First insights into the meiofauna community of a maerl bed in the Bay of Brest (Brittany)

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Summary: Maerl beds, particularly those of Brittany, are important, structurally complex biogenic coastal habitats that form a unique ecosystem with high benthic biodiversity. Although they are relatively well studied throughout Europe, several faunal groups of maerl beds, such as those belonging to the meiofauna, have received little attention. We investigated the meiofaunal abundance, distribution and community structure, with a focus on nematode biomass and diversity, in a maerl area in the Bay of Brest, Brittany, compared with that on a sandy beach (Anse de Dinan, Brittany). Meiofauna was five times more abundant on the maerl bed than on the sandy beach, and 1.5 times more diversified (12 vs. 8 taxa, respectively). Nematode diversity was more than three times higher on the maerl bed than on the sandy beach and showed a distinctive nematode community that was absent from the sandy beach. Maerl beds create more heterogeneous microhabitats and promote a higher diversification of meiofauna and nematode communities than sandy beaches.

Primeros conocimientos sobre la comunidad meiofáunica del lecho de maerl en la bahía de Brest (Bretaña)

Resumen: Los lechos de maerl y, en particular, los de Bretaña, son un importante hábitat costero biogénico y estructuralmente complejo, que forma un ecosistema único con una alta biodiversidad bentónica. A pesar de que varios grupos faunísticos son relativamente bien estudiados en toda Europa, aquellos pertenecientes a la meiofauna han recibido poca atención. Hemos investigado la abundancia, distribución y estructura de la comunidad de la meiofauna, con especial atención a la biomasa y diversidad de nematodos de un área de maerl en la bahía de Brest (Bretaña), en comparación con la de una playa de arena (Anse de Dinan, Bretaña). La meiofauna del maerl fue cinco veces más abundante que la de la playa arenosa, y 1,5 veces más diversificada (12 taxones frente a 8 respectivamente). La diversidad de nematodos del maerl fue más de tres veces mayor que la de la playa arenosa y mostró un único nematodo que, a su vez, resultó ausente en la playa arenosa. Los lechos de maerl crean microhábitats más heterogéneos y promueven una mayor diversificación de la meiofauna y las comunidades de nematodos que los hábitats de playas arenosas.

INTRODUCTION

Maerl (or rhodolith) beds are formed by accumulations of living and dead non-geniculate unattached coralline algae (Foster et al. 2013). They occur on a wide variety of bottoms, ranging from coarse sand to fine mud (Grall et al. 2006, Hall-Spencer et al. 2010). Extensive beds occur on open coasts worldwide, either in tide-swept channels or in sheltered areas where wave action and bioturbation are strong enough to prevent sediment burial and anoxia from sedimentation and to move maerl thalli (Foster et al. 2013). In Europe, maerl beds are reported in the Mediterranean Sea and all along the Atlantic Ocean coasts, from Portugal to Norway, but are rare in the English Channel, Irish Sea, North Sea and Baltic Sea (Grall et al. 2006). Strictly depending on light penetration, they can be found down to 30 m depth in the northeast Atlantic, to 90–100 m depth in the western Mediterranean, and to 180 m depth in the eastern Mediterranean (BIOMAERL Team 2003).

Maerl beds have been less investigated than other marine ecosystems such as kelp forests and seagrass beds (BIOMAERL Team 2003). However, some of the best-studied maerl beds are located on the European coasts, particularly in Brittany (Hall-Spencer et al. 2010), where they form a unique ecosystem with a complex three-dimensional matrix harbouring a higher benthic biodiversity than on other sublittoral bottoms (Grall et al. 2006). The associated organisms can either live inside and on the nodules or burrow into the coarse gravel and fossil nodules lying beneath the top living layer (Foster et al. 2013). Many of them are rare, highly specialized species that are mostly confined to this habitat (BIOMAERL Team 2003), but there are also juveniles of other organisms, including commercially important shellfish and fish (Hall-Spencer et al. 2010).

Maerl beds are threatened by anthropogenic activities, such as large-scale commercial extraction for use as a soil conditioner, dredging, bottom trawling, pollution, eutrophication, aquaculture and invasion of alien species such as *Crepidula fornicata* Linnaeus, 1758 (BIOMAERL Team 2003). Accordingly, since 1976 they have been included in EU and international conventions and strategies to preserve fragile marine ecosystems in Europe (BIOMAERL Team 2003). Furthermore, there are still some major gaps in the knowledge of benthic communities inhabiting maerl beds, one of them being meiofaunal studies (BIOMAERL Team 2003).

Meiofauna comprises microscopic protists and multicellular metazoans living in aquatic sediments that are retained between sieves with a standard mesh size of between 1000 and 32 μm (Giere 2009, Zeppilli et al. 2015a). They play a fundamental role in the benthic food web and in ecosystem functioning because of their high diversity and abundance, widespread distribution, rapid generation time and fast metabolic rates (Zeppilli et al. 2015a and references therein). In particular, their short generation time and the lack of pelagic larval dispersal makes them highly sensitive to natural and anthropogenic environmental alterations (Zeppilli et al. 2015a). Nematodes are among the most abundant and diverse meiofaunal metazoans, inhabiting all kind of sediments. They are widely used as indicators in biological monitoring (Semprucci et al. 2018) and are key organisms in the trophic dynamics of coastal ecosystems, having positive effects on bacterial growth and nutrient recirculation and directly competing with macrofauna for food resources (Leduc and Probert 2009).

The few studies on meiofauna suggest that maerl beds support a high biodiversity, including a high diversity of bivalves compared with other substrata (Jackson et al. 2004) and a new genus of Copepoda from the Irish west coast (McCormack 2006). Furthermore, a high species richness of foraminifera on Scottish coasts has led maerl beds to become an important near-shore habitat in regional studies of benthic foraminiferal distribution/ecology (Austin and Cage 2010).

This study aims to characterize (1) the meiofaunal abundance, vertical distribution and community structure of a maerl site located in the Bay of Brest, Brittany, France; (2) the taxonomic and functional diversity of maerl nematode assemblages; and (3) the richness and diversity of the maerl meiofauna compared with those from a sandy beach area (Anse de Dinan, Brittany, France).

MATERIALS AND METHODS

Study site and sampling strategy

The studied maerl bed is located in the semi-enclosed Bay of Brest (Brittany, NW France), which has a total area of 180 km^2, a maximum tidal amplitude of 8 m and an average depth of 8 m (Fig. 1). Water-exchange with the shelf waters (Iroise Sea) occurs through a narrow (2 km wide) and deep (40 m) channel (Grall et al. 2006), and two rivers (the Aulne, with a catchment area of 1842 km^2, and the Elorn, with a catchment area of 402 km^2) contribute freshwater inputs (Grall et al. 2006). Tidal action and regular wind-generated swell induce short-term variability in hydrological factors and enhance water mass mixing (Grall et al. 2006). Local hydrodynamics influences the sediment composition, which ranges from muds to coarse gravels, but there are also rocky substrata (Grall et al. 2006). Maerl beds cover 30% of the total surface area (Grall et al. 2006).

