Benthic foraminiferal biomonitoring in northern Norway:

Establishing reference conditions, Ecological Quality Statuses and responses to organic matter.

Anouk Tosca Klootwijk

Dissertation for the degree of Philosophiae Doctor (PhD)

Department of Geosciences
Faculty of Mathematics and Natural Sciences
University of Oslo
Norway

2021

Submitted: 16-09-2021

Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo
No. 2470

ISSN 1501-7710

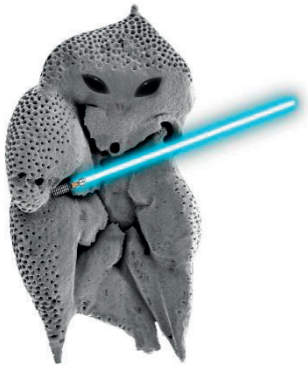
Cover: Hanne Baadsgaard Utigard.
Print production: Reprosentralen, University of Oslo.

"Our greatest weakness lies in giving up.
The most certain way to succeed is always to
try just one more time."

- **Thomas Edison**

"Focus on signal over noise.
Don't waste time on stuff that doesn't actually make things better."

- **Elon Musk**



MAY THE FORAM BE WITH YOU

Preface

This thesis was submitted to the Faculty of Mathematics and Natural Sciences at the University of Oslo, in agreement with the dissertation requirements for the degree of PhD

The basis for the current thesis comes from work that was conducted under the primary supervision of Prof. Dr. Elisabeth Alve and the supporting supervision of Dipl. Silvia Hess and Prof. Dr. Paul Renaud. This project was partly funded by the Norwegian Environment Agency (MD17SF8F99), the Research Council of Norway ('JellyFarm' project: RCN #244572), and the Fjord and Coast Flagship of the Fram Centre for Climate and the Environment ('EFFECTS' project).

Benthic foraminifera have been widely used to investigate environmental conditions at the seafloor, on both short (decades to centuries) and long geological time scales (e.g. millions of years). With the rise of the European Water Framework Directive in the year 2000, benthic foraminifera gained interest as an environmental biomonitoring tool. To further develop benthic foraminifera as a biomonitoring tool it is essential to gain a better understanding of their ecology and test the performance of the foraminiferal indices that have been developed so far.

The first paper of the current thesis established in situ reference using geochemical parameters (normalized to grain size total organic carbon, total organic carbon and total nitrogen ratios, stable carbon isotopes ($\delta^{13}C_{VPDB}$), and heavy metal concentrations; e.g. copper) and fossil benthic foraminiferal assemblages to assess potential impacts of fish farming activities in the two basins of inner Øksfjorden, northern Norway. This is to our knowledge the first application of the foraminiferal AZTI's Marine Biotic Index (fAMBI), fH_{log2}, $ES_{100,}$ and Norwegian Quality Index (fNQI), in northern Norway to assess the impact of fish farming. The second study investigated the benthic foraminiferal response to the addition of jellyfish detritus from *Periphylla periphylla* from the inner to the outer Kaldfjorden, northern Norway. The second study worked towards a better understanding of benthic foraminiferal ecology. The third study investigated the impact of the analysed size fraction (> 63 µm vs > 125 µm) on establishing the ecological quality status in northern Norway.

This thesis includes an introduction to the investigated topics, the aims and objectives, a description of the studied sites, the results in the form of the main findings of the two papers and one manuscript that came from this work (two published, submitted), and a general discussion section with concluding remarks.

Personal acknowledgements

I am grateful to my supervisors Prof. Elisabeth Alve, Silvia Hess, and Prof. Paul Renaud for allowing me to work on this exciting, diverse, and at times challenging research project. The trust you placed in me from the beginning by giving me the responsibility for growing the ^{13}C labelled algae used in the JellyFarm 2017 experiment was terrifying, but it helped me to develop the tools and skills needed to successfully complete this PhD project. Thank you for the good, exciting, and fun, scientific discussions we had over the years. I learned a great deal from those and I shall very greatly miss them.

I would like to thank the University of Oslo Department of Geoscience, the Norwegian Environment Agency (MD17SF8F99), the Research Council of Norway ('JellyFarm' project: RCN #244572), and the Fjord and Coast Flagship of the Fram Centre for Climate and the Environment ('EFFECTS' project), for funding the project.

Thank you:

- Co-authors for your input and help with the manuscripts.
- Current and former office mates for your support and all the fun.
- IT staff of the UiO geology department for your time and support.
- GEO-football team for the fun times.
- PhD mentors Henning Dypvik and Valerie Maupin for your support and guidance.
- UioDoc and UiO karrieresenteret for organising fantastic workshops.
- Bachelor and Master Students that I had the pleasure of working with over the years. It has truly been a pleasure and a lot of fun to work with you all. Your enthusiasm and sometimes very difficult questions kept me on my toes. I can only hope you learned as much from me as I learned from you.

I count myself lucky to have so many friends that supported me in building towards getting a PhD project and during this PhD. For without you I could not have gotten this far. To name a few: Nicole van Ettenkoven-Jastrzebski who has always been there for me in the past 18 years; Carl Ballantine for the fun, the much-needed discussions, and excellent help with the English language; Laurie Charrieau for our Monday chats that I cherish; Vincent Koffman for hearing me out and guiding me with his experience; Mischa Seas for his help and listening ear; Gidske Holck and Hans-Kristian Ekenes for their support; and last but not least Marjorie Parker for her

encouraging words and valuable insights. Now don't fret if I have not named you personally, you may plead your case for a beer.

This PhD thesis would also not have been here if it was not for the following people:
Martin Jansen former teacher at van Hall Larenstein in Leeuwarden, Gert van Ee from the water board Hoogheemraadschap Hollands Noorderkwartier, Professor William Austin of the University of St. Andrews in Scotland, and Professor Alison Specht at the time from the Southern Cross University in Lismore Australia.
Martin, thank you for supporting me in finding internships and letting me go to the other side of the world on my own even though it was against the rules. It made a tremendous difference in my life.
Gert, thank you for your support and for starting my love for microscopy during my first internship. Was het nou *Anacaena bipustulata* of *bicolor*?
Bill (William), thank you for giving me a job opening the door to academia for me.
Alison, if you had not taken a chance on a 19-year old student from the Netherlands in 2009 this PhD thesis would not have existed. The things a small, critically endangered snail can do.
I would like to thank all of you for cheering me on over the years, it means the world.

I am very grateful to Matthias Peatzel and Peter Hovgaard, Professor and former Professor at Høgskule på Vestlandet, for their fantastic support and belief in me over the years. It made a great difference.

Thank you Rob Klootwijk and Maria Sterkenburg (parents), for all those times you dropped me off and picked me up at airports, in cities, and even in countries. Thank you for always supporting me in my hunger to study and plans to go to whatever county I had set my eye on. It must not always have been easy to let me go, but you were always there to support me. Thank you for toughing out yet another one of my slightly insane endeavours, in yet another country.

Though words can never do justice: Thank you Kevin Saurin (my better half) for being an absolute champion during the past 9 years. I am sorry that it did not get better after the algae.
Just like "*Frodo would not have gotten far without Sam*" (LOTR), Anouk would not have gotten far without Kevin.

Anouk

List of publications

Papers and manuscripts

Paper 1 (published): Klootwijk, A.T., Alve, E., Hess, S., Renaud, P.E., Sørlie, C., Dolven, J.K., 2020. Monitoring environmental impacts of fish farms: Comparing reference conditions of sediment geochemistry and benthic foraminifera with the present. Ecological Indicators, volume: 120. https://doi.org/10.1016/j.ecolind.2020.106818.

Paper 2 (Published): Klootwijk, A.T., Sweetman, A.K., Hess, S., Alve, E., Dunlop, K.M. and Renaud, P.E., 2021. Benthic foraminiferal carbon cycling in coastal zone sediments: The influence of the assemblage structure and jellyfish detritus. Estuarine, Coastal and Shelf Science, p.107535. https://doi.org/10.1016/j.ecss.2021.107535

Paper 3 (Submitted): Does the analysed size fraction for benthic foraminifera influence the Ecological Quality Status? Indications from two northern Norwegian fjords. Submitted to Ecological Indicators.

Conference contributions

Klootwijk, A. T., Alve, E., Hess, S., Sørlie, C. (2020). Utilizing benthic foraminifera and geochemical parameters in modern stratigraphy as a tool to solve challenges in biomonitoring. Annual Geological Winter Meeting, Oslo, Norway. Abstract, oral presentation.

Klootwijk, A. T., Alve, E., Hess, S., Sørlie, C. (2019). The impact of fish farming in an arctic fjord investigated using geochemical parameters and benthic foraminiferal assemblages.
The Micropalaeontological Society Annual Conference 2019, Fribourgh, Switserland. Abstract, oral presentation.

Klootwijk, A. T., Alve, E., Hess, S., Renaud, P. (2018). Benthic foraminiferal response to carbon loading introduced by "jelly-falls": An ex-situ experiment using material from Kaldfjord (Northern Norway). International Symposium on Foraminifera, Edinburgh, Scotland. Abstract, oral presentation.

Klootwijk, A. T., Alve, E., Hess, S., Renaud, P. (2017). Changes in organic carbon composition and accumulation in Norwegian fjords during the past centuries: Implications for ecological quality status and fjords as carbon sinks.
MARINFORSK PhD-seminar 2017, Bergen, Norway. Abstract, oral presentation.

Table of Content

Journal publications and manuscript

Glossary

Terms	Abbreviations
AZTI's Marine Biotic Index	AMBI
Carbon uptake*:	
1) not normalised	1) C-uptake
2) normalised to rose Bengal (rB) densities	2) C-uptake$_{rB}$
3) normalised to biomass	3) C-uptake$_{bio}$
Constant Initial Concentration model	CIC
Constant Rate of Supply model	CRS
Ecological Quality Status	EcoQS
Ecological Group(s)	EG(s)
Experimental treatments*	Control (C) = phytodetritus Low (L) = phytodetritus + 10 g jellyfish High (H) = phytodetritus + 30 g jellyfish
Norwegian Quality Index	NQI
Total organic carbon	TOC
Total organic carbon normalised to % < 63 µm fraction in the sediment	TOC$_{63}$
Total organic carbon and total nitrogen ratio	C/N

- terms used in the second paper of this thesis

1. Introduction

This introduction provides background information on benthic foraminifera and their applications. Additionally, environmental biomonitoring, benthic foraminiferal distributions in fjords, jellyfish detritus as a carbon source, the potential of isotope tracer studies, and the use of size fractions in biomonitoring are introduced. In the final paragraph of the introduction, the aims and objectives of the current PhD thesis are provided.

1.1 Benthic foraminifera

Foraminifera represent the order of Foraminiferida in the Phylum Protista and their name translates as: "*Cytoplasmic body enclosed in a test or shell comprised of one or more interconnected chambers"* (Loeblich and Tappan, 1987, p. 7). Benthic foraminifera live predominantly in the upper 0.5 cm of the sediment, but can also much live deeper (up to 10 cm) in the sediment (e.g. Alve and Bernhard, 1995; Van Der Zwaan et al., 1999). The majority of foraminifera are microscopically small and make so-called shells, mostly referred to as tests, consisting of a single or multiple chambers. These tests are mostly made of either calcium carbonate or agglutinated sediment particles. After foraminifera die many of their tests preserve in the sediment forming so-called fossil assemblages, which can be found in marine sediments from the Cambrian (541-485.4 million years ago) to the present (Murray, 2006).

Benthic foraminifera are a major meiofaunal group in many marine sediments and respond rapidly to both natural, e.g. changes in the global climate, and human-induced environmental changes, e.g. physical disturbances, elevated levels of heavy metals, and eutrophication (Alve, 1995, 1991; Bouchet et al., 2018, 2012; Dijkstra et al., 2017; Duffield et al., 2015; Pochon et al., 2015; Sen Gupta, 1999). Benthic foraminifera, therefore, have many applications, but since the rise of the European Water Framework Directive (WFD, 2000/60/EC) the interest in benthic foraminifera as an environmental monitoring tool has increased (e.g. Alve et al., 2016; Schönfeld et al., 2012).

1.2 Environmental monitoring

The WFD is a set of non-legally binding guidelines and requirements that form an environmental monitoring protocol to control water pollution in coastal areas (2000/60/EC). From the WFD the Norwegian guidelines (Veileder, 02:2018) were derived based on the same principles but adjusted to fit the Norwegian coastal ecosystems. Biomonitoring is a large part of the guidelines, where the organisms that live in a water body are examined to assess the health of the environment, also referred to as environmental conditions. Traditionally biomonitoring is performed using macrofauna, but foraminifera have recently been implemented in the Norwegian guidelines (Veileder, 02:2018). The sediment geochemistry, e.g. total organic carbon (TOC) concentration or heavy metal concentrations, are mostly used as complementary to biomonitoring results. To assess the environmental conditions in a water body an Ecological Quality Status (EcoQS) is established, defined as either a High, Good, Moderate, Poor or Bad status (Veileder, 02:2018).

The EcoQS is established using diversity indices, e.g. Shannon-Wiener Index (H'; Shannon and Weaver, 1963) and Hurlbert rarefaction index (ES; Hurlbert, 1971), which are a way to show how many species are in a sample in combination with how evenly these species are distributed. Additionally, the AZTI's Marine Biotic Index (AMBI) is combined with a modified species richness index (SN) for macrofauna (Rygg, 2006) and the ES_{100} foraminifera (Alve et al., 2019) into the multi-metric Norwegian Quality Index (NQI). The AMBI is a sensitivity index where species are assigned to one of the five Ecological Groups (EG) based on their responses to organic matter enrichment. To further implement foraminifera into official monitoring systems, the H'_{log2}, ES_{100}, and NQI class boundary values for macrofauna were recently adapted to foraminifera using linear regressions to derive EcoQS class boundary values for foraminifera from the existing class boundary values of macrofauna (Alve et al., 2019).

According to the guidelines it is obligatory that water bodies under potential anthropogenic pressure are kept at or returned to so-called "reference conditions", defined as a Good or High EcoQS, that presumably existed before human impact. These references conditions are established from either similar seemingly un-impacted sites, historical data, modelling, and/or expert judgement (WFD, 2003/5/EC, p. 36-47). The first option is often not available and poses a problem with species their varying tolerance/sensitivity levels along with their geographical distributions (Grémare et al., 2009; Zettler et al., 2013). The second option is also often not available and an expert judgement lacks transparency for non-experts (Borja et al., 2012). Intensive fish farming is a major industry in Norway, which is most rapidly expanding in

northern Norway (Fiskeridirektoratet, 2021). In Norway, it is mandatory to monitor the environmental conditions in fjords with a known anthropogenic impact like fish farming.

The health of an aquatic body is also assed via a so-called chemical status that is often used as a supporting element (Veileder, 02:2018, p. 30). Copper, zinc, and nickel are heavy metals associated with fish farming and enter the marine system from either the anti-biofouling paint on the net pens or as constituents of fish feed (e.g. Brooks and Mahnken, 2003a; Burridge et al., 2010). The bulk sediment TOC, total organic carbon and total nitrogen ratios (C/N), and the stable carbon isotope signatures ($\delta^{13}C_{VPDB}$) have shown potential to identify organic matter input from fish farming activities (Kutti et al., 2007a). Previous studies suggest that organic carbon emissions from fish farming could have increased the primary productivity and organic carbon loading of fjord sediments, which in turn affected the benthic community (e.g. Holmer, 2010; Husa et al., 2014; Kutti et al., 2007; Sweetman et al., 2014a). These current studies investigating the impact of fish farming are difficult to interpret, as long time series (spanning pre-anthropogenic impact conditions) have not been established. This makes it challenging to exclude natural gradients as causes of the observed variabilities.

Sediment cores consist of sequentially deposited layers of substrate that can record changes in environmental conditions over time. Using sediment core records might it easier to exclude natural causes for observed variabilities in the sediment organic geochemistry and heavy metal concentrations. As the majority of benthic foraminiferal tests preserve the sediment, their assemblages in sediment cores can be used for the reconstruction of benthic environmental conditions far beyond any recorded historical data at the site itself (e.g. Alve et al., 2009; Bouchet et al., 2012; Dolven et al., 2013). The latter would circumvent potential problems with species their varying tolerance/sensitivity levels. Benthic foraminifera can thus be used to establish so-called in situ reference conditions, which makes them a powerful biomonitoring tool in assessing potential anthropogenic pressure factors like fish farming. To utilize benthic foraminifera as a biomonitoring tool it is, however, essential to gain a better understanding of their responses to anthropogenic pressure factors and their distribution within fjords.

1.3 Benthic foraminifera distributions in fjords

Fjords are transitional zones that connect terrestrial and oceanic systems. Fjords sediments are therefore often characterized by gradients of terrigenous versus marine organic matter input moving from the inner to the outer fjord (Faust and Knies, 2019; Syvitski et al., 1987). The contribution of terrestrial organic carbon to the sediment generally declines moving from the

inner to the outer fjord (Duffield et al., 2017; Heiskanen and Tallberg, 1999), and marine organic carbon is generally regarded as more labile (bio-available) than terrestrial organic carbon (e.g. Hedges and Keil, 1995). The quality and quantity of organic carbon input is known to alter benthic ecosystem functioning and community structure (e.g. Smith et al., 2008), but the mechanisms behind these interactions are poorly understood.

Previous research has shown distinctly different benthic foraminiferal assemblages from inner to outer fjords (Alve and Nagy, 1990; Duffield et al., 2017; Husum and Hald, 2004; Korsun and Hald, 2000). Differences in foraminiferal assemblage composition are considered related to differences in food availability, bottom water oxygenation, or substrate characteristics (e.g. Corliss, 1985). Changes in benthic foraminiferal assemblage composition can lead to changes in their C(carbon)-cycling capability (Gooday et al., 1992; Sweetman et al., 2009) and the ecosystem functions they perform. Additionally, differences in the assemblage composition may also affect the ability of foraminiferal assemblages to withstand environmental pressure factors like, e.g., fish farming. It is therefore important to increase our current understanding of benthic foraminiferal distributions within fjords.

1.4 Jellyfish detritus as a carbon source

Food sources for benthic communities mainly come from the water column above (pelagic zone), and both phyto- and zooplankton are regarded as common pelagic carbon sources. Sinking jellyfish particulate organic matter has, however, been shown an important pelagic carbon source to the benthic ecosystem (Lebrato et al., 2013; Sweetman et al., 2016; Woulds et al., 2016), which is believed to be increasing due to anthropogenic and climate-driven changes (Billett et al., 2006; Mills, 2001; Purcell et al., 2007). In Norway, fishing activities and increasingly darker coastal waters are thought to have contributed to mass occurrences of the jellyfish *Periphylla periphylla* in some fjords during the last decades (Aksnes et al., 2009; Sørnes et al., 2007; Sweetman and Chapman, 2011). *P. periphylla* is originally characterised as a cold and deep-water scyphozoan that only exists as a medusa. The species can adapt to a variety of environmental conditions unfavourable to fish making it highly competitive with its main food competitor (Condon et al., 2012; Tiller et al., 2017).

Recent observations suggest *P. periphylla* is becoming more abundant in northern Norwegian ecosystems, where it has established healthy populations in several fjords (Tiller et al., 2017). Jellyfish carrion fluxes can be rapidly scavenged at the seafloor (Dunlop et al., 2018; Sweetman et al., 2014), but experiments suggest that jellyfish decomposition increases the benthic O_2

demand (Chelsky et al., 2016, 2015; Condon et al., 2011; West et al., 2009) and causes significant shifts in benthic community functioning (Condon et al., 2011; Sweetman et al., 2016). The O_2 availability in the benthic environment regulates important biogeochemical processes and has large implications for the ecology and biology of benthic communities (Glud, 2008). Benthic foraminifera play important carbon processing roles in marine ecosystems (e.g. Middelburg et al., 2000), but little is known about how they process carbon within fjords, or how jellyfish detritus on the sediment may affect this role.

1.5 Isotope tracer studies

One successful method to assess benthic community functioning is through isotope tracer experiments. In such experiments, a food source (e.g. algae) is enriched in a naturally uncommon stable isotope (^{13}C or ^{15}N) which is then used to quantify consumers processing patterns and rates (e.g. Middelburg et al., 2000; Sweetman et al., 2016; Woulds et al., 2016). Feeding activities of benthic foraminifera have been successfully measured in previous isotope tracer studies (e.g. Enge et al., 2014; Moodley et al., 2002; Nomaki et al., 2005; Sweetman et al., 2009), which showed that benthic foraminifera play an important carbon processing roles in marine ecosystems.

Currently, little is known about how benthic foraminifera process carbon within fjords, or how jellyfish detritus on the sediment may affect this role. One former isotope tracer experiment showed that benthic foraminifera responded differently to a supplied food source under different oxygen concentrations (Enge et al., 2016). Another experiment showed that the foraminiferal carbon uptake can differ between spring and autumn depending on the species of foraminifera in the assemblage (Nomaki et al., 2005). Isotope tracer experiments are therefore a useful tool to assess the benthic foraminiferal response to jellyfish detritus from the inner region of a fjord to its outer region.

1.6 size fractions in foraminiferal research

The introduction of the European Water Framework Directive increased the interest in benthic foraminifera as a biomonitoring tool (e.g. Alve et al., 2016; Bouchet et al., 2021; Jorissen et al., 2018), which prompted the need to standardise the methods used to analyse benthic foraminiferal assemblages (see Schönfeld et al., 2012). The standardised method suggests samples should be washed over a 63 and 125 μm mesh, but that only the foraminiferal

assemblage of the > 125 µm fraction is to be analysed, unless research questions justify otherwise. The from the WFD derived Norwegian guidelines (Veileder, 02:2018) advises to follow the Dolven et al. (2013) method, which analysed benthic foraminiferal assemblages from the 63-500 µm fraction.

Benthic foraminifera assemblage compositions can substantially vary depending on the analysed size fraction (e.g. Lo Giudice Cappelli and Austin, 2019; Weinkauf and Milker, 2018). Analysing the > 63 µm is regarded as substantially more labour intensive (Schröder et al., 1987), but many scientific studies use this fraction as it is considered to contain the majority of environmental quality indicator species (e.g. Dolven et al., 2013; Duffield et al., 2017; Mojtahid et al., 2006). A study from the Norwegian Skagerrak found that the foraminiferal assemblages of the > 63 µm and > 125 µm fraction correlated suggesting a highly similar EcoQS, which indicates that the > 125 µm fraction may be good enough to establish the EcoQS (Bouchet et al., 2012). Another study from Nova Scotia, Canada, showed that benthic foraminifera can produce small (< 125 µm), yet relatively easy to identify adult tests and that analysing only the > 125 µm fraction could create artificially barren zones (Schröder et al., 1987). As intensive fish farming is most rapidly expanding in northern Norway (Fiskeridirektoratet, 2021), the influence of the analysed size fraction on establishing the EcoQS and environmental conditions in northern Norway should therefore be investigated.

1.7 Aim and objectives

Fjords in northern Norway, ca. 66° - 71° north, differ from their southern boreal counterparts as their drainage areas have a sparser vegetation cover and often lack a glacier in their catchment area which affects the sediment supply (Faust and Knies, 2019). Additionally, fjords in this region often lack a major river draining into the fjord (Wassmann et al., 1996). The sparser vegetation, lower sediment supply, and lack of major river input influence the environmental conditions in arctic fjords, which in turn affects the biological processes in these fjords (Syvitski et al., 1987). Little is known about benthic foraminiferal ecology in the investigated region, regarded as an up and coming fish farming region, with only a limited amount of published studies (e.g. Dijkstra et al., 2017; Husum and Hald, 2004).

The main aim of this PhD project was therefore to further develop benthic foraminifera as a biomonitoring tool and increase our understanding of benthic foraminiferal ecology in northern Norway.

To achieve this aim the following three objectives were addressed in the form of two published papers and a manuscript:

1) Establish in situ reference conditions using the sediment geochemistry and benthic foraminiferal records from sediment cores to assess potential environmental impacts of fish farming activities on the benthic environment in Inner Øksfjorden, northern Norway.
2) Quantify how *P. periphylla* detritus alters benthic foraminiferal microalgal-carbon uptake (C-uptake) from the inner to outer fjord using ^{13}C-labelled algae as a tracer in an ex-situ experiment.
3) Assess the influence of analysing the > 63 µm or > 125 µm fraction on establishing the EcoQS using the H'_{log2}, ES_{100}, NQI, and AMBI, and on interpreting the environmental conditions in northern Norway.

The first publication tested the applicability of the benthic foraminiferal indices H'_{log2}, ES_{100}, and NQI, and the AMBI from sediment core records to assess the potential impact of fish farming. The potential of the bulk sediment geochemistry (TOC_{63}, $\delta^{13}C_{VPDB}$, C/N ratios) and heavy metal concentrations (e.g. Nickel) from sediment core records to assess the impact of fish farming was also evaluated. The second paper contributed towards further understanding benthic foraminiferal ecology in coastal zones by studying foraminiferal C-uptake rates from the inner to the outer Kaldfjorden. The C-uptake rates in Kaldfjorden were studied in combination with added jellyfish detritus whilst taking in situ environmental parameters (e.g. sediment TOC_{63} concentrations) and sediment O_2 dynamics into consideration. Placing jellyfish detritus on the sediment thus gives an impression of how foraminifera respond to additional carbon and potential changes in the sediment O_2 dynamics. Understanding benthic foraminiferal ecology is essential for further developing foraminifera as a biomonitoring tool. By assessing the influence of the analysed size fraction on establishing the EcoQS, the third manuscript worked towards optimizing benthic foraminifera as a biomonitoring tool in northern Norway. This PhD thesis, therefore, contributed towards the current understanding of benthic foraminiferal ecology in northern Norway and towards further implementing benthic foraminifera as a biomonitoring tool.

2. Study area

In the current thesis two fjords in northern Norway were investigated (Fig. 1), Kaldfjorden (I) in the Troms kommune and Øksfjorden (II) in the Loppa kommune (Fig. 2 and 3). This section is to provide a brief description of the bathymetry of the coastal shelf outside of Kaldfjorden and Øksfjorden and the bathymetry of the fjords themselves. The influence of the bathymetry on the hydrological settings in the area and the fjords is also discussed. Finally, potential anthropogenic environmental pressure factors on the fjord are defined.

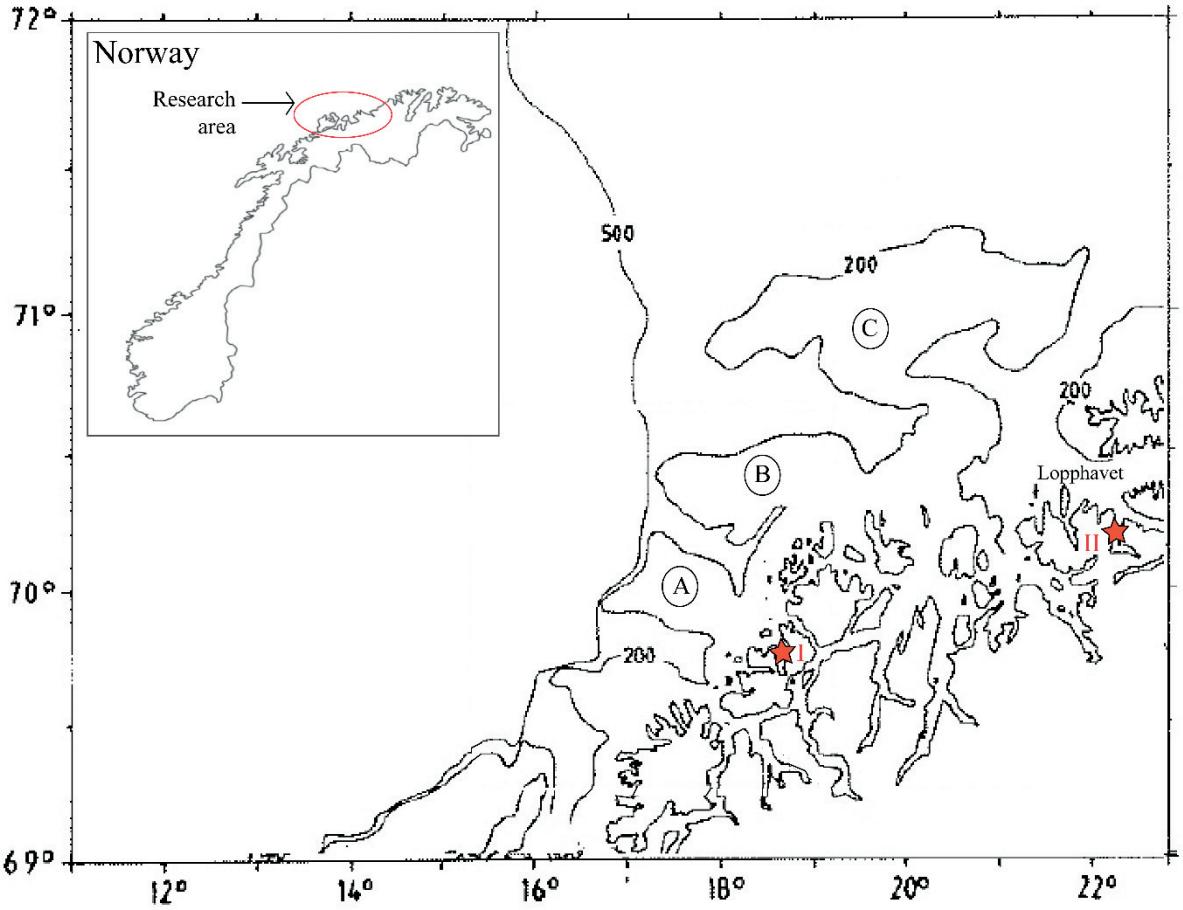


Fig. 1: Map showing Kaldfjorden (I) and Øksfjorden (II) as red stars. The banks are indicated as circled letters: Malangsgrunnen (A); Fugløybanken (B); and Nordvestbanken (C). The map was modified from Sundby, 1984.

2.1 Bathymetry and hydrology

Off the coast of Kaldfjorden and Øksfjorden, the continental shelf topography is dominated by three banks, the Malangsgrunnen (A), Fugløysbanken (B), and Nordvestbanken (C), which are separated by troughs (Sundby, 1984; Fig. 1). The hydrology in the region is highly influenced by the shelf topography, where Norwegian Coastal Water circulates over banks and Atlantic Water intrudes into the troughs (Sundby, 1984). The Norwegian Coastal Water is relatively cold with salinities < 35, whereas the Atlantic Water is relatively warm (4-6 °C) with salinities above 35 (Helland-Hansen and Nansen, 1909). Compared to the more southern fjords in Norway, fjords in northern Norway are considered more open to exchange with Norwegian Coast water and Atlantic water due to a greater sill depth (Holte et al., 2005; Wassmann et al., 1996).

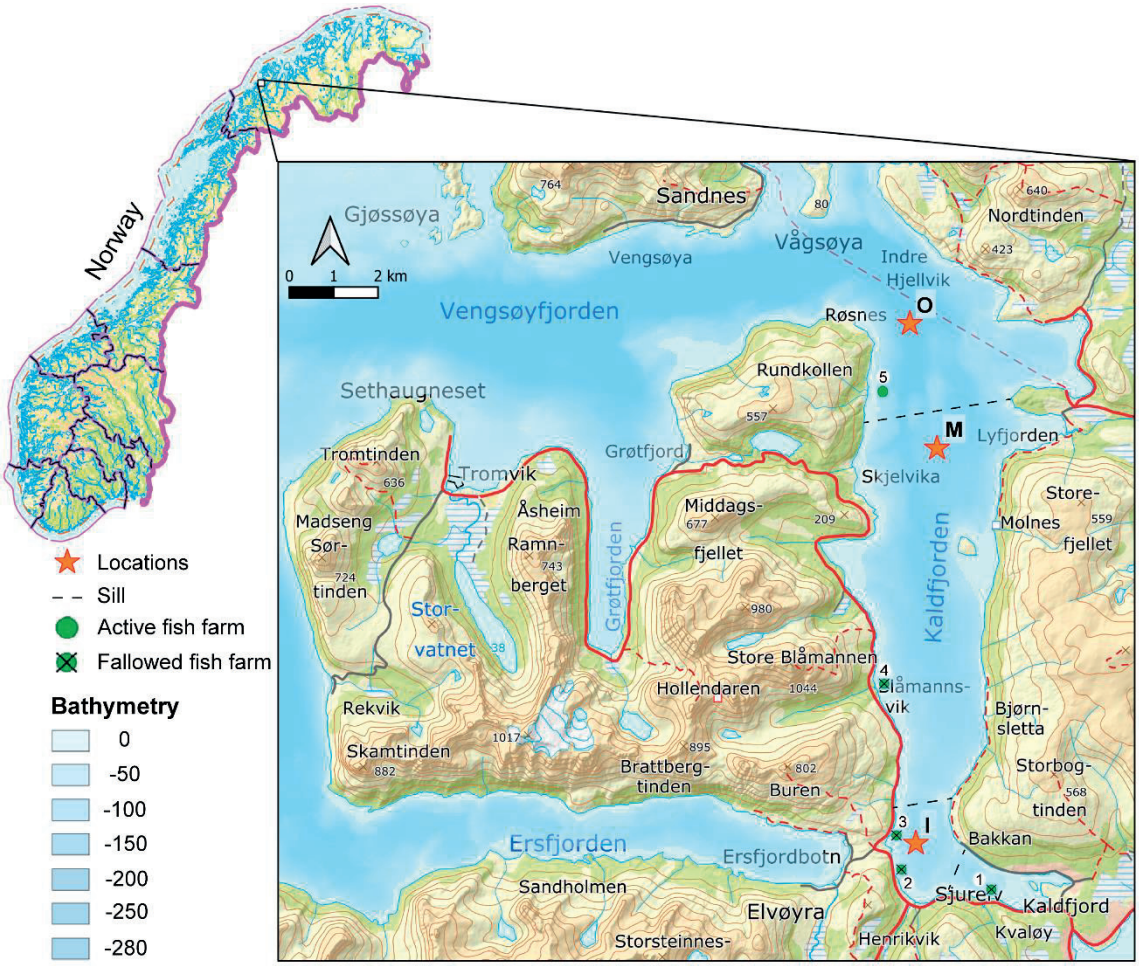


Fig. 2: Map of Kaldfjorden showing the Inner (I), Middle (M) and Outer (O) location and the connecting Vengsøyfjorden. The green circle represents Rongdalen, the fish farm in active use in September 2017. The green circles with a black cross represent the fallowed fish farms Sjurelv (1), Hendrikvika (2), Kræmarvika (3), and Blåmannsvika (4), which were not in active use in September 2017. This map is based on Norwegian Mapping Authority data (http://www.kartverket.no, 2020) and created with QGIS.

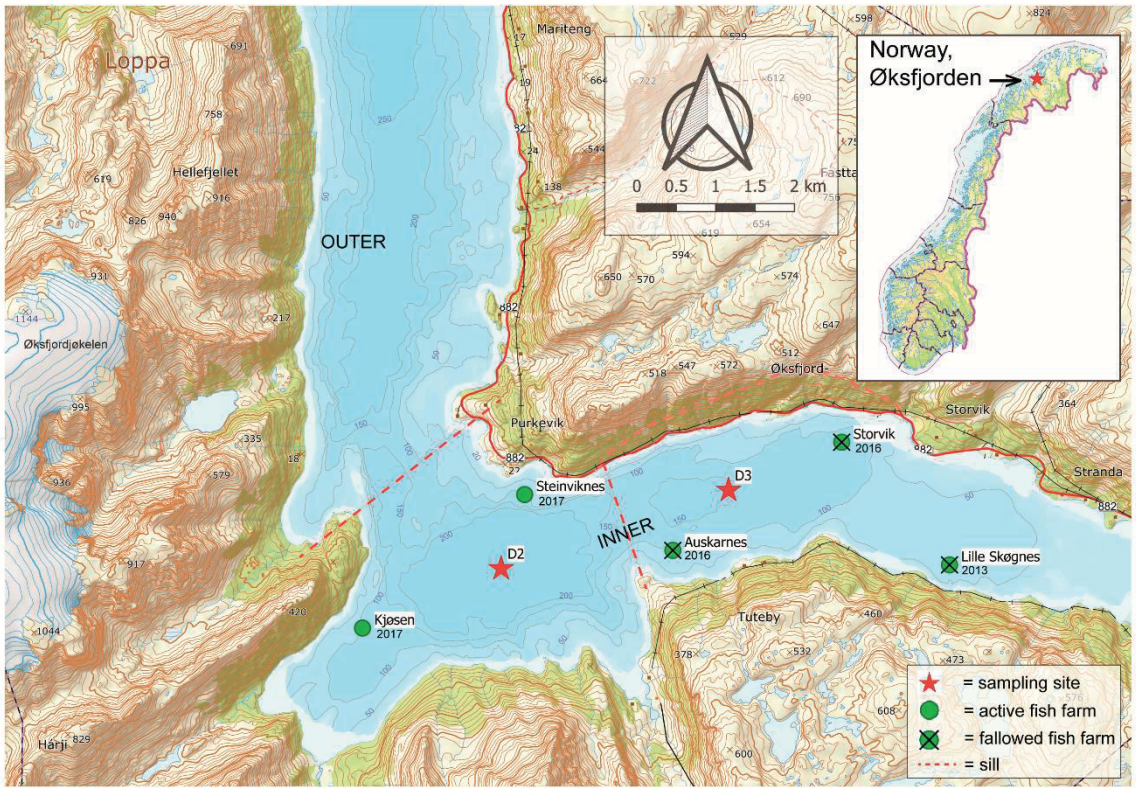


Fig. 3: Map of outer and inner Øksfjorden. The inner fjord consists of a main (D2) and a sub-basin (D3). The years under the names of the fish farms indicate the year at which they were in active use, or since when they were fallowed. (Modified from the QGIS Development Team (3.4.14-Madeira, 2020), map from Statens kartverk 2007).

The isotope tracer experiment was carried out using sediment from Kaldfjorden, Northern Norway. Kaldfjorden is a 16 km long fjord consisting of an innermost, inner, and middle basin, and an outer section that connects to Vengsøyfjorden. The basins and the outer section are approx. 40, 110, 150 and 240 meters deep, respectively, and at approx. 3.5, 13, and 15 km distance from the head of the fjord (Fig. 2). The innermost basin is separated from the inner basin by an approx. 50 m deep sill, which in turn is separated from the middle basin by an approx. 55 m deep sill. The middle basin and outer section are separated by a partial sill that is 75 m deep at the shallowest parts but with 150 m deep channels cutting through it. The outer section connects to Vengsøyfjorden without a sill. The basins are from here on referred to as the Innermost, Inner and Middle locations, and the outer section as the Outer location. The steep topography of the surrounding mountains continues into the bathymetry of Kaldfjorden.

