

“The effect of hydrodynamics on benthic macrofaunal composition and functioning under salmon fish farms”



Master of Science thesis in Marine Biology – Marine Biodiversity



Submitted by Carina Gunderstad – August 2015



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NOTE: C. GUNDERSTAD HAS PUBLISHED PART OF HER THESIS WORK IN THE FOLLOWING RESEARCH ARTICLE:

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Abstract

The fish farming industry has continued to increase over the last years, and salmon fish farms in Norway continue to grow in numbers. With this growing aquaculture, there is also a larger need to quantify the environmental effects that follow a net-pen fish farm, and to investigate which areas are best suited for fish farming. Also, the role of hydrodynamics could potentially alter the effects that the effluents have on the benthic ecosystem.

This study conducted a comparison of the benthic (1) abundance, (2) biomass, (3) biodiversity and (4) carbon uptake, at two different fish farms located in high and low water-flow environments, as well as control samples further away from each of the fish farms, to get information on how the ecosystem functions under the different hydrodynamic regimes. The carbon uptake by macrofauna was measured using stable isotope pulse chase experiments with ^{13}C .

Abundance, biomass and carbon uptake did not differ significantly between the two fish farms, while biodiversity was significantly higher under the high flow fish farm than under the low flow fish farm. Both fish farm sites are regarded as organically enriched, although the low flow fish farm site were more heavily enriched, with a more typical r-selected community structure and the large presence of the opportunistic polychaetes *Capitella capitata*, *Vigtorniella ardabilia*, and *Palpiphitime lobifera*, the latter two being bacterivores.

With the benthic community under both fish farms being equally effective in carbon uptake, although by different agents, either hydrodynamic regime can situate a well-functioning ecosystem.

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Introduction

As net-pen aquacultural fish farms continue to grow in numbers along the Norwegian coast (FAO, 2008), the many environmental effects need to be carefully monitored. One of the threats to the benthic environment is the accumulation of fish faeces and uneaten fish food that sinks to the bottom (Gowen and Bradbury, 1987, Weston, 1990, Lee et al., 2006). This changes the ecosystem functioning by *i*) reducing biodiversity (Gowen and Bradbury, 1987, Weston, 1990, Lee et al., 2006), *ii*) reducing bioturbation and increasing nutrient efflux from the sediment (Gowen and Bradbury, 1987, Heilskov et al., 2006), and *iii*) increasing the anaerobic metabolism of microbes (Holmer and Kristensen, 1992, Hargrave et al., 1993, Lee et al., 2006).

There is no general consensus on how nutrients from fish farms are spread with the water flow or how it affects the pelagic ecosystem (Olsen et al., 2008). When it comes to knowledge about the benthic environment under fish farms, some theoretical models suggest that there is less impact on the bottom in high flow waters than in stiller waters (Findlay and Watling, 1997, Kalantzi and Karakassis, 2006), while other investigations have proved that water flow do not have much effect on the degree of disturbance (Lee et al., 2006, Hall-Spencer et al., 2006). This study aims to add to the limiting understanding about sedimentary processes and recycling pathways when it comes to the benthos surrounding fish farms in high water flow- and low water flow environments (Sweetman et al., 2014), and consequently to help guide future management of where fish farms should be located.

My master's project was part of a large, joint project between NIVA, IMR, Unifob and UiB. The project was titled ECORAIS – ECOsystem Responses to Aquaculture Induced Stress. ECORAIS had the overall goal to “qualitatively and quantitatively describe fjord ecosystem responses to aquaculture induced stress with special regards to water-flow regimes”. The project therefore was providing knowledge that can assist management of fish farms in the future, and is in partial fulfilment of the Norwegian Research Council's agenda to achieve

“[...] *knowledge of possible environmental and ecological effects of discharge from aquaculture activities*” (“HAVBRUK – 3.1.3 Bærekraft-Miljømessige og økologiske effekter-Framskaffe kunnskap om mulige miljømessige og økologiske effekter ved utslipp fra oppdrettsaktivitet”).

ECORAIS’s main objective was to “qualitatively and quantitatively describe spatial and temporal scales of pelagic and benthic ecosystem functions under aquaculture stress, and the importance of high and low water flow regimes for transportation, storage and mineralization of nutrients”. It was divided into three part objectives:

- 1) To measure net-pen fish farm release of a) dissolved nutrient uptake by measuring growth rates in microalgae, and b) particulate material transportation using mussels (biofilters) and conventional sediment traps at logarithmic distances from net-pens in high and low water flow regimes.
- 2) To measure growth rates and nutrient storage (e.g. nitrogen) of macro algae at logarithmic distances from net-pens situated in high and low water flow regimes.
- 3) To explore macrofaunal communities, ecosystem functions (e.g. mineralization) in the benthic environment beneath net-pens and at logarithmic distances from fish pens in high and low water flow regimes.

My master thesis was part of the 3rd objective, and is called “*The effect of hydrodynamics on benthic macrofaunal composition and functioning under salmon fish farms*”, and some of the data have already been published in Limnology and Oceanography under the title “*Benthic ecosystem functioning beneath fish farms in different hydrodynamic environments*” (Sweetman et al., 2014).

To understand what happens in biogeochemical cycling and energy flow throughout an ecosystem, a powerful technique has been designed, called stable isotope pulse chase experiments. This is a process where a substrate is labelled with an isotopic tracer, and the substrate is then added to the samples that you want to test how the tracer flows through. In our experiment we used a culture of C-13 enriched diatoms which we distributed evenly over our sampled material. Our samples were then incubated to allow uptake of the tracer. Throughout the experiment we were able to measure the uptake of C-13 into respired dissolved inorganic carbon (DIC), and at the end of the experiment we could measure the uptake of C-13 that was incorporated into the organisms (Aspetsberger et al., 2007, Sweetman and Witte, 2008b). Thus we were able to quantify the carbon cycling and identify the responsible agents for the process (Middelburg et al., 2000, Witte et al., 2003b, Witte et al., 2003a), and thereby get an idea about how the ecosystem functions under the different flow regimes.

Analyses of abundance, biomass and biodiversity data from different sites under different flow regimes give information about the state of the different ecosystems. Pearson and Rosenberg's generalized successional model (1978) of how macrofaunal composition varies through different degrees of organic enrichment is frequently applied when discussing the state of a community under pollution stress. At low exposure to organic enrichment, a community comprise of a relatively high diversity of large-bodied species, and they can be found burrowing into the sediments down to 10 cm depth (Pearson and Rosenberg, 1978). These species are typically not very abundant in these circumstances, and are sometimes referred to as K-selected species (Clarke and Warwick, 1994). Following the enrichment gradient to the other end, the species become smaller and more abundant as they are specialized to live in areas that most species cannot. They are called opportunists, or r-selected species, and these communities are low in biodiversity, and the deeper sediments are low in oxygen meaning that the animals do not burrow into the sediments. A study of these measures are therefore important when assessing the effects that different hydrodynamics have on an ecosystem.

The hypotheses that I want to test throughout my master's thesis are:

H₀₍₁₎: There is no difference in benthic macrofaunal abundance, biomass or biodiversity at a site under a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

H₀₍₂₎: There is no difference in benthic macrofaunal abundance, biomass or biodiversity between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₀₍₃₎: There is no difference in benthic macrofaunal C-13 uptake between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₀₍₄₎: There is no difference in benthic macrofaunal C-13 uptake between a site close to a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

The complementary H₁ hypotheses are then as follows:

H₁₍₁₎: There is a difference in benthic macrofaunal abundance, biomass or biodiversity at a site under a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

H₁₍₂₎: There is a difference in benthic macrofaunal abundance, biomass or biodiversity between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₁₍₃₎: There is a difference in benthic macrofaunal C-13 uptake between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₁₍₄₎: There is a difference in benthic macrofaunal C-13 uptake between a site close to a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

Methods

Study site and experimental design

To find appropriate sampling sites to test my hypotheses several factors were considered. The goal was to compare a fish farm in a high water flow environment with a farm in low water flow environment, and it was desirable to test fish farms located in the same fjord so that they were more easily comparable. We therefore selected one salmon fish farm with a high current velocity ($4,7 \pm 3,7$ cm s⁻¹ at 75 m depth), located in the outer part of Hardangerfjorden – Farm 1 – and one salmon fish farm with a slow current velocity ($1,1 \pm 0,4$ cm s⁻¹ at 100 m depth), in the inner part of Hardangerfjorden – Farm 2 (Figure 1.). These categorizations are consistent with Valdemarsen et al (2012)’s documentation that current speeds under 2 cm s⁻¹ at 80 m depth are considered slow current velocities. Farm 1 had a farming license to a maximum hold of 2340 tons of salmon, while Farm 2 had a farming license to a maximum hold of 3120 tons of salmon.

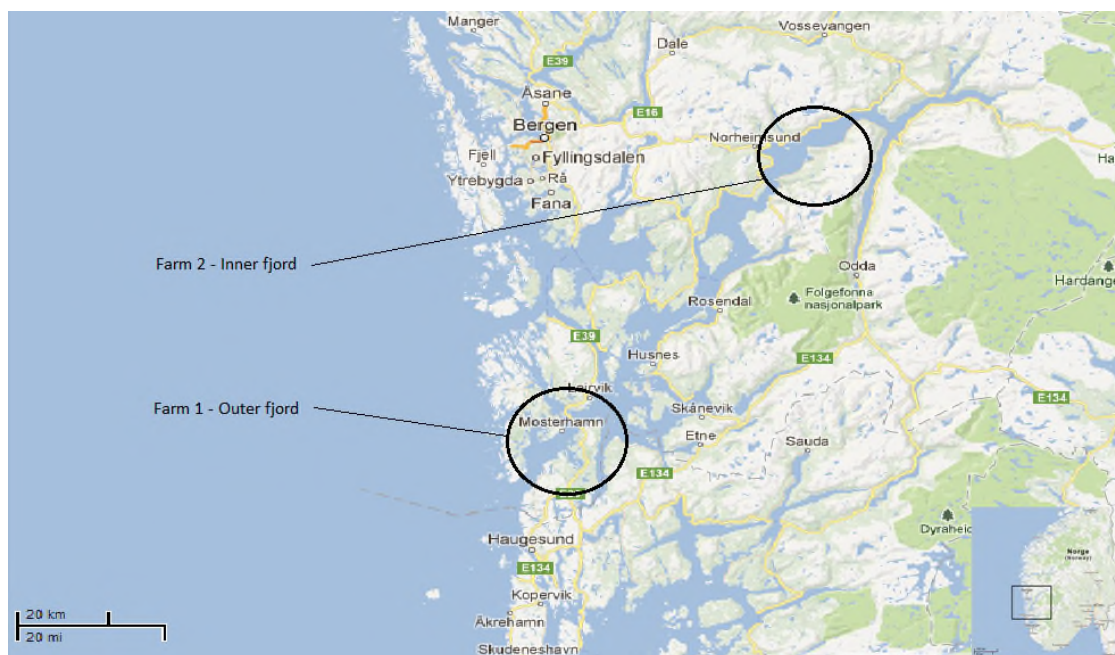


Figure 1. Map showing the locations of the two fish farms, Farm 1 – Outer fjord (high flow), and Farm 2 – Inner fjord (low flow).

Initial measurements of the flow regime and bottom structure were conducted to ensure that the fish farms were suitable for our desired experiments. When choosing how far downstream the samples should be taken, we assumed a logarithmic change in organic matter flux with distance from the farm to be able to see whether there was a difference in benthic community structure and function downstream from the farms. Samples were collected 50 metres away from Farm 1 (F1(0)), and 25 metres away from Farm 2 (F2(0)), while a distance of 500 metres downstream from both fish farm sites were considered sufficient distance to serve as control sites. We therefore have two sample sites per fish farm, leaving a total of four sites, with five to six samples/replicates collected at each site, 23 samples in total (Table 1). For further information on the study sites, see Sweetman et al. (2014).

| Fish farm | Farm 1 | | Farm 2 | |
|--------------------|-----------|------------|-----------|------------|
| Downstream | 50 metres | 500 metres | 25 metres | 500 metres |
| Sites | F1(0) | F1(500) | F2(0) | F2(500) |
| Samples/Replicates | F1(0)-R1 | F1(500)-R1 | F2(0)-R1 | F2(500)-R1 |
| | F1(0)-R2 | F1(500)-R2 | F2(0)-R2 | F2(500)-R2 |
| | F1(0)-R3 | F1(500)-R3 | F2(0)-R3 | F2(500)-R3 |
| | F1(0)-R4 | F1(500)-R4 | F2(0)-R4 | F2(500)-R4 |
| Controls | F1(0)-R5 | F1(500)-R5 | F2(0)-R5 | F2(500)-R5 |
| | F1(0)-R6 | | F2(0)-R6 | F2(500)-R6 |

Table 1. Two fish farms with two sites per farm (immediately under the fish farm and 500 metres downstream), and five to six samples per sample site (total of 23 samples). Replicates 5 and 6 were kept as control samples in terms of not adding labelled algae.

To be able to have samples to compare results to, some of the replicates were kept as control samples, meaning that there were no isotopic tracer added to these. We therefore have two control samples per sample station (suffix –R5 and –R6). The F1(500) site has only one control sample due to equipment failure.

Sampling methods and material

Field sampling

Sampling took place in March 2010. When collecting the samples, we used a US Naval electronics laboratory (USNEL) box-corer made by KC-Denmark to get relatively undisturbed sediment samples at 200 metres depth. We then took subsamples from the box corer with a benthic polycarbonate chamber, 20cm in diameter, 45cm in height (Figure 2.) The sediment depth was between 16 and 20 cm, and 0,2 μm filtered seawater was immediately added over the top of the sediment, after retrieval, to minimize disturbance (~45-49 cm). The chambers were sealed with a water tight lid, and within a few hours they were transported to a seawater bath in a temperature controlled lab where the rest of the experiment took place *ex situ*.

Pulse chase experiments

In the lab the chambers were placed in temperature-controlled water baths. We had a separate bath for control samples that were not incubated with isotopic tracer than for those that were (Figure 3.), but both baths were kept the same initial *in situ* temperature (8 degrees Celsius). The lids were designed with magnetically operated propellers to allow circulation, and air valves connected to an aquarium pump to allow oxygenation of the water mass within the chambers (Figure 2.). The oxygenation occurred only at different time intervals. A mechanism stirred the water carefully with the propellers continuously throughout the incubation to simulate the natural environment and to avoid stratification of the water mass. All chambers were allowed to settle for 72 hours before starting the experiment, as in Sweetman and Witte (2008a), and Sweetman et al. (2010).

Prior to the experiment, an algal culture of an axenic clone of the diatom *Skeletonema costatum* had been labelled with Carbon-13 using the methods of Sweetman and Witte (2008a). The spring bloom in temperate Norwegian fjords is partly made up by this particular diatom (Erga and Heimdal, 1984), and it would therefore serve as a realistic food source and allow us to trace the carbon cycle within our experiment. The labelled culture was then homogenized with a mortar, added to the chambers *ex situ*, and it then served as the isotopic tracer in this experiment. Please refer to

Sweetman et al. (2014) for details on how this algal culture of *S. costatum* was treated so that it could serve as an isotopic tracer. Approximately 142 mg of the tracer labelled with 28.4 mg of Carbon-13 was carefully added to every non-control chamber (16 chambers) using a syringe containing a mix of the tracer and filtered sea water. The propeller was running constantly and ensured that the algae were evenly distributed throughout the water column similar to the methods of Sweetman and Witte (2008a). We left the chambers to incubate for 48 hours, sampling the chamber water at different intervals to ensure that there was enough oxygen present, and aerating them with the aquarium pump when it was necessary. In addition to collecting macrofaunal samples from the cores at the end of the experiment, samples were also taken for bacterial phospholipid fatty acids, bacterial amino acid samples, porosity, density, O₂ micro profiles, dissolved inorganic carbon (DIC), bulk organic carbon, meiofauna and foraminifera, results of some of which can be found in Sweetman et al. (2014), and will not be discussed further here. Oxygen levels were measured using Winkler titration (KARL, 2007).

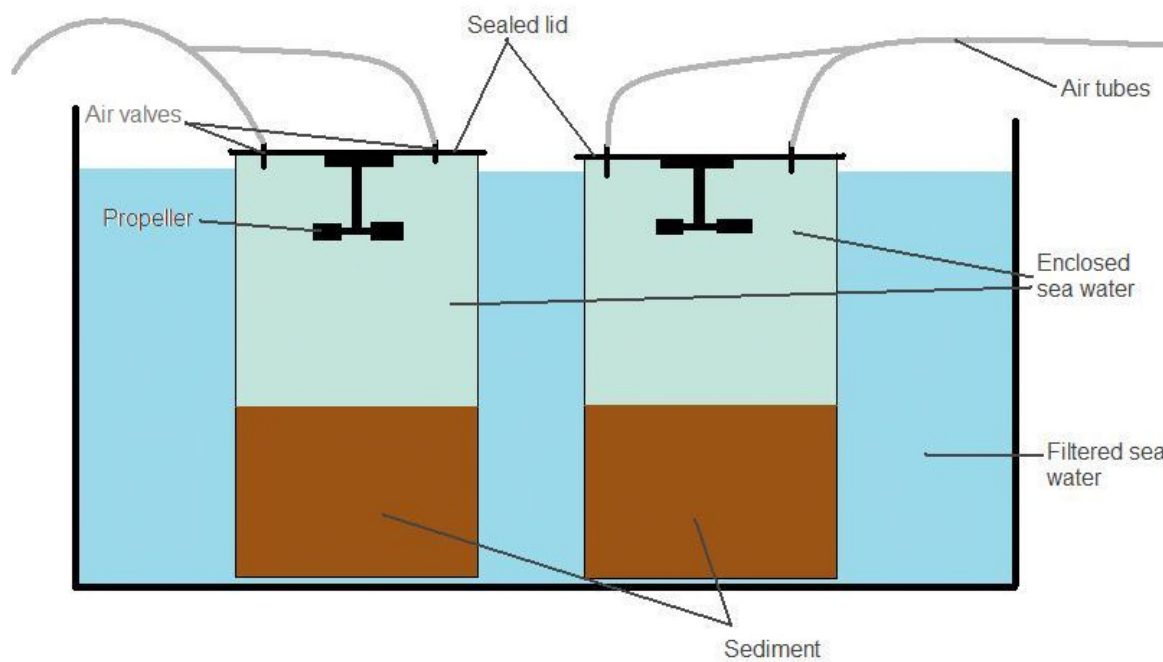


Figure 2. Schematic figure of the benthic chambers standing in the water bath.

