UiT The Arctic University of Norway

Department of Arctic and Marine Biology

Estimating effects of river runoff, predation, and fish carcasses on intertidal macrobenthic community and food-web structure in a sub-Arctic estuary

Frederike Hoppmann

Master's thesis in Biology BIO-3950, May 2024

Abstract

Coastal benthic organisms play an essential role in many ecosystem functions, such as organic matter utilization and regeneration of nutrients. In northern Norway, coastal ecosystems experience snowmelt-induced increased river runoff in early summer, arrival of poleward migrating predators, and invasive pink salmon runs, potentially affecting macrobenthic communities and food-web structures. This study investigated the impact of river runoff, predation, and carcasses of migratory fish on intertidal benthic macrofauna community and food-web composition in a fjord in northern Norway. Cage experiments were conducted at two sites, one more river-influenced (river site) and the other less river-influenced (marine site), from June (during increased river runoff) until fall (end of September/beginning of October, after increased river runoff) 2023. The total abundance and biomass, measures of biodiversity (taxon richness, Shannon index, evenness), and community structure of the macrobenthos were recorded for community analysis. Additionally, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of the five most abundant taxa (Oligochaeta indet., *Macoma calcarea*, Spionidae indet., *Euchone* sp., and Chironomidae indet.) were analyzed to identify changes in food-web composition. In fall, total benthic biomass showed an increase (marine site) and a decrease (river site) compared to June, while total abundance, measures of diversity, and community structure remained unchanged. The $\delta^{13}C$ values increased for several taxa from June to fall, indicating a shift in carbon sources from more terrestrial organic matter sources in June to marine organic matter in fall. The exclusion of predators increased total biomass at both sites and total abundance at the river site. Adding fish to simulate organic input by carcasses of migratory salmon did not influence the macrobenthos total abundance, biomass, or biodiversity, but fish was included to varying degrees into the diet of all taxa (indicated by higher $\delta^{15}N$ values in fall) at both sites. The study showed that river runoff, as well as predation and fish carcasses, have limited – yet some – effects on the benthic macrofauna community and food web.

Keywords: intertidal benthic macrofauna, stable isotopes, pink salmon, Norwegian fjord, cages, field experiment

Acknowledgments

I want to express my deepest gratitude to everyone who has contributed to this over-one-year master's thesis project. I am incredibly thankful for all the opportunities I have been given, the people I have met, and the many things I have learned during this time.

First and foremost, I would like to thank my supervisors, Markus Molis and Bodil Bluhm, for sharing their knowledge and passion about the intertidal zone and benthic organisms. Thank you for your time and patience and for always reaching out a hand whenever I had a bunch of question marks in my head.

A special thank you to Maeve McGovern and Rolf Gradinger – my supervisors of heart. You were a tremendous help in so many ways from the beginning, whether in the lab, in the field, or by providing me with additional data. I highly appreciate your encouragement and support throughout the whole time.

Additionally, I would like to thank all the fantastic people who helped in the field and the lab: Thank you, Christian Buschbaum, Johanna Hovinen, and Fride Tønning, for your expertise and for introducing me to the macrobenthic community. Thank you, Victoria, Femke, Emily, and Charly, for your assistance and our great talks. The project would not have worked without you.

Thank you to the Fram Center for financial support within the "Catchment to Coast" project and the project coordinators Amanda Poste and André Frainer.

I am thankful for my friends who have patiently listened to all the ups and downs during this time and rejoiced or built me up again. You made the many hours in the lab more enjoyable, encouraged me to think in other directions as well, and created awesome shorter and longer breaks, wonderfully distracting me from the stress.

Lastly, a heartfelt thank you to my family and the fluffies in the backyard. Thank you for always encouraging me to follow my dreams and for your endless support and trust. Thank you to my brother; you sparked my interest in studying in the Arctic, shared your love for Norway, and continuously backed me in my endeavors.

Thank you! Danke! Tusen takk! Tack så mycket! Dankjewel! Kiitos!

Table of Contents

List of Tables

List of Figures

1 Introduction

1.1 Estuaries

Estuaries have a major function in aquatic systems by linking freshwater and marine habitats. They occur where a river meets the ocean, creating a unique brackish habitat and posing physiological challenges for the organisms living within this habitat. In estuaries, environmental drivers like dissolved oxygen concentration, temperature, salinity, and river runoff have a large seasonal and inter-annual variability and structure estuarine communities (e.g., Kaiser & Williams 2011). In addition, in intertidal areas, organisms face periodic desiccation and reduced food availability during low tides. These factors make it challenging for organisms to live in intertidal estuarine habitats, but the benthic taxa that adapted to these conditions are essential for estuarine ecosystem functions. With activities such as respiration, biomass production, and bioturbation, benthic macrofauna process organic matter (OM) and make it accessible for other taxa in the food web (Villnäs et al. 2019).

As a consequence of climate change, more freshwater is expected to enter estuaries through rivers at high latitudes, e.g., due to increasing precipitation and thawing permafrost (Larsen et al. 2011, Bring & Destouni 2014, de Wit et al. 2016, Ahmed et al. 2020). River runoff can enhance nutrient concentrations in estuaries, which may affect the organisms in the intertidal zone. For example, Posey et al. (2006) showed that higher nutrient levels and the absence of predators increase macrofauna biomass while decreasing their abundance, indicating a complex response to nutrient availability.

1.2 Benthic communities

Benthic infauna communities are important components in coastal ecosystems. They, for example, utilize marine and terrestrial OC, regenerate nutrients, and provide food for organisms at higher trophic levels, which is why their composition and functional characteristics matter (Middelburg 2018, Thoms et al. 2018, Villnäs et al. 2019, McGovern et al. 2020). The extent to which benthic infauna contribute to ecosystem processes depends on the faunal community structure (e.g., individual abundance or functional groups such as feeding type or mobility; Kristensen 2000, Biles et al. 2002). Thus, environmental changes like increasing river runoff change community composition and, therefore, influence the functioning of an ecosystem (e.g., in terms of regeneration of nutrients or decomposition of OM; McGovern et al. 2020). This is

why it is essential to know what lives in coastal sediments, what affects these organisms, and how these organisms respond to changing environmental conditions. In northern Norway, common taxa in soft-bottom coastal habitats are for example polychaetes (e.g., *Pygospio elegans*, *Arenicola marine*, *Fabricia stellaris*), bivalves (e.g., *Macoma* sp.), and oligochaetes (Oug 2001). In the intertidal zone, species with limited mobility (e.g., the filter feeder *Pygospio elegans,* Taghon et al. 1980) have limited access to feed during low tide.

In glacial estuaries, benthic communities are primarily structured by river influence due to high sediment load. Close to the river mouth, sessile, tube-dwelling, and filter-suspension feeders occur in very low abundances, while motile and deposit feeders dominate. The opposite pattern is true for habitats further out in the fjord (Ugelstad 2019). In sub-Arctic fjords, benthic community structures also show a clear difference between inner and outer fjord as well as between different depths (Jordà Molina et al. 2019). According to the Remane model (1934) (Figure 1), macrobenthic invertebrate species richness follows a specific pattern along the salinity-based river-estuary-marine gradient. The model states that species richness is the lowest at a salinity of seven, with brackish species dominating. Below and above a salinity of seven, species richness strongly increases, with freshwater (<7) and marine species (>7) dominating, respectively; the total abundance and biomass are expected to be relatively equal. However, even though this model is widely applicable, it was created based on data from the Baltic Sea with overall brackish water conditions and is missing some information, e.g., the ability of marine organisms to tolerate and live in lower salinity systems (discussed in Whitfield et al. 2012). Other research indicates an increase in species diversity and a lower total abundance under more marine conditions and *vice versa* with more freshwater conditions (Ugelstad 2019).

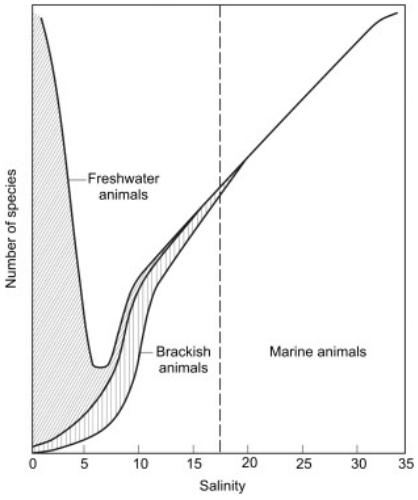


Figure 1. Remane model redraw by Withfield et al. 2012 of the original model by Remane 1934. The grey area represents freshwater animals, the white area below the curve represents marine animals, and the vertical striped area represents brackish animals. The vertical dashed line indicates the salinity of about 50 % of typical seawater.

1.3 Increased river runoff effects

Rivers collect catchment water and discharge it into the oceans, bringing terrestrial nutrients, OM, and contaminants into estuaries. The flow rate, as well as the transported nutrient amounts, strongly vary by river, season, and year. Especially in Arctic and sub-Arctic regions, river discharge plays an important role as a substantial source of terrestrial nutrients and dissolved organic matter for coastal areas (Frigstad et al. 2020). Here, the seasonal flux is extremely high during the snowmelt in early summer. During these few weeks, more than half of the total annual flux of freshwater, OM, suspended particulate matter, nutrients, and contaminants are delivered to coastal ecosystems (Finlay et al. 2006, Zolkos et al. 2020, Frigstad et al. 2020, Poste et al. 2021). As a result, light level, nutrient and organic carbon (OC) availability, and sedimentation rates in estuaries change substantially with season (Poste et al. 2021).

River runoff can have various impacts on coastal benthic communities. The nutrient input can increase primary production and this increased food availability can result in higher macrofauna densities (Montagna & Kalke 1992, McGovern et al. 2020). However, higher sedimentation rates can lead to "coastal darkening", reducing light intensity in estuaries. This, in turn, can decrease primary production and harm benthic communities (Edgar & Barrett 2000, Norkko et al. 2002, McGovern et al. 2019, Kokarev et al. 2021). River runoff can further reduce taxonomic and functional diversity through high environmental stress and high levels of disturbance (McGovern et al. 2020). Moreover, river runoff can influence the quality and quantity of OM in estuaries directly by transporting terrestrial-derived OM directly into estuaries (Monteith et al. 2007, Aksnes et al. 2009, Frigstad et al. 2013, de Wit et al. 2016), and indirectly by shaping environmental gradients, which influence benthic infauna community composition and functional characteristics that are accountable to what degree marine and terrestrial-derived OM are processed (Middelburg 2018, Thoms et al. 2018, Villnäs et al. 2019, McGovern et al. 2020). The utilization of terrestrial OM can be measured using stable isotopes of carbon. Lower $\delta^{13}C$ values (around -25 ‰ and lower) indicate the assimilation of terrestrial and higher $\delta^{13}C$ values (> -25 ‰) of marine OM (Dunton et al. 2012).

In general, the strength of the runoff impact depends on several factors such as the timing of increased flow, human activity, or upstream land use (Jickells 1998, Mattsson et al. 2015). The impact of river runoff tends to be highest at the river mouth and decreases further out, depending on the coastal morphometry and the degree of marine water exchange (Poste et al. 2021). In this study, two sites with different levels of river influence were selected to investigate whether

estuarine benthic organisms respond differently to increased river runoff after snowmelt during summer than organisms in a more marine and less river-influenced habitat.

1.4 Predation impact

Predation is one factor influencing and structuring communities and populations (Sih et al. 1985, Freestone et al. 2011, 2021, Guzman et al. 2019). It can regulate communities in multiple ways and make predator-prey interactions highly complex. Predators, for example, directly limit the abundance of prey species, leading to top-down control by predators. Thereby, predators can indirectly affect the abundance and composition of other species within the community, which can result in cascading effects throughout the food web (Pace et al. 1999). This concept was, among others, observed in a study by Estes & Duggins (1995). They demonstrated top-down control of sea otters on sea urchins, which in turn influenced the abundance and distribution of kelp forests. Thus, by regulating sea urchin populations through predation, sea otters indirectly promote the persistence of kelp forests.

Studies from lower latitudes show that the exclusion of predators can have a significant influence by increasing prey abundance, taxon richness, and biomass, as well as by altering community composition (Reise 1977, Freestone et al. 2011, 2021, Lavender et al. 2014). However, there is also evidence that this predator impact decreases with increasing latitude (Freestone et al. 2011, 2021). This assumption is confirmed by predator-exclusion studies conducted in polar regions, e.g., on Svalbard (Petrowski et al. 2015, Díaz et al. 2023). Possible reasons explaining this pattern can be, for instance, more abundant and divers predators, higher predation rates, longer interaction durations, and larger predator body sizes in lower than in higher latitudes (Freestone et al. 2021).

Climate change is leading to changing environmental conditions, such as rising temperatures and an increase in extreme weather events all over the world (Mainka & Howard 2010). This can affect predator-prey relationships (Molis et al. 2019), as scientists observe and expect several species to expand their distribution range poleward with increasing water temperatures (Rahel & Olden 2008, García Molinos et al. 2016). With increasing numbers or longer seasonal presence of predator species (such as fish, crabs, and birds) in northern Norway, future predation pressure on benthic macrofaunal prey may increase.

To investigate the influence of predators on benthic communities, experimental studies with cages that exclude predators from a certain benthic area have repeatedly been carried out in the

past (e.g., Reise 1977, Freestone et al. 2011, 2021, Lavender et al. 2014, Petrowski et al. 2015, Díaz et al. 2023). Manipulative experiments by either excluding or adding certain species proved to be suitable ways to identify links between species or mechanisms in community patterns (Volkenborn & Reise 2007, Petrowski et al. 2015, Molis et al. 2019). The present study followed this cage approach by using fully covered cages to exclude larger epibenthic predators and investigate their impact on intertidal macrobenthos communities.

1.5 Pink salmon in northern Norway

The non-native pink salmon (*Oncorhynchus gorbuscha*) is becoming progressively dominant in Norwegian waters after its fry was introduced in rivers in the Kola Peninsula in the 1960s (Mo et al. 2018). By 2017, its numbers had strongly increased to several thousand individuals in rivers along the Norwegian coast (Sandlund et al. 2019). The anadromous species migrates up the rivers in large numbers every other year to reproduce primarily in August (Sandlund et al. 2019). After spawning, the adults die, and the carcasses remain in the rivers or are flushed out into the estuaries. The carcasses contain a large amount of nutrients (Hindar et al. 2020), which can enter the water and increase primary production (Cederholm et al. 1999).

However, studies about the nutrient concentrations originating from pink salmon carcasses are lacking in Norway, and so is research about the consequences for other organisms within rivers and estuaries. A first investigation by Hansen (UiT master thesis, unpublished data) from northern Norway shows that large amounts of pink salmon carcasses highly increase riverine nutrient concentrations and bacterial abundances. Bacteria are food for some benthic protists and invertebrates, allowing carbon and nutrients from pink salmon carcasses to enter the food web. Whether and how this also affects other species in rivers and estuaries is unknown for Norway's waters.

Studies from Alaska indicate that anadromous salmon, including pink salmon, and their carcasses contribute a large proportion of nutrients (nitrogen and phosphor) to rivers (Gende et al. 2004). The degree of utilization of carcass-derived nutrients depends on many abiotic and biotic factors such as in-stream physical structure, river discharge, spawning densities, feeding macroinvertebrates and fish species (Piorkowski 1995, Cederholm et al. 1999). Fujiwara & Highsmith (1997) found higher $\delta^{15}N$ values in macroalgae (*Ulva* sp.), demonstrating the uptake of fish carcass-derived nutrients. Additionally, the carcasses can contribute to a change in benthic macroinvertebrate community structure with more chironomids and generally higher

species abundances (Monaghan & Milner 2008) since they serve as a food source for macroinvertebrates (e.g., Chaloner & Wipfli 2002, Winder et al. 2005). Studies that placed fish carcasses directly on top of the sediment showed an increase in scavengers, shredders, and collectors (Monaghan & Milner 2008, Dunlop et al. 2021).

The present study used fish pieces of migratory fish hanging over the sediment. This approach should simulate fish nutrients and OC input from rivers with spawning and dead pink salmon potentially reaching Norwegian estuaries.

1.6 Aims and hypotheses

The overall aims of this study are to investigate whether total abundance and biomass, taxa diversity, community composition, and food-web structure of an intertidal benthic macrofauna community is affected by:

1) increased river runoff after snowmelt in summer
2) predation
3) carcasses of migratory fish

This was done using an experimental cage setup at two different locations: one in an estuary (hereafter river site) and one in an area with reduced river-influence (hereafter marine site) in a fjord in northern Norway. Based on the given background, the following hypotheses were formulated:

H1.1 Total benthic macrofauna abundance and biomass are hypothesized to be higher in fall compared to June for both, the marine and river, sites, while biodiversity is expected to decrease. Overall, river runoff effects are predicted to be stronger at the river than at the marine site due to the reduced freshwater amount reaching the marine site.

H1.2 Benthic macrofauna is expected to feed less on terrestrial organic matter (reflected in higher $\delta^{13}C$ values) in fall compared to June, due to reduced river inputs and higher availability of marine organic matter from the summer phytoplankton bloom. This change is hypothesized to be more pronounced at the river than at the marine site.

H2.1 Predator exclusion is proposed to not change benthic macrofauna abundance, biomass, and biodiversity, assuming predators do not structure macrobenthic communities at high latitudes.

H3.1 The additional fish food source is hypothesized to increase total abundance and biomass of benthic macrofauna. The new food source is expected to attract scavenger taxa.

H3.2 Benthic macrofauna is expected to utilize the additional fish as a food source, resulting in higher $\delta^{15}N$ values in fish-carcass relative to control treatments at both sites.

2 Material and Methods

2.1 Study sites

The study took place in 2023 at two sites located in the Malangenfjord system in Troms county, northern Norway. The river station (69°34.1754 N, 18°48.7195 E) was located in Målselvfjord while the marine station (69°39.4369 N, 18°38.2147 E) was located at the mouth of Rossfjordstraumen (Figure 2). The river station is seasonally influenced by freshwater and suspended sediment inputs from the Målselv river (Målselva, Wassmann et al. 1996), with peak discharge typically observed in early June (Appendix 1). The marine station lacks this high river influence. In fall 2023, during the final sampling, the marine station had a water temperature of 9.9 °C, a sediment temperature (1 cm depth) of 9.8 °C, and a water salinity of 30.0 (pure seawater salinity is around 34). The water at the river station was 10.8 °C, the sediment 8.4 °C and the salinity was 0.0. The macroalgae *Ascophyllum nodosum*, *Fucus vesiculosus*, *Ulva lactuca* were abundant at both sites. A common bird that feeds on macrobenthos at both study sites is, for example, the oystercatcher *Haematopus ostralegus* (own observation). An overview of the water nutrient and particulate organic carbon (POC) and dissolved organic carbon concentrations at both study sites is given in Table 1 (NIVA, unpublished data). The water samples were taken during sampling, but their analysis was not part of the thesis project and, therefore, is not further explained. Yet, in combination with the salinity measurements, the water chemical indicators confirm that the river site was indeed more river- and runoff influenced compared to the marine site.

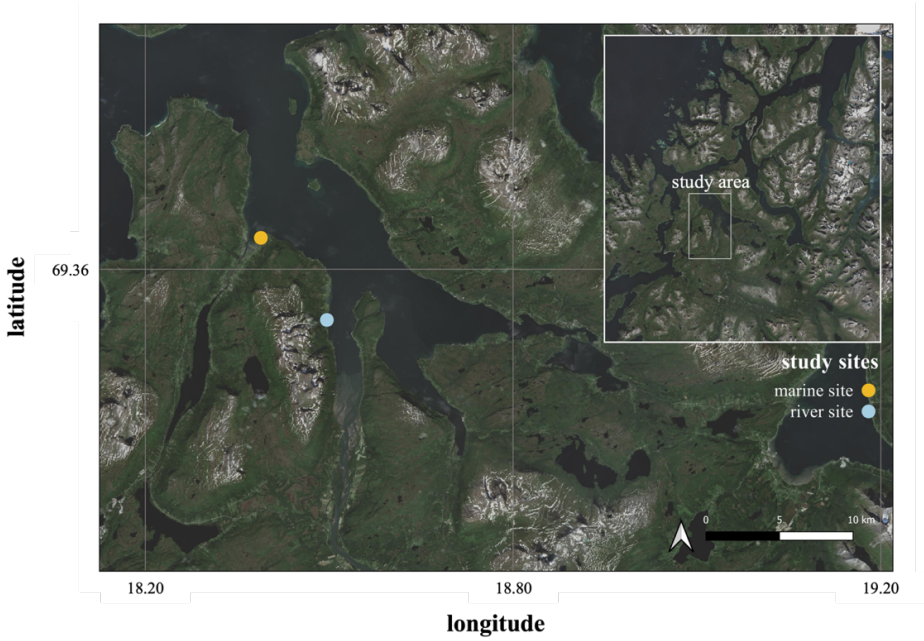


Figure 2. Map (1:190000) of the position of the two study sites in coastal areas in northern Norway.

Table 1. Water nutrient concentrations at both experimental sites during the two samplings in 2023. The values indicate the mean and standard deviation with sample sizes n = 1 or n = 4. POC = particulate organic carbon. DOC = dissolved organic carbon. Unpublished data provided by NIVA.

	marine site		river site	
	June	October	June	October
POC [µg/L]	351.74	69.35	811.14	174.86
DOC [mg/L]	2.00	2.00	1.29 ± 0.45	1.40
NO_2 & NO_3 [µg/L]	0.50	4.00	12.00 ± 0.00	25.00
PO_4 [µg/L]	2.00	1.00	1.50 ± 0.71	3.00
SiO_2 [µg/L]	1000.00	700.00	1530.00 ± 183.85	134.00

2.2 Study design and setup

The same cage experimental setup was installed at the marine and the river site during one low tide on 20.06.2023. The experiments at each site were deployed in triplicates with a random block design (Casler et al. 2015), in which each site had three blocks consisting of triplicates of four different treatments (Figure 3, 4). The treatments were randomly assigned inside each block with a total of 36 plots per site, 12 plots per block, including three treatment replicates. To aim to keep replicate measurements independent, the distance between the blocks was at least double the size of the block and the plots within each block had about 1 m distance from

each other. During the installation of the experimental setup, the height of each block at each site above low tide was measured. The marine site was about 45 cm (block 2 and 3) and 70 cm (block 1) above mean low tide, while the blocks at the river site were about 25 cm (block 3) and 42 cm (block 1 and 2) above low tide.

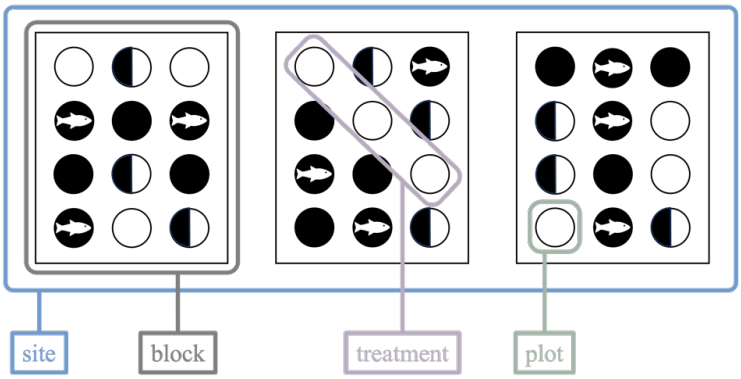


Figure 3. Overview of the experimental setup and terminology used. White circles represent the control treatments, half-black-half-white circles the partial-cage treatments, black circles the predator-exclusion treatments, and the black circles with a fish inside the fish-carcass treatments. The arrangement and shape of the blocks and the treatments within the blocks are for illustration and do not reflect the actual positions.

Figure 4. Photos of the three experimental blocks of the two study sites located in coastal northern Norway. Marine site: A) block 1, B) block 2, C) block 3; river site: D) block 1, E) block 2, F) block 3.

2.3 Treatments

To test for effects of cages, river runoff (control), predation, and fish carcasses, the experiment included four treatments with three cage types. All cylindrical cages (diameter: 30 cm, height: 13 cm) consisted of two PVC rings, one each at the bottom and top of the cages. In between, a polyethylene net (net size: 0.5 cm) was installed and fixed with cable ties (width: 3.6 mm) to the rings. During the installation of the cages in the field, it was made sure that the bottom rings were fully pushed into the sediment (about 5 cm deep) to prevent horizontal movements of infauna organisms. The cages were fixed by pushing three iron rods per cage (length: approx. 40 cm) into the sediment.

