FACULTY OF SCIENCES

Biology Department

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THE EFFECTS OF ORGANIC ENRICHMENT OF JELLY-FALLS AND AQUACULTURE ON MEIOBENTHIC COMMUNITY COMPOSITION AND FUNCTIONING: RESULTS FROM AN EX SITU TRACER EXPERIMENT

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Master's dissertation submitted to obtain the degree of Master of Science in Biology

Academic year: 2016 - 2017

GHENT UNIVERSITY

ABSTRACT (EN)

The intensive aquaculture and increase in magnitude of jellyfish blooms in fjord systems over the past decade has potentially major impacts on the seafloor, which is subjected to organic enrichment from fish farm depositions and gelatinous carcasses. This study investigated the separate and combined effects on the structure and functioning of meiobenthic communities from two different water depths in a lab experiment. Two different weights of jellyfish were added and isotope labelled algae were used as a tracer. Respiration was measured over the course of the experiment. Higher densities but a lower diversity of meiobenthos and nematodes were found in the vicinity of fish farms and at the lower water depth. Community composition also differed according to fish farm presence and water depth, but the impacts from fish farm depositions appeared to be lower at greater depth. Nematode biomass was higher in the presence of aquaculture, this could be the result of increasing dominance of relatively larger genera such as *Cheironchus*, *Dorylaimopsis* and *Marylynnia*. Food uptake was only affected by aquaculture depositions and water depth, while sediment community oxygen consumption experienced an interaction of depth and jellyfish addition. The general findings of this study do not indicate that the combination of the two stressors affected the seafloor in a more severe way than they did separately.

ABSTRACT (NL)

De intensieve aquacultuur en toename in omvang van kwallenbloei in fjordsystemen over het laatste decennium heeft mogelijks grote gevolgen voor de zeebodem, die wordt blootgesteld aan organische verrijking afkomstig van vis-kwekerijen en karkassen van dode kwallen. Deze studie onderzocht de aparte en gecombineerde effecten op de structuur en het functioneren van meiobenthosgemeenschappen afkomstig van twee waterdieptes. Twee verschillende gewichten aan kwal werden toegevoegd en isotoop-gelabelde algen werden gebruikt als merker. De respiratie werd gemeten over het verloop van het experiment. Op lagere diepte en in de omgeving van viskwekerijen werden hogere densiteiten maar een lagere diversiteit aan meiobenthos en nematoden gevonden. Gemeenschapssamenstelling verschilde ook afhankelijk van de aanwezigheid van een viskwekerij en waterdiepte, maar de effecten van viskwekerij-afzettingen bleken kleiner te zijn op grotere diepte. De nematode biomassa was hoger in de aanwezigheid van aquacultuur, dit was mogelijks het resultaat van verhoogde dominantie van relatief grotere genera zoals *Cheironchus*, *Dorylaimopsis* en *Marylynnia*. Voedselopname werd enkel beïnvloed door aquacultuur afzettingen en waterdiepte, terwijl de zuurstofconsumptie van de sedimentgemeenschap een interactie van waterdiepte en het toevoegen van de kwallen ondervond. De algemene bevindingen van deze studie wijzen niet op een grotere bedreiging van de zeebodem als gevolg van de combinatie van de twee stressoren.

Keywords: Aquaculture · Jelly-falls · Organic enrichment · Fjords · Meiobenthos · Nematodes · Stable isotopes · SCOC

INTRODUCTION

Benthic ecosystems largely depend on labile organic material that sinks from the water column to the seafloor as their energy and carbon source, especially in the deep sea. The timing and quantity of this input strongly impacts benthic community structure and ecosystem functioning (Smith et al., 2015). Many studies have assessed the response of benthic ecosystems to these seasonal inputs of phytodetritus (e.g. Franco et al., 2008b; Witte et al., 2003; Woulds et al., 2009), which is the most common source of organic matter input to the seafloor. On a more localised scale, other sources such as fish farm depositions and jellyfish carcasses can play an important role as additional food sources.

In recent years, marine aquaculture has increased enormously to provide an answer to the ever-growing global human population and overfished seas. The release of nutrients and other waste products, however, are a downside which may have severe impacts on the benthic ecosystem, resulting in increased anaerobic microbial metabolism (Sweetman et al., 2014) and often anoxic conditions in the sediment (Gray et al., 2002; Holmer et al., 2003, 2007). In turn, this leads to reduced biodiversity and altered species compositions of the benthic communities, usually with a shift to dominance of a few opportunistic species (Mirto et al., 2002, 2010, 2012; Neofitou et al., 2010). Opportunistic polychaetes such as *Capitella capitata*, for example, show a massive increase in abundance and biomass at the most heavily impacted sites (Kutti et al., 2007). Macrobenthos, in general, is more sensitive to low oxygen concentrations than meiobenthos (Josefson and Widbom, 1985; Weston, 1990). This suggests that meiofauna are relatively more important mineralisers of carbon as sediments become organically enriched (Duplisea and Hargrave, 1996).

The impact of fish farms located in shallow waters of the Mediterranean Sea tends to be very localised, often only observable within 20-50 m from the cages (Grego et al., 2009; Neofitou et al., 2010). More modern and high-production fish farms are preferably sited at off-coast locations with moderate hydrodynamics and deep water (Kutti et al., 2007, 2008) to disperse the waste over greater distances and reduce the impact directly beneath the cages. These can for instance be found in deep-sea fjords in Norway, which is the leading producer of Atlantic salmon in the world. However, Valdemarsen et al. (2012) showed that locating fish farms at deep water sites is not a universal solution for reducing benthic organic loading to sustainable levels. Deep-water habitats are often diverse and adapted to low input of organic matter (i. e. oligotrophic) and may therefore be highly sensitive to organic enrichment from fish farming. Kutti et al. (2007) reported that large-scale effects on the benthos were restricted to the nearest 250 m from the farm, which was moored at a water depth of 230 m.

Another potentially big contributor to the organic enrichment of the seafloor in fjord systems are jellyfish, as their populations are expanding along the Norwegian shelf margin (mainly *Periphylla periphylla*). Jellyfish are renowned for their ability to rapidly form massive, ephemeral blooms, which sink to the seafloor following senescence (Lebrato et al., 2012, 2013). These gelatinous carcasses (jelly-falls) can provide an important transport pathway for carbon (C) and nitrogen (N) to the seafloor (Sweetman and Chapman, 2015), but also pose a risk of smothering the sediment. The

accumulation of jellyfish material at the seafloor leads to greater microbial metabolism since the C:N ratio of bacteria (± 5-7:1, Goldman and Dennet, 2000) and jellyfish (e.g. *P. periphylla*: 5.6:1; Sweetman et al., 2016) are similar, leading to a more efficient bacterial degradation of gelatinous detritus. A substantial proportion of decomposition may already occur in the water column. Titelman et al. (2006) reported that approximately 95% of a specimen of *P. periphylla* decomposed within five days when suspended within the water column in Raunefjorden. This release of large amounts of organic carbon into the water column represents an important trophic link in the ecosystem (Titelman et al., 2006). *P. periphylla* can maintain year-round high populations in fjords because of their continuous spawning, high longevity and low mortality (Youngbluth and Båmstedt, 2001). Still, some fjords which currently house over 20,000 tons of jellyfish deal with mass die-offs in winter because of food shortage (Trondheim Fjord, J. Mork, pers. observation). If this trend spreads to other fjords, huge jelly-falls could become a recurring phenomenon.

The seafloor in fjords is subjected to two potentially major inputs of organic enrichment, which have been studied separately (Kutti et al., 2007; Riemann et al., 2006; Sweetman et al., 2014, 2016; Titelman et al., 2006), but never combined. The combined effect of both organic matter inputs may, however, be greater or smaller than just the sum of the effects from individual inputs (synergistic vs. additive and antagonistic effects; Darling and Côté 2008). Sweetman et al. (2016) already hypothesised that jelly-falls would exert a stronger impact on the seafloor in areas of high organic input such as fish farms. This Master's Thesis is performed in the framework of the Norwegian JellyFarm project which investigates the separate and combined effect of organic enrichment of aquaculture and jellyfish carcasses (jelly-falls) on biodiversity, hydrodynamics, biogeochemistry, and ecosystem services of benthic communities in Norwegian fjords. This study focusses on the effects of organic enrichment on the structure (densities, biomass, community composition) and the functioning (uptake ^{13}C-enriched algae) of meiobenthic communities with a special focus on nematodes. Nematodes in particular are often used as indicators for organic pollution since some species seem to proliferate in areas of organic loading (Moreno et al., 2008).

We performed a lab experiment in which we incubated natural sediments from a fish farm area and a control area from two locations at different water depths in Hardangerfjorden (Norway) and deposited ^{13}C-labeled algae and two different amounts of *P. periphylla* carcasses on the sediment. The jellyfish carcasses act as a stressor and their impact is indirectly referred from the potentially differential uptake of the labelled algae. The following hypotheses were tested: **(H1)** *Organic enrichment with jellyfish carcasses and fish farm waste products impact* ***a)*** *the structure (densities, biomass and diversity) and functioning (algal ^{13}C uptake) of meiobenthos and* ***b)*** *sediment community oxygen consumption (SCOC).* **(H2)** *The impact of organic enrichment on the meiobenthos and the SCOC differs with water depth.*

MATERIAL AND METHODS

Study system

Hardangerfjorden is a deep-sea fjord (max. depth 860 m) and one of the most important areas for aquaculture in Norway (Skogen et al., 2009). The fjord is separated from the open sea by a 160 m deep sill (Valdemarsen et al., 2012) and strong currents are present within the fjord system, which result in an exchange of water and nutrients with the coast (Skogen et al., 2009). *Periphylla periphylla* (Scyphozoa, Coronatae) is a perennial jellyfish that occurs year-round in many deep-sea fjords along the Norwegian coast (Sørnes et al., 2007; Youngbluth and Båmstedt, 2001). Water column darkening in fjords attracted the negative phototactic species and favours tactile predators (Aksnes et al., 2009), while the rise in sea temperature stimulates reproduction. This can lead to mass blooms such as in Lurefjorden, where the population currently exceeds 50,000 tons.

Study site and sampling

The sediment samples were collected in Hardangerfjorden, Norway, on board of the MS *Solvik* between the 27th and 31st of August, 2016. Two study sites at different depths were selected (Fig. 1): Hisdalen (462-480 m; "470m") and Onarheim (113-128 m; "120m"). At each study site, 8 box core deployments were performed in close proximity at about 100 m from the fish farm ("FF") and further off at approximately 500 m distance from the fish farm ("NF") (Table 1). The box cores were subsampled with plexiglass tubes with a diameter of 14 or 12 cm. The sediment which reached a height of 15 cm was carefully submerged with in situ, filtered (on a 32 µm mesh) seawater before transporting them to IRIS (International Research Institute of Stavanger, Norway), where they were maintained in the dark in water basins at in-situ temperature (8°C) for acclimatization. The cores were continuously supplied with fresh, cooled and sand-filtered seawater (salinity: 34.3±0.2) from a nearby fjord by a flow-through system via gravity feed. To check if the water flow brought in some additional meiofauna, we filtered it over a 32µm sieve for 3 hours at three separate occasions. The inflow of meiofauna was negligible (2 nematodes; 8 nematodes; 3 nematodes and 1 copepod). The *Periphylla periphylla* specimens that were used in the experiments were caught on the 30th of August during this same cruise with a zooplankton net in the region of Onarheim. They were stored frozen at -20°C until the start of the experiments.