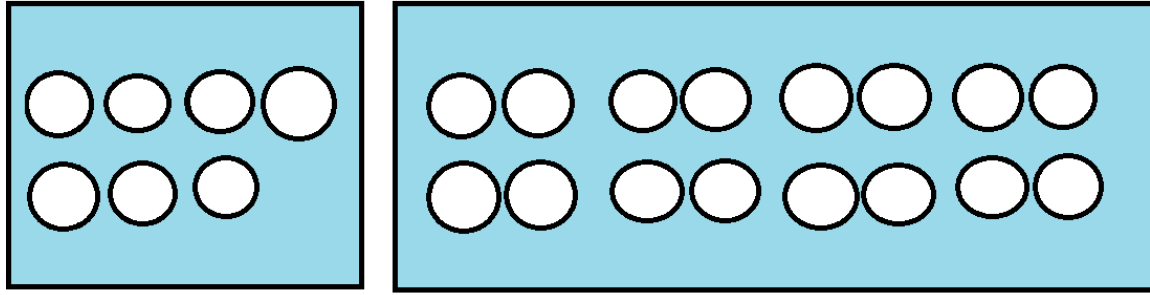


Figure 3. Schematic figure (bird perspective) of the benthic chambers in the two water baths. The controls without isotopic tracer were randomly placed in the left bath (7 chambers), while the rest of the chambers were randomly placed in the right bath (16 chambers).

Macrofaunal sampling and preparation for isotopic analysis

After the 48 hour incubation, the macrofauna was sampled from each chamber with a sub core (8 cm diameter) and, with the help of an extruder, the sediment was separated into 3 different horizons, 0-1 cm depth, 1-5 cm depth, and 5-10 cm depth. One sample was taken from all 3 horizons in each chamber, leaving a total of 69 samples. These samples were transferred to plastic bottles containing fresh, filtered 4 % buffered formaldehyde seawater to conserve the macrofauna for future sorting and analysis. The samples were sieved through a 500 μm mesh sieve, and macrofauna was sorted out using a dissection microscope and identified using appropriate identification keys. Separate sorting devices were used for labeled and unlabeled organisms to make sure there was no contamination with stable isotopes. A total of 9025 individual animals were counted (number of heads) and identified to the lowest possible level (Table 2), where e.g. polychaetes were determined to family, with the exception of a few species level identifications.

| Taxa | Phylum | Identification level |
|----------------|---------------|-----------------------------|
| Echiura | Annelida | class |
| Polychaeta | Annelida | family/species |
| Oligochaeta | Annelida | subclass |
| Pycnogonida | Arthropoda | class |
| Caprellidae | Arthropoda | family |
| Amphipoda | Arthropoda | order |
| Cumacea | Arthropoda | order |
| Harpacticoidae | Arthropoda | order |
| Tanaidacea | Arthropoda | order |
| Copepoda | Arthropoda | subclass |
| Hydrozoa | Cnidaria | class |
| Ophiuroidea | Echinodermata | class |
| Aplacophora | Mollusca | class |
| Bivalvia | Mollusca | class |
| Gastropoda | Mollusca | class |
| Scaphopoda | Mollusca | class |
| Caudofoveata | Mollusca | subclass |
| Solenogastres | Mollusca | subclass |
| Nematoda | Nematoda | phylum |
| Nemertea | Nemertea | phylum |
| Porifera | Porifera | phylum |
| Sipuncula | Sipuncula | phylum |

Table 2. Taxa encountered and lowest identification level determined.

The sorted fauna were transferred to tin capsules (5 x 9 mm) and dried in an oven at low temperature (35-45°C) over a period of several days. Calcareous fauna were transferred to double boated silver capsules and were decalcified using 2 M HCl before being dried a second time. The abundance and biodiversity data is based on number of heads, as some animals encountered was only fragments. Fragments are included in the biomass data, but not in the abundance data. The weight of the animals was carefully measured using an electronic microbalance (Sartorius M3P, d = 0.001 mg), or an analytical balance (Sartorius CPA224S, d = 0.1 mg) and kept between 0.004 mg and 3 mg per capsule. For some of the light weighted taxa (e.g. nematoda), individuals had to be pooled to gain the sufficient weight for IRMS analysis, like the methods of Aberle and Witte (2003), Kamp and Witte (2005), and Sweetman and Witte (2008b), while for some of the heavier taxa they had to be homogenized with a mortar and the desired amount (>0.004, <3.000 mg) of homogenized animal matter was added to the capsule. The capsules (a total of 1171 capsules) were rolled into compressed balls to get rid of any air in the capsules, and then sent to the University of California (UC Davis) for isotopic analysis. Isotopic ratios and biomass were measured using both

Europa Integra and Hydra 20/20 isotope ratio mass spectrometers for enriched and natural isotopes, respectively. Macrofaunal uptake of ^{13}C after 48 hours ($\text{mg } ^{13}\text{C}/\text{m}^2$) was calculated as the product of the excess ^{13}C (E) and carbon content in the animal. E is the difference between the labeled fraction (F) of a sample and the background sampled from the control chambers with no stable isotopes added:

$$E = F(\text{sample}) - F(\text{background}),$$

where

$$F = \frac{^{13}\text{C}}{^{13}\text{C} + ^{12}\text{C}} = \frac{R}{R + 1}$$

and

$$R = \frac{\delta^{13}\text{C}}{1000} + 1 \times RVPDB$$

where $RVPDB = 0.0112372$ and VPDB is Vienna Pee Dee Belemnite. If there were no unlabeled individual of a certain taxa in the background samples, the F value was obtained from a closely related organism with the same feeding guild and then used to calculate ^{13}C uptake (E).

Statistical analyses

All data was tested statistically using a combination of R (R Core Team, 2014) and Sigmaplot version 11 (Systat Software, Inc., San Jose California USA, www.sigmaplot.com). PRIMER-E (Clarke and Warwick, 1994) was used for graphical techniques and multivariate analysis such as taxa accumulation curves, K-dominance plot, rarefaction, MDS, ANOSIM, SIMPER and cluster analysis. A combination of Sigmaplot version 11, Microsoft Excel version 2010 and PRIMER-E (Clarke and Warwick, 2001) was used for graphical techniques. Before performing any statistical tests, the data was checked for normality and equal variance. Data was first transformed using square root, $\ln(+1)$ or $\log(+1)$, and if the transformed data failed to meet the parametric assumptions, a less powerful non-parametric test such as a Kruskal-Wallis or Mann-Whitney test was performed instead of a One- or Two-way Analysis of Variance. Significant results with a p-value of 0.05 or less was then examined using multiple comparison procedures such as post-hoc Tukey tests and Dunn's method.

Results

Abundance, biomass and biodiversity

Abundance and biomass trough different depth layers

All sites had most abundance in the mid layer, 1-5 cm (Figure 4.), except F2(0), which had the most abundance in the upper layer, 0-1 cm (72084 ± 18149 individuals pr m-2) and decreased with depth. When it comes to biomass, all sites had most macrofaunal biomass in the mid layer, except F1(500), which had the most biomass in the lower layer, 5-10 cm ($1020,79 \pm 428,70$ mg dry weight pr m-2) and increased with depth.

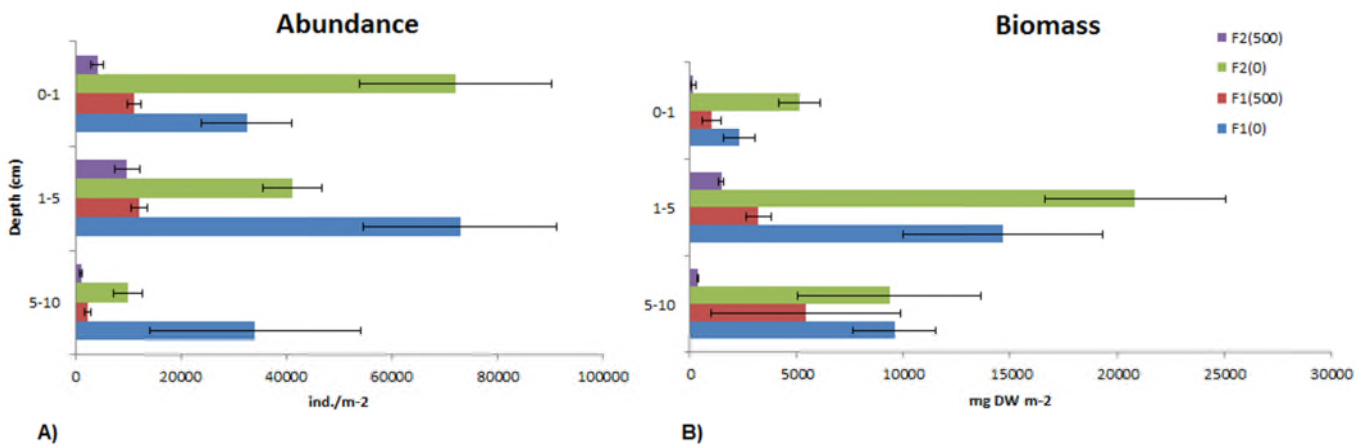


Figure 4. (A) Abundance (individuals pr m-2) and (B) biomass (mg dry weight pr m-2) at different depth layers at each site. Error bars indicate $SE \pm 1$ ($n = 6$), except for F1(500) where error bars indicate $SE \pm 1$ ($n = 5$).

Total abundance and biomass at each site

The sites under the fish farms had the most abundance (139526 ± 29730 ind. pr m^{-2} (F1(0)), 123212 ± 21202 ind. pr m^{-2} (F2(0)), Figure 5.), and also the most biomass ($26560,85 \pm 5945,59$ mg dw pr m^{-2} (F1(0)), $46102,85 \pm 4261,72$ mg dw pr m^{-2} (F2(0))). There is a larger difference between F1(0) and F1(500) in terms of abundance than in terms of biomass. Kruskal-Wallis tests suggested significant differences between the sites when it came to both abundance and biomass ($p < 0,001$), and Pairwise Multiple Comparison Procedures (Dunn's Method) showed that in terms of both abundance and biomass, only F2(500) differed significantly from other sites, with F2(500) having both significantly lower abundance and biomass values than F1(0) and F2(0) (both $p < 0,001$). There appear to be a large difference in abundance between the fish farm sites and the control sites, however the conservative non-parametric test showed no significant difference between the sites located in the low flow environment.

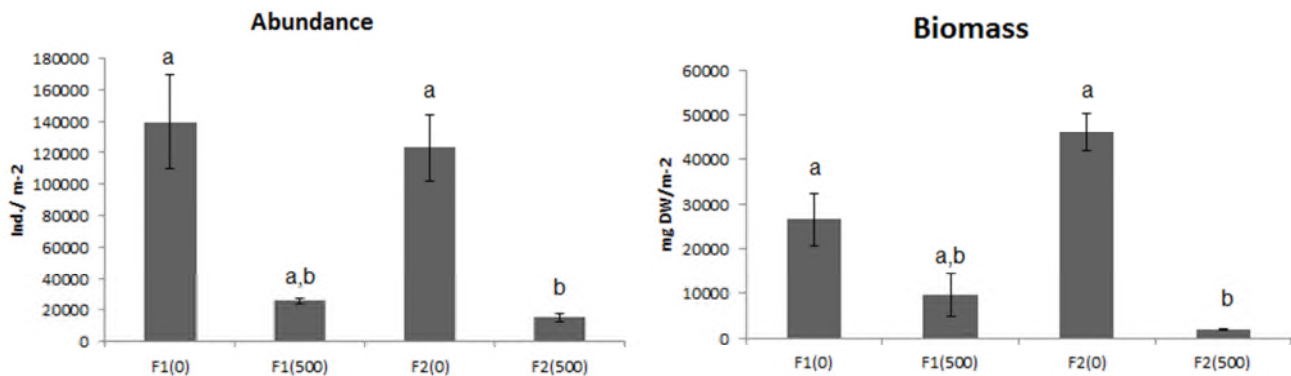


Figure 5. Abundance (individuals pr m^{-2}) and biomass (mg dry weight pr m^{-2}) at each site. Error bars indicate $SE \pm 1$ ($n = 6$), except for F1(500) where error bars indicate $SE \pm 1$ ($n = 5$). Statistically significant differences between the sites ($p = <0,05$) are represented by different letters.

As the analysis is restricted to macrofauna, and Nematoda usually is considered as meiofauna and hence excluded from some macrofaunal analyses (Weston, 1990), it is also interesting to look at the abundance when the nematodes are excluded (Figure 6). In that case, there is, by far, most abundance in F2(0). The small body size of the nematodes leaves no considerable difference in biomass.

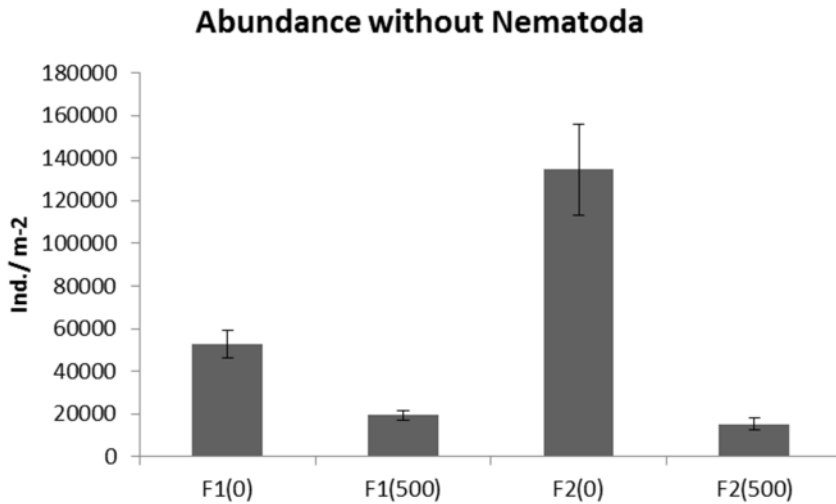


Figure 6. Abundance (individuals pr m-2) at each site. Error bars indicate SE ± 1 (n = 6), except for F1(500) where error bars indicate SE ± 1 (n = 5).

Biomass divided by abundance (nematodes included) show that the individuals were generally heavier in F2(0) (1,9 mg dw/ind), and F1(500) (1,7 mg dw/ind) compared to F1(0) and F2(500) (~0,7 mg dw/ind) (Figure 7 A). However, when nematodes are excluded, body size looks more equal between the fish farm sites, and the heavier individuals are found in the high flow control site (2,3 mg dw/ind) (Figure 7 B).

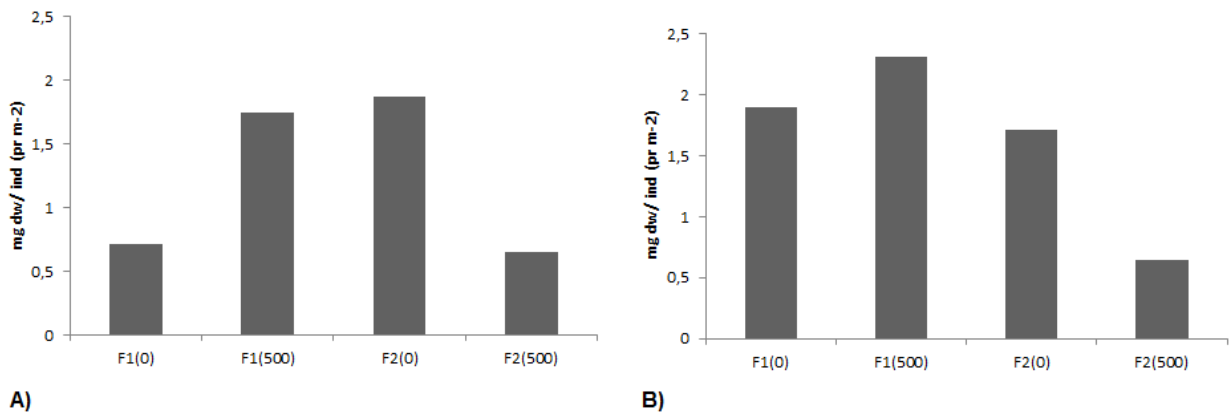


Figure 7. Biomass (mg dry weight pr m-2) divided by abundance (individuals pr m-2) shows average biomass pr individual at each site, Nematoda included in A, Nematoda excluded in B.

Nematoda are still included in the rest of the analyses, as are all individuals large enough to remain on a 500 µm mesh sieve.