The sandy beach site is located in the Anse de Dinan, Bay of Douarnenez, France (Fig. 1) and is characterized by a median particle size ranging from 140 to 200 mm, a low silt content (0.2%) and a fraction of dead shells ranging from 2% to 9% (Baldrighi et al. 2019).

Three replicate samples were collected by SCUBA divers in April 2012 at the maerl bed site (48°17.627′N, 4°26.470′W, 7 m depth, water temperature of 14°C and salinity of 33.9; Fig. 1) using Plexiglas corers (6 cm inner diameter) buried down to 5 cm depth. The sediment cores were sliced into five layers: Maerl Layer at the top (ML, including maerl without sediment), 0–1, 1–2, 2–3 and 3–4 cm. They were preserved in buffered 4%
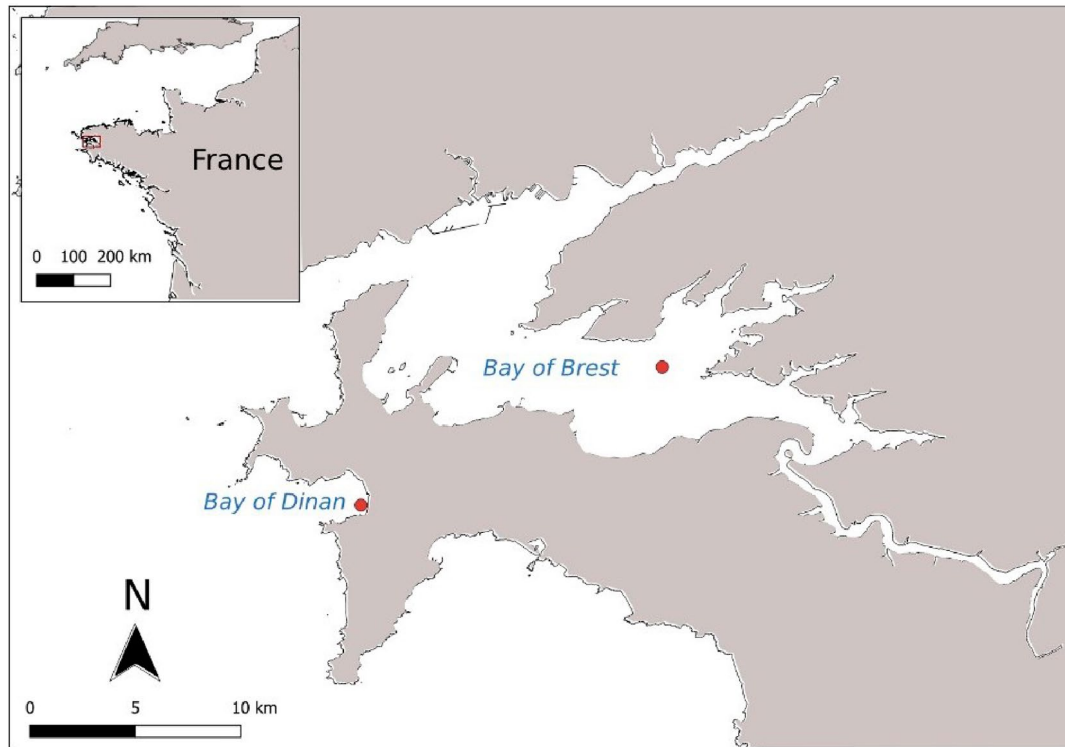
Fig. 1. – Location of the sampling sites: maerl bed (Bay of Brest) and sandy beach (Anse de Dinan) in Brittany, France.

formalin solution and stained with Rose Bengal (0.5 g l⁻¹). Samples collected below the maerl bed contained poorly sorted, very coarse sands with 3.5% of organic matter. At the sandy beach (48°14.109′N, 4°32.545′W, temperature of 14.4°C, salinity of 35.39; Fig 1), samples were collected in May 2012 at low tide in the intertidal, using Plexiglas corers (3.6 cm inner diameter). The samples consisted of three separates replicates of 15 cm depth cores and contained very well sorted fine sands with 1.5% of organic matter (see Carriço et al. 2013 and Baldrighi et al. 2019 for details). The authors are aware of the different sampling strategy adopted, i.e. a 5 cm sediment depth (maerl bed) vs. a 15 cm sediment depth (sandy beach). However, most meiofaunal organisms inhabit the top 5 cm of sediment (e.g. Ingels and Vanreusel 2013), allowing us to assume that comparisons between the two environments would not be substantially affected.

Meiofaunal and nematode analyses

All samples were sieved through 1000 µm and 32 µm mesh sizes. Meiofaunal organisms were extracted by Ludox centrifugation following Danovaro (2010), counted and classified to the highest taxonomic level using a stereomicroscope. At least 100 nematodes from each replicate were picked out randomly and mounted on permanent slides after formalin-ethanol-glycerol treatment for identification to the genus level with an optical microscope according to Platt and Warwick (1988) and the recent literature available (NeMys database, Bezerra et al. 2021). Species richness (SR), expected number of genera (51) and diversity indices (Shannon, H', Margalef D, Pielou evenness and J') were calculated for both meiofauna and nematodes with the DIVERSE routine (PRIMER 6+; Clarke and Gorley 2006). The nematodes were divided into four trophic groups following Wieser (1953): (1A) selective (bacterial) feeders with no buccal cavity or a fine tubular one; (1B) non-selective deposit feeders with a large but unarmed buccal cavity; (2A) epistrate or epigrowth (diatom) feeders with a scraping tooth or teeth in the buccal cavity; and (2B) predators/omnivores with a buccal cavity with large jaws. The index of trophic diversity (ITD) was calculated considering the relative contribution of each trophic group to the total (Gambi et al. 2003). Nematode biomass was calculated by biovolume, estimated from all specimens per replicate (Andrassy 1956). Then, dry weight (µg DW) was estimated by multiplying each body volume by an average density (1.13 g cm⁻³), and finally the biomass was expressed as carbon content (µg of C/10 cm²), which was considered to be 40% of dry weight (Feller and Warwick 1988).