Cultivation and 13C enrichment of algae

Dunaliella salina was cultured axenically at IRIS in artificial sea water modified with Walne's medium (Walne, 1970) and labelled by replacing the $NaH^{12}CO_3$ in the sea water by $NaH^{13}CO_3$. The flask was placed in an incubation chamber at 20°C with a 12:12-h light-dark period while the logarithmic growth was monitored by an automated size particle counter. Harvesting was done by centrifuging (5000 rpm, 20min) and rinsing for three times. The culture was then frozen at -40°C and submitted to lyophilisation, after which they were ground with a mortar and pestle. This labelling technique resulted in an average $\delta^{13}C$ value of 26788±37‰ (equalling 23.7 % ^{13}C).

Table 1. Sampling details of the cores taken between 27th-31st of August 2016. One extra box core was taken from Onarheim to compensate for a core that was dropped on the boat.

AKS	Date	Location		Depth	Coordinates
184	27/08/2016	Hisdalen	NF	462m	60 06.324N, 005 55.745E
185	28/08/2016	Hisdalen	FF	478m	60 07.535N, 005 55.608E
186	28/08/2016	Hisdalen	FF	479m	60 07.548N, 005 55.497E
187	28/08/2016	Hisdalen	FF	480m	60 07. 533N, 005 55.489E
188	28/08/2016	Hisdalen	FF	479m	60 07.467N, 005 55.500E
189	28/08/2016	Hisdalen	NF	468m	60 06.368N, 005 55.800E
190	29/08/2016	Onarheim	FF	128m	59 57.107N, 005 39.790E
191	29/08/2016	Onarheim	FF	127m	59 57.068N, 005 40.556E
195	29/08/2016	Onarheim	FF	126m	59 56.991N, 005 40.102E
192	29/08/2016	Onarheim	NF	113m	59 56.930N, 005 40.568E
193	29/08/2016	Onarheim	FF	128m	59 57.072N, 005 39.884E
194	29/08/2016	Onarheim	FF	127m	59 57.000N, 005 40.043E
196	30/08/2016	Onarheim	NF	117m	59 56.605N, 005 40.548E
197	30/08/2016	Onarheim	NF	113m	59 57.578N, 005 40.617E
198	30/08/2016	Onarheim	NF	115m	59 57.132N, 005 41.058E
206	31/08/2016	Hisdalen	NF	467m	60 06.390N, 005 55.669E
207	31/08/2016	Hisdalen	NF	468m	06 06.271N, 005 55.602E

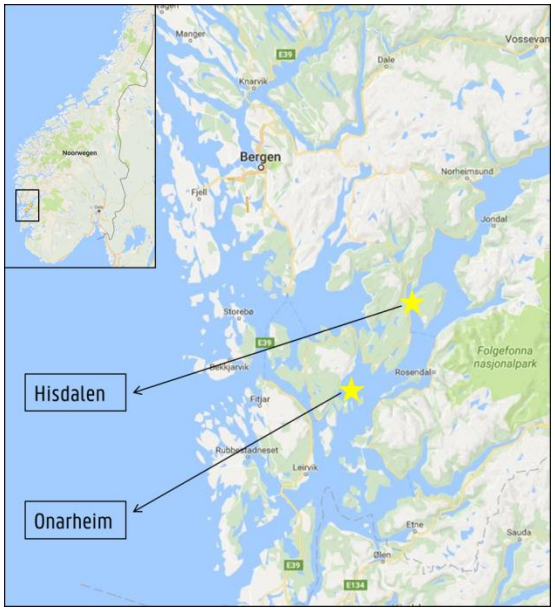

Fig. 1. Location of the two study areas within Hardangerfjorden, Norway (maps from Google).

Experimental set-up

To assess the effect of both aquaculture and jellyfish carcasses on the functioning of the benthos, ^{13}C-enriched *Dunaliella salina* algae were added to the sediment cores after 2 to 5 days of acclimatization. The experimental incubations were started at 4 different moments to spread work load of sample processing at the end of the experiment. The aim was to add 1 g C/m² of labelled algae. Assuming that the carbon content in those algae was 20%., 77 mg algae was added to the 14 cm Ø cores and 57 mg algae to the 12 cm Ø cores. After removing half of the water overlaying the sediment in the cores, the algae were dissolved in seawater in a 20ml syringe and gently introduced in close proximity of the sediment surface to assure an even distribution. The algae were left to settle for one hour, before the jellyfish carcasses were introduced.

From each study site, from both the FF and NF location, 4 cores were randomly assigned to the following treatments: No jellyfish addition ("C"), Low jellyfish carbon amount ("L"), High jellyfish carbon amount ("H"). Based on a carbon content of 0.023 g C / g wet weight (A. Sweetman, unpublished data), 46.59±0.55 g of thawed jellyfish was added to the 14 cm Ø cores and 34.13±0.29 g to the 12 cm Ø cores for the H treatment and 9.73±0.27 g and 7.00±0.14 g, respectively, for the L treatment. This equals 75 g jellyfish C/m² for the H treatment and 15 g jellyfish C/m² for the L treatment. This is a considerable larger amount than the jellyfish detritus input that has been recorded for Norwegian fjords (0-13.4 mg C/m², Sweetman and Chapman, 2011, 2015), but more similar to those documented in other areas (e.g. Gulf of Oman: 1.5-75 g C/m², Billett et al., 2006). This allowed us to study the seafloor impact from a large pulse of gelatinous detritus, as done by Sweetman et al. (2016). The thawed jellyfish was dabbed with tissues to remove excess water before weighing and cut up as less as possible to reach the target weight. The jellyfish were added to the cores using a large metal bolt to prevent them from floating. A bolt was also added to the control cores to standardize the procedure.

Immediately after the jellyfish addition, the cores were sealed with lids and the stirrers that were mounted under them were activated. This gently mixed the water inside the cores without re-suspending the sediment. The oxygen concentrations were measured for minimum 6 h by FireStingO_2 optic oxygen sensors from Pyro Science that were inserted in the cores through the lids. During this period the cores were disconnected from the water flow through system. The water volume in all cores was measured after concluding the experiment. The whole experiment was performed in the dark.

Sample processing and analytical procedures

The cores were processed after 48 hours of incubation. Seawater overlaying the sediment was removed with a syringe before the sediment was sliced from the surface to 5 cm sediment depth in three sections (0-1 cm, 1-2 cm, 2-5 cm). Each section was homogenized before subsampling with a 50-ml syringe: 20 ml from the 1 cm-layers and 60 ml from the 3 cm-layers. The 144 samples in total were stored on Li_2CO_3-buffered formalin (4%) until further processing at the Marine Biology Research Group at Ghent University. The samples were sieved over two stacked sieves (500µm and 32µm mesh) and rinsed with tap water. The fraction that was retained on the 32µm sieve underwent a triple density centrifugation (3000 rpm, 3 x 12 minutes) with the colloidal silica polymer LUDOX TM 40 (Heip et al., 1985) to separate the organic matter from the sediment. All meiofauna organisms were identified to taxon level according to Higgins and Thiel (1988) and counted. Counts were converted to densities per 10 cm² and the counts and densities of layers 0-1 and 1-2 were summed. Meiofauna analyses were performed on this 0-2 cm layer, this because the 2-5 cm layer counts were only finished after these first analyses were already performed and there was no time to redo them on the 0-5 cm data.

From the 0-1 cm sediment layer 100 nematodes were handpicked randomly and transferred to De Grisse I, II and III (Seinhorst, 1959) before being mounted on glass slides and identified to genus level based on the pictorial keys of Warwick et al., 1998) and the identification keys and original descriptions available on the Nemys website (www.Nemys.ugent.be, Guilini et al., 2017). Genera were classified into four trophic groups according to Wieser (1953): no buccal cavity - selective deposit feeders (1a), large but unarmed buccal cavity - non-selective deposit feeders (1b), buccal cavity with scraping tooth or teeth - epistrate or epigrowth feeders (2a) and buccal cavity with large jaws - predators/omnivores (2b). This was used to calculate the diversity trophic index (ITD) as follows: ITD = $\sum\theta^2$, where θ is the percentage of each trophic group (Heip et al., 1985). The 1b/2a-ratio was calculated as done in Lambshead (1986). The 1b/2a-ratio was considered useful because it has been shown that the 2a group is a constant factor but that contamination and eutrophication is associated with a relative increase in the 1b group. The genera were also given a colonisers-persisters (c-p) value according to (Bongers et al., 1991). If the genus was not explicitly mentioned, the value of the family was used. The maturity index (MI) was calculated as the weighted mean of the individual genus scores: MI = ∑c-p value(genus) x frequency(genus). Nematode biomass was calculated using the carbon content as measured by EA-IRMS (µgC/cup) divided by the number of nematodes in a sample cup times the number of nematodes per 10 cm² in the core.

Structural meiofauna and nematode diversity was assessed by calculating the Hill's indices, which are variably dependent on relative abundances and thus cover both taxon richness and evenness (H_0, H_1, H_2; Heip et al., 1998; Hill, 1973). With increasing order the indices become less sensitive to the rare, and more sensitive to the more abundant taxa or species (Soetaert and Heip, 1990). A sufficient number of meiofauna and nematode specimens in the samples allowed for the calculation of a rarefaction index, i.e. the expected number of higher taxa or genera, respectively, present in a sample of 51 individuals (ET(51) or EG(51); Hurlbert, 1971). Both Hill's indices and rarefaction indices were calculated using Primer v6.

Another 200 nematode specimens were handpicked randomly from the 0-1cm layer samples, rinsed in MilliQ water and transferred to a drop of MilliQ water in 5x8 mm tin cups. The cups were placed overnight in an oven at 60°C, securely folded and stored in a multi-well Microtitre plate. An elemental analyser-isotope ratio mass spectrometer (EA-IRMS; NIOZ, Yerseke, The Netherlands) was used to measure the carbon stable isotope ratios and carbon content. Stable isotope ratios are expressed in the δ notation with Vienna Pee Dee Belemnite (VPDB) as reference standard, and expressed in units of ‰, according to the standard formula $\delta^{13}C = [R_{sample} / R_{VPDB} - 1] \times 10^3$, where R is the ratio of $^{13}C/^{12}C$ ($R_{sample} = [(\delta^{13}C_{sample}/1000)+1] \times R_{VPDB}$) and R_{VPDB} is 0.0111802. Label uptake by the nematodes is reflected as enrichment in ^{13}C and is presented as $\Delta\delta^{13}C$ (‰), which indicates the increase in $\delta^{13}C$ of the sample, as compared to its natural background value, and is calculated as $\Delta\delta^{13}C$ (‰) = $\delta^{13}C_{sample} - \delta^{13}C_{background}$. We did not acquire the background nematode ^{13}C values yet and therefore, assumed that $\delta^{13}C_{background}$ is -21.64‰, as was measured the year before in Hardangerfjorden (water depth: 207 m) by Mevenkamp et al. (2017). Positive $\Delta\delta^{13}C$ values indicate that the organisms have acquired some of the introduced label. Absolute uptake of the label (I) is expressed in mg $^{13}C/m^2$ and calculated as $I = (F_{sample} - F_{background}) \times S$, where F is the ^{13}C fraction F= R / (R+1) and S is the total carbon stock (mg C/m^2) of the nematodes.