Abundance and biomass of present taxa groups

The most abundant taxon is Nematoda at the high flow fish farm site (F1(0) ~65%), while Polychaeta are the most abundant at all other sites (F1(500) ~ 35%, F2(0) ~ 97%, F2(500) ~ 75%)(Figure 8, Figure 10). Nematoda is the second most abundant group at F1(500) and F2(500) (25 and 13%, respectively), while the few individuals of nematodes at F2(0) make up less than 1%. The second most abundant group at F2(0) is therefore Crustacea with only 3%. The taxon that contributes most to biomass at each site is Polychaeta (F1(0) ~ 60%, F1(500) ~ 65%, F2(0) ~ 100%, F2(500) ~ 94%), while Ophiuroidea also contributes significantly at F1(0) and F1(500) (~ 26% and ~ 23%, respectively) (Figure 8, Figure 9.).

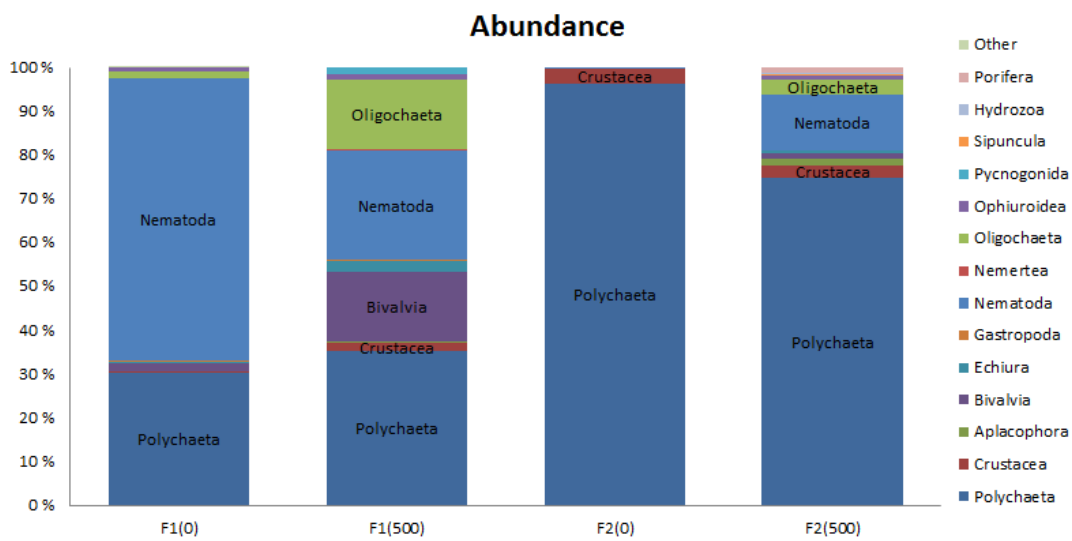


Figure 8. Percentage contribution to abundance (individuals pr m-2) by different taxa groups within each site.

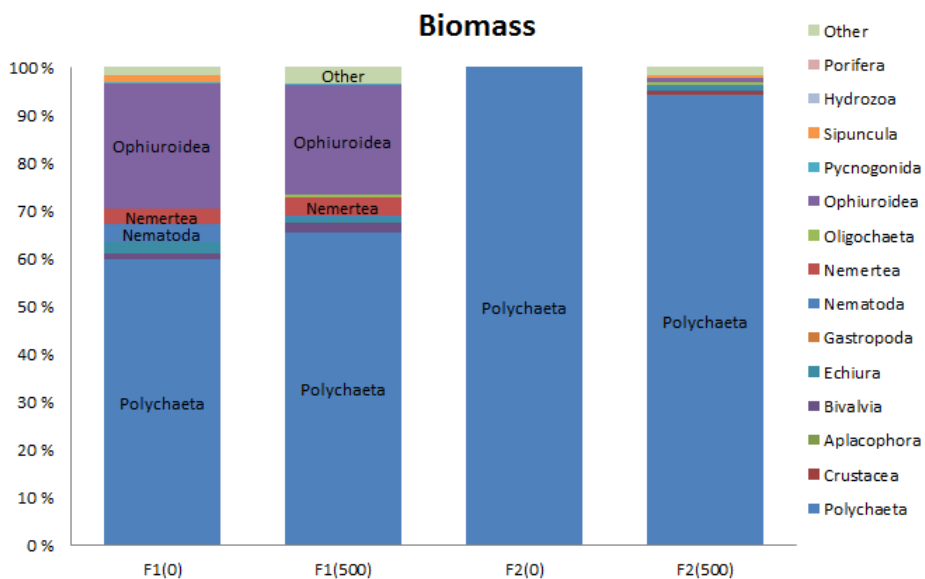


Figure 9. Percentage contribution to biomass (mg dry weight pr m-2) by different taxa groups within each site.

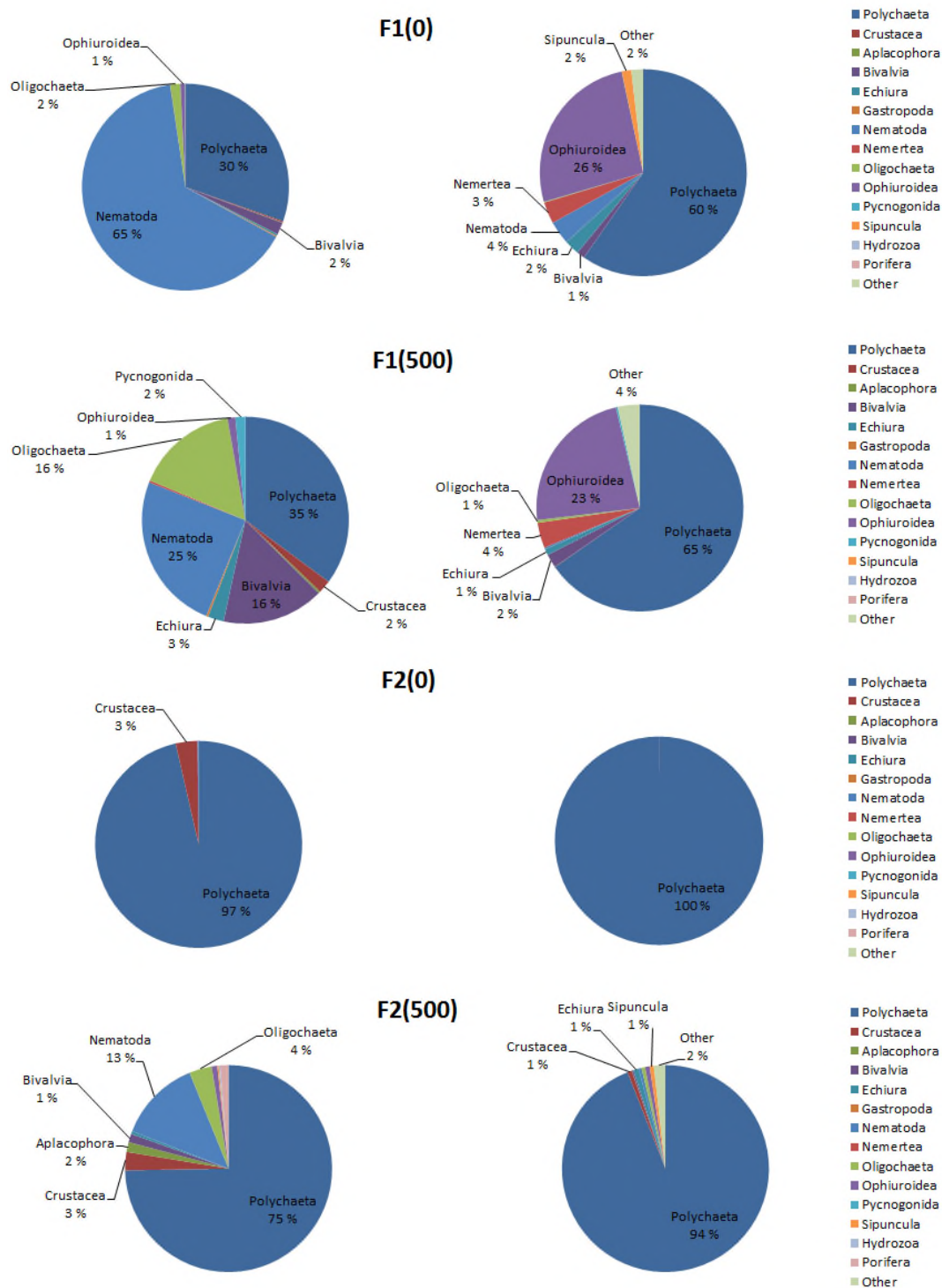


Figure 10. Percentage influence on abundance, ind/m² (A,C,E,G) and biomass, mg dw/m² (B,D,F,H), by different taxa groups at each site.

The taxon Polychaeta is represented by a number of different families, and many individuals have also been identified to species. With knowledge of present families and thereby feeding methods we also gain the possibility of learning more about the community structure. The most abundant polychaete family in all sites, except F1(0), is Capitellidae which contributes with 40 – 58% of the abundance of polychaetes (Figure 11, Figure 13 (A,C,G)). In F1(0), Capitellidae are barely outnumbered by Cirratulidae which contributes with 42% of the abundance (Figure 11, Figure 13 (A)). Cirratulidae is also numerous at F1(500) and F2(500) with 14% and 21 %, respectively, but they are barely present at F2(0) with only 0,02 % contribution to abundance. Dorvilleidae are also present at all sites, with 8 – 13%. At F2(0) 10 % of the 13% of the Dorvilleids is by the species *Palpiphitime lobifera*, but interestingly, the *P. lobifera* are not at all present at the 500 m sites, and only 0,15% at F1(0). *Vigtorniella ardabilia* is also a species that is only present at F2(0), and are quite dominant there with its 40% contribution to abundance (Figure 11, Figure 13 (E)).

Cirratulidae is a group that also adds expressively to biomass at all sites, with 38 – 49%, except for F2(0), where they are less than 1% of the biomass (Figure 11, Figure 12) Capitellidae amounts 28% to biomass at F1(0), and dominates biomass at F2(0) with 93% (Figure 12, Figure 13). Although *V. ardabilia* were quite numerous at F2(0), they do not make up much of the biomass (~ 4%), and while there are many polychaete groups that contribute to biomass at F1(0), F1(500), and F2(500), only three groups make up between 1 and 4% of the biomass at F2(0). *V. ardabilia* are one of those groups, with 4% of the biomass (Figure 12, Figure 13, Figure 13).

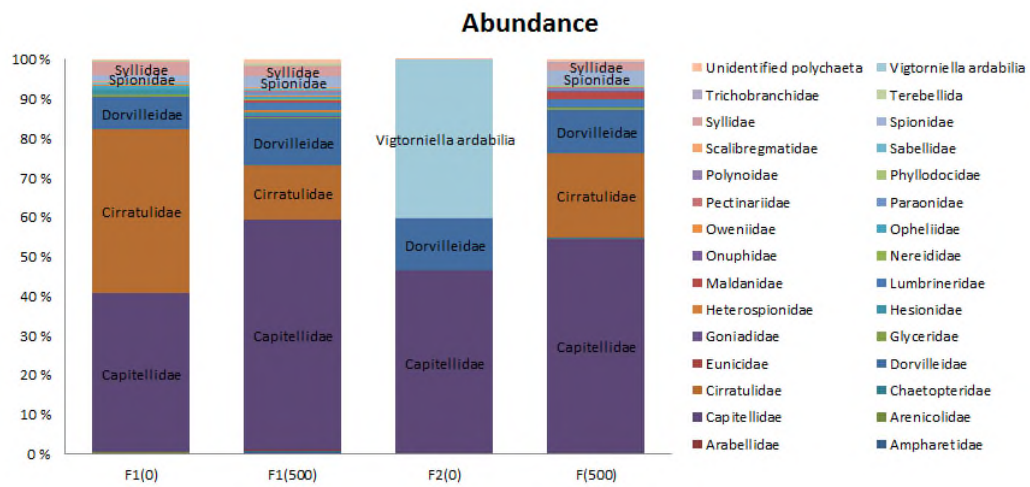


Figure 11. Percentage contribution to abundance (individuals pr m-2) by different polychaeta groups.

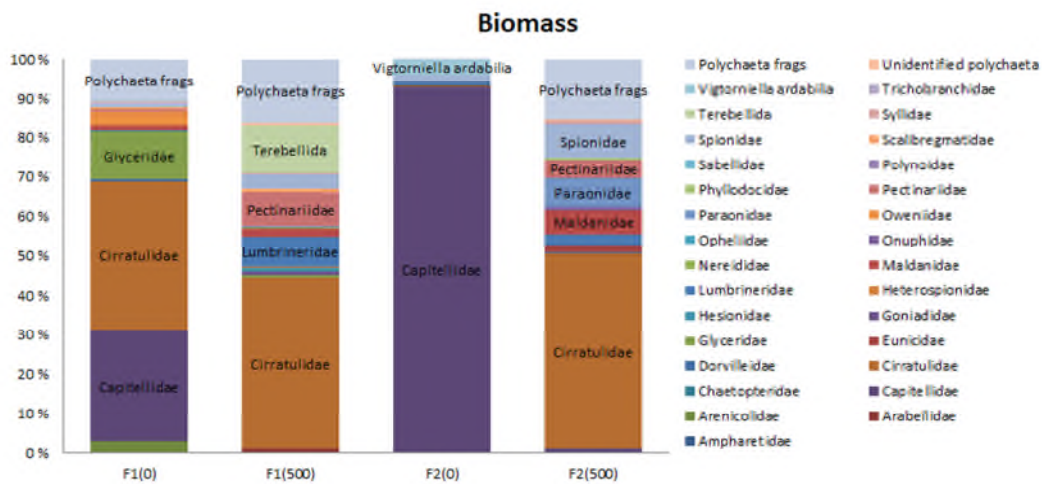


Figure 12. Percentage contribution to biomass (mg dw pr m-2) by different polychaeta groups.

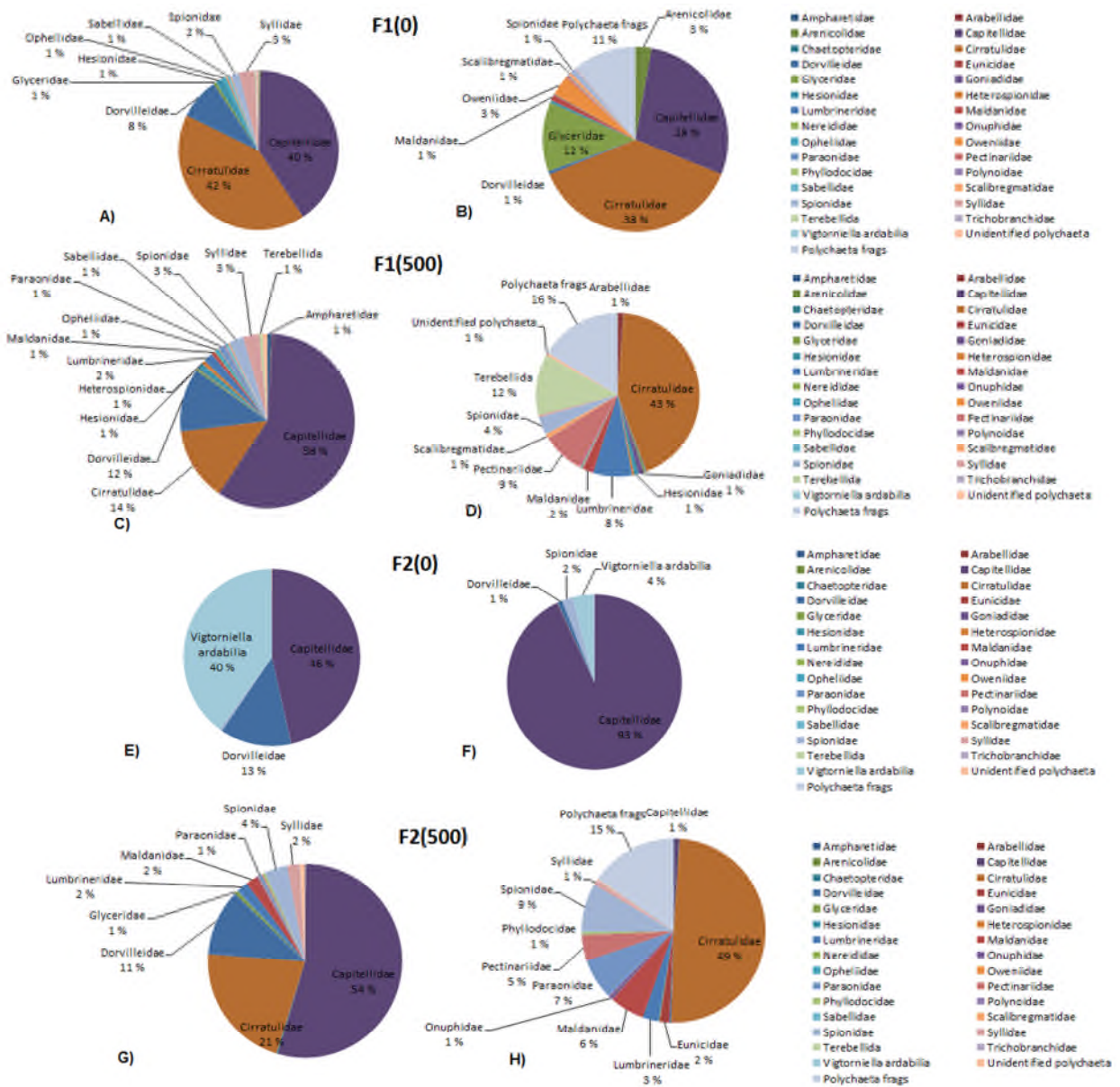


Figure 13. Percentage influence on abundance, ind/m² (A,C,E,G) and biomass, mg dw/m² (B,D,F,H), by different Polychaeta groups at each site.

