	5.5	36.3	11.6	0.954	present study
South Pacific	Feb 02	33°48.20' (S)	78°32.10' (W)	2,280	PC	35	51	5	17	5.5	36.6	11.2	0.964	present study
South Pacific	Feb 02	33°48.20' (S)	78°32.10' (W)	2,280	PC	26	44	3	10	5.2	36.9	10.3	0.959	present study
South Pacific	Feb 02	33°54.20' (S)	80°22.50' (W)	3,050	PC	52	59	4	14	5.8	41.5	13.2	0.978	present study
South Pacific	Feb 02	33°54.20' (S)	80°22.50' (W)	3,050	PC	41	47	3	11	5.3	33.6	10.2	0.949	present study
Equatorial Pacific	Nov 92	08°56.04' (N)	139°51.55' (W)	4,994	BC	n.a.	40	n.a.	n.a.	n.a.	26.6	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	08°55.80' (N)	139°52.30' (W)	4,991	BC	n.a.	49	n.a.	n.a.	n.a.	33.9	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	08°55.08' (N)	139°52.20' (W)	4,986	BC	n.a.	51	n.a.	n.a.	n.a.	33.3	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	05°05.00' (N)	139°39.00' (W)	4,447	BC	n.a.	46	n.a.	n.a.	n.a.	30.0	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	05°04.80' (N)	139°38.50' (W)	4,424	BC	n.a.	54	n.a.	n.a.	n.a.	34.5	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	05°04.42' (N)	139°38.90' (W)	4,446	BC	n.a.	46	n.a.	n.a.	n.a.	31.9	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	02°04.00' (N)	140°07.90' (W)	4,414	BC	n.a.	44	n.a.	n.a.	n.a.	30.7	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	02°03.96' (N)	140°08.06' (W)	4,409	BC	n.a.	51	n.a.	n.a.	n.a.	34.2	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	02°03.94' (N)	140°08.94' (W)	4,409	BC	n.a.	48	n.a.	n.a.	n.a.	31.6	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	00°06'40' (N)	139°44.10' (W)	4,307	BC	n.a.	47	n.a.	n.a.	n.a.	30.6	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	00°06.62' (N)	139°43.96' (W)	4,305	BC	n.a.	57	n.a.	n.a.	n.a.	35.8	n.a.	n.a.	Lambshead et al 2002
Equatorial Pacific	Nov 92	00°06.00' (N)	139°43.90' (W)	4,328	BC	n.a.	46	n.a.	n.a.	n.a.	33.1	n.a.	n.a.	Lambshead et al 2002
Southern Ocean	Mar 02	58°50.00' (S)	23°50.00' (W)	6,319	MC	34	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Vanhove et al 2004
Southern Ocean	Feb 96	71°34.00' (S)	12°27.00' (W)	588	MC/BC	68	75	3	23	5.5	27.1	11.4	0.820	present study
Southern Ocean	Feb 96	71°40.00' (S)	12°44.00' (W)	228	MC/BC	68	75	4	26	5.7	30.5	12.8	0.854	present study
Southern Ocean	Dec 94	72°30.00' (S)	175°00.00' (E)	460	BC	45	50	3	21	4.8	22.7	8.4	0.805	present study
Southern Ocean	Dec 94	74°00.00' (S)	175°00.00' (E)	570	BC	73	80	5	26	5.5	26.8	12.3	0.805	present study

Table S2. Results of Non Parametric Multivariate Multiple Regression

A

Marginal tests (Ecosystem functioning)			
Variable	% Var	F	P
SR	56.92	41.37	0.001
H'(log2)	34.36	21.05	0.001
ES(51)	40.76	26.14	0.001
$(H')^2$	42.62	27.70	0.001
D	52.45	36.76	0.001
Taxa richness	83.42	77.62	0.001
SR predators	21.33	11.98	0.001
Functional div.	53.94	38.26	0.001

Sequential tests (Ecosystem functioning)				
Variable	% Var	F	P	Cum (%)
Taxa richness	83.42	77.62	2e-4	46.9
SR	11.41	11.94	4e-4	53.3
ES(51)	6.60	7.41	3e-3	57.0

B

Marginal tests (Ecosystem efficiency)			
Variable	% Var	F	P
SR	76.16	35.12	0.001
H' (log2)	58.43	24.66	0.001
ES(51)	64.92	28.27	0.001
$(H')^2$	67.18	29.58	0.001
D	80.12	37.73	0.001
Taxa richness	53.01	21.80	0.001
SR predators	68.84	30.57	0.001
Functional div. (as Tot Num Trop. Tr.)	61.56	26.37	0.001