Biomass-specific respiration rates (R, d^{-1}) were calculated using both the Mahaut formula: $R = 0.0074 \times W^{-0.24}$ and the formula by de Bovée and Labat, corrected for in situ temperature (8°C) assuming Q10 is 2: $R = 0.0449 \times W^{-0.1456} \times \exp^{\ln(Q10)/10(T-20)}$ (de Bovee and Labat, 1993; Guilini et al., 2011; Mahaut et al., 1995), where W is the mean individual dry weight (µg C/individual), directly inferred from the carbon content measured by the EA-IRMS divided by the number of nematodes in the sample cup. To investigate whether the uptake of the nematodes was sufficient to meet their carbon requirements, the observed uptake values were compared with those required to maintain biomass-dependent respiration rates under a minimal nematode net growth efficiency (NGE) of 0.6 (indicated as assimilation/carbon demand; (Pape et al., 2013; van Oevelen et al., 2006). The theoretical carbon demand of the nematodes was calculated as follows: Carbon demand = NGE x R / (1 - NGE). The assimilation of the algal carbon by the nematodes was calculated as nematode ^{13}C uptake divided by the fractional abundance of ^{13}C in the algae.

Flux rates of O_2 (or SCOC) were calculated based on the regression slope of 4 h of measurements, except in four instances where it was only recorded for 1.2 h because of overnight computer failure. The intervals were chosen towards the end of the recordings or before a set threshold of 175 µmol O_2/L was exceeded. This guaranteed a minimum of 59% oxygen saturation (temperature: 8°C, salinity: 34; Ramsing and Gundersen, 2011). The last set of measurements only ran for 6 h, so we discarded these replicates, since Sweetman et al. (2016) showed that SCOC increased considerably during the first 24 h. The remaining intervals were all taken between 10 h and 20 h after the start of the measurements. The SCOC was calculated as follows: SCOC (mmol O_2/day/m²)=(((-slope/exp^{time})*24/area)*volume)/1000.

Data analyses

Univariate data, i.e. absolute uptake (I), % carbon demand, SCOC, diversity indices (Hill numbers: H_0, H_1, H_2; Expected number of Taxa/Genera: ET(51), EG(51)), Maturity Index (MI), Index of Trophic Diversity (ITD), 1b/2a-ratios, nematode biomass (µg C/10cm²) and densities, were analysed with parametric ANOVA tests in R v3.3.1 (R Core Team, 2013, http://www.R-project.org) using RStudio v0.98.1087 (RStudio Team, 2015, http://www.rstudio.com). "Depth", "Fish farm" and "Treatment" were treated as fixed factors, with two (120m and 470m), two (FF and NF) and three levels (C, L, H), respectively. A type II test was performed when no significant interactions were revealed in the type III test. When the assumptions for ANOVA could not be met, PERMANOVA was performed on a Euclidean distance similarity matrix instead, using unrestricted permutation of raw data.

Multivariate non-parametric permutational ANOVA (PERMANOVA) analyses were performed with PRIMER v6 and PERMANOVA+ add-on software (Anderson et al., 2008; Clarke and Gorley, 2006) to test for the differences in meiofauna and nematode community composition between the different sampling sites, also at different sediment depths (0-2 cm and 2-5 cm). Bray-Curtis similarity was used as resemblance measure on standardized, square-root or logarithmic transformed abundances. When incorporating sediment depth, two factors were added to the main model: "Replicate", nested in "Fish farm" as a random factor and "Layer" as a fixed factor, with four (1, 2, 3, 4) and two levels (0-2 cm, 2-5 cm) respectively. The presence of five factors in the PERMANOVA design proved difficulties, with incomplete replication at the lowest level, and "Treatment" was therefore discarded, since this factor was non-significant. Calculation of the Pseudo-F ratio and p value (significance level set at p = 0.05) required 9999 permutations of the residuals under a reduced model. *A posteriori* pair-wise tests were conducted where significant effects were found and a PERMDISP test checked the homogeneity of multivariate dispersions. Where only a restricted number of unique permutations was possible, p-values were obtained from Monte Carlo samplings (Anderson and Robinson, 2003). Nematode community composition patterns were visualized by non-metric multidimensional scaling (MDS) plots. To reveal the variability among and between nematode sample groups a SIMPER analysis was performed on standardized square-root transformed abundance data. The described results include information on the type of statistical test and the p-values; more details are provided in the tables in the Appendix.

RESULTS

Meiofauna assemblages

Total meiofauna densities in the 0-2 cm depth layer differed between FF and NF sites at both depths and between the two water depths ("Depth x Fish farm", PERMANOVA, Pseudo-F=4.979, p=0.032; Table A1; Fig. 2a). Highest densities were found at the FF sites and at 120 m depth (Fig. 2a). Densities of Nematoda, the most abundant taxon (94.5±3.5%), exhibit the same pattern ("Depth x Fish farm", PERMANOVA, Pseudo-F=5.991, p=0.019; Table A2; Fig. 2b). There was a dispersion effect on the "Depth" factor in both cases (PERMDISP: p<0.05). Copepoda, which are the second most abundant taxon (2.6±2.1%, 4±4 ind./10cm²), had higher densities at the NF site at 120 m depth compared to the FF sites at 120 m depth and the NF site at 470 m ("Depth x Fish Farm", PERMANOVA, Pseudo-F=16.239, p<0.001, Table A3; Fig. 2c) and also in the C versus the L and H treatments ("Treatment", PERMANOVA, Pseudo-F=3.696, p=0.032). There was a dispersion effect on both "Depth" and "Fish farm" (PERMDISP: p<0.01). Polychaeta, which occurred with 1.9±1.5% of the total meiofauna abundance (2±1 ind./10cm²), had higher densities in the FF sites compared to the NF sites ("Fish farm", PERMANOVA, Pseudo-F=5.549, p=0.025, Table A4; Fig. 2d) and in the C versus the L and H treatments ("Treatment", PERMANOVA, Pseudo-F:4.705, p=0.016). Other meiofauna taxa occurred with <0.5% relative abundance and include Nauplii (0.4±0.6%), Gastrotricha (0.1±0.2%), Bivalvia (0.1±0.1%), Cnidaria (0.1±0.2%), Ostracoda (0.1±0.1%) and Kinorhyncha (0.1±0.1%). Results of the statistical tests on the densities of these less abundant taxa is provided in Table A5-A10.

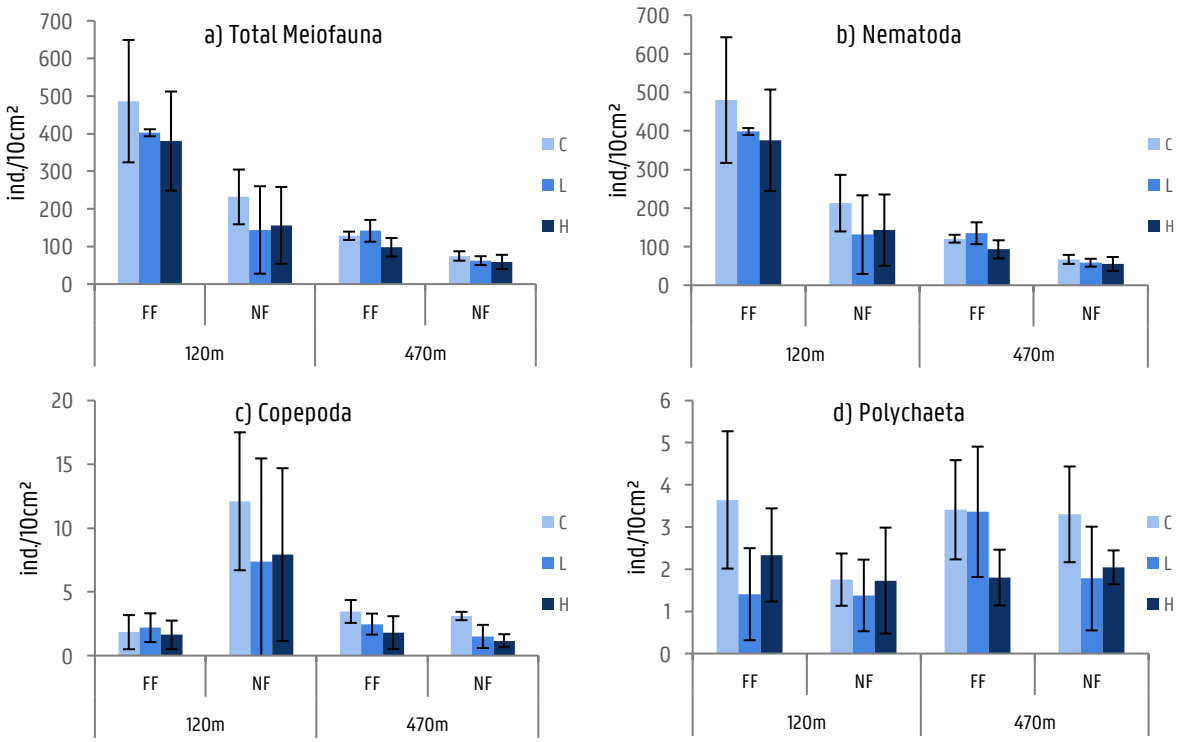

Fig. 2. Total densities (ind./10cm²) of the **a)** Meiofauna higher taxa, **b)** Nematoda, **c)** Copepoda and **d)** Polychaeta in the 0-2 cm layer.

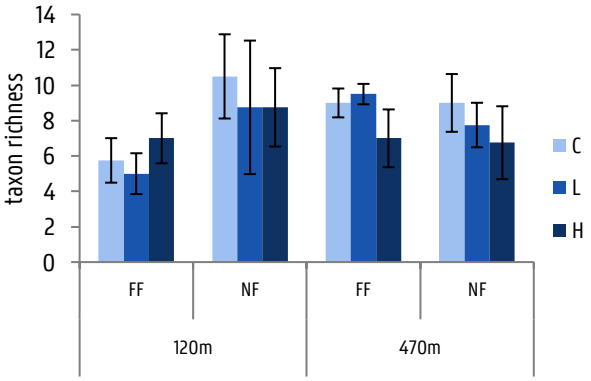

Fig. 3. Meiofauna taxon richness (H_0) in the 0-2 cm layer.