Statistical analysis

Differences in total meiofaunal abundance, total nematode biomass, nematode diversity between layers, total meiofaunal abundance and total nematode biomass between the maerl bed and the sandy beach were assessed by one-way analyses of variance (ANOVA). Prior to the ANOVAs, the homogeneity of variances was assessed by the Anderson-Darling test and, when necessary, data were square-root transformed. Tukey's HSD test was performed to assess significant
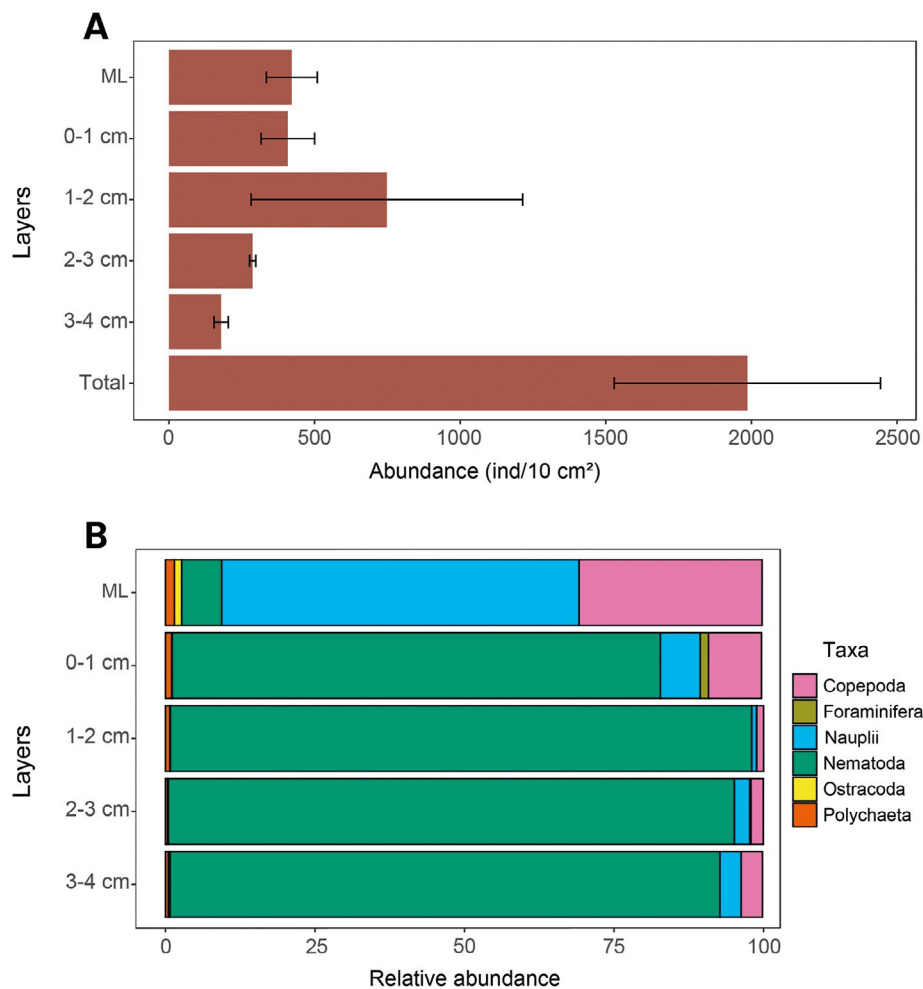
Fig. 2. – A, vertical distribution of total meiofaunal abundance in the maerl bed (ind/10 cm²). B, meiofaunal community structure in the maerl bed (as percentages of dominant higher taxa). Horizontal bars are standard deviations. ML, Maerl Layer at the top (including maerl without sediment).

between-level effects. The ANOVAs and Turkey's test were performed using the STATISTICA V.10 software. A one-way analysis of similarities (ANO-SIM) was used to assess between-layer differences in meiofauna community structure and nematode composition. The SIMPER routine (cut-off of 90%, on fourth-root transformed data) was used to determine the contribution of each meiofaunal taxon and nematode species to the total dissimilarity. ANOSIM and SIMPER analyses were performed using Primer 6+ (Clarke and Gorley 2006).

RESULTS

Maerl meiofauna community

The total meiofaunal abundance was 1986±457 ind/10 cm². The highest mean abundance occurred in layer 1–2 (748±466 ind/10 cm²) and decreased with increasing depth, being the lowest in layer 3–4 (179±25 ind/10 cm²) (Fig. 2A). The ML and layers 0–1 and 1–2 showed a significantly higher abundance than the deepest layer (ANOVA, $p < 0.05$).

A total of 12 (8±1) taxa characterized the maerl station, including Nematoda, Copepoda + nauplii, Polychaeta, Ostracoda, Kinorhyncha, Oligochaeta, Amphipoda, Cladocera, Gastropoda, Tardigrada, Isopoda and Foraminifera. From layer 0–1 to 3–4, Nematoda were the most abundant (82%–97%), followed by Copepoda (1%–9%) and their nauplii (1%–7%). Polychaeta accounted for 1% in layers 0–1 and 1–2 and Foraminifera for 1% in layer 0–1. In the ML, Copepoda (31%) with their nauplii (60%) were the most abundant (91%), followed by Nematoda (7%), Polychaeta (2%) and Ostracoda (1%) (Fig. 2B). Kinorhyncha, Oligochaeta, Amphipoda, Cladocera, Gastropoda, Tardigrada and Isopoda accounted for less than 1% of the total abundance at all layers and are together indicated as "other taxa". The community structure differed significantly between sediment layers (ANOSIM, R=44%; P=0.012) (Table S1A), with the differences being mainly due to the increasing abundance of Nematoda and the decreas-
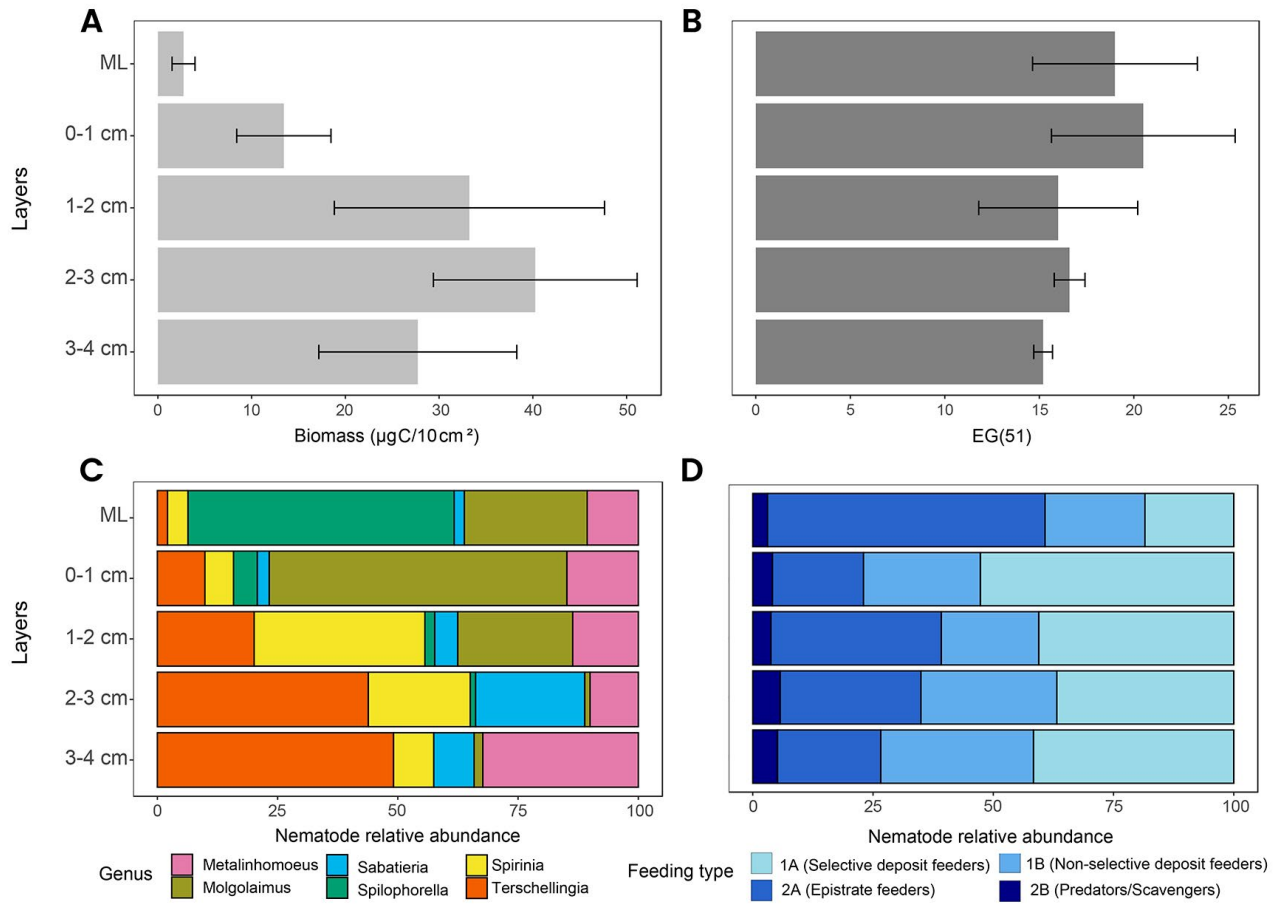
Fig. 3. – A. Vertical distribution of nematode biomass. B. Expected genus number (EG (51)). C. Most abundant nematode genera. D. Nematode trophic structure.