Øksfjorden consists of an inner and outer region but only the inner fjord was investigated, from here on referred to as Øksfjorden (Fig. 3). Øksfjorden is approximately 13 km long and separated from the outer region by a ca. 120 m deep sill and consists of two basins separated

by a ca. 100 m sill (Fig. 3). The area surrounding Øksfjorden is characterized by a steep topography with rocky slopes (Krauskopf, 1954), which continues in the fjords bathymetry.
No major rivers drain into Kaldfjorden or Øksfjorden (Fig. 2 and 3), but the glacier Øksfjordjøkelen drains into the inner and outer region of Øksfjorden from the western side. The water stratification in northern Norwegian fjords is considered weaker compared to fjords further south (Holte et al., 2005). The water column stratification in northern Norway is considered at its minimum during early spring after which it increases in May-September, followed by a decrease during late fall and winter (Keck and Wassmann, 1996; Wassmann et al., 1996). In Kaldfjorden, the maximum water column stratification in 2017 was from June until October, after which it decreased during November, and the water column was considered well mixed from December till May (Jones et al., 2020). In Øksfjorden, only CTD data from September 2017 was available, which did not indicate a strong stratification in September 2017.

Table 1: The bottom water O_2 concentrations, salinity, temperature, and water depth, of Kaldfjorden and Øksfjorden as measured in September 2017. For Kaldfjorden, the bottom water O_2 concentrations were provided by Angelika Renner (Norwegian Institute of Marine Research, Tromsø), and both salinity and temperature were obtained from Chierici et al. (2019).

Fjord	Location/ Basin	Water Depth m	Oxygen mmol/L	Oxygen ml/L	Salinity PSU	Temperature °C
Kaldfjorden	Inner	111	0.24	5.4*	34.1	7.1
Kaldfjorden	Middle	140	0.24	5.3*	34.3	6.5
Kaldfjorden	Outer	236	0.24	5.3*	34.4	6.4
Øksfjorden	Main	240	0.23	5.1	35	5.1
Øksfjorden	Sub-	160	0.26	5.8	35	5.6

*un-calibrated values

The hydrology measurements discussed in the next two paragraphs concern measurements taken in September 2017. The salinity in Kaldfjorden increased from 33.4 in the surface waters to ca. 34.4 in the bottom waters at all three locations (Chierici et al., 2019; Table 1). Dissolved O_2 measurements using a conductivity, temperature, depth mounted OxyGuard Profile sensor indicated an O_2 saturation of at least 80% in the seawater above the seafloor at all three locations in Kaldfjorden (Angelika Renner, Norwegian Institute of Marine Research, Tromsø pers. com.). The temperature in Kaldfjorden decreased from ca. 10 °C in the surface waters to ca. 6.6 °C in the bottom waters (Chierici et al., 2019).
In September 2017, the salinity in the water column increased from c.a. 33 in the surface to 35 in the bottom in both basins in Øksfjorden (Table 1). The temperature decreased from 9 °C in

the surface waters to 5.5 °C in the bottom waters in both basins (Table 1). The oxygen concentrations in Øksfjorden decreased from 6 mL L^{-1} (0.27 mol L^{-1}) in the surface to 5.5 mL L^{-1} (0.25 mol L^{-1}) in the bottom waters (Table 1). The measurements from Øksfjorden suggest that the inner fjord could be influenced by the relatively warm Atlantic waters, as proposed by Helland-Hansen and Nansen (1909) and Wassmann et al. (1996).

2.2 Anthropogenic activity

There are no large settlements, heavy industry or agricultural activities along Kaldfjorden or Øksfjorden (Fig. 2 and 3). In Kaldfjorden, a sewage wastewater outlet installed in 1983 discharges mechanically treated wastewater of ca. 500 households into the innermost basin at 12 m water depth (Helø and Lejon, 2009). The outlet is at ca. 3.5 km distance from the nearest sampling location in Kaldfjorden (Fig. 2). Fish farming activities have been conducted in Kaldfjorden since 1984 (Vågen, 2018), operating from five different locations. Fish farming locations Sjurelv, Henrikvika, and Kræmarvika in the innermost part have been permanently closed since 2001, 2010, and at least 2018, respectively. Kræmarvika was not in active use in September 2017. The two locations Blåmannsvik and Rogndalen further outwards are still in use, but only Rogndalen was in active use during sampling in 2017 (Vågen, 2018).
Øksfjorden is one of the most intensively fish farmed fjords in northern Norway (Bjørn et al., 2009). Since the start of production in Øksfjorden in 1996, licences increased from 1500 tonnes of fish per fish farm to 2700 tonnes in 2006 (Per-Arne Emaus, pers. com. 2020). Grieg Seafood ASA obtained the farming licences in 2005 and has since increased the production to 4000–8000 tonnes of fish per year (Odd Leknes pers. com. 2020). In total, Grieg Seafood ASA produced 62,700 tonnes of salmon using 75,500 tonnes of fish feed between 2005 and 2017 in Øksfjorden (Odd Leknes pers. com. 2020). During the sampling campaign in September 2017, the fish farms Steinviknes and Kjøsen were in active use (Fig. 3). Storvika and Auskarnes were being fallowed during sampling in 2017. Fish farming location Lille Skøgness has been permanently closed since 2013 due to deteriorating environmental conditions.

3. Methodology

This section provides a summary of the methods used in the two papers and the manuscripts where special attention is being paid to providing background information for the used methods. For the detailed methodology, see the papers and the manuscript in appendix I, II and III. Note that from here on the indices for foraminifera are referred to as the fH'_{log2}, fES_{100}, fNQI, and fAMBI, whereas the indices for macrofauna will be referred to as the mH'_{log2}, mES_{100}, mNQI, and mAMBI. In both fjords, samples were collected in September 2017.

3.1 Collecting sediment cores in Øksfjorden

To assess the impact of fish farming activities in Øksfjorden sediment cores were collected from the main basin (D2) and the sub-basin (D3) at approximately 240 m and 160 m water depth, respectively (Fig. 3). Sediment coring was performed using a twin-barrelled Gemini gravity corer (inner diameter 8 cm, Niemistö, 1974). With gravity corers, sediment core records spanning pre-anthropogenic impact can be obtained (e.g., Alve, 1991; Dolven et al., 2013; Duffield et al., 2017). The sequentially deposited layers of sediment in a core, i.e. the stratigraphy, provide a record of changes through time where the youngest sediments are on top and the oldest are at the bottom.

Two sediment cores from each basin in Øksfjorden were sectioned on deck, slicing the upper 20 cm into 1 cm thick slices and below 20 cm into 2 cm slices. Sediment core samples were kept frozen at –20 °C until further analyses. All sediment core samples were freeze-dried to obtain the porosity records which were used to assess the quality of the cores. The cores with porosity records that described the smoothest exponential-like decrease down-core were regarded as high quality and sent to the Environmental Radioactivity Research Centre, University of Liverpool, UK, for radiometric dating.

From samples from the dated sediment cores, the bulk sediment organic geochemistry (TOC, total organic carbon and total nitrogen ratios (C/N), and stable carbon isotopes ($\delta^{13}C_{VPDB}$)), heavy metal concentrations (e.g. copper), and grain size distributions (% < 63 µm) were obtained. The TOC was normalized to the sediment fine fraction (% < 63 µm), hereafter referred to as TOC_{63} (TOC_{63} = TOC + 18 × 1 − % <63 µm; (Veileder, 02:2018), to take into account the strong correlation between sediment grain size and TOC concentrations (Kennedy et al., 2002). In the current thesis, TOC_{63} class limits are according to the Norwegian guidelines in 2018 (Veileder, 02:2018; Table 2). The samples for heavy metal analyses were treated with 7 M

NHO_3 prior to the analyses of copper, zinc and nickel on a Gas Chromatography ICP Sector Field Mass Spectrometer by the ALS Laboratory Group Norway AS. The class limits used to determine the quality status based on the heavy metals are according to the Norwegian guidelines in 2018 (Veileder, 02:2018; Table 3).

Table 2: Table with the TOC_{63} class limits according to the Norwegian guidelines (Veileder, 02:2018, p. 170 Table, 9.23)

Parameter mg/g	**Classes**				
	High	**Good**	**Moderate**	**Poor**	**Bad**
TOC_{63}	0 - 20	20 - 27	27 - 34	34 - 41	41 - 200

Table 3: Table with the heavy metal class limits according to the Norwegian guidelines (Veileder, 02:2018, p. 209 - 211 Table, 11.11).

Parameter mg/kg DW*	**Classes**				
	High	**Good**	**Moderate**	**Poor**	**Bad**
Nickel (Ni)	0 - 30	30 - 42	42 - 271	271 - 533	> 533
Copper (Cu)	0 - 20	20 – 84		84 - 147	> 147
Zinc (Zn)	0 - 90	90 - 139	139 - 750	750 - 6690	> 6690

* Dry weight (DW)

In addition to the sediment core samples in Øksfjorden, three replicate surface samples (0 - 1 cm) were obtained from each station for living, rose Bengal (rB) stained, foraminiferal assemblages using the twin-barrelled Gemini corer. These samples were preserved and stored in 70 % ethanol 2 g L^{-1} rB mixture (Schönfeld et al., 2012), which consists of 70 % ethanol, 30 % fresh (tap) water and 2 g of rB powder. Previous research has shown that rB staining prior to washing yielded the best results in terms of colouration of the cytoplasm (Schönfeld et al., 2013).

3.2 Radiometric dating

The sediment core samples were analysed at the University of Liverpool (England) Environmental Radioactivity Research Centre for ^{210}Pb, ^{226}Ra and ^{137}Cs isotope concentrations (Becquerel kg^{-1}) by direct gamma assay on Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al., 1986). The ^{210}Pb dates were calculated using both the Constant Rate of Supply (CRS) and Constant Initial Concentration

(CIC) models (Appleby and Oldfield, 1978), and chronostratigraphic dates were determined from the ^{137}Cs records. ^{210}Pb is a natural radioactive isotope of lead with a half-life of 22.26 years and one of the most important radioisotopes used for dating sediments younger than 150 years (Appleby, 2001). The CRS model assumes a constant rate of supply of ^{210}Pb to the sediment record regardless of any variations in the sedimentation rate. The CIC model assumes that freshly deposited sediments all have the same initial ^{210}Pb concentration.

At sites with constant sedimentation rates, the simple CSR and CIC models are essentially equivalent. Differences may, however, occur when sedimentation rates have varied through time. Assessments as to which model is more appropriate are made using independent chronostratigraphic dates such as those determined from sediment records of the artificial fallout radionuclide ^{137}Cs (half-life 30.17 years). Significant levels of ^{137}Cs fallout from the atmospheric testing of high-yield thermonuclear weapons began in the early 1950s and persisted through to the early 1980s. Peak concentrations can be used to identify sediments deposited in 1963, the year of maximum fallout. In some parts of the world, a second peak recording fallout from the 1986 Chernobyl accident may be observed. Where neither of the simple models is in good agreement with the available chronostratigraphic dates, ^{210}Pb dates can still be determined by applying them in a piecewise way using the methods outlined in Appleby (2001). Adopting these procedures, the ^{210}Pb method has been found to give reliable results at a wide range of different locations.

In the main basin sediment core, the non-monotonic ^{210}Pb record immediately excluded the use of the CIC model. According to this model, unsupported ^{210}Pb concentrations must decline monotonically with depth. The ^{137}C record has two clearly defined peaks straddling a dense layer of sediment between 13 – 5 cm (Klootwijk et al., 2020; appx. I, supplementary material). The raw CRS model calculations suggest an early 1960s date for the deepest ^{137}Cs peak between 16 – 13 cm. The relatively low ^{210}Pb concentration within the dense layer coupled with the high ^{210}Pb concentrations immediately above suggests that this layer was deposited within a very short period of time. The second ^{137}Cs peak between 5 - 3 cm (Klootwijk et al., 2020; appx. I, supplementary material) therefore also records the ^{137}Cs deposited during the early 1960s period of peak fallout from the atmospheric nuclear weapons tests. The ^{210}Pb chronology for the main basin sediment core was calculated using the method outlined above. These results highlight the importance of determining both ^{210}Pb and ^{137}Cs records. For the sub-basin core, the ^{210}Pb record declined monotonically with depth and CRS and CIC model gave highly similar results.

3.3 Collecting box-cores in Kaldfjorden

In Kaldfjorden, sediment was collected at approx. 110, 140 and 235 m depth from the Inner, Middle and Outer locations respectively (Fig. 2). At each location, four replicate box-cores (KC Denmark, 34.5 × 29 cm, 1000 cm^2) were collected and sub-sampled using three, clear acrylic experimental chambers (inner diameter 14 cm) pushed 25-cm deep into the sediment. Directly after sub-sampling, each chamber was randomly assigned to a Control, Low, or High experimental treatment (C, L, H), where Low (10 g) and High (30 g) indicated the amount of jellyfish to be added at a later stage. By using a box-corer, the three chambers could be collected in one deployment, which ensured that the cores for the three experimental treatments came from a highly similar area. The latter was required to minimize potential underlying causes for potential differences between the experimental treatments.

Taking a box-corer also left enough space to obtain three additional smaller cores (inner diameter 4.7 cm) to take samples for bulk sediment organic geochemistry, grain-size analyses, living (rose Bengal (rB) stained) foraminiferal assemblages, and background ^{13}C isotope values of foraminiferal cytoplasm. From the smaller cores, the upper 1 cm was sectioned on deck, and the rB stained foraminiferal samples were preserved and stored in a 70 % ethanol 2 g L^{-1} rB mixture (Schönfeld et al., 2012). Samples for bulk sediment organic geochemistry, grain size analyses, and background ^{13}C isotopes were kept frozen at -20 °C until analysis.

3.4 Foraminiferal analyses

For the fossil foraminiferal analyses in Øksfjorden approximately 2 g of freeze-dried, gently homogenized sediment to ensure the aliquot was representative of the sample, was washed over 500 µm and 63 µm sieves and dried at 40 °C. From the 63 - 500 µm fraction material was taken at random and fully picked until > 250 specimens could be mounted on microfossil slides and identified to species level. The 0 - 1 cm sediment slices for the rB stained foraminifera analyses from both fjords were washed over a 63 µm and 500 µm mesh after which the 63 - 500 µm fraction was split using a modified Elmgren wet splitter (Elmgren, 1973). These splits were further washed over a 63 µm and 125 µm mesh after which both fractions were completely picked until > 200 individuals could be identified and mounted. Previous research has shown that analysing the uppermost centimetre is sufficient for bio-monitoring purposes (e.g. Barras et al., 2014; Schönfeld et al., 2012). Specimens in the > 500 µm (un-split sample) comprised < 6 % of the rB stained foraminiferal assemblages, and were therefore excluded from both the

fossil and rB stained assemblages. As some rB stained samples contained up to 1450 specimens, of small (< 125 µm), difficult to distinguish *Stainforthia fusiformis* and *S. feylingi* these species were grouped into a *Stainforthia* group in both the fossil and rB stained assemblages.

Wet and dry picking are commonly used for picking rB stained foraminifera, and both methods have been shown to provide an accurate estimation of the benthic foraminiferal diversities used for environmental quality assessments (Bouchet et al., 2012; Schönfeld et al., 2013). This is despite the absence of fragile non-fossilisable species in the dry assemblages, which suggest that assemblages not including non-fosilisable species give a good indication of the environmental conditions (Bouchet et al., 2012). Therefore, and to compare rB stained and fossil foraminiferal assemblages, non-fossilisable species were excluded from both the fossil and rB stained assemblages prior to analyses. In the current thesis, rB stained foraminifera were wet picked as this makes it easier to distinguish living foraminifera as the cell does not shrink during drying. Additionally, wet-picking is the recommended method in samples rich in organic debris (Schönfeld et al., 2013 and sources therein).

In the current thesis, the recently by Alve et al. (2019) adapted for the use on benthic foraminifera fH'_{log2} (Shannon and Weaver, 1963) and fES_{100} (Hurlbert, 1971) were calculated using the R-data software program (R Core Team, 2020). The H'_{log2} and ES_{100} are also referred to as diversity indices and combine the simple diversity, also known as the number of species, with a second variable that gives an estimation of what is often referred to as the evenness (Hurlbert, 1971; Rosenzweig, 1995; Shannon and Weaver, 1963). The evenness represents the proportions of species within an assemblage or community, also referred to as relative abundances. Diversity indices were introduced to improve the way the number of species is expressed by making them into continuous values (Rosenzweig, 1995). Diversity indices rise if the number of species goes up or the variation in species abundance goes down (Rosenzweig, 1995).

The fAMBI was calculated according to Alve et al. (2016) and the mAMBI according to Borja et al. (2000), where only species or groups of species assigned to EGs were used. The foraminiferal distributions amongst the EGs were calculated by summing the relative abundances of species or groups of species for each EG. The fAMBI and mAMBI are also referred to as sensitivity indices as they are derived from the proportions of individual abundance in one of the five EGs representing different responses to organic matter enrichment. The EGs are defined as follows: Group I the sensitive species; Group II the indifferent species; Group III the tolerant species; Group IV the 2nd order opportunists; and Group V the 1st order opportunists (Alve et al., 2016; Borja et al., 2000).

The underlying rationale of multi-metric indices, including the NQI, is that organisms reflect the quality of their environment by both the proportions of sensitive and tolerant species and the diversity of the assemblages or communities (Josefson et al., 2009). The NQI for macrofauna combines the mAMBI with a modified species richness index (SN), which are both normalized to their highest obtainable value and equally weighted (mNQI; Rygg, 2006). The NQI for foraminifera is based on the same principle but uses the fAMBI and the recently to foraminifera adapted fES_{100} (fNQI; Alve et al., 2019).
Due to < 100 individuals in the > 125 µm fraction in Kaldfjorden, the replicates from each location for both size fractions were pooled to calculate the indices in both fjords for the Klootwijk and Alve (submitted; appx. III) study.

3.5 Ecological Quality Status classification

The EcoQS is used to ensure that appropriate and obtainable environmental goals are set for water bodies. In the WFD, the EcoQS are defined as follows (WFD, 2003/5/EC, p. 48, Annex V Table 1.2):

1. High status (blue): no, or only very minor, deviations of the physicochemical, hydro-morphological, or biological quality elements due to anthropogenic pressure factors from those normally associated with that type of water body under undisturbed conditions are observed.
2. Good status (green): the values of biological quality elements show low levels of distortion resulting from human activity, but do not diverge much from those that would prevail under undisturbed conditions
3. Moderate status (yellow): the values of the biological quality elements diverge moderately from those normally found when no distorting anthropogenic pressure factors are present but indicate significantly more disturbed conditions compared to the conditions that would prevail under a good status.
4. Poor status (orange): the water body is showing evidence of major alterations to the values of the biological quality elements and the relevant biological communities have deviated substantially from those normally associated with that type of water body under undisturbed conditions.
5. Bad status (red): water bodies showing evidence of severe alterations to the values of the biological quality elements and in which large proportions of the relevant

biological communities normally associated with that type of water body in undisturbed conditions are absent.

The purpose of classifying a water body is to describe the environmental state in a way that is comprehendible to non-experts and to assess if measurements to counteract anthropogenic pressure factors are effective. According to the WFD, the border between Good (green) and Moderate (yellow) is the point at which a community regresses from an acceptable to an unacceptable state. The latter would require governmental interference to improve the EcoQS. In the current thesis, EcoQS class limits for the fH'_{log2}, fES_{100} and fNQI according to Alve et al. (2019), were used (Table 4). For the fAMBI no class limits for foraminifera have been defined, therefore the class limits for macrofauna according to Borja et al. (2003) were used (Table 4). The EcoQS class limits for macrofauna according to the Norwegian Guidelines (Veileder, 02:2018) were used (Table 5).

Table 4: Ecological Quality Status (EcoQS) class limits for the fH'_{log2}, fES_{100} and fNQI after Alve et al. (2019), and the fAMBI after Borja et al. (2003).

EcoQS	fH'_{log2} class limits	fES_{100} class limits	fAMBI class limits	fNQI class limits
High	5 - 3.4	35 - 18	0 - 1.2	1 - 0.54
Good	3.4 - 2.4	18 - 13	3.3 - 1.2	0.54 - 0.45
Moderate	2.4 - 1.8	13 - 11	4.3 - 3.3	0.45-0.31
Poor	1.8 - 1.2	11 - 9	5.5 - 4.3	0.31-0.13
Bad	0 - 1.2	9 - 0	5.5 - 7.0	0.13-0

Table 5: Ecological Quality Status (EcoQS) class limits for the mH'_{log2}, mES_{100} and mNQI after (Veileder, 02:2018) as used in the Klootwijk et al. (2020; appx. I) study in the current thesis.

EcoQS	mH'_{log2} class limits	mES_{100} class limits	mNQI class limits
High	4.8 – 3.2	39 – 19	0.9 - 0.72
Good	3.2 – 2.5	19 – 13	0.72 - 0.63
Moderate	2.5 – 1.6	13 – 8	0.63 – 0.49
Poor	1.6 – 0.8	8 – 4	0.49 – 0.31
Bad	0.8 - 0	4 - 0	0.31 - 0

3.7 Isotope tracer experiment

For the isotope tracer experiment, *Dunaliella tertiolecta* was grown as a labelled food source in the ½ IRM medium with additional selenite (Paassche et al., 1988). Replacing 25 % of the ^{12}C bicarbonate already present in the ½ IRM medium with $NaH^{13}CO_3$ ensured that the algae

incorporated enough ^{13}C to assess the foraminiferal Carbon-uptake (C-uptake). In the natural environment, the abundance of the ^{13}C isotope is ~1.1 %, and significantly increasing the ^{13}C isotope abundance above the natural value makes it possible to assess the amount of food that has been consumed by the studied organisms (e.g. Sweetman et al., 2016). The final concentration of ^{13}C in the algal carbon used in the experiment for this thesis was 21.6 ± 0.3 atom%.

Upon arrival at the Akvaplan-Niva research station in Kraknes (Research Innovation Station Kraknes, FISK), the experimental chambers were carefully filled with filtered seawater and placed in dark, temperature-controlled water baths (Fig. 4). The chambers were allowed to re-settle and geochemically stabilize for 4 days whilst being kept in an overflow system (Sweetman et al., 2016, 2014a), after which 77 mg of the ^{13}C labelled was added to each chamber to start the experiment (Fig. 4). After ensuring the algae were evenly mixed into the overlying water column, the stirrers were switched off for one hour, allowing the algae to settle on the sediment (Fig. 4). After one hour, a single piece of 10 (Low) or 30 (High) grams of thawed *P. periphylla* carrion, equivalent to 32 and 96 grams of jellyfish particulate C m^{-2} respectively, were carefully placed on the sediment surface of the chambers selected for jellyfish treatments (Fig. 4). After this, the chambers were left to incubate for 48 hours to ensure the uptake of labelled carbon and that no more than 30% of the O_2 available in the overlying water column was consumed during the incubation (Renaud et al., 2008; Sweetman et al., 2016).

After the incubation, oxygen micro-profile measurements were made using a UNISENSE 3D-O_2 micro-profiling system avoiding the jellyfish carrion as much as possible. During this process, a needle with a sensor was carefully inserted into the sediment until no more O_2 could be measured to obtain the O_2 gradient profile in the sediment. The obtained gradient profiles were used to determine the diffusive oxygen uptake (DOU; mmol O_2 m^{-2} d^{-1}) from a linear approximation to the O_2 gradient that is situated inside the diffusive boundary layer applying Fick's first law of diffusion (Glud, 2008). From the position of the sensor relative to the sediment-water interface, the oxygen concentrations at the sediment-water interface (OCI; mmol L^{-1}) and oxygen penetration depth (OPD; mm) were obtained.

To sample the experimental chambers, the upper centimetre of sediment (0 - 1 cm) was sliced off and carefully homogenized, after which 20 mL sediment was collected for foraminiferal analyses by transferring material into a syringe. The sub-samples were kept frozen till further analyses. In the laboratory, the sub-samples were thawed and washed over 63- and 500-µm meshes with artificial seawater (salinity 30) that was produced following the method described

by Enge et al. (2011). From the 63- to 500-µm size fraction, approximately 400 living individuals (including agglutinated specimens) were picked for cytoplasm analyses and identified to species level where possible.

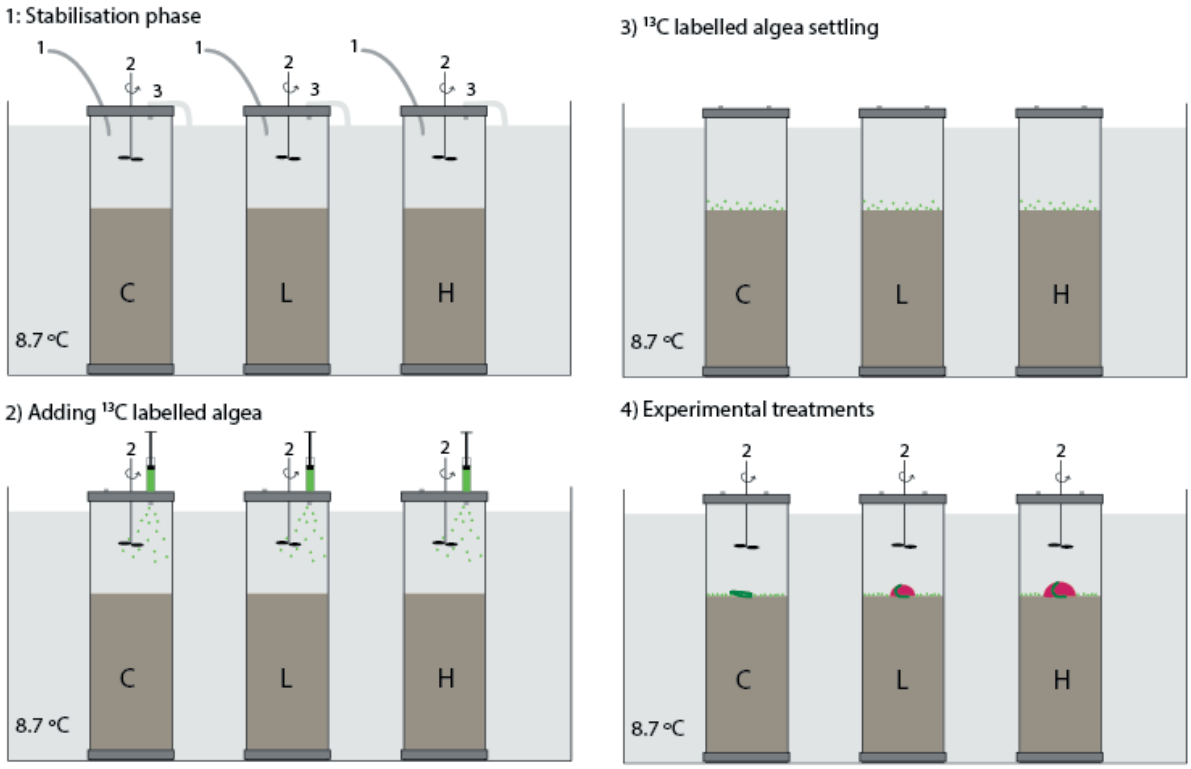


Fig. 4: Schematic representation of the experimental design, where the numbers 1, 2 and 3 represent the water inflow, stirrer and water overflow, respectively. The experimental treatments are depicted by the letters C, L and H representing the Control, Low and High treatment, respectively.

In addition to the samples from the experimental chambers, one sample from each location was analysed to obtain the natural (background) foraminiferal carbon isotope signatures. These samples were required to assess the amount of ^{13}C isotopes above the natural abundance which is needed to calculate the uptake of microalgal carbon (C-uptake; µg C_{algae} 10 cm^{-2} d^{-1}). To further investigate potential drivers behind the C-uptake, the C-uptake per 10 cm^2 was normalized to both rB assemblage densities by dividing it by the number of tests per 10 cm^{-2} (C-$uptake_{rB}$; ngC_{algae}/individual/d), and foraminiferal biomass by dividing by the biomass per 10 cm^{-2} (C-$uptake_{bio}$; $\mu gC_{algae}/\mu gC_{biomass}$). The number of foraminiferal tests per 10 cm^{-2} was obtained from the rB stained assemblages.

To obtain the bulk sediment stable carbon and nitrogen isotope signatures ($\delta^{13}C_{VPDB}$ and $\delta^{15}N_{air}$) and TOC_{63} and total nitrogen content the upper sediment centimetre (0–1 cm) from one core from each location was analysed. This was done to investigate possible underlying causes for

potential differences in the foraminiferal assemblage structure from the inner to the outer region of Kaldfjorden. A principal component was performed to investigate potential differences in the bulk sediment geochemistry (e.g. $\delta^{13}C_{VPDB}$ and TOC_{63}) and hydrological conditions (e.g. the bottom water salinity) amongst the locations. Prior to the principal component analyses the TOC_{63}, C/N ratios, stable carbon and nitrogen isotopes ($\delta^{13}C_{VPDB}$ and $\delta^{15}N_{air}$), and grain size distribution (% < 63 μm), in addition to the water depth (m), and bottom water O_2 concentration (mL L^{-1}), salinity, and temperature (°C), were standardised by subtracting the mean from the values and dividing that outcome by the standard deviations. It should be noted that the bottom water O_2 concentrations were provided by A. Renner (Norwegian Institute of Marine Research in Tromsø), and the bottom water salinity and temperature were provided by (Chierici et al., 2019).

Differences in the (arithmetic) mean foraminiferal C-uptake, C-$uptake_{bio}$, C-$uptake_{rB}$, DOU, OCI and OPD, were analysed using separate two-way Analyses of Variance (ANOVA) with experimental treatment (C, L, H) and location (Inner, Middle, Outer) as fixed factors. An ANOVA is a statistical method to separate the observed variance within a data set into different components that can be used for further statistical testing for levels of significance. For a two-way ANOVA, the two factors, e.g. experimental treatment and location, should in principle be independent. Any observed significant differences were further analysed using Tukey posthoc tests. After a significant outcome of an ANOVA, a Tukey post hoc test was performed to find out which specific group means are different by comparing all the possible pairs of the means with one another.

To visualize potential differences in foraminiferal assemblage composition amongst samples separate correspondence analyses were performed for the experiment and the rB stained samples. For both correspondence analyses, square-root transformed relative abundances of the 15 numerically dominant species in the assemblages from the experiment across all locations were used. The correspondence analysis of the rB stained assemblages also used the 15 numerically most dominant species in the assemblages from the experiment to investigate if the distribution of species amongst the locations was natural or a potential outcome of the experiment. In a correspondence analysis, the differences between relative values are analysed, where for example the inter-sample differences in relative abundances across the species can be used (Greenacre, 2017, Chap. 13). The square root transformation was performed for visual purposes only. All statistical analyses were performed using the statistical language R version 3.6.1 (R Core Team, 2019), where the correspondence analyses were performed using the "Vegan" package in R (version 2.5-5, Oksanen et al., 2010).

4. Results

This section provides a short introduction to the two papers and the manuscript after which the main findings are listed as bullet points. The results are presented in greater detail in appendix I, II and III for the first and second paper and third manuscript, respectively.

Paper 1: Monitoring environmental impacts of fish farms: Comparing reference conditions of sediment geochemistry and benthic foraminifera with the present

Authors: Anouk T. Klootwijk, Elisabeth Alve, Silvia Hess, Paul E. Renaud, Carsten Sørlie, Jane K. Dolven
Published: Ecological Indicators
Keywords: Biomonitoring, Aquaculture, Benthic foraminifera, Geochemical parameters, Macrofauna, Ecological Quality Status.

Intensive fish farming is a major industry, but the extent of organic matter and heavy metal pollution by fish farms is debated. In this paper, in situ reference conditions were established using geochemical parameters (TOC_{63}, C/N, $\delta^{13}C_{VPDB}$ TOC and heavy metals Zn, Cu and Ni) and fossil benthic foraminiferal assemblages in dated sediment cores to identify potential impacts of fish farming in the two basins of inner Øksfjorden, Northern Norway. The rB stained benthic foraminifera were used to assess the present-day environmental conditions. The fossil foraminiferal records were compared with the rB stained foraminifera, which in turn were compared with macrofaunal data.

Findings:

- Modern (ca. past 200 years) stratigraphic records from ^{210}Pb and ^{137}Cs dated sediment cores did not indicate that the benthic environment of the Øksfjorden basins has been impacted by fish farming activities.
- Both the geochemical parameters and benthic foraminiferal indices (fNQI, fAMBI), $fHlog_2$, ES_{100}) from the fossil assemblages showed no major deviations from references conditions.
- For most of the fossil assemblages > 85% could be assigned to the five EGS defined in the AMBI but for the 8-4 cm in the sub-basin core only 77 to 79 % could be assigned.

- The long-term (> 100 years) sediment core records also suggested that the concentrations of nickel are naturally high, as no deviations from reference conditions were observed. This is also the case for the TOC_{63} concentrations in this basin. Overall, the concentrations of the TOC_{63} and heavy metals were higher in the sub-basin compared to the main basin.
- The benthic foraminiferal absolute abundances (tests/g dry sediment) increased in the upper 3 cm of the sub-basin sediment core, and relative abundances of species within the EGs changed in the upper 5 cm of both sediment cores.
- Relative abundances *Brizalina skagerrakensis* and *Epistominella vitrea* increased in the upper 5 cm of the main basin core, but *B. skaggerakensis* was absent in the sub-basin core. *E. vitrea* only exhibited small changes in the sub-basin core.
- The high relative abundances of the *Stainforthia* group (*S. fusiformis* and *S. feylingi*) in the rB stained foraminiferal assemblages were in strong contrast with the fossil foraminiferal assemblages in Øksfjorden.
- The indices of the rB stained foraminifera and macrofauna resulted in the same or a higher similar EcoQS. The sensitivity index AMBI showed that opportunistic species and species tolerant to OM were more abundant in the foraminiferal assemblages compared to the macrofauna.

Paper 2: Benthic foraminiferal carbon cycling in coastal zone sediments: the influence of the assemblage structure and jellyfish detritus

Authors: Anouk T. Klootwijk, Andrew K. Sweetman, Silvia Hess, Elisabeth Alve, Katherine M. Dunlop, Paul E. Renaud.
Submitted to: Estuarine Coastal and Shelf Science
Keywords: Benthic foraminiferal carbon uptake; Sediment organic geochemistry; Jellyfish-detritus; Sediment O_2 dynamics; Fjord-to-coast gradient; northern Norway.

Benthic foraminiferal assemblage compositions have been shown to vary from the inner regions of fjords to the outer regions. These differences have been linked to differences in food availability, bottom water oxygenation or substrate characteristics. Benthic foraminifera play important carbon processing roles in marine ecosystems, but little is known about how they process carbon within fjords or how additional organic carbon loading from, e.g., jellyfish

detritus may affect this role. Jellyfish carrion is an important carbon source to the benthic ecosystem that is expected to increase in some regions in the future. Its potential impact on sediment biochemical processes is, however, not fully understood. The second manuscript used ^{13}C-labelled algae to quantify how jellyfish detritus may alter benthic foraminiferal microalgal-carbon uptake (C-uptake) from the inner to the outer fjord. To assess potential mechanisms for variations in C-uptake, foraminiferal biomass, density, and assemblage composition, in addition to sediment O_2 dynamics and environmental parameters (e.g. sediment TOC_{63}), were also investigated.

Findings:

- Benthic foraminiferal C-cycling strongly varied within the fjord with 20-fold higher C-uptake rates at the inner fjord location compared to the locations further outwards. Statistical testing showed that the difference between the inner fjord location and the outer two locations was significant, but the outer two locations did not significantly differ from one another. No significant effect of jellyfish addition on the C-uptake was detected.
- Normalising the foraminiferal C-uptake to the biomass ($C\text{-}uptake_{bio}$) and foraminiferal densities ($C\text{-}uptake_{rB}$) showed that the biomass explained just under 50% of the difference amongst the locations, whereas foraminiferal densities only explained 20%. Normalising the foraminiferal C-uptake rates resulted in the same statistically significant differences found for the non-normalised C-uptake rates.
- The foraminiferal assemblage composition at the inner fjord location was distinctly different from the two locations further outwards. The inner fjord location had higher relative abundances of *Bulimina marginata* and *Nonionella turgida* compared to the other two locations further outwards.
- Strong differences in the foraminiferal assemblage structure amongst the locations were not accompanied by strong differences in the environmental parameters investigated in this study.
- DOU were approx. 1.5-fold higher in cores were jellyfish detritus was placed on top of the sediment. Pairwise testing showed a significant difference between the Control (no jellyfish on the sediment) and the two jellyfish treatments (10 and 30 g of jellyfish on the sediment), but not between the jellyfish treatments themselves.

- The placement of jellyfish detritus on the sediment had a marginally significant effect on the OCI compared to the Control treatment. The OCI was not significantly different amongst the locations.
- The OPD was shallower by approx. 2.5 fold but not significantly different in cores where jellyfish detritus was placed on top of the sediment compared to the Control treatment. The OPD was significantly lower at the middle sampling location compared to the inner fjord location and the location furthest out of the fjord.
- The for none of the tested parameters did the observed differences dependent on the interaction between experimental treatments (C, L, H) and sampled location (from here on referred to as the interaction effect).

Paper 3: Does the analysed size fraction of benthic foraminifera influence the Ecological Quality Status and the interpretation of environmental conditions? Indications from two northern Norwegian fjords

Authors: Anouk T. Klootwijk and Elisabeth Alve.
Submitted to: Ecological Indicators
Keywords: Ecological quality status (EcoQS), benthic foraminiferal biomonitoring, foraminiferal test size, diversities indices, arctic region.

The introduction of the European Water Framework Directive increased the interest in benthic foraminifera as a biomonitoring tool. This prompted the need to standardise the methods used to analyse benthic foraminifera, including which sediment fraction to analyse. In some regions benthic foraminifera produce small (< 125 µm) adult tests and this study assessed the effect of analysing the > 63 µm or > 125 µm fraction on determining the EcoQS in two fjords in northern Norway. The EcoQs has been established using the fH'_{log2}, fES_{100}, fNQI, and fAMBI. Foraminiferal distributions amongst Ecological Groups (EGs) representing the sensitivity of species to organic matter enrichment were investigated for both size fractions to assess the potential loss of ecological information. Finally, the loss of species with ecological information was also assessed should only the > 125 µm fraction be analysed. This study provided new insights into benthic foraminiferal index functioning in an important fish farming region of Norway.

Findings:

- The fH'_{log2}, fES_{100}, and fNQI, from both the > 63 µm and > 125 µm fraction resulted in the same or highly similar EcoQS, with a Good (green) or High (blue) EcoQS. The same applied to the fAMBI, except in the sub-basin of Øksfjorden where the > 63 µm fraction showed a Moderate (yellow) EcoQS whereas the > 125 µm fraction reflected a Good (green).
- Of the investigated indices, the fAMBI was the most affected by the analysed size fraction as the fAMBI of the > 63 µm fraction in both fjords was approximately twice as high compared to the fAMBI of the > 125 µm fraction.
- In general, the > 63 µm fraction contained more foraminifera with a tolerant or opportunistic response to organic matter enrichment compared to the > 125 µm fraction, but this was especially the case in the sub-basin of Øksfjorden.
- The species *E. vitrea* (EG II), *Pullenia osloensis* (EG III), *Nonionella iridea* (EG III), the *Stainforthia* group (EG V), and *Textularia earlandi* (EG III), were mostly absent in the > 125 µm assemblage.
- The foraminiferal densities were 5 to 9-fold higher in the > 63 µm fraction compared to the > 125 µm fraction.

5. General discussion

This section provides a general discussion where the main discussion points from the manuscripts are presented and further discussed in relation to developing benthic foraminifera as a monitoring tool in northern Norway. For a detailed discussion of the main discussion points in this general discussion, please see the discussion sections of the first and second paper and the manuscript in appendix I, II and III, respectively.