The meiofauna community composition in the 0-2 cm layer differed not only between FF and NF sites at both water depths and according to water depth ("Depth x Fish Farm", PERMANOVA, Pseudo-F=13.434, p=0.0002, Table A11), but also between the C and L treatment ("Treatment", PERMANOVA, Pseudo-F = 2.426, p =0.038). The meiofauna community composition was also compared between the two sediment depth layers (i.e. 0-2 cm and 2-5 cm). Interestingly, the meiofauna community in both layers differed between both water depths ("Depth x Layer", PERMANOVA, Pseudo-F = 5.092, p = 0.001, Table A12) and between the FF and NF sites only in the upper 0-2 cm layer ("Fish Farm x Layer", PERMANOVA, Pseudo-F= 17.69, p = 0.0026, Table A12). The number of meiofauna taxa (H_0) at 120 m depth was lower at the FF site than at the NF site and compared to the FF site at 470 m depth (Fig. 3; Table 2a; "Depth x Fish Farm", PERMANOVA, Pseudo-F=15.06, p<0.001, Table A13). The two other Hill's indices (H_1, H_2) and the ET(51) were generally higher at NF sites compared to FF sites and at the FF site at 470 m depth compared to 120 m depth (Table 2a; "Depth x Fish Farm", PERMANOVA, Tables A14-A16). There was a dispersion effect on the depth factor in all of the index analyses (PERMDISP: p<0.05).

Table 2. Diversity indices for **a)** meiofauna (higher taxon, 0-2 cm) and **b)** nematodes (genera, 0-1 cm): Hill's indices (H_0, H_1, H_2); Expected number of meiofauna taxa and nematode genera with n=51 (ET(51), EG(51)); Maturity index (MI) and Index of trophic diversity (ITD, %). Standard deviation reported next to the mean index value.

	120FF						120NF						470FF						470NF					
	C		L		H		C		L		H		C		L		H		C		L		H	
a. Meiofauna																								
H_0	**5.8**	1.3	**7.0**	1.4	**5.0**	1.2	**10.5**	2.4	**8.8**	2.2	**8.8**	3.8	**9.0**	0.8	**7.0**	1.6	**9.5**	0.6	**9.0**	1.6	**6.8**	2.1	**7.8**	1.3
H_1	**2.0**	0.3	**1.8**	0.2	**2.0**	0.1	**4.1**	0.7	**3.6**	1.1	**4.2**	1.3	**3.4**	0.4	**3.3**	0.2	**3.3**	0.3	**4.3**	0.6	**3.5**	0.6	**3.4**	0.4
H_2	**1.5**	0.2	**1.4**	0.1	**1.5**	0.1	**2.9**	0.5	**2.5**	0.7	**3.0**	0.9	**2.5**	0.3	**2.3**	0.1	**2.4**	0.1	**3.1**	0.4	**2.5**	0.5	**2.5**	0.2
ET(51)	**1.6**	0.6	**1.5**	0.5	**1.6**	0.6	**3.2**	0.6	**2.8**	1.0	**3.2**	1.3	**2.8**	0.0	**2.6**	0.5	**2.7**	0.0	**3.5**	1.0	**2.8**	0.0	**2.9**	0.5
b. Nematodes																								
H_0	**21.7**	3.1	**16.7**	4.2	**16.3**	2.1	**27.3**	6.8	**29.3**	5.8	**23.7**	0.6	**25.0**	1.7	**27.0**	2.0	**27.7**	3.2	**35.3**	1.5	**34.7**	2.5	**33.0**	4.6
H_1	**18.6**	2.2	**14.0**	4.1	**13.5**	1.7	**24.7**	7.1	**26.7**	5.7	**21.0**	0.4	**21.6**	1.6	**23.8**	2.0	**24.3**	3.6	**32.3**	1.8	**31.4**	2.5	**30.6**	4.4
H_2	**15.7**	1.8	**11.9**	3.9	**11.2**	1.1	**22.1**	6.9	**24.4**	5.5	**18.7**	0.3	**17.6**	1.7	**20.5**	1.8	**20.8**	4.3	**29.3**	2.1	**28.5**	2.6	**28.0**	3.9
EG(51)	**16.1**	1.0	**13.2**	3.9	**12.6**	1.3	**21.3**	5.8	**22.0**	3.5	**18.3**	0.4	**18.6**	1.2	**20.0**	1.6	**20.4**	3.3	**25.4**	1.1	**24.9**	1.3	**24.1**	2.2
MI	**2.6**	0.2	**2.6**	0.2	**2.5**	0.1	**2.9**	0.1	**2.8**	0.2	**3.0**	0.1	**2.8**	0.0	**2.8**	0.1	**2.7**	0.0	**2.7**	0.1	**2.8**	0.2	**2.7**	0.1
ITD	**30.8**	2.3	**36.0**	0.9	**36.9**	6.0	**28.7**	1.2	**26.0**	0.1	**28.9**	2.1	**39.7**	5.8	**31.5**	3.4	**33.1**	2.8	**32.5**	2.3	**28.9**	1.3	**32.2**	3.3

Nematode assemblages

Nematode community composition at genus level differed between FF and NF sites at both water depths and between the two water depths (Fig. 4; "Depth x Fish Farm", PERMANOVA, Pseudo-F=4.661, p=0.002, Table A17). There was, however, a dispersion effect on both factors (PERMDISP: p<0.001). The same difference in community composition was found when considering the trophic groups ("Depth x Fish Farm", PERMANOVA, Pseudo-F= 10.464, p<0.001, Table A18). At 120 m depth, the ratio between deposit feeders (group 1) and predators, omnivores and epistrate feeders (group 2) is ca. 50:50, while at 470 m depth the deposit feeders make up 60-75% of the community (Fig. 5a). The 1b/2a-ratio was higher at 470 m depth as well ("Depth", ANOVA, F-value=29.029, p=1.562e-05, Table A19).

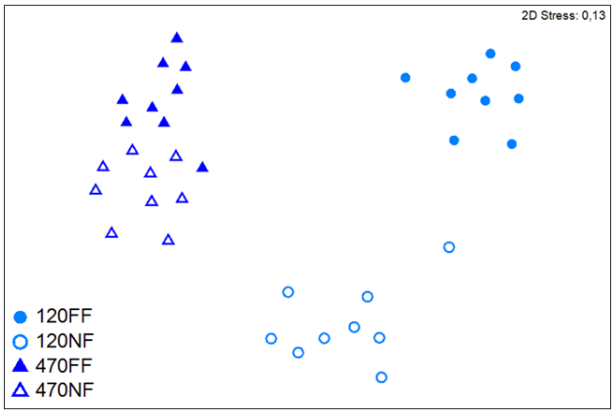

Fig. 4. MDS ordination of the nematode assemblages after square root transformation

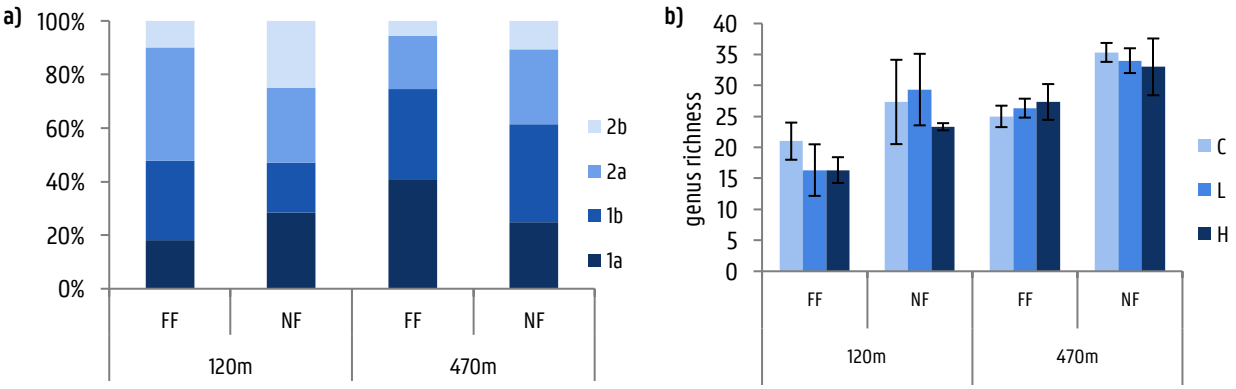

Fig. 5. a) Average relative abundance of the different trophic groups at the FF and NF sites at 120 m and 470 m depth. 1a – selective deposit feeders; 1b – non-selective deposit feeders; 2a – epistrate or epigrowth feeders; 2b – predators/omnivores (Wieser, 1953). **b)** Nematode genus richness (H_0) in the 0-1 cm layer.

The number of genera (H_0) was the highest at 470 m water depth (Fig 5b; Table 2b; "Depth", ANOVA, F-value=42.780, p=9.158e-07, Table A20) and at the NF sites ("Fish farm", ANOVA, F-value=45.2071, p=5.916e-07; Fig. 3b, Table 2b). The two other Hill's indices (H_1, H_2) and the EG(51) followed the same trend (Table 2b; "Depth" and "Fish farm", PERMANOVA, Tables A21-A23). The maturity index (MI; Table 2b) was higher at the NF site at 120 m depth than at the FF sites at both 120 and 470 m depth, while the MI was also higher at the FF site at 470 m depth than at 120 m depth ("Depth x Fish Farm", PERMANOVA, Pseudo-F=18.418, p<0.001, Table A24). There was a dispersion effect on the depth factor (PERMDISP: p<0.01).

The trophic diversity (ITD; Table 2b) was higher in C compared to L treatments, but only at 470 m depth ("Depth x Treatment", ANOVA, F-value=8.257, p=0.002; Table A25). There seemed to be a "Depth x Fish Farm x Treatment" interaction (p=0.046) as well, but the *a posteriori* pairwise tests did not reveal any significant interactions between factor levels.

A one-way SIMPER analysis on the combined factors "Depth" and "Fish Farm" showed that the similarity within FF and NF sites at both water depths ranged between 52.44-57.97% (Table 3a). *Molgolaimus* and *Sabatieria* were very well represented, with high contributions to all groups. *Cytolaimium*, *Paracyatholaimus* and *Cervonema* were typical high contributors at the 470 m locations, *Marylynnia, Cheironchus* and *Dorylaimopsis* were primarily found at the 120 m locations. The dissimilarities between study sites (Table 3b) were smallest between the NF and FF sites at 470 m depth (50.03%) and the largest between the FF sites at 120 m and 470 m depth (72.52%).