Sequential tests (Ecosystem efficiency)				
Variable	% Var	F	P	Cum. (%)
+D	80.12	37.73	2.0e-4	30.0
+SR predators	14.82	7.50	6.0e-4	35.6
+Taxa richness	8.981	4.74	6.6e-3	38.9

C

	SR	H' (log2)	ES(51)	$(H')^2$	D	Taxa richness	SR Predators
SR							
H' (log2)	0.90						
ES(51)	0.97	0.94					
$(H')^2$	0.96	0.98	0.98				
D	0.98	0.91	0.96	0.96			
Taxa richness	0.51	0.45	0.46	0.47	0.53		
SR Predators	0.62	0.55	0.56	0.57	0.61	0.37	
Tot Num trophic traits	0.90	0.87	0.88	0.89	0.88	0.52	0.56

Results of multiple regressions of indexes of biodiversity on (A) different measures of ecosystem functioning (Prokaryote C Production and total meiofaunal biomass) and (B) efficiency. % Var: percentage of variance explained by the variable. The correlation matrix among all pairs of explanatory variables of biodiversity deriving from the first analysis is also shown (C). Output from the analysis includes: (a) the results of the marginal tests (i.e. fitting each variable individually, ignoring other variables), followed by (b) the results of the forward selection procedure with the conditional tests (i.e. fitting each variable one at a time, conditional on the variables that are already included in the model). The multivariate multiple regressions were based on Euclidean distances. The forward selection of the predictor variables was done with tests by permutation. P-values were obtained using 4999 permutations of raw data for the marginal tests (tests of individual variables), while for all conditional tests, the program uses 4999 permutations of residuals under a reduced model. High correlations among many of the variables (e.g., between Species Richness and $(H')^2$ or between ES(51) and

Species Richness) helps to explain the choice of certain variables over others in the forward selection procedure.

Table S3. Permutational MANOVA on the Basis of the Bray-Curtis Dissimilarities on Untransformed Data

Source	df	SS	MS	F	P (perm)
COV	2	688.3	344.14	87.54	0.001
Time	1	158.6	158.63	27.87	0.090
Location	2	47.50	23.75	0.24	0.977
Site (Location)	6	779.2	129.87	0.84	0.590
Time × Location	2	1300.0	650.00	40.72	0.064
Time × Site (Location)	6	917.6	152.93	38.90	0.005
Res	34	1336.6	39.31		
Total	53	5775.5			

Source	Estimates of variance components
COV	5.45E+02
Time	12.00
Location	0
Site (Location)	0
Time × Location	77.63
Time × Site (Location)	66.12

Each test was based on 4999 permutations of appropriate units. The appropriate permutable units are indicated by the denominator mean square in each case and are shown in the final column. The analysis also includes the functional variable prokaryote C production and meiofaunal production as covariates. Estimates of variance components are also included.

Table S4. List of Predator Genera Encountered in Deep-Sea Sediments

1. *Bolbolaimus*
2. *Cheironchus*
3. *Choanolaimus*
4. *Chromaspirina*
5. *Cylicolaimus*
6. *Dolicholaimus*
7. *Doliolaimus*
8. *Enoploides*
9. *Enoplolaimus*
10. *Epacanthion*
11. *Gairleanema*
12. *Gammanema*
13. *Halichoanolaimus*
14. *Latronema*
15. *Mesacanthion*
16. *Mesacanthoides*
17. *Metasphaerolaimus*
18. *Oxyoncus*
19. *Pandolaimus*
20. *Paramesacanthion*
21. *Parasphaerolaimus*
22. *Pomponema*
23. *Ptycolaimellus*
24. *Rhabdodemania*
25. *Sigmophoranema*
26. *Siphonolaimus*
27. *Sphaerolaimus*
28. *Subsphaerolaimus*
29. *Synodontium*
30. *Synonchiella*
31. *Synonchium*
32. *Synonchus*
33. *Syringolaimus*
34. *Thalassironus*
35. *Thoracostomopsis*
36. *Trileptium*
37. *Tripyloides*
38. *Trissonchulus*
39. *Tubolaimoides*

References for Data Sources

Mediterranean Sea

a. Boetius, A., Scheibe, S., Tselepides, A., and Thiel, H. (1996). Microbial biomass and activities in deep-sea sediments of the eastern Mediterranean: trenches are benthic hotspots. Deep- Sea Res Part I 43, 1439-1460.
b. Danovaro, R., Manini, E., and Dell'Anno, A. (2002). Higher abundance of bacteria than of viruses in deep Mediterranean sediments. Appl. Environ. Microbiol. 68, 1468-1472.
c. Danovaro, R., Dinet, A., Duineveld, G., and Tselepides, A. (1999). Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions-Catalan Sea (western Mediterranean) and the Cretan sea (eastern Mediterranean). Progr. Oceanogr. 44, 287-312.
d. Gambi, C., and Danovaro, R. (2006). A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. Deep-Sea Res Part I 53, 1117-1134.