ing abundance of Copepoda along the sediment profile (SIMPER, Table S2). The sediment layers showed dissimilarities ranging from 30% (0–1 vs. 1–2 cm) to 74% (2–3 vs. 3–4 cm) (SIMPER, Table S1A).

The maerl nematode community

The mean total nematode biomass was 108.2±41.9 µg of C/10 cm². It increased along the sediment profile from 2.7±1.2 µg of C/10 cm² in the ML to 40.3±10.9 µg of C/10 cm² in layer 2–3 cm (Fig. 3A). There were 78 genera and 22 families of nematodes (Table S3). The expected number of genera (51) ranged from 15.2±0.5 in layer 3–4 to 20.5±4.9 in layer 0–1, showing a decreasing trend along the sediment profile (Fig. 3B, Table S4). The Shannon index ranged from 2.3±0.3 in layer 1–2 to 2.7±0.3 in the ML, and the Pielou index ranged from 0.7±0.1 in layers 0–1, 1–2 and 2–3 to 0.9±0 in the ML, indicating that all genera were equally represented (Table S4). There were no significant between-layer differences in any diversity index.

Linhomoeidae was the most abundant family (36%), followed by Desmodoridae (30%), Chromadoridae (9%), Comesomatidae (8%) and Xyalidae (4%). The most abundant genera were *Terschellingia* (21%). *Spir-*

inia (13%) *Molgolaimus* (14%), *Metalinhomoeus* (12%) and *Sabatieria* (7%). *Molgolaimus* was more abundant (39%) in layer 0–1 and decreased with depth to 1% in layer 3–4, and *Spilophorella* decreased with depth from 20% in the ML to 0% in layer 2–3. *Terschellingia* increased in abundance with depth from 1% in the ML to 35% in layer 3–4, and *Sabatieria* increased in abundance with depth from 1% in the ML to 16% in layer 2–3. *Metalinhomoeus* also increased in abundance with depth from 4% in the ML to 23% in layer 3–4. *Spirinia* increased in abundance from 2% in the ML to 28% in layer 1–2 and then dropped to 6% in layer 3–4 (Fig. 3C).

The nematode composition in the ML and layer 0–1 differed significantly from those at all other layers (ANOSIM, Global R=37%: p=0.004, Table S1B), mostly owing to the presence of *Terschellingia*, *Spirinia* and *Perspiria* at the deeper layers and *Molgolaimus* in the top 1 cm (SIMPER analysis, Table S5). The trophic structure of the nematode assemblage was 1A (40%), 2A (30%), 1B (25%), and 2B (5%), although the contribution of some trophic groups changed along the sediment profile. 1A were less abundant in the ML (18%) and reached the highest abundance in layer 0–1 (53%), while 1B and 2B did not change significantly across layers (Fig. 3D). On the other hand, 2A were

dominant in the ML (58%), showing the highest biomass (38.4 µg of C/10 cm²). 1B and 2B showed biomasses of 26.1 and 27.0 µg of C/10 cm², respectively, and 1A showed the lowest biomass (16.7 µg of C/10 cm²).

Maerl bed vs. sandy beach meiofauna

Total meiofaunal density in the maerl bed was five times higher than on the sandy beach (1.986±457 ind/10 cm² vs. 384±16 ind/10 cm², respectively; ANOVA, p<0.05) (Fig. 4). Twelve higher taxa were identified in the maerl bed vs. 8 on the sandy beach (Fig. 4), where Nematoda was the most abundant (96%), followed by Copepoda (3%). Cumacea, Gastrotricha, Isopoda, Ostracoda, Platyhelminthes and Tardigrada accounted for less than 1%. Total nematode biomass was significantly higher in the maerl bed than on the sandy beach (108.2±41.9 and 47.6±2.1 µg of C/10 cm²; ANOVA, p<0.05). Nematode diversity in the maerl bed was more than three times higher than on the sandy beach, where 11 families and 20 genera were identified (Fig. 4), including *Richtersia* (51%), *Trileptum* (9%), *Daptonema* and *Omicronema* (8% each) as the most abundant. Overall, 66 and 8 nematode genera were exclusive to the maerl bed and the sandy beach, respectively, with 12 being shared (Table S6). 1A dominated in the maerl bed (40%) and 1B on the sandy beach (72%). Overall, the maerl bed showed a lower ITD (0.32) than the sandy beach (0.62), indicating a greater trophic diversity in the maerl bed (Table S6).

DISCUSSION

Maerl meiofaunal and nematode assemblages

The high maerl meiofaunal abundance recorded in the Bay of Brest was similar to that found in other structurally complex and perennial habitats such as seagrass beds (Novack 1989, Pusceddu et al. 2014) and similar micro-habitat rich environments such as coral sediments (Semprucci et al. 2013). The highest meiofaunal abundance was found in layer 1–2, and it progressively decreased along the sediment profile. Conversely, meiofauna is often concentrated in the first few centimetres of sediment (Giere 2009). In the maerl bed, the meiofauna distribution likely responds to its complex architecture, allowing a higher organic and oxygen content subsuperficially. This complexity also protects the sediment below, because meiofaunal organisms are less exposed to hydrodynamic perturbations. Indeed, the low erosion, combined with organic accumulation and dispersal lowering, may favour an increase in abundance subsuperficially. Conversely, taxa living on the surface or between the maerl thalli are less protected from current or wave actions (Martínez et al. 2021).