Table 3. List of the nematode genera that contributed most (≥3%) to **a)** the similarity within or **b)** the dissimilarity between study sites in terms of genus composition based on relative abundances at 0-1 cm sediment depth.

a)

120m				470m			
FF (similarity: 56.16%)		**NF (similarity: 52.44%)**		**FF (similarity: 57.97%)**		**NF (similarity: 53.33%)**	
Genus	**%**	**Genus**	**%**	**Genus**	**%**	**Genus**	**%**
Marylynnia	22.3	*Molgolaimus*	9.2	*Molgolaimus*	18.8	*Cervonema*	8.7
Sabatieria	14.9	*Rhabdodemania*	9.1	*Cytolaimium*	8.2	*Cytolaimium*	8.5
Molgolaimus	10.4	*Sphaerolaimus*	8.9	*Paracyatholaimus*	7.6	*Molgolaimus*	8.0
Cheironchus	9.3	*Actinonema*	8.2	*Setosabatieria*	7.1	*Paracyatholaimus*	6.7
Dorylaimopsis	8.7	*Sabatieria*	8.1	*Cervonema*	6.8	*Acantholaimus*	5.7
Odontophora	3.4	*Daptonema*	6.4	*Subsphaerolaimus*	6.1	*Daptonema*	4.7
Odontophoroides	3.2	*Dorylaimopsis*	6.2	*Sabatieria*	5.6	*Sabatieria*	4.4
Microlaimus	3.1	*Pomponema*	5.5	*Pandolaimus*	4.5	*Halalaimus*	3.9
Rest	**24.7**	*Southerniella*	4.8	*Acantholaimus*	3.8	*Leptolaimus*	3.8
		Spilophorella	4.4	*Daptonema*	3.5	*Elzalia*	3.0
		Leptolaimus	4.3	*Pselionema*	3.0	**Rest**	**42.6**
		Marylynnia	4.0	**Rest**	**25**		
		Viscosia	3.8				
		Rest	**17.1**				

b)

"Depth"				"FF"			
120FF and 470FF (dissim.: 72.52%)		**120NF and 470NF (dissim.: 63.58%)**		**120FF and 120NF (dissim.: 65.40%)**		**470FF and 470NF (dissim.: 50.03%)**	
Genus	**%**	**Genus**	**%**	**Genus**	**%**	**Genus**	**%**
Marylynnia	8.9	*Cytolaimium*	4.5	*Marylynnia*	6.2	*Molgolaimus*	5.8
Molgolaimus	4.6	*Paracyatholaimus*	3.8	*Actinonema*	4.5	**Rest**	**94.2**
Cytolaimium	4.5	*Rhabdodemania*	3.7	*Rhabdodemania*	4.2		
Dorylaimopsis	4.3	*Cervonema*	3.5	*Cheironchus*	4.1		
Paracyatholaimus	4.1	*Actinonema*	3.4	*Pomponema*	3.4		
Cervonema	3.5	**Rest**	**81.1**	*Molgolaimus*	3.1		
Cheironchus	3.4			*Southerniella*	3.0		
Subsphaerolaimus	3.4			**Rest**	**71.5**		
Setosabatieria	3.1						
Rest	**60.2**						

Table 4. Nematode biomass (µg C/10cm²).

120m	FF	115.6 ± 57.8
	NF	30.8 ± 23.2
470m	FF	18.4 ± 6.3
	NF	9.7 ± 6.1

Nematode biomass was higher at 120 m compared to 470 m depth ("Depth", ANOVA, F-value=40.321, p=3.957e-07; Table A26) and at FF sites compared to NF sites ("Fish farm', ANOVA, F-value=31.794, p=3.097e-06; Table 4).

Stable isotope analysis

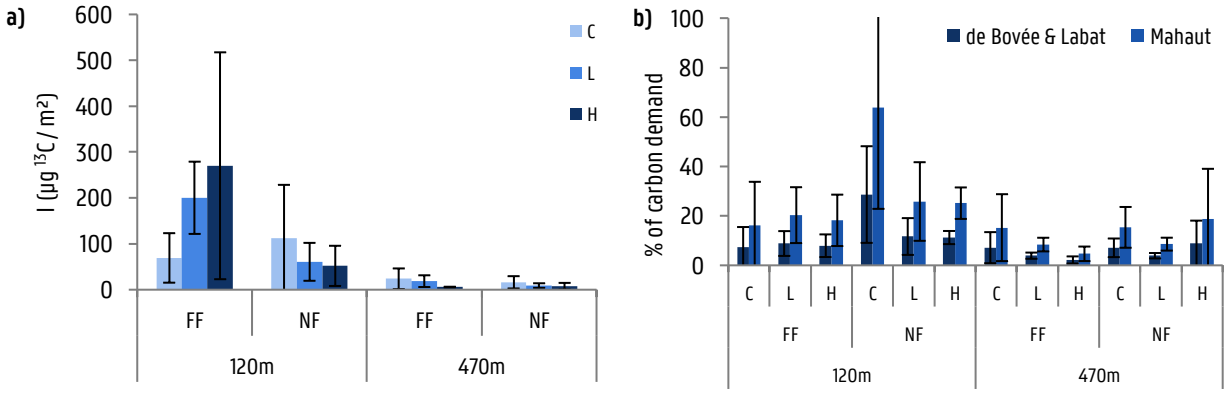

Fig. 6. a) Mean absolute uptake (µg $^{13}C/m^2$) of the labelled algae by the nematodes in the 0-1 cm sediment layer. **b)** % of carbon demand of the nematodes achieved by uptake of algal carbon.

Absolute uptake of ^{13}C was highest at FF sites ("Fish farm", ANOVA, F-value=65.658, p=2.973e-09, Table A27) and at 120 m water depth ("Depth", ANOVA, F-value=5.134, p=0.030; Fig. 6a). Interestingly, the factor depth explained 56.8% of the variation in absolute uptake and fish farm only 4%. In contrast, the % of carbon demand achieved by uptake of algal carbon is higher at the NF sites ("Fish farm", ANOVA, Table A28-A29, Fig. 6b) and at 120 m water depth ("Depth", ANOVA, p<0.001), no matter the respiration index used.

Sediment community oxygen consumption

SCOC was higher in both L and H treatments compared to the controls at 120 m water depth, in H treatments compared to L and C at 470 m depth and the L treatment yielded highest SCOC at 120 m depth ("Depth x Treatment", PERMANOVA, Pseudo-F=9.429, p=0.001; Fig. 7).

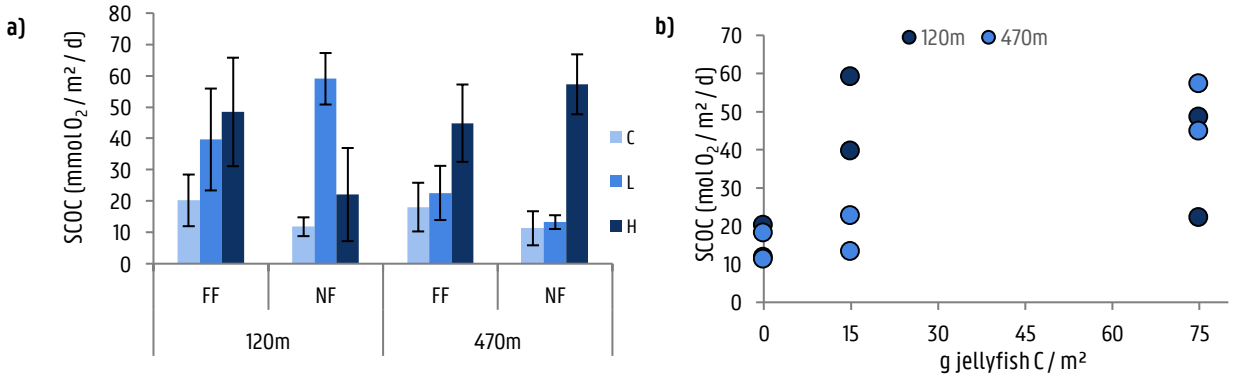

Fig. 7. a) SCOC (mmol O_2/m^2 day). NF locations have 2 replicates per treatment instead of 4. **b)** SCOC (mmol O_2/m^2 day) compared to the amount of jellyfish carbon added per m².

DISCUSSION

Two potentially major inputs of organic enrichment impacting deep fjord seafloors have been studied separately (Kutti et al., 2007; Riemann et al., 2006; Sweetman et al., 2014, 2016; Titelman et al., 2006), but never combined. This study shows the effects of a simulated jelly-fall in the presence and absence of fish farm depositions on the structure and functioning of meiobenthic communities at two water depths. It was found in general that the combination of fish farm presence, jelly-falls and water depth impacted the meiofauna and nematode community structure and functioning (food uptake), as well as the sediment community oxygen consumption.

Impact on meiofauna at higher taxon level

Total meiofauna densities were higher in sediments from FF sites. In previous studies that were carried out in the Mediterranean Sea, strong reductions in meiobenthic density in the vicinity of aquaculture farms have been reported (Grego et al., 2009; Mazzola, 2000; Mirto et al., 2002, 2012), except for the study by Mirto et al. (2010). However, the study of Sweetman et al. (2014) in a Norwegian fjord showed higher macrofaunal densities in sediments near the fish farms compared to the controls. Our findings support this trend for meiofauna as well. Highest densities were also found in sediment from 120 m depth compared to the 420 m area, which is in accordance with a general tendency of decreasing abundances of metazoan meiofauna with increasing depth (Gutzmann et al., 2004; Soetaert et al., 2009). Meiofauna assemblages consisted for nearly 95% of Nematoda, who were the main drivers behind these significant trends. Copepoda, the second largest contributor, did not follow this pattern and showed highest densities in NF sediment at 120 m depth. Jellyfish treatment (L and H) did not have an effect on the densities of Nematoda, which are known for their resilience, but it decreased the densities of Copepoda, Polychaeta, Bivalvia and Ostracoda. Kinorhyncha, who have been proposed as indicators of pristine environments (Grego et al., 2009; Mirto et al., 2012), proved to be sensitive to fish farm enrichment and had the lowest densities in FF sediment at 120 m depth. Cnidaria densities were not affected by any form of enrichment, nor water depth.

Meiofauna community composition was impacted by fish farm enrichment, water depth and jellyfish addition, as it differed between the L treatment and the controls. Comparison of the two sediment depth layers (0-2 cm and 2-5 cm) yielded an interesting result: only the assemblages of the upper layers (the one used for all other meiofauna results) differed between FF and NF sites. Hence, at higher meiobenthic taxon level, impact of fish farming seems to be limited to the upper 2 cm. The number of meiofauna taxa at 120 m depth was lower at the FF site than at the NF site and compared to the FF site at 470 m depth. This was due to the disappearance of taxa more sensitive to organic accumulation (Mirto et al., 2010, 2012). The two other Hill's indices and the ET(51) were generally lower at FF sites compared to NF sites and at the FF site at 120 m depth compared to 470 m depth. These lower values also point to a reduction in biodiversity in the vicinity of fish farms.

Impact on nematode assemblage composition

Nematode community composition was only affected by fish farm enrichment and water depth, not by the jellyfish treatments. The clear difference between nematode assemblages inhabiting FF and NF sites, as also corroborated by the MDS, reflects the different sensitivity of each genus to the organic enrichment. When considering the trophic groups as proposed by Wieser (1953), the clearest difference is seen between the two water depths. At 120 m depth, the ratio between deposit feeders (group 1) and predators, omnivores and epistrate feeders (group 2) is ca. 50:50, while at 470 m depth the deposit feeders make up 60-75% of the community. NF sites housed more predators and omnivores (2b), such as *Sphaerolaimus* which contributed nearly 9% to the similarity within NF sites at 120 m water depth. The 1b/2a ratio failed to detect differences in eutrophication and only showed a difference between water depths, which makes it an insensitive tool for this purpose. It was proposed by Lambshead (1986) and showed promising result in his study, unfortunately not in this case.