The control treatment aimed to test whether potential changes in macrobenthic community and food-web structure naturally occurred over time (e.g., through increased river runoff) or were caused by the treatments. This control treatment consisted of randomly selected untouched areas within a block without any cage construction, which were marked with cage rings during sampling.

The partial-cage treatment aimed to test whether the cages influenced the sediment organisms in the intertidal zone. Cages harbor the risk of confounding effects on response variables, e.g., by a cage-induced decrease in the water flow velocity (Miller & Gaylord 2007), which can result in identifying effects caused by the cages as treatment effects by mistake. To prevent this potential bias, partial cages were used (similar to other studies, e.g., Díaz et al. 2023). These cages aimed to find possible cage effects and, if they exist, to be used as the control for the predator-exclusion and fish-carcass treatment analyses to prevent false conclusions by cage artifacts. Therefore, partially open cages with a half-open top and three openings (7-8 cm × 14-15 cm) at the side were used. The openings should allow predators to enter and exit partial cages and maintain natural level of the predation pressure (Figure 5 A).

The predator-exclusion treatment aimed to exclude epibenthic predators from the study area to investigate how strong predation structures macrobenthic communities and food webs. Here, the cages were completely covered by the net on top and at all sides, not allowing larger predators to enter (Figure 5 B).

The fish-carcass treatment aimed to simulate the potential additional food source from fish carcasses of invasive pink salmon. The fish-carcass treatment cages were closed entirely at the top like the predator-exclusion cages and partly open at the sides with the same openings as the partial-cage cages. This design should prevent birds from reaching the fish from the top while

allowing consumers to enter the cages from the side. The fish were approximately 125 g frozen Atlantic salmon filets (*Salmo salar*) with skin (Coop Extra, bred in Norway) since pink salmon had not yet arrived at the Norwegian coast when setting up the experiments. The fish pieces were hanging in the middle inside the cages in a nylon sock (basic, ankle socks, transparency: 20 DEN) within a plastic net, and both were fixed with cable ties (width: 3.6 mm) to the net on top of the cages. A little stone inside the net prevented the fish from floating (Figure 5 C). To ensure a continuous presence of fish, the whole net-fish constructions were replaced periodically (first exchange: 21.07.2023, second exchange: 20.08.2023). During the replacement, neither the sediment in the cages was touched, nor the cages themselves were moved to avoid potential impacts on the organisms. A pilot study was conducted to determine the approximate time the fish pieces needed to rot, resulting in the replacement period. In the pilot study, the fish were placed in a similar construction as in the actual experiment in the intertidal zone and controlled regularly until they had finally rotted.

Figure 5. Photos of the three different cage types (diameter: 30 cm, height: 13 cm) used in three treatments. A) Partial-cage treatment used to test for cage effects, B) predator-exclusion treatment used to test for predation effects, and C) fish-carcass treatment used to test for effects of the fish hanging in the cage.

2.4 Sampling

The sampling for this thesis was part of the "Catchment to Coast" (C2C) project (https://framsenteret.no/forskning/fra-fjell-til-fjord-c2c/) and took place in two periods in 2023. Each sampling happened during one low tide. The first sampling was in June 2023 (20.06.2023) during the experiment installation. Three control samples were randomly taken from each block at both sites (18 in total) by making sure not to sample other treatment areas. The second period was in the fall of 2023 and consisted of two sampling days. On 28.09.2023, all plots of the marine site and on 02.10.2023, all plots of the river site were sampled (both samplings will be later referred to as fall samples). Overall, 90 plots, including 18 from the June period and 72 from the fall period, were sampled. The sampling itself was split into macrobenthos and food-web structure sampling, for which individual sediment samples were taken from each plot, respectively.

2.4.1 Macrobenthic community samples

To quantify macrobenthos total abundance and biomass, biodiversity metrics, and community structure, transparent PVC corers (diameter: 5.5 cm, height: approx. 20 cm) were used. Corers were pushed at least 10 cm into the sediment in the center of each plot, closed at the upper end with a rubber plug, and carefully drawn out of the sediment with the intact sediment core inside (Figure 6 A, B). The sample was wrapped at both ends with parafilm and aluminum foil on top to secure the sample during the transportation from the field to the lab. Samples within the corer were kept cool in coolers with ice packs until they were processed in the laboratory of UiT (The Arctic University of Norway, Tromsø) within four days after the sampling. Arriving in the laboratory, seawater was added to the cores.

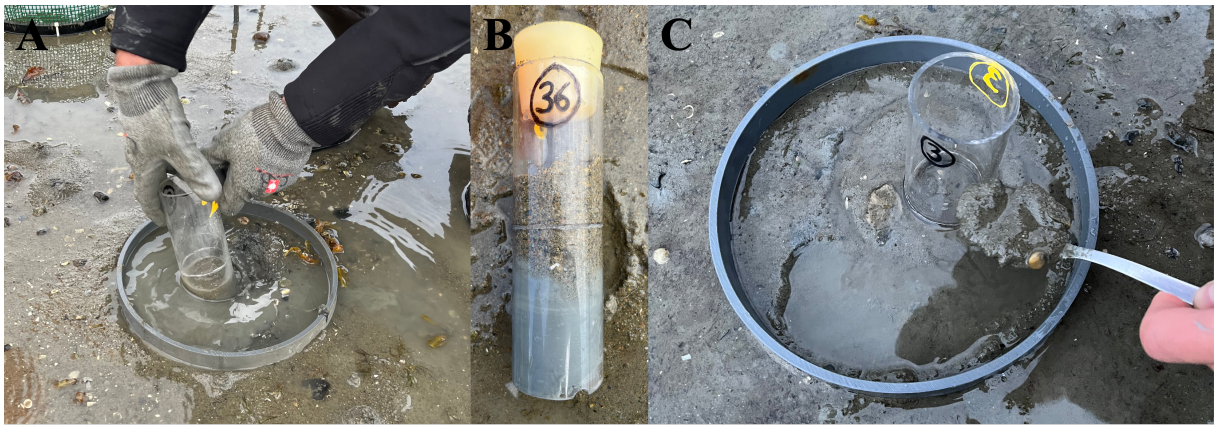


Figure 6. Sampling of the macrobenthic community and food-web structure sediment samples. A) Taking the macrobenthic community sample (control treatment) by pushing the core into the sediment. B) Macrobenthic community sample within the core before preparing for transportation. C) Taking the food-web structure sample (control treatment) by collecting the sediment around the community sample core.

Each sample was sieved in a 500 µm sieve. All organisms remaining in the sieve were sorted under a stereomicroscope (Leica and Wild Heerbrugg) and identified to the lowest possible taxonomic level with the help of expert expertise. The taxa names were standardized according to the World Register of Marine Species (WoRMS, accessed: 25.03.2024). Additionally, the number of individuals of each taxon was counted in each sample. To later determine the samples' biomass, all organisms of one plot were placed together in one pre-weighed tube. During the fall period, Oligochaeta indet., *Macoma calcarea*, *Pygospio elegans*, *Euchone* sp., Spionidae indet., and Chironomidae indet. were stored in separate tubes until they were later combined with the stable isotope samples. This separation was not done for the samples taken during the June sampling. The samples were dried at 60 °C in a drying oven (TERMAKS) to constant weight and measured using a balance (SARTORIUS, ED 1245, accuracy = 0.1 mg). See Appendix 12 for the list of macrobenthos abundance and biomass data.

Using the abundance and biomass data, the total abundance and biomass, taxon richness, Shannon Diversity Index, and Pielou's evenness were calculated for each plot. For calculating the biomass of the organisms, the weight of the empty tube was subtracted from the weight of the combined organisms and tube weight. The total biomass of all organisms of each sample, i.e., plot [g/24 cm^2] was calculated by combining all biomasses of the taxa belonging to the plot. Samples with a negative biomass were not included. These likely were a result of very small sample sizes and errors with the sensitive balance.

Based on abundance data, taxon richness (S) and the Shannon Diversity Index (H') were determined. The Shannon Diversity Index (hereafter Shannon Index; eq. 1) describes the diversity in a community, where the greater the diversity and the more complex the community, the higher the index value is (Shannon & Weaver 1963).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \quad [1]$$

S – number of taxa

p_i – proportion of taxon i in the community

Additionally, the Pielou's evenness (J; hereafter evenness; eq. 2), which describes how evenly individuals are distributed across taxa in a sample (Pielou 1966) was calculated. The evenness value ranges from 0 to 1; where 0 indicates the least evenness, i.e., all individuals in the sample are from one taxon, and 1 indicates the highest evenness, i.e., all taxa have the same number of individuals.

$$J = \frac{H'}{\log(S)} \quad [2]$$

H' – Shannon Diversity Index (to natural logarithm)

S – taxon richness (number of species)

2.4.2 Food-web structure samples

The food-web structure of the benthic infauna community was identified using stable isotope analyses. The stable isotope values of carbon and nitrogen (eq. 3) indicate the position of a taxon within the food web.

$$\delta^{13}C \text{ and } \delta^{15}N\ (‰) = [\ (R_{sample} - R_{standard}) / R_{standard}\ ] \times 1000 \qquad [3]$$

R_{sample} – ratio of heavy/light isotopes of X

$R_{standard}$ – ratio of reference standards (C: VPDB[1], Craig 1957; N: air[2], Mariotti 1983)

While $\delta^{13}C$ values indicate the nature of the food baseline, $\delta^{15}N$ values provide information about the trophic level of a taxon. A low $\delta^{13}C$ value (around -25 ‰ and lower) suggests the uptake of terrestrial food sources and a higher $\delta^{13}C$ value (> -25 ‰) the utilization of marine-derived OM (Dunton et al. 2012). When an organism feeds exclusively on one species, it is expected to have a 0.4 ‰ $\delta^{13}C$ higher value than its prey (Post 2002). When organisms feed, they accumulate a small amount of the heavier ^{15}N isotope of their prey, which is why a higher $\delta^{15}N$ value corresponds to a higher trophic level (Minagawa & Wada 1984). On average, an increase of about 3.4 ‰ in $\delta^{15}N$ indicates one higher trophic level, i.e., if an organism is exclusively feeding on one species, the consumer's $\delta^{15}N$ value is about 3.4 ‰ higher than the $\delta^{15}N$ value of the prey (Minagawa & Wada 1984, Post 2002). Since organisms nearly never feed on one food source alone, the $\delta^{13}C$ and $\delta^{15}N$ values combine the isotope values of several food sources, which is why organisms rarely show the theoretical trophic fractionation of around 0.4 ‰ ($\delta^{13}C$) and 3.4 ‰ ($\delta^{15}N$).

The isotopic enrichment in an organism is further depending on the isotopic turnover. This term refers to the time it takes for the isotopic signal of a new food source to be incorporated into the tissue of a given organism. In particular, the turnover time measures how quickly the isotopic signal is exchanged within the organism and can vary widely depending on the isotope, organism, and environmental conditions. Typically, the turnover is expressed as the isotopic

[1] VPDB = Vienna PeeDee Belemnite; primary reference for measurements of carbon isotopes

[2] air = atmospheric N_2; primary reference for measurements of nitrogen isotopes

half-life, i.e., the time of the half-way point of the isotope being replaced by the new food source within the organism (Vander Zanden et al. 2015). For example, the bivalve *Cerastoderma edule* has an isotopic turnover of about six days for $\delta^{13}C$ and eight days for $\delta^{15}N$ at 16 °C (Lefebvre & Dubois 2016).

For the stable isotope analyses, qualitative sediment samples were taken from each plot to determine the macrobenthic food-web structure. Therefore, the sediment within the entire plot area (except the area of the macrobenthic community sample) was collected and stored in little containers (Figure 6 C). Additionally, samples of potential food sources for the macrobenthos were collected (algae: *Ascophyllum nodosum*, *Fucus vesiculosus*, *Ulva lactuca*; leaves; water samples for POC). The stable isotope analysis of the pelagic particulate organic matter (POM) was not part of this thesis and therefore not further explained. The food web samples were handled the same way as the macrobenthic community samples in terms of transportation, storage, sieving, and identification. The aim was to sort out enough individuals to get three replicates per taxon of each plot of both sampling periods to ensure sufficient material (more than one mg dry mass per sample) for stable isotope analysis. The approximate number of individuals needed to constitute a sample was based on previous experience. Where insufficient material was obtained from a given sample, samples of the same taxon and plot from the abundance macrobenthic samples were combined with the food web samples to increase the available mass. Where taxa still had too few individuals, they were pooled with individuals of the same taxon from a different replicate of the same treatment. If the grouping was still not sufficient within one block, individuals of the same treatment from another block of the same site were pooled. Samples of potential carbon sources like leaves, macroalgae, and the salmon pieces in the cages were additionally analyzed. For larger individuals of the analyzed bivalve species, only muscle tissue was used. Samples with smaller bivalve individuals, of which the tissue could not be removed, were first treated like all other samples to get the $\delta^{15}N$ value and later acidified to obtain the $\delta^{13}C$ value of the OM (rather than a signal mixed with that of the carbonate shell), as described below.

All food-web samples were stored in microtubes (1.5 ml) in the freezer and subsequently dried in a freeze dryer (LABOCONCO, FreeZone Benchtop Freeze Dryer, Model 70020 2.5 L -50 °C Series) at -50 °C and 0.04 mbar for 24 h (Figure 7 A). Due to limited time, material, and funding, only Oligochaeta indet., *Macoma calcarea*, *Pygospio elegans*, *Euchone* sp., Spionidae indet., and Chironomidae indet. were analyzed. For the stable isotope analysis, *Pygospio elegans* and Spionidae indet. were grouped and analyzed together as Spionidae indet.. These

taxa were chosen because they were overall most abundant. In addition, Chironomidae indet. could indicate an important land-ocean impact since these insect larvae typically occur in freshwater ecosystems.

The dried samples were ground in their tubes using a tissue grinder (Kimble, mixer pellet pestle ss, size 0.5 ml). Between every sample, the used equipment was cleaned with 70 % ethanol and tissues. The homogenized samples were weighed into tin capsules (ELEMENTAR, S05 003 395, 5 x 3.5 mm) with a microbalance (accuracy: 0.001 mg; Figure 7 B) and stored in 96-well plates (Thermo SCIENTIFIC). The target weight was 1.00 – 5.00 mg dry mass with ideally ca. 80 µg nitrogen and 1600 µg carbon (UC Davis, accessed: 12.08.2023). As the samples repeatedly became statically charged during processing, an antistatic kit (HAUG GmbH & Co.KG, U-shaped electrode 3168, PRX U) was used. The generated electric field discharges the sample and thus prevents the small sample from escaping due to its static build-up during the work steps. Each sample was held in the electric field several times during processing, causing it to discharge.

To remove the inorganic carbon in the samples containing calcium carbonate (here small bivalves), a subsample of the dried powder was acidified (Jacob et al. 2005). Inorganic carbon has a higher $\delta^{13}C$ signature than OC and thus would skew the final $\delta^{13}C$ value. Drops of 1 N hydrochloric acid were added to the subsample until there was no visual reaction (i.e., gas release) anymore. The samples were subsequently dried in the drying oven at 60 °C for 72 h until all liquid had evaporated and weighed into tin capsules as described for non-acidified samples.

The final weighted samples were sent to the Stable Isotope Facility of UC Davis, California, USA for the $\delta^{13}C$ and $\delta^{15}N$ determination. The ^{13}C and ^{15}N ratios were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The received data included $\delta^{13}C_{VPDB}$ (‰), total C (µg), $\delta^{15}N_{Air}$ (‰), and total N (µg) values. The mean absolute accuracy for calibrated reference material was within ± 0.15 ‰ ($\delta^{13}C$) and ± 0.05 ‰ ($\delta^{15}N$). The mean standard deviation for the reference material was ± 0.14 ‰ ($\delta^{13}C$) and ± 0.10 ‰ ($\delta^{15}N$) (UC Davis). For the list of stable isotope data see Appendix 13.

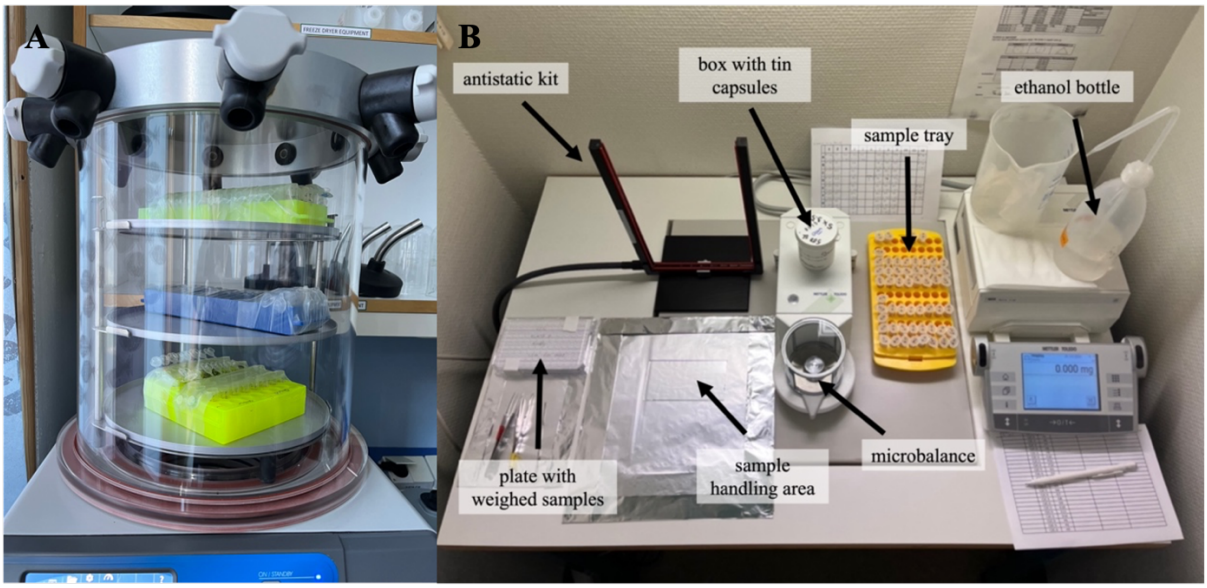


Figure 7. Pictures of two stable isotope processing steps in the laboratory. A) Stable isotope samples drying in the freeze dryer. B) Setup of weighing the stable isotope samples into tin capsules using the microbalance.

2.5 Data analyses

All analyses were performed in R (version 4.3.2; R Core Team, 2023). If not specified, *ggplot2* (Wickham 2016) was used to create the figures. The data were organized using the package *tidyverse* (Wickham et al. 2019). Statistical analyses were performed separately for samples of the two sites.

2.5.1 Macrobenthic community analyses

For each statistical analysis, the data (when using t-tests) or the residuals (when using ANOVA) were tested for normal distribution by using Shapiro-Wilk's test and for the homogeneity of variance by using Levene's test (*car* package; Fox & Weisberg 2019). If the data were not normally distributed, they were cube-transformed and checked for normal distribution and homogeneity of variances again. If the transformed data were still not normally distributed, the original data were used in the analyses.

To test for a cage effect, the fall-control and the partial-cage treatments were compared using t-tests. If the variances were homogeneous, a Student's t-test was used and if they were heterogeneous, a Welch t-test was used. If a cage effect on macrobenthos community and food-web structure was found, the tests for predator-exclusion and fish-carcass effects were conducted using the partial-cage treatment as the control. The analysis for a river runoff effect

followed the same procedure as for the cage effect. Except here, the differences between the samples taken in June (spring-control) and the control samples taken in fall (fall-control) were tested.

For the predator-exclusion and fish-carcass treatment effects, two-way ANOVAs (analysis of variance) were performed to test for treatment (fixed factor, three levels) and block (random factor, three levels) effects as well as their interaction treatment × block (*GAD* package; Sandrini-Neto & Camargo 2023). If the p-value of the interaction term was > 0.25, the variance of the interaction was combined with the residual variance of the full model and the analysis was repeated (Quinn & Keough 2002). The same procedure was followed for a non-significant block effect. A Tukey test was performed when the ANOVA revealed a significant treatment effect (p-value ≤ 0.05). In the case of non-homogeneous variances, the ANOVA was still performed. The use of an ANOVA with heterogeneous variances can lead to type I errors, i.e., finding differences where there are none. If the ANOVA does not find a difference, the possibility of a type I error is very low, and the ANOVA output can be used (Underwood 1997).

In addition, the statistical power for each t-test and ANOVA was calculated using the packages *pwr* (Student's t-test and ANOVA, Champely 2020) and *MKpower* (Welch t-test, Kohl 2023). The effect size for the power tests were calculated with the packages *effsize* (Torchiano 2020) for t-tests and *effectsize* (Ben-Shachar et al. 2020) for ANOVAs. A test power of < 0.8 was considered low and > 0.8 high (Cohen 1988).

Besides the statistical tests, the effect size (i.e., logarithm response ratio) was calculated as another approach to determine treatment effects using the package *metafor* (Viechtbauer 2010). The same package was used to create forest plots showing the effect size results. An effect size of ~ 0.2 was considered small, ~ 0.5 medium, and ~ 0.8 strong (Cohen 1988).

The relative abundance was analyzed with Permuted Multivariate analysis of variance (PERMANOVA; Anderson 2001) using adonis2 (treatment as fixed and block as random factor) to test for a treatment effect on the taxon community composition structure. Additionally, a non-metric multidimensional scaling (NMDS) plot was created to visualize the dissimilarity of community compositions of the treatments. To choose the optimal trade-off between stress and the number of dimensions, a scree plot for each NMDS was created (Appendix 2, 3), comparing the stress of NMDS with two to six dimensions. For both final NMDSs, four dimensions were chosen. The PERMANOVA and NMDS were based on

Bray-Curtis abundance-dissimilarity (Bray & Curtis 1957) and calculated using the *vegan* package (Oksanen et al. 2022).

2.5.2 Food-web structure analyses

The food-web structure was analyzed by testing for cage effects on the $\delta^{13}C$ and $\delta^{15}N$ values, river runoff effects on $\delta^{13}C$ values, and fish carcass effects on $\delta^{15}N$ values per study site. Principally, the statistical analyses followed the same structure as the macrobenthos analyses, except t-tests were used to identify the effects of the fish-carcass treatment on $\delta^{15}N$ values of the taxa at both sites. Neither the $\delta^{13}C$ nor $\delta^{15}N$ samples were balanced at either site, meaning not all taxa had the same sample size per treatment (including sometimes only one sample per treatment). This resulted in several limitations to the analyses of the river site. First, the cage effect analysis could not be done for Oligochaeta indet. and Spionidae indet.. Second, the river runoff effect (changes that occurred during summer) could only be tested on Oligochaeta. Third, t-tests for fish-carcass treatment effects could not be performed on Spionidae indet. at the marine and on Chironomidae indet and *Euchone* sp. at the river site. The same is true for the effect size and test power calculations.

3 Results

In total, 4977 individuals (marine: 3606; river: 1371) from 25 taxa were found. The overall most abundant taxa were Oligochaeta indet., *Macoma calcarea*, *Pygospio elegans*, *Euchone* sp., and Chironomidae indet. (Figure 8). Together, these five taxa comprised 95 % of the total abundance at the marine and 86 % at the river site.

The results will follow the same sequence as the hypotheses. Therefore, each section will state its corresponding hypothesis in the beginning.