Atlantic Ocean

a. Aller, J.Y. (1989). Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. Deep-Sea Res Part A 36, 901-934.
b. Antia, A.N., Maaßen, J., Herman, P., Voß, M., Scholten, J., Groom, S., and Miller P. (2001). Spatial and temporal variability of particle flux at the NW European continental margin. Deep-Sea Res Part II 48, 3083-3106.
c. Eardly, D.F., Carton, M.W., Gallagher, J.M., and Patching, J.W. (2001). Bacterial abundance and activity in deep-sea sediments from the eastern North Atlantic. Prog. Oceanogr. 50, 245-259.
d. Flach, F., Muthumbi, A., and Heip, C. (2002). Meiofauna and macrofauna community structure in relation to sediment composition at the Iberian margin compared to the Goban Spur (NE Atlantic). Progr. Oceanogr. 52, 433-457.
e. Galéron, J., Sibuet, M., Vanreusel, A., Mackenzie, K., Gooday, A.J., Dinet, A., and Wolff, G.A. (2001). Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. Progr. Oceanogr. 50, 303-324.
f. Harvey, H.R., Richardson, M.D., and Patton, J.S. (1984). Lipid composition and vertical distribution of bacteria in aerobic sediments of the Venezuela Basin. Deep-Sea Res 31, 403-413.
g. Heip, C., Duineveld, G., Flach, E., Graf, G., Helder, W., Herman, P.M.J., Lavaleye, M., Middelburg, J.J., Pfannkuche, O., Soetart, K., Soltwedel, T., de Stigter, H., Thomsen, L., Vanaverbeke, J., and de Wilde, P. (2001). The role of the benthic biota in sedimentary metabolism and sediment-water exchange process in the Goban Spur area (NE Atlantic). Deep-Sea Res Part II 48, 3223-3243.
h. Lambshead, P.J.D., Tietjen, J., Ferrero, T.J., and Jensen, P. (2000). Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. Mar Ecol Progr Ser 194, 159-167.
i. Lambshead, P.J.D., Tietjen, J., Glover, A., Ferrero, T.J., Thistle, D., Gooday, A.J. (2001). Impact of large-scale natural physical disturbance on the diversity of deep-sea North Atlantic nematodes. Mar Ecol Progr Ser 214, 121-126.
j. Lampitt, R.S., Antia, A.N. (1997). Particle flux in deep seas: regional characteristics sand temporal variability. Deep-Sea Res Part I 44, 1377-1403.
k. Relexans, J.C., Deming, J., Dinet, A., Gaillard, J.F., and Sibuet, M. (1996). Sedimentary organic matter and micro-meiobenthos with relation to trophic conditions in the tropical northeast Atlantic. Deep-Sea Res Part I 43, 1343-1368.
l. Richardson, M.D., and Young, D.K. (1987). Abyssal benthos of the Venezuela basin, Carribean Sea: standing stock considerations. Deep-Sea Res Part I 34, 145-164.
m. Thistle, D., and Sherman, K.M. (1985). The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep-Sea Res Part A 32, 1077-1088.

n. Tietjen, J.H. (1984). Distribution and species diversity of deep-sea nematodes in the Venezuela basin. Deep-Sea Res Part A 31, 119-132.
o. Tietjen, J.H. (1989). Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. Deep-Sea Res Part A 36, 1579-1594.
p. Tietjen, J.H., Deming, J.W., Rowe, G.T., Macko, S., and Wilke, R.J. (1989). Meiobenthos of the Hatteras Abyssal Plain and Puerto Rico Trench: abundance, biomass and associations with bacteria and particulate fluxes. Deep-Sea Res Part A 36, 1567-1577.
q. Vanaverbeke, J., Soetart, K., Heip, C., and Vanreusel, A. (1997). The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). J. Sea Res. 38, 93-107.
r. Vanreusel, A., Vincx, M., Bett, B.J., Rice, A.L. (1995). Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply. Int Revue ges Hydrobiol 80, 287-296.
s. Waniek, J.J., Schulz-Bull, D.E., Blanz, T., Prien, R.D., Oschlies, A., and Muller, T.J. (2005). Interrannual variability of deep water particle flux in relation to production and lateral sources in the northeast Atlantic. Deep-Sea Res Part I 52, 33-50.
t. Wolff, G.A., Boardman, D., Horsfall, I., Sutton, I., Davis, N., Chester, R., Ripley, M., Lewis, C.A, Rowland, S.J., Patching, J., Ferrero, T., Lambshead, P.J.D, and Rice A.L. (1995). The biogeochemistry of sediments from the Madeira Abyssal Plain – Preliminary results. Int Revue ges Hydrobiol 80, 333-349.