The number of genera confirmed the results of previous studies since it increased with water depth and decreased in the vicinity of fish farms (Mirto et al., 2002, 2014), as did the other two Hill's indices and the EG(51). Two additional indices that are useful tools in determining the environmental quality status of an ecosystem, are the Maturity Index and the Index of Trophic Diversity (Marques et al., 2010). The general principle of the Maturity Index is based on the different strategies of nematode assemblage in relation to different disturbances. Low values indicate a high stress level since opportunistic genera (i.e. colonisers) increase in abundance in adverse conditions. The NF sites at 120 m water depth scored higher than FF sites at both depths and the FF sites at 470 m depth scored higher than those at 120 m depth. This means that FF sites are more disturbed and disturbance decreases with water depth, which supports the rest of our findings. The MI of NF sediments at 120 m depth was very similar to that of FF and NF sediments at 470 m depth. The Index of Trophic Diversity is generally used to correlate the trophic diversity of nematodes with pollution levels (Heip et al., 1985; Mirto et al., 2002), ranging from 25% (highest trophic diversity) to 100% (lowest trophic diversity, i.e., one trophic guild completely dominates nematode density). All four guilds are well represented in each site, with a maximum ITD of nearly 40%. The ITD was only significantly higher in controls compared to L treatment at 470 m depth though, which is not consistent with the MI. Therefore, the ITD was not able to detect disturbance as was hoped, and this concern had already been expressed by e.g. Mirto et al. (2002), Moreno et al. (2011) and Soto et al. (2017).

SIMPER analysis revealed that the similarity within FF and NF sites at both water depths ranged between 52.44-57.97%. *Sabatieria* was a big contributor to all assemblages. It is a tolerant genus that has shown resilience to long periods of O_2 deficiency (Modig and Ólafsson, 1998) and is often shown to increase its dominance in organic enriched or even polluted sediments (Mirto et al., 2002; Moreno et al., 2008). Together with *Dorylaimopsis* and *Cheironchus* it was recently considered a good indicator of extreme environmental disturbance (Soto et al., 2017). *Molgolaimus* was another tolerant genus that made up a big part of all assemblages. *Cheironchus* contributed 9.3% to the similarity within FF sediment at 120 m depth and was absent from NF at the same depth, showing a clear preference for organically enriched sediments.

Setosabatieria, which had previously been described as a highly sensitive genus (Mirto et al., 2002), contributed 7.1% to FF sediments at 470 m depth, which is even more than *Sabatieria* in these sediments. *Cytolaimium*, *Paracyatholaimus* and *Cervonema* were three genera that were abundant in both FF and NF sites at 470 m depth. *Cytolaimium* and *Paracyatholaimus* were exclusively found at 470 m depth while a few *Cervonema* specimens were also found in NF sediment at 120 m depth. This suggests that the organic enrichment from the fish farm was not that disruptive to the nematode community composition at 470 m depth. The dissimilarities between study sites were smallest between the NF and FF sites at 470 m depth (50.03%) and the largest between the FF sites at 120 m and 470 m depth (72.52%), as also illustrated in the MDS ordination.

Nematode biomass was higher at 120 m compared to 470 m water depth and at FF sites compared to NF. At 120 m depth, the biomass was more than three times higher in FF sites. Mirto et al. (2002) already found that there was a difference in terms of body size related to eutrophication, with nematodes from beneath fish farm cages having significantly higher body weights than those in non-impacted sites. On the other hand, Duplisea and Hargrave (1996) did not find any difference in body mass beneath the cages. Meiofaunal biomass of organically enriched environments can become increasingly dominated by large specimens when compared to non-enriched environments (Moore and Bett, 1989). Nematode genera with relatively greater body size such as *Cheironchus*, *Dorylaimopsis* and *Marylynnia* were dominant at FF sites of 120 m depth, which corroborates this theory.

Impact on food uptake

Absolute uptake of labelled carbon was higher in the nematodes from FF sites. This was in correlation with the larger biomass of these nematodes assemblages. Differential uptake by nematode genera can also have played a role. For instance, *Sabatieria*, which is known for its high uptake and active migration towards food (Franco et al., 2008a, 2008b; Guilini et al. 2011), was much more abundant in FF sediment at 120 m depth. In contrast, nematode communities from NF sediments managed to fulfil a larger percentage of their carbon demand. This is also a consequence of their much lower total biomass compared to FF communities. Uptake of labelled carbon was highest in sediments from 120 m water depth. In situ, SCOC decreases with greater water depth as a result of organic matter decay while it sinks through the water column (Andersson et al., 2004; Soetaert et al., 2009). Greater water depth also allows greater organic matter dispersion with less localised disturbance effects. Possibly, the benthic communities from 470 m depth were adapted to this lower input to the extent that a short-term input of food (algae and jelly) could not be processed as quickly. It should also be kept in mind that because the algae were only added to the sediment surface, only short-term, near-surface C-cycling processes could be quantified.

The carbon uptake of the nematodes was not affected by treatment. A substantial portion of the uptake is assumed to have been by bacteria, as was the case in Sweetman et al. (2016). Bacterial uptake of photodetrital carbon was significantly higher in the presence of jellyfish, while macrofaunal uptake was higher without the jellyfish addition. This was expected because of the similar C:N ratios of bacteria and jellyfish, which leads to a more efficient bacterial

degradation of the gelatinous detritus. However, as nematodes are not as sensitive to low oxygen concentrations as macrofauna, their uptake is not expected to be as much lower than that of bacteria in this case (Duplisea and Hargrave, 1996).

Impact on sediment community oxygen consumption

SCOC was only impacted by water depth and jellyfish treatment. There was no significant difference between SCOC at NF and FF sites. This does not corroborate our hypothesis 1b, since only enrichment by jellyfish carcasses seems to have had an impact. This also contrasts the findings of Sweetman et al. (2014), where SOC rates were significantly higher at sediments from FF sites under both hydrodynamic regimes. The L treatment yielded a significantly higher SCOC at 120 m water depth than at 470 m. SCOC is correlated to total biomass (macrofaunal and bacteria, Sweetman et al., 2014). Since nematode biomass was higher at 120 m sites, which could explain the higher SCOC of the L treatment.

There were a few limitations associated with this study. Firstly, our method of measuring SCOC was inferior to the one used by Sweetman et al. (2014, 2016), who let the cores reoxygenate in between incubations. As we measured the SCOC continuously overnight, hypoxia could not be prevented. This was overcome by setting a threshold of 175 µmol O2/L (equalling 59% oxygen saturation) and only using intervals above this threshold. Although short-term hypoxia has little to no effect on the density, diversity, community composition and vertical density profiles of nematodes (Taheri et al., 2014), this should be kept in mind when comparing the results of this study with others. Also, the addition of the algae in itself likely boosted respiration rates, but since they were added to all cores, differences between the sites and treatments could still be assessed (Sweetman et al., 2014).

It makes sense to compare our results to those of Sweetman et al. (2016), who measured the SCOC of fjord sediment cores taken at a water depth of 100 m, after which 3.6 gC/m² labelled algae and 27.4 gC/m² of thawed *P. periphylla* was added. The control treatments yielded an SCOC of on average 20 mmol O_2/m²d (derived from graph, Sweetman et al., 2016), which corresponds well with our results (15.7±7.3mmol O_2/m²d). After addition of the jellyfish, SCOC followed a parabolic curve through time (Sweetman et al., 2016): it increased significantly during the first 24 h, after which it reached a plateau and started decreasing again after approximately 60 h. Our intervals were all taken between 10 and 20 h following addition of the jellyfish carcasses, which corresponds with an increase from 29±2.6 to about 58 mmol O_2/m²d (derived from graph, Sweetman et al., 2016. The L and H treatment added 15 gC/m² and 75 gC/m², respectively, and the yielded SCOC values did not exceed this range much. This could imply that the findings of Sweetman et al. (2016) can be generalized to larger jelly-fall loadings and a water depth ranging at least from 100 to 470 m. Overall, addition of the jellyfish carcasses had a significant and rapid effect on benthic ecosystem processes. For instance, SCOC in the cores subjected to the H treatment was nearly double that of the controls. This is consistent with the study of West et al. (2009), where addition of the jellyfish led to an average 209% increase in SCOC compared to the controls.

CONCLUSION

This study confirmed that the impact of a fish farm moored in a deep-sea fjord is larger in circumference than in the shallow waters of the Mediterranean Sea, as the effects are discernible at least 100 m away from the cages. However, the similar maturity index and community composition of control sites at 120 m depth compared to both fish farm and non-fish farm sites at 470 m depth could indicate that the organic enrichment from the fish farm was not that disruptive to the nematode community composition at the greatest depth. Further research involving different water depths is needed to determine the generality of these findings. It will be interesting to compare the food uptake of bacteria and macrofauna with that of the nematodes, as additional bacterial and macrofaunal samples were taken from the cores in function of the JellyFarm Project. In this experiment, the addition of jellyfish carcasses only affected the densities of a few meiofauna taxa and the sediment community oxygen consumption. This would imply that the combined effect of jelly-falls and aquaculture did not disrupt the seafloor of Norwegian fjords in a greater way than the separate stressors did.

ACKNOWLEDGEMENTS

Special thanks to the whole JellyFarm WP2-team at IRIS, who taught me a lot about the set-up and execution of an experiment, Dr. Katja Guilini who helped whenever she could with centrifugation of samples, counting of meiofauna and spending many hours of checking and correcting my nematode identifications. Also, the quality of this manuscript would be way lower without her advice and corrections. The last-minute guidance from Prof. Dr. Ann Vanreusel was also greatly appreciated. Last but not least, I want to thank Annick Van Kenhove and Guy De Smet for their tremendous work assisting with handpicking of nematodes and counting meiofauna. I would have had a lot less data to incorporate in this paper if it were not for them.

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APPENDIX

The factors based on which we find significant differences are indicated in red in the tables. The results of ANOVA and PERMDISP analysis and pairwise tests are provided with an asterisk code to indicate the significance level: '***' : p < 0.001 '**': p < 0.01 '*' : p < 0.05.