Taxa richness

Taxa richness refers to the number of taxa represented in the different samples. A Kruskal-Wallis test ($p = 0,003$) followed by a Pairwise Multiple Comparison Procedure (Dunn's Method) showed that the average number of taxa at F2(0) were significantly lower than the high flow sites ($p < 0,05$) while the other sites showed no significant difference from each other (Figure 14).

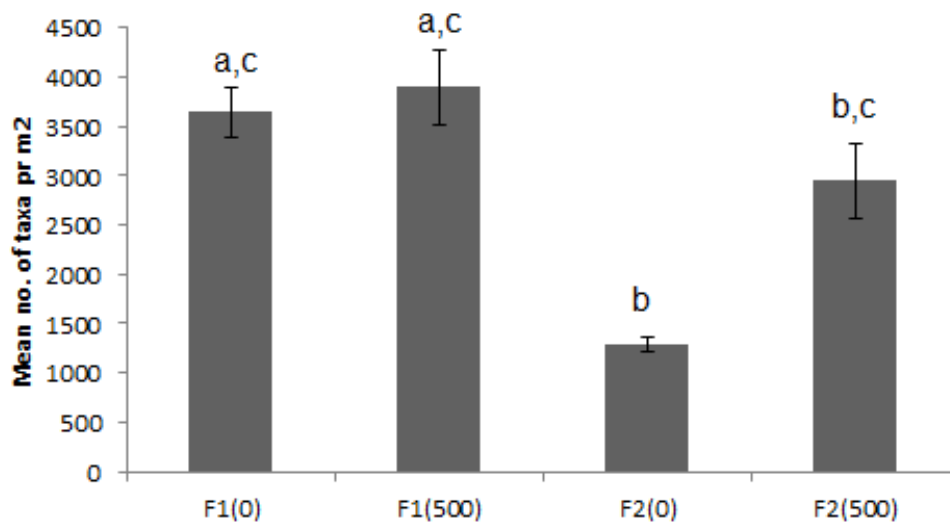


Figure 14. Average number of taxa present at each site (pr m²). Error bars indicate $SE \pm 1$ ($n = 6$), except for F1(500) where error bars indicate $SE \pm 1$ ($n = 5$). Statistically significant differences between the sites ($p < 0,05$) are represented by different letters.

Taxa evenness

Taxa evenness refers to how close in numbers each taxon is, within the samples. Even if there are many taxa present, there could be a knowingly difference in how many numbers are present of each taxa. If each taxon is close in numbers with the rest, there is a higher evenness than if there are many individuals of a some taxa and few of other taxa. Taxa evenness is here represented by Pielou's evenness (J') and is calculated as:

$$J' = \frac{H'}{H'_{max}}$$

where H' is Shannon's diversity index and $H'_{max} = \log(s)$, where s is the number of species (PIELOU, 1966).

A Kruskal-Wallis test ($p < 0,001$) on taxa evenness numbers followed by a Pairwise Multiple Comparison Procedure (Dunn's Method) showed that F1(0) had significantly lower taxa evenness than both control sites (500m sites), while F2(0) only had significantly lower taxa evenness than the high flow control cite ($p < 0,005$)(Figure 15). The other combinations showed no significant differences.

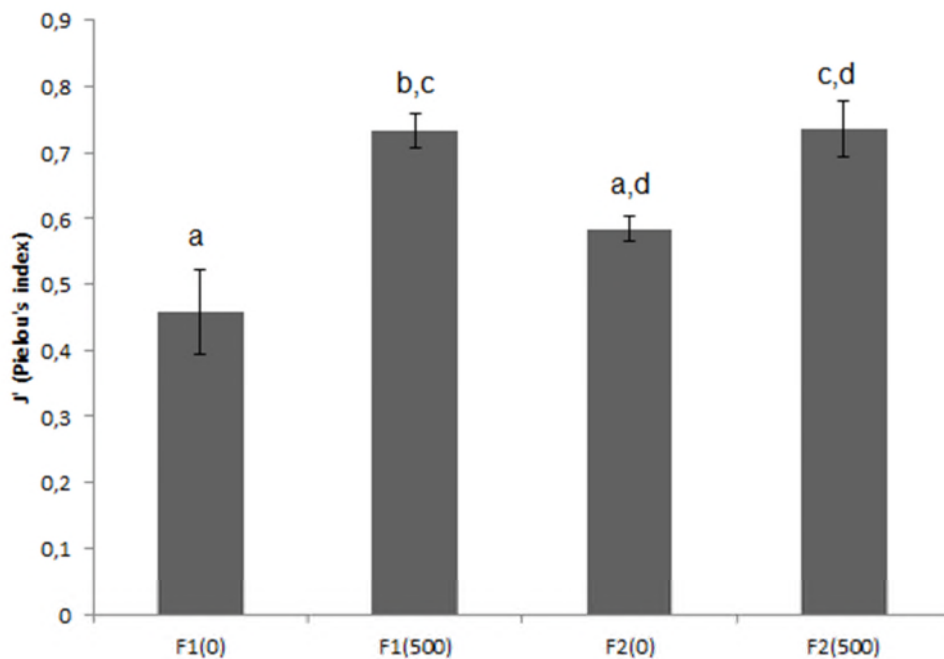


Figure 15. Taxa evenness represented by J' (Pielou's index) at each site. Error bars indicate $SE \pm 1$ ($n = 6$), except for F1(500) where error bars indicate $SE \pm 1$ ($n = 5$). Statistically significant differences between the sites ($p < 0,05$) are represented by different letters.

Taxa accumulation

The taxa accumulation curve gives us an indicator whether the community is thoroughly enough sampled. If the curves level off, then it is less likely that one might find another taxon present if one would have sampled the community once more. F2(0) levels off rapidly with 10 taxa present at the last two samples (Figure 16). F1(500) and F2(500) show a tendency to level off after 4 and 5 samples, with 37 and 34 taxa present, respectively, and while F1(0) also appears to be levelling off, with 31 and 33 numbers of taxa present at the last two samplings, more samples should have been taken at all sites except F2(0) to make sure that the curves levelled off completely.

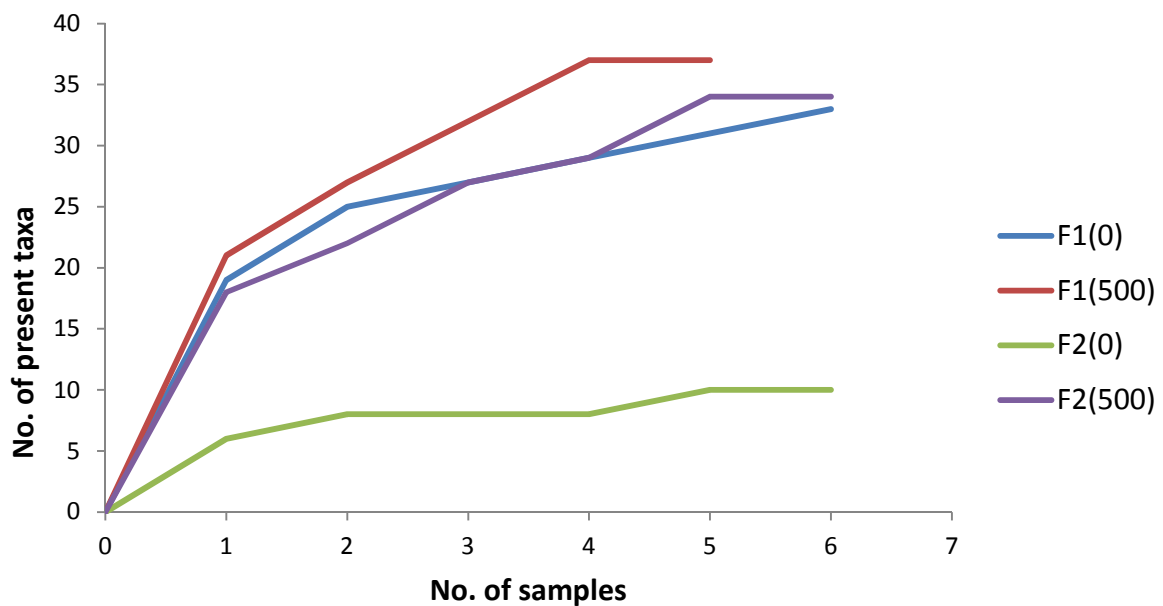


Figure 16. Taxa accumulation curve shows how many different taxa are present after each sample (replicate).

When it comes to dominance, a k-dominance plot of curves shows a cumulative ranked abundance plotted against taxa rank, and in this case, a steep curve indicates low diversity (Clarke and Warwick, 2001), because if a one or a few taxa dominates from an early stage, it does not leave room for high diversity. F1(0) differs slightly from the others, with the curves showing a great variance in both trend and starting point, indicating that the different replicates within the sample location are varied in terms of taxa composition (Figure 17). The curves from F2(0) rise quickly and become very steep. This means that a few taxa dominate from an early stage, leaving little room for high diversity.

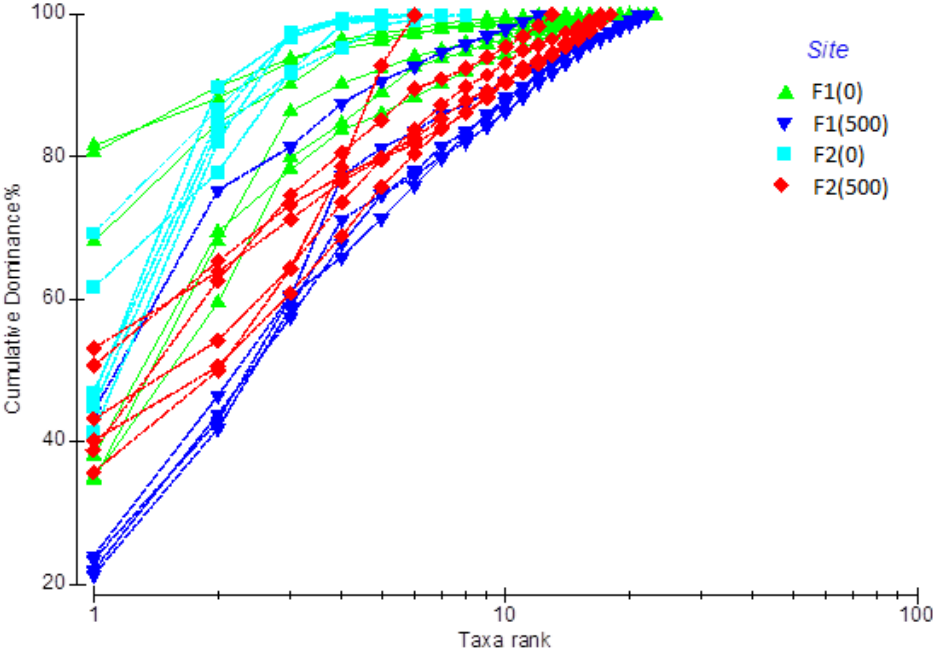


Figure 17. K-dominance plots of all replicates within each site.

Rarefaction

Rarefaction curves are plots of the number of individuals (x-axis) against the number of species/taxa (y-axis), and a rarefaction analysis essentially says that the steeper and more elevated the curve is, the more diversity there is within the community (Clarke and Warwick, 2001). In this case the plot shows that F2(0) seems to reach an asymptote with just 6 to 8 number of different taxa, suggesting that the community is dominated by a few taxa that are very abundant (~800 individuals)(Figure 18). F1(500) and F2(500) are far from reaching an asymptote, proving that they both are collected from a community that is highly diverse (~15 to 21 taxa), although not as abundant (~60 to 120 individuals). F1(0) have not reached an asymptote either, and displays higher abundance (~200 to 1200 individuals) than either of the control sites, and higher diversity (~13 to 23 taxa) than the low flow fish farm site (F2(0)). The \pm 95% confidence interval show that F1(0) has significantly lower diversity than the controls, and that F2(0) has significantly lower diversity than all other sites.

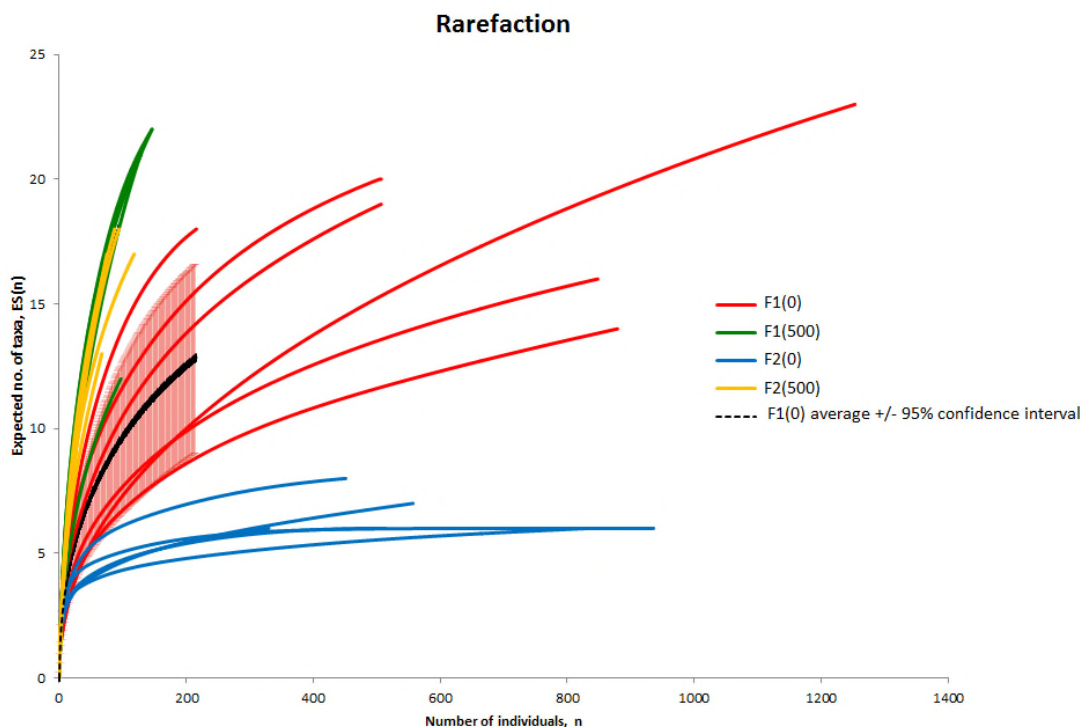


Figure 18. Rarefaction curves for all samples, including the average for F1(0) (black line) with a +/- 95% confidence interval (pink area).

MDS, ANOSIM, SIMPER

The obvious clusters in the MDS ordination clearly shows that resemblance is highest within each site, and also that F2(0) differs more from the other sites (Figure 19).

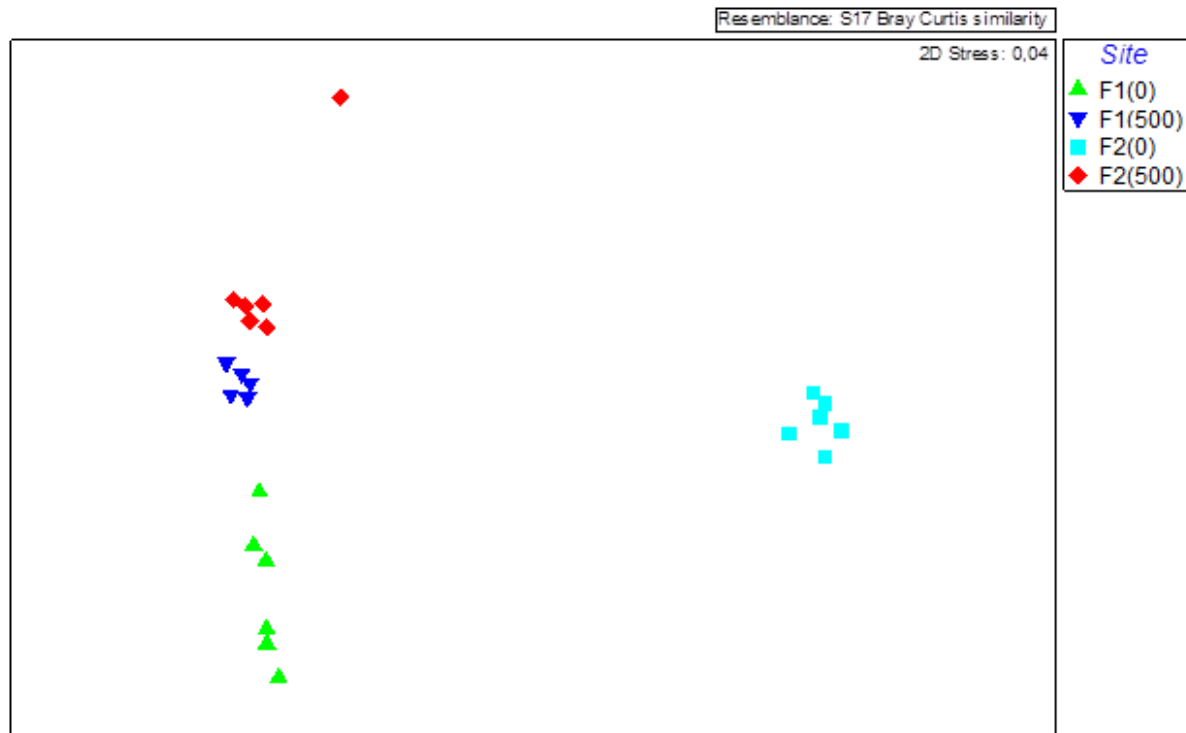


Figure 19. MDS ordination on standardized abundance data (no. of individuals/m²) of all replicate samples.