5.1 Organic geochemistry and heavy metals in sediment cores

The lack of major changes in the bulk sediment TOC_{63} and $\delta^{13}C_{VPDB}$ in the sediment cores records from Øksfjorden could be due to a combination of the large distances to the fish farms, relatively low sedimentation rates and well-oxygenated bottom waters (Klootwijk et al., 2020; this thesis). These factors may have affected the preservation of organic waste from the fish farms. Sediment core records from Klootwijk et al. (2020; appx. I) showed that the Moderate TOC_{63} classification of the upper 3 cm of sediment in the main basin of Øksfjorden reflects pre-1960s (prior to fish farming) reference conditions. A moderate status would require government action to improve the status (WFD 2000/60/EC), however, in the main basin of Øksfjorden, this would mean deviating from the natural conditions which is in conflict with the WFD aims and objectives.

Previous research found that copper concentrations in sediments near fish farm cages treated with anti-biofouling paint were in most cases within the ranges found under untreated cages (Brooks and Mahnken, 2003a). The surrounding bedrock of Øksfjorden is known for its high concentrations of copper, zinc and nickel (Krauskopf, 1954; Reimann and Caritat de, 1998). The main reason that the concentrations in the sediment were lower is probably because those only reflect the acid leached portion of the metals (Klootwijk et al., 2020; appx. I). There were thus stronger indications that the heavy metals concentrations reflected the bedrock rather than fish farming activities.

Overall, the sediment organic geochemistry and heavy metal records in Øksfjorden remained stable during at least the past century giving no indication of any impact from fish farming in the basins (Klootwijk et al., 2020). The sediment core records from Klootwijk et al. (2020; this thesis) thus seem to support former studies investigating spatial gradients that found no changes in heavy metal concentrations (Brooks and Mahnken, 2003a), TOC concentrations, or

particulate organic matter and carbon outside a 100 to 500 m radius from fish farms (Brooks and Mahnken, 2003b; Carroll et al., 2003; Kutti et al., 2007a).

Heavy metals are known to have an affinity for finer sediment fractions (e.g. Barbanti and Bothner, 1993; Brook and Moore, 1988; Sternal et al., 2017; Zonta et al., 1994), but are not corrected for differences in grain size distributions. The heavy metal concentrations were higher in the main basin of Øksfjorden compared to the sub-basin, which for nickel resulted in a moderate quality status in the main basin (Klootwijk et al., 2020; appx. I). Sediments in the main basin of Øksfjorden had an on average 26 % higher percentage of fine grains (< 63 µm) compared to the sub-basin, not including the rapid deposition layer (Klootwijk et al., 2020, appx. I). The study in Øksfjorden thus suggests a 26 % difference in the quantity of grains smaller than 63 µm could potentially lead to a large enough difference in heavy metal concentrations to have an effect on the quality status.

5.2 Using foraminiferal indices in northern Norway

In both Kaldfjorden and Øksfjorden, the environmental conditions have not greatly deviated from reference conditions as indicated by the Good or High EcoQS of the fH'_{log2}, fES_{100}, and fNQI from rB stained foraminiferal assemblages of the > 63 µm fraction (Klootwijk et al., 2020; appx. I; Klootwijk and Alve, submitted; appx. III). That there were no major deviations from references conditions was also indicated by preliminary results from a paleoenvironmental study in Kaldfjorden (Vågen, 2018) and down-core sediment geochemistry and fossil foraminiferal records of Øksfjorden (Klootwijk et al., 2020; appx. I). Overall, Kaldfjorden appeared relatively un-impacted by anthropogenic activities, and no clear indication of an impact of former or present fish farming activities was observed in the basins of Øksfjorden.

The fAMBI of the north-east Atlantic region was developed using predominantly data sets from below the arctic circle (Alve et al., 2016), but the high percentages of foraminifera assigned to EGs in Klootwijk et al. (2020; appx. I) and Klootwijk and Alve (submitted; appx. III) showed that fAMBI can also be applied in northern Norway. This is in contrast with the mAMBI that has been reported to not optimally reflect environmental pressure factions in Norway, which is believed to be due to using both northern and southern European data set to assign species to the EGs (Rygg and Norling, 2013). Comparing fAMBI and mAMBI is therefore not straightforward, and the mAMBI scores were lower compared to the fAMBI scores whilst the other indices gave similar EcoQS for foraminifera and macrofauna (Klootwijk et al., 2020; appx. I). The Moderate (yellow) status of the fAMBI (Klootwijk and Alve, submitted; appx.

III) and a substantially lower mAMBI (Klootwijk et al., 2020; appx. I) in the sub-basin of Øksfjorden may indeed indicate a discrepancy between the two parameters.

Sediment core records of the species distributions amongst the EGs suggest that EGs have the potential to reveal even subtle changes in the environmental conditions (Klootwijk et al., 2020; appx. I). The Klootwijk and Alve (in prep; appx. III) study, however, suggests that this signal could be relatively sensitive to the analysed size fraction. In Kaldfjorden and Øksfjorden, the > 63 µm fraction contained more foraminifera indicating an increase in organic matter input (EG III and V) compared to the > 125 µm fraction, which is in line with findings from previous studies (e.g. Alve, 2003; Lo Giudice Cappelli and Austin, 2019). The fossil foraminiferal assemblages of Øksfjorden were not picked in separate splits, but it is possible that the subtle shift in species distributions amongst EGs (Klootwijk et al., 2020; appx. I) would not be observed if only the > 125 µm fraction was analysed.

According to Aubry and Elliott (2006) environmental indicators, including indices, should serve three basic functions: 1) simplify, 2) quantify and 3) communicate complex information. Previous research has shown the potential of compiling sensitive and stress-tolerant foraminiferal species into separate groups to evaluate the quality of benthic ecosystems (Barras et al., 2014). The EGs as defined in the AMBI would provide an easy to interpret and standardized approach of using groups of species to communicate the health of a water body. There is, however, a certain number of stress-tolerant species naturally occur in benthic environments without any obvious anthropogenic pressure factors (Barras et al., 2014). Nevertheless, using EGs to monitor anthropogenic stress factors can be widely applied in Europe sience the AMBI has been established for the north-east Atlantic and Arctic region (Alve et al., 2016), the Mediterranean (Jorissen et al., 2018), and European intertidal areas and transitional waters (Bouchet et al., 2021).

The diversity, sensitivity and multi-metric indices are, however, limited in that they rely on the accurate identification and separation of foraminiferal species. Using foraminiferal absolute abundances and densities could be a solution as it does not require correctly identifying species. Foraminiferal densities and benthic foraminiferal accumulation rates have been previously used for biomonitoring purposes (e.g. Alve, 1995; Duffield et al., 2017; Mojtahid et al., 2006). In the sub-basin of Øksfjorden, an abrupt increase in foraminiferal absolute abundances in the sediment core records could represent a response to increased organic matter loading from fish farming (Klootwijk et al., 2020; appx. I). Kaldfjorden, however, appeared practically unpolluted (Vågen, 2018), suggesting that the low densities are natural indicating that low densities are not necessarily a sign of anthropogenic pressure factors. The current study,

however, indicates that the use of foraminiferal densities for biomonitoring in naturally transitional zones like fjords should probably be limited to long-term sediment core records (see Klootwijk et al. (2020)).

5.3 Size fractions, the EcoQS and interpreting environmental conditions

Previous studies found that a number of species present in smaller size fractions were absent in larger size fractions (e.g. Lo Giudice Cappelli and Austin, 2019; Weinkauf and Milker, 2018), which is in line with results from Kaldfjorden and Øksfjorden (Klootwijk and Alve, submitted; appx. III). The fH'_{log2}, $f ES_{100}$ and fNQI from the > 63 µm and > 125 µm fraction, however, resulted in the same or similar EcoQS (Klootwijk and Alve, submitted; appx. III). The same applied to the fAMBI, except in the sub-basin of Øksfjorden which had moderate EcoQS. In the sub-basin of Øksfjorden, especially, more foraminifera with a tolerant or opportunistic response to organic matter enrichment occurred in the > 63 µm fraction than in the > 125 µm fraction which seems to be reflected in the lower NQI of this fraction compared to the > 125 µm fraction. If the results from the Klootwijk and Alve (submitted; appx. III) study are applicable to other fjords in northern Norway, the latter suggests that the NQI of the > 63 µm fraction should reflect potential anthropogenic pressure factors better than the > 125 µm fraction in this region.

In both Kaldfjorden and Øksfjorden, the *Stainforthia* group and *E. vitrea* were mostly absent in the > 125 µm fraction (Klootwijk and Alve, submitted; appx. III). *E. vitrea* has been positively associated with phytodetritus (e.g. Duffield et al., 2015) and has been shown useful for interpreting changes in primary productivity in sediment cores (Klootwijk et al., 2020; appx. I). *S. fusiformis*, a prominent member of the *Stainforthia* group, occurred in the living assemblages of the 100 – 1000 µm fraction of Malangen with relative abundances predominantly < 2 % but with 9 % at one location (Husum and Hald, 2004; Katrine Husum pers. com.). *S. fusiformis* has a strong seasonal acme (Gustafsson and Nordberg, 2001) and the Klootwijk et al. (2020; appx. I) study indicated that high relative abundances of the *Stainforthia* group in the living assemblages of the sub-basin in Øksfjorden could be a bloom event. Sampling during blooming events should be avoided according to the Schönfeld et al. (2012) protocol. The Klootwijk and Alve, submitted; appx. III) study suggests that analysing the > 125 µm may avoid potential problems with the strong seasonal acme of the *Stainforthia* group. Analysing this fraction would, however, mostly exclude *E. vitrea* from the assemblages which would affect interpreting paleoenvironmental conditions in sediment cores.

Overall, analysing the > 125 µm appeared mostly sufficient for determining the EcoQS in relatively unpolluted fjords in northern Norway, but potential anthropogenic pressure or long-term environmental changes would be better reflected by the assemblages from the > 63 µm fraction.

5.4 In situ reference conditions and low sedimentation rate settings

Sedimentation rates in Øksfjorden were relatively low (0.5 – 1.1 mm yr^{-1}; Klootwijk et al. 2020; appx. I) compared to 1.4 – 5.1 mm yr^{-1} in Lysefjorden (Duffield et al., 2017) or 2 – 10 mm yr^{-1} in the Inner Oslofjord (Dolven et al., 2013). Besides affecting the preservation of organic matter, the relatively low sedimentation rates in Øksfjorden also led to a relatively high degree of time-averaging of the fossil assemblages. Time-averaging is the accumulation of foraminiferal tests from a succession of previous living assemblages over multiple years into one fossil assemblage (Murray, 2000). In Øksfjorden each 1 cm thick sediment sample represented 10 to 15 years (Klootwijk et al., 2020; appx. I). Fish farming waste fluxes strongly vary depending on the production cycle, usually 2-years, and the fallowing periods (Kutti et al., 2007a; Zhulay et al., 2015). As time-averaging can dampen such short-term variability (Duffield et al., 2017; Martin, 1999; Schafer, 2000), any potential response of the fossil foraminifera to fish farming in Øksfjorden may have been lost due to time-averaging.

In Øksfjorden, the production of fish officially started in 1996, after which the production rapidly intensified. The relatively low sedimentation rates mean that a potential impact of the intensification should only be recorded in the upper 2 to 3 cm of the cores (Klootwijk et al., 2020; appx. I), which makes it difficult to establish potential trends in the data records. Furthermore, the subtle changes in the fossil foraminiferal records occurred in the upper 5 cm of the sediment cores (Klootwijk et al., 2020; appx. I), which, according to the radiometric dating, includes pre-fish framing conditions. It is, therefore, difficult to exclude other causes, e.g. changes in the water column or increased riverine input as a result of global climate change, for the observed subtle changes.

Relatively low sedimentation rates may pose another challenge when analysing fossil foraminiferal records to obtain in situ reference conditions. Though the largest proportion of living foraminifera can be found in the upper 0.5 cm of the sediment (e.g. Alve and Bernhard, 1995), burrowing infaunal species can be found > 4 cm deep in the sediment (e.g. Corliss, 1991). The relatively low sedimentation rates in Øksfjorden (Klootwijk et al., 2020; appx. I) mean that burrowing species can potentially travel 10 to 15 years back in time with each per

centimetre. Additionally, potential sediment reworking by macrofauna (bioturbation) would have a larger impact on sediment cores in areas with low sedimentation rates compared to areas with high sedimentation rates. Both foraminifera burrowing into the sediment and macrofauna reworking the sediment could complicate the interpretation of sediment core records in areas with low sedimentation rates.

It is impossible to quantify or estimate to what extend foraminiferal borrowing and bioturbation by macrofaunal affected the sediment cores in Øksfjorden, but a potential influence of these factors cannot be ruled out. Fjords in northern Norway often lack a glacier in their catchment area (Faust and Knies, 2019) or a major river draining into the fjord (Wassmann et al., 1996) which affects the sediment supply. Additionally, the region is comprised of rocks that have a high resistance to chemical weathering (Krauskopf, 1954; Rea et al., 1996). This suggests that sedimentation rates could be relatively low in other fjords, besides Øksfjorden, in northern Norway as well. Northern Norway is an up and coming fish farming region (Fiskeridirektoratet, 2021), and relatively low sedimentation rates may have implications for assessing the impact of fish farming using in situ reference conditions derived from sediment cores in an important fish farming region.

5.5 Benthic foraminiferal C-uptake and environmental parameters

The carbon-cycling study in Kaldfjorden showed that foraminiferal C-uptake rates can strongly vary within fjords and that the foraminiferal biomass plays an important role (Klootwijk et al., 2021; appx. II). Strong variations in the C-uptake rates in different environmental settings were observed by former studies (e.g. Enge et al., 2016; Nomaki et al., 2005; Woulds et al., 2016), and the influence of the biomass was also previously observed (Moodley et al., 2005, 2000; Woulds et al., 2016, 2009). Normalising the foraminiferal C-uptake to the foraminiferal densities indicated that the foraminifera at the Inner location assimilated significantly more algal carbon per individual than at the other two locations (Klootwijk et al., 2021; appx. II). This suggests that the assemblage composition also played a role in the C-uptake.

The cytoplasm of *B. marginata*, *N. turgida*, and *N. iridea* frequently had a bright green-to-green-brownish colour in the Klootwijk et al. (2021; appx. II) study. This suggests that it is likely that these species actively ingested the fresh algal detritus supplied in the C-uptake experiment. In Kaldfjorden, both the experimental and rB stained foraminiferal assemblages at the Inner location were characterized by higher relative abundances of *B. marginata* and *N. turgida* than the two locations further outwards (Klootwijk et al., 2021; appx. II). Both *B.*

marginata and *N. turgida* are found in fjords along the entire Norwegian coastline (Murray and Alve, 2016), and previous studies found higher relative abundances of *B. marginata* in the inner regions of fjords compared to further outwards (Duffield et al., 2017; Husum and Hald, 2004). Should the foraminiferal distribution in Kaldfjorden be representative for other fjords, then these inner fjord regions could be sites of relatively high foraminiferal C-cycling activity.

The distinct differences in benthic foraminiferal assemblage structure amongst the locations in Kaldfjorden were not accompanied by strong differences in the sediment organic geochemistry (Klootwijk et al., 2021; appx. II), unlike in previous studies (e.g. Duffield et al., 2017; Mojtahid et al., 2006). The environmental parameters in Klootwijk et al. (2021; this thesis) were however measured only once in September and are thus a snapshot in time that may not be typical of the environmental conditions. Minor differences in the sediment organic geochemistry indicated a slightly higher primary productivity at the Inner location (Klootwijk et al., 2021; appx. II), which could potentially be related to a higher riverine input in the inner region compared to the outer region (Lalande et al., 2020).

In Kaldfjorden the number of small rivers draining into the fjord decreases towards the outer fjord (Fig. 2). Riverine input can influence important biochemical processes, e.g. primary productivity (Frigstad et al., 2020; McKee et al., 2004), and the macrofaunal community has been reported to feed on terrestrial organic matter from riverine input (Kokarev et al., 2021; McGovern et al., 2020; McMahon et al., 2021). Additionally, one study found the highest macrofaunal community biomass closest to the river outlet in their inner to outer fjord transect (McGovern et al., 2020). It is plausible that riverine input has some influence on the Inner location of Kaldfjorden that has yet to be further defined, and the Klootwijk et al. (2021; appx. II) study highlights a complex trophic system.

Fjords in northern Norway generally lack a major river coming draining into the fjord, which affects the sediment input (Wassmann et al., 1996). Additionally, they are generally considered to be more open to exchange with Norwegian Coastal water and Atlantic water compared to the more southern boreal fjords (Holte et al., 2005; Wassmann et al., 1996). This combination could potentially affect the preservation of seasonal organic matter fluxes, especially more labile marine organic matter fluxes, in the sediment as there is enough time and O_2 to degrade organic matter deposited on the sediment. Additionally, the relatively high foraminiferal C-cycling rate at the Inner location of Kaldfjorden compared to the other two locations (Klootwijk et al., 2021; appx. II) indicate that especially at this location deposited organic matter may be rapidly processed. It is possible that a combination of these three factors played a role in why no major

differences in the sediment organic geochemistry were observed in Kaldfjorden, but other still to be identified factors may also play a role.

5.6 Relations between foraminiferal C-uptake, jellyfish detritus and sediment O_2 dynamics

That the foraminiferal C-uptake did not significantly change when jellyfish detritus was placed on the top of the sediment could be due to some challenges associated with the experimental set-up. Foraminifera are known to be sensitive to changes in environmental conditions (e.g. Sen Gupta, 1999), and the Control treatment involved manipulating the in situ environmental conditions by adding phytodetrital carbon. It is possible that the added phytodetritus affected foraminifera at the Middle and Outer location to such an extent that the additional jellyfish detritus on top of the sediment had no further effect (Klootwijk et al., 2021; appx. II). Alternatively, the foraminifera at these two locations may not have fed on the ^{13}C labelled algae due to feeding preferences. The opaque light yellow-brownish coloured cytoplasm of *P. Osloensis* and *Bolivina pseudopunctata,* characteristic species for the Middle and Outer location, suggests that these two species, but potentially also other species, probably did not feed on the provided fresh phytodetritus (Klootwijk et al. (2021; appx. II). This may partially explain the low C-uptake rates at the outer two locations, and it complicates establishing a response to jellyfish detritus using ^{13}C labelled micro-algal detritus.

The findings from the Klootwijk et al. (2021; appx. II) study supported previous suggestions (based on indirect evidence) that the presence of jellyfish on top of the sediment can affect pore-water O_2 conditions (Chelsky et al., 2016; Sweetman et al., 2016). Previously, *B. marginata* has been shown to reduce its physiological activity when O_2 concentrations declined (Bernhard and Alve, 1996). The mean C-uptake rates at the Inner location in Kaldfjorden, albeit not significant, were somewhat lower when jellyfish was placed on the sediment (Klootwijk et al., 2021; appx. II). It is possible that at the Inner location the lower OCI and OPD when jellyfish detritus was placed on top of the sediment negatively affected *B. marginata* and potentially also other species (Klootwijk et al., 2021; appx. II). There appeared to be no obvious relationship between the OCI, OPD and foraminiferal uptake rates at the outer two locations in Kaldfjorden (Klootwijk et al., 2021; appx. II). Therefore, the effect of changes in the O_2 dynamics and thus jellyfish detritus on foraminiferal C-uptake rates seems little, and the assemblage composition, e.g. the presence of *B. marginata*, could play a role if any effect can be observed at all.

The O_2 uptake at the sediment-water interface (DOU) in Kaldfjorden could indicate that the benthic communities reached their carbon processing saturation or that the presence of jellyfish detritus on the sediment had a stronger effect than the additional carbon from the jellyfish (Klootwijk et al., 2021; appx. II). In the experiment jellyfish detritus never covered the entire sediment surface, and during the incubation the water column was mixed by stirrers to prevent stratification (Klootwijk et al., 2021; appx. II). The jellyfish detritus on top of the sediment may have obstructed the O_2 diffusion into the sediment creating a smothering-like effect. This could be an effect of the cylindrical and enclosed experimental chamber, but a previous study showed that bottom water currents can compile jellyfish carcasses on the sediment (Billett et al., 2006). Jellyfish detritus could thus have another effect on benthic ecosystems on top of the added carbon, and its effect on the benthic ecosystem may therefore differ from, e.g., phytodetritus.

5.7 Inner regions of northern Norwegian fjords: a perspective from Kaldfjorden and Øksfjorden

The results from the experimental study by Klootwijk et al. (2021; appx. II) suggest that the areas in coastal zones where the highest amounts of organic carbon are being processed may also be the most sensitive to changes in the sediment O_2 dynamics. This would make these areas vulnerable to changes in riverine input but also anthropogenic carbon enrichment. In the sub-basin Øksfjorden, an abrupt change in foraminiferal absolute abundances assemblages in the sediment core record suggests that the environmental conditions may have started to deviate from reference conditions (Klootwijk et al., 2020; appx. I). Such a change was not observed in the main basin of Øksfjorden where the foraminiferal absolute abundances remained stable over time (Klootwijk et al., 2020; appx. I). In Øksfjorden, the sub-basin is closer to the head of the fjord than the main basin, which could indicate that the inner region of Øksfjorden is more sensitive to changes in environmental conditions compared to further outwards.

In both Kaldfjorden and Øksfjorden, the fish farms in the inner regions have been permanently closed. In Kalfjorden, fish farming locations Sjurelv, Henrikvika, and Kræmarvika have been permanently closed since 2001, 2010, and at least 2018, respectively. From these locations, Sjurelv is closest to the head of the fjord, and Kræmarvika is furthest outwards though still in the inner basin of Kaldfjorden (Fig. 2). In Øksfjorden, the fish farming location Lille Skøgness has been permanently closed since 2013 due to deteriorating environmental conditions (Velvin and Emaus, 2015; Fig. 3), and fish farms Storvik and Auskarnes were being fallowed in 2017. The permanent closure of fish farms in the inner regions of both fjords indicates that also

macrofaunal communities in these regions may be relatively sensitive to changes in the environmental conditions compared to further outwards.

5.8 Potential challenges in foraminiferal biomonitoring in northern Norway

Global climate change will likely lead to an increase in the annual mean precipitation in the high-latitudes of the Northern Hemisphere (IPCC AR5 Synthesis Report, 2014; p. 60), which would increase the freshwater run-off into fjords. Additionally, the type of vegetation in these high-latitude regions is likely to rapidly change where the physical biomass is also expected to increase (Box et al., 2019). This could change the quantity and quality of terrestrial organic matter input in northern Norwegian fjords, as already observed in some boreal Norwegian fjords (Aksnes et al., 2009; Frigstad et al., 2020). The Klootwijk et al. (2021; appx. II) study suggests that the Inner location in Kaldfjorden may be sensitive to changes in riverine input, which could make this location vulnerable to global climate change. The study also indicated that the foraminiferal distribution in Kaldfjorden may be representative of other fjords as well. It is, therefore, important to gain a better understanding of the environmental factors that drove the differences in benthic foraminiferal structure in Kaldfjorden.

Previous studies on the link between salmon farms, ambient nutrient levels and phytoplankton density are equivocal (Brooks and Mahnken, 2003b; Jansen et al., 2018; Quiñones et al., 2019), but nutrient inputs from fish farms could be one factor leading to increased productivity. Alternatively, changes in the water column as a result of global climate change can affect primary productivity (e.g. Sommer and Lengfellner, 2008; Winder and Sommer, 2012). A large number of observations over the last decades in all ocean basins showed changes in abundances and distributions of phytoplankton, especially in the polar regions (IPCC AR5 Synthesis Report, 2014; p. 51). Additionally, riverine input could also play a yet to be defined role in phytoplankton blooms (Frigstad et al., 2020; McKee et al., 2004). A combination of the above-mentioned factors can lead or may have already led to changes in benthic environments in northern Norway, which might make it difficult to separate these factors in sediment core records.

Some opportunistic species, e.g. *S. fusiformis*, are known for their strong seasonal acme (e.g. Gustafsson and Nordberg, 2001), which can influence the interpretation of both the present and paleo-environmental conditions (Klootwijk et al., 2020 [appx. I]; Klootwijk and Alve, submitted [appx. III]). In northern Norway, the main phytoplankton bloom occurs in April-May, but elevated fluxes of particulate organic carbon have been observed during autumn (Keck

and Wassmann, 1996; Lalande et al., 2020; Noji et al., 1993). In Malangen, a fjord just south of Øksfjorden, a seasonal study showed that the highest absolute foraminiferal abundances in northern Norway occurred during autumn (Gaute Rørvik Salomonsen pers. com.). Sampling during a blooming event may not give a representative impression of the prevailing environmental conditions of a water body. The Schönfeld et al. (2012) protocol suggests that sampling in autumn offers the best perennial consistency at latitudes between the tropics and polar regions, but it is still to be determined if this is the best time interval to sample in northern Norway.

6. Concluding remarks

The Klootwijk et al. (2020; appx. I) study highlighted the importance of establishing in situ reference conditions using fossil foraminiferal assemblages and geochemical parameters from sediment cores. The study in Øksfjorden supported previous studies based on only spatial gradients that found no major impact of fish farming outside a 100 to 500 m radius from the fish farms. Additionally, sediment core records from Øksfjorden showed a natural difference in the TOC_{63} and nickel concentrations between the basins, where the Moderate (yellow) classification of both parameters in the main basin reflected the in situ reference conditions. The Vågen (2018) paleoenvironmental study using sediment cores provided valuable information for the Klootwijk et al. (2021; appx. II) study by indicating that the observed variability in the foraminiferal assemblage structure in the second was most likely due to yet to be defined natural causes. The current thesis has thus shown that fossil foraminiferal assemblages can, despite potential challenges, be a valuable tool for both biomonitoring and increasing the current knowledge in benthic foraminiferal ecology.

The analysed size fraction may influence the interpretation of environmental conditions based on both fossil and rB stained foraminiferal assemblages. The Klootwijk and Alve (submitted; appx. III) study suggests that the subtle shift in species distributions amongst EGs observed in Klootwijk et al. (2020; appx. I) might not have been detected if only the > 125 µm fraction was analysed. Furthermore, the mostly absent *E. vitrea* in the > 125 µm fraction could make it impossible to identify potential changes in primary productivity if only this size fraction is analysed (Klootwijk and Alve, submitted; appx. III). In the sub-basin of Øksfjorden, more foraminifera with a tolerant or opportunistic response to organic matter enrichment occurred in the > 63 µm fraction than in the > 125 µm fraction, which was reflected in the lower NQI of this fraction compared to the > 125 µm fraction (Klootwijk and Alve, submitted; appx. III).

This suggests that potential anthropogenic pressure in northern Norway would be better reflected by the foraminiferal assemblages from the > 63 µm fraction.

The Klootwijk and Alve (submitted; appx. III) study indicated that analysing the > 125 µm should be mostly sufficient for determining the EcoQS in relatively unpolluted fjords in northern Norway. The same study, however, also indicated that the > 125 µm fraction gives a less complete picture of the environmental conditions compared to the > 63 µm fraction, which was also found by previous studies (e.g. Lo Giudice Cappelli and Austin, 2019). The WFD and Norwegian Guidelines are so-called "living" documents that are evaluated regularly and updated if necessary. This raises the question if these "living" documents should be further developed using the > 63 µm fraction or the > 125 µm fraction. The fAMBI was developed using both datasets from the > 63 µm fraction and the 125 µm fraction (Alve et al., 2016), and the class limits fH'_{log2}, fES_{100}, and fNQI have been adapted to foraminifera using the > 63 µm fraction (Alve et al., 2019). The Klootwijk and Alve (submitted; appx. III) study suggests that using the > 63 µm fraction to develop foraminiferal indices may not necessarily affect their applicability when analysing only the > 125 µm fraction.

The Klootwijk et al. (2021; appx. II) study showed that foraminiferal C-cycling strongly varied within Kaldfjorden. This was likely caused by a combination of the higher foraminiferal biomass, and high relative abundances of *Bulimina marginata* and *Nonionella turgida* at the Inner location compared to the Middle and Outer location. Strong differences in foraminiferal assemblage structure amongst the locations were not explained by strong differences in the investigated environmental parameters, but slight differences in primary productivity, potentially influenced by riverine input, or riverine input itself could have played yet to be defined roles (Klootwijk et al., 2021; appx. II). The sediment O_2 dynamics suggested that jellyfish detritus may the O_2 diffusion into the sediment (Klootwijk et al., 2021; appx. II). A potential effect of these short-term changes in the sediment O_2 dynamics on foraminiferal C-uptake was only observed at the inner-fjord location. This indicates that the effect of jellyfish detritus on foraminiferal C-uptake rates was little and that the coastal habitats where the highest amounts of organic carbon are being processed may also be the most sensitive to changes in the sediment O_2 dynamics. The Klootwijk et al. (2021; appx. II) study also suggests that foraminifera could play a role in selecting suitable locations for fish farms if we can further identify which assemblages are naturally more sensitive to environmental change.

7. Acknowledgments

I, the PhD candidate, would like to thank Peter G. Appleby, Emeritus Professor at University of Liverpool, United Kingdom for his assistance in writing the paragraph regarding the dating of the sediment cores from Øksfjorden. I would also like to thank the following people for providing personal comments in the papers and manuscript which have been used in their original form this thesis: Angelika Renner from the Institute of Marine Research; Gaute Rørvik Salomonsen from reNature AS, Norway; Katrine Husum from the Norwegian Polar institute in Tromsø, Norway; Per-Arne Emaus, Senior adviser at Akvaplan-NIVA in Alta, Norway; Odd Leknes, Biological controller at Grieg Seafood Finnmark in Finnmark, Norway. For all the people that helped during this PhD project please see the acknowledgements in the two papers (Appendix I and II) and the manuscript (Appendix III).

8. Taxonomic reference list

Brizalina skagerrakensis (Qvale and Nigam) = *Bolivina skagerrakensis* Qvale and Nigam, 1985

Bulimina marginata d'Orbigny, 1826

Bolivina pseudopunctata (Höglund) = Bolivinellina pseudopunctata Höglund, 1947

Epistominella vitrea Parker, 1953

Nonionella iridea Heron-Allen and Earland, 1932

Nonionella turgida (Williamson) = *Rotalina turgida* Williamson, 1858

Pullenia osloensis Feyling-Hanssen, 1994

Stainforthia feylingi Knudsen and Seidenkrantz, 1994

Stainforthia fusiformis (Williamson) = *Bulimina pupoides* d'Orbigny var *fusiformis* Williamson, 1858

Textularia earlandi Parker, 1952

9. References

Aksnes, D.L., 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. https://doi.org/10.3354/meps08120

Alve, E., 2003. A common opportunistic foraminiferal species as an indicator of rapidly changing conditions in a range of environments. Estuar. Coast. Shelf Sci. 57, 501–514. https://doi.org/10.1016/S0272-7714(02)00383-9

Alve, E., 1995. Benthic foraminiferal responses to estuarine pollution: a review. J. Foraminifer. Res. https://doi.org/10.2113/gsjfr.25.3.190

Alve, E., 1991. Benthic foraminifera in sediment cores reflecting heavy metal pollution in Sorfjord , western Norway. J. Foraminifer. Res. 21, 1–19. https://doi.org/10.2113/gsjfr.21.1.1

Alve, E., Bernhard, J.M., 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. Mar. Ecol. Prog. Ser. 116, 137–152. https://doi.org/10.3354/meps116137

Alve, E., Hess, S., Bouchet, V.M.P., Dolven, J.K., Rygg, B., 2019. Intercalibration of benthic foraminiferal and macrofaunal biotic indices: An example from the Norwegian Skagerrak coast (NE North Sea). Ecol. Indic. 96, 107–115. https://doi.org/10.1016/j.ecolind.2018.08.037

Alve, E., Korsun, S., Schönfeld, J., Dijkstra, N., Golikova, E., Hess, S., Husum, K., Panieri, G., 2016. Foram-AMBI: A sensitivity index based on benthic foraminiferal faunas from North-East Atlantic and Arctic fjords, continental shelves and slopes. Mar. Micropaleontol. 122, 1–12. https://doi.org/10.1016/j.marmicro.2015.11.001

Alve, E., Nagy, J., 1990. Main features of foraminiferal distribution reflecting estuarine hydrography in Oslo Fjord. Mar. Micropaleontol. 16, 181–206. https://doi.org/10.1016/0377-8398(90)90003-5

Appleby, P.G., 2001. Chronostratigraphic techniques in recent sediments. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Vol. 1: Basin Analysis, Coring and Chronological Techniques, vol. 1. https://doi.org/10.1007/0-306-47669-X_9

Appleby, P.G., Nolan, P.J., Gifford, D.W., Godfrey, M.J., Oldfield, F., Anderson, N.J., Battarbee, R.W., 1986. 210Pb dating by low background gamma counting. Hydrobiologia 143, 21–27. https://doi.org/10.1007/BF00026640

Appleby, P.G., Oldfield, F., 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. Catena 5, 1–8. https://doi.org/10.1016/S0341-8162(78)80002-2

Aubry, A., Elliott, M., 2006. The use of environmental integrative indicators to assess seabed disturbance in estuaries and coasts: Application to the Humber Estuary, UK. Mar. Pollut. Bull. 53, 175–185. https://doi.org/10.1016/j.marpolbul.2005.09.021

Barbanti, A., Bothner, M.H., 1993. A procedure for partitioning bulk sediments into distinct grain-size fractions for geochemical analysis. Environ. Geol. 21, 3–13. https://doi.org/10.1007/BF00775044

Barras, C., Jorissen, F.J., Labrune, C., Andral, B., Boissery, P., 2014. Live benthic foraminiferal faunas from the French Mediterranean Coast: Towards a new biotic index of environmental quality. Ecol. Indic. 36, 719–743. https://doi.org/10.1016/j.ecolind.2013.09.028

Bernhard, J.M., Alve, E., 1996. Survival, ATP pool, and ultrastructural characterization of benthic foraminiferafrom Drammensfjord (Norway): Response to anoxia. Mar. Micropaleontol. 28, 5–17. https://doi.org/10.1016/0377-8398(95)00036-4

Billett, D.S.M., Bett, B.J., Jacobs, C.L., Rouse, I.P., Wigham, B.D., 2006. in the deep Arabian Sea Mass deposition of jellyfish. Limnol. Oceanogr. 51, 2077–2083.

Bjørn, P.A., Uglem, I., Kerwath, S., Sæther, B.S., Nilsen, R., 2009. Spatiotemporal distribution of Atlantic cod (Gadus morhua L.) with intact and blocked olfactory sense during the spawning season in a Norwegian fjord with intensive salmon farming. Aquaculture 286, 36–44. https://doi.org/10.1016/j.aquaculture.2008.08.038

Borja, Á., Dauer, D.M., Grémare, A., 2012. The importance of setting targets and reference conditions in assessing marine ecosystem quality. Ecol. Indic. 12, 1–7. https://doi.org/10.1016/j.ecolind.2011.06.018

Borja, A., Franco, J., Muxika, I., 2003. Classification tools for marine ecological quality assessment: the usefulness of macrobenthic communities in an area affected by a submarine outfall. ICES C. 2003/Session J-02, Tallinn, Est. Sept. 24-28 1–10.

Borja, A., Franco, J., Pérez, V., 2000. A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40, 1100–1114. https://doi.org/10.1016/S0025-326X(00)00061-8

Bouchet, V.M.P., Alve, E., Rygg, B., Telford, R.J., 2012. Benthic foraminifera provide a promising tool for ecological quality assessment of marine waters. Ecol. Indic. 23, 66–75. https://doi.org/10.1016/j.ecolind.2012.03.011

Bouchet, V.M.P., Frontalini, F., Francescangeli, F., Sauriau, P.G., Geslin, E., Martins, M.V.A., Almogi-Labin, A., Avnaim-Katav, S., Di Bella, L., Cearreta, A., Coccioni, R., Costelloe, A., Dimiza, M.D., Ferraro, L., Haynert, K., Martínez-Colón, M., Melis, R., Schweizer, M., Triantaphyllou, M. V., Tsujimoto, A., Wilson, B., Armynot du Châtelet, E., 2021. Indicative value of benthic foraminifera for biomonitoring: Assignment to ecological groups of sensitivity to total organic carbon of species from European intertidal areas and transitional waters. Mar. Pollut. Bull. 164. https://doi.org/10.1016/j.marpolbul.2021.112071

Bouchet, V.M.P., Telford, R.J., Rygg, B., Oug, E., Alve, E., 2018. Can benthic foraminifera serve as proxies for changes in benthic macrofaunal community structure? Implications for the definition of reference conditions. Mar. Environ. Res. 137, 24–36. https://doi.org/10.1016/j.marenvres.2018.02.023

Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.J.W., Brown, R., Bhatt, U.S., Euskirchen, E.S., Romanovsky, V.E., Walsh, J.E., Overland, J.E., Wang, M., Corell, R.W., Meier, W.N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., Olsen, M.S., 2019. Key indicators of Arctic climate change: 1971-2017. Environ. Res. Lett. 14. https://doi.org/10.1088/1748-9326/aafc1b

Brook, E.J., Moore, J.N., 1988. Particle-size and chemical control of As, Cd, Cu, Fe, Mn, Ni, Pb, and Zn in bed sediment from the Clark Fork River, Montana (U.S.A.). Sci. Total Environ. 76, 247–266. https://doi.org/10.1016/0048-9697(88)90111-8

Brooks, K.M., Mahnken, C.V.W., 2003a. Interactions of Atlantic salmon in the Pacific Northwest environment. III. Accumulation of zinc and copper. Fish. Res. 62, 295–305. https://doi.org/10.1016/S0165-7836(03)00065-1

Brooks, K.M., Mahnken, C.V.W., 2003b. Interactions of Atlantic salmon in the Pacific northwest environment. II. Organic wastes, Fisheries Research. https://doi.org/10.1016/S0165-7836(03)00064-X

Burridge, L., Weis, J.S., Cabello, F., Pizarro, J., Bostick, K., 2010. Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. Aquaculture 306, 7–23. https://doi.org/10.1016/j.aquaculture.2010.05.020

Carroll, M.L., Cochrane, S., Fieler, R., Velvin, R., White, P., 2003. Organic enrichment of sediments from salmon farming in Norway: Environmental factors, management practices, and monitoring techniques. Aquaculture 226, 165–180. https://doi.org/10.1016/S0044-8486(03)00475-7

Chelsky, A., Pitt, K.A., Ferguson, A.J.P., Bennett, W.W., Teasdale, P.R., Welsh, D.T., 2016.