Table A1: Total meiofauna densities (0-2 cm)

PERMANOVA table of results (Log(X+1)transformed) → PERMDISP: Depth*

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	12.287	12.287	84.007	<0.001	9819	41.40%	
FF	1	9.039	9.039	61.796	<0.001	9829	30.50%	
Treatment	2	0.943	0.472	3.224	0.051	9957		
DepthxFF	1	0.728	0.728	4.979	0.032	9822	2.50%	120FF>470FF***; 120NF>470NF**; FF>NF***
DepthxTreatment	2	0.417	0.208	1.425	0.247	9948		
FFxTreatment	2	0.772	0.386	2.639	0.081	9950		
DepthxFFxTreatment	2	0.206	0.103	0.705	0.491	9942		
Res	36	5.266	0.146					
Total	47	29.657						

Table A2: Nematoda densities (0-2 cm)

PERMANOVA table of results (Log(X+1)transformed) → PERMDISP: Depth**

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	12.728	12.728	88.053	<0.001	9819	41%	
FF	1	10.029	10.029	69.382	<0.001	9827	32.30%	
Treatment	2	0.838	0.419	2.8985	0.069	9948		
DepthxFF	1	0.866	0.866	5.991	0.019	9833	2.80%	120FF>470FF***; 120NF>470NF**; FF>NF***
DepthxTreatment	2	0.427	0.214	1.4775	0.237	9941		
FFxTreatment	2	0.709	0.355	2.4535	0.096	9951		
DepthxFFxTreatment	2	0.209	0.105	0.72347	0.485	9946		
Res	36	5.204	0.145					
Total	47	31.011						

Table A3: Copepoda densities (0-2 cm)

PERMANOVA table of results (Log(X+1)transformed) → PERMDISP: Depth**; FF**

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	2.044	2.044	8.395	0.006	9831	10%	
FF	1	1.622	1.622	6.664	0.014	9833	7.90%	
Treatment	2	1.8	0.9	3.696	0.032	9962	4.40%	C>L*, C>H**
DepthxFF	1	3.953	3.953	16.239	<0.001	9853	19.30%	120NF>470NF***; 120NF>120FF**
DepthxTreatment	2	0.195	0.097	0.4	0.677	9950		
FFxTreatment	2	1.432	0.716	2.942	0.065	9958		
DepthxFFxTreatment	2	0.645	0.322	1.324	0.28	9949		
Res	36	8.763	0.243					
Total	47	20.453						

Table A4: Polychaeta densities (0-2 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	3.995	3.995	3.206	0.081	9852		
FF	1	6.914	6.915	5.549	0.025	9850	8.90%	FF>NF
Treatment	2	11.725	5.863	4.705	0.016	9958	15.10%	C>L*, C>H**
DepthxFF	1	0.913	0.913	0.732	0.402	9860		
DepthxTreatment	2	3.397	1.699	1.363	0.273	9954		
FFxTreatment	2	2.01	1.005	0.806	0.449	9958		
DepthxFFxTreatment	2	3.936	1.968	1.579	0.226	9953		
Res	36	44.862	1.246					
Total	47	77.752						

Table A5: Nauplii densities (0-2 cm)

PERMANOVA table of results (4^{th} root transformed) → PERMDISP: Depth***

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	0.01	0.01	0.137	0.708	9829		
FF	1	1.588	1.588	22.486	<0.001	9825	19.10%	
Treatment	2	0.101	0.05	0.712	0.491	9943		
DepthxFF	1	3.207	3.207	45.418	<0.001	9818	38.70%	470FF>120FF***; 120NF>470NF**; 120NF>120FF***
DepthxTreatment	2	0.031	0.016	0.221	0.804	9953		
FFxTreatment	2	0.561	0.280	3.970	0.029	9953	6.80%	NF(C)>FF(C)***; FF(H>C)*
DepthxFFxTreatment	2	0.259	0.13	1.834	0.176	9953		
Res	36	2.542	0.071					
Total	47	8.299						

Table A6: Gastrotricha densities (0-2 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	1.159	1.159	6.451	0.009	9787	13%	120>470
FF	1	0.273	0.273	1.521	0.240	9819		
Treatment	2	0.02	0.01	0.056	0.953	9949		
DepthxFF	1	0.419	0.419	2.332	0.144	9818		
DepthxTreatment	2	0.107	0.054	0.299	0.766	9957		
FFxTreatment	2	0.248	0.124	0.69	0.542	9954		
DepthxFFxTreatment	2	0.207	0.103	0.576	0.596	9949		
Res	36	6.467	0.18					
Total	47	8.9						

Table A7: Bivalvia densities (0-2 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	0.35	0.35	12.755	<0.001	9792	16.50%	120>470
FF	1	0.007	0.007	0.268	0.614	9804		

Treatment	2	0.508	0.254	9.254	<0.001	9965	24%	C>L*, C>H**
DepthxFF	1	0.037	0.037	1.343	0.263	9807		
DepthxTreatment	2	0.104	0.052	1.9	0.159	9949		
FFxTreatment	2	0.016	0.008	0.283	0.776	9956		
DepthxFFxTreatment	2	0.111	0.055	2.018	0.141	9954		
Res	36	0.988	0.027					
Total	47	2.12						

Table A8: Cnidaria densities (0-2 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy
Depth	1	0.003	0.003	0.105	0.768	9823	
FF	1	0.058	0.058	1.781	0.2	9813	
Treatment	2	0.033	0.017	0.508	0.633	9964	
DepthxFF	1	0.041	0.041	1.25	0.285	9796	
DepthxTreatment	2	0.198	0.1	3.047	0.05	9968	
FFxTreatment	2	0.041	0.02	0.627	0.562	9946	
DepthxFFxTreatment	2	0.059	0.03	0.911	0.425	9967	
Res	36	1.171	0.033				
Total	47	1.604					

Table A9: Ostracoda densities (0-2 cm)

PERMANOVA table of results (4^{th} root transformed)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	0.112	0.112	1.681	0.199	9842		
FF	1	1.125	1.125	16.86	<0.001	9829	23%	NF>FF
Treatment	2	0.393	0.196	2.944	0.067	9961		
DepthxFF	1	0.22	0.22	3.297	0.08	9818		
DepthxTreatment	2	0.553	0.276	4.142	0.023	9951	11.30%	120(C>L)*; 470(C>H*and L>H)*; 120H>470H*
FFxTreatment	2	0.069	0.035	0.52	0.589	9963		
DepthxFFxTreatment	2	0.025	0.012	0.186	0.833	9950		
Res	36	2.402	0.067					
Total	47	4.898						

Table A10: Kinorhyncha densities (0-2 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	0.043	0.043	4.806	0.032	9677	8.50%	
FF	1	<0.001	<0.001	0.001	0.978	9671		
Treatment	2	0.017	0.008	0.933	0.404	9955		
DepthxFF	1	0.069	0.069	7.786	0.008	9682	13.80%	470FF>120FF**; 120NF>120FF*
DepthxTreatment	2	0.024	0.012	1.348	0.274	9949		
FFxTreatment	2	0.027	0.013	1.512	0.234	9951		
DepthxFFxTreatment	2	0.002	0.001	0.127	0.872	9946		

Res	36	0.319	0.009
Total	47	0.5	

Table A11: Meiofauna community composition (higher taxon level, 0-2 cm)

PERMANOVA table of results (Log(X+1) transformed) → PERMDISP: Depth**

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	1296.3	1296.3	21.071	<0.001	9938	19.3%	
FF	1	1677.7	1677.7	27.27	<0.001	9940	25%	
Treatment	2	298.48	149.24	2.426	0.024	9945	4.5%	C,L*
DepthxFF	1	826.47	826.47	13.434	<0.001	9952	12.3%	120FF,470FF**; 120NF,470NF***; 120FF,120NF***; 470FF,470NF**
DepthxTreatment	2	166.73	83.364	1.355	0.225	9939		
FFxTreatment	2	147.45	73.727	1.198	0.311	9940		
DepthxFFxTreatment	2	75.67	37.835	0.615	0.767	9932		
Res	36	2214.7	61.521					
Total	47	6703.5						

Table A12: Meiofauna community composition (higher taxon level, 0-2 cm and 2-5 cm)

PERMANOVA table of results (sqrt transformed) → PERMDISP: FF***, Layer***

Source	df	SS	MS	Pseudo-F	P(perm)	Unique Perms	P(MC)	Redundancy	Pair-Wise tests
Depth	1	574.64	574.64	12.516	0.003	9918	<0.001	6.3%	
FF	1	502.01	502.01	8.119	0.028	35	0.002	5.5%	
Layer	1	3652	3652	114.34	<0.001	9821	<0.001	39.8%	
Replicate(FF)	6	371.02	61.836	1.962	0.012	9904	0.015		
DepthxFF	1	399.39	399.39	8.699	0.008	9808	0.002	4.4%	120FF, 120NF*; 120FF, 470FF*; 120NF, 470NF*
DepthxLayer	1	218.99	218.99	5.092	0.017	9949	0.01	2.40%	0-2cm120, 0-2cm470***; 2-5cm120, 2-5cm470**
FFxLayer	1	564.99	564.99	17.69	0.002	9886	<0.001	6.20%	0-2cmFF, 0-2cmNF*
DepthxRepl(FF)	6	275.48	45.914	1.457	0.11	911	0.116		
Repl(FF)xLayer	6	191.63	31.939	1.014	0.441	9923	0.449		
DepthxFFxLayer	1	142.83	142.83	3.321	0.043	9946	0.041		0-2cm120(NF,FF)*; 120FF, 470FF*
DepthxRepl(FF)xLayer	6	258.07	43.011	1.365	0.152	9909	0.153		
Res	64	2016.6	31.51						
Total	95	9167.7							

Table A13: Meiofauna taxon richness (H_0, 0-2 cm)

PERMANOVA table of results (sqrt transformed) → PERMDISP: Depth*

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	0.177	0.177	1.652	0.205	9844		
FF	1	0.708	0.708	6.618	0.014	9824	9.20%	
Treatment	2	0.363	0.181	1.694	0.195	9952		
DepthxFF	1	1.612	1.612	15.06	<0.001	9812	20.80%	120NF>120FF***; 470FF>120FF***
DepthxTreatment	2	0.625	0.312	2.918	0.061	9945		
FFxTreatment	2	0.19	0.095	0.887	0.419	9948		
DepthxFFxTreatment	2	0.217	0.108	1.012	0.373	9938		
Res	36	3.853	0.107					
Total	47	7.743						

Table A14: Meiofauna taxon diversity (H_1, 0-2 cm)

PERMANOVA table of results (no transformation) → PERMDISP: Depth***

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	4.180	4.180	10.542	0.004	9817	8.70%	
FF	1	18.26	18.26	46.048	<0.001	9829	38.20%	
Treatment	2	1.379	0.69	1.739	0.188	9957		
DepthxFF	1	8.399	8.399	21.182	<0.001	9836	17.60%	470FF>120FF***; 120NF>120FF***; 470NF>470FF*
DepthxTreatment	2	0.653	0.327	0.824	0.448	9954		
FFxTreatment	2	0.362	0.181	0.457	0.632	9952		
DepthxFFxTreatment	2	0.356	0.178	0.449	0.645	9961		
Res	36	14.275	0.397					
Total	47	47.865						

Table A15: Meiofauna taxon diversity (H_2, 0-2 cm)

PERMANOVA table of results (no transformation) → PERMDISP: Depth***

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	2.172	2.172	12.743	0.002	9837	10.10%	
FF	1	8.588	8.588	50.379	<0.001	9834	39.80%	
Treatment	2	0.841	0.421	2.467	0.101	9950		
DepthxFF	1	3.095	3.095	18.158	<0.001	9843	14.40%	470FF>120FF***; 120NF>120FF***; 470NF>470FF**
DepthxTreatment	2	0.303	0.152	0.889	0.417	9948		
FFxTreatment	2	0.222	0.111	0.65	0.523	9942		
DepthxFFxTreatment	2	0.21	0.105	0.615	0.540	9963		
Res	36	6.137	0.171					
Total	47	21.567						