An analysis of similarity between groups (ANOSIM) gives R values of the comparison between sites. When the R value is close to zero, the null hypothesis is true, essentially saying that similarities between groups and within groups (among replicates) are the same on average, while an R value of 1 indicates that replicates within the group are more similar to each other than any replicates from different groups (Clarke and Warwick, 2001). F2(0) gives the value of 1 when compared to the other sites, proving that that site is very distinctive from the rest (Table 3).

| Groups | R-Statistic |
|------------------|-------------|
| F1(0), F1(500) | 0,896 |
| F1(0), F2(0) | 1 |
| F1(0), F2(500) | 0,876 |
| F1(500), F2(0) | 1 |
| F1(500), F2(500) | 0,621 |
| F2(0), F2(500) | 1 |

Table 3. ANOSIM output of R-value between sites.

A hierarchical cluster analysis also shows that, in terms of resemblance, the replicates are more similar within their site, than to other sites, and also within the same location (high flow vs. low flow) (Figure 20).

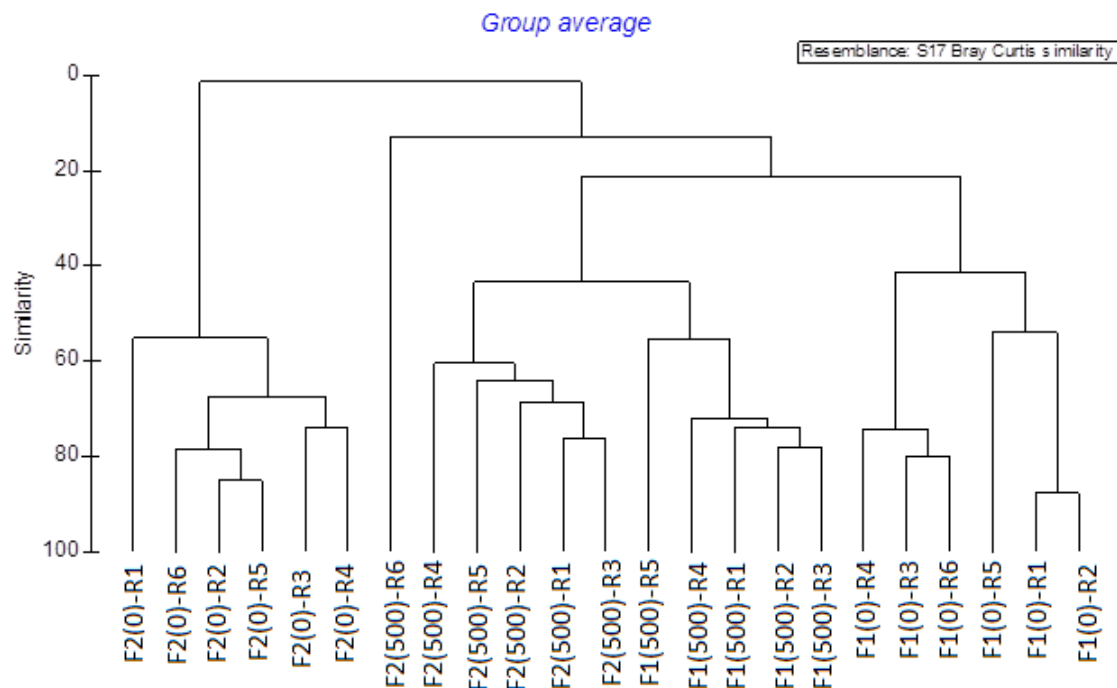


Figure 20. Hierarchical cluster analysis based on group abundance average.

A SIMPER analysis gives values of which taxa groups that contribute most to the dissimilarity between the sites, in terms of percentage (Appendix A). Although there were only two group comparisons that gave a value of significantly lower abundance between sites (Figure 5, F2(500) vs. both F1(0) and F2(0)), a SIMPER analysis gives a value that shows a great difference between some sites in terms of taxa- and species composition, and the relative abundance of those different taxa and species (Appendix A). The group comparisons that are most different is when F2(0) are compared to the others. They show a dissimilarity of 98,69 %, 98,60 %, 98,58 % (compared to F1(500), F1(0), and F2(500), respectively). These differences are mainly caused by a large presence of *V. ardabilia*, *C. capitata* and *P. lobifera* at F2(0) while they are absent at all other sites. However, the high abundance of nematodes at F1(0) also cause a large part of the dissimilarity between F1(0) and F2(0), as there were only 1 nematode present, in average, at F2(0). The high nematode abundance at F1(0) cause most of the dissimilarity when compared to both control sites, as they were only present in low numbers further downstream from the fish farms. The control are most similar when compared to each other with 61,09 % dissimilarity.

Macrofaunal carbon uptake

Uptake at different sites

The carbon uptake in F2(0) demonstrates the highest carbon consumption rate, with an average of $53,69 \pm 7,56$ mg carbon uptake per m² each day (Figure 21). Also, the other site immediately under the other fish farm, F1(0), demonstrate quite a high uptake ($36,14 \pm 0,22$ mg C) compared to the sites 500 metres downstream to the farms (F1(500) $9,98 \pm 2,36$ mg C, F2(500) $13,3 \pm 2,63$ mg C). Statistical tests (Kruskal-Wallis ($p = 0.005$), Tukey test) reveal that the only significant difference in uptake is when F2(0) is compared to F1(500) and F2(500) and that means that there is a significantly higher uptake of carbon at F2(0) than the 500 metres sites ($p < 0,05$).

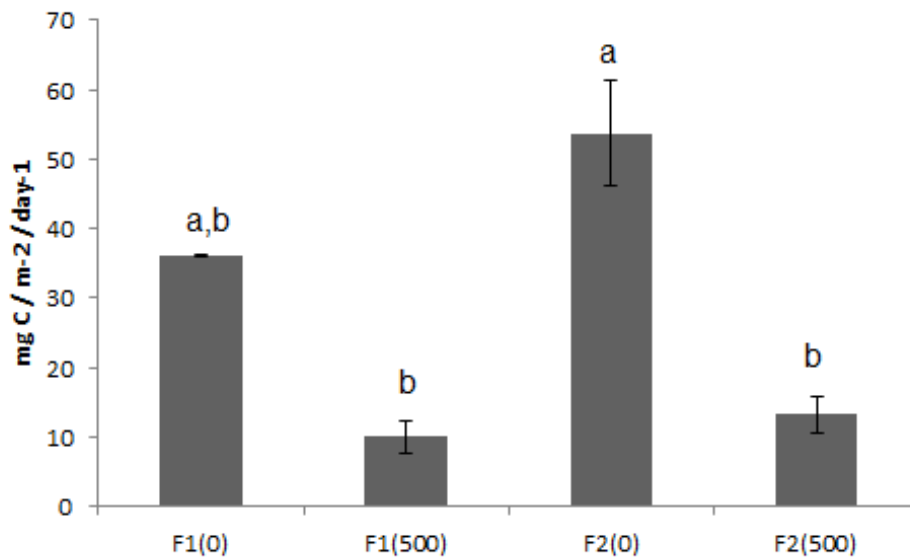


Figure 21. Total average carbon uptake (mg C/m²/day-1) at each site. Error bars indicate SE ± 1 (n = 4). Statistically significant differences between the sites ($p < 0,05$) are represented by different letters.

Uptake at different sediment layers

Figure 22(A) demonstrates that all sites have a higher amount of carbon uptake in the middle layer, 1 – 5 cm, than any other layer. Not surprisingly, the lower layer, 5 – 10 cm, has the least carbon uptake. To compare with the pattern shown by biomass distribution throughout the layers (Figure 22(B)), they are very similar, only, in terms of biomass, there is the least weight in the upper layer instead of the lower layer. The middle layer has the most weight, as well as the most carbon uptake.

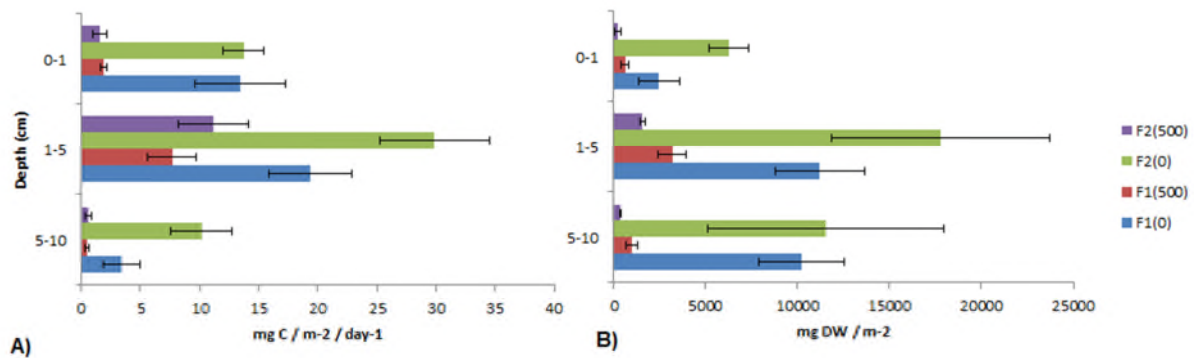


Figure 22. (A) Total carbon uptake (mg C/m²/day-1) and (B) biomass (mg dry weight pr m²) at different depth layers at each site. The bars in B are different to biomass bars in Figure 4 because this comparison is based on the exact same four replicates for both A and B (carbon uptake surveys have four replicates, while other macrofaunal surveys have 5-6 replicates). Error bars indicate SE ± 1 (n = 4).

Uptake in different polychaete feeding guilds

Of the total carbon uptake, polychaetes are responsible for 94 %, while the other groups combined only make up a total of 6 % (Figure 23). A closer look at the polychaetes allows for a better understanding of how the ecosystem functions, as different polychaete families and species have different preferences for food and resilience to environmental stress factors. Capitellids consume 56 % of the overall carbon uptake, while the second most carbon consuming family is the Cirratulidae with 22 % (Figure 24). Looking at the different sites and the taxa that are greatest in consuming carbon, Cirratulids are a large group at all sites except at the low flow fish farm site (F2(0)) where they are absent (Figure 25). Instead, Capitellids are the most important taxa at this site taking up 87 %. Capitellids are also important at the other fish farm site (F1(0) with 40 %), but they are insignificant at the control sites when it comes to carbon consumption (Figure 25).

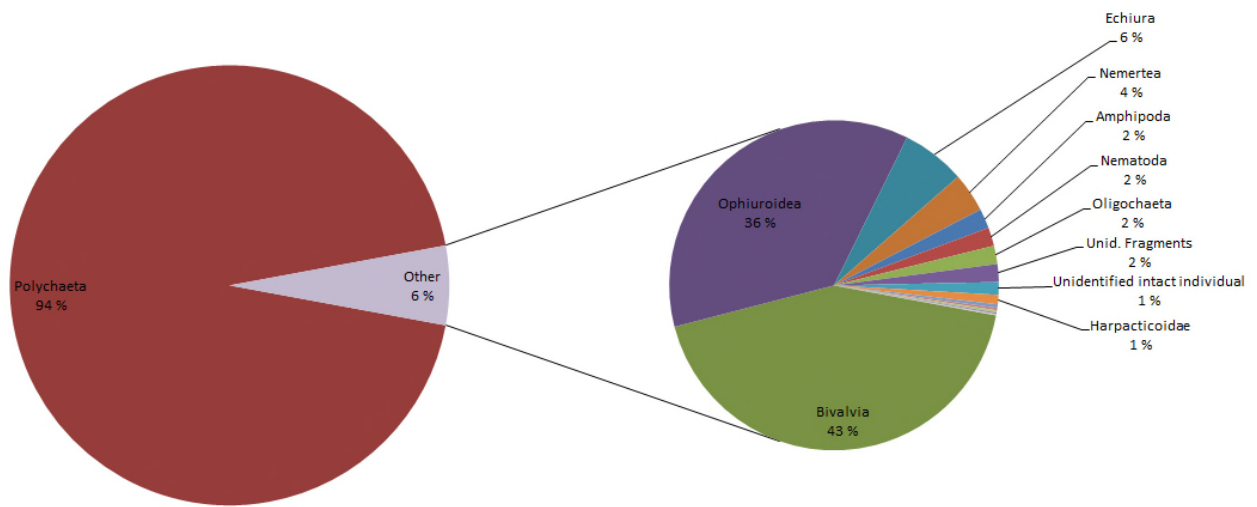


Figure 23. Pie chart demonstrates percent contribution to total carbon uptake for all four sites combined.

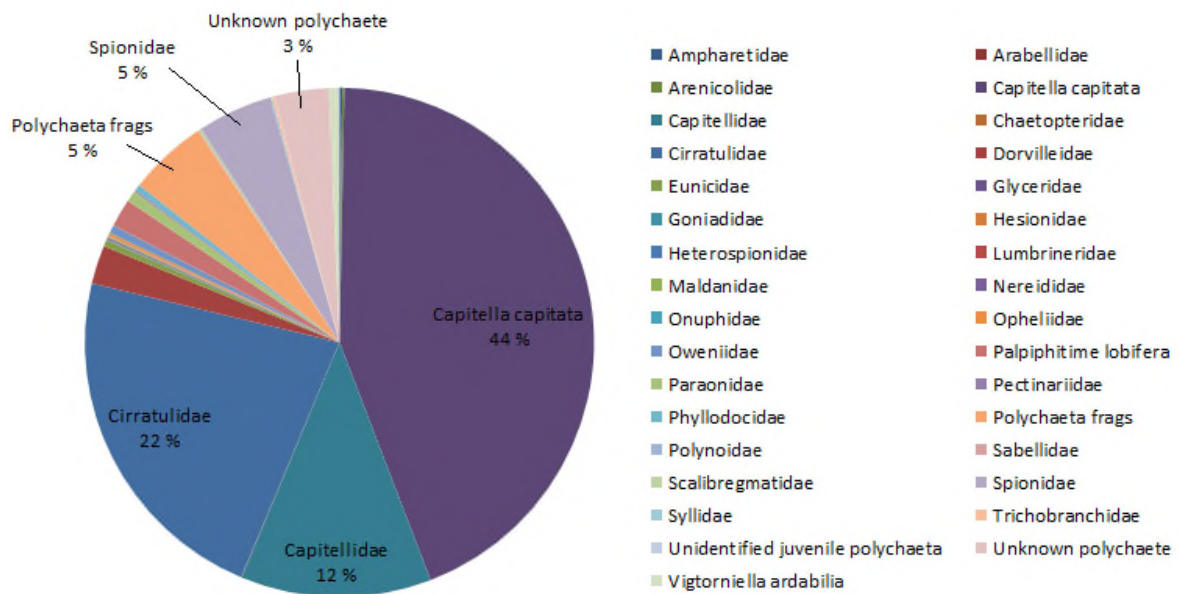


Figure 24. . Percentage contribution to total polychaete C-uptake (mg C/m-2/day-1) by different polychaete taxa.

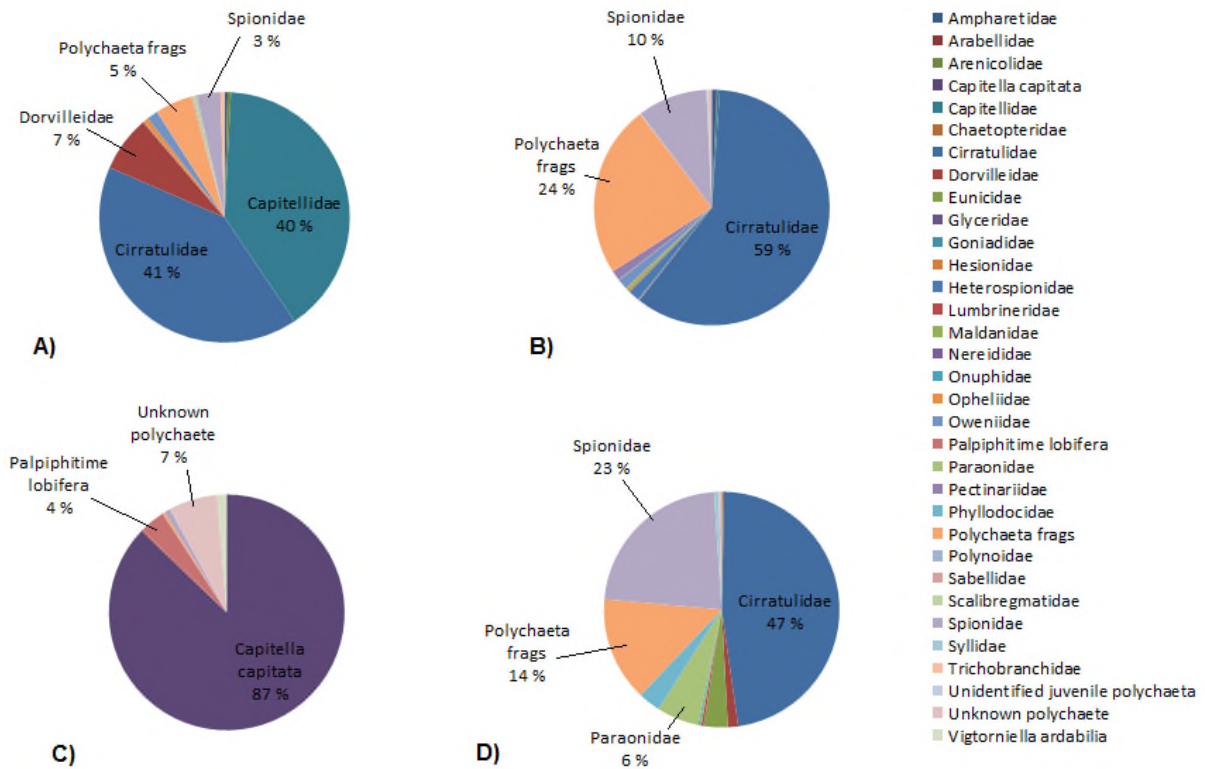


Figure 25. Percentage contribution to polychaete C uptake (mg C/m²/day-1) at different sites by each polychaete taxa. A is F1(0), B is F1(500), C is F2(0), D is F2(500).