Decomposition of jellyfish carrion in situ: Short-term impacts on infauna, benthic nutrient fluxes and sediment redox conditions. Sci. Total Environ. 566–567, 929–937. https://doi.org/10.1016/j.scitotenv.2016.05.011

Chelsky, A., Pitt, K.A., Welsh, D.T., 2015. Biogeochemical implications of decomposing jellyfish blooms in a changing climate. Estuar. Coast. Shelf Sci. 154, 77–83. https://doi.org/10.1016/j.ecss.2014.12.022

Chierici, M., Jones, E., Lødemel, H.H., 2019. Variability of the marine CO2 system, dissolved inorganic nutrients and stable oxygen isotopic ratio (δ18O) in Kaldfjorden in northern Norway from 2016 to 2018. https://doi.org/10.21335/NMDC-646962623

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.E., Purcell, J.E., Malej, A., Mianzan, H., Uye, S.I., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous Zooplankton in the world's oceans. Bioscience 62, 160–169. https://doi.org/10.1525/bio.2012.62.2.9

Condon, R.H., Steinberg, D.K., Del Giorgio, P.A., Bouvier, T.C., Bronk, D.A., Graham, W.M., Ducklow, H.W., 2011. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc. Natl. Acad. Sci. U. S. A. 108, 10225–10230. https://doi.org/10.1073/pnas.1015782108

Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. Mar. Micropaleontol. 17, 195–236. https://doi.org/10.1016/0377-8398(91)90014-W

Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. Nature 314, 4–7.

Dijkstra, N., Junttila, J., Skirbekk, K., Carroll, J., Husum, K., Hald, M., 2017. Benthic foraminifera as bio-indicators of chemical and physical stressors in Hammerfest harbor (Northern Norway). Mar. Pollut. Bull. 114, 384–396. https://doi.org/10.1016/j.marpolbul.2016.09.053

Dolven, J.K., Alve, E., Rygg, B., Magnusson, J., 2013. Defining past ecological status and in situ reference conditions using benthic foraminifera: A case study from the Oslofjord, Norway. Ecol. Indic. 29, 219–233. https://doi.org/10.1016/j.ecolind.2012.12.031

Duffield, C., Alve, E., Andersen, N., Andersen, T., Hess, S., Strohmeier, T., 2017. Spatial and temporal organic carbon burial along a fjord to coast transect: A case study from Western Norway. The Holocene 095968361769058. https://doi.org/10.1177/0959683617690588

Duffield, C.J., Hess, S., Norling, K., Alve, E., 2015. The response of Nonionella iridea and other benthic foraminifera to “fresh” organic matter enrichment and physical disturbance. Mar. Micropaleontol. 120, 20–30. https://doi.org/10.1016/j.marmicro.2015.08.002

Dunlop, K.M., Jones, D.O.B., Sweetman, A.K., 2018. Scavenging processes on jellyfish carcasses across a fjord depth gradient. Limnol. Oceanogr. 63, 1146–1155. https://doi.org/10.1002/lno.10760

Elmgren, R., 1973. Methods of sampling sublittoral soft bottom meiofauna. Oikos Suppl. 15, 112–120.

Enge, A.J., Nomaki, H., Ogawa, N.O., Witte, U., Moeseneder, M.M., Lavik, G., Ohkouchi, N., Kitazato, H., Kučera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Mar. Ecol. Prog. Ser. 438, 129–142. https://doi.org/10.3354/meps09298

Enge, A.J., Witte, U., Kucera, M., Heinz, P., 2014. Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian margin (Arabian Sea). Biogeosciences 11, 2017–2026. https://doi.org/10.5194/bg-11-2017-2014

Enge, A.J., Wukovits, J., Wanek, W., Watzka, M., Witte, U.F.M., Hunter, W.R., Heinz, P., 2016. Carbon and nitrogen uptake of calcareous benthic foraminifera along a depth-related oxygen gradient in the OMZ of the Arabian Sea. Front. Microbiol. 7, 1–12. https://doi.org/10.3389/fmicb.2016.00071

Faust, J.C., Knies, J., 2019. Organic Matter Sources in North Atlantic Fjord Sediments. Geochemistry, Geophys. Geosystems 20, 2872–2885. https://doi.org/10.1029/2019GC008382

Fiskeridirektoratet, 2021. Antall merder og lokaliteter i bruk 2005-2021.

Frigstad, H., Kaste, Ø., Deininger, A., Kvalsund, K., Christensen, G., Bellerby, R.G.J., Sørensen, K., Norli, M., King, A.L., 2020. Influence of Riverine Input on Norwegian Coastal Systems. Front. Mar. Sci. 7, 1–14. https://doi.org/10.3389/fmars.2020.00332

Glud, R.N., 2008. Oxygen dynamics of marine sediments. Mar. Biol. Res. 4, 243–289. https://doi.org/10.1080/17451000801888726

Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., 1992. The role of benthic foraminifera in deep-sea food webs and carbon cycling, in: Deep-Sea Foodchains and the Global Carbon Cycle. pp. 63–91. https://doi.org/10.1007/978-94-011-2452-2

Greenacre, M., 2017. Correspondance Analysis in Practice, CRC Press, 2nd Edn. Boca Raton, FL: Chapman & Hll/CRC. https://doi.org/10.1017/CBO9781107415324.004

Grémare, A., Labrune, C., Vanden Berghe, E., Amouroux, J.M., Bachelet, G., Zettler, M.L., Vanaverbeke, J., Fleischer, D., Bigot, L., Maire, O., Deflandre, B., Craeymeersch, J., Degraer, S., Dounas, C., Duineveld, G., Heip, C., Herrmann, M., Hummel, H., Karakassis, I., Kędra, M., Kendall, M., Kingston, P., Laudien, J., Occhipinti-Ambrogi, A., Rachor, E., Sardá, R., Speybroeck, J., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Włodarska-Kowalczuk, M., Zenetos, A., 2009. Comparison of the performances of two biotic indices based on the MacroBen database. Mar. Ecol. Prog. Ser. 382, 297–311. https://doi.org/10.3354/meps08030

Gustafsson, M., Nordberg, K., 2001. Living (stained) benthic foraminiferal response to primary production and hydrography in the deepest part of the Gullmar Fjord, Swedish west coast, with comparisons to Höglund's 1927 material. J. Foraminifer. Res. 31, 2–11. https://doi.org/10.2113/0310002

Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Mar. Chem. 49, 81–115. https://doi.org/10.1016/0304-4203(95)00008-F

Heiskanen, A.S., Tallberg, P., 1999. Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. Hydrobiologia 393, 127–140. https://doi.org/10.1023/A:1003539230715

Helland-Hansen, B., Nansen, F., 1909. The Norwegian SeaThe Norwegian Sea: Its Physical Oceanography Based upon the Norwegian Researches, 1900-1904. j.Hjort Rep. Nor. Fish. Mar. Investig. vol. II, R. Dep. Trade, Navig. Ind. Kristiania, Norw. 390. https://doi.org/10.2307/1776951

Helø, G., Lejon, R., 2009. Hovedplan avløp og vannmiljø 2009-2018 sak 113/09 1–156.

Holmer, M., 2010. Environmental issues of fish farming in offshore waters: Perspectives, concerns and research needs. Aquac. Environ. Interact. 1, 57–70. https://doi.org/10.3354/aei00007

Holte, B., Oug, E., Dahle, S., 2005. Soft-bottom fauna and oxygen minima in sub-arctic north Norwegian marine sill basins. Mar. Biol. Res. 1, 85–96. https://doi.org/10.1080/17451000510019033

Hurlbert, S.H., 1971. The Nonconcept of Species Diversity : A Critique and Alternative Parameters. Ecol. Soc. Am. 52, 577–586. https://doi.org/10.2307/1934145

Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K., Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). Mar. Biol. Res. 10, 241–252. https://doi.org/10.1080/17451000.2013.810754

Husum, K., Hald, M., 2004. Modern Foraminiferal Distribution in the Subarctic Malangen Fjord and Adjoining Shelf, Northern Norway. J. Foraminifer. Res. 34, 34–48. https://doi.org/10.2113/0340034

IPCC Climate Change AR5 Synthesis Report, 2014. , IPCC. https://doi.org/10.1016/S0022-0248(00)00575-3

Jansen, H.M., Broch, O.J., Bannister, R., Cranford, P., Handå, A., Husa, V., Jiang, Z., Strohmeier, T., Strand, 2018. Spatio-temporal dynamics in the dissolved nutrient waste plume from Norwegian salmon cage aquaculture. Aquac. Environ. Interact. 10, 385–399. https://doi.org/10.3354/AEI00276

Jones, E.M., Renner, A.H.H., Chierici, M., Wiedmann, I., Lødemel, H.H., Biuw, M., 2020. Seasonal dynamics of carbonate chemistry, nutrients and CO_2 uptake in a sub-Arctic fjord. Elem Sci Anth 8, 41. https://doi.org/10.1525/elementa.438

Jorissen, F., Nardelli, M.P., Almogi-Labin, A., Barras, C., Bergamin, L., Bicchi, E., El Kateb, A., Ferraro, L., McGann, M., Morigi, C., Romano, E., Sabbatini, A., Schweizer, M., Spezzaferri, S., 2018. Developing Foram-AMBI for biomonitoring in the Mediterranean: Species assignments to ecological categories. Mar. Micropaleontol. 140, 33–45. https://doi.org/10.1016/j.marmicro.2017.12.006

Josefson, A.B., Blomqvist, M., Hansen, J.L.S., Rosenberg, R., Rygg, B., 2009. Assessment of marine benthic quality change in gradients of disturbance: Comparison of different Scandinavian multi-metric indices. Mar. Pollut. Bull. 58, 1263–1277. https://doi.org/10.1016/j.marpolbul.2009.05.008

Keck, A., Wassmann, P., 1996. Temporal and spatial patterns of sedimentation in the subarctic fjord malangen, Northern Norway. Sarsia 80, 259–276. https://doi.org/10.1080/00364827.1996.10413600

Klootwijk, A.T., Alve, E., n.d. submitted to Ecological Indicators 06-09-2021. Does the analysed size fraction of benthic foraminifera influence the Ecological Quality Status and the interpretation of environmental conditions? Indications from two northern Norwegian fjords.

Klootwijk, A.T., Alve, E., Hess, S., Renaud, P.E., Sørlie, C., Dolven, J.K., 2020. Monitoring environmental impacts of fish farms : Comparing reference conditions of sediment geochemistry and benthic foraminifera with the present. Ecol. Indic. 120, 106818. https://doi.org/10.1016/j.ecolind.2020.106818

Klootwijk, A.T., Sweetman, A.K., Hess, S., Elisabeth Alve, K., Dunlop, M., Renaud, P.E., 2021. Benthic foraminiferal carbon cycling in coastal zone sediments: the influence of

the assemblage structure and jellyfish detritus. Estuar. Coast. Shelf Sci. https://doi.org/10.1016/j.ecss.2021.107535

Kokarev, V., Tachon, M., Austad, M., McGovern, M., Reiss, H., 2021. Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales. Estuar. Coast. Shelf Sci. 252, 107271. https://doi.org/10.1016/j.ecss.2021.107271

Korsun, S., Hald, M., 2000. Seasonal dynamics of benthic foraminifera in a glacially fed fjord of svalbard, european arctic. J. Foraminifer. Res. 30, 251–271. https://doi.org/10.2113/0300251

Krauskopf, K.B., 1954. Igneous and Metamorphic Rocks of the Øksfjord Area , Vest-Finnmark ., in: Norges Geologiske Undersökelse, Arbok 188. pp. 29–50.

Kutti, T., Ervik, A., Hansen, P.K., 2007a. Effects of organic effluents from a salmon farm on a fjord system. I. Vertical export and dispersal processes. Aquaculture 262, 367–381. https://doi.org/10.1016/j.aquaculture.2006.10.010

Kutti, T., Hansen, P.K., Ervik, A., Høisæter, T., Johannessen, P., 2007b. Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. Aquaculture 262, 355–366. https://doi.org/10.1016/j.aquaculture.2006.10.008

Lalande, C., Dunlop, K., Renaud, P.E., Nadaï, G., Sweetman, A.K., 2020. Seasonal variations in downward particle fluxes in Norwegian fjords. Estuar. Coast. Shelf Sci. 241, 106811. https://doi.org/10.1016/j.ecss.2020.106811

Lebrato, M., de Jesus Mendes, P., Steinberg, D.K., Cartes, J.E., Jones, B.M., Birsa, L.M., Benavides, R., Oschlies, A., 2013. Jelly biomass sinking speed reveals a fast carbon export mechanism. Limnol. Oceanogr. 58, 1113–1122. https://doi.org/10.4319/lo.2013.58.3.1113

Lo Giudice Cappelli, E., Austin, W.E.N., 2019. Size Matters: Analyses of Benthic Foraminiferal Assemblages Across Differing Size Fractions. Front. Mar. Sci. 6, 1–8. https://doi.org/10.3389/fmars.2019.00752

Loeblich, A.R., Tappan, H., 1987. Foraminiferal genera and their classification. Von Nostrand Reinhold Co., New York. 869.

Martin, R., 1999. Taphonomy and temporal resolution of fora- miniferal assemblages. In: Sen Gupta BK (ed.) Modern Foraminifera. New York: Kluwer Academics Publishers, pp. 281–298., n.d. https://doi.org/10.1007/0-306-48104-9

McGovern, M., Poste, A.E., Oug, E., Renaud, P.E., Trannum, H.C., 2020. Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords.

Estuar. Coast. Shelf Sci. 240, 106774. https://doi.org/10.1016/j.ecss.2020.106774

McKee, B.A., Aller, R.C., Allison, M.A., Bianchi, T.S., Kineke, G.C., 2004. Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: Benthic boundary layer and seabed processes. Cont. Shelf Res. 24, 899–926. https://doi.org/10.1016/j.csr.2004.02.009

McMahon, K.W., Ambrose, W.G., Reynolds, M.J., Johnson, B.J., Whiting, A., Clough, L.M., 2021. Arctic lagoon and nearshore food webs: Relative contributions of terrestrial organic matter, phytoplankton, and phytobenthos vary with consumer foraging dynamics. Estuar. Coast. Shelf Sci. 257, 107388. https://doi.org/10.1016/j.ecss.2021.107388

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R., 2000. The fate of intertidal microphytobenthos carbon: An in situ 13C-labeling study. Limnol. Oceanogr. 45, 1224–1234. https://doi.org/10.4319/lo.2000.45.6.1224

Mills, C.E., 2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68. https://doi.org/10.1023/A:1011888006302

Mojtahid, M., Jorissen, F., Durrieu, J., Galgani, F., Howa, H., Redois, F., Camps, R., 2006. Benthic foraminifera as bio-indicators of drill cutting disposal in tropical east Atlantic outer shelf environments. Mar. Micropaleontol. 61, 58–75. https://doi.org/10.1016/j.marmicro.2006.05.004

Moodley, L., Boschker, H.T.S., Middelburg, J.J., Pel, R., Herman, P.M.J., De Deckere, E., Heip, C.H.R., 2000. Ecological significance of benthic foraminifera: ^{13}C Labelling experiments. Mar. Ecol. Prog. Ser. 202, 289–295. https://doi.org/10.3354/meps202289

Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M.J., Heip, C.H.R., 2002. Bacteria and foraminifera: Key players in a short-term deep-sea benthic response to phytodetritus. Mar. Ecol. Prog. Ser. 236, 23–29. https://doi.org/10.3354/meps236023

Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., Heip, C.H.R., 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. J. Mar. Res. 63, 457–469. https://doi.org/10.1357/0022240053693662

Murray, J.W., 2006. Ecology and applications of benthic foraminifera, Ecology and Applications of Benthic Foraminifera. https://doi.org/10.1017/CBO9780511535529

Murray, J.W., 2000. the Enigma of the Continued Use of Total Assemblages in Ecological Studies of Benthic Foraminifera. J. Foraminifer. Res. 30, 244–245.

https://doi.org/10.2113/0300244

Murray, J.W., Alve, E., 2016. Benthic foraminiferal biogeography in NW European fjords: A baseline for assessing future change. Estuar. Coast. Shelf Sci. 181, 218–230. https://doi.org/10.1016/j.ecss.2016.08.014

Niemistö, L., 1974. A gravity corer for studies of soft sediment. Merentutkimuslait. Julk./Havsforskningsinst Helsinki 238, 33–38.

Noji, T.T., Noji, C.I.M., Barthel, K.G., 1993. Pelagic-benthic coupling during the onset of winter in a northern Norwegian fjord. Carbon flow and fate of suspended particulate matter. Mar. Ecol. Prog. Ser. 93, 89–99. https://doi.org/10.3354/meps093089

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments. Limnol. Oceanogr. 50, 134–146. https://doi.org/10.4319/lo.2005.50.1.0134

Paassche, E., Erga, S.R., 1988. Phosphorus and nitrogen limitation of phytoplankton in the inner Oslofjord (Norway). https://doi.org/0036-4827

Pochon, X., Wood, S.A., Keeley, N.B., Lejzerowicz, F., Esling, P., Drew, J., Pawlowski, J., 2015. Accurate assessment of the impact of salmon farming on benthic sediment enrichment using foraminiferal metabarcoding. Mar. Pollut. Bull. 100, 370–382. https://doi.org/10.1016/j.marpolbul.2015.08.022

Purcell, J.E., Uye, S.I., Lo, W.T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. Mar. Ecol. Prog. Ser. 350, 153–174. https://doi.org/10.3354/meps07093

Quiñones, R.A., Fuentes, M., Montes, R.M., Soto, D., León-Muñoz, J., 2019. Environmental issues in Chilean salmon farming: a review. Rev. Aquac. 11, 375–402. https://doi.org/10.1111/raq.12337

R Core team, 2020. R Core Team. R A Lang. Environ. Stat. Comput. R Found. Stat. Comput. , Vienna, Austria. ISBN 3-900051-07-0, URL http//www.R-project.org/.

Rea, B.R., Whalley, W.B., Rainey, M.M., Gordon, J.E., 1996. Blockfields, old or new? Evidence and implications from some plateaus in northern Norway. Geomorphology 15, 109–121. https://doi.org/10.1016/0169-555X(95)00118-O

Reimann, C., Caritat de, P., 1998. Geochemical atlas of Finland, Part2: Geological Survey of Finland, Espoo, Finland, 218 (Koljonen, T. (ed), 1992), in: Chemical Elements in the Environment. Spriner, p. 398. https://doi.org/10.1016/0009-2541(94)90076-0

Rosenzweig, M.L., 1995. Species diversity in space and time., Cambridge University Press,

1995.

Rygg, B., 2006. Developing indices for quality-status classification of marine soft-bottom fauna in Norway.

Rygg, B., Norling, K., 2013. Norwegian Sensitivity Index (NSI) for marine macroinvertebrates, and an update of Indicator Species Index (ISI), NIVA report 6475.

Schafer, C.T., 2000. Monitoring nearshore marine environments using benthic foraminifera: Some protocols and pitfalls. Micropaleontology 46, 161–169.

Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Abramovich, S., Almogi-Labin, A., du Chatelet, E.A., Barras, C., Bergamin, L., Bicchi, E., Bouchet, V., Cearreta, A., Di Bella, L., Dijkstra, N., Disaro, S.T., Ferraro, L., Frontalini, F., Gennari, G., Golikova, E., Haynert, K., Hess, S., Husum, K., Martins, V., McGann, M., Oron, S., Romano, E., Sousa, S.M., Tsujimoto, A., 2012. The FOBIMO (FOraminiferal BIo-MOnitoring) initiative-Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. Mar. Micropaleontol. 94–95, 1–13. https://doi.org/10.1016/j.marmicro.2012.06.001

Schönfeld, J., Golikova, E., Korsun, S., Spezzaferri, S., 2013. The Helgoland Experiment – assessing the influence of methodologies on Recent benthic foraminiferal assemblage composition. J. Micropalaeontology 32, 161–182. https://doi.org/10.1144/jmpaleo2012-022

Schröder, C.J., Scott, D.B., Medioli, F.S., 1987. CAN SMALLER BENTHIC FORAMINIFERA BE IGNORED IN PALEOENVIRONMENTAL ANALYSES? J. foram 17, 101–105.

Sen Gupta, B.K., 1999. Modern foraminifera, Kluwer Academic Publishers. https://doi.org/https://doi.org/10.1007/0-306-48104-9

Shannon, C.E., Weaver, W., 1963. The Mathematical Theory of Communication. University of Illinois Press.

Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23, 518–528. https://doi.org/10.1016/j.tree.2008.05.002

Sørnes, T.A., Aksnes, D.L., Båmstedt, U., Youngbluth, M.J., 2007. Causes for mass occurrences of the jellyfish Periphylla periphylla: A hypothesis that involves optically conditioned retention. J. Plankton Res. 29, 157–167. https://doi.org/10.1093/plankt/fbm003

Sternal, B., Junttila, J., Skirbekk, K., Forwick, M., Carroll, J.L., Pedersen, K.B., 2017. The

impact of submarine copper mine tailing disposal from the 1970s on Repparfjorden, northern Norway. Mar. Pollut. Bull. 120, 136–153. https://doi.org/10.1016/j.marpolbul.2017.04.054

Sundby, S., 1984. Influence of bottom topography on the circulation at the continental shelf off northern Norway. Fisk. Skr. Ser. Havundersøkelser 17, 501–519.

Sweetman, A.K., Chapman, A., 2011. First observations of jelly-falls at the seafloor in a deep-sea fjord. Deep. Res. Part I Oceanogr. Res. Pap. 58, 1206–1211. https://doi.org/10.1016/j.dsr.2011.08.006

Sweetman, A.K., Chelsky, A., Pitt, K.A., Andrade, H., van Oevelen, D., Renaud, P.E., 2016. Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. Limnol. Oceanogr. 61, 1449–1461. https://doi.org/10.1002/lno.10310

Sweetman, A.K., Norling, K., Gunderstad, C., Haugland, B.T., Dale, T., 2014a. Benthic ecosystem functioning beneath fish farms in different hydrodynamic environments. Limnol. Oceanogr. 59, 1139–1151. https://doi.org/10.4319/lo.2014.59.4.1139

Sweetman, A.K., Smith, C.R., Dale, T., Jones, D.O.B., 2014b. Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. Proc. R. Soc. B Biol. Sci. 281, 1–8. https://doi.org/10.1098/rspb.2014.2210

Sweetman, A.K., Sommer, S., Pfannkuche, O., Witte, U., 2009. Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord. J. Foraminifer. Res. 39, 15–22. https://doi.org/10.2113/gsjfr.39.1.15

Syvitski, P.M., Burrell, D.C., Skei, J.M., 1987. Fjords. Processes and Products. Springer-Verlag 379.

Tiller, R.G., Borgersen, Å.L., Knutsen, Ø., Bailey, J., Bjelland, H.V., Mork, J., Eisenhauer, L., Liu, Y., 2017. Coming Soon to a Fjord Near You: Future Jellyfish Scenarios in a Changing Climate. Coast. Manag. 45, 1–23. https://doi.org/10.1080/08920753.2017.1237239

Vågen, H., 2018. Temporal changes of the benthic environmental conditions in a subarctic fjord with aquaculture activity A geochemical and micropaleontological study. Thesis, Master Sci. Nat.

Van Der Zwaan, G.J., Duijnstee, I.A.P., Den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifers: Proxies or problems? A review of paleocological concepts. Earth Sci. Rev. 46, 213–236. https://doi.org/10.1016/S0012-8252(99)00011-2

Veileder (02:2018), Klassifisering av miljøtilstand i vann (Økologisk og kjemisk klassifiseringssystem for kystvann, grunnvann, innsjøer og elver., 2018.

Velvin, R., Emaus, P.A., 2015. Grieg Seafood Finnmark; Miljøovervåking i Øksfjorden, Loppa kommune 2015. 1–43.

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. https://doi.org/10.1016/0924-7963(95)00037-2

Water Framework Directive 2000/60/EC: establishing a framework for Community action in the field of water policy, 2000. 72. https://doi.org/10.1039/AP9842100196

Weinkauf, M.F.G., Milker, Y., 2018. The effect of size fraction in analyses of benthic foraminiferal assemblages: A case study comparing assemblages from the >125 and >150µm size fractions. Front. Earth Sci. 6, 1–10. https://doi.org/10.3389/feart.2018.00037

West, E.J., Welsh, D.T., Pitt, K.A., 2009. Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. Hydrobiologia 616, 151–160. https://doi.org/10.1007/s10750-008-9586-7

WFD, 2003. Common Implementation Strategy for the Water Framework Directive (2003/60/EC). Guidance Document No. 5. Transitional and Coastal Waters - typology, reference conditions and classification systems., Produced by Working Group 2.4 - Coast.

Woulds, C., Andersson, J.H., Cowie, G.L., Middelburg, J.J., Levin, L.A., 2009. The short-term fate of organic carbon in marine sediments: Comparing the Pakistan margin to other regions. Deep. Res. Part II Top. Stud. Oceanogr. 56, 393–402. https://doi.org/10.1016/j.dsr2.2008.10.008

Woulds, C., Bouillon, S., Cowie, G.L., Drake, E., Middelburg, J.J., Witte, U., 2016. Patterns of carbon processing at the seafloor: The role of faunal and microbial communities in moderating carbon flows. Biogeosciences 13, 4343–4357. https://doi.org/10.5194/bg-13-4343-2016

Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., Speybroeck, J., Tagliapietra, D., Van Hoey, G., Ysebaert, T., 2013. On the Myths of Indicator Species: Issues and Further Consideration in the Use of Static Concepts for Ecological Applications. PLoS One 8. https://doi.org/10.1371/journal.pone.0078219

Zhulay, I., Reiss, K., Reiss, H., 2015. Effects of aquaculture fallowing on the recovery of

macrofauna communities. Mar. Pollut. Bull. 97, 381–390. https://doi.org/10.1016/j.marpolbul.2015.05.064

Zonta, R., Zaggia, L., Argese, E., 1994. Heavy metal and grain-size distributions in estuarine shallow water sediments of the Cona Marsh (Venice Lagoon, Italy). Sci. Total Environ. 151, 19–28. https://doi.org/10.1016/0048-9697(94)90482-0

Journal publications and manuscript:

Paper I (Published):

Klootwijk, A.T., Alve, E., Hess, S., Renaud, P.E., Sørlie, C., Dolven, J.K., 2020. Monitoring environmental impacts of fish farms: Comparing reference conditions of sediment geochemistry and benthic foraminifera with the present. Ecological Indicators, volume: 120. https://doi.org/10.1016/j.ecolind.2020.106818.

Ecological Indicators 120 (2021) 106818

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Monitoring environmental impacts of fish farms: Comparing reference conditions of sediment geochemistry and benthic foraminifera with the present

Anouk T. Klootwijk[a,*], Elisabeth Alve[a], Silvia Hess[a], Paul E. Renaud[b], Carsten Sørlie[a,c], Jane K. Dolven[d,e]

[a] Department of Geosciences, University of Oslo, PO Box 1047 Blindern, 0316 Oslo, Norway
[b] Akvaplan-niva, Fram Centre for Climate and the Environment, 9296 Tromsø, Norway and University Centre on Svalbard, 9171 Longyearbyen, Norway
[c] NCC Infrastructure Division Office, Division Civil Engineering, PO Box 93 Sentrum, NO-0101 Oslo, Norway
[d] University of South-Eastern Norway, Kjølnes ring 56, 3901 Porsgrunn, Norway
[e] Biologg.no, Minnehallveien 27B, 3290 Stavern, Norway

ARTICLE INFO

Keywords:
Biomonitoring
Aquaculture
Benthic foraminifera
Geochemical parameters
Macrofauna
Ecological Quality Status

ABSTRACT

Intensive fish farming is a major industry, but the extent of organic matter (OM) and heavy metal pollution by fish farms is debated. This study established in situ reference conditions using geochemical parameters and fossil benthic foraminiferal assemblages in dated sediment cores to identify potential impacts of fish farming in two basins of the inner Øksfjord, Northern Norway. Living (rose Bengal stained) benthic foraminifera were used to assess the present day environmental conditions. The fossil foraminiferal records were compared with the living foraminifera, which in turn were compared with macrofaunal data. Long-term (> 100 yrs) sediment core records of the geochemical parameters (TOC_{63}, C/N, $\delta^{13}C_{VPDB}$ TOC and heavy metals) and foraminiferal indices (Norwegian Quality Index (fNQI), AZTI's Marine Biotic Index (fAMBI), $fHlog_2$, ES_{100}) did not indicate an impact from fish farming through time. Long-term changes in foraminiferal absolute abundances and relative abundances of ecological groups (EGs) reflecting organic matter (OM) tolerance suggest that the OM supply slightly increased compared to reference conditions. Relative abundances of *Brizalina skagerrakensis* and *Epistominella vitrea*, previously associated with phytodetrital input, suggest a minor increase in primary productivity compared to reference conditions. The *Stainforthia* group (*S. fusiformis* and *S. feylingi*), indicative of OM enrichment, in the living foraminiferal assemblages may indicate a response to fish farming activities, but foraminiferal seasonality could not be excluded as a potential cause. The indices of both fossil and living foraminifera, in addition to the macrofauna showed a good to high Ecological Quality Status (EcoQS) through time and at present. This indicates that environmental conditions have been and still are acceptable.

1. Introduction

Since the industrial revolution, population growth has led to increased inputs of anthropogenic organic carbon (OC) in many coastal areas. One major but relatively little studied source of anthropogenic OC and nutrients is intensive fish farming (Henderson et al., 1997; Husa et al., 2014; Johnsen and Lunestad, 1993; Kutti et al., 2008). It is estimated that a fish farm with 2910 tonnes of salmon produces 300 tonnes of organic waste per 2-year growth cycle (Kutti et al., 2007a; Zhulay et al., 2015). Previous studies suggest that OC emissions from fish farming have increased the primary productivity and OC loading of fjord sediments, with consequences for ecosystem functioning and benthic community structure (Holmer, 2010; Husa et al., 2014; Kutti et al., 2007b; Sweetman et al., 2016, 2014). Currently these studies based on spatial differences are difficult to interpret, as long time-series (spanning pre-anthropogenic impact conditions) have not been established. This makes it challenging to exclude natural gradients as causes of observed variabilities.

As a tool to manage and protect coastal water bodies in Europe, the Water Framework Directive (WDF, 2000/60/EC) was introduced. The WFD uses five categories (high, good, moderate, poor or bad) to classify a water body in order to define the Ecological Quality Status (EcoQS). According to the WFD it is mandatory that water bodies are returned to so called "reference conditions", defined as good or high EcoQS that

* Corresponding author.
E-mail address: a.t.klootwijk@geo.uio.no (A.T. Klootwijk).

https://doi.org/10.1016/j.ecolind.2020.106818
Received 20 March 2020; Received in revised form 30 July 2020; Accepted 4 August 2020

presumably existed before human impact. From the WFD the Norwegian guidelines (Veileder, 02:2018) were derived based on the same principles but adjusted to fit the Norwegian coastal ecosystems. Currently reference conditions are established from seemingly un-impacted "pristine sites", historical data, modelling or expert judgement (WDF, 2000/60/EC, p. 36–47). The first two options are often not available, so expert judgement is the best broadly available approach to constrain reference conditions (Borja et al., 2012). The latter, however, lacks transparency and is often incomprehensible for non-experts (Borja et al., 2012).

Benthic foraminiferal assemblages can provide estimates of in situ reference conditions (Alve et al., 2009), as the empty tests of many species preserve in the sediment forming fossil assemblages. Previous studies have shown that benthic foraminifera rapidly respond to changing environmental conditions, and steps have been made to implement them as a biomonitoing tool (e.g. Alve et al., 2009; Bouchet et al., 2012; Dolven et al., 2013; Schönfeld et al., 2012). Foraminifera can also provide environmental information at locations where a low abundance of macrofauna hampers their usability (Schönfeld et al., 2012). In environmental monitoring, benthic macrofauna is the traditionally used biological quality element. Whilst selected heavy metals and total organic carbon (TOC) are used as supporting elements to define the chemical status (Veileder, 02:2018, p. 30). In aquaculture related biomonitoring, geochemical parameters like sediment stable carbon isotopes ratios ($\delta^{13}C_{VPDB}$ TOC) and organic Carbon and total Nitrogen (C/N) ratios have shown potential to determine the dispersal of fish-farm waste (Kutti et al., 2007a). These parameters are well documented for successfully tracing sources of the organic matter (OM) in coastal systems (Kuliński et al., 2014; Mayr et al., 2011; Meyers, 1994; Sauer et al., 2016).

The main objectives of this study are to establish reference conditions and assess the potential environmental impacts of fish farming activities on the benthic environment of the Øksfjord, northern Norway. The study is based on the long-term (> 100 yrs) records of geochemical parameters and benthic foraminifera in dated sediment cores. This is the first combined down-core application of geochemical parameters (TOC_{63}, $\delta^{13}C_{VPDB}$ TOC, C/N ratios and heavy metals) with foraminiferal indices (Shannon-Wiener; fH'_{log2}, Hurlberts rarefaction; fES_{100}, multimetric Norwegian Quality Index; fNQI; fAMBI (Alve et al., 2019, 2016)), to investigate potential temporal changes introduced by fish farming. An additional aim is to assess the present day EcoQS based on living (rose Bengal (rB) stained) benthic foraminiferal assemblages and compare it with ecological assessments based on macrofauna and the fossil foraminiferal record. This study is another step towards integrating foraminifera in the governmental monitoring protocols.

2. Study area

This study was carried out in the inner Øksfjord, Loppa kommune, Northern Norway (Fig. 1). The inner fjord is separated from the outer fjord by a ca. 120 m deep sill, and the inner fjord consists of two basins separated by a ca. 100 m sill. The basins in the inner Øksfjord are referred to as the main basin and the sub-basin, and have maximum depths of 240 and 160 m, respectively (Fig. 1). The fjord area is characterized by a steep topography and bathymetry with rocky slopes (Krauskopf, 1954). The glacier Øksfjordjøkelen drains into the inner and outer fjord from the western side, but apart from that, no other substantial rivers drain into the inner fjord. Water column stratification in northern Norway is at a minimum during early spring followed by an increase in May-September, after which it decreases during late fall and winter (Keck and Wassmann, 1996; Wassmann et al., 1996). The stratification is also less and the water exchange is stronger compared to Norway's boreal fjords (Holte et al., 2005).

There are no large settlements, heavy industry or agricultural activities along the inner Øksfjord. The fjord is, however, one of the most intensively fish farmed fjords in northern Norway (Bjørn et al., 2009). Norway's aquaculture pioneered in the early 1970s (Berge, 2000), but fish farming in the Øksfjord started in 1996 (Per-Arne Emaus, pers. com. 2020). Since the start of production, licences increased from 1500 tonnes of fish per fish farm to 2700 tonnes in 2006 (Per-Arne Emaus, pers. com. 2020). Grieg Seafood ASA obtained the licences in 2005 and has since increased the production to 4000–8000 tonnes of fish per year (Odd Leknes, Grieg Seafood, pers. com. 2020). From 2011 to 2013, five fish farms were operating simultaneously in the inner Øksfjord (Fig. 1). Since 2013, one location (Lille Skognes) has been permanently closed due to deteriorating environmental conditions in the innermost part of the fjord (Odd Leknes, pers. com. 2020). During sampling in September 2017, the fish farms Auskarnes and Storvik were both being fallowed. The fallowing period started in 2016. In September 2017, two farms (Steinviknes and Kjøsen) were in active use (Fig. 1). In total, Grieg Seafood ASA produced 62,700 tonnes of salmon using 75,500 tonnes of fish feed between 2005 and 2017 in the inner Øksfjord (Odd Leknes, Grieg Seafood, pers. com. 2020).

3. Materials and methods

Sediment cores were collected from the main basin (D2) and the sub-basin (D3) in early September 2017 (Fig. 1, Table 1). Sediment coring was performed using a twin-barrelled Gemini gravity corer (inner diameter 8 cm, Niemistö, 1974). Two sediment cores from each basin were sectioned on deck, slicing the upper 20 cm into 1 cm thick slices and below 20 cm into 2 cm slices. In addition, three replicate surface samples (0–1 cm) were obtained from each station for living (rB stained) foraminiferal assemblage analyses. These samples were preserved and stored in a 70% ethanol/2 g L^{-1} rB mixture (Schönfeld et al., 2012). Three replicate grab samples were taken at each station for macrofaunal analysis using a van Veen grab (0.1 m^2, 36 × 28 cm). The macrofauna samples were carefully washed on deck using a 1 mm sieve and preserved in a rB stained 4% formaldehyde mixture neutralized with borax. Hydrographic measurements (temperature, salinity, oxygen concentration) were performed in each basin using a SAIV CTD model SD204.

All sediment core samples were freeze dried to obtain the down-core porosity records that were used to assess the quality of the cores. Cores D2-6A (main basin) and D3-3B (sub-basin) were sent to the Environmental Radioactivity Research Centre, University of Liverpool, UK, and analysed for ^{210}Pb, ^{226}Ra and ^{137}Cs by direct gamma assay on Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al., 1986). ^{210}Pb dates were calculated using both the Constant Rate of Supply (CRS) and Constant Initial Concentration (CIC) models (Appleby and Oldfield, 1978), and possible chronostratigraphic dates determined from the ^{137}Cs records. The dating results of D3-3B showed that reference conditions might not have been reached. Therefore the longer, not radiometrically dated, D3-13A core was used as an extension of the shorter D3-3B core (from here on D3-3B/13A) as the sediment porosities of both cores showed a good correlation. This correlation was further strengthened by good correlations between the geochemical parameters (bulk sediment TOC, C/N ratios and $\delta^{13}C_{VPDB}$ TOC).

Grain size distributions were determined using a Beckman Coulter LS13320 with laser diffraction at the Department of Geoscience, University of Oslo. The bulk sediment TOC, total nitrogen and $\delta^{13}C_{VPDB}$

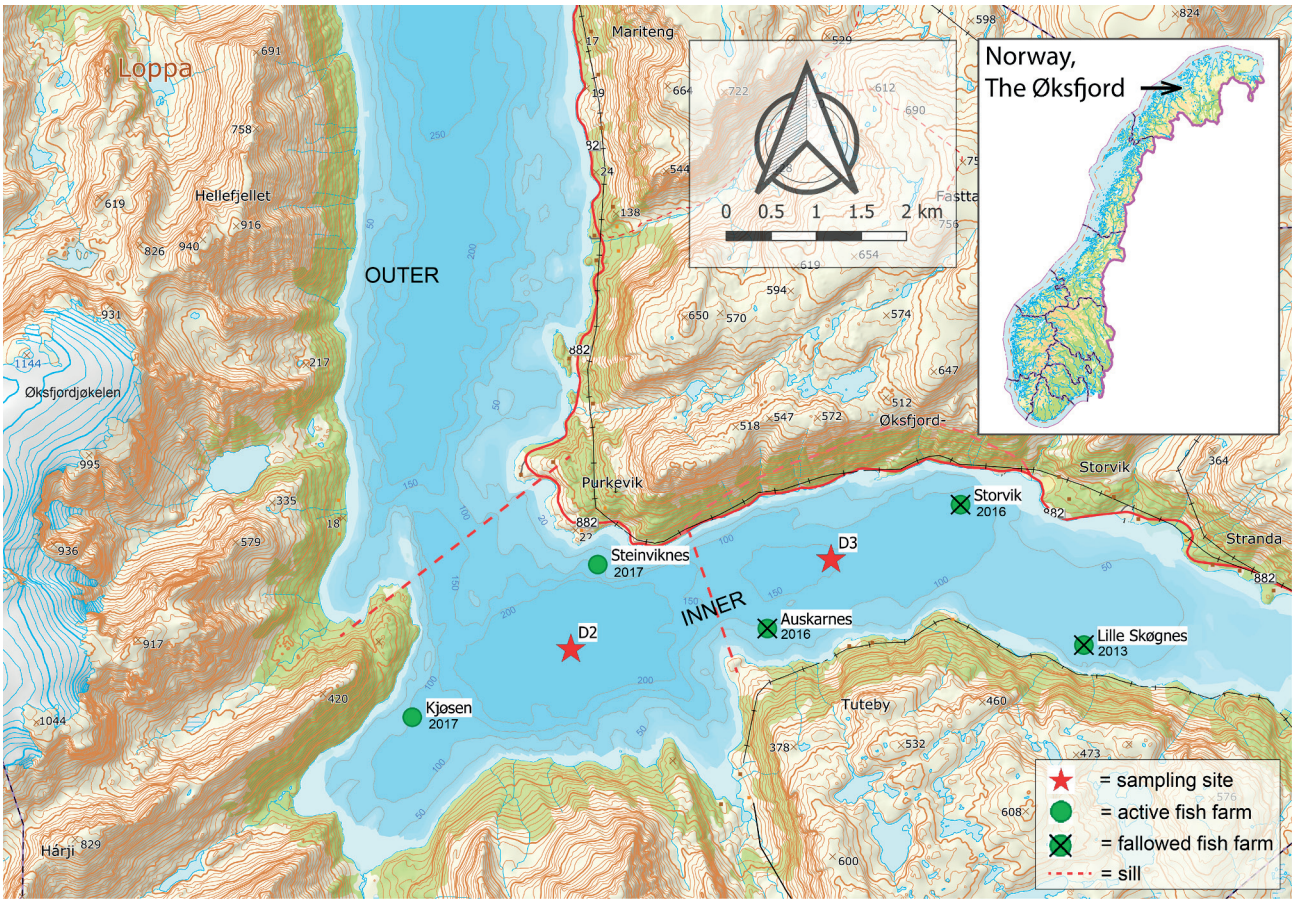


Fig. 1. Map of the outer and inner Øksfjord. The inner fjord consist of a main (D2) and a sub-basin (D3). The years under the names of the fish farms indicate the year at which they were active, or since when they were fallowed. (Modified from the QGIS Development Team (3.4.14-Madeira, 2020), map from Statens kartverk (2007)).