Table A16: Meiofauna taxon diversity (ET(51), 0-2 cm)

PERMANOVA table of results (no transformation) → PERMDISP: Depth***

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	3.830	3.830	21.133	<0.001	9820	14.60%	
FF	1	10.381	10.381	57.274	<0.001	9849	39.60%	
Treatment	2	0.976	0.488	2.693	0.077	9946		
DepthxFF	1	3.834	3.834	21.153	<0.001	9841	14.60%	470FF>120FF***; 120NF>120FF***; 470NF>470FF**
DepthxTreatment	2	0.29	0.145	0.799	0.457	9957		
FFxTreatment	2	0.2	0.029	0.546	0.573	9944		
DepthxFFxTreatment	2	0.183	0.091	0.504	0.608	9960		
Res	36	6.525	0.181					
Total	47	26.217						

Table A17: Nematode community composition (genus level, 0-1 cm)

PERMANOVA table of results (sqrt transformed) → PERMDISP: Depth***, FF*

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	20841	20841	19.605	<0.001	9921	30.50%	
FF	1	9470.6	9470.6	8.909	<0.001	9926	13.90%	
Treatment	2	2466.3	1233.1	1.16	0.251	9894		
DepthxFF	1	4954.8	4954.8	4.661	<0.001	9926	7.30%	120FF, 120NF***; 470FF, 470NF***; 120FF, 470FF***; 120NF, 470NF***
DepthxTreatment	2	1871	935.5	0.88003	0.662	9880		
FFxTreatment	2	2256.8	1128.4	1.0615	0.387	9894		
DepthxFFxTreatment	2	889.45	444.72	0.41835	0.998	9877		
Res	24	25513	1063					
Total	35	68263						

Table A18: Nematode community composition (feeding groups, 0-1 cm)

PERMANOVA table of results (sqrt transformed) → PERMDISP non-sign.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	2779.7	2779.7	13.97	<0.001	9946	21.80%	
FF	1	1392.1	1392.1	6.997	<0.001	9964	11.40%	
Treatment	2	643.34	321.67	1.617	0.18	9957		
DepthxFF	1	2153.7	2153.7	10.824	<0.002	9959	15.90%	120FF, 120NF***; 470FF, 470NF***; 120FF, 470FF***; 120NF, 470NF**
DepthxTreatment	2	131.85	65.926	0.331	0.867	9959		
FFxTreatment	2	1002.2	501.1	2.518	0.05	9947		
DepthxFFxTreatment	2	270.11	135.06	0.679	0.639	9948		
Res	24	4775.4	198.98					
Total	35	13148						

Table A19: Nematode 1b/2a-ratio (feeding groups, 0-1cm)

Anova Table (Type II tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	6.023	1	29.029	1.562e-05 ***	49.4%	470>120
FF	0.248	1	1.197	0.285		
Treatment	0.062	2	0.151	0.861		
Depth:FF	0.136	1	0.655	0.426		
Depth:Treatment	0.102	2	0.245	0.785		
FF:Treatment	0.443	2	1.067	0.36		
Depth:FF:Treatment	0.206	2	0.496	0.615		
Residuals	4.979	24				
Total	12.199					

Table A20: Nematode genus richness (H_0, 0-1 cm)

Anova Table (Type II tests)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	568.03	1	42.781	9.158e-07 ***	35.3%	470>120
FF	600.25	1	45.207	5.916e-07 ***	37.3%	NF>FF
Treatment	28.39	2	1.069	0.359		
Depth:FF	1.36	1	0.103	0.752		
Depth:Treatment	35.39	2	1.333	0.283		
FF:Treatment	18.50	2	0.697	0.508		
Depth:FF:Treatment	38.39	2	1.446	0.255		
Residuals	318.67	24				
Total	1608.98					

Table A21: Nematoda diversity (H_1, 0-1 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	515.27	515.27	39.787	0.0001	9822	32.50%	470>120
FF	1	647.18	647.18	49.971	0.0001	9826	40.80%	NF>FF
Treatment	2	25.62	12.81	0.98913	0.3806	9942		
DepthxFF	1	0.72761	0.72761	5.62E-02	0.8156	9840		
DepthxTreatment	2	35.536	17.768	1.3719	0.2723	9958		
FFxTreatment	2	15.665	7.8325	0.60478	0.5453	9948		
DepthxFFxTreatment	2	35.931	17.966	1.3872	0.2716	9957		
Res	24	310.82	12.951					
Total	35	1586.8						

Table A22: Nematoda diversity (H_2, 0-1 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	416.55	416.55	33.858	<0.001	9849	27.20%	470>120
FF	1	713.04	713.04	57.958	<0.001	9848	46.60%	NF>FF
Treatment	2	19.529	9.7645	0.794	0.463	9949		
DepthxFF	1	0.058	0.058	0.005	0.946	9853		

DepthxTreatment	2	36.711	18.356	1.492	0.244	9952
FFxTreatment	2	12.187	6.094	0.495	0.615	9951
DepthxFFxTreatment	2	36.044	18.022	1.465	0.245	9948
Res	24	295.27	12.303			
Total	35	1529.4				

Table A23: Nematoda diversity (EG(51), 0-1 cm)

PERMANOVA table of results (no transformation)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	
Depth	1	223.44	223.44	30.821	<0.001	9832	29.30%	470>120
FF	1	308.45	308.45	42.548	<0.001	9846	40.40%	NF>FF
Treatment	2	15.703	7.851	1.083	0.346	9954		
DepthxFF	1	4.458	4.458	0.615	0.436	9819		
DepthxTreatment	2	18.065	9.033	1.246	0.304	9953		
FFxTreatment	2	6.931	3.465	0.478	0.619	9947		
DepthxFFxTreatment	2	11.959	5.98	0.825	0.452	9957		
Res	24	173.99	7.25					
Total	35	763						

Table A24: Nematoda Maturity Index (MI, 0-1 cm)

PERMANOVA table of results (no transformation) → PERMDISP: Depth**

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	<0.001	0.036	0.022	0.878	9833		
FF	1	0.233	0.233	14.605	<0.001	9841	22.80%	
Treatment	2	0.004	0.002	0.113	0.893	9946		
DepthxFF	1	0.294	0.294	18.418	<0.001	9824	28.70%	470FF>120FF**; 120NF>470NF*; 120NF>470FF***
DepthxTreatment	2	0.04	0.02	1.266	0.300	9946		
FFxTreatment	2	0.025	0.012	0.774	0.471	9950		
DepthxFFxTreatment	2	0.045	0.022	1.397	0.276	9953		
Res	24	0.383	0.016					
Total	35	1.024						

Table A25: Nematoda Trophic Diversity Index (ITD, 0-1 cm)

Anova Table (Type III tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)		Redundancy	Pair-wise tests(PERMANOVA)
(Intercept)	35.172	1	4199.647	2.2e-16	***	15.3%	
Depth	0.094	1	11.24	0.003	**		
FF	0.007	1	0.798	0.381			
Treatment	0.056	2	3.356	0.052			
Depth:FF	0.012	1	1.467	0.238			
Depth:Treatment	0.138	2	8.257	0.002	**	22.5%	470(C)>120(C)**; 470(C>L)*
FF:Treatment	0.052	2	3.131	0.062			
Depth:FF:Treatment	0.059	2	3.503	0.046	*	9.6%	/
Residuals	0.201	24					
Total	0.619						

Table A26: Nematode biomass (0-1 cm)

Anova Table (Type II tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	20.652	1	40.321	3.957e-07 ***	34.2%	120>470
FF	16.285	1	31.794	3.097e-06 ***	27%	FF>NF
Treatment	1.8375	2	1.794	0.183		
Depth:FF	1.3651	1	2.665	0.112		
Depth:Treatment	2.1042	2	2.054	0.145		
FF:Treatment	1.5102	2	1.474	0.244		
Depth:FF:Treatment	0.2902	2	0.283	0.755		
Residuals	16.391	32				
Total	60.435					

Table A27: Nematode absolute uptake ^{13}C (0-1 cm)

Anova Table (Type II tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	54.180	1	65.658	2.973e-09 ***	56.8%	120>470
FF	4.237	1	5.134	0.031 *	4.4%	FF>NF
Treatment	1.868	2	1.132	0.335		
Depth:FF	0.870	1	1.054	0.312		
Depth:Treatment	3.936	2	2.385	0.108		
FF:Treatment	2.463	2	1.492	0.240		
Depth:FF:Treatment	1.443	2	0.874	0.427		
Residuals	26.406	32				
Total	95.403					

Table A28: % of carbon demand achieved by algal carbon uptake (0-1 cm, Mahaut respiration index)

Anova Table (Type II tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	9.677	1	16.014	<0.001 ***	26.6%	120>470
FF	2.782	1	4.604	0.04 *	7.6%	NF>FF
Treatment	0.783	2	0.648	0.53		
Depth:FF	0.012	1	0.019	0.891		
Depth:Treatment	0.496	2	0.410	0.667		
FF:Treatment	0.986	2	0.816	0.451		
Depth:FF:Treatment	2.363	2	1.955	0.158		
Residuals	19.338	32				
Total	36.437					

Table A29: % of carbon demand achieved by algal carbon uptake (0-1 cm, de Bovée and Labat respiration index)

Anova Table (Type II tests, log transformed)

	Sum Sq	Df	F value	Pr(>F)	Redundancy	
Depth	8.683	1	14.506	<0.001 ***	26%	120>470
FF	2.902	1	4.848	0.035 *	8.7%	NF>FF
Treatment	0.851	2	0.711	0.499		
Depth:FF	0.014	1	0.024	0.878		
Depth:Treatment	0.402	2	0.336	0.717		
FF:Treatment	0.936	2	0.716	0.466		
Depth:FF:Treatment	2.428	2	2.028	0.148		
Residuals	19.156	32				
Total	33.372					

Table A30: Sediment community oxygen consumption (SCOC, based on 4h of measuring O_2 concentrations in the water column)

PERMANOVA table of results (Log(X+1)transformed) → PERMDISP: FF*

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	Redundancy	Pair-Wise tests
Depth	1	0.307	0.307	1.956	0.180	9837		
FF	1	0.457	0.457	2.915	0.097	9829		
Treatment	2	5.189	2.595	16.539	<0.001	9954	38.1%	
DepthxFF	1	0.011	0.011	0.068	0.791	9826		
								120(C<L)**; 120(C<H)*; 470(C<H)**; 470(L<H)***;
DepthxTreatment	2	2.959	1.479	9.429	0.001	9938	21.7%	120(L)>470(L)**
FFxTreatment	2	0.250	0.125	0.797	0.464	9956		
DepthxFFxTreatment	2	1.315	0.657	4.190	0.028	9946	9.70%	470FF(C<H)*
Res	24	3.765	0.157					
Total	35	13.615						