Pacific Ocean

a. Brown, C.J., Lambshead, P.J.D., Smith, C.R., Hawkins, L.E., and Farley, R. (2001). Phytodetritus and the abundance and biomass of abyssal nematodes in the central, equatorial Pacific. Deep-Sea Res Part I 48, 555-565.
b. Danovaro, R., Della Croce, N., Dell'Anno, A., and Pusceddu, A. (2003). A depocenter of organic matter at 7800m depth in the SE Pacific Ocean. Deep-Sea Res Part I 50, 1411-1420.
c. Danovaro, R., Gambi, C., and Della Croce, N. (2002). Meiofauna hotspot in the Atacama Trench (Southern Pacific Ocean). Deep-Sea Res Part I 49, 843-857.
d. Gambi, C., Vanreusel, A., and Danovaro, R. (2003). Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench (Southern Pacific Ocean). Deep-Sea Res Part I 50, 103-117.
e. Glover, A.G., Smith, C.R., Paterson, G.L.J, Wilson, G.D.F, Hawkins, L., and Sheader M. (2002). Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. Mar. Ecol. Prog. Ser. 240, 157-170.
f. Hernes, P.J., Hedges, J.I., Peterson, M.L., Wakeham, S.G., and Lee, C. (1996). Neutral carbohydrate geochemistry of particulate material in the central equatorial Pacific. Deep-Sea Res Part II 43, 1181-1204.
g. Honjo, S., Dymond, J., Collier, R., and Manganini, S.J. (1995). Export production of particles to the interior of the equatorial Pacific Ocean during the 1992 EqPac experiment. Deep-Sea Res Part II 42, 831-870.
h. Lambshead, P.J.D., Brown, C.J., Ferrero T., Mitchell N.J., Smith, C.R., Hawkins, L.E., and Tietjen J. (2002). Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific. Mar. Ecol. Progr. Ser. 236, 129-135.
i. Smith, C.R., Berelson, W., Demaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H., and Stephens, M. (1997). Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. Deep-Sea Res Part II 44, 2295-2317.
j. Smith, K.L.Jr, Baldwin, R.J., Karl, D.M., and Boetius, A. (2002). Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre. Deep-Sea Res Part I 49, 971-990.

Southern Ocean

a. Fabiano, M., and Danovaro, R. (1998). Enzymatic activity, bacterial distribution and organic matter composition in sediments of the Ross Sea (Antarctica). Appl. Environ. Microbiol. 64, 3838-3845.

b. Fabiano, M., and Danovaro, R. (1999). Meiofauna distribution and mesoscale variability in two sites of the Ross sea (Antarctica) with contrasting food supply. Pol. Biol. 22, 115-123.
c. Langone, L., Frignani, M., Ravaioli, M., and Bianche, C. (2000). Particles fluxes and biogeochemical processes in an area influenced by seasonal retreat of the ice margin (northwestern Ross sea, Antarctica). J. Mar. Syst. 27, 221-234.
d. Manachini, B. (1997). Biodiversity of nematode assemblages in the Antarctic sea bed. Thesis for degree of Master of Science in Nematology. University of Gent. 75 pp.
e. Schluter, M., Rutger van der Loeff, M.M., Holby, O., and Kuhn, G. (1998). Silica cycle in surface sediments of the South Atlantic. Deep-Sea Res Part I 45, 1085-1109.
f. Vanhove, S., Arntz, W., and Vincx, M. (1999). Comparative study of the nematode communities in the southerneastern Weddell Sea shelf and slope (Antarctica). Mar. Ecol. Prog. Ser. 181, 237-256.
g. Vanhove, S., Vermeeren, H., and Vanreusel, A. (2004). Meiofauna towards the South Sandwich trench (750-6300 m) focus on nematodes. Deep-Sea Res Part II 51, 1665-1687.