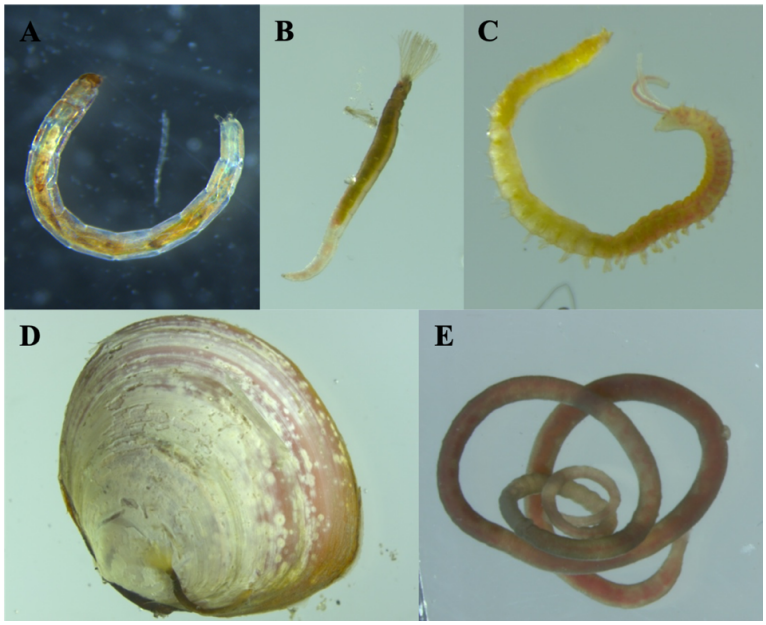


Figure 8. Photos showing the five most abundant intertidal macrobenthos taxa found in this study. A) Chironomidae indet., B) *Euchone* sp., C) *Pygospio elegans*, D) *Macoma calcarea*, E) Oligochaeta indet.. Photos: Johanna Hovinen

3.1 Cage effects

The test for cage effects was conducted as a prerequisite to the subsequent hypotheses testing.

Non of Student's t-test showed a significant difference between the fall-control and the partial-cage treatments at either site, i.e., no cage effect was found (Appendix 4, 5). The test power of the Student's t-tests were very low (0.051 – 0.318) at both study sites, which can be a reason for not detecting cage effects. Yet, in one case, the test power was high (0.940 for total biomass at the river site), and the test itself still did not identify a cage effect. The effect sizes provided limited evidence for a cage effect (Appendix 6). Here, a medium-size cage effect was found for the total biomass at both study sites.

For the stable isotope analyses, limited cage effects were found on $\delta^{13}C$ and $\delta^{15}N$ values at both sites (Appendix 7). Student's t-tests revealed a significant cage effect on the $\delta^{13}C$ values of Oligochaeta indet. at the marine site and $\delta^{15}N$ values of Spionidae indet. at the river site. No cage effect was determined for any other taxa and isotope (Appendix 8). The test power for the $\delta^{13}C$ analysis of Chironomidae indet., Oligochaeta indet., and Spionidae indet. at the marine site was very high. The test power of the remaining Student's t-tests at the marine and river sites was low (Appendix 8). The effect sizes (all < 0.1) did not show any influence of the cage on the taxa's $\delta^{13}C$ and $\delta^{15}N$ values at the marine site or the river site (Appendix 9, 10).

Due to the limited cage effects on the macrobenthos community and stable isotope values, the following analyses on total abundance and biomass, taxon richness, Shannon Index, and evenness, as well as $\delta^{13}C$ and $\delta^{15}N$ values for predator-exclusion and fish-carcass effects were performed using the partial-cage treatment as the comparison treatment.

3.2 River runoff effects

3.2.1 Macrobenthic community

H1.1: Total benthic macrofauna abundance and biomass are hypothesized to be higher in fall compared to June for both, the marine and river, sites, while biodiversity is expected to decrease. Overall, river runoff effects are predicted to be stronger at the river than at the marine site due to the reduced freshwater amount reaching the marine site.

A river runoff effect was not detected on the total abundance and biomass or on the three diversity measurements at the marine and river site (Figure 9). Student's t-test did not identify significant differences in any of the five variables between June and fall, i.e., during and after the melting season. The test powers were low, which can also be a reason for not detecting any river runoff effects in the statistical analyses (Table 2).

Table 2. Student's t-test and test power results for a river runoff effect on total abundance, total biomass, taxon richness, Shannon Index, and evenness at the marine and the river site. df = 16. The asterisk indicates df = 14.

	marine site		**river site**	
	Student's t-test	**test power**	**Student's t-test**	**test power**
total abundance	t = 0.02, p = 0.988	0.133	t = -0.38, p = 0.708	0.148
total biomass	t = 0.62, p = 0.541	0.447	t = -0.36, p = 0.725	0.061
taxon richness	t = -0.23, p = 0.822	0.050	t = 0.47, p = 0.647	0.081
Shannon Index	t = -0.42, p = 0.679	0.222	t = 0.97, p = 0.349	0.319
evenness	t = 0.31, p = 0.759	0.084	*t = 0.58, p = 0.573	0.447

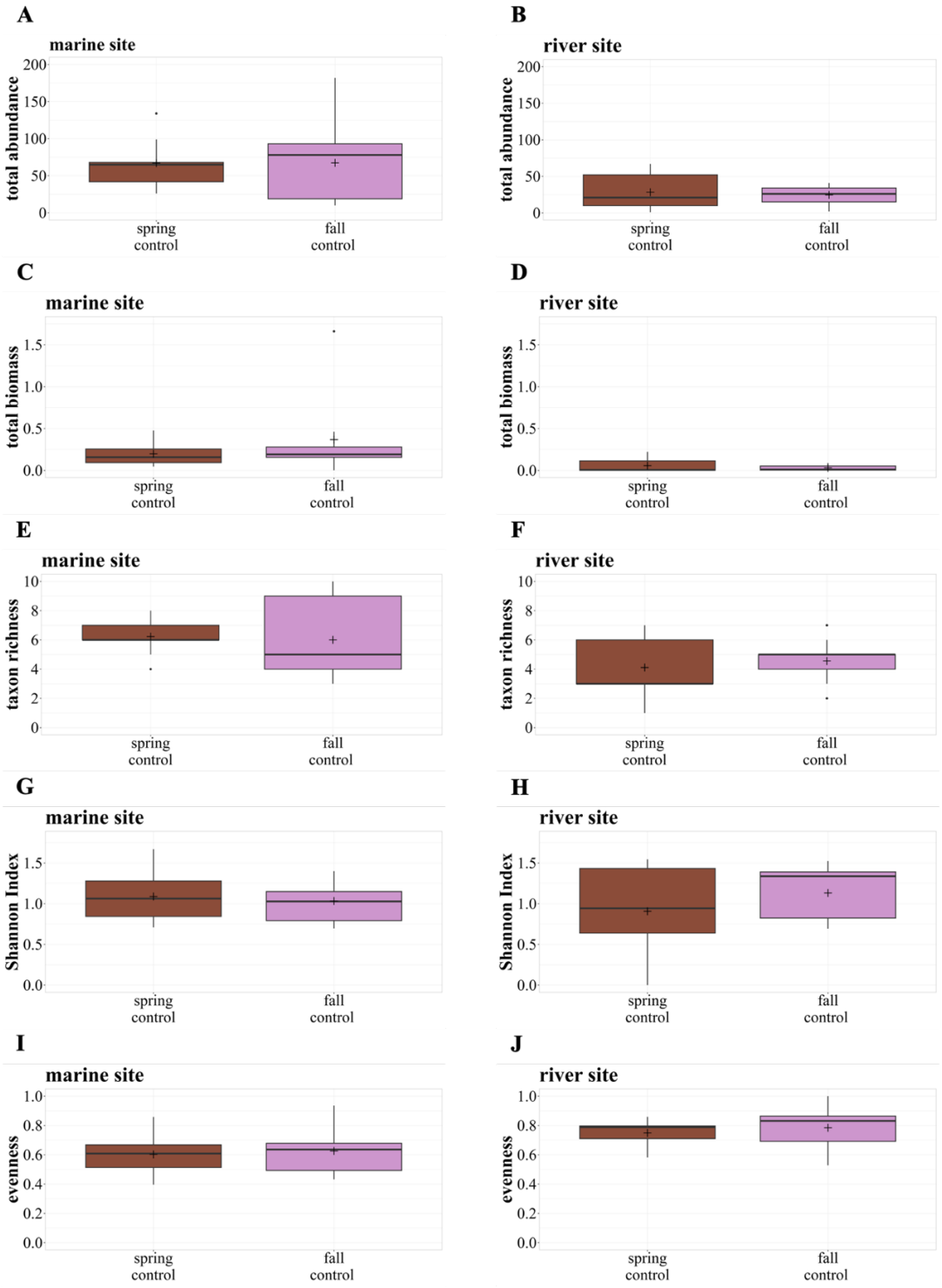


Figure 9. Boxplots showing no detectable river runoff effects (n = 18, evenness river n = 16) on the different macrobenthic measurements. Total macrobenthic abundance at A) the marine site and B) the river site. Total macrobenthic biomass [g dry mass/24 cm^2] at C) the marine site and D) the river site. Taxon richness [number of taxa/24 cm^2] at E) the marine and F) the river site. Shannon Index at G) the marine and H) the river site. Evenness of at I) the marine and J) the river site. The runoff effect is based on the comparison between the spring-control (brown) and the fall-control (rose) treatments. The boxes indicate the interquartile range (IQR) of the median (black thickened line). Whiskers represent the largest and lowest value within 1.5 times and black dots mark outliers. The black cross represents the mean.

The effect sizes revealed limited river runoff (or other seasonal change) effects on macrobenthic total abundance, total biomass, and biodiversity. Only the total biomass experienced a medium effect (increase at the marine and decrease at the river site). River runoff had a small effect on all remaining variables (total abundance, taxon richness, Shannon Index, and evenness; Figure 10).

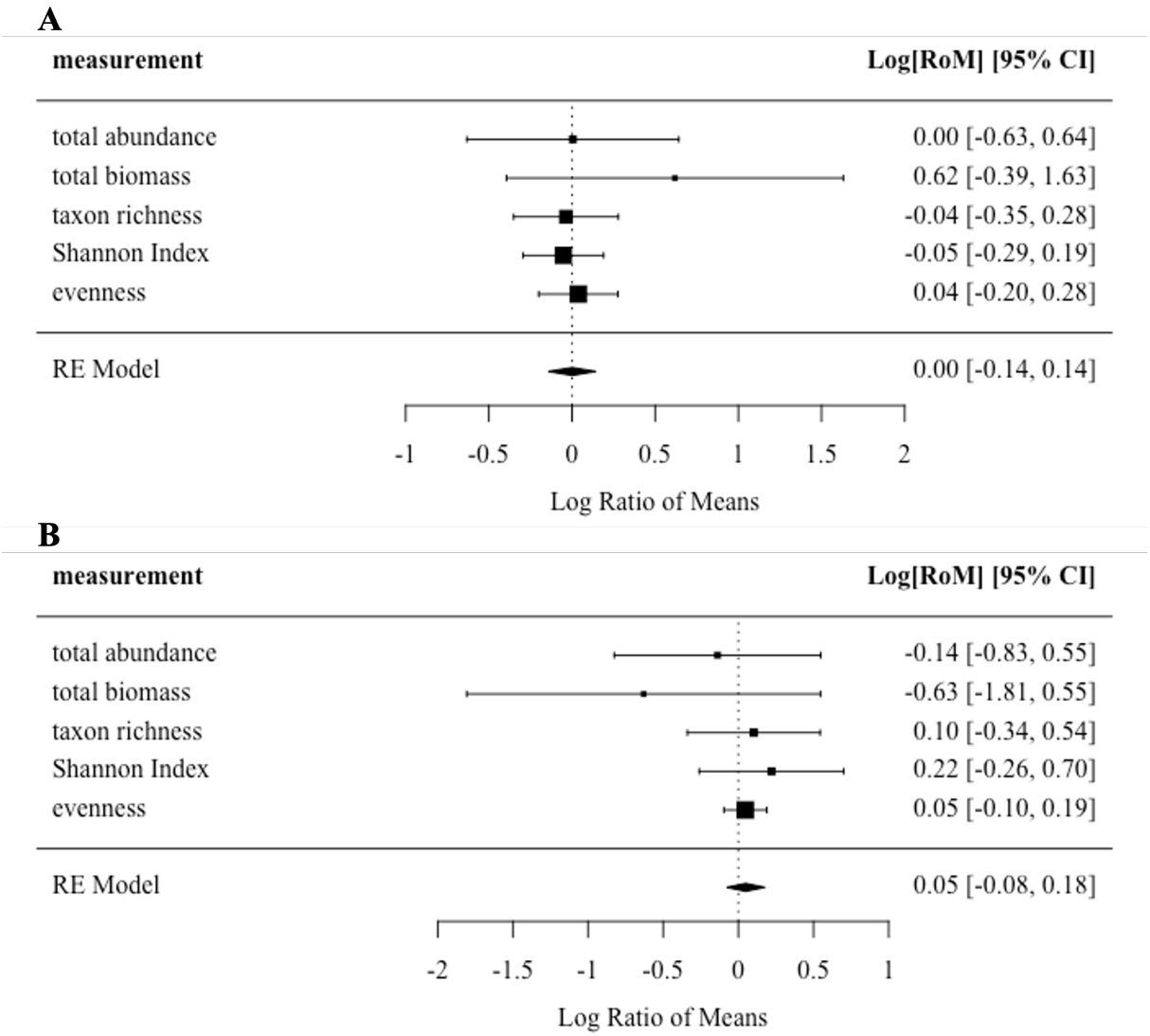


Figure 10. Effect size of the river runoff effect (comparison of the spring-control and the fall-control treatments) on the total abundance, total biomass, taxon richness, Shannon index, and evenness of intertidal macrobenthos for the marine (A) and the river (B) site. The boxes represent the estimated mean effect size, the size of the boxes the proportion of the weight of the measurement to the pooled effect size estimate (RE Model), and the whiskers the 95% confidence interval. The log ratio of means (Log [RoM]) and the 95 % confidence interval ([95% CI]) are shown in the right column. The dotted line indicates the log ratio of means of zero, meaning the cage caused no difference.

The NMDS plots showed no distinct difference between the macrobenthic communities in summer and fall. Additionally, the 95 % confidence ellipses had a large overlap at either site, meaning the benthic macrofauna community composition did not change during the melting season (Figure 11). The PERMANOVA did not determine a river runoff effect on the taxon composition of the benthic macrofauna at either study site (Table 3).

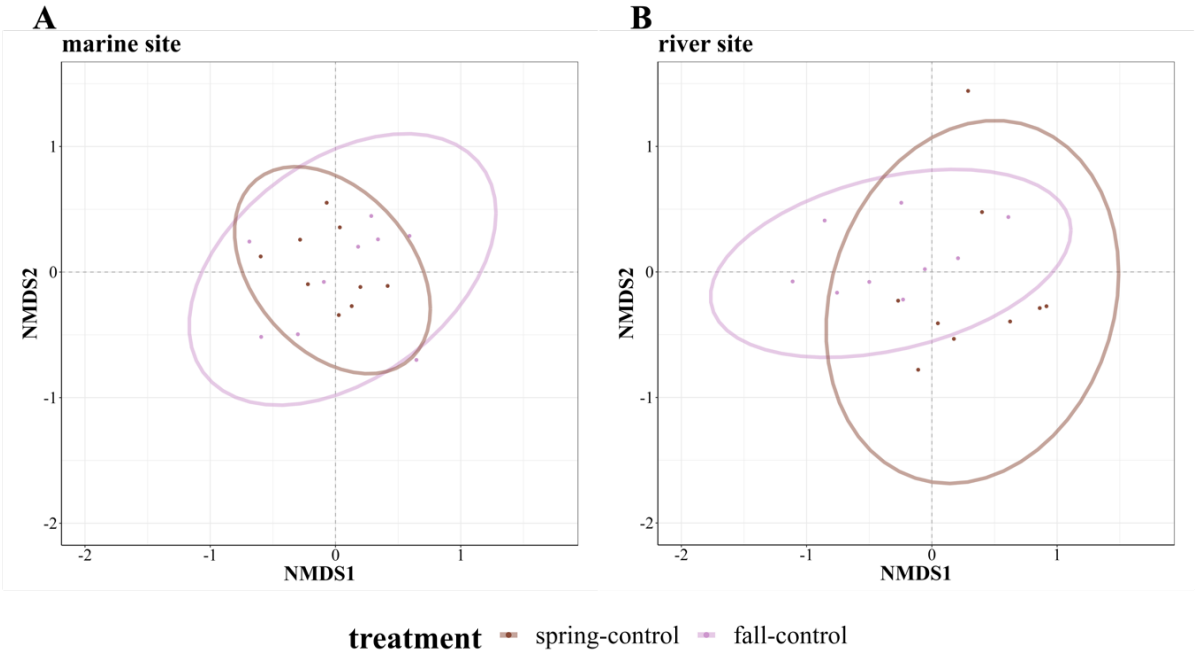


Figure 11. Non-metric multidimensional scaling (NMDS) plots of the first two axes showing the similarity in macrobenthic community composition of the spring-control (brown) and the fall-control (rose) treatments at the marine (A) and river site (B). The dashed lines indicate NMDS1 and NMDS2 values of zero. Each point represents one community sample of one treatment. The distance between points indicates the relative difference in community composition based on Bray-Curtis similarity. Ellipses represent the 95 % confidence interval. n = 9 for each season and site. Stress level = 0.1028 for both sites.

Table 3. PERMANOVA results suggesting no river runoff effects on the benthic macrofauna community composition at the marine and the river site. Treatment was included as a fixed factor and block as a random factor. Df are the degrees of freedom, SSq is the sum of squares, R^2 the proportion of total SSq, and pseudo-F is the ratio of among-to-within group variance.

	marine site					river site				
	df	**SSq**	**R^2**	**F**	**p**	**df**	**SSq**	**R^2**	**F**	**p**
treatment	1	0.14912	0.06179	1.0538	0.322	1	0.2818	0.07236	1.248	0.248
residual	16	2.26426	0.93821			16	3.6123	0.92764		
total	17	2.41338	1.00000			17	3.8941	1.00000		

3.2.2 Food-web structure

H1.2: Benthic macrofauna is expected to feed less on terrestrial organic matter (reflected in higher $\delta^{13}C$ values) in fall compared to June, due to reduced river inputs and higher availability of marine organic matter from the summer phytoplankton bloom. This change is hypothesized to be more pronounced at the river than at the marine site.

The Student's t-tests provide evidence for an assimilated terrestrial OM on stable isotope values during the snowmelt-induced increased river runoff in June (Figure 12). At the marine site, the $\delta^{13}C$ values of *Euchone* sp. and Oligochaeta indet. were significantly higher in fall after snowmelt (Table 4). However, $\delta^{13}C$ values of Chironomidae indet., *Macoma calcarea*, and Spionidae indet. did not show such an effect. At the river site, a river runoff effect was found with significantly higher $\delta^{13}C$ values of Oligochaeta indet. in fall after the snowmelt (Table 4, Figure 12 B).

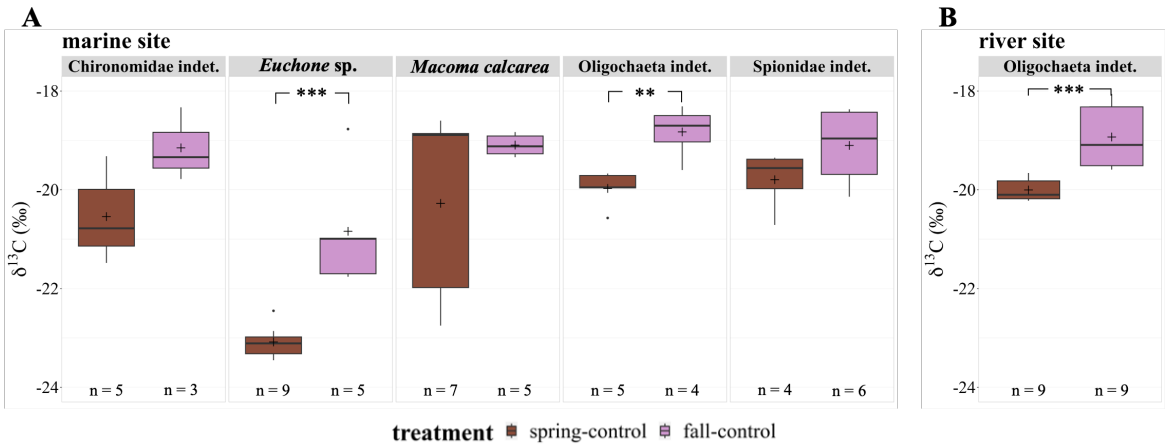


Figure 12. Boxplots showing the river runoff or other seasonal effects on the taxa's $\delta^{13}C$ values at A) the marine and B) the river site. The runoff effect is the difference between the spring-control (brown) and the fall-control (rose) treatments. Asterisks indicate significant differences (< 0.01 with **, < 0.001 with ***). Other symbols and their explanations as in Figure 9.

Table 4. Student's t-test and test power results for a river runoff effect on the taxa's $\delta^{13}C$ values at the marine and the river site. Significant p-values are marked in bold. Asterisk marks performed Welch t-test.

	marine site				river site			
	Student's t-test			test power	Student's t-test			test power
$\delta^{13}C$	df	t	p		df	t	p	
Chironomidae indet.	6	-2.28	0.063	0.584	-	-	-	-
Euchone sp.	12	-5.40	**<0.001**	0.987	-	-	-	-
Macoma calcarea	10	-1.38	0.198	0.215	-	-	-	-
Oligochaeta indet.	7	-3.74	**0.007**	0.770	9.96	-5.09	***<0.001**	0.097
Spionidae indet.	8	-1.47	0.179	0.690	-	-	-	-

All effect sizes of the runoff effect on the $\delta^{13}C$ values of the different taxa at the marine site were < 0.1 and considered small effects (Figure 13). The Oligochaeta $\delta^{13}C$ values from the river site detected small effects either ($\delta^{13}C$: -0.06 [-0.08, -0.03]).

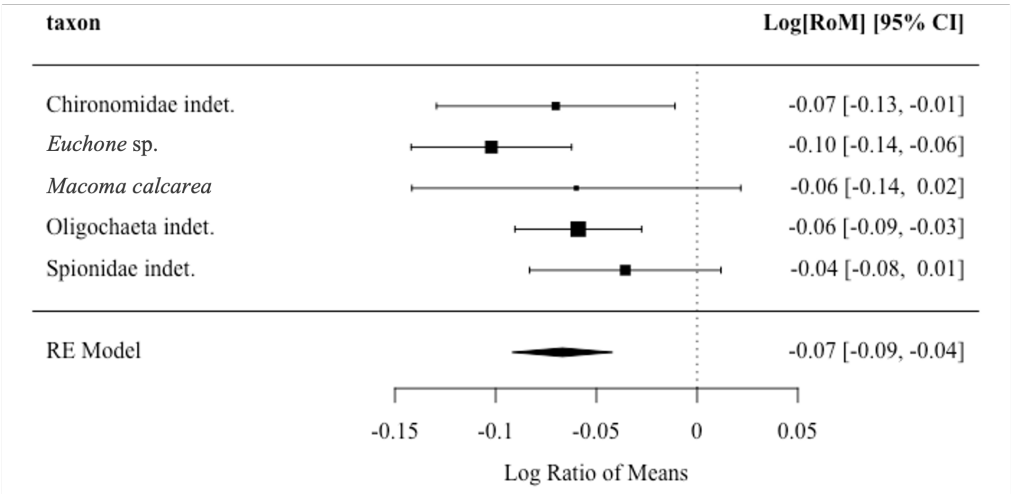


Figure 13. Effect size of the river runoff (comparison of the spring-control and the fall-control treatment) on the $\delta^{13}C$ values of the different taxa at the marine site. Symbols and their explanations as in Figure 10.

The $\delta^{13}C$ values of potential food sources showed a very negative value for leaves as well as rather negative POM values after the snowmelt in fall than during the snowmelt in June at the river site. The rather high $\delta^{13}C$ values of the three macroalgae identified them as a marine food source (Table 5).

Table 5. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) in ‰ of potential food source samples for intertidal benthic macrofauna. N is the sample size for each food source, while the values indicate the mean and standard deviation. POM = particulate organic matter of water.

	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Ascophyllum nodosum	3	-17.37 ± 0.34	3.55 ± 0.42
Fucus vesiculosus	3	-16.43 ± 0.59	4.34 ± 0.12
Ulva lactuca	3	-22.42 ± 1.91	4.57 ± 0.31
Salmo salar	6	-24.73 ± 0.62	6.88 ± 0.16
leaves	2	-32.92 ± 0.21	2.26 ± 1.46
POM, marine site, June	1	-20.96	4.16
POM, marine site, Fall	1	-24.28	4.52
POM, river site, June	1	-23.45	4.46
POM, river site, Fall	1	-24.37	4.2

3.3 Predator exclusion and fish carcass effects

3.3.1 Macrobenthic community

H2.1: Predator exclusion is proposed to not change benthic macrofauna abundance, biomass, and biodiversity, assuming predators do not structure macrobenthic communities at high latitudes.