TOC, samples were analysed using an Elemental Analyser–Isotope Ratio Mass Spectrometry (EA-IRMS) at the ISO-Analytical Ltd. stable isotope analysis laboratory in Crewe, UK. Prior to the TOC and $\delta^{13}C_{VPDB}$ TOC, analyses samples were acidified with 1 M HCl. The TOC was normalized to the sediment fine fraction (% < 63 μm), as only the TOC_{63} can be used for classification in the Norwegian guidelines (TOC_{63} = TOC + 18 × 1 − % < 63 μm; Veileder, 02:2018). After initially starting with every second sample, the % < 63 μm fraction varied only little in the 42–22 cm interval of core D2-6A. Grain size measurements were therefore interpolated for the samples not analysed in this interval. Samples were treated with 7 M HNO_3 prior to the analyses of copper (Cu), zinc (Zn) and nickel (Ni) on a Gas Chromatography ICP Sector Field Mass Spectrometer by the ALS Laboratory Group Norway AS. Heavy metal concentrations were analysed from the undated D3-13A and D2-5A core, as the sediment porosity records were highly similar to those of the other cores taken in the basins.

For the fossil foraminiferal analyses, approximately 2 g of freeze-dried, gently homogenized sediment to ensure the aliquot represented the sample, was washed over 500 μm and 63 μm sieves and dried. From the 63–500 μm fraction, material was taken at random and fully picked, until > 250 specimens could be mounted on microfossil slides and identified to species level. The total number of specimens > 500 μm in the assemblages was small (< 6%) and therefore not included. For the living foraminiferal analyses, samples were washed through 63 μm and 500 μm sieves after which the 63–500 μm fraction was split using a modified Elmgren wet splitter (Elmgren, 1973). For one eighth of the sample, all living (rB stained) foraminifera were picked and mounted. To compare living foraminiferal assemblages with fossil foraminiferal records, non-fossilizable species were excluded from living assemblages (Bouchet et al., 2012). Due to large numbers of juvenile *Stainforthia*

Table 1
Basin, location, water depth, CTD results obtained at the sampling sites, the obtained cores and their length.

Site	Basin	Coordinates	Water depth (m)	BW* O_2 (ml/L^{-1})	BW* O_2 (mol/L^{-1})	BW* Salinity	BW* Temperature (°C)	Sediment cores + length
D2	Main	70°08.6456 N 22°17.7542 E	240	5.13	0.23	35	5.1	D2-6A = 42 cm D2-5B = 46 cm
D3	Sub-	70°08.8295 N 22°22.5421 E	160	5.77	0.26	35	5.6	D3-3B = 14 cm D3-13A = 30 cm

* Bottom Water.

fusiformis and *S. feylingi*, and *Cibicides refulgens* and *C. lobatulus*, the *Stainforthia* and *Cibicides* species were grouped into a *Stainforthia* group and a *Cibicides* group.

After fixation, macrofaunal samples were sorted in the laboratory under 10× magnification. Living specimens were identified to the lowest practical taxonomic level and counted in the EN ISO-IEC 17025 accredited laboratories at Akvaplan-niva, Tromsø, Norway. The EN ISO-IEC 17025 is set of internationally accepted standards for laboratories that perform testing, sampling or calibration.

Species diversity indices H'_{log2} (Shannon and Weaver, 1963) and ES_{100} (Hurlbert, 1971) were calculated using the R-data software program (R Core team, 2020). The OM sensitivity index AMBI was calculated according to Alve et al. (2016) for foraminifera (fAMBI) and Borja et al. (2000) for the macrofauna (mAMBI). For the calculation of fAMBI and mAMBI only taxa and groups assigned to the ecological groups (EGs) were used, as described in Alve et al. (2016) and Borja et al. (2000). The multi-metric Norwegian Quality Index (NQI) for foraminifera was calculated after Alve et al., 2019 (fNQI) and for macrofauna *sensu* the Norwegian guidelines (Veileder 02:2018 (mNQI)). For both the living foraminiferal assemblages and macrofauna, index values represent the arithmetic mean of three replicates after which only the averages were reported and, when applicable, used to assess EcoQS (Borja and Muxika, 2005). To further explore the palaeo-environmental conditions the five EGs of Alve et al. (2016), representing different responses to OM enrichment, were used. For the EGs, the relative abundances of assigned species, and species groups, were calculated using the sum of assigned species and groups only, after which the relative abundances were summed for each EG. Absolute abundances of the fossil foraminifera were calculated as the number of tests per gram dry sediment (test/g sediment). For the radiometrically dated upper 6 cm of core D3-3B, the Benthic Foraminifera Accumulation Rates (BFAR) were calculated according to Herguera and Berger (1991). *Stainforthia fusiformis*, a member of the *Stainforthia* group, is considered a first order opportunist, indicative of excess OM enrichment according to Alve et al. (2016). *Brizalina skagerrakensis* and *Epistominella vitrea* were used as species indicative of increased phytodetrital input (Asteman et al., 2018 and sources therein; Duffield et al., 2015). For the foraminifera taxonomic references, see Appendix A.

4. Results

4.1. Hydrocast data

The salinity in the water column increased from ~33 in the surface to 35 in both the Øksfjord basins (Supplementary Appendix A, Table 1). The temperature decreased from 9 °C in the surface to 5.5 °C in the bottom waters (Supplementary Appendix A, Table 1). The oxygen concentrations in the fjord decreased from 6 mL/L (0.27 μmol/L^{-1}) in the surface to 5.5 mL/L (0.25 μmol/L^{-1}) in the bottom waters (Supplementary Appendix A, Table 1).

4.2. Chronologies of the sediment cores

The sediment cores D2-6A and D3-3B could be radiometrically dated back to the mid-1800s and 1920s, respectively (Table 2, Fig. 2). In the main basin D2-6A core, the ^{210}Pb and ^{137}Cs records were both dominated by a major non-monotonic feature, between 13 and 5 cm, in which concentrations were significantly lower than in samples directly above and below (Table 2, Fig. 2). This feature coincides closely with a layer of dense, compact sediment amounting to around 73 kg m^{-2} in a ± 8 cm thick layer. ^{210}Pb calculations using the CRS model showed that the otherwise exponentially declining ^{137}Cs record was split into two distinct peaks, one immediately above the dense layer and the other immediately below. In the sub-basin D3-3B core concentrations of fallout ^{210}Pb declined exponentially with depth down to 6 cm, after which the signal was lost. Excluding the 13–5 cm interval in the main basin D2-6A core, sedimentation rates and sediment accumulation rates in both basins appear to have been relatively stable, averaging 0.9 mm yr^{-1} and 0.35 kg m^{-2} yr^{-1} in core D2-6A and 0.6 mm yr^{-1} and 0.53 kg m^{-2} yr^{-1} in core D3-3B.

4.3. Geochemical parameters and grain size

In core D2-6A from the main basin, the TOC_{63} concentrations from 42 to 14 cm varied between 29 and 38 mg/g (2.8–3.3% TOC) (Fig. 3). Between 13 and 5 cm, values were lower and varied between 9 and 17 mg/g (0.2–2.3% TOC) (Fig. 3). In the upper 5 cm of core D2-6A the concentration gradually increased from 22 to 28 mg/g (2.0–2.7% TOC). In the D3-3B/13A core from the sub-basin the TOC_{63} concentrations

Table 2
The radiometric dates, sediment accumulation rates (kg m^{-2} yr^{-1}) and sedimentation rates (mm yr^{-1}) from the D2-6A and D3-3B core.

Main basin D2-6A				Sub basin D3-3B			
Depth (cm)	Date AD	Sedimentation		Depth (cm)	Date AD	Sedimentation	
		kg m^{-2} $^{-1}$	mm yr^{-1}			kg m^{-2} yr^{-1}	mm yr^{-1}
0	2017			0	2017		
0.5	2013	0.37	1.1	0.5	2012	0.53	0.9
2.5	1995	0.37	1	1.5	1999	0.53	0.7
3.5	1983	0.37	0.8	2.5	1985	0.53	0.6
4.5	1969	0.37	1.2	3.5	1967	0.53	0.5
5.5	1967	3.58	5.6	4.5	1948	0.53	0.5
6.5	1965	9.86	13.1	5.5	1926	0.53	0.5
8.5	1964	20.65	24.6				
10.5	1964	20.65	23.8				
12.5	1963	10.39	10.5				
14.5	1960	0.34	1.2				
16.5	1928	0.34	0.6				
18.5	1897	0.34	0.6				
21	1858	0.34	0.6				

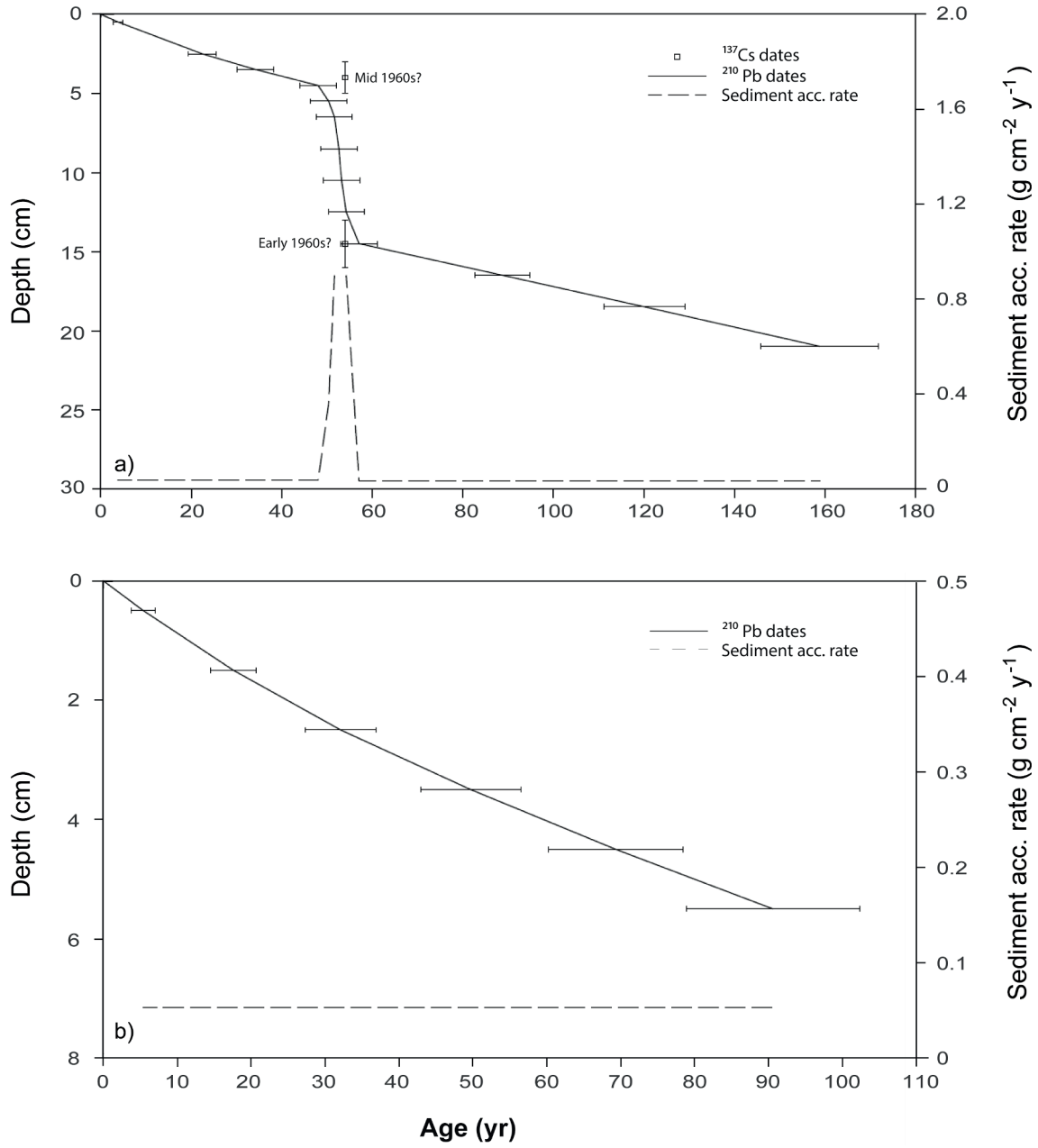


Fig. 2. Radiometic chronologies for a) core D2-6A from the main basin, and b) core D3-3B from the sub-basin. NB: axes have different scales.

showed a minor increase from ± 7 mg/g (0.5% TOC) to 17 mg/g (1.3% TOC) (Fig. 3) in the uppermost part (0–1 cm). The uncorrected % TOC values in parentheses are shown in Appendix B Tables B.1 and B.2.

The $\delta^{13}C_{VPDB}$ TOC and C/N ratios in the sediment cores from both basins, not including the 13–5 cm interval in D2-6A, showed no major changes (Fig. 3), and the concentrations of Cu, Zn and Ni showed only small variations through time (Fig. 3). In both basins, concentrations including the 13–5 cm interval in D2-6A, varied as follows: Cu = 16–75, Zn = 31–130 and Ni = 27–87 mg/kg.

The sediment fraction < 63 µm in core D2-6A had the lowest values in the 13–5 cm interval (28–80%), with only 28% fine fraction between 12 and 11 cm (Fig. 3). In core D3-3B/13A the sediment fraction < 63 µm fraction varied between 50 and 96% (Fig. 3).

4.4. Fossil foraminiferal assemblages

The fossil foraminiferal indices showed no clear tendency in both cores and varied as follows; fH'_{log2} = 3.3–4.5, fES_{100} = 17–28, fNQI = 0.57–0.76 (Fig. 4). In the D2-6A core, the fAMBI scores ranged from 1.4 to 2.6, apart from in the 13–5 cm interval where they ranged from 0.7 to 1.8 (Fig. 4). In the upper 3 cm of core D3-3B/13A, the fAMBI scores were somewhat higher compared to the lower part, ranging from 2.9 to 3.1 compared 1.2 to 2.5 below (Fig. 4). For most samples > 85% of the fossil foraminiferal assemblages could be assigned to one of the five EGs defined in the fAMBI. For the 8–4 cm interval in core D3-3B only between 77 and 79% could be assigned. The EG distributions showed that in both cores, D2-6A and D3-3B/13A, relative abundance of EG III were higher than EG I in the upper 5–6 cm (Fig. 5).

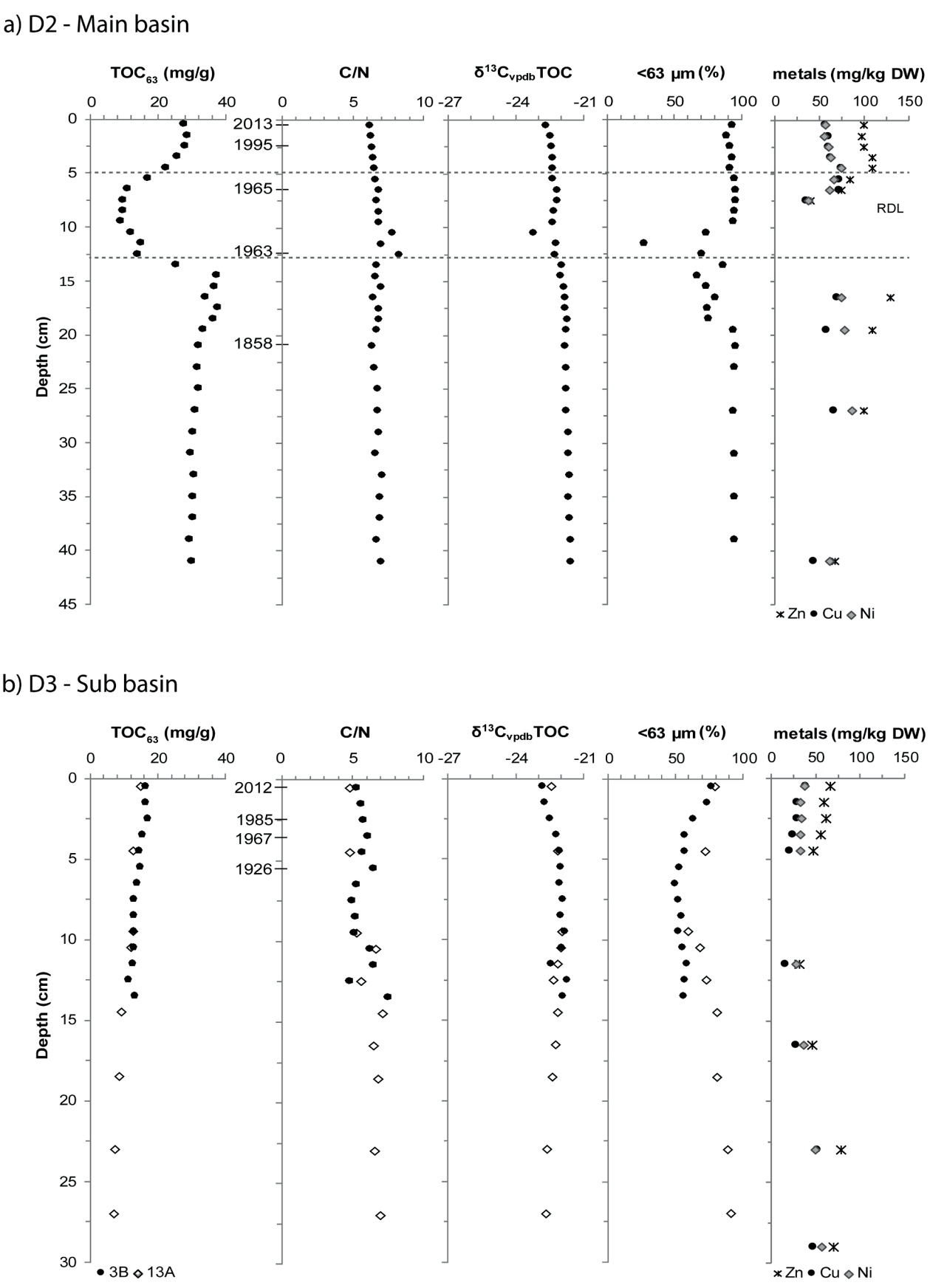


Fig. 3. The geochemical parameters, TOC_{63} (mg/g), C/N ratios, bulk sediment carbon isotopes ($\delta^{13}C_{VPDB}$ TOC), fraction < 63 µm (%) and heavy metal concentrations of Zinc (Zn), Copper (Cu) and Nickel (Ni) (mg/kg Dry Weight) plotted for a) the main and b) the sub-basin. RDL = re-deposited layer.

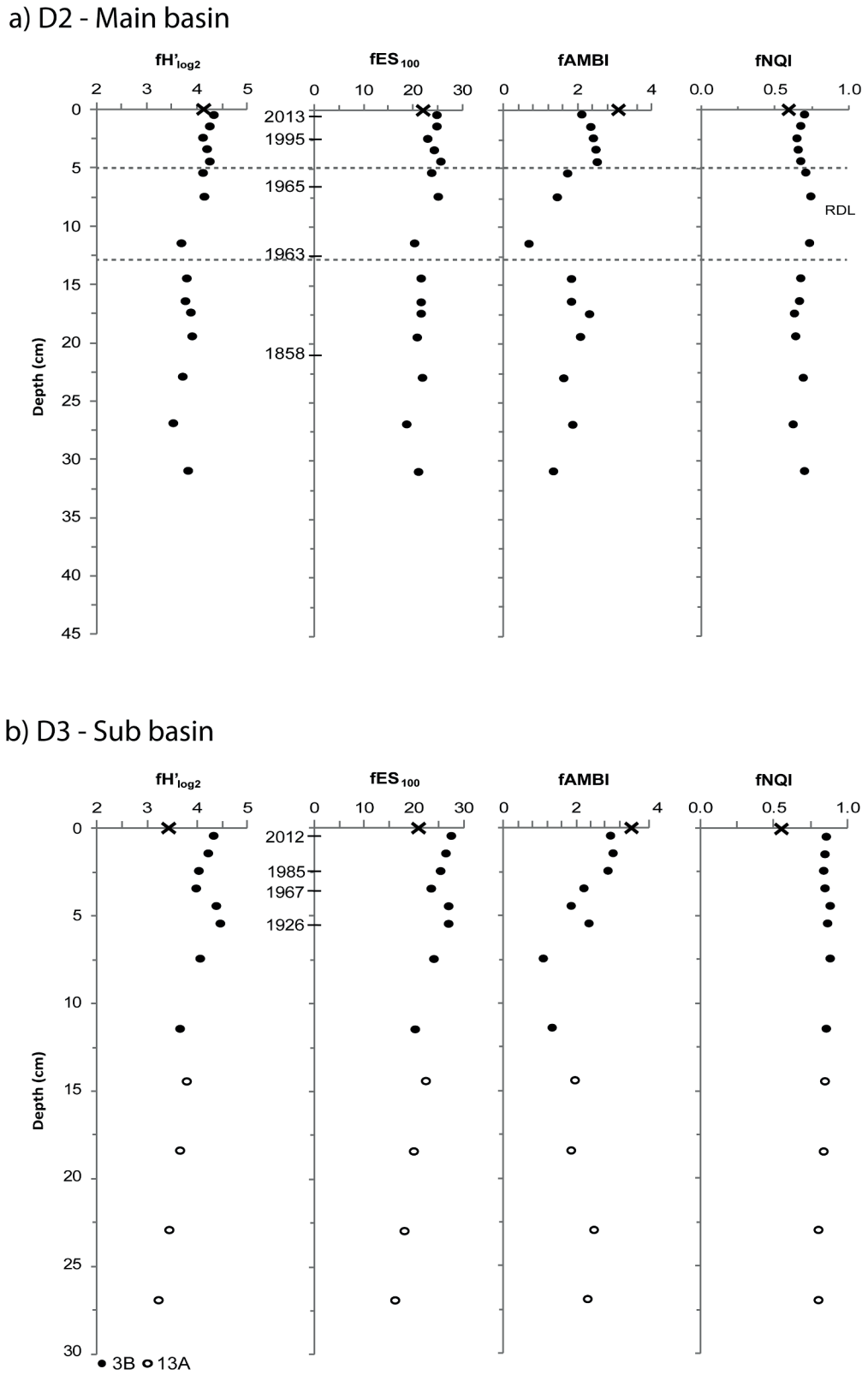


Fig. 4. The diversity indices (fH'_{log2} and fES_{100}), sensitivity index fAMBI and the fNQI plotted for a) the main and b) the sub-basin. Circles = fossil data and crosses = living foraminiferal assemblage data. RDL = re-deposited layer.

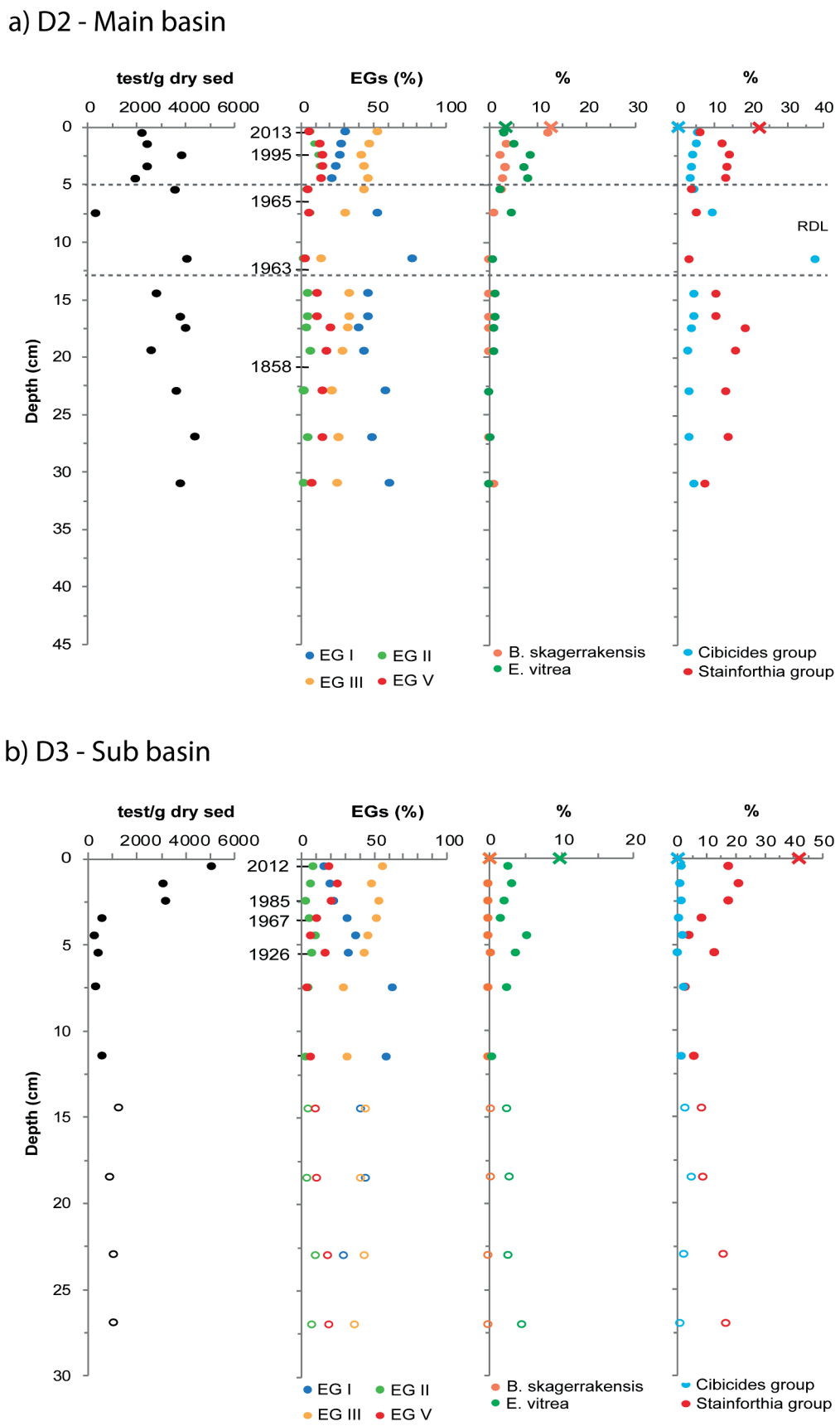


Fig. 5. The foraminiferal absolute abundances (test/g dry sediment), relative abundances of the Ecological Groups (EGs %) and relative abundances of the indicator species (%) plotted for a) the main and b) the sub-basin. Circles represent = fossil data and crosses = the living foraminiferal assemblage data. In b) D3 – Sub basin open circles = D3-13A and filled circles = D3-3B. RDL = re-deposited layer.

Table 3
Macrofauna and living foraminiferal indices, averages of three replicates. Colour coding of the classification according to Norwegian guidelines (Veileder, 02:2018) and Alve et al., 2019. Colour coding of the statuses is shown in the legend below the table.

Site	D2	D3	D2	D3
Indices	*macrofauna*	*macrofauna*	*foraminifera*	*foraminifera*
H'_{log2}	3.3	2.6	4.0	3.4
ES_{100}	18	19	22	20
AMBI	2.1	2.3	3.1	3.5
NQI	0.69	0.71	0.58	0.54

Status	High	Good	Moderate	Poor	Bad

The absolute abundances of the fossil assemblages in the D2-6A core varied between 1975 and 4436 tests/g dry sediment, except for one sample at 7–8 cm where 388 tests/g dry sediment were found (Fig. 5). In core D3-3B/13A, absolute abundances were relatively stable in the lower part (30–6 cm), ranging between 372 and 1299 tests/gr dry sediment, compared to the rapid increase in the upper 3 cm from 625 till 5074 tests/g dry sediment (Fig. 5). The BFAR were only calculated for the radiometrically dated upper 6 cm of core D3-3B/13A, as the absolute abundances only changed in D3-3B/13A. In this interval, they increased from 18 to 33 test/cm^2/year to 165–269 test/cm^2/year.

In both sediment cores, the *Stainforthia* group showed no overall trend and varied in relative abundance between 5 and 20% (Fig. 5). Relative abundances of the *Cibicides* group were generally below 10% in both cores, except for a peak at 11–12 cm in core D2-6A where the abundance was 38% (Fig. 5). In the upper 5 cm of core D2-6A, the combined relative abundances of *B. skagerrakensis* and *E. vitrea* ranged from 5 to 15% compared to 0–1% in the lower part (Fig. 5). In core D3-3B/13A, relative abundances of *E. vitrea* exhibited small changes and *B. skagerrakensis* was almost absent (Fig. 5).

4.5. Living foraminiferal assemblages

Living foraminifera indices were as follows; fH'_{log2} = 4.1 and 3.4, fES_{100} = 22 and 21, fNQI = 0.59 and 0.56, fAMBI 3.1 and 3.5 for D2 and D3, respectively (Fig. 4). Relative abundances of *B. skagerrakensis* and *E. vitrea* in the living assemblages were 13% and 4% at D2 and 0.1% and 10% at D3 (Fig. 5). For the *Stainforthia* group relative abundances in the living assemblages were 22% at D2 and 42% at D3 (Fig. 5).

4.6. Macrofauna

The macrofaunal diversity indices (mH'_{log2}, mES_{100}) and the mNQI were as follows; at D2, mH'_{log2} = 3.3, mES_{100} = 18, mNQI = 0.69, and at D3, mH'_{log2} = 2.6, mES_{100} = 19, mNQI = 0.71 (Table 3). The mAMBI scores were similar at both sites, 2.1 at D2 and 2.3 at D3. Of the macrofauna, between 96% and 98% could be assigned to the five EGs that were used to calculate the mAMBI for D2 and D3, respectively.

5. Discussion

5.1. Continuity of the sedimentary record

The ^{210}Pb concentrations declined exponentially in both cores, giving no indication of dredging or trawling activities in the inner-Øksfjord (Fig. 2). The interruption of the ^{137}Cs and ^{210}Pb records suggests that the 13–5 cm interval in the D2-6A core is a re-deposited layer (RDL) (Supplementary Appendix B, Table 2, Fig. 2). This re-deposited layer was deposited during an event in the early 1960s, as is shown by the maximum ^{137}Cs fallout from the atmospheric testing of nuclear weapons. Shell fragments, coarse grains, and high relative abundances of the *Cibicides* group at the base of the RDL indicate that the event was a sub-aqueous slide (Figs. 3 and 5). Members of the *Cibicides* group prefer high-energy areas with coarse sediment and hard substrates (Mackensen et al., 1985; Schönfeld, 2002), suggesting that the RDL material came from the shallower areas of the Øksfjord with more suitable conditions for these taxa. Fossil *Cibicides* specimens appeared worn and in some instances missed the final chambers throughout both cores, which supports the hypotheses regarding transportation.

In the sub-basin D3-3B core, there was no evidence of a peak in the ^{137}Cs record for the 1963 fallout maximum. This could be the result of large standard errors in the measurements, low isotope concentrations, or minor bioturbation as suggested by width of the peak in the ^{137}Cs dating record. In core D3-3B, no evidence of an RDL was found in the percent < 63 μm fraction or the foraminiferal record itself either.

5.2. Establishing reference conditions

There are no large settlements, heavy industry or agricultural activities along the inner-Øksfjord. This leaves fish farming activities the most noticeable remaining source of human impact on the fjord. Fish farming was conducted on a relatively small scale, until Grieg Seafood ASA rapidly increased the production in 2005 (Odd Leknes, pers. com. 2020). It is thus reasonable to assume that the relatively stable conditions in pre-1960 sediment records from D2 and D3 are only minimally affected by human activities, and thus represent the reference conditions.

5.3. Temporal patterns of the abiotic parameters

The fish farms in the Øksfjord are situated in rocky, steeply inclined areas that could not be sampled (Fig. 1). The sampling sites in the Øksfjord were thus between 1 and 2 km away from the farms. Previously no changes in TOC concentrations, and particulate organic matter and carbon (POM and POC) fluxes have been observed outside a 100 to 500 m radius from fish farms (Brooks and Mahnken, 2003a; Carroll et al., 2003; Kutti et al., 2007a; Lalande et al., 2020). A previous study using fatty acids, $\delta^{13}C_{VPDB}$, and C/N ratios, however, suggested that some of the organic fish farming waste was transported > 1 km away (Kutti et al., 2007a), though this is less than < 2.7% of the total waste (Bannister et al., 2016). The lack of major changes in the $\delta^{13}C_{VPDB}$ TOC, and C/N ratios (Fig. 3), suggest that the sampling locations in the Øksfjord are probably too far away to have a realistic impact on these parameters. Furthermore, the sedimentation rates in the Øksfjord are relatively low (between 0.5 and 1.1 mm yr^{-1}, Table 2) compared to e.g. 1.4–5.1 mm yr^{-1} in Lysefjorden (Duffield et al., 2017)

or 2–10 mm yr^{-1} in the Inner Oslofjord (Dolven et al., 2013). In addition, the bottom waters in the Øksfjord are well oxygenated in autumn as shown in this study (Table 1), and previous biomonitoring reports (Velvin and Emaus, 2015). The oxygenated bottom waters in combination with low sedimentation rates could have affected the preservation of any potential fish farm OM in the Øksfjord basins.

In nearby Repparfjorden no fish farm is present and TOC_{63} concentrations ranged from 8.4 mg/g to 27.3 mg/g (Sternal et al., 2017). The Øksfjord TOC_{63} concentrations are predominantly within this range, but below the RDL (19–14 cm) in core D2-6A concentrations were higher. The sediments below the RDL in D2-6A, however, were deposited pre 1960s when no fish farms were present in the Øksfjord during reference conditions. Furthermore, according to the Norwegian guidelines, the TOC_{63} concentrations in sediments from the upper 3 cm of core D2-6A are classified as indicating a moderate impact (Appendix B Table B.1, Supplementary Appendix C, Veileder 02:2018). During the time interval these sediments were deposited (± 1995–2017), fish farms were active. The long-term sediment core records, however, showed that the moderate status reflects the reference conditions at site D2, as TOC_{63} concentrations in pre-1960s sediments have a moderate status as well. Overall, sediment geochemistry records suggest that the environmental conditions in the Øksfjord basins have remained relatively stable during at least the past century (Fig. 3).

The heavy metals Cu and Zn are used in monitoring studies to detect the impact of fish farming as their main sources are assumed to be anti-biofouling paint on the cages and fish feed (Brooks and Mahnken, 2003b; Burridge et al., 2010; Dean et al., 2007). However, a study investigating Cu concentrations in sediments near fish farm cages found that in most cases Cu concentrations in sediments under anti-biofouling paint treated cages were within the range found under untreated cages (Brooks and Mahnken, 2003b). The metal concentrations of Cu, Zn and Ni in the Øksfjord could reflect the surrounding bedrock. The bedrock surrounding the Øksfjord is comprised of gabbro (Krauskopf, 1954; Rea et al., 1996), which is known for its high concentrations of up to 90 mg/kg Cu, 100 mg/kg Zn and 130 mg/kg Ni (Reimann and Caritat, 1998). Biomonitoring studies only use the acid leached portion of the metals (e.g. Turner and Olsen, 2000), which is probably the main reason for the lower metal concentrations in the Øksfjord sediments compared to the bedrock. The Ni concentrations in core D2-6A have a moderate status according to the Norwegian guidelines, which would require governmental intervention to lower the concentrations (Appendix B Table B.1, Supplementary Appendix D, Veileder 02:2018). However, the sediment core records, again, showed that this reflects the natural background status in the Øksfjord. The lack of major variations in the heavy metal concentrations throughout the Øksfjord sediment cores (Fig. 3), suggests that the metal concentrations reflect bedrock rather than fish farming.

5.4. The use of biotic indices

Time averaging of the fossil assemblages could have influenced the fossil foraminiferal indices in the Øksfjord. Time averaging is the accumulation of foraminiferal tests from a succession of previous living assemblages over multiple years into one fossil assemblage (Murray, 2000). Due to low sedimentation rates, the fossil foraminiferal assemblages in each sample are time averaged over 10 to 15 years in the Øksfjord. Fish farming waste fluxes strongly vary depending on the farm's production cycle, usually 2-years, and the fallowing periods (Kutti et al., 2007a; Zhulay et al., 2015). As time averaging dampens such short-term variability (Duffield et al., 2017; Martin, 1999; Schafer, 2000), any potential responses of the fossil foraminifera indices that would occur on these time scales potentially lost in the Øksfjord records (Fig. 4).

Since they are not affected by time averaging, the living foraminiferal assemblages are more likely to reflect the recent OM input from the two active fish farms in the Øksfjord (Fig. 1). The indices of the living and fossil foraminiferal assemblages suggest no major change from the reference EcoQS in either basin (Appendix B Tables B.1 and B.2, Supplementary Appendix E, Fig. 4), reflecting good to high EcoQS according to Alve et al. (2019). The macrofauna indices from this study (Supplementary Appendix G, Table 3) and previous biomonitoring studies in the Øksfjord (Velvin and Emaus, 2015) also indicate good to high EcoQS according to the Norwegian guidelines (Veileder 02:2018).