Among the 12 taxa identified, nematodes were the most abundant in all sediment layers except in the ML, where the community was dominated by Copepoda with their nauplii. Nematodes are well-known to penetrate deeply into sediments thanks to their specialized morphology and high tolerance to anaerobic conditions
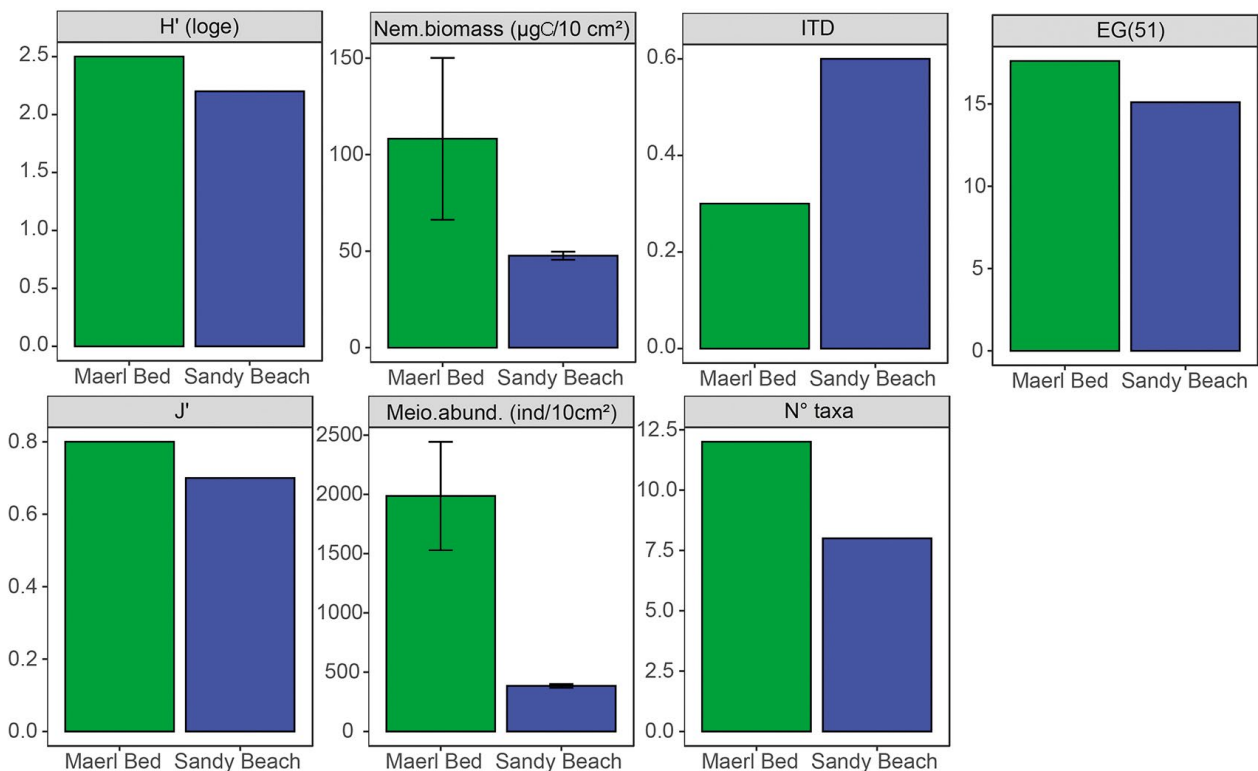

Fig. 4. – Shannon index (H'), nematode biomass (µg of C/10 cm²), trophic diversity index (ITD) values, expected genus number (EG (51)), equitability evenness (J'), meiofaunal abundance and number of higher meiofauna (N° taxa). Vertical bars are standard deviations.

(Heip et al. 1985), while hydrodynamism can also contribute to the dispersal of the specimens into deeper layers (Zeppilli et al. 2014). Consequently, nematodes were less abundant in the ML, possibly because of the low shelter inherent to its particular architecture, but probably also to a higher predation pressure (Grall et al. 2006).

Copepods and nauplii were particularly abundant in the ML, resembling coral sediment assemblages (Semprucci et al. 2013). This could be related to the additional food resources (macroepiphytic algae and microphytobenthos production) associated with maerl beds (Grall et al. 2006). In addition, the swimming ability of crustaceans, compared with other meiofaunal groups, allows them to speedily return to the seafloor after being resuspended in the water column by current or waves (e.g. Colangelo et al. 2001, Zeppilli et al. 2015b). However, their numbers decreased along the sediment profile, despite the coarse sediment that has been suggested to promote their presence (Colangelo et al. 2001), likely due to their high sensitivity to oxygen depletion or anoxia, unlike nematodes (Moodley et al. 2000).

Some genera of Chromadoridae are almost entirely restricted to upper sediment layers (Platt 1977). Accordingly, the epistrate feeders *Spilophorella* and *Spirinia* showed high abundances in the ML and layer 1–2, respectively, and decreased along the sediment profile, probably because of lowering food availability (Pusceddu et al. 2009). *Terschellingia* and *Sabatiera* penetrated deep into the sediment, having their highest abundances in layers 3–4 and 2–3, respectively. *Terschellingia*, a selective deposit feeder, is usually found in anoxic sediments (Wieser 1960). *Sabatieria*, a non-selective deposit feeder displaying a wide range of ecological preferences (Steyaert 1999), is also known to be a facultative anaerobic organism, a trait allowing it to inhabit suboxic or anoxic sediment layers, so it is thus a common deeper-living nematode (Jensen 1987). *Metalinhomoeu*s was present in all sediment layers, but was particularly abundant in layer 3–4. This genus is known to be associated with subtidal silt or muddy sediments (Wieser 1960), being frequent in sediments with low oxygen levels (Heip et al. 1985). It also has a body morphology that allows it to dig quickly up and down into the sediment, passing easily from reduced to well-oxygenated zones (Jensen 1987). Surprisingly, we found no families typically associated with 3D complex substrates, such as Epsilonematidae and Draconematidae from corals or hard substrates (Raes et al. 2008, Zeppilli et al. 2015b). Therefore, our data support the hypothesis that maerl nematodes benefit mainly from the sediments below the bed, instead of the 3D rhodoliths, which mainly act as a protective layer for the sediments and assemblages below. Moreover, all trophic groups were equally represented in all layers, allowing us to suggest possible differences in food sources along the sediment profile. This may well help reduce the number of competitive interactions, while allowing the different feeding groups to coexist in small sediment patches.

Maerl bed vs. sandy beach

Maerl beds are known to harbour higher macrofaunal biodiversity than bare sediments (Foster et al. 2013), and meiofauna is no exception. In the maerl bed, its abundance was five times higher, and its taxa diversity 1.5 times higher than on the sandy beach. Obviously, nematodes were also more numerous (three times), as was the number of exclusive genera (66). The functional diversity (i.e. trophic diversity) was also higher in the maerl bed. All trophic groups were represented: bacterial and epistrate feeders (1A and 2A respectively) dominated in the maerl bed, while the non-selective deposit feeders (1B) dominated on the sandy beach. Thus, maerl beds seemed to host a rich meiofaunal community and a unique and peculiar nematode community, which is clearly distinguishable from those inhabiting sandy beach ecosystems. Accordingly, maerl beds seem to harbour a rich and specific meiofaunal community that may serve as potential prey for these predator/omnivore nematodes. The physical presence of complex maerl thalli, combined with the numerous resources provided, may explain the difference in meiofaunal diversity between these habitats. Moreover, the sandy beach samples were collected at low tide in the intertidal. This may have also affected the community composition and richness, since only well-adapted fauna can survive the extreme conditions arising from long-term exposure (e.g. higher radiation, salinity and oxygen availability variation) (Baldrighi et al. 2019 and literature therein).