H3.1: The additional fish food source is hypothesized to increase total abundance and biomass of benthic macrofauna. The new food source is expected to attract scavenger taxa.

For both study sites, the comparison of the predator-exclusion and the fish-carcass treatments with the partial-cage did not determine a treatment or block effect on the macrobenthos total abundance, total biomass, and biodiversity (Figure 14, Table 6). The ANOVAs only identified a significant treatment-block interaction for the total abundance at the marine site and block effects on the Shannon Index and the evenness at the marine site (Table 6).

At the marine site, the test power of the ANOVAs was very low (total abundance: $p = 0.055$; total biomass: $p = 0.087$; taxon richness: $p = 0.059$; Shannon Index: $p = 0.050$; evenness: $p = 0.057$). The same was true at the river site (total abundance: $p = 0.082$; total biomass: $p = 0.099$, taxon richness: $p = 0.050$; Shannon Index: $p = 0.050$; evenness: $p = 0.050$).

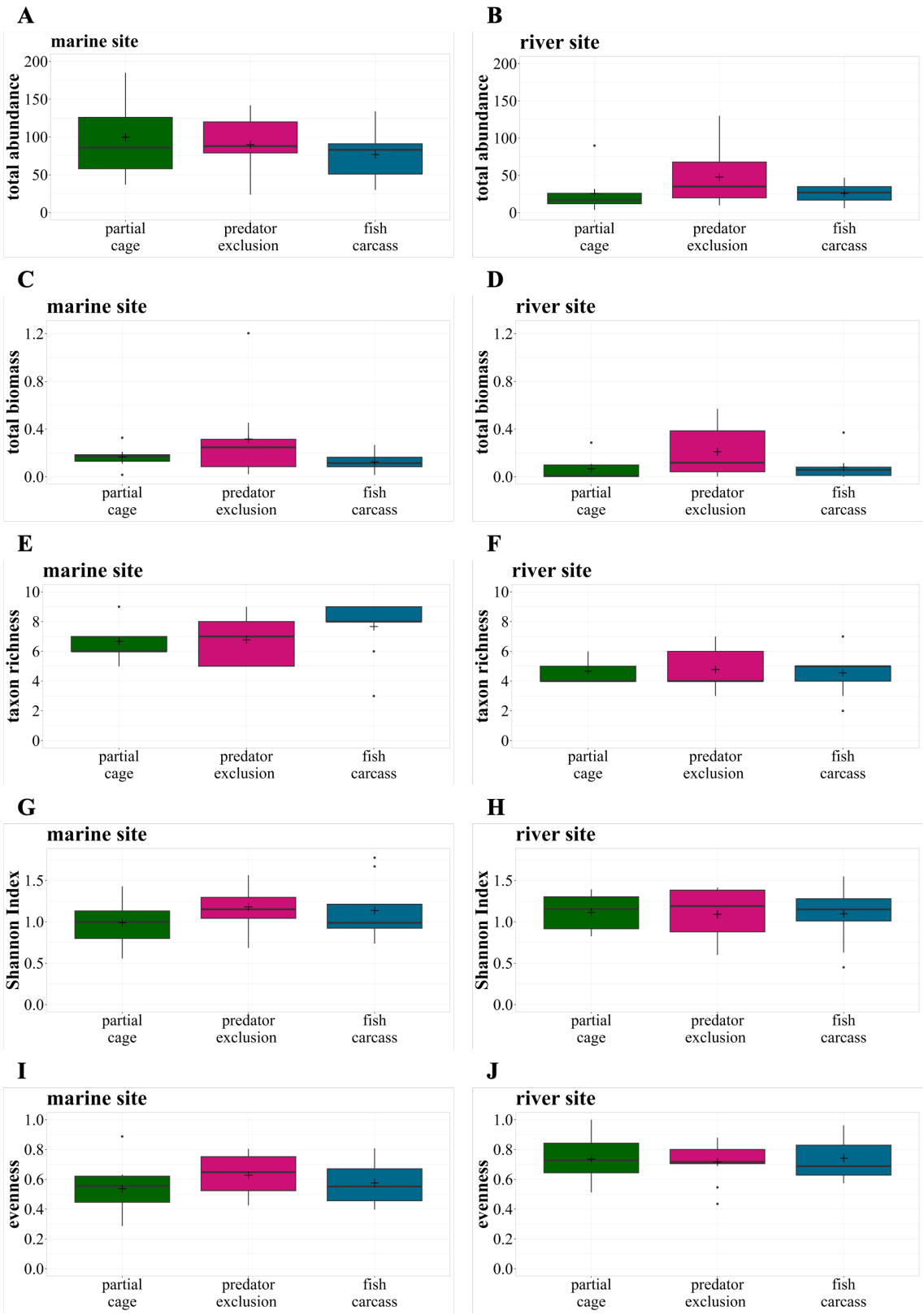


Figure 14. Boxplots showing limited treatment effects (n = 18) of the predator-exclusion (pink) and fish-carcass (blue) treatments in comparison with the partial-cage (green) treatment. Total abundance [per 24 cm^2] at A) the marine and B) the river site. Total biomass [g dry mass/24 cm^2] at C) the marine and D) the river site. Taxon richness [number of taxa/24 cm^2] at E) the marine and F) the river site. Shannon Index at G) the marine and H) the river site. Evenness at I) the marine and J) the river site. Symbols and their explanations as in Figure 9.

Table 6. Results of the two-way ANOVA testing the effects of the different treatments (partial-cage, predator-exclusion, and fish-carcass) on total abundance, total biomass, taxon richness, Shannon Index, and evenness for each study site. The analysis included treatment (t) as a fixed factor and block (b) as a random factor. The model was adjusted by removing the random factor interaction (b × t) if $p > 0.25$ (pooling 1), followed by removing the random factor block if $p > 0.25$ (pooling 2). The Mean Square denominators (MSq_{den}) indicate which Mean Squares (MSq) were used to calculate the F value. The degrees of freedom are reported under df, while the Sum of Squares can be found under SSq. Bold marked values indicate a significant ($p \leq 0.05$) result.

source	**marine site – total abundance**						**river site – total abundance**					
	df	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**	**df**	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**
b	2	6290.7	3145.3	2.80	0.088	b × t	2	2793.6	1396.8	1.94	0.168	pooling 1
t	2	2374.2	1187.1	0.30	0.757	b × t	2	2904.2	1452.1	2.02	0.156	pooling 1
b × t	4	15879.1	3969.8	3.53	**0.027**	residuals	4	3305.6	826.4	1.19	0.351	residuals
residuals	18	20240.7	1124.5				18	12545.3	697.0			
pooling 1	no pooling						22	15850.9	720.5			
pooling 2	no pooling						no pooling					

source	**marine site – total biomass**						**river site – total biomass**					
	df	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**	**df**	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**
b	2	0.100	0.050	1.83	0.185	pooling 1	2	0.024	0.012	0.54	0.588	pooling 1
t	2	0.085	0.042	1.55	0.235	pooling 1	2	0.112	0.056	2.64	0.092	pooling 2
b × t	4	0.114	0.029	1.056	0.407	residuals	4	0.080	0.020	0.88	0.495	residuals
residuals	18	0.488	0.027				18	0.407	0.022			
pooling 1	22	0.602	0.027				22	0.487	0.022			
pooling 2	no pooling						24	0.511	0.021			

source	**marine site – taxon richness**						**river site – taxon richness**					
	df	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**	**df**	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**
b	2	9.852	4.926	1.82	0.186	pooling 1	2	1.556	0.778	0.43	0.659	pooling 1
t	2	5.407	2.704	1.00	0.385	pooling 1	2	0.222	0.111	0.06	0.938	pooling 2
b × t	4	10.370	2.593	0.95	0.460	residuals	4	2.222	0.556	0.26	0.898	residuals
residuals	18	49.333	2.741				18	38.000	2.111			
pooling 1	22	59.704	2.714				22	40.222	1.828			
pooling 2	no pooling						24	41.778	1.741			

source	**marine site – Shannon Index**						**river site – Shannon Index**					
	df	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**	**df**	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**
b	2	1.181	0.590	12.49	**<0.001**	pooling 1	2	0.128	0.064	0.74	0.490	b × t
t	2	0.180	0.090	1.90	0.173	pooling 1	2	0.003	0.001	0.01	0.990	b × t
b × t	4	0.239	0.060	1.34	0.294	residuals	4	0.600	0.150	1.74	0.186	residuals
residuals	18	0.801	0.045				18	1.553	0.086			
pooling 1	22	1.040	0.047				no pooling					
pooling 2	no pooling						no pooling					

source	**marine site – evenness**						**river site – evenness**					
	df	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**	**df**	**SSq**	**MSq**	**F**	**p**	**MSq_{den}**
b	2	0.268	0.134	12.03	**<0.001**	b × t	2	0.007	0.004	0.19	0.827	b × t
t	2	0.037	0.019	0.70	0.549	b × t	2	0.003	0.002	0.04	0.964	b × t
b × t	4	0.106	0.027	2.38	0.090	residuals	4	0.173	0.043	2.37	0.091	residuals
residuals	18	0.201	0.011				18	0.329	0.018			
pooling 1	no pooling						no pooling					
pooling 2	no pooling						no pooling					

The effect sizes revealed mostly small effects of the predator-exclusion and fish-carcass treatments on the macrobenthos community (Figure 15). However, the predator-exclusion treatment resulted in a medium (marine site) and strong increase (river site) of total biomass and a medium total abundance increase (river site).

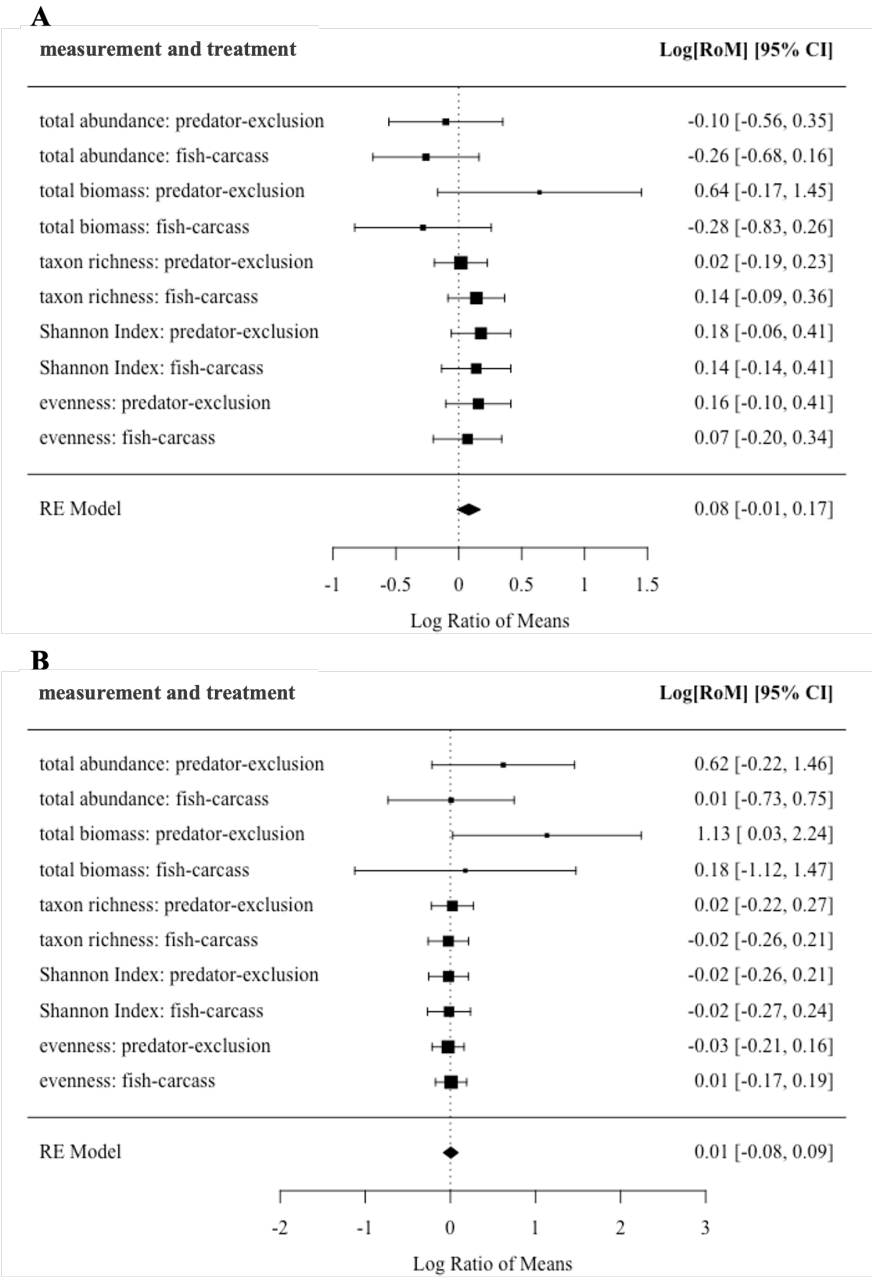


Figure 15. Effect size of the predator-exclusion and the fish-carcass treatments on the total abundance, total biomass, taxon richness, Shannon index, and evenness for A) the marine and B) the river site. Symbols and their explanations as in Figure 10.

The NMDS plots showed no clear distinction between the partial-cage, predator-exclusion, and fish-carcass treatment communities at either the marine or the river site. The large overlap of the treatment ellipses suggests that the benthic macrofauna community composition did not change when predators were excluded or when fish was added as an additional food source (Figure 16). The PERMANOVA did not detect any influence of the predator-exclusion and fish-carcass treatments on the benthic macrofauna community either (Table 7).

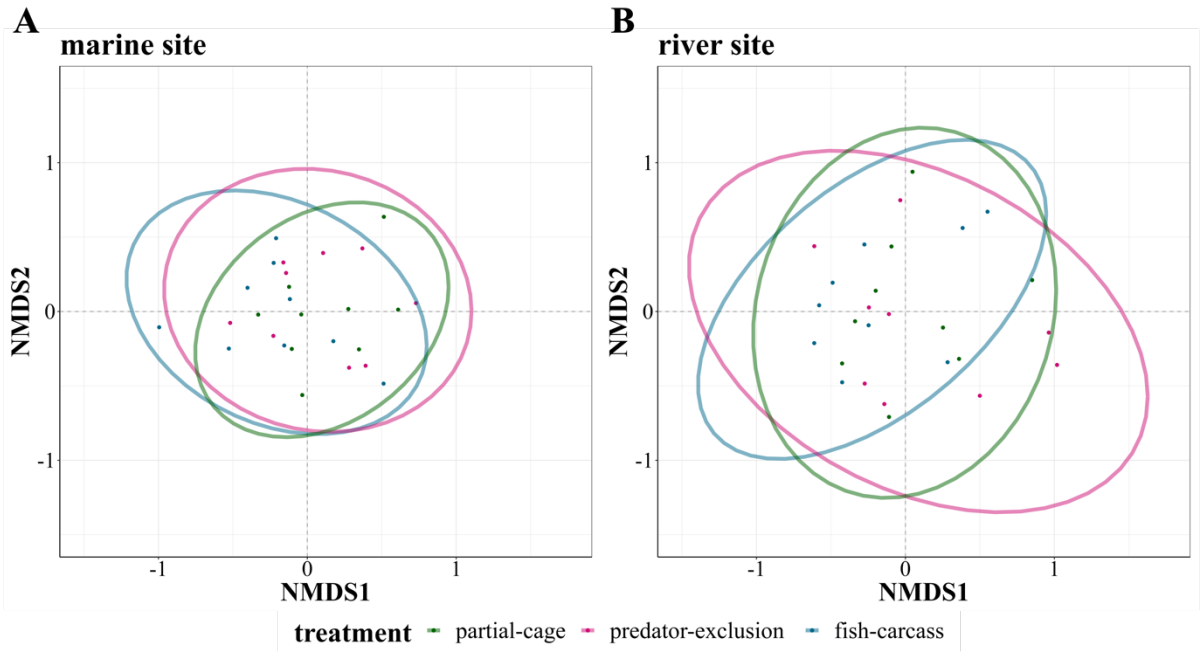


Figure 16. Non-metric multidimensional scaling (NMDS) plots of the first two axes showing the similarity in macrobenthic community composition of the partial-cage (green), predator-exclusion (pink), and fish-carcass (blue) treatments at the marine (A) and river site (B). Symbols and their explanations as in Figure 11. n = 9 for each season and site. Stress level = 0.1204 for both sites.

Table 7. Summary of PERMANOVA results testing for a treatment influence (predator-exclusion and fish-carcass) on the benthic macrofauna community composition at the marine and the river site. Treatment was included as a fixed factor and block as a random factor. Abbreviations as in Table 3.

	marine site					river site				
	df	**SSq**	**R^2**	**pseudo-F**	**p**	**df**	**SSq**	**R^2**	**pseudo-F**	**p**
treatment	2	0.13	0.05	0.60	0.72	2	0.28	0.05	0.63	0.84
residual	24	2.54	0.95			24	5.35	0.95		
total	26	2.66	1.00			26	5.64	1.00		

3.3.2 Food-web structure

H3.2: Benthic macrofauna is expected to utilize the additional fish as a food source, resulting in higher $\delta^{15}N$ values in fish-carcass relative to control treatments at both sites.

At the marine site, the Student's t-tests found significant increases in the $\delta^{15}N$ values of *Euchone* sp. and Oligochaeta indet. due to the fish-carcass treatment, indicating the uptake of fish OM. No significant effects of the fish-carcass treatment were determined on the $\delta^{15}N$ values for Chironomidae indet. and *Macoma calcarea* (Figure 17 A, Table 8). The test power for all Student't t-tests at the marine site was low (Table 8).

At the river site, the Student's t-tests detected a significant increase in $\delta^{15}N$ values for Spionidae indet. caused by the fish-carcass treatment and thus, the feeding of them on OM of the fish. For Oligochaeta indet. the fish-carcass treatment did not significantly change the $\delta^{15}N$ values (Figure 17 B, Table 8). The Welch t-test did not identify a significant difference in $\delta^{15}N$ values due to the fish-carcass treatment for *Macoma calcarea* either (Table 8). The test power for the analyses at the river site was also low (< 0.2), only the test power of the $\delta^{15}N$ analysis for Spionidae indet. was high (Table 8).

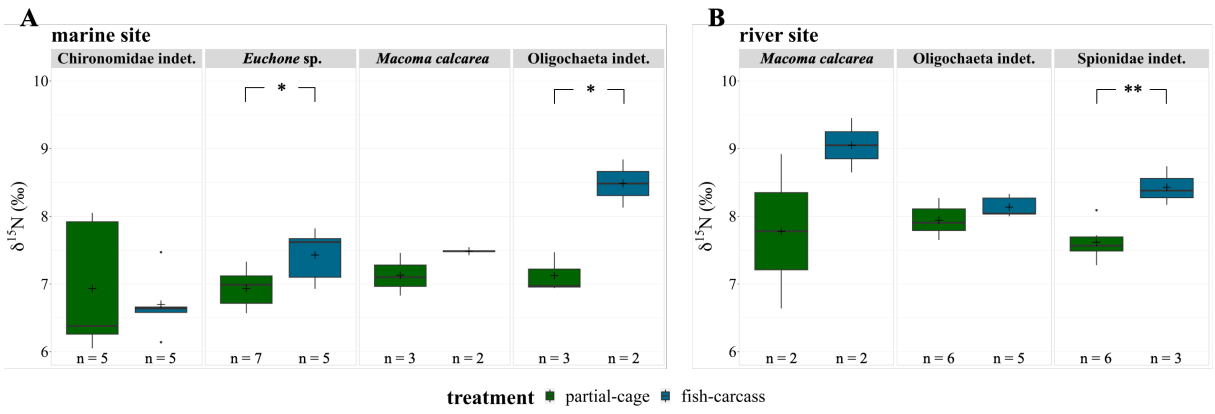


Figure 17. Boxplots showing the treatment effects on the $\delta^{15}N$ values of intertidal macrobenthos for A) the marine and B) the river site. The effects were based on the comparison between fish-carcass (blue) treatment with the partial-cage (green) treatment. The fish-carcass had a $\delta^{15}N$ value of 6.88 ± 0.16 ‰. Asterisks indicate significant differences (< 0.05 with *, < 0.01 with **). Other symbols and their explanations as in Figure 9.

Table 8. Student's t-test and test power results for fish-carcass treatment effects on the $\delta^{15}N$ values of the taxa at the marine and the river site. Significant p-values are marked in bold. Asterisk marks performed Welch t-test.

	marine site				river site			
	Student's t-test			test power	Student's t-test			test power
$\delta^{15}N$	df	t	p		df	t	p	
Chironomidae indet.	8	0.48	0.642	0.321	-	-	-	-
Euchone sp.	10	-2.54	**0.030**	0.109	-	-	-	-
Macoma calcarea	3	-1.51	0.229	0.152	1.24	-1.05	*0.456	0.078
Oligochaeta indet.	3	-3.93	**0.029**	0.320	9	-1.57	0.152	0.158
Spionidae indet.	-	-	-	-	7	-4.12	**0.004**	0.998

All effect sizes of the fish-carcass treatment only provided small effects (< 0.2) on the $\delta^{15}N$ values of all taxa at both study sites (Figure 18).

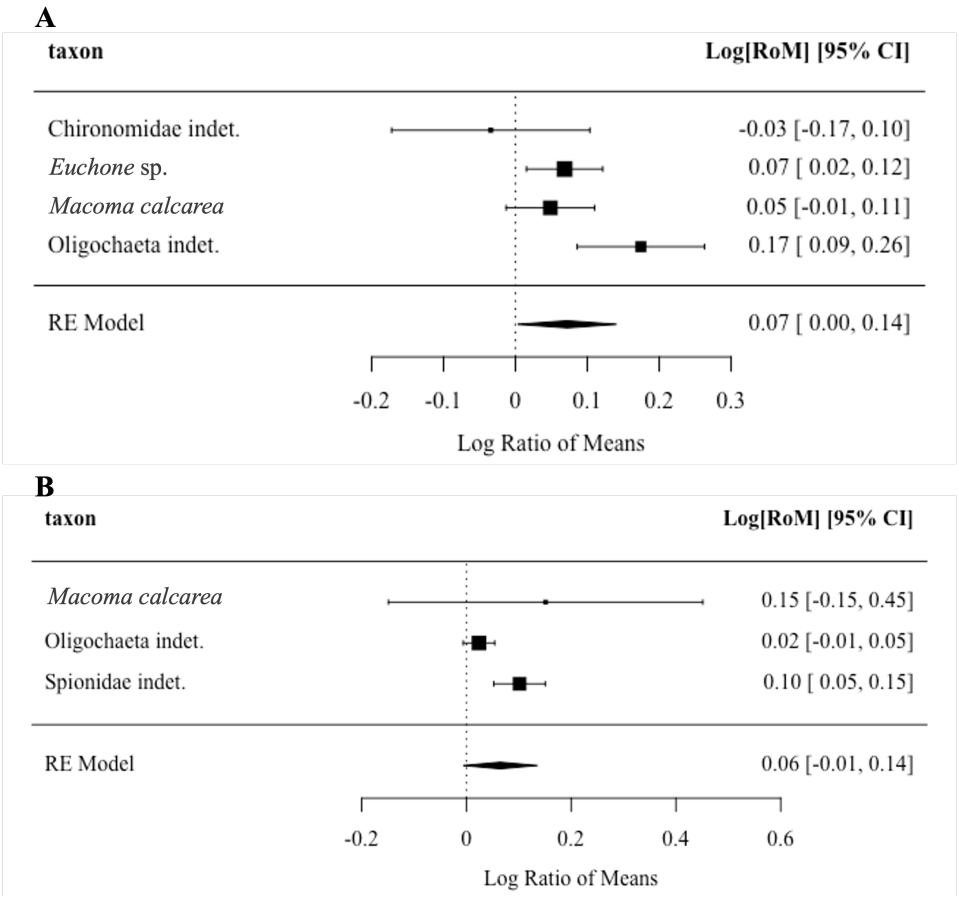


Figure 18. Effect size of the fish-carcass treatments on the $\delta^{15}N$ values of the different taxa at A) the marine site and B) the river site. Symbols and their explanations as in Figure 10.