Currently, comparing the fAMBI of the living foraminifera and the mAMBI is not straightforward. Species that are sensitive or indifferent to OM enrichment (Alve et al., 2016; Borja et al., 2000) are more abundant in the macrofauna compared to the living foraminiferal assemblages, as shown by the lower mAMBI than fAMBI (Table 3). Previous studies have shown that benthic foraminifera are potentially more sensitive to environmental degradation than macrofauna (Bouchet et al., 2020; Denoyelle et al., 2010). The mAMBI, however, may not optimally reflect environmental pressure gradients in Norwegian coastal waters (Rygg and Norling, 2013). This is thought to be due to using both Northern and Southern European data of macroinvertebrates to assign species to the five EGs (Rygg and Norling, 2013). This creates problems as species may exhibit varying sensitivity/tolerance levels along their different geographical distributions (Grémare et al., 2009; Zettler et al., 2013). This is less of a problem for the fAMBI as species are assigned to the EGs using data from the North Atlantic region only (Alve et al., 2016). However, both the living foraminifera fAMBI and mAMBI indicate that the present day conditions have deviated only minorly, if at all, from reference conditions in the Øksfjord basins.

5.5. Foraminiferal absolute abundances, Ecological groups and indicator species

The correlation between increased OM supply and increases in benthic foraminifera absolute abundances and BFAR is well known (e.g. Fontanier et al., 2002; Gooday, 1988; Rudnick, 1989). The use of these parameters for biomonitoring purposes was illustrated by Alve (1995), Duffield et al. (2017) and Hess et al. (2020), but they have not yet been systematically explored. Pearson and Rosenberg (1978) showed that when OM supply increases the number of individuals and biomass of macrofauna rise before a change in the number of taxa is observed. These increases in absolute abundances can occur rapidly. This is shown by the immediate response of the macrofauna after a pipe-line discharging organic waste was installed, and an immediate recovery when the pipe-line outlet was relocated (Borja et al., 2003). The abrupt increase of fossil foraminifera absolute abundances in the D3-3B/13A core could thus represent the first response to an increase in OM loading (Fig. 5). This is supported by the BFAR, which has been shown to reflect changes in OM supply (Herguera and Berger, 1991). In core D2-6A, the absolute abundances do not change throughout the core but they are higher than in most of the samples from core D3-3B/13A. A change in OM supply from reference conditions is also suggested by the sediment core records of the EGs. Foraminiferal species sensitive to OM input are in EG I (e.g. *Cassidulina reniforme*) whereas EG III (e.g. *B. marginata*) contains species tolerant to excess OM enrichment. For the EGs see Supplementary Appendices E and F, where species are assigned to EGs according to Alve et al. (2016). The shift of fossil assemblages dominated by EG I to EG III is subtle (Fig. 5), but suggests that the OM supply has changed compared to reference conditions.

The use of indicator species has been questioned due to differences in stress tolerance along natural environmental gradients and geographic regions (Grémare et al., 2009; Zettler et al., 2013). The species *B. skagerrakensis* and *E. vitrea* are considered indicator species for

increased phytodetrital input (Asteman et al., 2018 and sources therein; Duffield et al., 2015). Relative abundances of these two species in long term sediment core records and living foraminiferal assemblages may suggests an increase in primary productivity compared to reference conditions in the Øksfjord (Fig. 5). Previous studies on the link between salmon farms, ambient nutrient levels and phytoplankton density are equivocal (Brooks and Mahnken, 2003a; Jansen et al., 2018; Quiñones et al., 2019), but nutrient inputs from fish farms may be one factor leading to increased productivity in the Øksfjord. Alternatively, changes in the water column as a result of global climate change could have affected the primary productivity (e.g. Sommer and Lengfellner, 2008; Winder and Sommer, 2012).

The *Stainforthia* group reflects the opportunistic life strategy of *S. fusiformis*, a member of EG V (Alve et al., 2016), which is considered highly adapted to deal environmental stress like for example OM enrichment (Alve, 2003). The *Stainforthia* group strongly influenced the diversity indices and fAMBI scores of the living foraminiferal assemblages in the Øksfjord. The high relative abundances of the *Stainforthia* group in the living assemblages are not observed in the fossil assemblages of the Øksfjord (Fig. 5). This could in part be due to time averaging dampening the present day signal in the fossil assemblages because of the low sedimentation rates. In addition, some of the thin *Stainforthia* tests disintegrated during picking which could point to a preservation issue. However, despite their relatively thin tests, members from the *Stainforthia* group were present throughout both sediment cores (Fig. 5). *S. fusiformis* has the ability to rapidly increase in abundance with seasonal changes showing the highest abundances from May till September in the Gullmarfjord (Gustafsson and Nordberg, 2001). This seasonal acme could have caused the high relative abundances observed in the living assemblages of the Øksfjord. In Malangen, a fjord just south of the Øksfjord, a seasonal study showed that the highest absolute foraminiferal abundances in northern Norway occurred during autumn (Gaute Rørvik Salomonsen pers. com.). In northern Norway, the main phytoplankton bloom occurs in April-May, but elevated fluxes of POC have also been observed during autumn (Lalande et al., 2020; Noji et al., 1993; Wassmann et al., 1996). The high relative abundances of the *Stainforthia* group in the living assemblages could thus be a result of seasonality, rather than a response to fish farming.

6. Conclusions

This study illustrated the importance of integrating sediment core records of geochemical parameters and benthic foraminifera in environmental monitoring systems. Sediment geochemistry and benthic foraminiferal indices from dated sediment cores showed no deviations from reference conditions. Long-term changes in foraminiferal absolute abundances, relative abundances of the EGs and indicator species suggest the OM supply slightly increased during recent decades compared to reference conditions. The sediment core records also showed that the moderate classification of TOC_{63} and Ni in core D2-6A reflected the natural background conditions. The Ecological Quality Status (EcoQS) from the fossil and living foraminifera, in addition to the macrofauna, classified as good to high. This indicates that good environmental conditions persisted during at least the past century and in the present. Overall, there is no clear indication of an impact of former and present fish farming in the Øksfjord basins.

CRediT authorship contribution statement

Anouk T. Klootwijk: Conceptualization, Investigation, Data curation, Formal analysis, Writing - original draft. **Elisabeth Alve:** Conceptualization, Funding acquisition, Project administration, Writing - review & editing. **Silvia Hess:** Conceptualization, Funding acquisition, Writing - review & editing. **Paul E. Renaud:** Conceptualization, Funding acquisition, Writing - review & editing. **Carsten Sørlie:** Data curation. **Jane K. Dolven:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the following people: the crew of Brattholmen (MMSI257602700), Charlotte, Jack, Simon and Runar; Per-Arne Emaus, Odd Leknes and Gaute Rørvik Salomonsen for their personal comments; Professor Peter Appleby and Dr Gayane Piliposyan for the radiometric dating; Mufak Naoroz for assisting laboratory analyses; Carl Ballantine for helping during the writing process; Beata Sternal for providing her TOC and grain size data; Andrey Sikorski (polychaetes), Jesper Hansen (molluscs), Hans Petter Mannvik (echinoderms), and Roger Velvin (other taxa) for the macrofaunal analyses. The authors would also like to thank the two anonymous reviewers for their valuable comments on the manuscript. This project was partly funded by the Norwegian Environment Agency (MD17SF8F99) and the Research Council of Norway ('JellyFarm' project: RCN #244572).

Appendix A. Taxonomic list of the benthic foraminifera

Brizalina skagerrakensis (Qvale and Nigam) = *Bolivina skagerrakensis* Qvale and Nigam, 1985
Bulimina marginata d'Orbigny, 1826
Cassidulina reniforme Nørvang, 1945
Cibicides lobatulus (Walker and Jacob) = Nautilus lobatulus Walker and Jacob, 1798
Cibicides refulgens Montfort, 1808
Epistominella vitrea Parker, 1953
Stainforthia feylingi Knudsen and Seidenkrantz, 1994
Stainforthia fusiformis (Williamson) = Bulimina pupoides d'Orbigny var. fusiformis Williamson, 1858

Appendix B. Geochemical and foraminiferal parameters

Table B.1
The D2-6A porosity (%), uncorrected TOC (%), Fine fraction (% < 63 μm), TOC_{63} (mg/g), N (%), C/N ratios, $\delta^{13}C_{VPDB}$, fES_{100}, fAMBI, fNQI, $fHlog_2$, and the D2-5B porosity (%), Cu (mg/kg), Zn (mg/kg), Ni (mg/kg). Classification of the geochemical parameters and foraminiferal parameters are according to the Veileder (02:2018) and Alve et al. (2019), respectively.

Status	High	Good	Moderate	Poor	Bad

Core	Interval	Porosity	TOC	Fine fraction	TOC_{63}	N	C/N	$\delta^{13}C_{V-PDB}$	fES_{100}	fAMBI	fNQI	$fHlog_2$	Core	Interval	Porosity	Cu	Zn	Ni
	(cm)	(%)	(%)	(%<63μm)	(mg/g)	(%)		(‰)						(cm)	(%)	(mg/kg)	(mg/kg)	(mg/kg)
D2-6A	0-1	76	2.66	94	28	0.42	6.27	-22.67	25	2.14	0.71	4.36	D2-5B	0-1	76	57	100	57
D2-6A	1-2	71	2.66	89	29	0.42	6.32	-22.45	25	2.41	0.69	4.28	D2-5B	1-2	71	61	97	56
D2-6A	2-3	68	2.63	92	28	0.41	6.37	-22.41	23	2.45	0.66	4.16	D2-5B	2-3	65	60	100	60
D2-6A	3-4	64	2.42	93	25	0.37	6.47	-22.35	24	2.52	0.67	4.25	D2-5B	3-4	60	63	110	63
D2-6A	4-5	59	2.06	92	22	0.32	6.53	-22.36	26	2.57	0.69	4.30	D2-5B	4-5/5-6 A	55	75	110	75
D2-6A	5-6	54	1.62	95	17	0.25	6.59	-22.35	24	1.78	0.72	4.17	D2-5B	4-5/5-6 B	49	72	85	66
D2-6A	6-7	49	1.01	96	11	0.15	6.90	-22.18					D2-5B	6-7	45	72	75	62
D2-6A	7-8	46	0.87	96	9	0.13	6.68	-22.17	25	1.47	0.76	4.19	D2-5B	7-8	36	35	40	38
D2-6A	8-9	47	0.88	95	10	0.13	6.87	-22.30					D2-5B	8-9	26			
D2-6A	9-10	44	0.78	94	9	0.11	6.88	-22.37					D2-5B	9-10	45			
D2-6A	10-11	35	0.74	74	12	0.09	7.81	-23.20					D2-5B	10-11	59			
D2-6A	11-12	25	0.20	28	15	0.03	7.00	-22.22	21	0.72	0.74	3.74	D2-5B	11-12	60			
D2-6A	12-13	33	0.88	71	14	0.11	8.34	-22.28					D2-5B	12-13	61			
D2-6A	13-14	54	2.30	87	25	0.34	6.73	-21.95					D2-5B	13-14	61			
D2-6A	14-15	60	3.13	68	37	0.47	6.66	-22.04	22	1.85	0.68	3.83	D2-5B	14-15	62			
D2-6A	15-16	59	3.19	74	36	0.46	7.00	-21.89					D2-5B	15-16	62			
D2-6A	16-17	59	3.05	81	34	0.47	6.51	-21.80	22	1.85	0.68	3.81	D2-5B	16-17	54	70	130	75
D2-6A	17-18	60	3.31	75	38	0.48	6.89	-21.81	22	2.34	0.64	3.93	D2-5B	17-18	69			
D2-6A	18-19	61	3.20	75	36	0.47	6.85	-21.74					D2-5B	18-19	61			
D2-6A	19-20	61	3.21	94	33	0.48	6.73	-21.77	21	2.13	0.65	3.94	D2-5B	19-20	60	58	110	79
D2-6A	20-22	60	3.10	96	32	0.48	6.41	-21.82					D2-5B	20-22	60			
D2-6A	22-24	59	3.08	95	32	0.47	6.58	-21.76	22	1.64	0.70	3.76	D2-5B	22-24	60			
D2-6A	24-26	58	3.09	95	32	0.46	6.79	-21.78					D2-5B	24-26	61			
D2-6A	26-28	57	3.00	95	31	0.44	6.83	-21.79	19	1.89	0.64	3.56	D2-5B	26-28	59	66	100	87
D2-6A	28-30	57	2.95	95	30	0.43	6.89	-21.65					D2-5B	28-30	58			
D2-6A	30-32	56	2.86	95	29	0.43	6.60	-21.65	21	1.36	0.71	3.87	D2-5B	30-32	58			
D2-6A	32-34	56	2.96	95	30	0.42	7.08	-21.63					D2-5B	32-34	56			
D2-6A	34-36	56	2.93	95	30	0.42	6.95	-21.68					D2-5B	34-36	56			
D2-6A	36-38	55	2.93	95	30	0.42	6.95	-21.61					D2-5B	36-38	55			
D2-6A	38-40	54	2.85	95	29	0.42	6.75	-21.57					D2-5B	38-40	55			
D2-6A	40-42	55	2.92	95	30	0.41	7.06	-21.58					D2-5B	40-42	55	44	68	62

Table B.2
The D3-3B/13A porosity (%), uncorrected TOC (%), Grain size (% < 63 μm), TOC_{63} (mg/g), N (%), C/N ratios, $\delta^{13}C_{VPDB}$, fES_{100}, fAMBI, fNQI, $fHlog_2$ and the D3-13A porosity (%), Cu (mg/kg), Zn (mg/kg), Ni (mg/kg). Classification of the geochemical parameters and foraminiferal parameters are acording to the Veileder (02:2018) and Alve et al. (2019), respectively.

Status	High	Good	Moderate	Poor	Bad

Core	Interval	Porosity	TOC	Fine fraction	TOC_{63}	N	C/N	$\delta^{13}C_{V-PDB}$	fES_{100}	fAMBI	fNQI	$fHlog_2$	Core	Interval	Porosity	Cu	Zn	Ni
	(cm)	(%)	(%)	(%<63μm)	(mg/g)	(%)		(‰)						(cm)	(%)	(mg/kg)	(mg/kg)	(mg/kg)
D3-3B	0-1	58	1.25	77	17	0.24	5.30	-22.81	28	2.99	0.69	4.35	D3-13A	0-1	63	38	66	37
D3-3B	1-2	50	1.19	74	17	0.21	5.60	-22.69	27	3.05	0.66	4.24	D3-13A	1-2	54	29	59	32
D3-3B	2-3	45	1.07	64	17	0.18	5.82	-22.45	26	2.91	0.66	4.06	D3-13A	2-3	50	29	61	34
D3-3B	3-4	37	0.80	58	16	0.13	6.10	-22.20	24	2.27	0.68	4.00	D3-13A	3-4	44	24	55	32
D3-3B	4-5	36	0.69	57	15	0.12	5.67	-22.04	27	1.92	0.75	4.40	D3-13A	4-5	41	20	47	32
D3-3B	5-6	30	0.65	53	15	0.10	6.48	-22.02	27	2.41	0.72	4.50	D3-13A	11-12	26	16	31	27
D3-3B	6-7	28	0.50	50	14	0.09	5.33	-22.06					D3-13A	16-17	41	27	46	36
D3-3B	7-8	27	0.47	53	13	0.09	5.01	-21.90	24	1.16	0.76	4.07	D3-13A	22-24	35	52	78	49
D3-3B	8-9	26	0.50	55	13	0.09	5.27	-21.98					D3-13A	28-30	36	47	70	56
D3-3B	9-10	25	0.45	53	13	0.09	5.17	-21.82										
D3-3B	10-11	24	0.50	56	13	0.08	6.26	-21.96										
D3-3B	11-12	26	0.55	59	13	0.09	6.47	-22.44	21	1.40	0.69	3.67						
D3-3B	12-13	26	0.39	57	12	0.08	4.84	-21.69										
D3-3B	13-14	24	0.55	56	13	0.07	7.52	-21.92										
D3-13A	0-1	63	1.14	80	15	0.24	4.79	-22.42										
D3-13A	4-5	41	0.79	73	13	0.16	4.86	-22.15										
D3-13A	9-10	29	0.54	60	13	0.10	5.28	-21.95										
D3-13A	10-11	27	0.65	69	12	0.10	6.65	-22.01										
D3-13A	12-13	27	0.52	73	10	0.09	5.60	-22.31										
D3-13A	14-15	29	0.59	82	9	0.08	7.17	-22.12	23	2.01	0.68	3.82						
D3-13A	16-17	29	0.53			0.08	6.54	-22.25										
D3-13A	18-19	29	0.52	81	9	0.08	6.83	-22.38	20	1.92	0.65	3.67						
D3-13A	22-24	35	0.54	89	7	0.08	6.61	-22.59	18	2.53	0.58	3.46						
D3-13A	26-28	35	0.55	92	7	0.08	7.00	-22.64	17	2.35	0.57	3.26						

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106818.

References

Alve, E., 2003. A common opportunistic foraminiferal species as an indicator of rapidly changing conditions in a range of environments. Estuar. Coast. Shelf Sci. 57, 501–514. https://doi.org/10.1016/S0272-7714(02)00383-9.

Alve, E., 1995. Benthic foraminiferal responses to estuarine pollution: a review. J. Foraminifer. Res. https://doi.org/10.2113/gsjfr.25.3.190.

Alve, E., Hess, S., Bouchet, V.M.P., Dolven, J.K., Rygg, B., 2019. Intercalibration of benthic foraminiferal and macrofaunal biotic indices: An example from the Norwegian Skagerrak coast (NE North Sea). Ecol. Indic. 96, 107–115. https://doi.org/10.1016/j.ecolind.2018.08.037.

Alve, E., Korsun, S., Schönfeld, J., Dijkstra, N., Golikova, E., Hess, S., Husum, K., Panieri, G., 2016. Foram-AMBI: a sensitivity index based on benthic foraminiferal faunas from North-East Atlantic and Arctic fjords, continental shelves and slopes. Mar. Micropaleontol. 122, 1–12. https://doi.org/10.1016/j.marmicro.2015.11.001.

Alve, E., Lepland, A., Magnusson, J., Backer-Owe, K., 2009. Monitoring strategies for re-establishment of ecological reference conditions: possibilities and limitations. Mar. Pollut. Bull. 59, 297–310. https://doi.org/10.1016/j.marpolbul.2009.08.011.

Appleby, P.G., Nolan, P.J., Gifford, D.W., Godfrey, M.J., Oldfield, F., Anderson, N.J., Battarbee, R.W., 1986. 210Pb dating by low background gamma counting. Hydrobiologia 143, 21–27. https://doi.org/10.1007/BF00026640.

Appleby, P.G., Oldfield, F., 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported 210Pb to the sediment. Catena 5, 1–8. https://doi.org/10.1016/S0341-8162(78)80002-2.

Asteman, P.I., Risebrobakken, B., Moros, M., Binczewska, A., Dobosz, S., Jansen, E., Sławińska, J., Bąk, M., 2018. Late Holocene palaeoproductivity changes: a multi-proxy study in the Norwegian Trench and the Skagerrak, North Sea. Boreas 47, 238–255. https://doi.org/10.1111/bor.12264.

Bannister, R.J., Johnsen, I.A., Hansen, P.K., Kutti, T., Asplin, T., 2016. Changes in benthic sediment conditions under an atlantic salmon farm at a deep, well-flushed coastal site. Aquac. Environ. Interact. 5, 2408–2419. https://doi.org/10.3354/aei00092.

Berge, D.M., 2000. Samfunn, entreprenørskap og kunnskapsspredning i norsk fiskeoppdrett på 1970-tallet., in: Innovasjonspolitikk, Kunnskapsflyt Og Regional Utvikling, Trondheim: Tapir Akademisk Forlag. pp. 159–178.

Bjørn, P.A., Uglem, I., Kerwath, S., Sæther, B.S., Nilsen, R., 2009. Spatiotemporal distribution of Atlantic cod (Gadus morhua L.) with intact and blocked olfactory sense during the spawning season in a Norwegian fjord with intensive salmon farming. Aquaculture 286, 36–44. https://doi.org/10.1016/j.aquaculture.2008.08.038.

Borja, Á., Dauer, D.M., Grémare, A., 2012. The importance of setting targets and reference conditions in assessing marine ecosystem quality. Ecol. Indic. 12, 1–7. https://doi.org/10.1016/j.ecolind.2011.06.018.

Borja, A., Franco, J., Muxika, I., 2003. Classification tools for marine ecological quality assessment: the usefulness of macrobenthic communities in an area affected by a submarine outfall. ICES C. 2003/Session J-02, Tallinn. Est. Sept. 24–28, 1–10.

Borja, A., Franco, J., Pérez, V., 2000. A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40, 1100–1114. https://doi.org/10.1016/S0025-326X(00)00061-8.

Borja, A., Muxika, I., 2005. Guidelines for the use of AMBI (AZTI's Marine Biotic Index) in the assessment of the benthic ecological quality. Mar. Pollut. Bull. 50, 787–789. https://doi.org/10.1016/j.marpolbul.2005.04.040.

Bouchet, V.M.P., Alve, E., Rygg, B., Telford, R.J., 2012. Benthic foraminifera provide a promising tool for ecological quality assessment of marine waters. Ecol. Indic. 23, 66–75. https://doi.org/10.1016/j.ecolind.2012.03.011.

Bouchet, V.M.P., Deldicq, N., Baux, N., Dauvin, J., Pezy, J., Seuront, L., Méar, Y., 2020. Benthic foraminifera to assess ecological quality statuses: the case of salmon fish farming. Ecol. Indic. 117.

Brooks, K.M., Mahnken, C.V.W., 2003a. Interactions of Atlantic salmon in the Pacific northwest environment. II. Organic wastes. Fish. Res.. https://doi.org/10.1016/S0165-7836(03)00064-X.

Brooks, K.M., Mahnken, C.V.W., 2003b. Interactions of Atlantic salmon in the Pacific Northwest environment. III. Accumulation of zinc and copper. Fish. Res. 62, 295–305. https://doi.org/10.1016/S0165-7836(03)00065-1.

Burridge, L., Weis, J.S., Cabello, F., Pizarro, J., Bostick, K., 2010. Chemical use in salmon aquaculture: a review of current practices and possible environmental effects. Aquaculture 306, 7–23. https://doi.org/10.1016/j.aquaculture.2010.05.020.

Carroll, M.L., Cochrane, S., Fieler, R., Velvin, R., White, P., 2003. Organic enrichment of sediments from salmon farming in Norway: environmental factors, management practices, and monitoring techniques. Aquaculture 226, 165–180. https://doi.org/10.1016/S0044-8486(03)00475-7.

Dean, R.J., Shimmield, T.M., Black, K.D., 2007. Copper, zinc and cadmium in marine cage fish farm sediments: an extensive survey. Environ. Pollut. 145, 84–95. https://doi.org/10.1016/j.envpol.2006.03.050.

Denoyelle, M., Jorissen, F.J., Martin, D., Galgani, F., Miné, J., 2010. Comparison of

benthic foraminifera and macrofaunal indicators of the impact of oil-based drill mud disposal. Mar. Pollut. Bull. 60, 2007–2021. https://doi.org/10.1016/j.marpolbul.2010.07.024.
Dolven, J.K., Alve, E., Rygg, B., Magnusson, J., 2013. Defining past ecological status and in situ reference conditions using benthic foraminifera: a case study from the Oslofjord, Norway. Ecol. Indic. 29, 219–233. https://doi.org/10.1016/j.ecolind.2012.12.031.
Duffield, C., Alve, E., Andersen, N., Andersen, T., Hess, S., Strohmeier, T., 2017. Spatial and temporal organic carbon burial along a fjord to coast transect: a case study from Western Norway. Holocene 095968361769058. https://doi.org/10.1177/0959683617690588.
Duffield, C.J., Hess, S., Norling, K., Alve, E., 2015. The response of Nonionella iridea and other benthic foraminifera to "fresh" organic matter enrichment and physical disturbance. Mar. Micropaleontol. 120, 20–30. https://doi.org/10.1016/j.marmicro.2015.08.002.
Elmgren, R., 1973. Methods of sampling sublittoral soft bottom meiofauna. Oikos Suppl. 15, 112–120.
Fontanier, C., Jorissen, F., Licari, L., Alexandre, A., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. Deep Sea Res. Part I. Oceanogr. Res. Pap. 49, 751–785. https://doi.org/10.1016/s0967-0637(01)00078-4.
Gooday, A.J., 1988. A response by benthic Foraminifera to the deposition of phytodetritus in the deep sea. Nature 332, 70–73. https://doi.org/10.1038/332070a0.
Grémare, A., Labrune, C., Vanden Berghe, E., Amouroux, J.M., Bachelet, G., Zettler, M.L., Vanaverbeke, J., Fleischer, D., Bigot, L., Maire, O., Deflandre, B., Craeymeersch, J., Degraer, S., Dounas, C., Duineveld, G., Heip, C., Herrmann, M., Hummel, H., Karakassis, I., Kędra, M., Kendall, M., Kingston, P., Laudien, J., Occhipinti-Ambrogi, A., Rachor, E., Sardá, R., Speybroeck, J., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Włodarska-Kowalczuk, M., Zenetos, A., 2009. Comparison of the performances of two biotic indices based on the MacroBen database. Mar. Ecol. Prog. Ser. 382, 297–311. https://doi.org/10.3354/meps08030.
Gustafsson, M., Nordberg, K., 2001. Living (stained) benthic foraminiferal response to primary production and hydrography in the deepest part of the Gullmar Fjord, Swedish west coast, with comparisons to Höglund's 1927 material. J. Foraminifer. Res. 31, 2–11. https://doi.org/10.2113/0310002.
Henderson, R.J., Forrest, D.A.M., Black, K.D., Park, M.T., 1997. The lipid composition of sealoch sediments underlying salmon cages. Aquaculture 158, 69–83. https://doi.org/10.1016/S0044-8486(97)00207-X.
Herguera, J.C., Berger, W.H., 1991. Paleoproductivity from benthic foraminifera abundance: glacial to postglacial change in the west-equatorial Pacific. Geology 19, 1173–1176. https://doi.org/10.1130/0091-7613(1991)019<1173:PFBFAG>2.3.CO;2.
Hess, S., Alve, E., Andersen, T.J., Joranger, T., 2020. Defining ecological reference conditions in naturally stressed environments – how difficult is it? Mar. Environ. Res. 156. https://doi.org/10.1016/j.marenvres.2020.104885.
Holmer, M., 2010. Environmental issues of fish farming in offshore waters: Perspectives, concerns and research needs. Aquac. Environ. Interact. 1, 57–70. https://doi.org/10.3354/aei00007.
Holte, B., Oug, E., Dahle, S., 2005. Soft-bottom fauna and oxygen minima in sub-arctic north Norwegian marine sill basins. Mar. Biol. Res. 1, 85–96. https://doi.org/10.1080/17451000510019033.
Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecol. Soc. Am. 52, 577–586. https://doi.org/10.2307/1934145.
Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K., Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). Mar. Biol. Res. 10, 241–252. https://doi.org/10.1080/17451000.2013.810754.
Jansen, H.M., Broch, O.J., Bannister, R., Cranford, P., Handå, A., Husa, V., Jiang, Z., Strohmeier, T., Strand,, 2018. Spatio-temporal dynamics in the dissolved nutrient waste plume from Norwegian salmon cage aquaculture. Aquac. Environ. Interact. 10, 385–399. https://doi.org/10.3354/AEI00276.
Johnsen, R., Lunestad, B., 1993. Environmental distribution of organic waste from a marine fish farm. Aquaculiure 118, 229–244. https://doi.org/10.1016/0044-8486(93)90459-C.
Keck, A., Wassmann, P., 1996. Temporal and spatial patterns of sedimentation in the subarctic fjord malangen, Northern Norway. Sarsia 80, 259–276. https://doi.org/10.1080/00364827.1996.10413600.
Krauskopf, K.B., 1954. Igneous and Metamorphic Rocks of the Øksfjord Area, Vest-Finnmark. In: Norges Geologiske Undersökelse, Arbok, vol. 188. pp. 29–50.
Kuliński, K., Kedra, M., Legezyńska, J., Gluchowska, M., Zaborska, A., 2014. Particulate organic matter sinks and sources in high Arctic fjord. J. Mar. Syst. 139, 27–37. https://doi.org/10.1016/j.jmarsys.2014.04.018.
Kutti, T., Ervik, A., Hansen, P.K., 2007a. Effects of organic effluents from a salmon farm on a fjord system. I. Vertical export and dispersal processes. Aquaculture 262, 367–381. https://doi.org/10.1016/j.aquaculture.2006.10.010.
Kutti, T., Ervik, A., Høisæter, T., 2008. Effects of organic effluents from a salmon farm on a fjord system. III. Linking deposition rates of organic matter and benthic productivity. Aquaculture 282, 47–53. https://doi.org/10.1016/j.aquaculture.2008.06.032.
Kutti, T., Hansen, P.K., Ervik, A., Høisæter, T., Johannessen, P., 2007b. Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. Aquaculture 262, 355–366. https://doi.org/10.1016/j.aquaculture.2006.10.008.
Lalande, C., Dunlop, K., Renaud, P.E., Nadaï, G., Sweetman, A.K., 2020. Seasonal variations in downward particle fluxes in Norwegian fjords. Estuar. Coast. Shelf Sci. 241, 106811. https://doi.org/10.1016/j.ecss.2020.106811.
Mackensen, A., Sejrup, H.P., Jansen, E., 1985. the distribution of living benthic foraminifera on the continental slope and rise off southwest Norway. Mar. Micropaleontol. 9, 275–306. https://doi.org/10.1016/0377-8398(85)90001-5.
Martin, R., 1999. Taphonomy and temporal resolution of fora- miniferal assemblages. In: Sen Gupta, B.K. (Ed.) Modern Foraminifera. Kluwer Academics Publishers, New York, pp. 281–298., n.d. https://doi.org/10.1007/0-306-48104-9.
Mayr, C.C., Försterra, G., Häussermann, V., Wunderlich, A., Grau, J., Zieringer, M., Altenbach, A.V., 2011. Stable isotope variability in a chilean fjord food web: Implications for N- and C-cycles. Mar. Ecol. Prog. Ser. 428, 89–104. https://doi.org/10.3354/meps09015.
Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chem. Geol. 114, 289–302. https://doi.org/10.1016/0009-2541(94)90059-0.
Murray, J.W., 2000. The enigma of the continued use of total assemblages in ecological studies of benthic foraminifera. J. Foraminifer. Res. 30, 244–245. https://doi.org/10.2113/0300244.
Niemistö, L., 1974. A gravity corer for studies of soft sediment. Merentutkimuslait. Julk./Havsforskningsinst Helsinki 238, 33–38.
Noji, T.T., Noji, C.I.M., Barthel, K.G., 1993. Pelagic-benthic coupling during the onset of winter in a northern Norwegian fjord. Carbon flow and fate of suspended particulate matter. Mar. Ecol. Prog. Ser. 93, 89–99. https://doi.org/10.3354/meps093089.
Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. An Annu. Rev. 16, 229–311. https://doi.org/10.2983/035.034.0121u1.10.
Quiñones, R.A., Fuentes, M., Montes, R.M., Soto, D., León-Muñoz, J., 2019. Environmental issues in Chilean salmon farming: a review. Rev. Aquac. 11, 375–402. https://doi.org/10.1111/raq.12337.
R Core team, 2020. R A Lang. Environ. Stat. Comput. R Found. Stat. Comput., Vienna, Austria. ISBN 3-900051-07-0, URL http//www.R-project.org/.
Rea, B.R., Whalley, W.B., Rainey, M.M., Gordon, J.E., 1996. Blockfields, old or new? Evidence and implications from some plateaus in northern Norway. Geomorphology 15, 109–121. https://doi.org/10.1016/0169-555X(95)00118-O.
Reimann, C., Caritat de, P., 1998. Geochemical atlas of Finland, Part2: Geological Survey of Finland, Espoo, Finland, 218. In: Koljonen, T (Ed), 1992. Chemical Elements in the Environment. Springer, p. 398. https://doi.org/10.1016/0009-2541(94)90076-0.
Rudnick, D., 1989. Time lags between the deposition and meiobenthic assimilation of phytodetritus. Mar. Ecol. Prog. Ser. 50, 231–240. https://doi.org/10.3354/meps050231.
Rygg, B., Norling, K., 2013. Norwegian Sensitivity Index (NSI) for marine macroinvertebrates, and an update of Indicator Species Index (ISI), NIVA report 6475.
Sauer, S., Hong, W.-L., Knies, J., Lepland, A., Forwick, M., Klug, M., Eichinger, F., Baranwal, S., Crémière, A., Chand, S., Schubert, C.J., 2016. Sources and turnover of organic carbon and methane in fjord and shelf sediments off northern Norway. Geochem. Geophys. Geosystems 17, 4011–4031. https://doi.org/10.1002/2016GC006296.
Schafer, C.T., 2000. Monitoring nearshore marine environments using benthic foraminifera: Some protocols and pitfalls. Micropaleontology 46, 161–169.
Schönfeld, J., 2002. Recent benthic foraminiferal assemblages in deep high-energy environments from the Gulf of Cadiz (Spain). Mar. Micropaleontol. 44, 141–162. https://doi.org/10.1016/S0377-8398(01)00039-1.
Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Abramovich, S., Almogi-Labin, A., du Chatelet, E.A., Barras, C., Bergamin, L., Bicchi, E., Bouchet, V., Cearreta, A., Di Bella, L., Dijkstra, N., Disaro, S.T., Ferraro, L., Frontalini, F., Gennari, G., Golikova, E., Haynert, K., Hess, S., Husum, K., Martins, V., McGann, M., Oron, S., Romano, E., Sousa, S.M., Tsujimoto, A., 2012. The FOBIMO (FOraminiferal BIoMOnitoring) initiative-Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. Mar. Micropaleontol. 94–95, 1–13. https://doi.org/10.1016/j.marmicro.2012.06.001.
Shannon, C.E., Weaver, W., 1963. The Mathematical Theory of Communication. University of Illinois Press.
Sommer, U., Lengfellner, K., 2008. Climate change and the timing, magnitude, and composition of the phytoplankton spring bloom. Glob. Chang. Biol. 14, 1199–1208. https://doi.org/10.1111/j.1365-2486.2008.01571.x.
Sternal, B., Junttila, J., Skirbekk, K., Forwick, M., Carroll, J.L., Pedersen, K.B., 2017. The impact of submarine copper mine tailing disposal from the 1970s on Repparfjorden, northern Norway. Mar. Pollut. Bull. 120, 136–153. https://doi.org/10.1016/j.marpolbul.2017.04.054.
Sweetman, A.K., Chelsky, A., Pitt, K.A., Andrade, H., van Oevelen, D., Renaud, P.E., 2016. Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. Limnol. Oceanogr. 61, 1449–1461. https://doi.org/10.1002/lno.10310.
Sweetman, A.K., Norling, K., Gunderstad, C., Haugland, B.T., Dale, T., 2014. Benthic ecosystem functioning beneath fish farms in different hydrodynamic environments. Limnol. Oceanogr. 59, 1139–1151. https://doi.org/10.4319/lo.2014.59.4.1139.
Turner, A., Olsen, Y.S., 2000. Chemical versus enzymatic digestion of contaminated estuarine sediment: relative importance of iron and manganese oxides in controlling trace metal bioavailability. Estuar. Coast. Shelf Sci. 51, 717–728. https://doi.org/10.1006/ecss.2000.0725.
Veileder (02:2018), Klassifisering av miljøtilstand i vann (Økologisk og kjemisk klassifiseringssystem for kystvann, grunnvann, innsjøer og elver., 2018.
Velvin, R., Emaus, P.A., 2015. Grieg Seafood Finnmark. Miljøovervåking i Øksfjorden, Loppa kommune 2015, 1–43.
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. https://doi.org/10.1016/0924-7963(95)00037-2.
WDF, 2000. Common Implementation Strategy for the Water Framework Directive (2000/60/EC). Guidance Document No. 5. Transitional and Coastal Waters -

typology, reference conditions and classification systems., Produced by Working Group 2.4 – Coast.
Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698, 5–16. https://doi.org/10.1007/s10750-012-1149-2.
Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., Speybroeck, J., Tagliapietra, D., Van Hoey, G., Ysebaert, T., 2013. On the myths of indicator species: issues and further consideration in the use of static concepts for ecological applications. PLoS One 8. https://doi.org/10.1371/journal.pone.0078219.
Zhulay, I., Reiss, K., Reiss, H., 2015. Effects of aquaculture fallowing on the recovery of macrofauna communities. Mar. Pollut. Bull. 97, 381–390. https://doi.org/10.1016/j.marpolbul.2015.05.064.

Supplementary material Paper I: Radiometric dating graphs

Main Basin: D2-6A

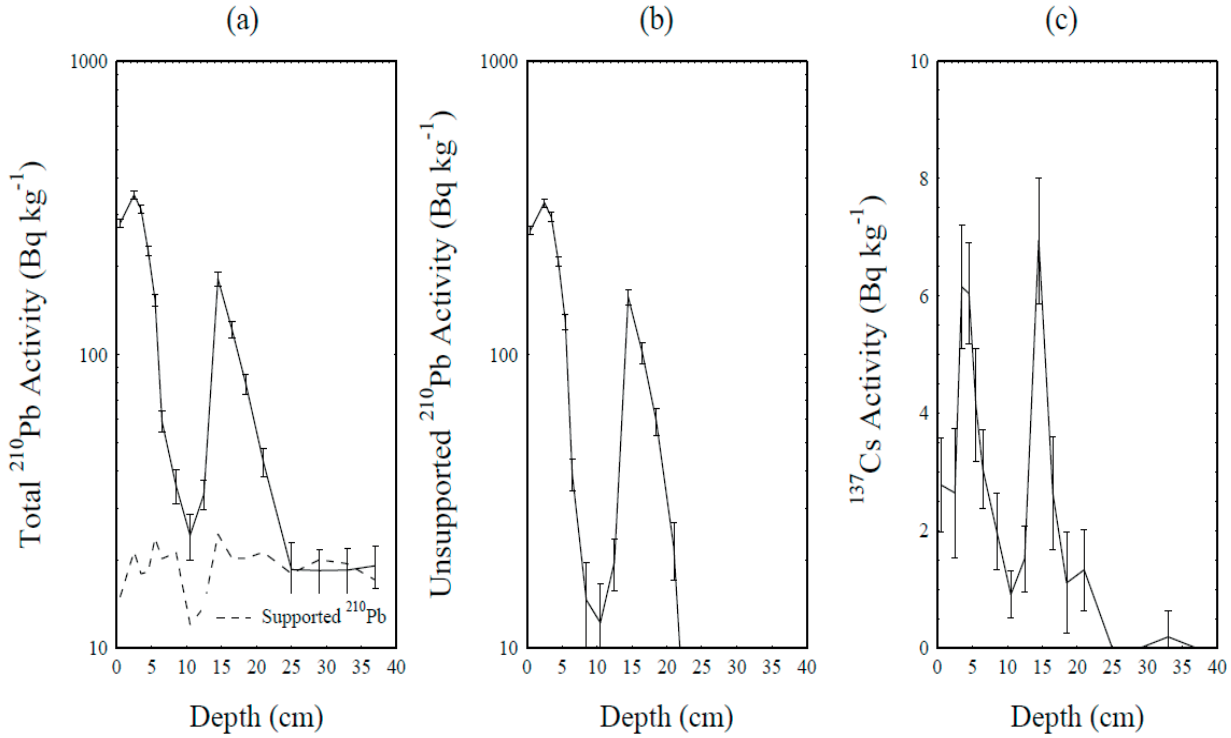


Figure 1: Fallout radionuclides in the main-basin sediment core (D2-6A) showing a) total and supported ^{210}Pb, b) unsupported ^{210}Pb, and c) ^{137}Cs concentrations, plotted against depth. The graphs come from the Øksfjorden dating report written by Professor emeritus Peter G. Appleby and Dr. Gayane Piliposyan.