When divided into groups according to feeding guild (group characterization from Levin et al. 2001), the Capitellids belong to the Sub-surface deposit feeders (SSDF), while Cirratulids are Surface feeders (SF)(Table 4). Other groups are Filter feeders (FF), Carnivores (CV), and Bacterivores (BV)(Table 4). The SSDF are responsible for 63 % of the total amount of carbon consumed by polychaetes, and they take up over 94 % of the carbon at F2(0)(46,73 ± 6,88 mg C/m²/day-1) and 44 % of the carbon at F1(0)(Figure 26 and Figure 27). The SF, with an uptake of 31 % of the total polychaete carbon consumption, are the most consuming group at all sites except at F2(0)(49 % at F1(0), 96 % at F1(500), and 86 % at F2(500)).(Figure 26 and Figure 27). Although BV only contribute to carbon uptake at the sites close to the fish farms, they are still responsible for 5 % of the overall carbon consumption (Figure 26 and Figure 27). A two-way ANOVA on the average amount of carbon consumed in total, followed by a Holm-Sidak multiple comparison procedure with a significance level of 0,05 suggest that SSDF take up a significantly larger amount of carbon than BV and CV (no significant results for the other group comparisons)(Figure 28).

| Taxa | Guild | Feeding mode |
|-----------------------|-------|---------------------------|
| Dorvilleidae | BV | Bacterivore |
| Palpiphitime lobifera | BV | Bacterivore |
| Vigtoniella ardabilia | BV | Bacterivore |
| Glyceridae | CV | Carnivore |
| Goniadidae | CV | Carnivore |
| Hesionidae | CV | Carnivore |
| Lumbrineridae | CV | Carnivore |
| Phyllodocidae | CV | Carnivore |
| Polynoidae | CV | Carnivore |
| Syllidae | CV | Carnivore |
| Chaetopteridae | FF | Filter feeder |
| Ampharetidae | SF | Surface feeder |
| Arenicolidae | SF | Surface feeder |
| Cirratulidae | SF | Surface feeder |
| Heterospionidae | SF | Surface feeder |
| Sabellidae | SF | Surface feeder |
| Spionidae | SF | Surface feeder |
| Trichobranchidae | SF | Surface feeder |
| Capitella capitata | SSDF | Subsurface deposit feeder |
| Capitellidae | SSDF | Subsurface deposit feeder |
| Maldanidae | SSDF | Subsurface deposit feeder |
| Opheliidae | SSDF | Subsurface deposit feeder |
| Paraonidae | SSDF | Subsurface deposit feeder |
| Pectinariidae | SSDF | Subsurface deposit feeder |
| Scalibregmatidae | SSDF | Subsurface deposit feeder |

Table 4. Taxa divided into feeding mode groups. The taxa that are not in the table were not determined high enough taxonomically to have an accurate feeding guild.

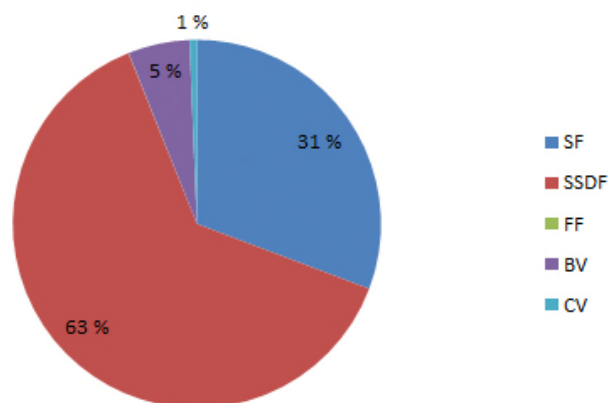


Figure 26. Pie chart demonstrates percent contribution to total carbon uptake by all feeding guilds for all four sites combined.

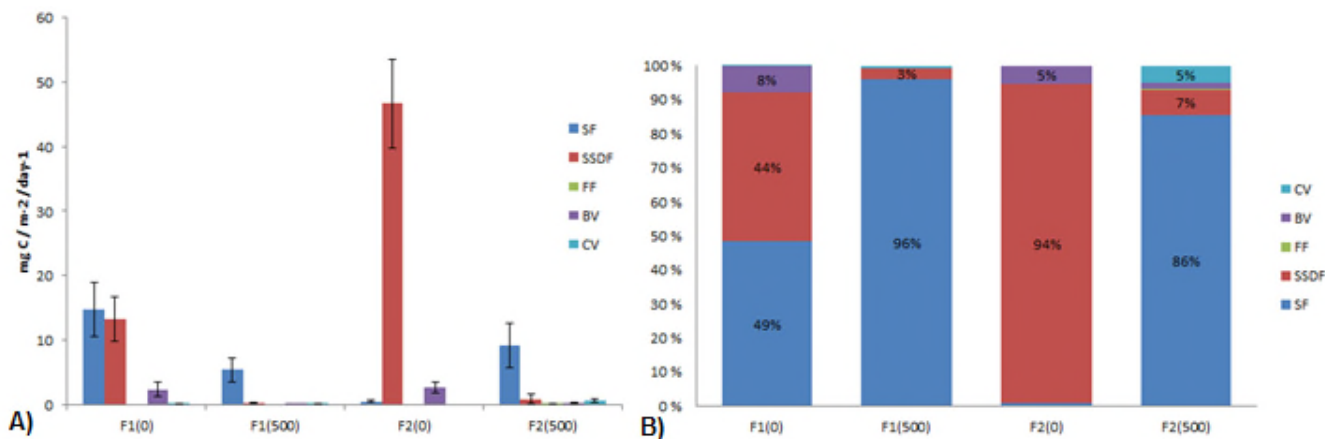


Figure 27. Average carbon uptake (mg C/m²/day-1) by each feeding guild, all samples (A), and demonstration of feeding guilds' contribution (percent) of carbon uptake, relative to total uptake within each sample (B). Error bars indicate SE ± 1 (n = 4).

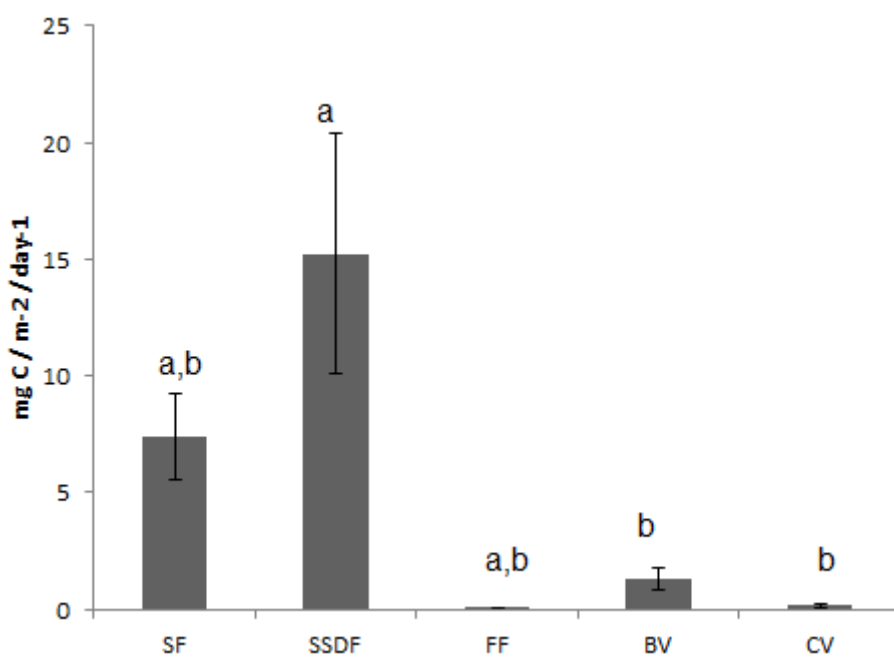


Figure 28. Total average carbon uptake by each feeding guild. Error bars indicate SE ± 1 (n = 4). Statistically significant differences between the sites (p = <0,05) are represented by different letters.

Discussion

The null hypotheses were:

H₀₍₁₎: There is no difference in benthic macrofaunal abundance, biomass or biodiversity at a site under a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

H₀₍₂₎: There is no difference in benthic macrofaunal abundance, biomass or biodiversity between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₀₍₃₎: There is no difference in benthic macrofaunal C-13 uptake between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₀₍₄₎: There is no difference in benthic macrofaunal C-13 uptake between a site close to a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

The complementary H₁ hypotheses are then as follows:

H₁₍₁₎: There is a difference in benthic macrofaunal abundance, biomass or biodiversity at a site under a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

H₁₍₂₎: There is a difference in benthic macrofaunal abundance, biomass or biodiversity between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₁₍₃₎: There is a difference in benthic macrofaunal C-13 uptake between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

H₁₍₄₎: There is a difference in benthic macrofaunal C-13 uptake between a site close to a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm.

Results and conclusion of the different hypotheses

Hypothesis 1

The low flow control site (F2(500)) displayed a significantly lower number of abundance and amount of biomass than both fish farm sites (0 m sites, $p < 0,001$). Consequently, in a low flow environment, when it comes to abundance and biomass, H₀(1) can be partially rejected in favour of the opposite; There is a difference in benthic macrofaunal abundance and biomass at a site under a salmon fish farm, compared to a site 500 metres downstream from that same salmon fish farm, but only when located in a low flow environment. The difference is that there is higher abundance and biomass at a site close to a low flow fish farm, than a site 500 metres further downstream.

H₀(1) can be rejected in favour of the opposite regarding biodiversity; There is a difference in benthic macrofaunal biodiversity at a site under a salmon fish farm compared to a site 500 metres downstream from that same salmon fish farm, and that difference is that there is higher biodiversity at a site 500 metres downstream than there is at the site close to the fish farm. This conclusion is supported by the 95 % confidence interval in the rarefaction analysis which showed that the high and low flow control sites are significantly more diverse than the high and low flow fish farm sites. Also, the statistics on taxa evenness/Pielou's evenness (J') supports the rejection of the H₀(1) hypothesis, although only in a high flow environment, as the high flow control site (F1(500)) had significantly higher diversity than the high flow fish farm site.

Hypothesis 2

H₀(2) cannot be rejected in terms of abundance and biomass, as the abundance and biomass numbers show no significant difference between the fish farm sites, nor between the control sites (Figure 5); There is no difference in benthic macrofaunal abundance nor biomass between a salmon

fish farm located in a high flow environment compared to a salmon fish farm located in a low flow environment.

According to the rarefaction (Figure 18), the low flow fish farm site had significantly lower diversity than the high flow fish farm site, thus H0(2) can be partially rejected in terms of diversity. Therefore, there is a difference in benthic macrofaunal biodiversity between a salmon fish farm located in a high flow environment compared to a salmon fish farm located in a low flow environment, when comparing sites are close to the fish farms. In such case, benthic biodiversity is higher in a high flow environment.

Hypothesis 3

The only statistically significant difference in macrofaunal c-uptake is when the low flow fish farm site is compared to either control sites. H0(3) cannot be rejected; There is no difference in benthic macrofaunal C-13 uptake between a salmon fish farm located in a high flow environment vs. a salmon fish farm located in a low flow environment.

Hypothesis 4

H0(4) can be partially rejected, and the alternate hypothesis can be assumed to be true, but only when the farm is located in a low flow environment; There is a difference in benthic macrofaunal C-13 uptake between a site close to a salmon fish farm compared to a site 500 metres downstream from the same salmon fish farm when the water flow is low. There is a higher uptake of C-13 close to a low flow fish farm than 500 metres downstream.

Discussion of abundance and biomass

Depth layers

Most animals were found in the mid layer, at 1-5 cm depth, except for the fish farm site located in a low flow environment, where the abundance was highest at the top layer, 0-1 cm deep. The reason why this site differs from the rest is most likely because there is such high organic loading, causing the deeper sediment layers to be deprived of oxygen to the extent that even the most anoxic tolerant species cannot live deeper (Pearson and Rosenberg, 1978, Nilsson and Rosenberg, 2000, Weston, 1990). This is consistent with the generalized model of macrobenthic succession along an enrichment gradient from Pearson and Rosenberg (1978). The surface layers are intermediately disturbed, and that allows for opportunistic specialists to dominate that area. They can become quite abundant with the lack of competition by organic intolerant species, however one would not expect them to grow large in size, as that would demand access to a larger supply of oxygen. This is the typical characterization of r-selected species, according to e.g. Clarke and Warwick (1994), which can often be found in organically enriched ecosystems. The high flow fish farm site also displays a relatively high abundance, although most in the mid layer. This is not surprising as a soft bottom environment make a desirable habitat for burrowing animals, and the stress of a high flow environment will reduce the size of the benthic diffusive layer and then allow more oxygen flux across the sediment-water interface (Glud et al., 2007). When it comes to biomass, however, the low flow fish farm site has the highest biomass in the mid layer, although the abundance is highest in the top. Further, it has more biomass than the high flow fish farm site in the mid layer. When processing the live samples, some of the animals were seen trying to escape by burrowing to deeper sediment depths. For that reason, this study does not make any definite conclusions with regard to the distribution of animals within the different layers.

Total abundance and biomass at each site

Abundance and biomass are both high at the fish farm sites, and relatively low at the control sites. Total average abundance ranged from 15087 to 139526 ind/m², while Capitellidae abundance ranged from 17043 to 64391 ind/m². These numbers are very high compared to the findings in other studies. Kutti et al. (2007) reported a total average abundance of 1530 to 14650 ind/m², and Capitellidae abundance of 12 to 5811 ind/m². Tsutsumi (1991) found total densities above 10000 individuals/m², though there were no exact numbers given. Capitellid numbers ranged between 3700 to 8800 ind/m² in the same study (Tsutsumi et al., 1991). There is no certainty as to why there are so high densities of macrofauna found in this present study compared to the previous

studies mentioned, although the location and climate, as well as the use of a 1,0 mm mesh sieve for macrofauna sorting, might cause some of the difference in numbers in Tsutsumi's case. As to the difference between Kutti et al.'s and this study's numbers could potentially be explained by a difference in the mooring system of the farms (farm allowed to move versus farm in fixed position, respectively), as well as the difference in depth under the farms.

As the fish farm sites were assumed to be heavily organically enriched by the effluents from the fish farm, and therefore experience low oxygen concentrations, one might anticipate that the low flow site would be so oxygen deprived that it was unfavorable for any organism to colonize. However, since both fish farm sites have elevated levels of abundance and biomass compared to the controls, some opportunistic species seem to have colonized these sites. Further, if we leave the nematodes out of the analysis (as they are too small to make a difference in biomass, and are often considered as meio- rather than macrofauna), the low flow fish farm have a much higher abundance than the high flow fish farm. These measures can be explained by the presence of small-bodied, opportunistic r-selected species at the fish farms sites, as typically seen when organic enrichment becomes more extensive (Pearson and Rosenberg, 1978, Nilsson and Rosenberg, 2000, Clarke and Warwick, 1994, Weston, 1990).

Abundance and biomass of present taxa groups

At both fish farm sites the abundance was elevated by only a few taxa, nematodes at the high flow site, and Crustacea along with Polychaeta at the low flow site. However, the first two taxa do not contribute much to biomass. In fact, polychaetes make up most of the biomass at all sites, but also some ophiuroids at the high flow site. The absence of ophiuroids at the low flow sites may indicate that the organic loading is too high for them, while polychaeta have many different families and species that are considered enrichment-tolerant opportunists that can specialize and colonize areas unfavorable for other taxa. In these areas, polychaetes can be quite numerous. The many taxa that make up the abundance at the control sites supports the idea that further from the fish farms, less organic loading make it a more hospitable area for many different taxa. The animals compete with each other, and therefore no single taxa get a chance to become dominant.

Although not as tolerant as Capitellidae (*Capitella* sp.), the cirratulids are also said to be common in enriched environments (Pearson and Rosenberg, 1978), and Cirratulidae are the most numerous at all sites except the low flow fish farm site. Spionidae and Syllidae are quite abundant at the control sites, whereas there are more Capitellida and Dorvilleidae at the high flow fish farm site.