Our study documented novel findings on the abundance, structure and diversity of the meiofauna and nematode communities characterizing the maerl beds from the Bay of Brest. Our results suggest that maerl beds create a more heterogeneous environment, richer in microhabitats, that promotes highly diversified meiofaunal and nematode assemblages in the sediments below, which proved to be particularly rich when compared with more homogenous environments lacking the protective rhodolith layer (e.g. a sandy beach). Maerl beds, which have been largely neglected in meiofaunal studies, have been shown to harbour high meiofaunal assemblages with a very complex structure and a high functional diversity. Therefore, their protection may be crucial for marine biodiversity preservation.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link: http://scimar.icm.csic.es/scimar/supplm/sm05230esm.pdf

First insights into the meiofauna community of a maerl bed in the Bay of Brest (Brittany)

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Supplementary material

Table S1. – ANOSIM (R statistic), significance level (P) and SIMPER results (Diss., Dissimilarity %). A. most abundant higher meiofaunal taxa. B. nematode species.

A

Group	R statistic %	P	Diss. %
ML, 0-1 cm	41	0.01	39
ML, 1-2 cm	37	0.01	39
ML, 2-3 cm	15	0.02	59
ML, 3-4 cm	42	0.02	32
0-1 cm, 1-2 cm	59	0.01	30
0-1 cm, 3-4 cm	100	0.01	63
1-2 cm, 2-3 cm	22	0.02	49
1-2 cm, 3-4 cm	100	0.01	67
2-3 cm, 3-4 cm	17	0.04	74

B

Group	R statistic %	P	Diss. %
ML, 0-1 cm	33	0.02	65
ML, 1-2 cm	67	0.01	74
ML, 2-3 cm	67	0.01	73
ML, 3-4 cm	83	0.01	75
0-1 cm, 1-2 cm	30	0.02	52
0-1 cm, 2-3 cm	44	0.01	58
0-1 cm, 3-4 cm	83	0.01	60
1-2 cm, 2-3 cm	19	0.03	51
1-2 cm, 3-4 cm	25	0.04	47
2-3 cm, 3-4 cm	8	0.04	49

Table S2. – SIMPER analysis showing the contribution of meiofaunal taxa to between-layer dissimilarity. Contrib.%, contribution %; Cum.%, cumulative %.

Groups ML & 0-1 cm			Groups ML & 1-2 cm			Groups ML & 2-3 cm			Groups ML & 3-4 cm		
Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%
Nematoda	45.78	45.78	*nauplii*	32.3	32.3	Nematoda	31.98	31.98	Nematoda	33.28	33.28
nauplii	21.84	67.62	Copepoda	26.64	58.94	*nauplii*	27.64	59.62	*nauplii*	32.16	65.44
Copepoda	15.26	82.87	Nematoda	20.67	79.61	Copepoda	23.97	83.6	Copepoda	16.84	82.28
Foraminifera	4.93	87.8	Polichaeta	6.61	86.22	Polichaeta	6.58	90.18	Ostracoda	8.16	90.44
Ostracoda	3.86	91.66	Ostracoda	4.94	91.15						

Groups 0-1 cm & 1-2 cm			Groups 0-1 cm & 2-3 cm			Groups 0-1 cm & 3-4 cm			Groups 1-2 cm & 2-3 cm		
Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%	Taxon	Contrib%	Cum.%
Nematoda	52.33	52.33	Nematoda	69.7	69.7	Nematoda	42.81	42.81	Nematoda	62.73	62.73
nauplii	12.48	64.81	Copepoda	8.23	77.93	*nauplii*	28.38	71.19	*nauplii*	11.79	74.52
Copepoda	10.92	75.73	Polichaeta	5.99	83.92	Copepoda	17.08	88.27	Copepoda	10.38	84.9
Foraminifera	9.03	84.76	Foraminifera	5.23	89.14	Foraminifera	2.86	91.13	Polichaeta	4.26	89.16
Polichaeta	7.34	92.1	*nauplii*	4.99	94.13				Foraminifera	4.16	93.32

Groups 1-2 cm & 3-4 cm			Groups 2-3 cm & 3-4 cm		
Taxon	Contrib%	Cum %	Taxon	Contrib%	Cum.%
nauplii	35.24	35.24	*nauplii*	39.66	39.66
Nematoda	27.14	62.39	Copepoda	27.44	67.09
Copepoda	23.57	85.96	Nematoda	17.44	84.54
Polichaeta	4.36	90.32	Polichaeta	5.6	90.14

Table S3. – List of nematode families, genera and putative species found in the maerl bed.

Family	Genus	Species
Chromadoridae	*Acantholaimus*	*Acantholaimus* sp1
Chromadoridae	*Actinonema*	*Actinonema* sp1
Leptolaimidae	*Antomicron*	*Antomicron* sp1
Diplopeltidae	*Campylaimus*	*Campylaimus* sp1
Anticomidae	*Cephalanticoma*	*Cephalanticoma* sp1
Chromadoridae	*Chromadora*	*Chromadora* sp1
Chromadoridae	*Chromadora*	*Chromadora* sp2
Chromadoridae	*Chromadorella*	*Chromadorella* sp1
Chromadoridae	*Chromadoridae* spp.	*Chromadoridae* spp.
Chromadoridae	*Chromadorita*	*Chromadorita* sp1
Xyalidae	*Cobbia*	*Cobbia* sp1
Comesomatidae	*Comesomatidae* spp.	*Comesomatidae* spp.
Comesomatidae	*Comesoma*	*Comesoma* sp1
Comesomatidae	*Comesomoides*	*Comesomoides* sp1
Cyartonematidae	*Cyartonema*	*Cyartonema* sp1
Xyalidae	*Daptonema*	*Daptonema* sp1
Desmoscolecidae	*Desmoscolex*	*Desmoscolex* sp1
Camacolaimidae	*Diodontolaimus*	*Diodontolaimus* sp1
Comesomatidae	*Dorylaimopsis*	*Dorylaimopsis* sp1
Draconematidae	*Draconema*	*Draconema* sp1
Chromadoridae	*Euchromadora*	*Euchromadora* sp1
Linhomoeidae	*Eumorpholaimus*	*Eumorpholaimus* sp1
Enchelidiidae	*Eurystomina*	*Eurystomina* sp1