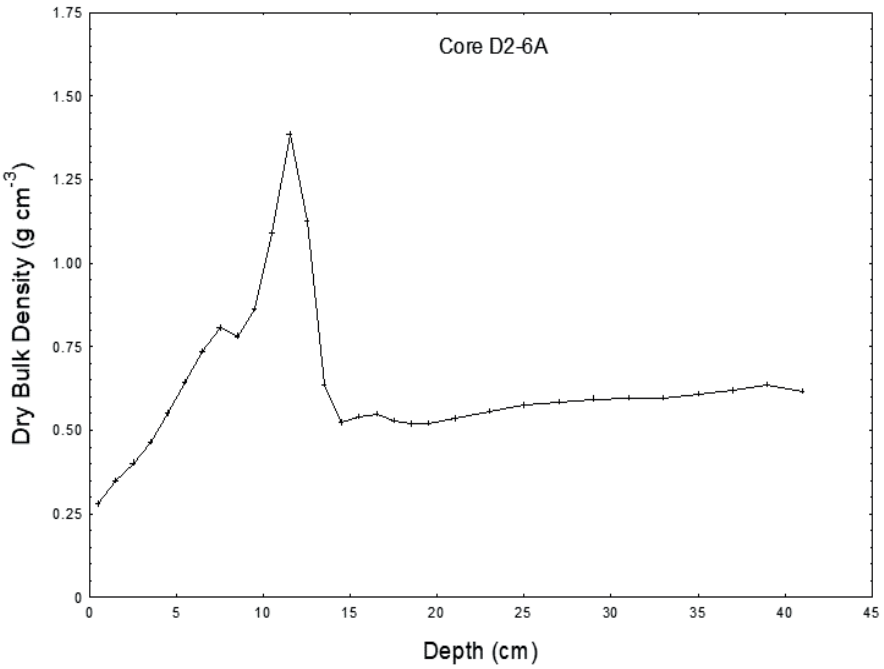


Figure 2: The sediment dry bulk density plotted against depth. The graph comes from the Øksfjorden dating report written by Professor emeritus Peter G. Appleby and Dr. Gayane Piliposyan.

Sub-basin: D3-3B

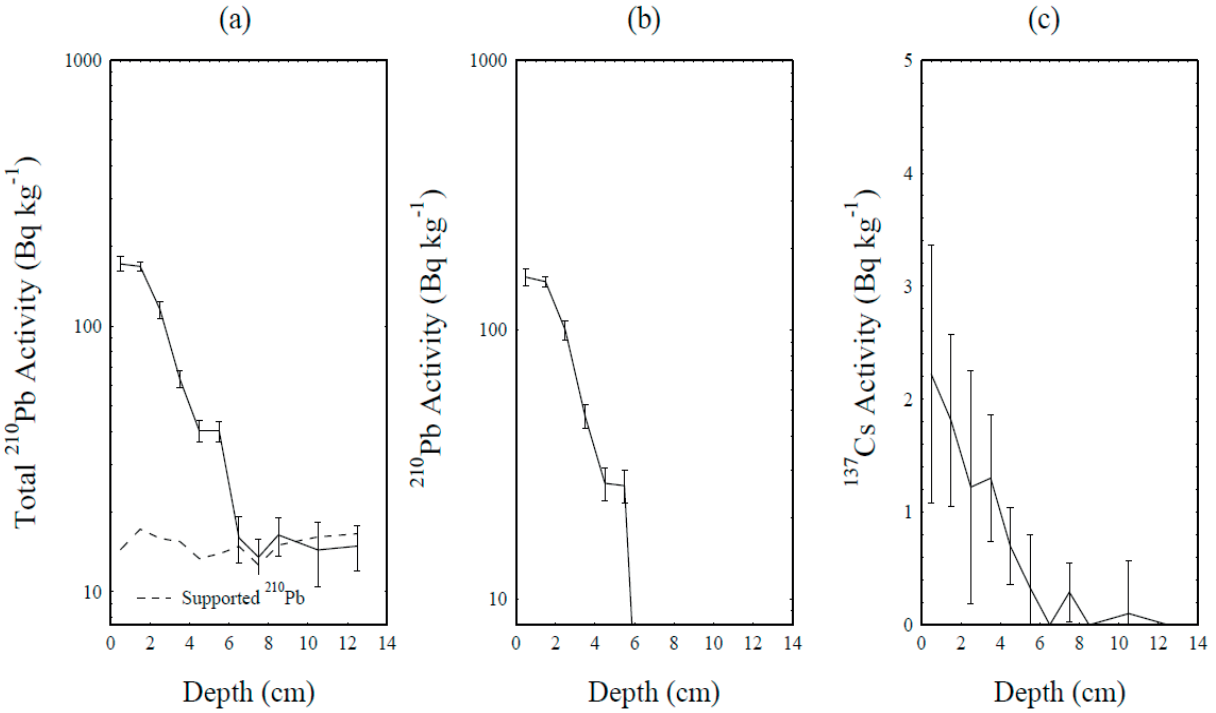


Figure 3: Fallout radionuclides in the sub-basin sediment core (D3-3B) showing a) total and supported ^{210}Pb, b) unsupported ^{210}Pb, and c) ^{137}Cs concentrations, plotted against depth. The graphs come from the Øksfjorden dating report written by Professor emeritus Peter G. Appleby and Dr. Gayane Piliposyan.

Paper II (Published):

Klootwijk, A.T., Sweetman, A.K., Hess, S., Alve, E., Dunlop, K.M. and Renaud, P.E., 2021. Benthic foraminiferal carbon cycling in coastal zone sediments: The influence of the assemblage structure and jellyfish detritus. Estuarine, Coastal and Shelf Science, p.107535. https://doi.org/10.1016/j.ecss.2021.107535.

Estuarine, Coastal and Shelf Science 261 (2021) 107535

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Benthic foraminiferal carbon cycling in coastal zone sediments: The influence of the assemblage structure and jellyfish detritus

Anouk T. Klootwijk [a,*], Andrew K. Sweetman [b], Silvia Hess [a], Elisabeth Alve [a], Kathrine M. Dunlop [c,1], Paul E. Renaud [c,d]

[a] Department of Geosciences, University of Oslo, PO box, 1047 Blindern, 0316, Oslo, Norway
[b] Deep-Sea Ecology and Biogeochemistry Research Group, The Lyell Centre for Earth and Marine Science, Heriot-Watt University, Edinburgh, UK
[c] Akvaplan-niva, Fram Centre for Climate and the Environment, 9296, Tromsø, Norway
[d] University Centre in Svalbard, 9171, Longyearbyen, Norway

ARTICLE INFO

Keywords:
Benthic foraminiferal carbon uptake
Sediment organic geochemistry
Jellyfish-detritus
Sediment O_2 dynamics
Fjord-to-coast gradient
Northern Norway

ABSTRACT

Jellyfish carrion is an important carbon source to the benthic ecosystem that is expected to increase in some regions in the future, but its potential impact on sediment biochemical processes is not fully understood. Benthic foraminifera play important carbon processing roles in marine ecosystems but little is known about how they process carbon within fjords, or how jellyfish detritus on the sediment may affect this role. This study is the first to use ^{13}C-labelled algae to quantify how jellyfish detritus may alter benthic foraminiferal microalgal-carbon uptake (C-uptake) from the inner to outer fjord. To assess potential mechanisms for variations in C-uptake, foraminiferal biomass, density, and assemblage composition, in addition to the sediment O_2 dynamics and environmental parameters (e.g. sediment total organic carbon [TOC] content) were investigated. Benthic foraminiferal C-cycling strongly varied within the fjord with 20-times higher C-uptake rates at the inner-fjord location compared to the locations further outwards. This difference was likely caused by the higher foraminiferal biomass and relative abundances of *Bulimina marginata* and *Nonionella turgida* at the inner location. Strong differences in foraminiferal assemblage structure amongst the locations were not explained by major differences in the investigated environmental parameters. Changes in sediment O_2 dynamics suggested that jellyfish detritus obstructed O_2 diffusion into the sediment. A potential effect of these changes on the C-uptake was only observed at the inner location, indicating the effect of jellyfish detritus on foraminiferal C-uptake rates was little and dependent on the benthic foraminiferal assemblage composition (e.g. the presence of *B. marginata*). This suggests that the areas in coastal zones where the highest amounts of organic carbon are being processed may also be the most sensitive to changes in the sediment O_2 dynamics, which would make them vulnerable to changes in riverine input and anthropogenic organic carbon enrichment.

1. Introduction

Fjords are transitional zones that connect terrestrial and oceanic systems and are characterized by gradients of terrigenous vs marine organic matter input moving from the inner fjord towards the outer region (Faust and Knies, 2019; Syvitski et al., 1987). The contribution of terrestrial organic carbon to the sediment generally declines moving from the inner fjord to the outer fjord (Duffield et al., 2017; Heiskanen and Tallberg, 1999), and marine organic carbon is generally regarded as more labile than terrestrial organic carbon for benthic ecosystems (e.g. Hedges and Keil, 1995). However, terrestrial carbon can comprise at least half of the organic carbon delivery to coastal sediment (Schlünz and Schneider, 2000). The quality and quantity of organic carbon input is known to alter benthic ecosystem functioning and community structure (e.g. Smith et al., 2008) but the mechanisms behind these interactions are poorly understood. Studying benthic environments in coastal zones will offer further insight into the mechanisms behind those interactions.

Benthic foraminifera are an abundant meiofaunal group in many marine sediments and respond rapidly to changing environmental

* Corresponding author. University of Oslo, P.O. box 1047, Blindern, 0316, Oslo, Norway.
E-mail addresses: a.t.klootwijk@geo.uio.no, anoukklootwijk@gmail.com (A.T. Klootwijk).
[1] present address: Institute of Marine Research, 9007 Tromsø, Norway.

https://doi.org/10.1016/j.ecss.2021.107535
Received 10 April 2021; Received in revised form 23 July 2021; Accepted 26 July 2021
Available online 3 August 2021

conditions (e.g. Sen Gupta, 1999). Benthic foraminiferal assemblage compositions have been shown to vary from the inner to outer fjord (Alve and Nagy, 1990; Duffield et al., 2017; Korsun and Hald, 2000), but also between adjacent fjord basins (Klootwijk et al., 2020). Differences in foraminiferal assemblage composition have been shown to be related to differences in food availability, bottom water oxygenation or substrate characteristics. Changes in benthic foraminiferal assemblage composition can lead to changes in their C (carbon)-cycling activity (Gooday et al., 1992; Sweetman et al., 2009), and the ecosystem functions they perform.

Sinking jellyfish particulate organic matter is an important pelagic carbon source to the benthic ecosystem (Lebrato et al., 2013; Sweetman et al., 2014b, 2016; Sweetman and Chapman, 2011, 2015) and is believed to be increasing in some areas due to anthropogenic and climate-driven changes (Billett et al., 2006; Mills, 2001; Purcell et al., 2007). In Norway, fishing activities and increasingly darker coastal waters are thought to have contributed to mass occurrences of the jellyfish *Periphylla periphylla* in some fjords during the last decades (Aksnes et al., 2009; Sørnes et al., 2007; Sweetman and Chapman, 2011). *P. periphylla* is originally characterised as a cold and deep-water scyphozoan that is mostly rare and exists only as a medusa. The species can adapt to a variety of environmental conditions unfavourable to fish and is therefore highly competitive with its main food competitor (Condon et al., 2012; Tiller et al., 2017). Recent observations suggest *P. periphylla* is becoming more abundant in northern Norwegian ecosystems where it has established healthy populations in several fjords (Tiller et al., 2017). Jellyfish carrion fluxes can be rapidly scavenged at the seafloor (Dunlop et al., 2018; Sweetman et al., 2014a, b), but experiments have shown that jellyfish decomposition increases the benthic O_2 demand (Chelsky et al., 2015, 2016; Condon et al., 2011; Sweetman et al., 2016; West et al., 2009) and causes significant shifts in benthic community functioning (Condon et al., 2011; Sweetman et al., 2016).

One successful method to assess benthic community functioning is through isotope tracer experiments. In such experiments, a food source is enriched with a stable isotope (^{13}C or ^{15}N) which is used to quantify consumers processing patterns and rates (e.g. Middelburg et al., 2000; Sweetman et al., 2016; Woulds et al., 2016). The feeding activities of benthic foraminifera have been successfully measured in previous isotope tracer studies (e.g. Enge et al., 2014; Moodley et al., 2002; Nomaki et al., 2005; Sweetman et al., 2009), which showed that benthic foraminifera play important carbon processing roles in marine ecosystems. Currently, however, little is known about how benthic foraminifera process carbon within fjords, or how jellyfish detritus may affect this role.

The aim of this study was to quantify how *P. periphylla* detritus alters benthic foraminiferal microalgal-carbon uptake (C-uptake) from the inner to outer fjord using ^{13}C-labelled algae as a tracer in an ex situ experiment. To address this aim, the following null hypotheses were tested: benthic foraminiferal C-uptake did not 1) *change when P. periphylla detritus was added;* 2) *differ from the inner to outer fjord;* and 3) *exhibit an interaction effect of P. periphylla addition and the sampled location.* To investigate potential influences of the foraminiferal assemblage structure on the C-uptake, the biomass, densities and assemblage composition of foraminifera were also evaluated. In addition, the role of environmental parameters, including the bulk sediment organic geochemistry and bottom water characteristics, in driving the foraminiferal assemblage structure and functioning was investigated. The sediment O_2 dynamics were explored using the same hypotheses as for the foraminiferal C-uptake and the results were compared with the foraminiferal C-uptake to investigate potential relationships. This is the first study investigating foraminiferal C-uptake from the inner region of a fjord to the outer region in combination with added jellyfish detritus, sediment O_2 dynamics and in situ environmental parameters. Therefore, this study will significantly contribute to our understanding of benthic foraminiferal functioning in coastal zone settings.

2. Material and methods

2.1. Site description

The ex situ experiment was carried out using sediment from Kaldfjorden, Northern Norway. Kaldfjorden is a 16 km long fjord consisting of an innermost, inner, and middle basin alongside an outer section that connects to Vengsøyfjorden. The basins and the outer section are approx. 40, 110, 150 and 240 m deep respectively, and are located at approx. 3.5, 13, and 15 km distance from the head of the fjord (Fig. 1). The innermost basin is separated from the inner basin by an approx. 50 m deep sill, which in turn is separated from the middle basin by a sill at approx. 55 m water depth. The middle basin and outer section are separated by a partial sill that is 75 m deep at the shallowest parts but with 150 m deep channels cutting through it. The outer section connects to Vengsøyfjorden without a sill. The basins are from here on referred to as the Innermost, Inner and Middle location, and the outer section as the Outer location.

There are no major rivers draining into Kaldfjorden (Fig. 1) and the maximum water column stratification is found from June until October (Jones et al., 2020). This stratification erodes during November and the water column is well mixed from December until May (Jones et al., 2020). In September 2017, the month when the samples for this study where obtained, the salinity in Kaldfjorden increased slightly from 33.4 in the surface waters to approx. 34.4 in the bottom waters at all three locations (Chierici et al., 2019). The sills between the basins and outer section are much deeper than the observed pycnocline, and do not obstruct the water exchange between the basins. Dissolved O_2 measurements from a Conductivity, Temperature, and Depth mounted OxyGuard Profile sensor from September 2017 indicated an O_2 saturation of at least 80 % in the seawater above the seafloor at all three locations in Kaldfjorden (Angelika Renner, Norwegian Institute of Marine Research, Tromsø, pers. com.). A sewage wastewater outlet installed in 1983 at the head of the fjord approx. 3.5 km away from the Inner location discharges mechanically treated wastewater from approx. 500 households into the fjord at 12 m water depth (Helø and Lejon, 2009).

2.2. Sediment sampling

Sediment was collected at approx. 110, 140 and 235 m depth from the Inner, Middle and Outer locations in Kaldfjorden respectively, in September 2017. At each location, four replicate box-cores (KC Denmark, 34.5 × 29 cm, 1000 cm^2) were collected and sub-sampled using three, clear acrylic experimental chambers (inner diameter 14 cm) pushed 25-cm deep into the sediment. Directly after sub-sampling, each chamber was randomly assigned to a Control, Low, or High experimental treatment (C, L, H), where Low and High indicated the amount of jellyfish to be added at a later stage. The chambers were transported to the Akvaplan-niva research station in Kraknes (Research Innovation Station Kraknes, FISK) for the experiment. From each box-core, an additional three smaller cores (inner diameter 4.7 cm) were taken to obtain samples for bulk sediment organic geochemistry, grain-size analyses, living (rose Bengal (rB) stained) foraminiferal assemblages and background ^{13}C isotope values of foraminiferal cytoplasm. The cores were visually assessed for disturbance, after which the two least disturbed surfaces were selected for the foraminiferal analyses, leaving the third for grain-size analyses and bulk sediment organic geochemistry. From the smaller cores, the upper 1 cm was sectioned on deck, and the rB-stained foraminiferal samples were preserved and stored in a 70% ethanol 2 g L^{-1} rB mixture (Schönfeld et al., 2012). Samples for bulk sediment organic geochemistry and background ^{13}C isotopes were kept frozen at −20 °C until analysis.

2.3. Preparation of ^{13}C labelled algae

The marine alga *Dunaliella tertiolecta*, was used as a labelled food

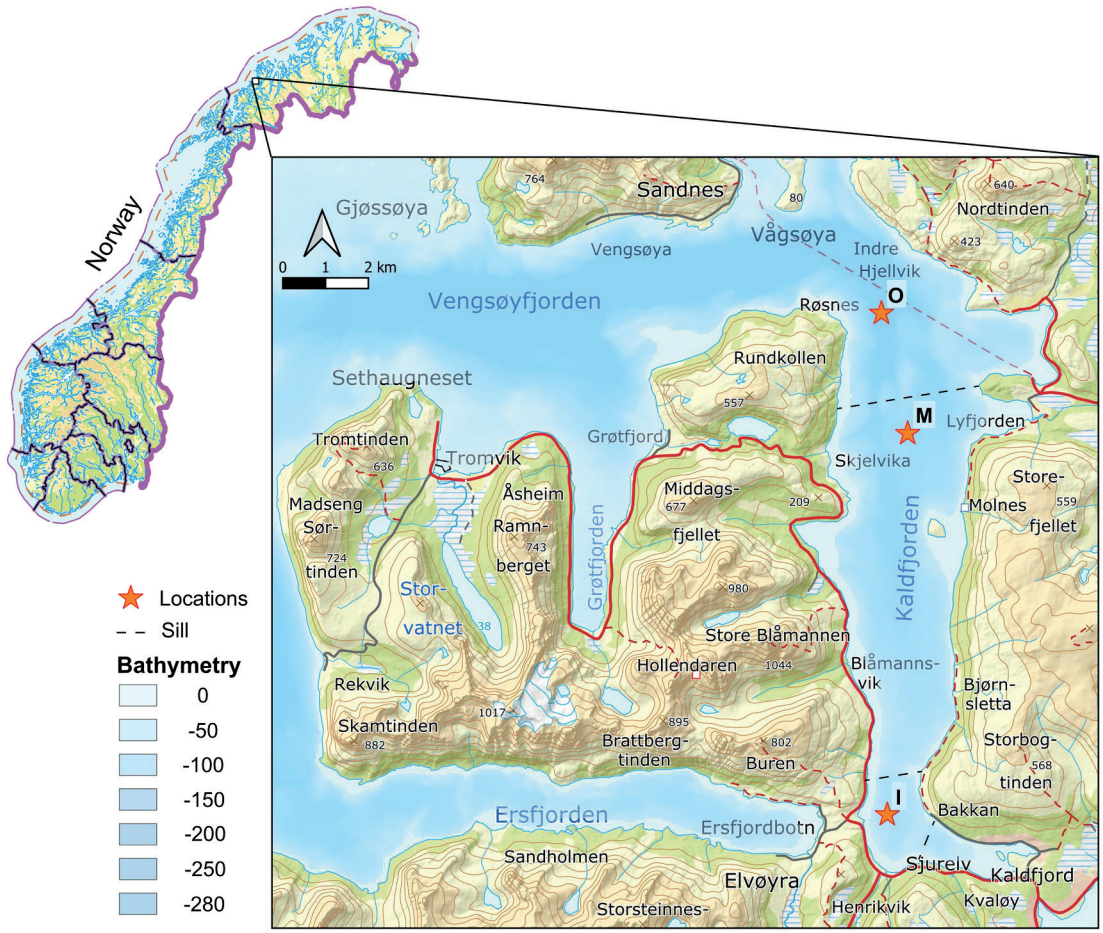


Fig. 1. Map of Kaldfjorden showing the Inner (I), Middle (M) and Outer (O) location and the connecting Vengsøyfjorden (based on Norwegian Mapping Authority data (http://www.kartverket.no, 2020) created with QGIS).

source. It was cultured at 19 °C (16 h light: 8 h dark cycle) in sterilized pre-filtered natural seawater containing the Eppley et al. (1967) IMR 1/2 medium with additional selenite (Paassche et al., 1988). To the IMR 1/2 medium approximately 5×10^{-4} mol L^{-1} of $NaH^{13}CO_3$ was added to replace 25 % of the ^{12}C bicarbonate in the seawater with $NaH^{13}CO_3$. The algae were harvested by centrifugation (500 G; 20 min), after which the obtained pellets were re-suspended and rinsed three times with sterilized, pre-filtered and unlabelled seawater to remove inorganic ^{13}C-labelled carbon. Finally, the algal pellets were lyophilized to obtain a powder. The final concentration of ^{13}C in the algal carbon was 21.6 ± 0.3 atom% (SE, $n = 3$).

2.4. Experimental design

Upon arrival at the research station, the experimental chambers were carefully filled with 60-μm filtered seawater pumped from 60 m depth. Chambers were immediately placed in dark, temperature controlled (approx. 8.7 °C) water baths and kept in a flow-through system with filtered seawater for 4 days (Fig. 2). These four days allowed the sediment to re-settle and geochemically stabilize (Sweetman et al., 2014a,b, 2016). During this phase, the chamber waters were allowed to exchange and overflow into the surrounding water bath, which maintained the independence of replicates. To start the experiment the overflow system was switched off and 77 mg of dry algae was re-hydrated and added to each chamber using a syringe (Fig. 2). Spread out over 1 m, 77 mg would be equivalent to 1 g organic C m^{-2}, assuming that the algae contain 20 % carbon (Sweetman et al., 2014), which is equal to approximately 10 days of carbon flux during the spring bloom (Lalande et al., 2020). After ensuring the algae were evenly mixed into the overlying water column, the stirrers were switched off for 1 h allowing the algae to settle on the sediment (Fig. 2). After 1 h, a single piece of 10 (Low), or 30 (High) grams of thawed *P. periphylla* carrion previously collected from Lurefjorden, Norway, equivalent to 32 and 96 g of jellyfish particulate C m^{-2} respectively, were carefully placed on the sediment surface of the chambers selected for jellyfish treatments. The jellyfish detritus was weighted down using a plastic-coated metal ring to counteract the buoyancy of the jellyfish (Fig. 2). A plastic-coated ring was also added to the chambers that received no jellyfish (Control) to standardize the procedure (Fig. 2). In no case did jellyfish carrion cover the entire surface of the sediment during the experiment. After the addition of algae and jellyfish, the chambers were left to incubate for 48 h after closing the chambers and reactivating the stirrers (Fig. 2). The duration of incubation was chosen to ensure the uptake of labelled carbon and that no more than 30 % of the O_2 available in the overlying water column was consumed during the incubation (Renaud et al., 2008; Sweetman et al., 2016).

2.5. Sediment O_2 micro-profiling

After the experiment, O_2 micro-profile measurements were made using a UNISENSE 3D-O2 micro-profiling system avoiding the jellyfish carrion as much as possible. Sensors were calibrated using a 2-point calibration and used to determine the diffusive O_2 uptake (DOU; mmol O_2 m^{-2} d^{-1}) from a linear approximation to the O_2 gradient situated inside the diffusive boundary layer applying Fick's first law of diffusion (Glud, 2008). From the position of the sensor relative to the

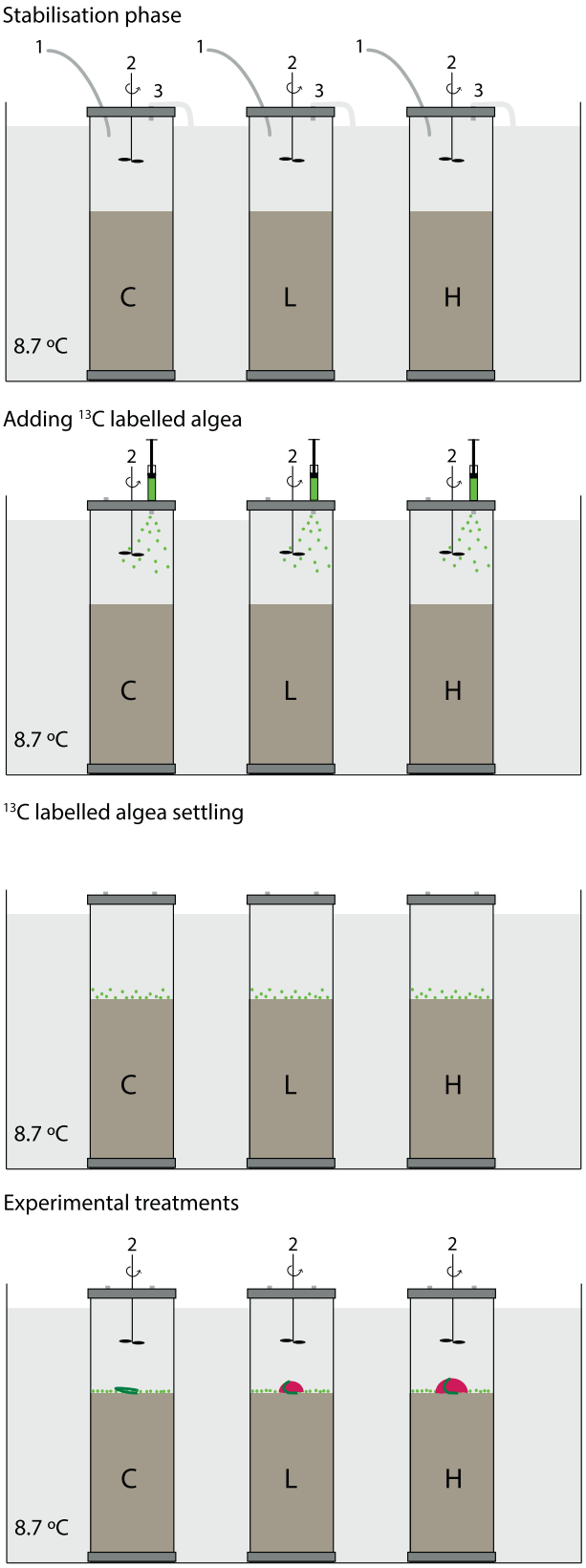


Fig. 2. Schematic representation of the experimental design, where the numbers 1, 2 and 3 represent the water inflow, stirrer and water overflow, respectively. The experimental treatments are depicted by the letters C, L and H representing the Control, Low and High treatment, respectively.

sediment-water interface, O_2 concentrations at the interface (OCI; mmol L^{-1}) and O_2 penetration depth (OPD; mm) were obtained.

2.6. Foraminiferal analyses

After micro-profiling, the overlying seawater was removed to prepare for the sub-sampling of the experimental chambers. To sub-sample the experimental chambers, the upper centimetre of sediment (0–1 cm) was sliced off and gently homogenized after which 20 mL sediment was collected for foraminiferal analyses by transferring material into a syringe. The sub-sample was kept frozen at −20 °C until further analyses. In the laboratory, the sub-samples were thawed and washed over 63- and 500-μm meshes with artificial seawater (salinity 30) that was produced following the method described by Enge et al. (2011). From the 63- to 500-μm size fraction, material was taken at random and picked until approx. 400 living individuals (including agglutinated specimens) could be selected for cytoplasm analyses and identified to species level where possible. One sample from each location was analysed to obtain the natural (background) foraminiferal carbon isotope signatures following the same procedure. The distinction between living and dead foraminifera was based on the visual observations of definite cytoplasm in the test in at least the majority of the older chambers (e.g. Moodley et al., 2002; Nomaki et al., 2005).

The picked foraminifera were carefully and individually cleaned using a brush to remove adhering particles and kept frozen until processing for isotope analysis. In preparation for the isotope analysis, the samples were rinsed 3 times with filtered artificial seawater followed by Milli-Q water (3 times) to remove any remaining particles and salt. After the final cleaning the foraminifera were transferred into silver capsules for decalcification. Decalcification included three HCl (4 %) treatments to ensure that all inorganic foraminiferal carbonate was removed. The samples were dried at 40 °C for 4 h in between treatments and for 16 h for the final drying step. Decalcification ensured that only foraminiferal cytoplasmic carbon remained for C-uptake analyses.

For the living (rB-stained) foraminiferal analyses, the upper 1 cm from the smaller cores was washed through 63-μm and 500-μm sieves using tap water, after which the 63 to 500-μm fraction was split using a modified Elmgren wet splitter (Elmgren, 1973). For the Inner location one eight of the sample was fully picked for living foraminifera, while one quater of was picked for the samples from the Middle and Outer. All specimens were mounted on microfossil slides and identified to species level where possible.

2.7. Carbon uptake calculations

For each sample (s) foraminiferal cytoplasm total carbon content (μgC_s; biomass) and stable carbon isotope ratio ($\delta^{13}C_s$; ‰) were measured using an Elemental Analyser – Isotope ratio Mass Spectrometer (Flash 112 EA and Delta V IRMS, Thermo) at the Royal Netherlands Institute for Sea Research, Yerseke. The first step to determine the C-uptake rates is to calculate the $\delta^{13}C_s$ against the Vienna Pee Dee Belemnite standard ($R_{VPDB} = 0.0112372$) and convert it into atom%$^{13}C_s$ as shown in equation (1).

$$\text{atom\%}^{13}C_s = (100 \times (\delta^{13}C_s / 1000 + 1) \times R_{VPDB})/(1 + (\delta^{13}C_s / 1000 + 1) \times R_{VPDB}) \quad (1)$$

The second step is to calculate the amount of ^{13}C isotopes above background (atom%$^{13}C_b$), referred to as excess (E_s), according to Middelburg et al. (2000) using equation (2).

$$E_s = (\text{atom\%}^{13}C_s - \text{atom\%}^{13}C_b)/ 100 \quad (2)$$

Background (atom%$^{13}C_b$) values, represent the natural amount of ^{13}C atoms in foraminiferal cytoplasm.

The third step is to determine the amount of ^{13}C isotopes incorporated (U_{s_iso}) by taking the product of the excess ^{13}C (E_s) and the biomass

(μgC_s) as shown in equation (3).

$$U_{s\_iso} = E_s \times \mu gC_s \quad (3)$$

The final step is to determine the phytodetrital carbon content (C-uptake) for each sample (I_{s_algae}; μgC_{algae}) by dividing the U_{s_iso} by the amount of ^{13}C isotopes in the added algae (atom%$^{13}C_{algae}$) which in turn must be divided by 100 using equation (4):

$$I_{s\_algae} = U_{s\_iso}/(atom\%^{13}C_{algae}/\ 100) \quad (4)$$

The foraminiferal densities (individuals cm^{-2}) derived from rB-stained assemblages were divided by the number of foraminifera picked for the experiment. This fraction was used to standardize the foraminiferal C-uptake to area, and only the foraminiferal C-uptake rates standardized to area (μgC_{algae} 10 cm^{-2} d^{-1}) are presented in the results. To further investigate potential drivers behind the C-uptake, the C-uptake per 10 cm^2 was normalised to both rB assemblage densities by dividing it by the number of tests per 10 cm^{-2} (C-uptake$_{rB}$; ngC_{algae}/individual/d), and foraminiferal biomass by dividing by the biomass per 10 cm^{-2} (C-uptake$_{bio}$; $\mu gC_{algae}/\mu gC_{biomass}$).

2.8. Sediment organic geochemistry

To obtain the sediment total organic carbon (TOC) and nitrogen content and stable carbon and nitrogen isotope signatures ($\delta^{13}C_{VPDB}$ and $\delta^{15}N_{air}$), the upper sediment centimetre (0–1 cm) from one core from each location was analysed using an Elemental Analyser–Isotope Ratio Mass Spectrometry at the ISO-Analytical Ltd. stable isotope analysis laboratory in Crewe, UK. Unlike the samples used to measure total nitrogen, the TOC samples were acidified with 1M HCl acid, after which they were neutralized by repeated washing with distilled water and then oven dried at 40 °C prior to analysis. The TOC and total nitrogen were used to derive total organic carbon and total nitrogen ratios (C/N). The TOC was normalised to the sediment fine fraction (% < 63 μm), hereafter referred to as TOC_{63} (TOC_{63} = TOC + 18 × 1 − % <63 μm; Veileder, 02:2018), to take into account the strong correlation between sediment grain size and TOC concentrations (Kennedy et al., 2002). Grain size distributions, performed on non-acidified samples, were determined using a Beckman Coulter LS13320 with laser diffraction at the Department of Geoscience, University of Oslo.

2.9. Statistical analysis

Differences in the (arithmetic) mean foraminiferal C-uptake, C-uptake$_{bio}$, C-uptake$_{rB}$, DOU, OCI and OPD were analysed using separate two-way Analyses of Variance (ANOVA) with experimental treatment (C, L, H) and location (Inner, Middle, Outer) as fixed factors. As one of the O_2 micro-profiles could not be used, unbalanced type III ANOVAs were used for the DOU, OCI and OPD. Significant differences were further analysed using Tukey post-hoc tests. Prior to analysis, the data were checked to determine whether the parametric assumptions were met using the Shapiro-Wilk normality test and Levene's homogeneity of variances test. Data was root-transformed when necessary. ANOVA analyses are relatively robust to deviations from a normal distribution (Underwood, 1996), so if the data were not normally distributed the critical α was adjusted from 0.05 to 0.01. When data sets were normally distributed, an α of 0.05 was chosen as a criterion for significance. All statistical analyses were performed using the statistical language R version 3.6.1 (R Core Team, 2019). For all parameters tested for significance, the standard error and mean were derived from 12 measurements. Except for the DOU, OCI and OPD from the Middle location where only 11 measurements were available.

To visualize potential differences in foraminiferal assemblage composition amongst samples separate correspondence analyses were performed for the experiment and the rB-stained samples. For both correspondence analyses, square-root transformed relative abundances of the 15 numerically dominant species in the assemblages from the experiment across all locations were used. The remaining taxa were grouped and termed as "Rest". Due to the difficulties in distinguishing the *Cassidulina* species in water, the species were grouped into two groups: Group I = *C. laevigata* and *C. neoteretris*; Group II = *C. obtusa*, *C. reniforme* and *C. bradyi*. The correspondence analyses were performed using the "Vegan" package in the R-data software program (version 2.5–5, Oksanen et al., 2010). To assess potential differences in environmental conditions amongst the locations the bulk sediment TOC_{63}, C/N ratios, stable carbon and nitrogen isotopes ($\delta^{13}C_{VPDB}$ and $\delta^{15}N_{air}$), and grain size distribution (% < 63 μm), in addition to the water depth (m), and bottom water O_2 concentration (mL L^{-1}), salinity, and temperature (°C), were standardized by subtracting the mean and dividing by the standard deviations before performing a principal component analysis. An overview of the terms and corresponding abbreviations is given in Table 1.

3. Results

3.1. Foraminiferal carbon uptake

The mean foraminiferal non-normalized C-uptake (Fig. 3a), was 25.0 ± 4.4, 1.0 ± 0.2, and 1.5 ± 0.4 μgC_{algae} 10 cm^{-2} d^{-1} at the Inner, Middle and Outer location, respectively. Mean C-uptake rates differed significantly amongst the locations (ANOVA, $p < 0.001$), with the Inner location having a significantly higher C-uptake (approx. 20-fold) than the other two locations. The C-uptake did not significantly differ between the Middle and Outer location. No significant effect of jellyfish addition on C-uptake was detected (ANOVA, $p = 0.921$), nor were differences in the non-normalized C-uptake rates dependent on the interaction between experimental treatments (C, L, H) and sampled location (from here on referred to as the interaction effect) (ANOVA, $p = 0.453$). The mean non-normalized C-uptake rates for the treatments ranged between approx. 7.5 and 11.1 μgC_{algae} 10 cm^{-2} d^{-1}.

The total foraminiferal biomass was 61.6 ± 7.6, 19.6 ± 1.2, and 23.3 ± 2.6 μgC $sample^{-1}$ for the Inner, Middle and Outer location, respectively. When normalised to biomass, the foraminiferal mean C-uptake$_{bio}$ was 0.8 ± 0.1, 0.3 ± 0.1, and 0.4 ± 0.1 $\mu gC_{algae}/\mu gC_{biomass}$ at the Inner, Middle and Outer location, sequentially. The difference amongst the locations was significant (ANOVA, $p < 0.001$), with a lower (approx. 2.3-fold) but still significant difference between the Inner location and the other two locations, which did not significantly differ from each other (Fig. 3b). Differences in C-uptake$_{bio}$ amongst the treatments ranged from approx. 0.49 to 0.51 $\mu gC_{algae}/\mu gC_{biomass}$ and were not significant (ANOVA, $p = 0.972$), nor was the interaction effect (ANOVA, $p = 0.292$).

The foraminiferal densities derived from the rB-stained samples were

Table 1
List of terms and corresponding abbreviations.