The low flow fish farm site is quite distinguishable from the other sites in terms of the most dominant taxa, as the crysopetalid *Vigtorniella ardabilia* is the most abundant, while, in addition to *Capitella* sp, there is also a large presence of *Palpiphitime lobifera*. *V. ardabilia* is a relatively new species of “carpet worm”, described in 2009 (Wiklund et al.) from a whale fall in Sweden and from underneath a fish farm in Norway, and is a bacterivore observed feeding on bacterial mats that often lies beneath fish farms and is a consequence of heavy organic loading. Although very numerous, they are small, specialized opportunistic worms, and do not contribute much to biomass, and may therefore be considered as typical r-selected species (Clarke and Warwick, 1994). *Palpiphitime lobifera* is another specialized species that are present at the low flow fish farm site, previously described from whale falls and underneath fish farms (also known as *Ophrytrocha lobifera*)(Oug, 1978, Wiklund et al., 2009a). The presence of these two species of bacterivores supports the assumption that the low flow fish farm site is very organically enriched.

Discussion of biodiversity

The low flow fish farm site has significantly less taxa richness than both high flow farm sites, as seen when comparing the number of different taxa that were present at the different sites. Also, these numbers show that there is less taxa richness at the low flow farm site than the low flow control site, although not confirmed by the statistical analysis. Pielou's index show that there is less taxa evenness at the fish farm sites than their control sites, although not supported by statistically significant numbers at the low flow site in this case either. This lack of significance can be due to the less powerful conservative non-parametrical statistical tests performed. The taxa accumulation curve show that there is no reason to believe that more samples from the low flow fish farm site would give higher diversity, as the curve is completely levelled off at that site. Rarefaction and hierarchical cluster analysis show that there are more similarities between the high flow fish farm site and either control site, rather than between the two fish farm sites. The rarefaction analysis shows that both fish farm sites are significantly less diverse than the control sites, and further, it even shows that the low flow fish farm site is significantly less than the high flow fish farm. The k-dominance plot demonstrates that there is a high dominance by only a few taxa at the low flow fish farm, and also at some of the samples from the high flow farm site. But the high flow farm curves are not as steep, which allows more taxa within the community. Together, these analyses mean that there is less biodiversity at a site in a low flow environment, compared to a site in a high flow environment, when the sites are close to the fish farms. Further downstream, there is no significant difference between a high and low flow environment.

Carbon can be a limiting factor as food source when it comes to population size (Pearson, 1980, Rosenberg, 1995). Underneath salmon fish farms, large quantities of fecal matter and leftover food sinks to the bottom and generally leads to organic enrichment of the surrounding sediments (Pearson and Rosenberg, 1978, Carroll et al., 2003) and sometimes oxygen depletion (Pearson and Rosenberg, 1978). Some taxa and species are more specialized to handle these conditions, and they can sometimes colonize and dominate in these areas, leading to large abundances of few species. The low flow fish site appears to be in such a state, as biomass and abundance numbers are high, but diversity is low. The taxa that has colonized the low flow fish farm site is quite conspicuous; the opportunistic organically tolerant *C. capitata*, along with the two bacterivore species *V. ardabilia* and *P. lobifera*. The control sites are both considered relatively diverse communities, and the SIMPER analysis along with the hierarchical cluster analysis on group abundance numbers shows

that they are quite similar in taxa composition and abundances; no single taxa dominate the community, instead there is high diversity of different taxa. In addition to the significant differences in diversity between the high and low flow fish farm sites, the SIMPER analysis shows that in community taxa composition, the high flow fish farm site is more similar to the control sites than the low flow fish farm site, especially if the numerically dominant, but insignificantly small nematodes from the high flow site is not considered. There is, however, a presence of capitellids at the high flow farm site suggesting a slight tendency to organic enrichment, although not so enriched that it is unfavorable for organically less tolerant species. Moreover, there is a complete absence of the two bacterivores at all sites except at the low flow farm, further supporting that the low flow fish farm site comprise a heavily organically enriched community. To be able to detect if the community at this site has reached a “peak of opportunists” and whether it is on the border to becoming anoxic, more samples should be taken along a gradient of organic enrichment (Pearson and Rosenberg, 1978).

Discussion of carbon uptake

There appears to be higher carbon remineralization at the sites close to the fish farms rather than at the control sites further downstream, and carbon consumption also seem to be higher at the low flow fish farm site compared to the high flow site. Yet, the only statistical significant difference is that there is a higher carbon uptake at the fish farm site located in a low flow environment, than at a site 500 metres downstream from that same fish farm. Carbon uptake naturally follows the same trend as biomass, meaning that where there is most macrofaunal biomass, there is also most carbon remineralization. This is also true when comparing it within the different sediment depth categories, and when comparing the taxa responsible for the carbon consumption to the polychaete taxa that dominate biomass. A rapid subduction of the added carbon is facilitated by sub-surface deposit feeders, so there is a higher uptake of carbon 1 – 5 cm down in the sediment than in the upper layer (0 – 1 cm). Capitellids are the main carbon consumers at the low flow farm site, and are the second most consuming group at the high flow farm site, but surface feeding cirratulids are the main carbon consumers at all other sites. Spionids, which also are surface feeders, also contribute to a large part of the carbon consumption in the control sites, while dorvilleids are the third most important group in terms of carbon consumption at the high flow farm site. Despite the high abundance of *V. ardabilia* in the low flow farm samples, they exerted little to biomass and carbon uptake, which is to be expected as they are considered to feed on bacterial mats, so longer experiments would most likely have been needed to see any uptake of labelled carbon, as this first has to route through the bacteria. The large presence and rapid carbon remineralization rate of the sub-surface deposit feeding polychaete family Capitellidae at both fish farm sites show that these individuals are important facilitators to ecosystem functioning in these circumstances (Norling et al., 2007), as other representatives from this feeding group are responsible for retarded uptake of carbon in other communities and ecosystems (Sweetman et al., 2010). As there cannot be detected any statistical difference in carbon uptake between the two fish farm sites, this essentially means that the two different communities are both well-functioning ecosystems in terms of macrofaunal carbon uptake.

Conclusion

Abundance, biomass and carbon uptake did not differ much from the high flow fish farm site to the low flow fish farm site, neither did bacterial biomass nor bacterial carbon uptake (Sweetman et al., 2014). In fact, the only factor that differs significantly between the two farms is the biodiversity, which is higher under the high flow fish farm. The two different communities have found different ways of dealing with the effluents from the fish farms, but both are still highly functioning ecosystems. The subject of the importance of biodiversity for the resilience of an ecosystem has been discussed by scientists for a long time (MacArthur, 1955, Odum, 1969, Paine, 1969, Walker, 1995, McCann, 2000, Elmqvist et al., 2003). It is argued, among others, that diversity gives rise to ecosystem stability, but also that it is necessary to have certain species, e.g. keystone species, and functional groups of individuals “that are capable of differential response” (McCann, 2000). So in any natural community, it is desirable to have such resilience against fluctuations in the environment, which can, or cannot, come from human interactions with nature. However, when the time comes for a fish farm to cease production, and remove its cages, the ultimate outcome is usually for the benthic habitat to bounce back to its initial natural state, in which the rest of the regional community is. If the benthic community is resilient to the changes that the cessation induces, it may take more time to reach that state. Karakassis (1999) recorded that even 23 months after cessation, the community was still dominated by opportunists such as *Capitella cf. captata*, and even periods of 12 to 14 years have been recorded at various organic effluent disposal sites (Johnson and Frid, 1995, Moore and Rodger, 1991). If the final goal, after a cessation of a fish farm, is for the community to reach its initial state and faunal composition, then more investigations should be performed to find out whether the amount of biodiversity has an effect on the time an ecosystem needs to reach the final successional stage. However, when choosing a location for placement of fish farms, if only considering the degree of functioning by the ecosystem, both well-flushed and more quiescent watered ecosystems can be considered, as both may be fully capable of processing the present levels of organic loading from the salmon fish farms.

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Appendix A - Dissimilarity

| <i>Groups F1(0) & F1(500)</i> | | | | | | | |
|-----------------------------------|-------------|---------------|---------|---------|----------|-------|--|
| Average dissimilarity = 75,17 | | | | | | | |
| Species | Group F1(0) | Group F1(500) | Av.Diss | Diss/SD | Contrib% | Cum.% | |
| | Av.Abund | Av.Abund | | | | | |
| Nematoda | 453 | 32 | 41,57 | 1,7 | 55,3 | 55,3 | |
| Capitellidae | 86 | 1 | 12,71 | 1,79 | 16,91 | 72,2 | |
| Cirratulidae | 89 | 20 | 9,52 | 1,14 | 12,67 | 84,87 | |
| Oligochaeta | 11 | 21 | 2,06 | 1,11 | 2,74 | 87,61 | |
| Dorvilleidae | 17 | 1 | 1,92 | 1,18 | 2,56 | 90,17 | |

| <i>Groups F1(0) & F2(0)</i> | | | | | | | |
|---------------------------------|-------------|-------------|---------|---------|----------|-------|--|
| Average dissimilarity = 98,60 | | | | | | | |
| Species | Group F1(0) | Group F2(0) | Av.Diss | Diss/SD | Contrib% | Cum.% | |
| | Av.Abund | Av.Abund | | | | | |
| Nematoda | 453 | 1 | 30,74 | 1,63 | 31,18 | 31,18 | |
| Vigtorniella ardabilia | 0 | 278 | 21,04 | 1,95 | 21,34 | 52,52 | |
| Capitella capitata | 0 | 238 | 19,64 | 2,09 | 19,92 | 72,44 | |
| Capitellidae | 86 | 3 | 7,16 | 1,97 | 7,27 | 79,71 | |
| Cirratulidae | 89 | 0 | 7,11 | 1,3 | 7,21 | 86,92 | |
| Palpiphitime lobifera | 0 | 74 | 5,53 | 2 | 5,61 | 92,52 | |

| <i>Groups F1(500) & F2(0)</i> | | | | | | | |
|-----------------------------------|---------------|-------------|---------|---------|----------|-------|--|
| Average dissimilarity = 98,69 | | | | | | | |
| Species | Group F1(500) | Group F2(0) | Av.Diss | Diss/SD | Contrib% | Cum.% | |
| | Av.Abund | Av.Abund | | | | | |
| Vigtorniella ardabilia | 0 | 278 | 34,71 | 2,88 | 35,17 | 35,17 | |
| Capitella capitata | 0 | 238 | 33,51 | 2,65 | 33,96 | 69,13 | |
| Palpiphitime lobifera | 0 | 74 | 9,15 | 3,06 | 9,27 | 78,4 | |

| | | | | | | |
|--------------|----|---|------|------|------|-------|
| Nematoda | 32 | 1 | 4,56 | 2,6 | 4,62 | 83,02 |
| Bivalvia | 21 | 0 | 2,99 | 1,92 | 3,03 | 86,05 |
| Oligochaeta | 21 | 0 | 2,99 | 1,54 | 3,03 | 89,08 |
| Cirratulidae | 20 | 0 | 2,93 | 1,71 | 2,97 | 92,06 |

Groups F1(0) & F2(500)

Average dissimilarity = 84,55

| Species | Group F1(0) | Group F2(500) | Av.Diss | Diss/SD | Contrib% | Cum.% |
|--------------|-------------|---------------|---------|---------|----------|-------|
| | Av.Abund | Av.Abund | | | | |
| Nematoda | 453 | 10 | 47,95 | 2,04 | 56,72 | 56,72 |
| Capitellidae | 86 | 1 | 14,22 | 1,65 | 16,82 | 73,53 |
| Cirratulidae | 89 | 34 | 9,86 | 1,14 | 11,66 | 85,19 |
| Bivalvia | 13 | 1 | 2,26 | 1,05 | 2,67 | 87,86 |
| Dorvilleidae | 17 | 2 | 2,06 | 1,25 | 2,44 | 90,3 |

Groups F1(500) & F2(500)

Average dissimilarity = 61,09

| Species | Group F1(500) | Group F2(500) | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---------------|---------------|---------------|---------|---------|----------|-------|
| | Av.Abund | Av.Abund | | | | |
| Nematoda | 32 | 10 | 11,75 | 1,77 | 19,23 | 19,23 |
| Cirratulidae | 20 | 34 | 9,86 | 1,7 | 16,14 | 35,36 |
| Bivalvia | 21 | 1 | 9,56 | 2,31 | 15,65 | 51,01 |
| Oligochaeta | 21 | 3 | 9,31 | 1,74 | 15,24 | 66,25 |
| Syllidae | 4 | 3 | 1,87 | 1,27 | 3,07 | 69,32 |
| Spionidae | 4 | 6 | 1,59 | 1,18 | 2,6 | 71,92 |
| Echiura | 3 | 0 | 1,55 | 1,07 | 2,53 | 74,45 |
| Maldanidae | 1 | 3 | 1,49 | 0,87 | 2,44 | 76,89 |
| Lumbrineridae | 3 | 3 | 1,18 | 1,04 | 1,94 | 78,83 |
| Pycnogonida | 2 | 0 | 0,99 | 3,12 | 1,61 | 80,44 |
| Dorvilleidae | 1 | 2 | 0,79 | 0,95 | 1,3 | 81,74 |
| Hesionidae | 2 | 0 | 0,77 | 1,21 | 1,25 | 83 |
| Capitellidae | 1 | 1 | 0,75 | 0,88 | 1,23 | 84,22 |

| | | | | | | |
|--------------------|---|---|------|------|------|-------|
| Ophiuroidea | 2 | 1 | 0,71 | 1,15 | 1,17 | 85,39 |
| Unknown polychaeta | 1 | 1 | 0,7 | 1,24 | 1,15 | 86,54 |
| Paraonidae | 2 | 1 | 0,65 | 1,17 | 1,07 | 87,61 |
| Ampharetidae | 1 | 0 | 0,6 | 0,84 | 0,98 | 88,58 |
| Amphipoda | 2 | 1 | 0,52 | 1,33 | 0,85 | 89,44 |
| Glyceridae | 1 | 1 | 0,52 | 1,2 | 0,85 | 90,28 |

Groups F2(0) & F2(500)
Average dissimilarity =
98,58

| Species | Group F2(0) | Group F2(500) | Av.Diss | Diss/SD | Contrib% | Cum.% |
|------------------------|-------------|---------------|---------|---------|----------|-------|
| | Av.Abund | Av.Abund | | | | |
| Vigtorniella ardabilia | 278 | 0 | 37,62 | 2,99 | 38,16 | 38,16 |
| Capitella capitata | 238 | 0 | 36,54 | 2,62 | 37,07 | 75,23 |
| Palpiphitime lobifera | 74 | 0 | 9,91 | 3,22 | 10,05 | 85,28 |
| Cirratulidae | 0 | 34 | 5,24 | 1,67 | 5,32 | 90,6 |

Appendix B – Raw data (Abundance, biomass and C-uptake)