4 Discussion

4.1 River runoff effects

4.1.1 Macrobenthic community

Neither the total abundance nor the biodiversity or community structure of intertidal macrobenthos in the Målselv area changed significantly at either the marine or river site after snowmelt in fall compared to June, which rejects most parts of hypothesis 1.1. Interestingly, however, the total macrobenthic biomass after snowmelt was higher at the marine site and lower at the river site compared to during snowmelt – also partly rejecting hypothesis 1.1.

The higher total biomass at the marine site after snowmelt can result from higher nutrient concentrations supplied during snowmelt and increased river runoff. Even though the marine site was considered to be less river influenced, the NO_2 and NO_3 concentrations in the water were, in fact, eight times higher in fall than in June by the time of sampling, suggesting this area also benefits from river runoff through input of nutrients (Table 1). Further, Målselva runoff seems to reach the marine site of this study and dominate the freshwater in the surface layer during freshet (personal communication A. Renner, Institute of Marine Research (IMR)). This river impact associated with higher nutrient concentrations at the marine site can lead to higher primary production and hence, more food availability for macrobenthos. Data on monthly nutrient fluxes from 2017 until 2023 indicate that most NO_3 from the Målselva arrives before the maximum discharge in May (2023) or June (2017 – 2022) (Appendix 1). Although the phytoplankton spring bloom typically happens before the snowmelt in the study area (April/May), the increased riverine nutrient input may support a second bloom in summer (July until September) (Appendix 1, Frigstad et al. 2020). If this process was extended to the marine site, intertidal organisms would have more food available after than during snowmelt, which would allow benthic biomass to increase.

Contradictory to the marine site, the total biomass at the river site was lower in fall than in June, i.e., after than during snowmelt. This finding is also contradictory to that of McGovern et al. (2020), who found higher biomass after increased river runoff close to the river mouth. The reason for the lower total biomass observed in the present study at the more river-influenced site may be the high sedimentation loads that can come down the river during the snowmelt. In 2023, the peak in suspended particulate matter in the study area was reached around the discharge peak in May (Appendix 1). The sediment can reduce light availability after the

snowmelt and thus lower primary production (Frigstad et al. 2020). The runoff from the Målselva is high in fine inorganic sediment and can cause high light attenuation (personal observation). Perhaps this effect was strong enough to sufficiently limit algal food availability on the sediment surface that it constrained macrobenthic biomass production in the subsequent months.

How total abundances of macrobenthos could persist when biomass declined at the river site in fall, remains unexplained. While recruits perhaps would have been expected to settle by then, they likely had not done so yet. A study from the Irish intertidal zone found the highest total mean recruits in May/April and fall starting in September (Watson & Barnes 2004). If the same was true in northern Norway this potentially could have increased the total abundance in the present study. However, for *Macoma balthica*, for instance, it can take between 18 and 31 days for larvae to develop (Drent 2002), suggesting that the benthos in the present study might not have been developed as fast by the time of sampling in fall, which can resulted in stable total abundance data. Additionally, predation could have lowered the recruitment effect since the exclusion of larger epibenthic predators in the present study resulted in an increase in total abundance at least at the river site.

Biodiversity metrics were not affected by the increased snowmelt-driven river runoff but the river site had an overall lower taxon richness than the marine site. A previous study related reduced species richness near the river outflow compared to marine conditions farther out in the fjord to high sedimentation, providing some evidence that river runoff lowers biodiversity (McGovern et al. 2020). The lower taxon richness at the river site compared to the marine site further agrees with the Remane model (1934) predicting lower species richness in brackish habitats, which could be an indication of the taxa being adapted to the environmental conditions on a longer time scale.

Further, the lower taxon richness at the river site and the absence of its changes from spring to fall could have resulted from high environmental disturbance, e.g., ice scouring. Ice scouring harms benthic communities, followed by an increase in diversity and abundance after recovery (Gutt 2001, Conlan & Kvitek 2005). However, frequently scoured areas may not or just very slowly recover after several years due to a slow growth rate of cold-water species (Gutt 2001). The recovery of a soft-bottom community in the high Canadian Arctic, for example, took several years (Conlan & Kvitek 2005) and boulders in the Beaufort Sea shelf in Alaska showed a recolonization of only 10 % after seven years (Konar 2013). The river site of the present study faced ice scouring at the beginning of the sampling year (personal communication M. Molis).

Thus, the ice scouring at the river site, which might have been very strong before sampling in spring, resulted in low taxon richness, and the recovery took longer than the experimental period, possibly explaining why biodiversity did not increase from spring to fall.

Overall, the different macrobenthic community parameters only partially provide evidence for higher river runoff effects at the river site than at the marine site, rejecting the last part of hypothesis 1.1. Based on the argumentation above, a stronger river influence at the river site compared to the marine site is only observed for the total macrobenthic biomass (which decreased at the river and increased at the marine site). All other macrobenthic community parameters did not show differences between the two sites, which is probably due to the unexpectedly stronger river influence at the marine site.

4.1.2 Food-web structure

The average $\delta^{13}C$ increase of all taxa by 1.33 ‰ at the marine site and 1.07 ‰ for Oligochaeta at the river site from June to fall provides evidence that macrobenthos assimilated terrestrial OM during increased river runoff and rather sourced marine OM later in the season – confirming hypothesis 1.2. In agreement with the present study, previous research near the study site found decreasing $\delta^{13}C$ values in macrobenthos with increased terrestrial input during the snowmelt as the organisms tend to utilize the terrestrial OM (McGovern et al. 2020), which typically has lower $\delta^{13}C$ values than marine OM (< -25 ‰; Dunton et al. 2012). However, even during runoff season, the $\delta^{13}C$ values of the analyzed macrobenthos in the present study ranged between -24 and -18 ‰ at both sites, indicating primarily feeding on marine algae and to a less extent on terrestrial matter.

In more detail, the increase in $\delta^{13}C$ in macrobenthos in fall at both sites can be due to the lower river discharge, given that the maximum discharge from Målselva in 2023 was in May and the freshwater flow in fall less than in June (Appendix 1). Hence, by the time of sampling in fall, the freshwater amount was less and the proportion of marine water increased again. In this context, it remains unclear why the isotope POM values in the water in fall showed lower $\delta^{13}C$ values at both sites compared to June (Table 1), although values were still higher than reported by McGovern et al. (2020) (-27.7 ‰), suggesting being rather marine-derived (-24.28 ‰ at the marine and -24.37 ‰ at the river site).

The higher $\delta^{13}C$ values of macrobenthos after the snowmelt than before can result from the organisms primarily feeding on the phytoplankton bloom in summer. Unpublished monitoring data (Appendix 1) show that in 2023, the summer bloom lasted from June until October and, therefore, before and during the sampling at the end of September and the beginning of October. Support for this idea comes from rather fast isotopic turnover in intertidal macrobenthos. For macrobenthos of temperate latitudes, the isotopic turnover is typically one to a few weeks (water temperature: 15.9 °C; Lefebvre & Dubois 2016), suggesting that the $\delta^{13}C$ values of the organisms in the present study were able to show a response to phytoplankton summer bloom by the time of sampling in fall. Additionally, this isotopic turnover time provides evidence that the lower $\delta^{13}C$ values of the organisms in June compared to fall can result from the increased river runoff given sampling happened four weeks after peak discharge of Målselva on May 22nd (Appendix 1).

Addressing the part of hypothesis 1.2 that possible river runoff effects are more substantial at the river than at the marine site is only possible for Oligochaeta indet. due to insufficient material of other taxa for stable isotope analysis from the river site. The $\delta^{13}C$ values of Oligochaeta do not reflect stronger impacts of river runoff at the river site than at the marine site. At both study sites, the mean $\delta^{13}C$ values for during (marine: -19.97 ‰, river: -20.00 ‰) and after snowmelt (marine: -18.83 ‰, river: -18.93 ‰) were very similar and the mean increase from June to fall was just slightly higher at the marine site (marine: 1.14 ‰, river: 1.07 ‰). These similar responses in $\delta^{13}C$ at both sites could result from the fact that the marine site was probably more river-influenced than expected (personal communication A. Renner, IMR). The isotopic signal suggests that sufficient amounts of terrestrial OM were able to reach the marine site and caused lower $\delta^{13}C$ values during compared to after snowmelt and to a similar degree as at the river site.

In the present study, all taxa showed an increase in $\delta^{13}C$ values after the increased river runoff in fall. However, while the degree of the increase varied between taxa, there was no evidence that this variation in $\delta^{13}C$ increase can be explained by the taxa's feeding mode as there was no clear connection between feeding mode and $\delta^{13}C$ increase, i.e., taxa with the same feeding mode showed different strong increases, while taxa with different feeding modes exhibited similar $\delta^{13}C$ increases. *Euchone* sp., and *Macoma calcarea*, for example, are both filter feeders (Kędra et al. 2010) and while the $\delta^{13}C$ values of *Euchone* sp., increased by 2.24 ‰ after snowmelt, the $\delta^{13}C$ of *Macoma calcarea* increased by only half of that (1.18 ‰). At the same time, the $\delta^{13}C$

values of deposit feeding Oligochaeta (Kędra et al. 2010) showed a similar increase (1.14 ‰ at the marine site) as *Macoma calcarea*.

4.2 Predator exclusion effects

4.2.1 Macrobenthic community

The increase in total macrobenthos abundance at the river site and biomass at either site partly rejects hypothesis 2.1, while the lack of changes in biodiversity and community composition are as predicted. The increase in total biomass at either site aligns with the results of Posey et al. (2006), who found evidence that benthic biomass increases in the absence of predators and in combination with nutrient enhancement. In the present study, nutrient increase was caused by river runoff; while the total macrobenthic biomass at the marine site increased by 90 %, the total biomass at the river site increased by 211 %, suggesting a positive interaction between the absence of predators, additional nutrients through river runoff, and the increase of macrobenthos biomass. Moreover, the higher total biomass at both study sites may indicate individual growth in the absence of epibenthic predators. The body weight per individual at the marine site increased by 111 % and at the river site by 67 % in the predator-exclusion treatment. This increase may have resulted from the organisms having more time to feed and grow during the absence of predators.

The higher total abundance of macrobenthos in the absence of predators at the river site suggests that the exclusion of predators may have favored the survival of recruits. It is, however, rather likely that the sampling of the present study in fall was too early to identify any changes in the macrobenthos abundance in response to recruitment (discussed in section 4.1.1). Since the total abundance increased at the river and not at the marine site, the suspected reproductive event might have been sped up in response to the higher nutrient concentrations (NO_2, NO_3, and PO_4) at the river site. Even though this idea cannot be tested with the available data, research from McGovern et al. (2020) found an increase in abundance and biomass due to river influence.

The results of the biodiversity and community composition analyses are consistent with other studies that found a low to no impact of predation on benthic communities at higher compared to lower latitudes (Freestone et al. 2011, 2021, Petrowski et al. 2015, Díaz et al. 2023). Therefore, it is likely that this study provides further evidence that epibenthic predators have a minor impact on benthic macrofauna communities at higher latitudes, at least on macrobenthic diversity and community composition. This low influence can be due to the overall low predator

abundances, diversity, or predation rates (Petrowski et al. 2015, Freestone et al. 2021), which can result in low predation pressure and hence be a negligible factor in structuring benthic macrofauna communities. The present study did not include monitoring the presence of predators. The only observations happened during the sampling periods in June and fall in which the bird Eurasian oystercatcher and single crabs of the genus *Hyas* spp. were present. Thus, it remains questionable whether the missing predator effects on macrobenthic diversity indeed resulted from the absence of predators or have another cause.

Alternatively to a low predator abundance, another reason for the limited impact of predation on macrobenthos diversity might be the high abiotic stress benthic organisms face in intertidal zones and at higher latitudes. In polar intertidal zones, benthic organisms must deal with substantial diurnal and seasonal variations in temperature, light, salinity, ice cover, and food availability (e.g., Gutt 2001, Kaiser & Williams 2011). According to the environmental stress model (ESM, Menge & Sutherland 1987), predation impact on individuals and communities decreases with increasing environmental stress when predators are more strongly negatively affected by environmental stress than the prey. This implies that predation is a less important structuring factor in benthic communities in polar than temperate regions (Petrowski et al. 2015, Molis et al. 2019, Díaz et al. 2023) and likely in sub-polar regions (as in the present study) with similar environmental conditions, too.

4.3 Fish carcass effects

4.3.1 Macrobenthic community

The fish-carcass treatment did not change total abundance and biomass, biodiversity, and community composition of macrobenthos, thus rejecting hypothesis 3.1. It remains questionable whether this finding is due to a true lack of influence of the fish on the macrobenthos or the experimental design. Studies from lakes and streams in Alaska do show effects of salmon and their carcasses on benthic organisms. They primarily reported increased abundance and biomass of macroinvertebrates due to nutritious input of the salmon (Wipfli et al. 1998, McLennan et al. 2019). Other studies described an increased growth rate of macrobenthos, standing stock for certain feeding guilds (shredders and collectors), and increased abundance for Chironomidae (Chaloner & Wipfli 2002, Monaghan & Milner 2008).

One reason for the lack of fish carcass effects on the macrobenthic community in the present study could have been the method that was used. The fish piece was hanging a few centimeters

above the sediment and was not in contact with the sediment. This design was intended to simulate the nutrients and OM of the fish potentially coming from the river. However, studies showing an increase in scavengers, shredders, and collectors through fish carcasses placed the fish directly on top of the sediment (Monaghan & Milner 2008, Dunlop et al. 2021) instead of hanging the fish over the sediment. Hence, the organisms in the present could not reach the fish without detaching from the seafloor and might not have considered it as a food source, which is, however, contradictory to the trophic marker data discussed below (section 4.3.2).

The possibility that the fish piece might not have released enough nutrients or food particles to cause an effect seems unlikely given the fish was mostly degraded when it was replaced every few weeks to maintain the input. Moreover, the fish piece (about 125 g) may have been too small to cause detectable effects, as the studies conducted in Alaska that found an effect on macrobenthos had larger amounts of fish (up to several ten thousand individuals; Wipfli et al. 1998). To create a more comparable setting to the studies from Alaska and to investigate the effects higher amounts of fish carcasses have on intertidal macrobenthos in northern Norway, future studies that consider these aspects should be conducted. These studies could either increase the amount of fish hanging in the cages to increase the load of nutrients and OM or take macrobenthos samples in estuaries facing high numbers of spawning and dead pink salmon.

Furthermore, periods of strong currents from the tide may have transported the nutrients and OM from the fish away, reducing the concentrations reaching the sediment below the fish, and leading to weakened effects of the fish on the macrobenthic community. Nutrient concentrations from the fish and the sediment and stable isotope samples of the sediment below the fish were not taken, which could have given evidence for this theory.

In addition, chlorophyll *a* concentration in the sediment could indicate whether the fish affected lower trophic levels. Cederholm et al. (1999) showed that primary production increased (in rivers and streams) due to salmon carcass nutrients. In relation to the C2C project in which this study took place, chlorophyll *a* measurements were taken. However, a first look at the data did not show a higher chlorophyll *a* concentration for the fish-carcass treatment compared to the control at both study sites (Appendix 11).

4.3.2 Food-web structure

Significant higher $\delta^{15}N$ values of *Euchone* sp. and Oligochaeta indet. at the marine site and Spionidae indet. at the river site as well as trends for higher $\delta^{15}N$ values for all other taxa at both sites (except one decrease in $\delta^{15}N$ values for Chironomidae at the marine site) in the fish-carcass treatment partly confirm hypothesis 3.2, namely – that the study taxa assimilated the OC from the fish. This finding is consistent with stream studies indicating that aquatic macroinvertebrates can be enriched in ^{15}N, resulting from including organic salmon matter in their diet (Schuldt & Hershey 1995, Bilby et al. 1996). They found ^{15}N enrichments in macroinvertebrates from 1 – 4 ‰ during a study period of half a year (Schuldt & Hershey 1995) and over a year (Bilby et al. 1996).

However, the isotopic enrichment of the taxa in the present study is low (on average 0.49 ‰ at the marine and 0.76 ‰ at the river site), with the highest $\delta^{15}N$ value increase in Oligochaeta at the marine site with 1.36 ‰, suggesting either a small contribution from the fish to the diet of the taxa or a slow isotopic turnover. The fish itself had a mean $\delta^{15}N$ value of 6.88 ‰, while the values of the taxa ranged from 6.70 – 8.49 ‰ at the marine and from 8.14 – 9.05 ‰ at the river site. If the taxa would have fed exclusively on the fish, their $\delta^{15}N$ values were expected to be around 10.28 ‰ in the fish-carcass treatment ($\delta^{15}N$ values of the fish plus 3.4 ‰ enrichment per trophic level, Minagawa & Wada 1984, Post 2002). Thus, the smaller isotopic enrichment observed here suggests a small contribution of the fish in the diet of the taxa. Alternatively, a slow isotopic turnover rate of the taxa would mean that the organisms fed on the fish but the accumulation of the isotopic signal of the fish in the taxa's tissue took time. Hence, it is possible that the taxa fed more on the fish than the $\delta^{15}N$ values showed at the time of measurement. However, studies investigating the isotopic turnover of macrobenthos conclude a turnover of about one to a few weeks for macrobenthos (Lefebvre & Dubois 2016), meaning that if the macrobenthos had fed to a strong extent on the fish, the isotopic turnover would have been fast enough to be visible as a strong $\delta^{15}N$ increase in the fish-carcass treatment. Thus, it is more likely that the small increase in $\delta^{15}N$ values in the fish-carcass treatment provides evidence that the taxa included the fish in their diet but fed to a larger extent on other food sources.

As other studies found increased $\delta^{15}N$ values in primary producers in streams and estuarine macroalgae after a salmon run in Alaska (Kline et al. 1990, Schuldt & Hershey 1995, Fujiwara & Highsmith 1997), conducting the present experiment for a more extended period in combination with stable isotope analyses of the micro- and macroalgae could determine if fish

carcasses affect the trophic structure of northern Norwegians intertidal zones after a longer period of time. This could be an approach to investigate whether the nutrients from fish carcasses are taken up by primary producers before entering the macrobenthic food-web and higher trophic levels (Kline et al. 1990).

4.4 Critical reflection

The results need to be taken with caution. All test powers for the macrobenthos community analyses were low (< 0.8; Cohen 1988), which can explain why changes over time, through predator exclusion, and the addition of fish carcasses were not found using statistical tests, even though some data showed a trend towards an increase or decrease in the different treatments. To investigate whether the treatments still influenced the macrobenthic community despite the lack of statistically significant differences, the effect sizes of each community parameter per treatment were calculated. They showed, for example, that the absence of predators, on average, increased the total biomass of macrobenthos. However, all values that showed a medium or large effect also had a large variance. In the stable isotope data, several analyses provided significant differences with both, high and low test power. At the same time, all effect sizes of the stable isotope data of all treatments indicated small effects, suggesting that the differences that were detected by statistical tests resulted from several influencing factors and not just from the tested one. Summarized, the combination of the two analysis approaches in the present study can identify whether treatment effects on macrobenthic communities did not occur and can provide evidence of whether treatment effects did occur. For the fish-carcass treatment, for instance, besides no statistical differences, the effect sizes of the macrobenthic community were also small (< 0.28), emphasizing no fish carcass effects on the intertidal macrobenthic community.

Moreover, the statistical comparison between the two study sites to investigate the difference in river runoff effects was not possible due to missing site replicates. To be able to statistically test whether e.g., the taxon richness is lower at the river site due to the higher river runoff influence (i.e., for a difference between the two sites), it would be necessary to add independent site replicates; at least two site replicates with high river runoff and two site replicates with low river runoff. Both study sites were influenced to a different degree by Målselva and rather function as subsamples than independent replicates. A statistical comparison of the two sites in context of river runoff influence would result in pseudo-replication (Hurlbert 1984).

5 Conclusion and outlook

Cage experiments at two sites with different degrees of river influences were used to investigate the impact of river runoff, predation, and carcasses of migratory fish on intertidal benthic macrofauna communities and carbon and nitrogen stable isotopes. The results indicated decreased total biomass through increased river runoff during snowmelt closer to the river and an increase further away. The $\delta^{13}C$ values were lower during snowmelt with either more and less river influence, suggesting the uptake of terrestrial OM. The exclusion of predators revealed an overall increase in total biomass as well as higher total abundances closer to the river. The addition of fish did not alter the macrobenthic community, although it led to higher $\delta^{15}N$ values for some taxa, implying the assimilation of fish OM from macrobenthos. In conclusion, river runoff influenced the macrobenthic community and food web-structure, while predation and fish carcasses had rather limited effects.

The present study highlights the complexity of macrobenthic communities and the food web in the intertidal zone. It underlines the need to measure central components within the ecosystem (e.g., chlorophyll *a* and nutrient concentrations) and emphasizes further research in this field. This study represents a "snapshot" of the effects of river runoff, predation, and carcasses of migratory fish on benthic macrofauna. Environmental and biological drivers that structure intertidal macrobenthos have high spatial, seasonal, and annual variation. The volume and content of river runoff in Norway, for example, varies between rivers and years (Kaste et al. 2023). Further, the presence of predators, their abundance, and the occurrence of pink salmon can change. The range extensions of predators (e.g., Atlantic cod in Kortsch et al. 2015, and red king crab in Fuhrmann et al. 2015), among other factors due to rising temperatures following climate change, alter food-web structures and can increase predation pressure on native species. McLennan et al. (2019) showed that higher macroinvertebrate abundance and biomass due to salmon carcasses last for one year after the carcass addition and it is possible that pink salmon is becoming more abundant where temperatures rise (Hindar et al. 2020). Due to the importance of macrobenthos for the ecosystem (e.g., through regeneration of nutrients and OM utilization), it is crucial to further investigate the changing drivers and understand their interactions with benthic organisms.

Hence, many questions arise from the findings of this study: Is the river runoff impact on macrobenthic community and food-web structure stronger in other years than in the present study? How does stronger predation pressure by potentially more predators alter the

macrobenthic community? How is the intertidal benthic macrofauna community and food-web structure influenced in Norwegian estuaries with high numbers of pink salmon, and how long does a possible impact take and last?

To address these questions, sampling should be conducted frequently before, during, and after the snowmelt season as well as for a longer period. This approach could identify changes in the macrobenthos community and food preferences that occur earlier or later than in this study. Additionally, repetition over several years can identify varying effects with different environmental conditions and whether new predators increase predation pressure. Lastly, the impact of fish carcasses on macrobenthos in coastal areas could be investigated with entire carcasses or in regions with the influence of rivers where pink salmon reproduce.

6 References

Ahmed R, Prowse T, Dibike Y, Bonsal B, O'Neil H (2020) Recent Trends in Freshwater Influx to the Arctic Ocean from Four Major Arctic-Draining Rivers. Water 12:1189.

Aksnes DL, Dupont N, Staby A, Fiksen Ø, Kaartvedt S, Aure J (2009) Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. Mar Ecol Prog Ser 387:39–49.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Ben-Shachar M, Lüdecke D, Makowski D (2020) effectsize: Estimation of Effect Size Indices and Standardized Parameters. Journal of Open Source Software, 5(56), 2815. doi: 10.21105/joss.02815.

Bilby RE, Fransen BR, Bisson PA (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can J Fish Aquat Sci 53:164–173.

Biles CL, Paterson DM, Ford RB, Solan M, Raffaelli DG (2002) Bioturbation, ecosystem functioning and community structure. Hydrol Earth Syst Sci 6:999–1005.

Bray JR, Curtis JT (1957) An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecol Monogr 27:326–349.

Bring A, Destouni G (2014) Arctic Climate and Water Change: Model and Observation Relevance for Assessment and Adaptation. Surv Geophys 35:853–877.

Casler MD, Vermerris W, Dixon RA (2015) Replication Concepts for Bioenergy Research Experiments. BioEnergy Res 8:1–16.

Cederholm CJ, Kunze MD, Murota T, Sibatani A (1999) Pacific Salmon Carcasses: Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems. Fisheries 24:6–15.

Chaloner DT, Wipfli MS (2002) Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. J North Am Benthol Soc 21:430–442.

Champely S (2020) _pwr: Basic Functions for Power Analysis_. R package version 1.3-0, <https://CRAN.R-project.org/package=pwr>.

Cohen J (1988) Statistical Power Analysis for the Behavioral Sciences, 2nd ed. Erlbaum, Hillsdale, NJ.

Conlan KE, Kvitek RG (2005) Recolonization of soft-sediment ice scours on an exposed Arctic coast. Mar Ecol Prog Ser 286:21–42.