Family	Genus	Species
Oncholaimidae	*Filoncholaimus*	*Filoncholaimus* sp1
Oxystominidae	*Halalaimus*	*Halalaimus* sp1
Leptolaimidae	*Halaphanolaimus*	*Halaphanolaimus* sp1
Selachinematidae	*Halichoanolaimus*	*Halichoanolaimus* sp1
Monhysteridae	*Halomonhystera*	*Halomonhystera* sp1
Chromadoridae	*Karkinochromadora*	*Karkinochromadora* sp1
Cyatholaimidae	*Kraspedonema*	*Kraspedonema* sp1
Comesomatidae	*Laimella*	*Laimella* sp1
Leptolaimidae	*Leptolaimus*	*Leptolaimus* sp1
Leptolaimidae	*Leptolaimus*	*Leptolaimus* sp2
Linhomoeidae	*Linhomoeus* spp.	*Linhomoeus* spp.
Linhomoeidae	*Linhomoeus*	*Linhomoeus* sp1
Linhomoeidae	*Linhomoeus*	*Linhomoeus* sp2
Xyalidae	*Linhystera*	*Linhystera* sp1
Cyatholaimidae	*Longicyatholaimus*	*Longicyatholaimus* sp1
Desmodoridae	*Molgolaimus*	*Molgolaimus* sp1
Cyatholaimidae	*Marylynnia*	*Marylynnia* sp1
Linhomoeidae	*Megadesmolaimus*	*Megadesmolaimus* sp1
Desmodoridae	*Metachromadora*	*Metachromadora* sp1
Cyatholaimidae	*Metacyatholaimus*	*Metacyatholaimus* sp1
Xyalidae	*Metadesmolaimus*	*Metadesmolaimus* sp1
Linhomoeidae	*Metalinhomoeus* spp.	*Metalinhomoeus* spp.
Linhomoeidae	*Metalinhomoeus*	*Metalinhomoeus* sp1
Linhomoeidae	*Metalinhomoeus*	*Metalinhomoeus* sp2
Linhomoeidae	*Metalinhomoeus*	*Metalinhomoeus* sp3
Sphaerolaimidae	*Metasphaerolaimus*	*Metasphaerolaimus* sp1
Xyalidae	*Manganonema*	*Manganonema* sp1
Monhysteridae	*Monhysteridae* spp.	*Monhysteridae* spp.
Oxystominidae	*Nemanema*	*Nemanema* sp1
Chromadoridae	*Neochromadora*	*Neochromadora* sp1
Oncholaimidae spp.	*Oncholaimidae* spp.	*Oncholaimidae* spp.
Oncholaimidae	*Oncholaimus*	*Oncholaimus* sp1
Cyatholaimidae	*Paracyatholaimus*	*Paracyatholaimus* sp1
Comesomatidae	*Paracomesoma*	*Paracomesoma* sp1
Linhomoeidae	*Paralinhomoeus*	*Paralinhomoeus* sp1
Cyatholaimidae	*Cyatholaimidae*	*Cyatholaimidae*
Cyatholaimidae	*Paralongicyatholaimus*	*Paralongicyatholaimus* sp1
Enchelidiidae	*Pareurystomina*	*Pareurystomina* sp1
Axonolaimidae	*Parodontophora*	*Parodontophora* sp1
Desmodoridae	*Perspiria*	*Perspiria* sp1
Comesomatidae	*Pierrickia*	*Pierrickia* sp1
Chromadoridae	*Prochromadorella*	*Prochromadorella* sp1
Chromadoridae	*Prochromadorella*	*Prochromadorella* sp2
Xyalidae	*Promonhystera*	*Promonhystera* sp1
Oncholaimidae	*Prooncholaimus*	*Prooncholaimus* sp1
Chromadoridae	*Ptycholaimellus*	*Ptycholaimellus* sp1
Desmoscolecidae	*Quadricoma*	*Quadricoma* sp1
Comesomatidae	*Sabatieria*	*Sabatieria* sp1

Family	Genus	Species
Comesomatidae	*Setosabatieria*	*Setosabatieria* sp1
Sphaerolaimidae	*Sphaerolaimus*	*Sphaerolaimus* sp1
Chromadoridae	*Spiliphera*	*Spiliphera* sp1
Chromadoridae	*Spilophorella* spp.	*Spilophorella* spp.
Chromadoridae	*Spilophorella*	*Spilophorella* sp1
Chromadoridae	*Spilophorella*	*Spilophorella* sp2
Desmodoridae	*Spirinia*	*Spirinia* sp1
Chromadoridae	*Steineridora*	*Steineridora* sp1
Chromadoridae	*Steineridora*	*Steineridora* sp2
Desmodoridae	*Stilbonematinae*	*Stilbonematinae*
Xyalidae	*Stylotheristus*	*Stylotheristus* sp1
Desmodoridae	*Stygodesmodora*	*Stygodesmodora* sp1
Selachinematidae	*Synonchiella*	*Synonchiella* sp1
Ironidae	*Syringolaimus*	*Syringolaimus* sp1
Linhomoeidae	*Terschellingia* spp.	*Terschellingia* spp.
Linhomoeidae	*Terschellingia*	*Terschellingia* sp1
Linhomoeidae	*Terschellingia*	*Terschellingia* sp2 (*cf.longicaudata*)
Monhysteridae	*Thalassomonhystera*	*Thalassomonhystera* sp1
Xyalidae	*Theristus*	*Theristus* sp1
Thoracostomopsidae	*Thoracostomopsis*	*Thoracostomopsis* sp1
Xyalidae	*Trichoteristus*	*Trichoteristus* sp1
Desmoscolecidae	*Tricoma*	*Tricoma* sp1
Thoracostomopsidae	*Trileptium*	*Trileptium* sp1
Oncholaimidae	*Viscosia*	*Viscosia* sp1
Oxystominidae	*Wieseria*	*Wieseria* sp1
Xyalidae spp.	*Xyalidae* spp.	*Xyalidae* spp.

Table S4. – Nematode diversity indices in the maerl bed: species richness (SR), Margalef diversity (D), Pielou evenness (J'), expected genus number (EG(51)) and Shannon index (H').

Layers	SR	D	J'	EG(51)	H'
ML	19.0±4.4	4.8±1.2	0.9±0.0	19.0±4.4	2.7±0.3
0-1 cm	31.7±6.0	6.6±1.4	0.7±0.1	20.5±4.9	2.5±0.6
1-2 cm	24.7±6.0	4.9±1.3	0.7±0.0	16.0±4.2	2.3±0.3
2-3 cm	26.3±1.5	5.2±0.3	0.7±0.0	16.6±0.8	2.4±0.2
3-4 cm	22.0±1.4	4.4±0.1	0.8±0.0	15.2±0.5	2.4±0.1

Table S5. – SIMPER analysis showing the contribution of nematode species to between-layer dissimilarity. The ten most contributing taxa are reported. The following abbreviations were used: Contrib.%, contribution%; Cum.%, cumulative %.