| Higher taxa | Taxa | F1(0) | | | F1(500) | | |
|--------------------|-----------------------|-------------------------|------------------------------|----------------------------|-------------------------|------------------------------|----------------------------|
| | | average abundance / m-2 | biomass (mg dryweight / m-2) | c uptake (mg C/ m-2/day-1) | average abundance / m-2 | biomass (mg dryweight / m-2) | c uptake (mg C/ m-2/day-1) |
| Aplacophora | Aplacophora total | 99 | 0 | 0 | 80 | 0 | 0 |
| | Caudofoveata | 66 | 36,9277383 | 0,00904825 | 40 | 48,8318022 | 0,012456863 |
| | Solenogastres | 33 | 54,6090093 | 0 | 40 | 0,7819384 | 0,000350154 |
| Bivalvia | | 2653 | 331,11225 | 0,84757366 | 4098 | 207,458729 | 1,245001254 |
| Crustacea | Amphipoda | 33 | 0,73480337 | 0,00034476 | 358 | 5,12951354 | 0,000692119 |
| | Caprellidae | 33 | 1,57234646 | 0,00650769 | 40 | 0 | 4,41055E-05 |
| | Copepoda | 0 | 0 | 0 | 0 | 0 | 0 |
| | Crustacea total | 298 | 3,70031593 | | 517 | 5,12951354 | |
| | Cumacea | 133 | 1,39316611 | 0,01256538 | 0 | 0 | 0 |
| | Harpacticoidae | 99 | 0 | 0,00014666 | 40 | 0 | 2,39272E-05 |
| | Tanaidacea | 0 | 0 | 0 | 80 | 0 | 0,003023332 |
| Echiura | | 398 | 620,199905 | 0,07932881 | 637 | 90,2365835 | 0,243755611 |
| Gastropoda | | 265 | 4,95859587 | 0,00222062 | 80 | 0,50061567 | 0,00018539 |
| Hydrozoa | | 0 | 0 | 0 | 0 | 0 | 0 |
| Nematoda | | 90155 | 964,511014 | 0,08429656 | 6366 | 26,1543421 | 0,001881433 |
| Nemertea | | 33 | 900,714132 | 0,11321461 | 80 | 384,546485 | 0,077013333 |
| Oligochaeta | | 2188 | 33,276145 | 0,03842745 | 4098 | 42,0839909 | 0,042042605 |
| Ophiuroidea | | 962 | 6953,38973 | 1,51858614 | 318 | 2242,67922 | 0,318307751 |
| Polychaeta | Ampharetidae | 66 | 4,57774455 | 0,08993334 | 239 | 1,58774439 | 0,040678626 |
| | Arabellidae | 0 | 0 | 0 | 40 | 33,8800946 | 0,004256965 |
| | Arenicolidae | 99 | 416,595382 | 0,09500136 | 0 | 0 | 0 |
| | Capitella capitata | 0 | 0 | 0 | 0 | 0 | 0 |
| | Capitellidae | 17043 | 4224,4574 | 8,600334 | 239 | 2,69404173 | 0,020560017 |
| | Chaetopteridae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Cirratulidae | 17607 | 5621,33533 | 8,99408684 | 3979 | 1426,67157 | 3,565545858 |
| | Dorvilleidae | 3448 | 83,6691529 | 1,56779401 | 119 | 6,53726565 | 0,002599419 |
| | Eunicidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Glyceridae | 232 | 1799,08675 | 0,0160516 | 119 | 11,2024682 | 0,00300411 |
| | Goniadidae | 0 | 0 | 0 | 40 | 35,1182838 | 0,002716938 |
| | Hesionidae | 564 | 68,6297674 | 0,01712815 | 318 | 28,3419402 | 0,004033612 |
| | Heterospionidae | 0 | 0 | 0 | 199 | 13,9422315 | 0,089375676 |
| | Lumbrineridae | 0 | 0 | 0 | 517 | 254,822119 | 0,009385083 |
| | Maldanidae | 0 | 157,336201 | 0,00228925 | 199 | 70,958465 | 0,026162721 |
| | Nereididae | 0 | 0 | 0 | 40 | 2,65879995 | 0,001011408 |
| | Onuphidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Opheliidae | 365 | 16,0547361 | 0,13331478 | 199 | 1,847038 | 0,010424259 |
| | Oweniidae | 99 | 516,944857 | 0,31265049 | 40 | 2,64830074 | 0,08668515 |
| | Palpiphitima lobifera | 66 | 1,04951403 | 0 | 0 | 0 | 0 |
| | Paraonidae | 0 | 0 | 0 | 318 | 10,1651512 | 0,003197634 |
| | Pectinariidae | 33 | 68,1863158 | 0,0223566 | 40 | 281,331242 | 0,102385881 |
| | Phyllodocidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Polychaeta fragments | | 1632,96321 | 1,04742687 | | 538,784924 | 1,421499796 |
| | Polychaeta total | 42342 | 15857,6627 | | 9032 | 6330,49255 | |
| | Polynoidae | 0 | 0 | 0 | 40 | 1,25678388 | 0,000776621 |
| | Sabellidae | 232 | 22,2634561 | 0,03864971 | 159 | 0,59147854 | 0,00710798 |
| Scalibregmatidae | 99 | 92,2368562 | 0,10890661 | 80 | 30,357438 | 0,004982786 | |
| Spionidae | 696 | 139,821972 | 0,61560376 | 796 | 118,087515 | 0,573231793 | |
| Syllidae | 1359 | 13,560169 | 0,00315033 | 875 | 13,3366032 | 0,007853904 | |
| Terebellida | 99 | 8,51363475 | 0 | 159 | 401,875468 | 0,004877208 | |
| Trichobranchidae | 66 | 31,3322969 | 0,10875968 | 0 | 0 | 0 | |

| | | | | | | |
|-------------------------------|-----|------------|------------|-----|------------|-------------|
| Unidentified polychaeta | 166 | 2,18813244 | 0,00070799 | 279 | 18,019708 | 0,036425532 |
| Vigtorniella ardabilia | 0 | 0 | 0 | 0 | 0 | 0 |
| Porifera | 0 | | 0 | 0 | | 0 |
| Pycnogonida | 66 | 5,7310385 | 0,00095503 | 398 | 27,6040709 | 0,016930172 |
| Scaphopoda | 0 | 0 | 0 | 0 | 0 | 0 |
| Sipuncula | 33 | 395,911944 | 0 | 0 | 0 | 0 |
| Unidentified | 33 | 351,378495 | 0,057709 | 0 | 0 | 0 |
| Unidentified fragments | | 46,766825 | 0,00873724 | | 284,15927 | 0,069206826 |

| Higher taxa | Taxa | F2(0) | | | F2(500) | | |
|--------------------|-----------------------|-------------------------|------------------------------|----------------------------|-------------------------|------------------------------|----------------------------|
| | | average abundance / m-2 | biomass (mg dryweight / m-2) | c uptake (mg C/ m-2/day-1) | average abundance / m-2 | biomass (mg dryweight / m-2) | c uptake (mg C/ m-2/day-1) |
| Aplacophora | Aplacophora total | 0 | 0 | 0 | 232 | 0,5693585 | 0 |
| | Caudofoveata | 0 | 0 | 0 | 99 | 18,0174175 | 0,00390464 |
| | Solenogastres | 0 | 0 | 0 | 33 | 4,04617031 | 0,00077144 |
| Bivalvia | | 0 | 0 | 0 | 199 | 4,91335078 | 0,00123412 |
| Crustacea | Amphipoda | 0 | 0 | 0 | 166 | 13,6032923 | 0,08405835 |
| | Caprellidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Copepoda | 0 | 0 | 0 | 99 | 3,38769271 | 0,00022537 |
| | Crustacea total | 4211 | 10,8520143 | | 431 | 14,1446274 | |
| | Cumacea | 0 | 0 | 0 | 33 | 0 | 0 |
| | Harpacticoidae | 4211 | 10,8520143 | 0,04026824 | 0 | 0 | 0 |
| | Tanaidacea | 0 | 0 | 0 | 133 | 0,5413351 | 0,01497471 |
| Echiura | | 0 | 0 | 0 | 66 | 16,8739776 | 0,00172527 |
| Gastropoda | | 0 | 0 | 0 | 0 | 0 | 0 |
| Hydrozoa | | 0 | 0 | 0 | 33 | 1,97311745 | 0,00046385 |
| Nematoda | | 199 | 0,39550082 | 8,47223E-05 | 1956 | 9,74763776 | 0,00281281 |
| Nemertea | | 0 | 0 | 0 | 0 | 0 | 0 |
| Oligochaeta | | 0 | 0 | 0 | 531 | 11,5442663 | 0,0086796 |
| Ophiuroidea | | 0 | 0 | 0 | 133 | 14,4622974 | 0,05865473 |
| Polychaeta | Ampharetidae | 0 | 0 | 0 | 33 | 1,82626619 | 0,00127575 |
| | Arabellidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Arenicolidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Capitella capitata | 47349 | 29887,8997 | 31,09612132 | 0 | 0 | 0 |
| | Capitellidae | 497 | 32182,7707 | 0 | 166 | 13,6548405 | 0,00559466 |
| | Chaetopteridae | 0 | 0 | 0 | 66 | 0,8954842 | 0,02170418 |
| | Cirratulidae | 33 | 27,8181167 | 0 | 6698 | 772,028611 | 4,10850368 |
| | Dorvilleidae | 232 | 317,902241 | 0,052393546 | 298 | 4,6242756 | 0,12327381 |
| | Eunicidae | 0 | 0 | 0 | 0 | 26,846248 | 0,28452762 |
| | Glyceridae | 0 | 0 | 0 | 166 | 2,33596955 | 0,00084458 |
| | Goniadidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Hesionidae | 0 | 0 | 0 | 33 | 0,48792202 | 0 |
| | Heterospionidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Lumbrineridae | 0 | 0 | 0 | 597 | 44,3855427 | 0,02935868 |
| | Maldanidae | 0 | 0 | 0 | 630 | 95,6623379 | 0,0165972 |
| | Nereididae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Onuphidae | 0 | 0 | 0 | 66 | 12,5761802 | 0,01773383 |
| | Opheliidae | 0 | 0 | 0 | 0 | 0 | 0 |
| | Oweniidae | 0 | 0 | 0 | 33 | 1,10902702 | 0,00051155 |
| | Palpiphitime lobifera | 14689 | 292,272997 | 1,272834765 | 0 | 0 | 0 |
| | Paraonidae | 0 | 0 | 0 | 166 | 113,960675 | 0,49695881 |
| | Pectinariidae | 0 | 0 | 0 | 66 | 71,1987584 | 0,00062747 |
| | Phyllodocidae | 0 | 0 | 0 | 133 | 8,04882804 | 0,26707983 |

| | | | | | | |
|-------------------------------|--------|------------|-------------|-------|------------|------------|
| Polychaeta fragments | | 50,0553182 | 0,11684044 | | 241,159736 | 1,24502131 |
| Polychaeta total | 118803 | 35314,0334 | | 11273 | 1935,59997 | |
| Polynoidae | 0 | 0 | 0 | 0 | 0 | 0 |
| Sabellidae | 0 | 0 | 0 | 0 | 0 | 0 |
| Scalibregmatidae | 0 | 0 | 0 | 0 | 0 | 0 |
| Spionidae | 663 | 684,141851 | 0,313062435 | 1194 | 133,434288 | 1,95955168 |
| Syllidae | 0 | 0 | 0 | 630 | 12,9462842 | 0,05629487 |
| Terebellida | 0 | 0 | 0 | 0 | 0 | 0 |
| Trichobranchidae | 0 | 0 | 0 | 33 | 1,3938908 | 0,00027078 |
| Unidentified polychaeta | 133 | 1,86233358 | 2,412993469 | 265 | 4,27542659 | 0,03363099 |
| Vigtorniella ardabilia | 55207 | 1351,43488 | 0,474662198 | 0 | 0 | 0 |
| Porifera | 0 | | 0 | 199 | | 0 |
| Pycnogonida | 0 | 0 | 0 | 0 | 0 | 0 |
| Scaphopoda | 0 | 0 | 0 | 33 | 7,28141963 | 0 |
| Sipuncula | 0 | 0 | 0 | 33 | 13,4892597 | 0,00206 |
| Unidentified | 0 | 0 | 0 | 0 | 3,73253941 | 0,00084463 |
| Unidentified fragments | 0 | 0 | 0 | | 2,05515399 | 0,01013875 |

Appendix C – Statistical results

Abundance

Kruskal-Wallis One Way Analysis of Variance on Ranks

| Group | N | Missing | Median | 25 % | 75 % |
|---------|---|---------|----------|----------|----------|
| F1(0) | 6 | 0 | 134883,8 | 85943,67 | 193472,7 |
| F1(500) | 5 | 0 | 25663,74 | 22381,16 | 29045,78 |
| F2(0) | 6 | 0 | 106633,8 | 83705,55 | 175617,5 |
| F2(500) | 6 | 0 | 16114,44 | 10693,22 | 19894,37 |

H = 18,100 with 3 degrees of freedom. (P = <0,001)

All Pairwise Multiple Comparison Procedures (Dunn's Method)

| Comparison | Diff of Ranks | Q | P<0,05 | |
|--------------------|---------------|-------|-------------|------------------|
| F1(0) vs F2(500) | 14,167 | 3,618 | Yes | |
| F1(0) vs F1(500) | 9,033 | 2,2 | No | |
| F1(0) vs F2(0) | 0,667 | 0,17 | Do Not Test | Do Not Test = No |
| F2(0) vs F2(500) | 13,5 | 3,448 | Yes | |
| F2(0) vs F1(500) | 8,367 | 2,037 | Do Not Test | |
| F1(500) vs F2(500) | 5,133 | 1,25 | No | |

Biomass

Kruskal-Wallis One Way Analysis of Variance on Ranks

| Group | N | Missing | Median | 25 % | 75 % |
|---------|---|---------|----------|----------|----------|
| F1(0) | 6 | 0 | 23914,22 | 14058,54 | 37693,14 |
| F1(500) | 5 | 0 | 4591,776 | 3489,021 | 18441,74 |
| F2(0) | 6 | 0 | 46133,05 | 35010,36 | 55608,18 |
| F2(500) | 6 | 0 | 1861,32 | 1803,212 | 2413,263 |

H = 18,769 with 3 degrees of freedom. (P = <0,001)

All Pairwise Multiple Comparison Procedures (Dunn's Method)

| Comparison | Diff of Ranks | Q | P<0,05 |
|--------------------|---------------|-------|-------------|
| F2(0) vs F2(500) | 16,333 | 4,171 | Yes |
| F2(0) vs F1(500) | 10,033 | 2,443 | No |
| F2(0) vs F1(0) | 5,333 | 1,362 | Do Not Test |
| F1(0) vs F2(500) | 11 | 2,809 | Yes |
| F1(0) vs F1(500) | 4,7 | 1,144 | Do Not Test |
| F1(500) vs F2(500) | 6,3 | 1,534 | No |

Taxa richness

Kruskal-Wallis One Way Analysis of Variance on Ranks

| Group | N | Missing | Median | 25 % | 75 % |
|---------|---|---------|--------|-------|-------|
| F1(0) | 6 | 0 | 18,5 | 15,5 | 20,75 |
| F1(500) | 5 | 0 | 21 | 16,5 | 22 |
| F2(0) | 6 | 0 | 6 | 6 | 7,25 |
| F2(500) | 6 | 0 | 17 | 11,25 | 18 |

H = 13,947 with 3 degrees of freedom. (P = 0,003)

All Pairwise Multiple Comparison Procedures (Dunn's Method)

| Comparison | Diff of Ranks | Q | P<0,05 |
|--------------------|---------------|-------|-------------|
| F1(500) vs F2(0) | 13,833 | 3,368 | Yes |
| F1(500) vs F2(500) | 6,833 | 1,664 | No |
| F1(500) vs F1(0) | 2,333 | 0,568 | Do Not Test |
| F1(0) vs F2(0) | 11,5 | 2,937 | Yes |
| F1(0) vs F2(500) | 4,5 | 1,149 | Do Not Test |
| F2(500) vs F2(0) | 7 | 1,788 | No |

Taxa evenness

Kruskal-Wallis One Way Analysis of Variance on Ranks

| Group | N | Missing | Median | 25 % | 75 % |
|---------|---|---------|--------|-------|-------|
| F1(0) | 6 | 0 | 0,478 | 0,292 | 0,609 |
| F1(500) | 5 | 0 | 0,761 | 0,678 | 0,775 |
| F2(0) | 6 | 0 | 0,601 | 0,529 | 0,625 |
| F2(500) | 6 | 0 | 0,717 | 0,654 | 0,791 |

H = 17,091 with 3 degrees of freedom. (P = <0,001)

All Pairwise Multiple Comparison Procedures (Dunn's Method)

| Comparison | Diff of Ranks | Q | P<0,05 |
|--------------------|---------------|-------|--------|
| F1(500) vs F1(0) | 13,633 | 3,32 | Yes |
| F1(500) vs F2(0) | 10,967 | 2,67 | Yes |
| F1(500) vs F2(500) | 1,467 | 0,357 | No |
| F2(500) vs F1(0) | 12,167 | 3,107 | Yes |
| F2(500) vs F2(0) | 9,5 | 2,426 | No |
| F2(0) vs F1(0) | 2,667 | 0,681 | No |

C-uptake

Kruskal-Wallis One Way Analysis of Variance on Ranks

| Group | N | Missing | Median | 25 % | 75 % |
|---------|---|---------|--------|--------|--------|
| F1(0) | 4 | 0 | 36,172 | 35,702 | 36,555 |
| F1(500) | 4 | 0 | 8,491 | 6,467 | 14,982 |
| F2(0) | 4 | 0 | 52,059 | 40,287 | 68,734 |
| F2(500) | 4 | 0 | 12,152 | 8,93 | 18,795 |

H = 13,059 with 3 degrees of freedom. (P = 0,005)

All Pairwise Multiple Comparison Procedures (Tukey Test)

| Comparison | Diff of Ranks | q | P<0,05 |
|--------------------|---------------|-------|-------------|
| F2(0) vs F1(500) | 44 | 4,621 | Yes |
| F2(0) vs F2(500) | 36 | 3,781 | Yes |
| F2(0) vs F1(0) | 16 | 1,68 | No |
| F1(0) vs F1(500) | 28 | 2,941 | No |
| F1(0) vs F2(500) | 20 | 2,1 | Do Not Test |
| F2(500) vs F1(500) | 8 | 0,84 | Do Not Test |

Feeding guild vs site

Two-way ANOVA

| Response: uptake | Df | Sum sq | Mean sq | F value | Pr(>F) |
|------------------|----|--------|---------|---------|---------------|
| guild | 4 | 5088,4 | 1272,11 | 13,7484 | 2,109e-07 *** |
| site | 3 | 1921,4 | 640,48 | 6,922 | 0,0006258 *** |
| guild:site | 9 | 7528,4 | 836,49 | 9,0404 | 1,226e-07 *** |
| Residuals | 45 | 4163,7 | 92,53 | | |

Holm-Sidak multiple comparison procedure

| Comparison | Diff of Means | t | Unadjusted P | Critical Level | Significant? |
|-------------|---------------|--------|--------------|----------------|--------------|
| SSDF vs. CV | 14,865 | 3,977 | <0,001 | 0,005 | Yes |
| SSDF vs. BV | 15,147 | 3,728 | <0,001 | 0,006 | Yes |
| SSDF vs. SF | 7,774 | 2,08 | 0,042 | 0,006 | No |
| SF vs. CV | 7,091 | 1,897 | 0,063 | 0,007 | No |
| SF vs. BV | 7,373 | 1,815 | 0,075 | 0,009 | No |
| SSDF vs. FF | 11,595 | 1,398 | 0,168 | 0,01 | No |
| SF vs. FF | 3,821 | 0,461 | 0,647 | 0,013 | No |
| FF vs. BV | 3,551 | 0,421 | 0,676 | 0,017 | No |
| FF vs. CV | 3,27 | 0,394 | 0,695 | 0,025 | No |
| CV vs. BV | 0,282 | 0,0693 | 0,945 | 0,05 | No |