Craig H (1957) Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim Cosmochim Acta 12:133–149.

de Wit HA, Valinia S, Weyhenmeyer GA, Futter MN, Kortelainen P, Austnes K, Hessen DO, Räike A, Laudon H, Vuorenmaa J (2016) Current Browning of Surface Waters Will Be Further Promoted by Wetter Climate. Environ Sci Technol Lett 3:430–435.

Díaz MJ, Buschbaum C, Renaud PE, Valdivia N, Molis M (2023) Limited predatory effects on infaunal macrobenthos community patterns in intertidal soft-bottom of Arctic coasts. Ecol Evol 13:e9779.

Drent J (2002) Temperature responses in larvae of *Macoma balthica* from a northerly and southerly population of the European distribution range. J Exp Mar Biol Ecol 275:117–129.

Dunlop K, Renaud PE, Berge J, Jones DOB, Harbour RP, Tandberg AHS, Sweetman AK (2021) Benthic scavenger community composition and carrion removal in Arctic and Subarctic fjords. Polar Biol 44:31–43.

Dunton KH, Schonberg SV, Cooper LW (2012) Food Web Structure of the Alaskan Nearshore Shelf and Estuarine Lagoons of the Beaufort Sea. Estuaries Coasts 35:416–435.

Edgar GJ, Barrett NS (2000) Effects of Catchment Activities on Macrofaunal Assemblages in Tasmanian Estuaries. Estuar Coast Shelf Sci 50:639–654.

Estes JA, Duggins DO (1995) Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. Ecol Monogr 65:75–100.

Finlay J, Neff J, Zimov S, Davydova A, Davydov S (2006) Snowmelt dominance of dissolved organic carbon in high-latitude watersheds: Implications for characterization and flux of river DOC. Geophys Res Lett 33.

Fox J, Weisberg S (2019) _An R Companion to Applied Regression_, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

Freestone AL, Osman RW, Ruiz GM, Torchin ME (2011) Stronger predation in the tropics shapes species richness patterns in marine communities. Ecology 92:983–993.

Freestone AL, Torchin ME, Jurgens LJ, Bonfim M, López DP, Repetto MF, Schlöder C, Sewall BJ, Ruiz GM (2021) Stronger predation intensity and impact on prey communities in the tropics. Ecology 102:e03428.

Frigstad H, Andersen T, Hessen DO, Jeansson E, Skogen M, Naustvoll L-J, Miles MW, Johannessen T, Bellerby RGJ (2013) Long-term trends in carbon, nutrients and stoichiometry in Norwegian coastal waters: Evidence of a regime shift. Prog Oceanogr 111:113–124.

Frigstad H, Kaste Ø, Deininger A, Kvalsund K, Christensen G, Bellerby RGJ, Sørensen K, Norli M, King AL (2020) Influence of Riverine Input on Norwegian Coastal Systems. Front Mar Sci 7.

Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM (2015) Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. J Sea Res 106:1–13.

Fujiwara M, Highsmith RC (1997) Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. Mar Ecol Prog Ser 158:205–216.

García Molinos J, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, Pandolfi JM, Poloczanska ES, Richardson AJ, Burrows MT (2016) Climate velocity and the future global redistribution of marine biodiversity. Nat Clim Change 6:83–88.

Gende SM, Quinn TP, Willson MF, Heintz R, Scott TM (2004) Magnitude and Fate of Salmon-Derived Nutrients and Energy in a Coastal Stream Ecosystem. J Freshw Ecol 19:149–160.

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biol 24:553–564.

Guzman LM, Germain RM, Forbes C, Straus S, O'Connor MI, Gravel D, Srivastava DS, Thompson PL (2019) Towards a multi-trophic extension of metacommunity ecology. Ecol Lett 22:19–33.

Hindar K, Hole LR, Kausrud KL, Malmstrøm M, Rimstad E, Robertson L, Sandlund OT, Thorstad EB, Vollset K, de Boer H, Eldegard K, Järnegren J, Kirkendall LR, Måren IE, Nilsen EB, Rueness EK, Nielsen A, Velle G (2020) Assessment of the risk to Norwegian biodiversity and aquaculture from pink salmon (*Oncorhynchus gorbuscha*). Scientific Opinion of the Panel on Alien Organisms and Trade in Endangered Species of the Norwegian Scientific Committee for Food and Environment. 1-157.

Hurlbert SH (1984) Pseudoreplication and the Design of Ecological Field Experiments. Ecol Monogr 54:187–211.

Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. Mar Ecol Prog Ser 287:251–253.

Jickells TD (1998) Nutrient Biogeochemistry of the Coastal Zone. Science 281:217–222.

Jordà Molina È, Silberberger MJ, Kokarev V, Reiss H (2019) Environmental drivers of benthic community structure in a deep sub-arctic fjord system. Estuar Coast Shelf Sci 225:106239.

Kaiser MJ, Williams PJ leB (2011) Marine Ecology: Processes, Systems, and Impacts. OUP Oxford.

Kaste Ø, Gundersen CB, Sample J, McGovern M, Skancke LB, Allan I, Jenssen MTS, Bæk K, Skogan OA (2023) The Norwegian River Monitoring Programme 2022 – water quality status and trends. Norsk institutt for vannforskning (NIVA).

Kline TC, Goering JJ, Mathisen OA, Poe PH, Parker PL (1990) Recycling of Elements Transported Upstream by Runs of Pacific Salmon: I, $\delta^{15}N$ and $\delta^{13}C$ Evidence in Sashin Creek, Southeastern Alaska. Can J Fish Aquat Sci 47:136–144.

Kohl M (2023) _MKpower: Power Analysis and Sample Size Calculation_. R package version 0.7, <https://github.com/stamats/MKpower>.

Kokarev VN, Vedenin AA, Polukhin AA, Basin AB (2021) Taxonomic and functional patterns of macrobenthic communities on a high Arctic shelf: A case study from the East Siberian Sea. J Sea Res 174:102078.

Konar B (2013) Lack of recovery from disturbance in high-arctic boulder communities. Polar Biol 36:1205–1214.

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc B Biol Sci 282:20151546.

Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. In: Life at Interfaces and Under Extreme Conditions. Liebezeit G, Dittmann S, Kröncke I (eds) Springer Netherlands, Dordrecht, p 1–24

Kędra M, Gromisz S, Jaskuła R, Legeżyńska J, Maciejewska B, Malec E, Opanowski A, Ostrowska K, Włodarska-Kowalczuk M, Węsławski J (2010) Soft bottom macrofauna of an All Taxa Biodiversity Site: Hornsund (77°N, Svalbard). Pol Polar Res 31:309–326.

Larsen S, Andersen T, Hessen DO (2011) Climate change predicted to cause severe increase of organic carbon in lakes. Glob Change Biol 17:1186–1192.

Lavender JT, Dafforn KA, Johnston EL (2014) Meso-predators: A confounding variable in consumer exclusion studies. J Exp Mar Biol Ecol 456:26–33.

Lefebvre S, Dubois S (2016) The stony road to understand isotopic enrichment and turnover rates: insight into the metabolic part. Vie Milieu-Life Environ 66:305–314.

Mainka SA, Howard GW (2010) Climate change and invasive species: double jeopardy. Integr Zool 5:102–111.

Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303:685–687.

Mattsson T, Kortelainen P, Räike A, Lepistö A, Thomas DN (2015) Spatial and temporal variability of organic C and N concentrations and export from 30 boreal rivers induced by land use and climate. Sci Total Environ 508:145–154.

McGovern M, Evenset A, Borgå K, de Wit HA, Braaten HFV, Hessen DO, Schultze S, Ruus A, Poste A (2019) Implications of Coastal Darkening for Contaminant Transport, Bioavailability, and Trophic Transfer in Northern Coastal Waters. Environ Sci Technol 53:7180–7182.

McGovern M, Poste AE, Oug E, Renaud PE, Trannum HC (2020) Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords. Estuar Coast Shelf Sci 240:106774.

McLennan D, Auer SK, Anderson GJ, Reid TC, Bassar RD, Stewart DC, Cauwelier E, Sampayo J, McKelvey S, Nislow KH, Armstrong JD, Metcalfe NB (2019) Simulating nutrient release from parental carcasses increases the growth, biomass and genetic diversity of juvenile Atlantic salmon. J Appl Ecol 56:1937–1947.

Menge BA, Sutherland JP (1987) Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. Am Nat 130:730–757.

Middelburg JJ (2018) Reviews and syntheses: to the bottom of carbon processing at the seafloor. Biogeosciences 15:413–427.

Miller LP, Gaylord B (2007) Barriers to flow: The effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. J Exp Mar Biol Ecol 344:215–228.

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140.

Mo TA, Thorstad EB, Sandlund OT, Berntsen HH, Fiske P, Uglem I (2018) The pink salmon invasion: a Norwegian perspective. J Fish Biol 93:5–7.

Molis M, Beuchel F, Laudien J, Włodarska-Kowalczuk M, Buschbaum C (2019) Ecological Drivers of and Responses by Arctic Benthic Communities, with an Emphasis on Kongsfjorden, Svalbard. In: The Ecosystem of Kongsfjorden, Svalbard. Advances in Polar Ecology, Hop H, Wiencke C (eds) Springer International Publishing, Cham, p 423–481

Monaghan KA, Milner AM (2008) Salmon carcasses as a marine-derived resource for benthic macroinvertebrates in a developing postglacial stream, Alaska. Can J Fish Aquat Sci 65:1342–1351.

Montagna PA, Kalke RD (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. Estuaries 15:307–326.

Monteith DT, Stoddard JL, Evans CD, de Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, Keller B, Kopácek J, Vesely J (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450:537–540.

Norkko A, Thrush SF, Hewitt JE, Cummings VJ, Norkko J, Ellis JI, Funnell GA, Schultz D, MacDonald I (2002) Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. Mar Ecol Prog Ser 234:23–42.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) _vegan: Community Ecology Package_. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>.

Oug E (2001) Polychaetes in intertidal rocky and sedimentary habitats in the region of Tromsø, northern Norway. Sarsia 86:75–83.

Pace ML, Cole JJ, Carpenter SR, Kitchell JF, Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488.

Petrowski S, Molis M, Schachtl K, Buschbaum C (2015) Do bioturbation and consumption affect coastal Arctic marine soft-bottom communities? Polar Biol 39:2141–2153.

Pielou EC (1966) The measurement of diversity in different types of biological collections. J Theor Biol 13:131–144.

Piorkowski RJ (1995) Ecological effects of spawning salmon on several southcentral Alaskan streams - ProQuest. https://www.proquest.com/docview/304161063?pq-origsite=gscholar&fromopenview=true&sourcetype=Dissertations%20&%20Theses (accessed March 19, 2024)

Posey MH, Alphin TD, Cahoon L (2006) Benthic community responses to nutrient enrichment and predator exclusion: Influence of background nutrient concentrations and interactive effects. J Exp Mar Biol Ecol 330:105–118.

Post DM (2002) Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. Ecology 83:703–718.

Poste A, Kaste Ø, Frigstad H, de Wit H, Harvey T, Valestrand L, Deininger A, Bryntesen T, Delpech L-M, Christensen G (2021) The impact of the spring 2020 snowmelt floods on physicochemical conditions in three Norwegian river-fjord-coastal systems. Norsk institutt for vannforskning (NIVA).

Quinn GP, Keough MJ (2002) Experimental Design and Data Analysis for Biologists. Cambridge University Press.

R Core Team (2023) R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Rahel FJ, Olden JD (2008) Assessing the Effects of Climate Change on Aquatic Invasive Species. Conserv Biol 22:521–533.

Reise K (1977) Predator exclusion experiments in an intertidal mud flat. Helgoländer Wiss Meeresunters 30:263–271.

Remane A (1934) Die Brackwasserfauna: Mit besonderer Berücksichtigung der Ostsee. Zoologischer Anzeiger.

Sandlund OT, Berntsen HH, Fiske P, Kuusela J, Muladal R, Niemelä E, Uglem I, Forseth T, Mo TA, Thorstad EB, Veselov AE, Vollset KW, Zubchenko AV (2019) Pink salmon in Norway: the reluctant invader. Biol Invasions 21:1033–1054.

Sandrini-Neto L, Camargo MG (2023) GAD: an R package for ANOVA designs from general principles. Available on CRAN.

Schuldt JA, Hershey AE (1995) Effect of Salmon Carcass Decomposition on Lake Superior Tributary Streams. J North Am Benthol Soc 14:259–268.

Shannon CE, Weaver W (1963) The mathematical theory of communication. University of Illinois Press.

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, Competition, and Prey Communities: A Review of Field Experiments.

Taghon GL, Nowell ARM, Jumars PA (1980) Induction of Suspension Feeding in Spionid Polychaetes by High Particulate Fluxes. Science 210:562–564.

Thoms F, Burmeister C, Dippner JW, Gogina M, Janas U, Kendzierska H, Liskow I, Voss M (2018) Impact of Macrofaunal Communities on the Coastal Filter Function in the Bay of Gdansk, Baltic Sea. Front Mar Sci 5.

Torchiano M (2020) _effsize: Efficient Effect Size Computation_. doi:10.5281/zenodo.1480624 <https://doi.org/10.5281/zenodo.1480624>, R package version 0.8.1, <https://CRAN.R-project.org/package=effsize>.

UC Davis, Stable Isotope Facility of UC Davis, California, USA (2023) Available from https://stableisotopefacility.ucdavis.edu/sample-weight-calculator. Accessed 2023-08-12

Ugelstad CP (2019) Riverine and glacier influence on infaunal benthic communities in Isfjorden, Svalbard. Master thesis, UiT Norges arktiske universitet

Underwood AJ (1997) Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable Isotope Turnover and Half-Life in Animal Tissues: A Literature Synthesis. PLoS ONE 10:e0116182.

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. Journal of Statistical Software, 36(3), 1-48. https://doi.org/10.18637/jss.v036.i03

Villnäs A, Janas U, Josefson AB, Kendzierska H, Nygård H, Norkko J, Norkko A (2019) Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter. Mar Ecol Prog Ser 622:31–48.

Volkenborn N, Reise K (2007) Effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion. J Sea Res 57:78–88.

Wassmann P, Svendsen H, Keck A, Reigstad M (1996) Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J Mar Syst 8:53–71.

Watson DI, Barnes DKA (2004) Temporal and spatial components of variability in benthic recruitment, a 5-year temperate example. Mar Biol 145:201–214.

Whitfield AK, Elliott M, Basset A, Blaber SJM, West RJ (2012) Paradigms in estuarine ecology – A review of the Remane diagram with a suggested revised model for estuaries. Estuar Coast Shelf Sci 97:78–90.

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. _Journal of Open Source Software_, *4*(43), 1686. doi:10.21105/joss.01686 <https://doi.org/10.21105/joss.01686>.

Winder M, Schindler DE, Moore JW, Johnson SP, Palen WJ (2005) Do bears facilitate transfer of salmon resources to aquatic macroinvertebrates? Can J Fish Aquat Sci 62:2285–2293.

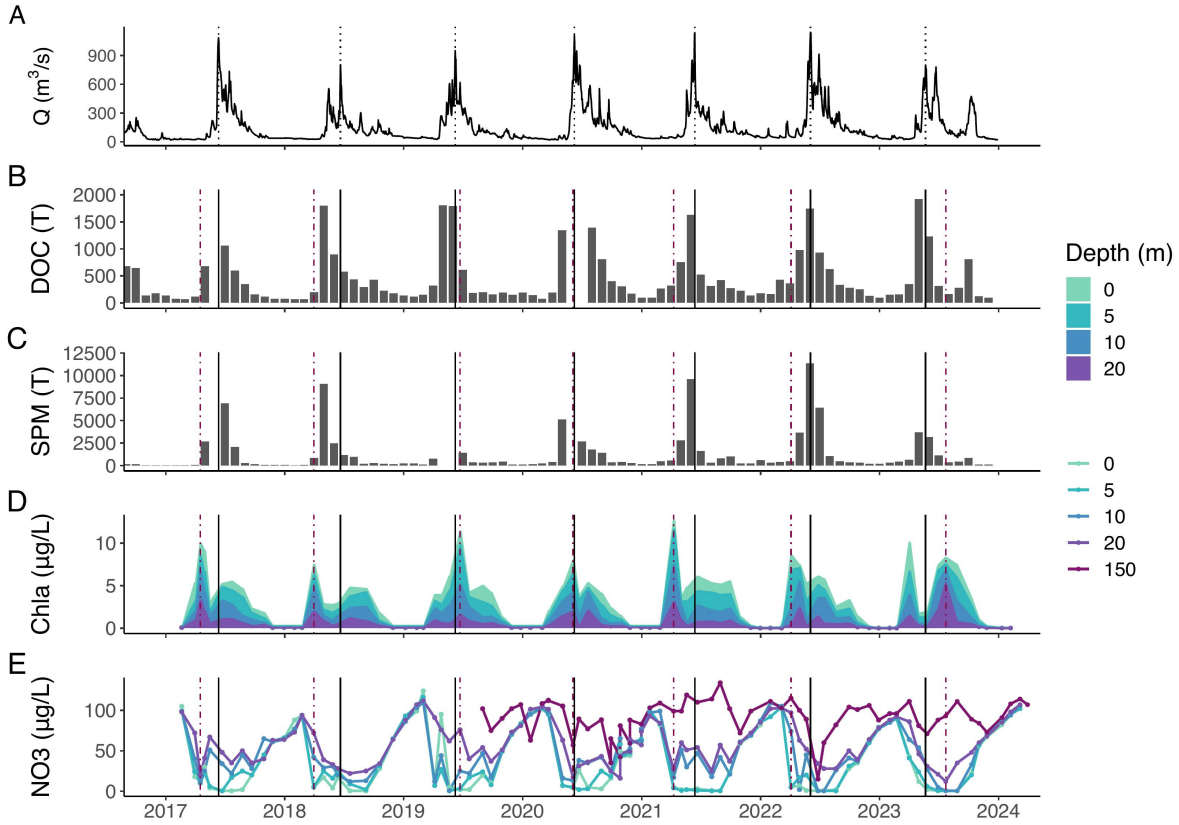
Wipfli MS, Hudson J, Caouette J (1998) Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Can J Fish Aquat Sci 55:1503–1511.

WoRMS Editorial Board (2024) World Register of Marine Species. Available from https://www.marinespecies.org. Accessed 2024-03-25. doi:10.14284/170.

Zolkos S, Krabbenhoft DP, Suslova A, Tank SE, McClelland JW, Spencer RGM, Shiklomanov A, Zhulidov AV, Gurtovaya T, Zimov N, Zimov S, Mutter EA, Kutny L, Amos E, Holmes RM (2020) Mercury Export from Arctic Great Rivers. Environ Sci Technol 54:4140–4148.

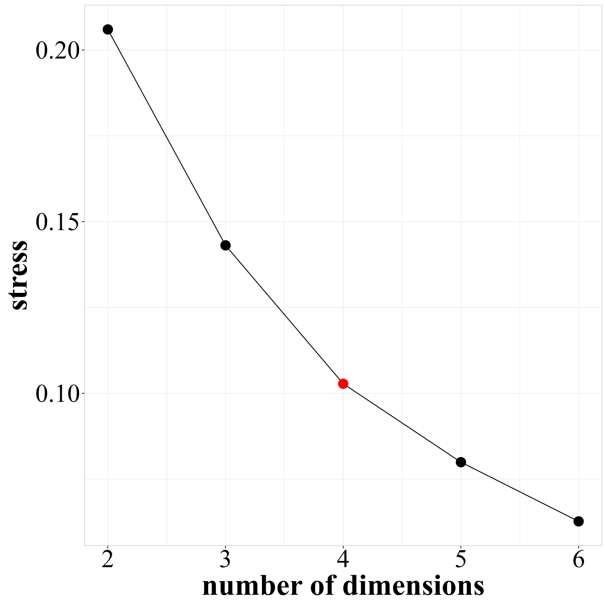
7 Appendix

Appendix 1



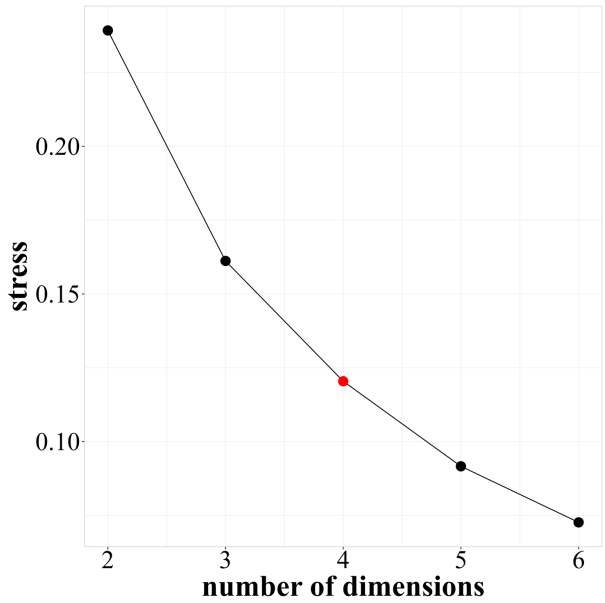
A) Discharge from Målselva measured by NVE at Målselvfossen, B) Dissolved organic carbon flux from Målselva (if no bar = missing data), C) Suspended particulate matter from Målselva, D) Chlorophyll *a* concentrations in the surface waters in Straumsfjorden (located a bit further out in the fjord compared to marine site of the present study), E) nitrate concentrations at Straumsfjorden. Vertical lines illustrate timing of the peak of the spring flood (black) and peak Chlorophyll *a* concentrations in the fjord (dotted, red). Figure made by Maeve McGovern based on unpublished NVE and NIVA monitoring data.

Appendix 2



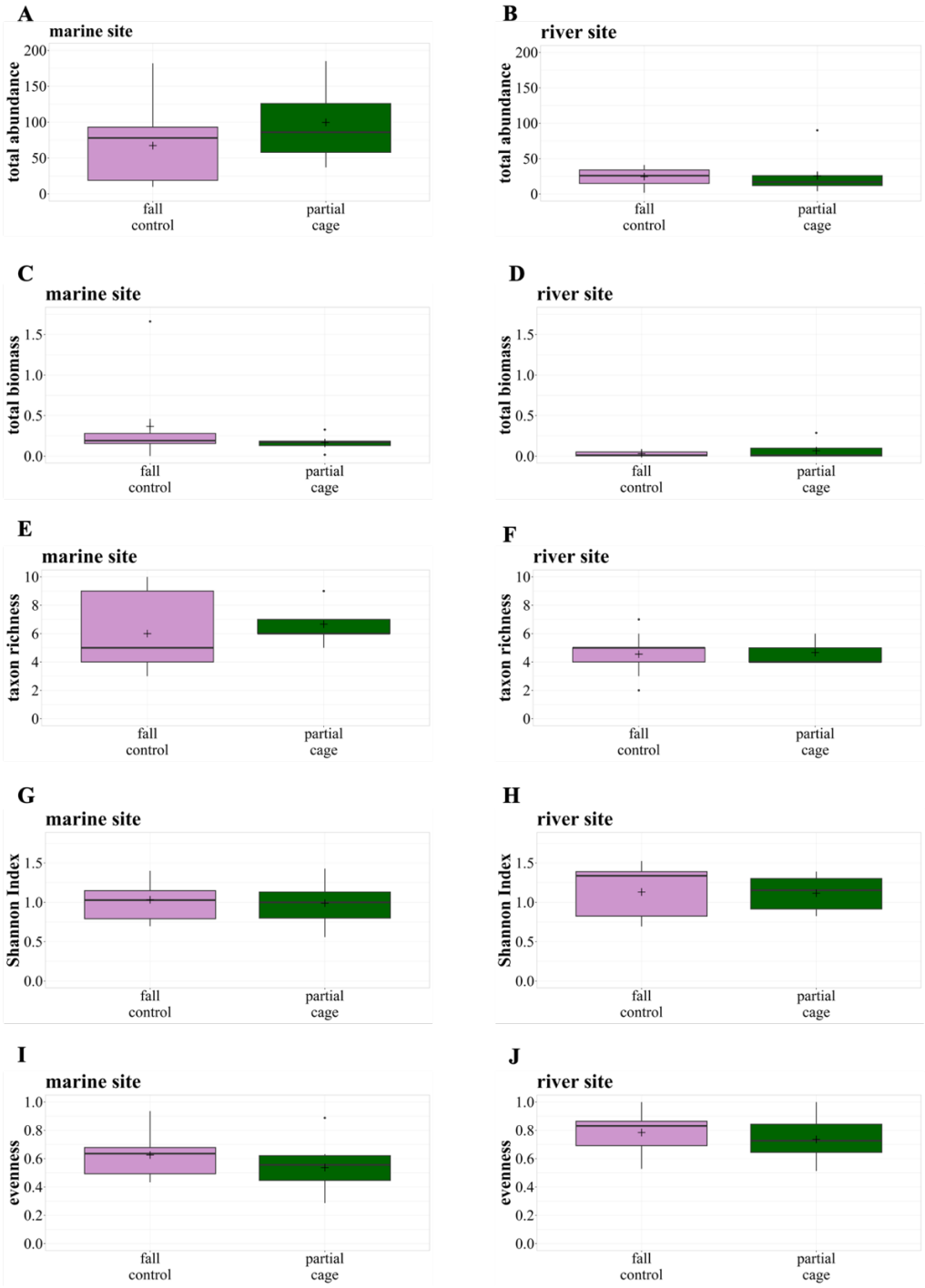
Number of dimensions in relation to stress values of the NMDS (river runoff effect). The red point marks the number of dimensions used in the corresponding NMDS.