Groups ML & 0-1 cm			Groups ML & 1-2 cm			Groups ML & 2-3 cm		
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
Terschellingia sp1	3.59	3.59	*Spirinia* sp1	5.16	5.16	*Terschellingia* sp2 (cf. *longicaudata*)	5.25	5.25
Molgolaimus sp1	2.89	6.48	*Terschellingia* sp2 (cf. *longicaudata*)	4.1	9.26	*Spirinia* sp1	4.21	9.46
Metalinhomoeus sp1	2.71	9.18	*Terschellingia* sp1	3.3	12.56	*Sabatieria* sp1	4.13	13.6
Sphaerolaimus sp1	2.63	11.81	*Halichoanolaimus* sp1	3.26	15.82	*Terschellingia* spp	3.1	16.69
Spirinia sp1	2.51	14.32	*Metalinhomoeus* sp1	3.21	19.03	*Halaphanolaimus* sp1	2.51	19.2
Halalaimus sp1	2.42	16.74	*Parodontophora* sp1	2.87	21.9	*Steineridora* sp1	2.35	21.55
Xyalidae	2.34	19.08	*Sabatieria* sp1	2.78	24.68	*Perspiria* sp1	2.22	23.77
Parodontophora sp1	2.33	21.4	*Linhomoeus* sp2	2.53	27.21	*Linhomoeus* sp2	2.21	25.98
Chromadorella sp1	2.30	23.7	*Xyalidae* spp.	2.26	29.47	*Chromadorella* sp1	2.17	28.15
Metalinhomoeus spp	2.13	25.83	*Chromadorella* sp1	2.2	31.67	*Spilophorella* sp1	2.17	30.32
Groups ML & 3-4 cm			**Groups 0-1 & 1-2 cm**			**Groups 0-1 & 2-3 cm**		
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
Terschellingia sp2 (cf. *longicaudata*)	5.53	5.53	*Terschellingia* sp2 (cf. *longicaudata*)	3.01	9.83	*Terschellingia* sp2 (cf. *longicaudata*)	3.86	3.86
Metalinhomoeus spp	4.3	9.84	*Pierrickia* sp1	3.16	6.82	*Molgolaimus* sp1	3.68	7.54
Perspiria sp1	3.52	13.36	*Spirinia* sp1	3.66	3.66	*Steineridora* sp1	2.86	10.4
Halichoanolaimus sp1	3.51	16.87	*Metalinhomoeus* sp2	2.46	12.29	*Diodontolaimus* sp1	2.46	12.86
Metalinhomoeus sp1	3.36	20.23	*Steineridora* sp1	2.34	14.63	*Perspiria* sp1	2.45	15.31
Linhomoeus sp2	3.27	23.5	*Daptonema* sp1	2.34	16.96	*Spirinia* sp1	2.37	17.69
Sabatieria sp1	3.27	26.77	*Linhomoeus* sp2	2.16	19.13	*Metalinhomoeus* sp2	2.3	19.98
Spirinia sp1	3.27	30.04	*Sphaerolaimus* sp1	2.11	21.24	*Sabatieria* sp1	2.18	22.16
Metalinhomoeus sp2	3.01	33.06	*Chromadora* sp1	2.07	23.31	*Daptonema* sp1	2.08	24.24
Terschellingia sp1	2.61	35.66	*Monhysteridae* spp.	2.06	25.38	*Leptolaimus* sp1	2.04	26.28
Groups 0-1 & 3-4 cm			**Groups 1-2 & 2-3 cm**			**Groups 1-2 & 3-4 cm**		
Species	Contrib%	Cum.%	Species	Contrib%	Cum.%	Species	Contrib%	Cum.%
Perspiria sp1	4.28	4.28	*Molgolaimus* sp1	3.17	3.17	*Perspiria* sp1	6	6
Terschellingia sp2 (cf. *longicaudata*)	3.98	8.26	*Halichoanolaimus* sp1	3.03	6.21	*Theristus* sp1	3.55	9.54
Molgolaimus sp1	3.54	11.8	*Marylynnia* sp1	3.03	9.23	*Molgolaimus* sp1	3.37	12.91
Metalinhomoeus sp2	3.47	15.26	*Perspiria* sp1	3.02	12.25	*Metalinhomoeus* sp2	3.12	16.04
Halalaimus sp1	3.11	18.38	*Halaphanolaimus* sp1	2.87	15.12	*Metalinhomoeus* spp	3.05	19.09
Steineridora sp1	2.94	21.32	*Metalinhomoeus* sp1	2.56	17.68	*Terschellingia* spp	2.87	21.96
Pierrickia sp1	2.85	24.17	*Metalinhomoeus* spp	2.38	20.06	*Spirinia* sp1	2.79	24.75
Sphaerolaimus sp1	2.53	26.69	*Linhomoeus* sp1	2.35	22.4	*Linhomoeus* sp1	2.7	27.45
Linhomoeus sp2	2.32	29.01	*Leptolaimus* sp1	2.35	24.75	*Halalaimus* sp1	2.48	29.93
Daptonema sp1	2.3	31.31	*Metalinhomoeus* sp2	2.3	27.05	*Leptolaimus* sp1	2.41	32.34

Groups 2-3 & 3-4 cm		
Species	Contrib%	Cum.%
Metalinhomoeus spp	3.76	3.76
Halichoanolaimus sp1	3.35	7.11
Diodontolaimus sp1	3.28	10.38
Theristus sp1	3.28	13.66
Leptolaimus sp1	3.14	16.8
Perspiria sp1	3.08	19.87
Terschellingia spp	2.7	22.58
Metalinhomoeus sp2	2.68	25.25
Halalaimus sp1	2.62	27.87
Chromadoridae spp.	2.54	30.42

Table S6. – Meiofaunal abundance, number of higher taxa, nematode biomass, diversity (Shannon index (H'), equitability evenness (J'), expected genus number (EG(51)) and trophic diversity index (ITD)). List of exclusive and shared genera of nematodes between the maerl bed and the sandy beach.

	Maerl bed	Sandy beach	Maerl/ Sandy beach
Meiofaunal abundance (ind/10 cm^2)	1986±457	384±16	
N° taxa	12	8	
Nematode biomass (µgC/10 cm^2)	108.2±41.9	47.6±2.1	
H' (loge)	2.5	2.2	
J'	0.8	0.7	
EG(51)	18	15	
ITD	0.3	0.6	
Genera of nematodes	*Acantholaimus*	*Chaetonema*	*Comesoma*
	Actinonema	*Dasynemoides*	*Daptonema*
	Antomicron	*Desmodora*	*Molgolaimus*
	Campylaimus	*Gonionchus*	*Neochromadora*
	Cephalanticoma	*Microlaimus*	*Paracomesoma*
	Chromadora	*Omicronema*	*Parodontophora*
	Chromadorella	*Richtersia*	*Promonhystera*
	Chromadorita	*Xyala*	*Spirinia*
	Cobbia		*Stylotheristus*
	Comesomoides		*Trichotheristus*
	Cyartonema		*Trileptium*
	Cyatholaimidae		*Viscosia*
	Desmoscolex		
	Diodontolaimus		
	Dorylaimopsis		
	Draconema		
	Euchromadora		
	Eumorpholaimus		
	Eurystomina		
	Filoncholaimus		
	Eurystomina		
	Filoncholaimus		
	Halalaimus		
	Halaphanolaimus		
	Halichoanolaimus		
	Halomonhystera		
	Karkinochromadora		
	Kraspedonema		
	Laimella		
	Leptolaimus		
	Linhomoeus		
	Linhystera		
	Longicyatholaimus		
	Marylynnia		
	Megadesmolaimus		
	Metachromadora		

Maerl bed	Sandy beach	Maerl/ Sandy beach
Metacyatholaimus		
Metadesmolaimus		
Metalinhomoeus		
Metasphaerolaimus		
Nemanema		
Oncholaimus		
Paracyatholaimus		
Paralinhomoeus		
Paralongicyatholaimus		
Pareurystomina		
Perspiria		
Pierrickia		
Prochromadorella		
Prooncholaimus		
Ptycholaimellus		
Quadricoma		
Sabatieria		
Setosabatieria		
Sphaerolaimus		
Spiliphera		
Spilophorella		
Steineridora		
Stilbonematinae		
Stygodesmodora		
Synonchiella		
Syringolaimus		
Terschellingia		
Thalassomonhystera		
Theristus		
Thoracostomopsis		
Tricoma		