Appendix 3



Number of dimensions in relation to stress values of the NMDS (predator-exclusion and fish-carcass effects). The red point marks the number of dimensions used in the corresponding NMDS.

Appendix 4



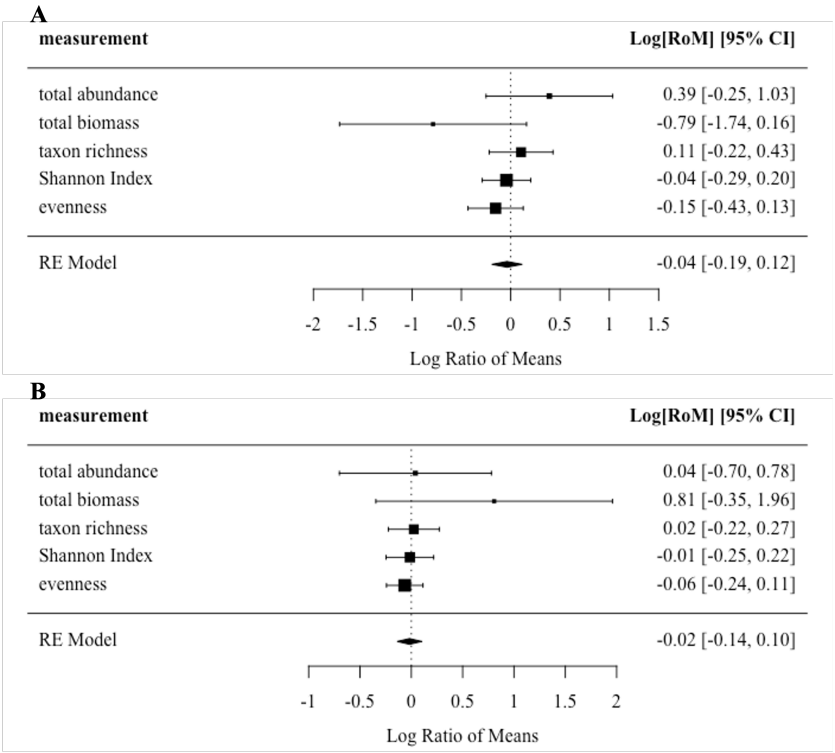
Boxplots showing no cage effects (n = 18, evenness river n = 16) on the different macrobenthic measurements [per 24 cm^2]. Total abundance at A) the marine site and B) the river site. Total biomass [g/24 cm^2] at C) the marine site and D) the river site. Taxon richness at E) the marine and F) the river site. Shannon Index at G) the marine and H) the river site. Evenness of at I) the marine and J) the river site. The cage effect is based on the comparison between the fall-control (rose) and the partial-cage (green) treatments. Symbols and their explanations as in Figure 9.

Appendix 5

Student's t-test and test power results for a cage effect on total abundance, total biomass, taxon richness, Shannon Index, and evenness at the marine and the river site. df = 16

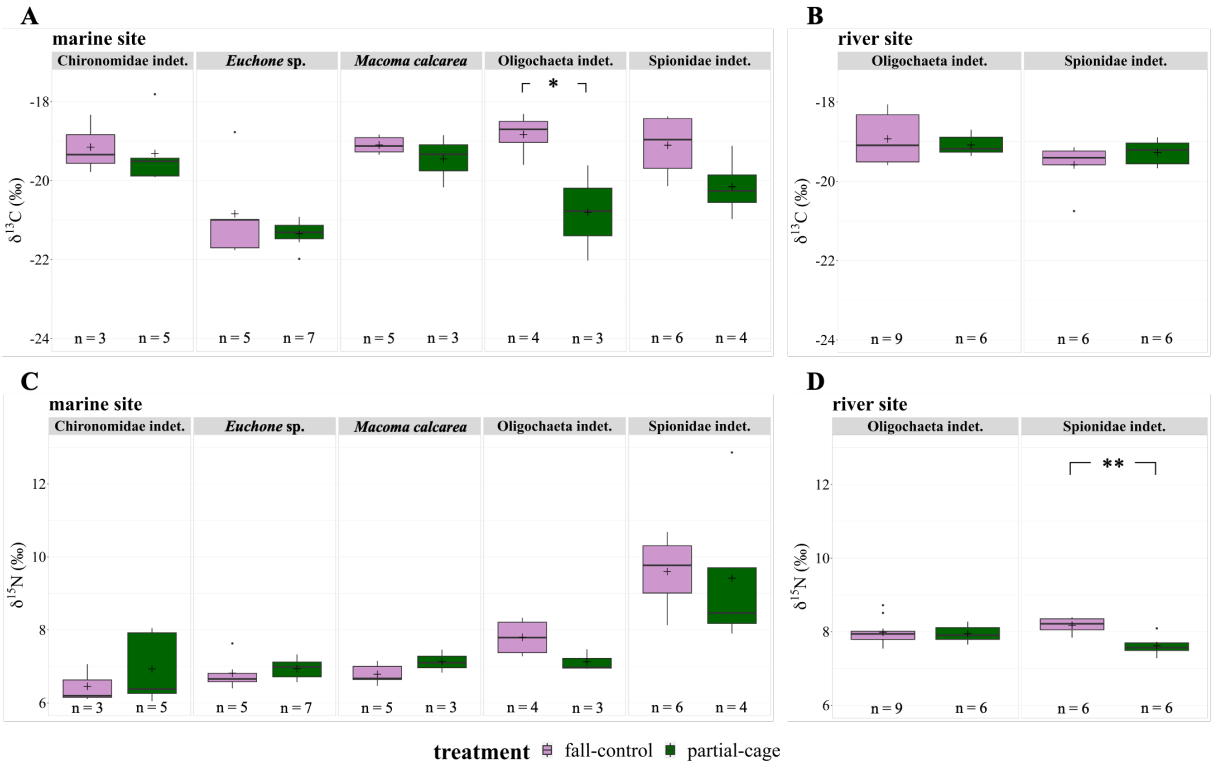
	marine site		river site	
	Student's t-test	**test power**	**Student's t-test**	**test power**
total abundance	t = -1.28, p = 0.219	0.268	t = 0.10, p = 0.920	0.109
total biomass	t = 1.18, p = 0.254	0.318	t = -0.83, p = 0.420	0.940
taxon richness	t = -0.66, p = 0.520	0.051	t = -0.19, p = 0.850	0.068
Shannon Index	t = 0.34, p = 0.737	0.114	t = 0.12, p = 0.906	0.059
evenness	t = 1.08, p = 0.296	0.243	t = 0.71, p = 0.488	0.260

Appendix 6



Effect size of the cages themselves (comparison of fall-control and partial-cage treatments) on the total abundance, total biomass, taxon richness, Shannon index, and evenness for A) the marine and B) the river site. Symbols and their explanations as in Figure 10.

Appendix 7



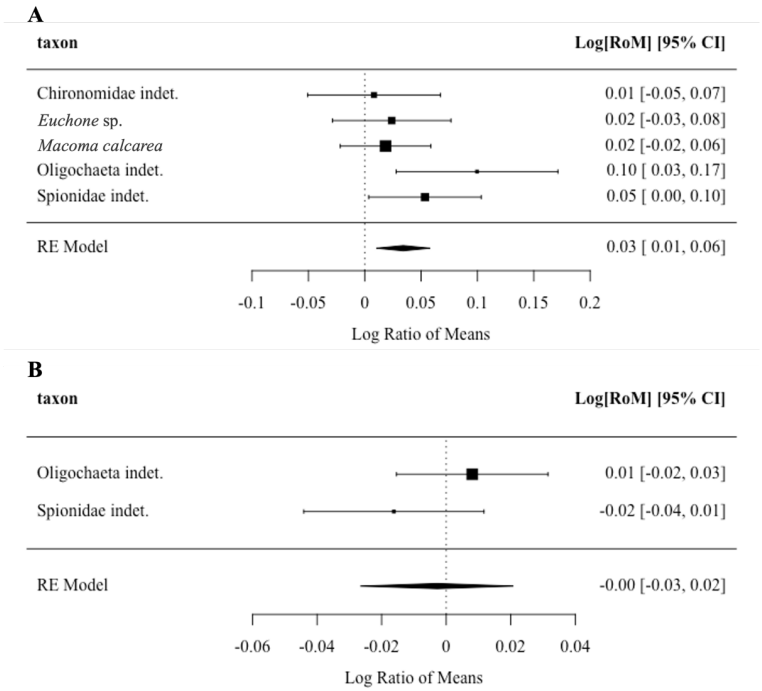
Boxplots showing the $\delta^{13}C$ and $\delta^{15}N$ values for the fall-control (rose) and the partial-cage (green) treatments of the analyzed taxa at the marine and river site. The difference between the two treatments is described as the cage effect. $\delta^{13}C$ values for all analyzed taxa at A) the marine and B) the river site. $\delta^{15}N$ values for all analyzed taxa at C) the marine and D) the river site. Asterisks indicate significant differences (< 0.05 with *, < 0.01 with **). Other symbols and their explanations as in Figure 9.

Appendix 8

Student's t-test and test power results for a cage effect on all taxa's $\delta^{13}C$ and $\delta^{15}N$ values at the marine and the river site. Significant p-values are marked bold.

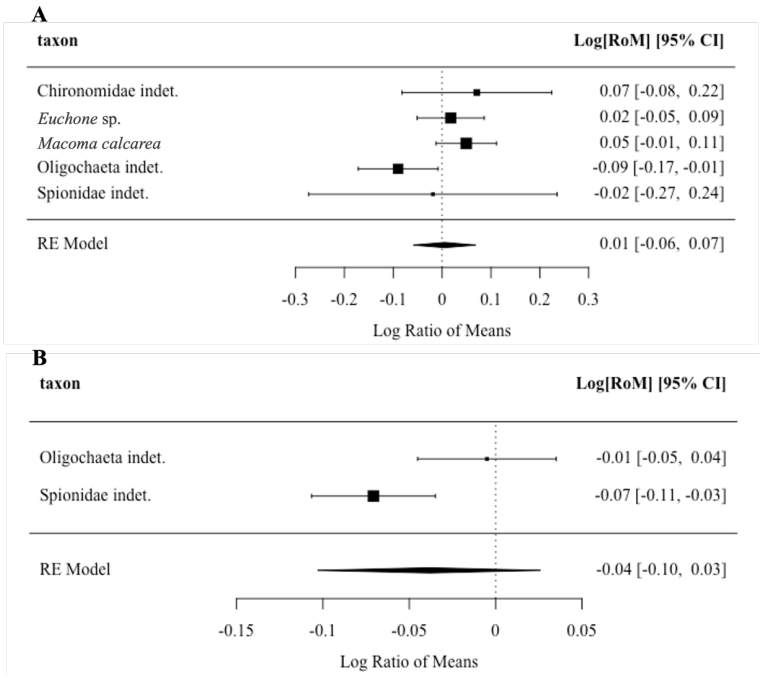
	marine site				**river site**			
		Student's t-test		**test power**		**Student's t-test**		**test power**
$\delta^{13}C$	**df**	**t**	**p**		**df**	**t**	**p**	
Chironomidae indet.	6	2.29	0.062	0.959	-	-	-	-
Euchone sp.	10	1.06	0.315	0.277	-	-	-	-
Macoma calcarea	6	1.14	0.296	0.050	-	-	-	-
Oligochaeta indet.	5	2.95	**0.032**	0.999	13	0.59	0.568	0.272
Spionidae indet.	8	2.09	0.070	0.875	10	-1.13	0.283	0.133
$\delta^{15}N$								
Chironomidae indet.	6	-0.19	0.859	0.198	-	-	-	-
Euchone sp.	10	-0.55	0.593	0.050	-	-	-	-
Macoma calcarea	6	-1.61	0.158	0.258	-	-	-	-
Oligochaeta indet.	5	1.95	0.109	0.224	13	0.22	0.828	0.149
Spionidae indet.	8	0.17	0.869	0.079	10	3.91	**0.003**	0.233

Appendix 9



Effect size the cages had on the $\delta^{13}C$ values of the different taxa at A) the marine and B) the river site. Symbols and their explanations as in Figure 10.

Appendix 10



Effect size the cages had on the $\delta^{15}N$ values of the different taxa at A) the marine and B) the river site. Symbols and their explanations as in Figure 10.

Appendix 11

Mean Chlorophyll *a* concentrations (µg/g dry weight) with standard deviation for all four treatments that were sampled in fall 2023. Unpublished data provided by Rolf Gradinger (UiT).

	marine site		river site	
treatment	**n**	**Chlorophyll a**	**n**	**Chlorophyll a**
fall-control	6	5.33 ± 1.25	6	5.82 ± 1.35
partial-cage	6	7.79 ± 1.11	6	5.37 ± 0.99
predator-exclusion	6	7.79 ± 0.99	6	5.86 ± 1.45
fish-carcass	6	7.66 ± 0.95	6	5.93 ± 1.94

Appendix 12 – Macrobenthos abundance and biomass data

SITE	BLOCK	TREATMENT	TREATMENT_1	OLIGOCHAETA	PYGOSPIO	CHIRONOMIDAE	EUCHONE	CAPITELLA	TURBELLARIA	MALACOCEROS	ARENICOLA	NEMATODA
Marine	1	C1	C	14	9	9	53	0	0	0	0	3
Marine	1	C2	C	49	18	3	106	0	1	0	0	0
Marine	1	C3	C	0	4	0	19	0	0	0	0	0
Marine	1	F1	F	6	11	1	61	2	0	2	0	2
Marine	1	F2	F	5	5	5	65	1	0	2	0	0
Marine	1	F3	F	1	7	1	66	2	0	2	0	0
Marine	1	FC1	FC	8	10	0	98	0	0	0	0	0
Marine	1	FC2	FC	14	15	2	87	2	0	0	0	5
Marine	1	FC3	FC	10	18	6	102	0	0	0	0	0
Marine	1	PC1	PC	4	10	3	55	0	0	0	0	0
Marine	1	PC2	PC	4	4	4	35	0	0	1	0	0
Marine	1	PC3	PC	4	12	9	93	1	0	1	0	1
Marine	2	C1	C	1	13	0	61	0	0	0	0	0
Marine	2	C2	C	3	13	3	72	0	0	0	0	1
Marine	2	C3	C	0	5	0	5	0	0	0	0	0
Marine	2	F1	F	3	9	1	31	0	0	0	0	0
Marine	2	F2	F	0	18	0	32	1	0	0	0	0
Marine	2	F3	F	17	15	1	97	0	1	0	0	1
Marine	2	FC1	FC	4	16	1	47	0	0	0	0	0
Marine	2	FC2	FC	1	2	5	17	0	0	0	0	0
Marine	2	FC3	FC	2	12	12	57	0	0	0	0	1
Marine	2	PC1	PC	1	11	8	161	0	0	0	0	0
Marine	2	PC2	PC	2	22	3	89	0	0	0	1	0
Marine	2	PC3	PC	2	15	7	129	0	0	0	2	0
Marine	3	C1	C	4	10	0	4	0	0	0	0	0
Marine	3	C2	C	13	7	3	56	7	0	3	0	2
Marine	3	C3	C	0	7	0	1	1	0	0	0	1
Marine	3	F1	F	9	10	3	35	7	0	2	0	5
Marine	3	F2	F	7	3	10	70	0	0	2	0	1
Marine	3	F3	F	0	10	2	7	0	0	6	0	1
Marine	3	FC1	FC	30	8	12	26	0	0	2	0	3
Marine	3	FC2	FC	11	6	0	5	1	0	0	1	0
Marine	3	FC3	FC	11	19	22	53	0	0	1	0	6
Marine	3	PC1	PC	2	9	3	37	1	0	1	0	1
Marine	3	PC2	PC	14	13	0	56	0	0	0	0	2
Marine	3	PC3	PC	6	10	0	13	0	0	0	0	7
River	1	C1	C	14	7	5	0	0	0	0	0	5
River	1	C2	C	1	1	0	0	0	0	0	0	0
River	1	C3	C	4	22	4	2	0	0	0	0	0
River	1	F1	F	1	21	5	0	0	0	0	0	0
River	1	F2	F	26	3	1	0	0	0	0	0	1
River	1	F3	F	5	0	0	0	0	0	0	0	0
River	1	FC1	FC	16	15	0	0	0	0	0	0	0
River	1	FC2	FC	0	5	2	0	0	0	0	0	0
River	1	FC3	FC	15	37	14	0	0	2	0	0	0
River	1	PC1	PC	6	5	3	0	0	1	0	0	0
River	1	PC2	PC	10	11	0	0	2	0	0	0	1
River	1	PC3	PC	9	0	0	0	0	0	0	0	0
River	2	C1	C	6	25	1	0	0	0	0	0	0
River	2	C2	C	7	4	0	2	1	0	0	0	0
River	2	C3	C	24	14	2	0	0	0	0	0	0
River	2	F1	F	16	10	2	1	0	0	0	0	0
River	2	F2	F	1	3	1	0	0	0	0	0	0
River	2	F3	F	6	4	5	0	0	0	0	0	0
River	2	FC1	FC	52	27	1	49	0	0	0	0	1
River	2	FC2	FC	13	11	10	1	0	0	0	0	0
River	2	FC3	FC	57	2	3	0	0	0	0	0	0
River	2	PC1	PC	15	4	3	1	0	0	0	0	0
River	2	PC2	PC	2	12	1	0	0	0	0	0	0
River	2	PC3	PC	69	5	1	0	0	0	0	0	9
River	3	C1	C	16	6	2	0	0	0	0	0	0
River	3	C2	C	3	1	1	0	0	0	0	0	0
River	3	C3	C	9	8	2	0	0	0	0	0	0
River	3	F1	F	15	21	6	4	0	0	0	0	0
River	3	F2	F	7	0	1	0	0	0	0	0	0
River	3	F3	F	9	1	3	0	0	0	0	0	0
River	3	FC1	FC	8	7	0	0	0	0	0	0	0
River	3	FC2	FC	3	5	20	0	0	1	0	0	0
River	3	FC3	FC	9	0	0	0	0	0	0	0	0
River	3	PC1	PC	1	0	1	0	0	0	0	0	0
River	3	PC2	PC	5	3	1	0	0	0	0	0	0
River	3	PC3	PC	20	6	3	0	0	0	1	0	0
Marine	1	TC	TC	11	5	1	71	0	0	0	1	0
Marine	1	TC	TC	3	2	0	28	0	0	0	0	3
Marine	1	TC	TC	7	11	2	106	0	0	0	0	0
Marine	2	TC	TC	6	15	0	40	0	0	0	0	0
Marine	2	TC	TC	1	9	0	52	0	1	0	0	0
Marine	2	TC	TC	0	6	0	18	0	0	0	0	1
Marine	3	TC	TC	11	18	0	31	1	0	0	0	1
Marine	3	TC	TC	7	13	0	11	2	0	0	0	2
Marine	3	TC	TC	23	10	0	30	0	0	0	0	1
River	1	TC	TC	4	1	0	0	5	0	0	0	0
River	1	TC	TC	0	1	0	0	0	0	0	0	0
River	1	TC	TC	12	37	0	0	3	0	0	0	0
River	2	TC	TC	10	2	1	2	5	0	0	0	0
River	2	TC	TC	26	9	0	18	0	0	0	0	0
River	2	TC	TC	27	12	1	9	0	0	0	0	0
River	3	TC	TC	7	4	0	1	14	0	0	0	0
River	3	TC	TC	4	0	0	0	0	0	0	0	0
River	3	TC	TC	8	1	0	0	0	0	0	0	0

YOLDIELLA LUCIDA	MACOMA	HYDROBIA NEGLECTA	AMPHIPODA	ETEONE	OWENIIDAE	CAUDOFOVEATA	SPIONIDAE	CAPITELLIDAE	CARDIDAE	LITTORINA	COPEPODA	ISOPODA
0	1	0	0	1	0	0	0	2	0	1	0	0
0	1	0	1	0	0	0	1	1	1	0	0	0
0	1	0	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	1	5
0	1	0	0	0	0	0	0	0	0	0	0	1
0	2	0	1	0	0	0	0	0	0	1	0	0
0	3	0	0	0	0	0	0	0	1	0	0	0
0	2	1	0	0	0	0	0	0	0	0	0	1
1	3	0	1	0	0	0	0	0	0	0	0	1
0	4	0	1	0	0	0	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0	0	0	0	0
0	4	0	1	0	0	0	0	0	0	0	0	0
0	2	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	1	0	0	0
0	2	0	0	0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	1	0	0
0	8	0	0	0	0	0	0	0	3	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0
0	2	0	1	1	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0	1	1	0	0
0	2	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	1	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0	0
0	2	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	2	0	1	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0	1
0	1	0	1	1	0	0	0	0	0	1	0	0
0	2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0	0	0	2	0
0	2	0	0	0	0	0	0	0	0	0	0	2
0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	2	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	5	0	0	3	1
0	0	0	1	0	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	0	0	0	1	0
0	1	0	0	0	0	0	0	3	0	0	3	0
0	0	0	0	0	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	1	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	1	2
0	0	0	0	0	0	0	0	2	0	0	6	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	6	0
0	1	0	0	0	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	6	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	4	0
0	0	0	0	0	0	0	0	0	0	0	6	1
0	0	0	0	0	0	0	0	0	0	0	0	1
0	1	0	3	0	0	0	0	0	0	0	23	0
0	0	0	0	0	0	0	0	4	0	0	0	0
0	1	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	17	1
0	1	0	0	0	0	1	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	1
0	3	0	0	0	3	0	0	4	0	0	0	0
0	2	0	0	0	0	0	0	1	0	0	0	0
0	3	1	4	0	0	0	0	0	0	0	0	0
0	1	0	0	0	3	0	0	0	0	0	0	0
0	1	0	1	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0	0	0	0	0
0	6	0	1	0	0	0	0	0	0	0	0	0
0	2	0	1	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0	0	0
0	1	0	0	0	5	0	0	7	1	0	0	0
0	1	0	0	0	4	0	0	8	0	0	0	0
0	1	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	0	0

GASTROPODA	POLYNOIDAE	PHYLLODOCIDAE	DRYMASS
0	0	0	0,1492
0	0	0	0,4609
0	0	0	1,6612
0	0	0	0,0159
0	0	0	0,1103
0	0	0	0,2184
0	0	0	1,2046
0	0	0	0,2072
0	0	0	0,2774
0	0	0	0,1707
0	0	0	0,3277
0	0	0	0,1779
0	0	0	0,1553
0	0	0	0,2159
0	0	0	0,1881
1	0	0	0,2672
0	0	0	0,0174
0	0	0	0,1642
0	0	0	0,4543
0	0	0	0,0853
0	0	0	0,3147
0	0	0	0,1855
0	0	0	0,1112
0	0	0	0,1308
0	0	0	0,1916
0	0	0	0,2802
0	0	0	0,0017
0	0	0	0,1149
0	0	0	0,1383
0	0	0	0,0846
0	0	0	0,2476
0	0	0	0,0217
0	0	0	0,0449
0	0	0	0,2104
0	0	0	0,1723
0	0	0	0,0170
0	0	0	0,0635
0	0	0	0,0000
0	0	0	0,0880
0	0	0	0,0118
0	0	0	0,0640
0	0	0	0,0016
0	0	0	0,3919
0	0	0	0,0019
0	0	0	0,5696
0	0	0	0,0023
0	0	0	0,0097
0	0	0	0,2865
0	0	0	0,0524
0	0	0	0,0008
0	0	0	0,0113
0	0	0	0,0811
0	0	0	0,0000
0	0	0	0,0584
0	0	0	0,2952
0	0	0	0,0423
0	0	0	0,0298
0	0	0	0,1087
0	0	0	0,0023
0	0	0	0,0903
0	0	0	0,0039
0	0	0	0,0464
0	0	0	0,0057
0	0	0	0,1059
0	0	0	0,3711
0	0	0	0,0328
0	1	1	0,0619
0	0	0	0,1182
0	0	0	0,3854
0	0	0	0,0018
0	0	0	0,0995
0	0	0	0,0085
0	0	0	0,0933
0	0	0	0,1980
0	0	0	0,3712
0	0	0	0,1578
0	0	0	0,0464
0	0	0	0,0765
0	0	0	0,4777
0	0	0	0,1041
0	0	0	0,2552
0	0	0	0,0020
0	0	0	0,0001
0	0	0	0,0220
0	0	0	0,0061
0	0	0	0,1395
0	0	0	0,1138
0	0	0	0,2217
0	0	0	0,0009
0	0	0	0,0046

sample_ID	year	site	block	treatment	taxon	weight_[mg]	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{Air}$ (‰)	cabron comment	nitrogen comment
M-7	2023	Marine	2	TC	Macoma	2,451	-9,20	6,31		
M-8	2023	Marine	2	TC	Macoma	2,908	-9,50	6,20		
M-29	2023	Marine	3	TC	Macoma	2,142	-10,83	6,22		
R-11	2023	River	2	TC	Macoma	3,502	-9,09	5,93		
M-69	2023	Marine	NA	NA	A. nodosum	1,860	-17,68	3,14		Precision decreases for samples containing less than 20ugN
M-70	2023	Marine	NA	NA	A. nodosum	1,673	-17,43	3,55		Precision decreases for samples containing less than 20ugN
M-71	2023	Marine	NA	NA	A. nodosum	1,214	-17,00	3,97		Precision decreases for samples containing less than 20ugN
M-72	2023	Marine	NA	NA	F. nesianiosus	1,441	-17,00	4,28		Precision decreases for samples containing less than 20ugN
M-73	2023	Marine	NA	NA	F. nesianiosus	1,397	-16,46	4,26		Precision decreases for samples containing less than 20ugN
M-74	2023	Marine	NA	NA	F. nesianiosus	1,100	-15,82	4,47		Precision decreases for samples containing less than 20ugN
M-75	2023	Marine	NA	NA	U. lactuca	1,337	-23,08	4,58		Precision decreases for samples containing less than 20ugN
M-76	2023	Marine	NA	NA	U. lactuca	1,196	-23,92	4,88		Precision decreases for samples containing less than 20ugN
M-77	2023	Marine	NA	NA	U. lactuca	1,328	-20,27	4,26		Precision decreases for samples containing less than 20ugN
M-1	2023	Marine	2	TC	Chironomidae	1,095	-19,99	7,21		
M-2	2023	Marine	2	TC	Chironomidae	1,042	-19,32	6,69		
M-3	2023	Marine	2	TC	Euchone	1,155	-23,32	6,00		
M-4	2023	Marine	2	TC	Euchone	1,112	-23,35	6,13		
M-5	2023	Marine	2	TC	Euchone	1,176	-22,98	5,87		
M-6	2023	Marine	2	TC	Euchone	1,550	-23,18	6,12		
M-10 + M-11	2023	Marine	2	TC	Oligo. & Spionidae	1,239	-20,00	7,45		
M-12	2023	Marine	2	TC	Macoma	1,365	-10,10	6,25		
M-13	2023	Marine	2	TC	Macoma	1,116	-18,60	8,39		
M-21 + M-39	2023	Marine	2+3	TC	Oligochaeta	1,579	-19,56	8,15		
M-25	2023	Marine	3	TC	Euchone	1,126	-22,45	6,23		
M-27	2023	Marine	3	TC	Euchone	1,805	-23,11	6,23		
M-30	2023	Marine	3	TC	Chironomidae	1,024	-21,14	6,22		
M-31	2023	Marine	3	TC	Chironimodae	1,477	-20,78	6,33		
M-32	2023	Marine	3	TC	Spionidae	1,054	-19,73	8,43		
M-33	2023	Marine	3	TC	Spionidae	1,122	-19,35	8,26		
M-35	2023	Marine	3	TC	Oligochaete	1,728	-19,67	7,33		
M-36	2023	Marine	3	TC	Oligochaete	1,772	-20,57	7,31		
M-37	2023	Marine	3	TC	Oligochaete	1,614	-19,95	7,51		
M-38	2023	Marine	3	TC	Spionidae	1,548	-19,39	8,46		
M-43	2023	Marine	3	TC	Macoma	1,273	-22,75	6,59		
M-47	2023	Marine	3	TC	Macoma	1,362	-22,47	6,55		
M-49	2023	Marine	3	TC	Macoma	1,804	-18,89	8,18		
M-52	2023	Marine	1	TC	Macoma	1,554	-18,88	8,29		
M-53 + M-54	2023	Marine	1	TC	Macoma	1,460	-18,84	8,47		
M-55	2023	Marine	1	TC	Euchone	1,507	-23,03	6,42		
M-56	2023	Marine	1	TC	Euchone	1,317	-22,86	6,26		
M-57	2023	Marine	1	TC	Euchone	1,333	-23,45	6,27	Precision decreases for samples containing less than 100ugC	
M-62	2023	Marine	1	TC	Chironimodae	1,103	-21,48	6,14		
M-66	2023	Marine	1	TC	Spionidae	1,276	-20,71	7,94		
M-67	2023	Marine	1	TC	Oligochaete	1,173	-19,71	7,09		
M-68	2023	Marine	1	TC	Oligochaete	1,800	-19,96	7,04		
R-1	2023	River	1	TC	Macoma	1,484	-19,45	7,37		
R-2	2023	River	1	TC	Macoma	1,246	-19,36	7,88		
R-3	2023	River	1	TC	Oligochaete	1,715	-19,78	7,06		
R-4	2023	River	1	TC	Oligochaete	1,504	-20,10	7,21		
R-5	2023	River	1	TC	Oligochaete	1,669	-20,18	7,14		
R-7	2023	River	2	TC	Oligochaete	1,411	-20,19	7,10		
R-8	2023	River	2	TC	Oligochaete	1,581	-20,22	6,86		

R-9	2023	River	2	TC	Oligochaete	1,474	-20,16	6,90		
R-12	2023	River	2	TC	Chironimodae	1,290	-20,56	5,11	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
R-15	2023	River	2	TC	Macoma	1,368	-19,41	8,30		
R-16	2023	River	2	TC	Macoma	1,003	-19,45	7,73		
R-17	2023	River	2	TC	Macoma	1,278	-19,96	7,54		
R-18	2023	River	2	TC	Macoma	1,382	-19,57	7,67		
R-19	2023	River	2	TC	Macoma	1,083	-19,47	8,19		
R-23	2023	River	3	TC	Oligochaete	1,153	-19,82	7,05		
R-24	2023	River	3	TC	Oligochaete	1,230	-19,66	7,07		
R-25	2023	River	3	TC	Oligochaete	1,453	-19,92	7,08		
R-27	2023	River	3	TC	Macoma	1,102	-18,88	7,96		
R-28	2023	River	3	TC	Macoma	1,190	-19,09	8,15		
F-3	2023	NA	NA	NA	Salmon	1,620	-24,26	6,94		
F-4	2023	NA	NA	NA	Salmon	1,781	-24,26	7,06		
F-1	2023	NA	NA	NA	Salmon	2,067	-25,78	6,61		
F-5	2023	NA	NA	NA	Salmon	1,155	-25,03	6,82		
F-2	2023	NA	NA	NA	Salmon	1,595	-24,19	6,89		
F-6	2023	NA	NA	NA	Salmon	1,100	-24,87	6,97		
M-215	2023	Marine	1	C1	Macoma	2,323	-9,73	6,47		
M-117	2023	Marine	1	C3	Macoma	2,433	-10,65	6,64		
M-91	2023	Marine	1	F3	Macoma	2,297	-11,54	7,50		
M-177	2023	Marine	1	FC1	Macoma	2,044	-9,87	6,84		
M-207	2023	Marine	1	FC2	Macoma	2,269	-14,24	7,00		
M-218	2023	Marine	1	PC1	Macoma	2,284	-10,48	6,83		Precision decreases for samples containing less than 20ugN
M-189	2023	Marine	2	C1	Macoma	2,448	-7,40	7,15		
M-100	2023	Marine	2	C2	Macoma	2,965	-10,35	6,67		
M-203	2023	Marine	2	F3	Macoma	2,125	-10,77	7,47		
M-107	2023	Marine	2	FC3	Macoma	2,466	-9,66	7,82		
M-79	2023	Marine	2	PC1	Macoma	2,388	-9,20	7,10		
M-229	2023	Marine	3	C2	Macoma	2,272	-7,78	7,00		
M-83	2023	Marine	3	FC1	Macoma	2,538	-10,62	7,68		
M-121	2023	Marine	3	PC2	Macoma	2,442	-6,49	7,46		
R-142	2023	River	2	C3	Macoma	2,124	-14,08	6,27		
R-106	2023	River	2	FC1	Macoma	2,128	-15,76	6,38		
R-118	2023	River	2	PC3	Macoma	2,071	-8,41	6,64		
R-146	2023	River	3	F1	Macoma	2,416	-6,82	7,70		
M-194	2023	Marine	NA	NA	Leaves	1,230	-33,07	3,29		Precision decreases for samples containing less than 20ugN
M-195	2023	Marine	NA	NA	Leaves	1,026	-32,77	1,22		Precision decreases for samples containing less than 20ugN
M-214	2023	Marine	1	C1	Oligochaeta	0,893	-18,31	7,28		
M-115	2023	Marine	1	C3	Oligochaeta	1,195	-19,60	7,41		
M-178	2023	Marine	1	FC1	Oligochaeta	1,944	-19,26	7,34		
M-206	2023	Marine	1	FC2	Oligochaeta	1,280	-19,09	7,40	Precision decreases for samples containing less than 100ugC	
M-221	2023	Marine	1	PC1	Oligochaeta	1,174	-22,02	6,97	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference
M-199	2023	Marine	2	F3	Oligochaeta	1,097	-20,69	8,84		
M-103	2023	Marine	2	FC3	Oligochaeta	1,370	-18,37	6,93	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-164	2023	Marine	2	PC3	Oligochaeta	1,590	-20,77	6,94	Contained less carbon than smallest reference	Precision decreases for samples containing less than 20ugN
M-151	2023	Marine	3	C1	Oligochaeta	1,034	-18,56	8,17		
M-226	2023	Marine	3	C2	Oligochaeta	1,464	-18,84	8,33		
M-169	2023	Marine	3	F2	Oligochaeta	1,668	-19,37	8,13		
M-86	2023	Marine	3	FC1	Oligochaeta	1,264	-19,32	7,75		
M-146	2023	Marine	3	PC3	Oligochaeta	1,365	-19,61	7,47		
R-32	2023	River	1	C1	Oligochaeta	1,267	-18,24	8,72		
R-102	2023	River	1	C2	Oligochaeta	1,069	-19,09	7,59		

R-138	2023	River	1	C3	Oligochaeta	1,173	-19,14	8,51		
R-135	2023	River	1	F2	Oligochaeta	1,235	-18,47	8,27		
R-68	2023	River	1	F3	Oligochaeta	1,128	-19,07	8,00		
R-78	2023	River	1	FC1	Oligochaeta	1,129	-19,02	7,70		
R-151	2023	River	1	FC3	Oligochaeta	1,491	-18,70	7,85		
R-112	2023	River	1	PC1	Oligochaeta	1,066	-18,81	8,27		
R-129	2023	River	1	PC2	Oligochaeta	1,503	-19,24	7,77		
R-36	2023	River	1	PC3	Oligochaeta	1,235	-19,12	7,96		
R-97	2023	River	2	C1	Oligochaeta	1,210	-19,56	7,79		
R-83	2023	River	2	C2	Oligochaeta	0,780	-19,51	7,54		
R-140	2023	River	2	C3	Oligochaeta	1,659	-19,59	7,94		
R-120	2023	River	2	FC1	Oligochaeta	1,592	-20,02	6,78		
R-121	2023	River	2	FC1	Oligochaeta	1,263	-19,70	7,26		
R-148	2023	River	2	FC2	Oligochaeta	1,608	-19,39	7,75		
R-63	2023	River	2	FC3	Oligochaeta	1,461	-19,45	7,51		
R-49	2023	River	2	PC1	Oligochaeta	1,880	-19,27	7,65		
R-107	2023	River	2	PC2	Oligochaeta	1,840	-7,37	6,51		
R-116	2023	River	2	PC3	Oligochaeta	1,829	-19,36	8,16		
R-60	2023	River	3	C1	Oligochaeta	1,545	-18,32	8,01		
R-41	2023	River	3	C2	Oligochaeta	1,423	-18,86	7,81		
R-157	2023	River	3	C3	Oligochaeta	1,357	-18,06	7,94		
R-144	2023	River	3	F1	Oligochaeta	1,659	-18,84	8,04		
R-59	2023	River	3	F2	Oligochaeta	1,198	-19,37	8,04		
R-73	2023	River	3	F3	Oligochaeta	1,220	-18,73	8,33		
R-34	2023	River	3	FC1	Oligochaeta	1,154	-18,73	8,02		
R-90	2023	River	3	FC2	Oligochaeta	1,138	-18,73	7,78	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
R-47	2023	River	3	FC3	Oligochaeta	1,227	-19,27	7,53		
R-86	2023	River	3	PC2	Oligochaeta	1,166	-18,70	7,85		
R-155	2023	River	1	FC3	Oligochaeta	1,962	-18,81	7,86		
M-216	2023	Marine	1	C1	Euchone	1,996	-20,98	6,81	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-118	2023	Marine	1	C3	Euchone	1,305	-20,99	6,40	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-97	2023	Marine	1	F1	Euchone	1,281	-19,14	7,82		
M-95	2023	Marine	1	F3	Euchone	1,486	-21,82	6,93	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-181	2023	Marine	1	FC1	Euchone	1,338	-21,23	6,70		
M-204	2023	Marine	1	FC2	Euchone	1,773	-20,30	6,89	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-219	2023	Marine	1	PC1	Euchone	1,983	-21,31	6,80		
M-158	2023	Marine	1	PC2	Euchone	1,705	-21,38	6,57		
M-193	2023	Marine	2	C1	Euchone	1,073	-21,70	7,63	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-98	2023	Marine	2	C2	Euchone	1,259	-21,76	6,66	Contained less carbon than smallest reference	Precision decreases for samples containing less than 20ugN
M-187	2023	Marine	2	F2	Euchone	1,284	-22,38	7,67		
M-202	2023	Marine	2	F3	Euchone	1,226	-22,02	7,62		
M-137	2023	Marine	2	FC2	Euchone	1,697	-21,38	6,67	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-105	2023	Marine	2	FC3	Euchone	1,367	-21,72	6,62		
M-78	2023	Marine	2	PC1	Euchone	1,511	-21,15	6,63		
M-165	2023	Marine	2	PC3	Euchone	1,648	-20,92	6,99	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-228	2023	Marine	3	C2	Euchone	1,387	-18,77	6,58	Contained less carbon than smallest reference	Precision decreases for samples containing less than 20ugN
M-171	2023	Marine	3	F2	Euchone	1,180	-21,46	7,10	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-82	2023	Marine	3	FC1	Euchone	1,165	-20,01	6,60		
M-127	2023	Marine	3	FC3	Euchone	1,230	-21,82	6,49		
M-129	2023	Marine	3	PC1	Euchone	1,270	-21,56	7,21		
M-124	2023	Marine	3	PC2	Euchone	1,235	-21,11	7,33		
M-142	2023	Marine	3	PC3	Euchone	1,551	-21,98	7,03		
M-89	2023	Marine	1	F1	Chironomidae	1,685	-18,83	6,14		

M-93	2023	Marine	1	F3	Chironomidae	1,951	-20,37	6,58	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-205	2023	Marine	1	FC2	Chironomidae	1,557	-18,65	6,96		
M-222	2023	Marine	1	PC1	Chironomidae	1,185	-17,81	6,26	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-191	2023	Marine	2	C1	Chironomidae	1,674	-18,33	7,06	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-99	2023	Marine	2	C2	Chironomidae	1,119	NA	7,84	Below detection	Contained less nitrogen than smallest reference
M-186	2023	Marine	2	F2	Chironomidae	1,387	-18,66	7,47		
M-198	2023	Marine	2	F3	Chironomidae	1,248	-19,58	6,64		
M-136	2023	Marine	2	FC2	Chironomidae	1,517	-17,61	5,85	Contained less carbon than smallest reference	Precision decreases for samples containing less than 20ugN
M-104	2023	Marine	2	FC3	Chironomidae	1,981	-19,29	5,89		
M-81	2023	Marine	2	PC1	Chironomidae	1,833	-19,43	6,05		
M-161	2023	Marine	2	PC3	Chironomidae	1,484	-19,51	7,92	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference
M149	2023	Marine	3	C1	Chironomidae	1,228	-19,34	6,11		
M-225	2023	Marine	3	C2	Chironomidae	1,442	-19,78	6,20		
M-167	2023	Marine	3	F2	Chironomidae	1,157	-19,75	6,66		
M-87	2023	Marine	3	FC1	Chironomidae	1,347	-20,00	6,18		
M-128	2023	Marine	3	FC3	Chironomidae	1,324	-19,32	6,23		
M-130	2023	Marine	3	PC1	Chironomidae	1,159	-19,91	8,05		
M-125	2023	Marine	3	PC2	Chironomidae	1,038	-19,88	6,38		
R-30	2023	River	1	C1	Chironomidae	1,633	-21,89	7,04	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference
R-92	2023	River	3	FC2	Chironomidae	1,403	NA	13,60	Below detection	Contained less nitrogen than smallest reference
M-212	2023	Marine	1	C1	Spionidae	1,567	-18,48	9,81	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference in run
M-119	2023	Marine	1	C3	Spionidae	1,085	-19,44	10,47		
M-180	2023	Marine	1	FC1	Spionidae	1,475	-19,55	10,53		
M-211	2023	Marine	1	FC2	Spionidae	1,804	-21,09	10,95	Precision decreases for samples containing less than 100ugC	Precision decreases for samples containing less than 20ugN
M-220	2023	Marine	1	PC1	Spionidae	1,794	-20,10	7,90		
M-192	2023	Marine	2	C1	Spionidae	1,383	-20,14	10,68		
M-101	2023	Marine	2	C2	Spionidae	1,123	-19,77	8,13	Contained less carbon than smallest reference in run	Precision decreases for samples containing less than 20ugN
M-185	2023	Marine	2	F2	Spionidae	1,419	-22,76	15,49		
M-106	2023	Marine	2	FC3	Spionidae	1,517	-19,36	7,49		
M-80	2023	Marine	2	PC1	Spionidae	1,621	-20,97	8,27	Contained less carbon than smallest reference in run	Contained less nitrogen than smallest reference in run
M-163	2023	Marine	2	PC3	Spionidae	1,216	-20,41	8,65	Contained less carbon than smallest reference in run	Precision decreases for samples containing less than 20ugN
M-152	2023	Marine	3	C1	Spionidae	1,333	-18,37	9,73		
M-227	2023	Marine	3	C2	Spionidae	1,375	-18,41	8,77	Contained less carbon than smallest reference in run	Precision decreases for samples containing less than 20ugN
M-147	2023	Marine	3	PC3	Spionidae	1,846	-19,12	12,86		
R-31	2023	River	1	C1	Spionidae	1,149	-19,34	8,39		
R-139	2023	River	1	C3	Spionidae	1,252	-20,75	8,38	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference in run
R-101	2023	River	1	F1	Spionidae	1,067	-20,08	8,74		
R-81	2023	River	1	FC1	Spionidae	1,230	-19,72	8,16		
R-54	2023	River	1	FC2	Spionidae	1,447	-19,58	8,00		
R-152	2023	River	1	FC3	Spionidae	1,087	-19,59	8,00		
R-113	2023	River	1	PC1	Spionidae	1,324	-19,63	7,62		
R-98	2023	River	2	C1	Spionidae	1,380	-19,20	8,26		
R-84 + R-141	2023	River	2	C1+C2	Spionidae	1,839	-19,14	8,01		
R-133	2023	River	2	F1	Spionidae	1,166	-19,62	8,38		
R-123	2023	River	2	FC1	Spionidae	1,172	-19,47	7,34		
R-149	2023	River	2	FC2	Spionidae	1,835	-19,33	8,39		
R-51	2023	River	2	PC1	Spionidae	1,232	-19,34	7,28		
R-108	2023	River	2	PC2	Spionidae	1,029	-19,02	7,72		
R-117	2023	River	2	PC3	Spionidae	1,193	-19,67	7,48		
R-62	2023	River	3	C1	Spionidae	1,719	-19,62	7,84		
R-158	2023	River	3	C3	Spionidae	1,750	-19,47	8,17		
R-145	2023	River	3	F1	Spionidae	1,950	-19,91	8,17		
R-33	2023	River	3	FC1	Spionidae	1,268	-19,49	8,06		

R-91	2023	River	3	FC2	Spionidae	1,414	-19,96	9,52	Contained less carbon than smallest reference	Contained less nitrogen than smallest reference in run
R-95	2023	River	3	PC1	Spionidae	1,223	-18,89	7,51		
R-87 + R-160	2023	River	3	PC2+PC3	Spionidae	1,494	-19,08	8,09		
R-82	2023	River	1	FC1	Macoma	1,378	-18,64	7,91		
R-53	2023	River	1	FC2	Macoma	1,212	-18,68	8,10		
R-154	2023	River	1	FC3	Macoma	1,317	-18,82	8,19		
A-R-142	2023	River	2	C3	Macoma acid	1,333	-19,25	6,22		
R-46	2023	River	2	F3	Macoma	1,323	-19,00	8,65		
A-R-106	2023	River	2	FC1	Macoma acid	1,875	-19,67	6,28		
R-130	2023	River	2	FC1	Macoma	1,557	-18,57	7,09		
R-65	2023	River	2	FC3	Macoma	1,679	-18,49	7,42		
A-R-118	2023	River	2	PC3	Macoma acid	1,593	-19,55	6,81		
R-76	2023	River	3	F3	Macoma	1,806	-18,34	9,45		
R-93	2023	River	3	FC2	Macoma	1,929	-18,48	7,95		
R-163	2023	River	3	PC3	Macoma	1,120	-18,15	8,92		
A-M-215	2023	Marine	1	C1	Macoma acid	0,906	-18,83	6,40		
A-M-117	2023	Marine	1	C3	Macoma acid	1,952	-19,34	6,98		
A-M-91	2023	Marine	1	F3	Macoma acid	1,895	-19,31	7,36		
A-M-177	2023	Marine	1	FC1	Macoma acid	1,487	-18,90	7,35		
A-M-207	2023	Marine	1	FC2	Macoma acid	1,208	-18,98	7,24		
A-M-218	2023	Marine	1	PC1	Macoma acid	1,480	-20,17	7,23		
A-M-189	2023	Marine	2	C1	Macoma acid	1,945	-18,91	7,48		
A-M-100	2023	Marine	2	C2	Macoma acid	1,841	-19,12	7,09		
A-M-203	2023	Marine	2	F3	Macoma acid	1,325	-20,29	7,96		
A-M-107	2023	Marine	2	FC3	Macoma acid	1,745	-19,90	7,71		
A-M-79	2023	Marine	2	PC1	Macoma acid	1,670	-19,33	7,44		
A-M-229	2023	Marine	3	C2	Macoma acid	1,330	-19,27	7,34		
A-M-83	2023	Marine	3	FC1	Macoma acid	1,138	-19,76	7,77		
A-M-121	2023	Marine	3	PC2	Macoma acid	1,325	-18,85	7,62		
R-122	2023	River	2	FC1	Oligochaeta	1,630	-19,60	7,13