Terms	Abbreviations
Analysis of Variance	ANOVA
Carbon uptake:	
1) not normalized	1) C-uptake
2) normalized to rose Bengal (rB) densities	2) C-uptake$_{rB}$
3) normalized to biomass	3) C-uptake$_{bio}$
Diffusive O_2 uptake	DOU
Experimental treatments	Control (C) = phytodetritus Low (L) = phytodetritus + 10 g jellyfish High (H) = phytodetritus + 30 g jellyfish
O_2 concentration sediment water interface	OCI
O_2 penetration depth	ODP
Total organic carbon, normalized to % < 63 μm fraction in the sediment	TOC_{63}
Total organic carbon and total nitrogen ratio	C/N

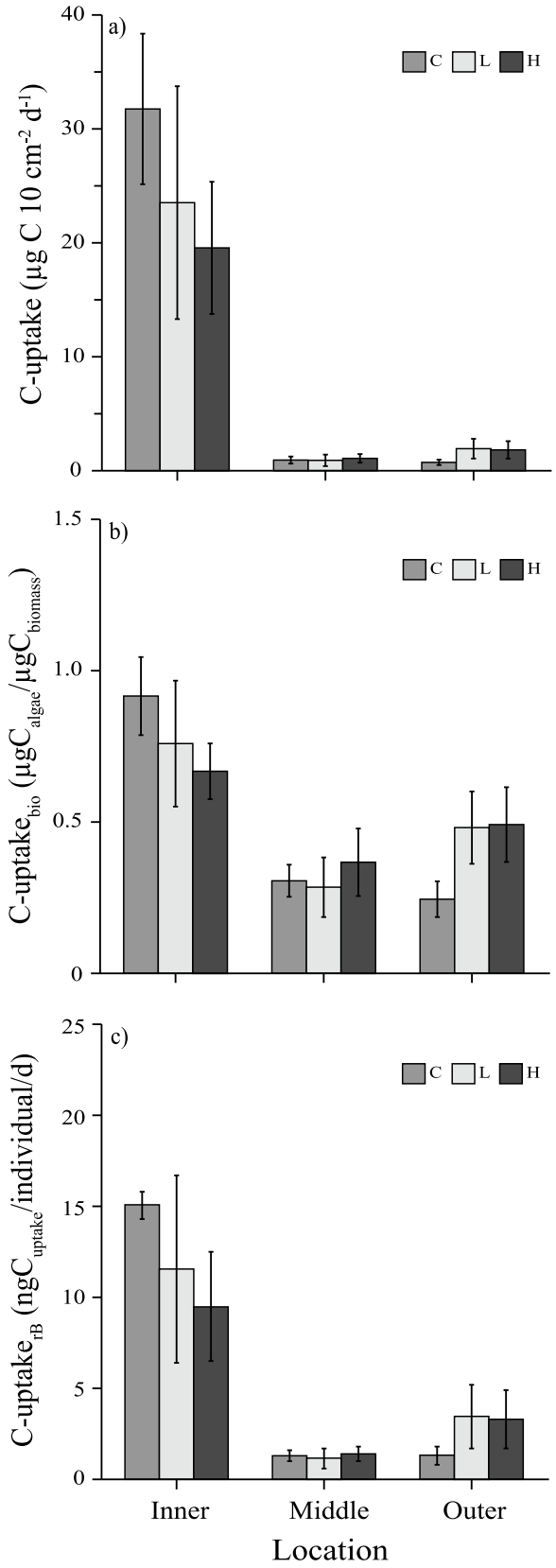


Fig. 3. The arithmetic means of a) carbon uptake (µgC 10 cm^{-2} d^{-1}), b) carbon uptake normalised to biomass ($\mu gC_{algae}/\mu gC_{biomass}$) and c) normalised to rB densities (ngC_{algae}/individual/d) for each treatment at each location. The experimental treatments are depicted in grey tones: C = phytodetritus only; L = phytodetritus +10 g Jelly; H = phytodetritus +30 g Jelly. Error bars denote ± standard error ($n = 12$).

2071 ± 365, 698 ± 90 and 583 ± 33 individuals per 10 cm^{-2}. Note that the mean foraminiferal densities and standard errors were derived from four samples. Normalising the C-uptake to the rB-densities, resulted in mean C-$uptake_{rB}$ rates of 12.0 ± 2.0, 1.3 ± 0.2 and 2.7 ± 0.8 ngC_{algae}/individual/d at the Inner, Middle and Outer locations, respectively. The difference amongst the locations was significant (ANOVA, $p < 0.001$), with a significant approx. 6-fold higher C-$uptake_{rB}$ at the Inner location compared to the other locations (Fig. 3c). There was no significant difference between the Middle and Outer location. The differences amongst the experimental treatments were not significant (ANOVA, $p = 0.975$), and mean C-$uptake_{rB}$ rates ranged from approx. 5.9 to 4.7 ± 1.5 ngC_{algae}/individual/d. There was no significant interaction effect (ANOVA, $p = 0.386$).

3.2. Foraminiferal assemblage-composition

The first two axes of the correspondence analyses explained 74.2 % and 61.6 % of the total variability in the foraminiferal assemblage composition from experimental cores and the rB-stained samples, respectively (Fig. 4). The 15 most abundant taxa as determined from the experiment assemblages (Table 2) comprised 79–95 % of the assemblages in the experimental cores, and 58–82 % of the rB-stained assemblages, respectively.

For the experimental assemblages, this was expressed by higher relative abundances of *Bulimina marginata*, *Nonionella turgida*, and *Adercotryma glomeratum*, and lower relative abundances of *Bolivina pseudopunctata*, *Nonionella iridea*, *Pullenia olsoensis,* and *Fissurina* cf. *laevigata* at the Inner location (Fig. 4a, Table 2). For the rB-stained assemblages, this separation was expressed by higher relative abundances of *B. marginata*, *N. turgida*, *Hyalinea balthica,* and *A. glomeratum*, and lower relative abundances of *P. olsoensis, Epistominella vitrea*, *N. iridea*, and the *Cassidulina* groups at the Inner location (Fig. 4b, Table 2). Small agglutinated foraminiferal species (e.g. *Reophax* cf *micaceus*) were less abundant in the experiment than in the rB-stained assemblages (Table 2). In this study the cytoplasm of *B. marginata*, *N. turgida*, *A. glomeratum*, *N. iridea*, and *H. balthica*, amongst some other less site specific (e.g. *E. vitrea*) or abundant species, often had a bright green or green-brownish colour.

A smaller portion of the variation was explained by the variability amongst samples, where the second axes of the correspondence analyses explained 9.7 % and 13.2 % for the experimental and rB-stained assemblages, respectively (Fig. 4). The correspondence analyses also showed that there was no clear difference in assemblage compositions between the different experimental treatments, as samples with a Control, Low and High treatment occurred amongst each another (Fig. 4a).

3.3. Environmental variables

The first axis of the principal component analysis performed on the environmental parameters explained >99% of the variance amongst the locations, where the depth explained most of the variance (Fig. 5). The bulk sediment TOC_{63}, % < 63 µm fraction, $\delta^{13}C_{VPDB}$, total nitrogen, $\delta^{15}N_{air}$, and C/N ratios varied only slightly amongst the locations (Table 3), as did the bottom water O_2 concentration, salinity and temperature (Table 3).

3.4. Sediment O_2 dynamics

DOU rates were approx. 1.5-fold higher (ANOVA, $p = 0.028$) in cores where jellyfish detritus was placed on top of the sediment (Fig. 6a). For the experimental treatments, the mean DOU rates were 6.1 ± 0.5, 8.8 ± 0.8 mmol O_2 $d^{-1}$and 9.4 ± 1.3 mmol O_2 d^{-1} for the Control, Low and High treatment, respectively. Pairwise testing showed a significant difference between the Control and the two jellyfish treatments but not between the jellyfish treatments. No significant location effect (ANOVA = 0.428; mean DOU range 6.1–8.6 mmol O_2 d^{-1}), or interaction effect

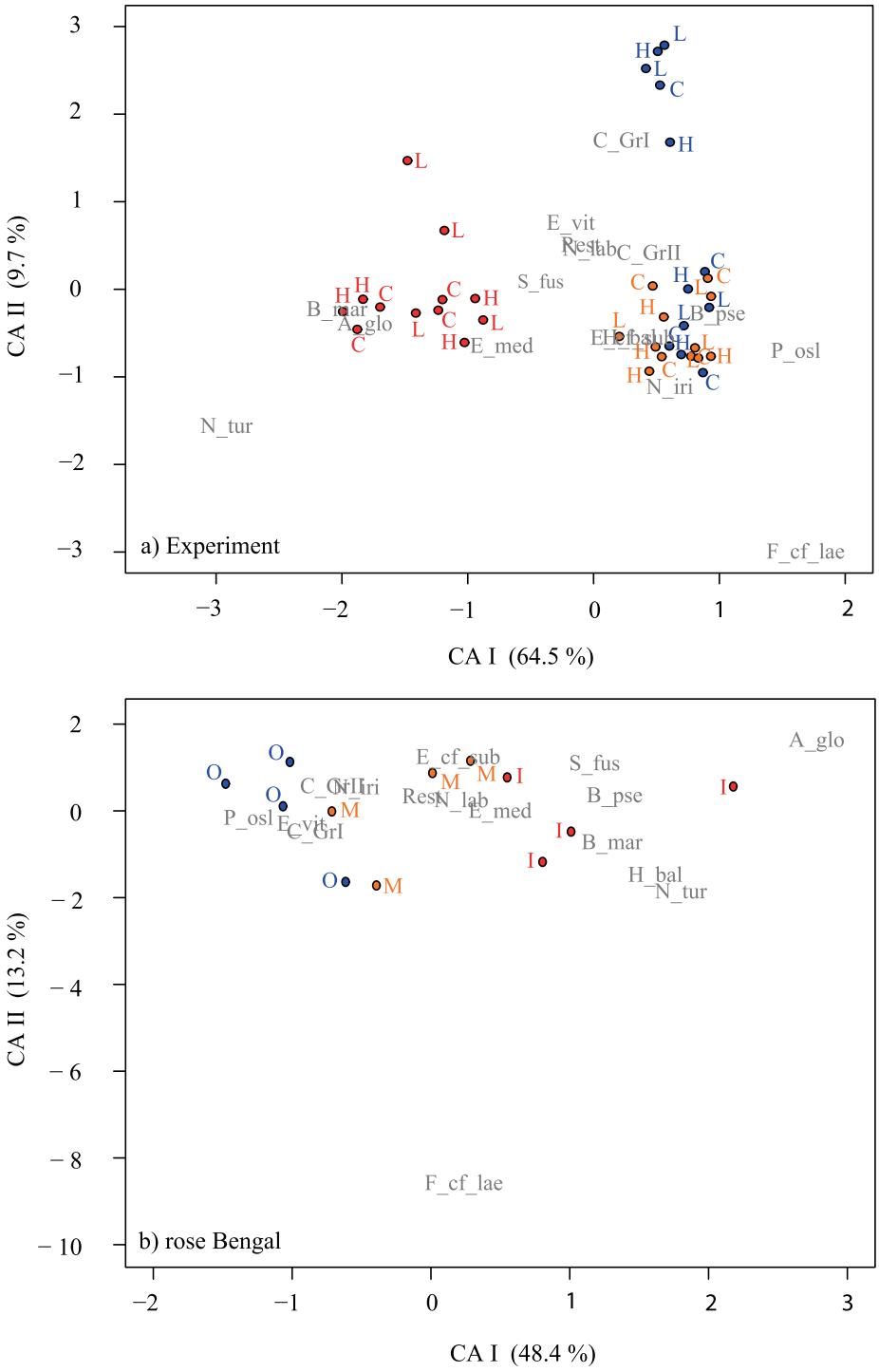


Fig. 4. Biplots showing the correspondence analyses results of the 15 numerically dominant species across all locations in the assemblages from the experiment, for a) experiment samples and b) rose Bengal field samples. The locations are depicted in the colours, red = Inner, orange = Middle, and blue = Outer, where the coloured dots represent the centre of mass for each sample. In a) the –C, -L and –H stand for the Control, Low and High treatment, respectively. In b) the -I, -M and -O stand for the Inner, Middle and Outer location, respectively; as also indicated by the colours. The species name abbreviations are depicted in grey (for full names see Table 2), and represent the centre of mass of the species within the ordination plane.

(ANOVA, $p = 0.825$) was observed amongst the DOU rates.

The addition of jellyfish had a marginally significant effect on the OCI (ANOVA, $p = 0.011$ therefore > 0.01) compared to the Control treatment (Fig. 6b). The mean concentrations were 0.13 ± 0.02, 0.09 ± 0.01 mmol L^{-1} and 0.05 ± 0.01 mmol L^{-1} for the Control, Low and High treatment, respectively. The OCI was not significantly different amongst the locations (ANOVA, $p = 0.035$) and there was no significant interaction effect (ANOVA, $p = 0.236$). The mean OCI concentrations were 0.11 ± 0.02, 0.05 ± 0.02 mmol L^{-1} and 0.12 ± 0.02 mmol L^{-1} for the Inner, Middle and Outer location, respectively.

The OPDs were shallower by approx. 2.5-fold but did not show a significant difference (ANOVA, $p = 0.011$ therefore > 0.01) in cores where jellyfish was added versus the Control treatment (Fig. 6c). The mean OPDs were 2.5 ± 0.7 (SE, $n = 12$), 0.8 ± 0.2 mm (SE, $n = 12$), and 1.1 ± 0.3 mm (SE, $n = 11$) for the Control, Low and High treatment, respectively. The OPDs were significantly different amongst the locations (ANOVA, $p < 0.001$), with a significantly lower OPD at the Middle location (mean OPD was 0.5 ± 0.2 mm, [SE, $n = 11$]) compared to the Inner and Outer locations where the mean OPD was 1.9 ± 0.3 and 2.0 ± 0.5 mm (*SE*, n = 12), respectively. OPD at the Inner and Outer locations did not vary significantly, and the interaction term was also not significant (ANOVA, $p = 0.328$).

Table 2
Arithmetic mean relative abundances of species used in the correspondence analysis of both the experiment and the rose Bengal stained samples for each location. Species explaining most of the variance on the first axis are marked bold. Error bars denote ± standard error (experiment: SE, $n = 12$; and rose Bengal stained: SE, $n = 4$).

		Inner		Middle		Outer	
Species	**Abbreviation**	(%)	SE	(%)	SE	(%)	SE
		Experiment					
Adercotryma glomeratum	**A_glo**	**3.1**	**0.4**	**0.4**	**0.1**	**0.3**	**0.1**
Bolivina pseudopunctata	**B_pse**	**0.9**	**0.2**	**3.9**	**0.4**	**4.0**	**0.5**
Bulimina marginata	**B_marg**	**10.8**	**1.4**	**0.7**	**0.2**	**0.7**	**0.2**
Cassidulina group I	C_GrI	14.6	1.4	29.0	3.1	18.4	1.0
Cassidulina group II	C_GrII	14.7	1.9	20.1	1.6	22.8	1.2
Egerelloides medius	E_med	2.7	0.3	0.6	0.2	1.3	0.2
Elphidium cf *subarcticum*	E_cf_sub	5.7	1.0	5.0	0.6	10.5	0.9
Epistominella vitrea	E_vit	5.9	0.9	4.1	0.8	4.2	0.5
Fissurina* cf *laevigata	**F_cf_lae**	**0.1**	**0.1**	**1.9**	**0.5**	**2.9**	**0.2**
Hyalinea baltica	H_bal	1.7	0.3	1.5	0.3	2.8	0.3
Nonionella iridea	**N_iri**	**2.2**	**0.4**	**4.5**	**1.0**	**4.6**	**0.3**
Nonionella labradorica	N_lab	3.5	0.9	3.5	1.0	2.8	0.3
Nonionella turgida	**N_tur**	**10.7**	**2.0**	**0.5**	**0.2**	**0.1**	**0.0**
Pullenia osloensis	**P_osl**	**0.5**	**0.2**	**11.3**	**0.7**	**9.3**	**1.3**
Stainforthia fusiformis	S_fusi	8.9	1.2	4.2	0.4	3.4	0.5
Grouped remaining species	Rest	14.0	1.2	11.0	0.6	9.8	0.7
Small agglutinated spp		11.1	0.9	4.4	0.5	4.1	0.3
		rB stained					
Adercotryma glomeratum	**A_glo**	**1.7**	**0.6**	**0.8**	**0.2**	**0**	**0**
Bolivina pseudopunctata	B_pse	2.4	0.6	1.2	0.5	0.8	0.5
Bulimina marginata	**B_marg**	**8.4**	**2.2**	**0.7**	**0.1**	**1.2**	**0.3**
***Cassidulina* group I**	**C_GrI**	**6.9**	**1.7**	**7.4**	**1.4**	**23.1**	**6.8**
***Cassidulina* group II**	**C_GrII**	**2.2**	**0.7**	**3.2**	**0.5**	**4.8**	**0.9**
Egerelloides medius	E_med	4.5	1.3	3.9	0.3	1.9	0.8
Elphidium cf *subarcticum*	E_cf_sub	2.5	1.1	1.8	0.8	3.0	0.8
Epistominella vitrea	**E_vit**	**5.9**	**2.6**	**16.9**	**4.0**	**17.1**	**3.2**
Fissurina cf *laevigata*	F_cf_lae	0.1	0.1	0.1	0.1	0.1	0.1
Hyalinea balthica	**H_bal**	**1.2**	**0.3**	**0.5**	**0.0**	**0.5**	**0**
Nonionella iridea	**N_iri**	**7.8**	**2.7**	**8.0**	**0.6**	**10.1**	**3.6**
Nonionella labradorica	N_lab	2.0	0.3	2.4	0.6	1.4	0.6
Nonionella turgida	N_tur	**7.2**	**2.9**	**2.6**	**1.2**	**2.0**	**0.9**
Pullenia osloensis	P_osl	**2.6**	**0.2**	**12.4**	**3.2**	**8.5**	**1.4**
Stainforthia fusiformis	S_fusi	16.6	6.2	11.0	4.7	4.0	1.7
Grouped remaining species	Rest	28.6	5.4	27.3	3.1	22.9	1.5
Small agglutinated spp		22.0	4.2	19.1	3.2	14.3	1.3

4. Discussion

4.1. Foraminiferal C-uptake

Earlier isotope tracer studies have shown that foraminiferal C-uptake rates can vary greatly, ranging from 0.01 to 8.5 μg C 10 cm^{-2} d^{-1} in different environmental settings (e.g. Enge et al., 2016; Nomaki et al., 2005; Woulds et al., 2016). The range of published C-uptake rates encompassed C-uptake rates from the Middle and Outer locations in Kaldfjorden, but the rates from the Inner location were over twice as high as the highest value published so far. The 8.5 μg C 10 cm^{-2} d^{-1} observed by Enge et al. (2016) must however be regarded as the minimum foraminiferal C-uptake, since only the 9 most abundant species in the >125 μm size fraction were analysed (Enge et al., 2014, 2016). The C-uptake in Kaldfjorden could be underestimated as despite careful selection, foraminifera that died during the experiment but appeared alive may have been selected for C-uptake analyses as their cytoplasm had little time to decay in the 2-day experiment. The 20-fold higher foraminiferal C-uptake rate at the Inner location in Kaldfjorden highlights a clear contrast in foraminiferal C-cycling from the inner to the outer fjord (Fig. 3a). Previously differences in foraminiferal C-uptake have been attributed to differences in assemblage composition, biomass, feeding preferences of species, and foraminiferal vs microbial activity (e.g. Enge et al., 2016; Sweetman et al., 2009; Woulds et al., 2016). The differences amongst locations in Kaldfjorden could be caused by differences in one or more of three factors: 1) total biomass; 2) foraminiferal densities; and 3) assemblage composition.

The high C-uptake at the Inner location seemed partly caused by the relatively high foraminiferal biomass, as the C-uptake rates normalised to biomass showed that the total biomass explained just under 50 % of the difference amongst the locations (Fig. 3b). The results from Kaldfjorden are in agreement with previous findings (Middelburg et al., 2000; Moodley et al., 2005; Woulds et al., 2009, 2016) that have shown that the relative biomass of different faunal groups played an important role in the C-uptake rates. Foraminiferal densities and biomass are non-exclusive factors as higher foraminiferal densities often result in a higher biomas. The current study showed that while less important than biomass, differences in foraminiferal densities explained approx. 20 % of the differences in the C-uptake rates amongst the locations (Fig. 3c). The rB-densities normalised results thus showed that foraminifera at the Inner location assimilated significantly more algal carbon per individual than at the other two locations. This indicates that the assemblage composition also plays a role in the foraminiferal C-uptake.

Previous studies have found that C-uptake rates vary greatly amongst foraminiferal species (Lintner et al., 2020; Wukovits et al., 2018), and tend to be driven by a select few species in the assemblage (Enge et al, 2014, 2016; Linshy et al., 2014; Nomaki et al., 2005). In Kaldfjorden both the experimental and rB-stained foraminiferal assemblages at the Inner location were characterized by higher relative abundances of *B. marginata* and *N. turgida* than the two locations further outwards (Table 2). Studies have shown that species in the family Buliminidae (such as *B. marginata*) are especially effective phytodetrital carbon consumers (Enge et al., 2014; Nomaki et al., 2005, 2006). Species in the family Nonionidae have also been positively associated with fresh phytodetrital input (e.g. Duffield et al., 2015; Gooday and Hughes, 2002). As the cytoplasm of *B. marginata*, *N. turgida*, and *N. iridea* in this

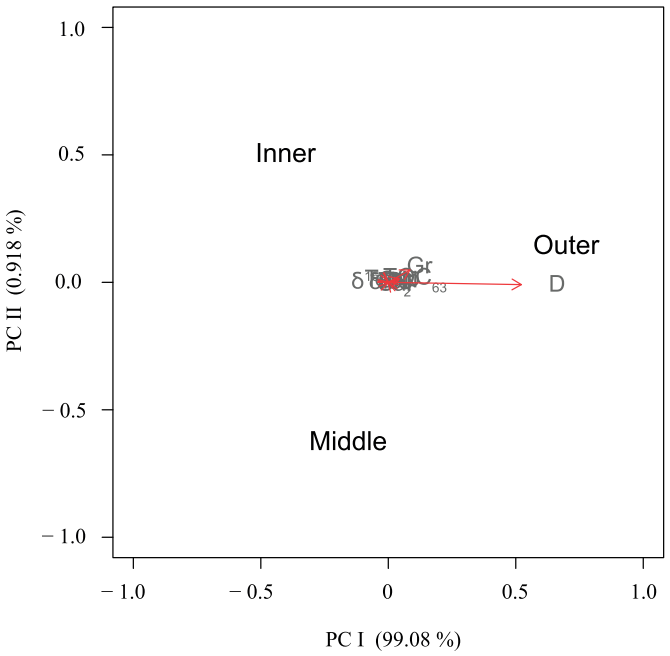


Fig. 5. Principal component analysis of the in situ-environmental variables: normalised total organic carbon (TOC_{63}; mg g^{-1}); grain size (Gr; % < 63 μm); stable carbon isotope ratio ($\delta^{13}C$; $\delta^{13}C_{VPDB}$); total nitrogen (TN; %); stable nitrogen isotopes ($\delta^{15}N$; $\delta^{15}N_{air}$); and total carbon and total nitrogen ratios (C/N); water depth (D; m); and bottom water O_2concentration (mL L^{-1}); salinity (Sal); and temperature (Temp; °C). Note that the organic geochemistry parameters represent bulk sediment samples.

study frequently had a bright green-to-green-brownish colour it is likely that these species actively ingested the fresh algal detritus supplied in the experiment. Alternatively, these species could have incorporated a fresh algal detritus source that was present during sampling, but this is less likely as the main phytoplankton bloom in northern Norway occurs in April–May (Lalande et al., 2020). *E. vitrea* was distributed evenly amongst the sampled locations in Kaldfjorden (Fig. 4) and was therefore not considered responsible for the differences in C-uptake rates amongst the locations. The species containing a green cytoplasm coloration however, confirmed previous suggestions that this species responds positively to fresh phytodetrital carbon input (Duffield et al., 2015; Klootwijk et al., 2020). Overall, the 20 times higher foraminiferal C-uptake at the Inner location in Kaldfjorden seems likely due to the higher biomass and foraminiferal densities in combination with higher relative abundances of *B. marginata* and *N. turgida* at this location.

4.2. Foraminiferal assemblage composition

The foraminiferal assemblages in Kaldfjorden contained species that are found in fjords along the entire Norwegian coastline (e.g. Murray and Alve, 2016). Previous studies indicate that *B. marginata* and agglutinated foraminifera (e.g. *A. glomeratum*) are common species in foraminiferal assemblages from relatively shallow inner fjord regions (Alve, 1991; Alve and Nagy, 1990; Austin and Sejrup, 1994; Husum and Hald, 2004; Klootwijk et al., 2020). Small agglutinated foraminiferal species were, however, less abundant in the experimental assemblages than in the rB-stained assemblages (Table 2) and virtually no tests of e.g. *Reophax* cf *micaceus* were observed in the experimental assemblages. This suggests that some of the more fragile tests from smaller agglutinated species may have been destroyed whilst processing the experimental samples. As carbon processing is often primarily determined by total biomass (e.g. Woulds et al., 2016, Fig. 3), the C-uptake rates in Kaldfjorden are considered relatively unaffected by the lack of C-uptake from smaller agglutinated foraminifera as their contribution can be considered negligible.

Previous studies using both long-term (several 100 years) sediment core records and living foraminifera, found higher relative abundances of *B. marginata* and agglutinated foraminifera (incl. *A. glomeratum*) in the inner region of the fjord compared to further outwards (Duffield et al., 2017; Husum and Hald, 2004), which is in line with the results from this study. Long-term sediment core records dating back to times without anthropogenic influences found no major changes in relative abundances of *B. marginata* and members of the Nonionidae family in the inner part of Øksfjorden, northern Norway (Klootwijk et al., 2020). Preliminary results from sediment cores taken in Kaldfjorden suggest that anthropogenic activities had little impact on foraminifera at the Inner location, as the assemblage composition did not greatly change over time (Vågen, 2018). This and previous studies thus indicate that *B. marginata* and *N. turgida*, considered important species for the C-uptake at the Inner location in Kaldfjorden, might naturally occur in relatively high abundances in the inner regions of fjords. If the foraminiferal species distribution in this study is representative for other fjords, than these inner regions could be sites of relatively high foraminiferal C-cycling activity.

4.3. Environmental parameters

Previous studies that observed large differences in benthic foraminiferal assemblage composition and densities were accompanied by strong differences in sediment organic geochemistry (e.g. Duffield et al., 2017; Mojtahid et al., 2009). The same has also been observed for macrofauna (McGovern et al., 2020), though another study found that strong differences in macrobenthic community composition were only weakly correlated with environmental parameters (Kokarev et al., 2021). In Kaldfjorden the foraminiferal assemblage composition, biomass, and density differed greatly amongst the locations, but the environmental parameters differed only slightly (Fig. 5). The environmental parameters were however only measured once in September, and as such are a snapshot in time that may not be typical of the environmental conditions. Marine organic matter C/N ratios are typically lower than 8, and marine particulate organic carbon $\delta^{13}C_{VPDB}$ typically ranges from approx. −21 ‰ to −18 ‰ (e.g. Lamb et al., 2006; Meyers, 1994). The low C/N ratios (< 6.2) from Kaldfjorden indicate a relatively strong contribution of marine organic matter to the sediment, though the slightly more negative $\delta^{13}C_{VPDB}$ value at the Inner location may indicate a marginally higher terrestrial organic matter input at this location

Table 3
The environmental parameters taken in September 2017. The bulk sediment geochemistry: normalized total organic carbon (TOC_{63}); grain size distribution; stable carbon isotope ratio ($\delta^{13}C_{VPDB}$); total nitrogen; stable nitrogen isotopes ($\delta^{15}N_{air}$); total organic carbon and total nitrogen ratios (C/N); in addition to the water depth, all from this study. Bottom water O_2 concentrations provided by A. Renner, bottom water salinity and temperature provided by Chierici et al. (2019).

Location	TOC_{63} mg g^{-1}	Grain size % < 63 μm	$\delta^{13}C_{VPDB}$ ‰	Total nitrogen %	$\delta^{15}N_{air}$ ‰	C/N	Water depth m	O_2* mL L^{-1}	Salinity	Temperature °C
Inner	25.0	75.4	−22.3	3.9	6.2	5.2	111	5.4	34.1	7.1
Middle	24.0	67.9	−21.8	2.9	5.8	6.2	140	5.3	34.3	6.5
Outer	34.2	91.9	−21.8	5.6	5.7	5.8	236	5.3	34.4	6.4

*un-calibrated values.

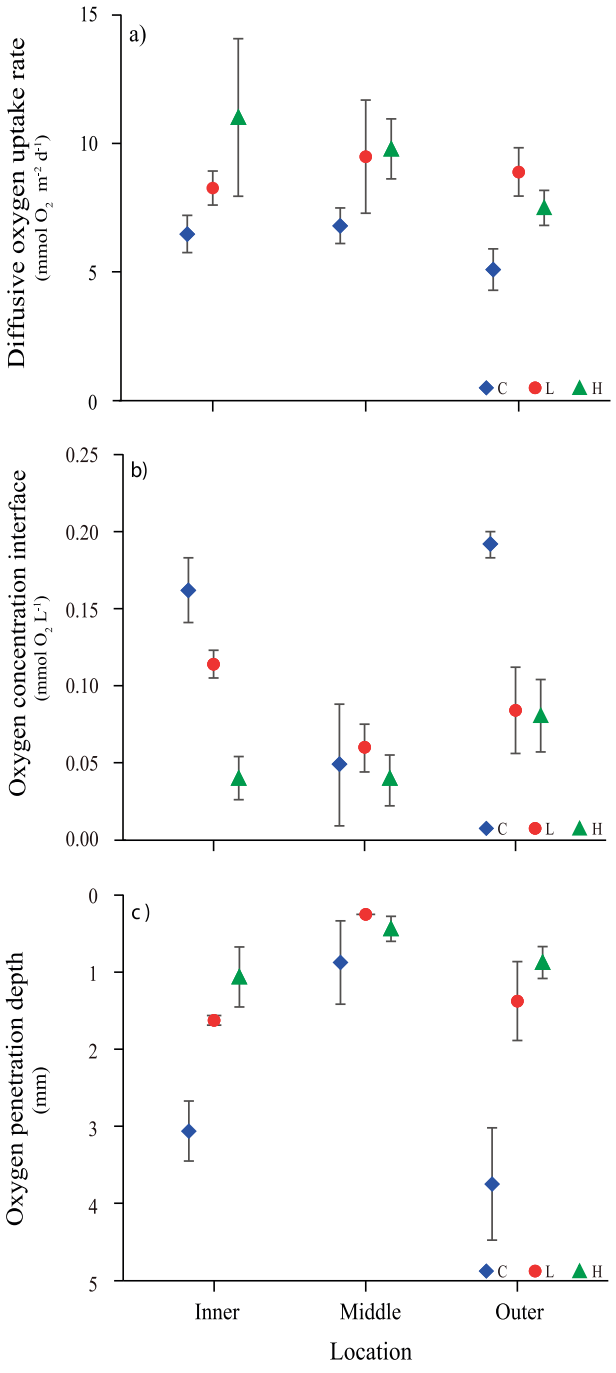


Fig. 6. Sediment O_2 dynamics: a) Diffusive O_2 Uptake (DOU, mmol O_2 m^{-2} d^{-1}); b) O_2 concentrations at the sediment water interface (OCI, mmol L^{-1}); and c) the O_2 penetration depth in the sediment (OP, mm). Note that the axis in c) is inverted. Experimental treatments are depicted by coloured symbols: C = phytodetritus only (blue diamond); L = phytodetritus + 10 gr Jelly (red circle); H = phytodetritus + 30 gr Jelly (green triangle). Error bars denote the ± standard error $n = 12$, except for the Middle location L treatment were $n = 11$.

(Table 3). These results are in agreement with sediment trap study results from Kaldfjorden that indicated a slightly higher primary productivity, potentially from a higher riverine input, at the inner region compared to the outer region (Lalande et al., 2020).

Marine organic carbon is, amongst other things, comprised of algal detritus from primary productivity, and is generally regarded as more labile (bio-available) than terrestrial organic carbon (e.g. Hedges and Keil, 1995). The slightly higher food quality at the Inner location in Kaldfjorden may have sustained the higher foraminiferal biomass at this location. Preliminary sediment core results from the Inner location in Kaldfjorden give no clear indication that the foraminiferal density has greatly changed due to anthropogenic influences (Vågen, 2018), suggesting that the causes for the high biomass at the Inner location are most likely natural. Previous studies have shown that riverine input may influence important biochemical processes, e.g. primary productivity (Frigstad et al., 2020; McKee et al., 2004), and the macrofaunal community has also been reported to feed on terrestrial organic matter from riverine input (Kokarev et al., 2021; McGovern et al., 2020; McMahon et al., 2021). Additionally, one study found the highest macrofaunal community biomass closest to the river outlet in their inner to outer fjord transect (McGovern et al., 2020). In Kaldfjorden, the number of small rivers draining into the fjord decreases towards the outer fjord (Fig. 1), and it is plausible that riverine input has some influence on the Inner location that has yet to be further defined. Overall, this study highlights a complex trophic system where strong differences in the foraminiferal assemblage structure did not coincide with major differences in environmental parameters that are typically linked with differences in foraminiferal assemblage structure.

4.4. *Foraminifera and jellyfish detritus*

In Kaldfjorden, the Low jellyfish treatment represented 66 % and the High jellyfish treatment 89 % of the annual particulate organic matter flux, which was estimated at approx. 11 g C m^{-2} yr^{-1} (Lalande et al., 2020). Previously, reduced macrofaunal C-uptake rates were observed in the presence of jellyfish detritus compared to samples without added jellyfish (Sweetman et al., 2016). Foraminiferal C-uptake rates in Kaldfjorden did not significantly change when jellyfish detritus was placed on top of the sediment (Fig. 3), which could be due to some challenges associated with this experimental study. Foraminifera are known to be sensitive to changes in the environmental conditions (e.g. Sen Gupta, 1999), and the Control treatment in this experiment involved manipulating the in situ environmental conditions by adding phytodetrital carbon. It is possible that the added phytodetritus affected the foraminifera at the Middle and Outer location to such an extent that the additional jellyfish detritus on top of the sediment had no additional effect (Fig. 3).

Additionally, using ^{13}C labelled algae as a tracer to assess the impact of jellyfish detritus on benthic foraminifera relies on the presumption that the foraminifera will feed on the algae. The green cytoplasm of the majority of species suggests they actively ingested the algal detritus, but not all species ingested the phytodetritus, which may be due to feeding preferences. For example, previous studies suggest that *P. osloensis* and *B. pseudopunctata*, characteristic species for the Middle and Outer location, do not feed on fresh phytodetritus (Alve and Bernhard, 1995; Das et al., 2006; Smart and Gooday, 1997). This was also indicated by their opaque light yellow-brownish coloured cytoplasm in this study, suggesting that these two species, and potentially also other species, did not feed on the provided fresh phytodetritus. The latter may have contributed to the relatively low C-uptake rates and could also partly explain the lack of a response to jellyfish detritus at the Middle and Outer location. The C-uptake rates from the outer two locations furthermore suggest that the species that did actively ingest algal detritus at these locations (e.g. *E. vitrea* and *N. iridea*) were not affected by jellyfish detritus (Fig. 3). Unlike at the two locations further outwards, the mean C-uptake rates at the Inner location in Kaldfjorden were somewhat lower, albeit not significant, when jellyfish was added (Fig. 3). This may indicate a reduction in the foraminiferal C-uptake in the presence of jellyfish detritus at the Inner location.

4.5. *Sediment O_2 dynamics*

DOU in sediments from Kaldfjorden was significantly higher by approx. 1.5-fold when jellyfish detritus was added (Fig. 6a), which is

consistent with previous studies (Sweetman et al., 2016; West et al., 2009). The remineralisation of older, less reactive organic matter in sediment decreases with increased carbon loading (van Nugteren et al., 2009), and the higher DOU measured when jellyfish detritus was added in this study should be a reflection of the microbial and meiofaunal response (Glud, 2008; Glud et al., 1994). The clear response of DOU to jellyfish detritus is in contrast with the foraminiferal C-uptake which only differed significantly amongst the locations. This suggests that foraminifera as a meiofaunal group were probably not the main driver behind the DOU in Kaldfjorden. The significant rise in DOU in sediments from Kaldfjorden was therefore likely due to increased microbial metabolism as previously observed by Sweetman et al. (2016) and Billett et al. (2006).

Scavengers and currents are known to disperse jellyfish carrion and thus reduce the concentrations at the sea floor (e.g. Dunlop et al., 2018; Sweetman et al., 2014; Sweetman and Chapman, 2011) and their absence in the experimental setting could have exaggerated both the concentrations and natural retention time of jellyfish carrion on top of the sediment. However, the Kalfjorden DOU were not significantly different between the two jellyfish detritus concentrations (Fig. 6a). This could indicate that the benthic communities reached their carbon processing saturation but also that the presence of jellyfish detritus on the sediment has a stronger effect than the additional carbon from the jellyfish. The latter would point to a smothering-like effect from the jellyfish detritus sitting on top the sediment obstructing O_2 diffusion into the sediment.

The almost significantly lower OCI and OPD at the Inner and Outer location when jellyfish was placed on top of the sediment (Fig. 6), suggests that the O_2 diffusion into the sediment was reduced. The findings from this study support previous suggestions (based on indirect evidence) that the presence of jellyfish on top of the sediment can affect pore-water O_2 conditions (Chelsky et al., 2016; Sweetman et al., 2016). Previously, *B. marginata* has been shown to migrate upwards and even out of the sediment (Alve and Bernhard, 1995), and reduce its physiological activity when O_2 concentrations decline (Bernhard and Alve, 1996). It is therefore possible that changes in pore-water O_2 conditions negatively affected *B. marginata* specimens (and potentially also other species) at the Inner location, and that the lower OCI and OPD induced by jellyfish detritus led to lower foraminiferal C-uptake rates. Though the OCI and ODP significantly differed between the Middle and Outer location the foraminiferal C-uptake rates did not, and there appeared to be no obvious relationship between the parameters at these locations (Figs. 5 and 6). This study suggests that short-term changes in OCI and OPD introduced by the addition of jellyfish detritus may only have had a marginal effect on benthic foraminiferal carbon processing, and that this effect could be dependent on the assemblage composition.

5. Summary and conclusions

Foraminiferal C-cycling varied strongly within the fjord with a 20-fold higher C-uptake at the inner-fjord location. This was likely caused by a combination of the higher foraminiferal biomass, and high relative abundances of *Bulimina marginata* and *Nonionella turgida* here compared to the middle and outer fjord location. The assemblage composition and foraminiferal biomass are thus considered important factors driving foraminiferal C-uptake rates. Strong differences in foraminiferal assemblage structure amongst the locations were not explained by strong differences in the investigated environmental parameters, but slight differences in primary productivity potentially influenced by riverine input or riverine input itself could have played yet to be defined roles. The non-significant differences in diffusive O_2 uptake rates between the jellyfish treatments (High and Low), in combination with the almost significantly lower O_2 concentrations at the sediment water interface and O_2 penetration depth when jellyfish was placed on top of the sediment at the Inner and Outer location, suggest that jellyfish detritus may obstruct O_2 diffusion into the sediment. A potential effect of short-term changes in the sediment O_2 dynamics on foraminiferal C-uptake was only observed at the inner-fjord location. This indicates that the effect of jellyfish detritus on foraminiferal C-uptake rates was little and that the assemblage composition, e.g. the presence of *B. marginata*, could play a role if any effect can be observed at all. The results from this study suggest that the coastal habitats where the highest amounts of organic carbon are being processed may also be the most sensitive to changes in the sediment O_2 dynamics. This would make these areas vulnerable to changes in riverine input but also anthropogenic organic carbon enrichment.

CRediT authorship contribution statement

Anouk T. Klootwijk: Writing – original draft, Formal analysis, Conceptualization, Resources, Visualization, Investigation, Writing – review & editing. **Andrew K. Sweetman:** Funding acquisition, Conceptualization, Formal analysis, Writing – review & editing, Project administration, Resources. **Silvia Hess:** Writing – review & editing, Investigation, Conceptualization, Supervision. **Elisabeth Alve:** Writing – review & editing, Investigation, Conceptualization, Supervision. **Kathy M. Dunlop:** Writing review and editing, Conceptualization, Investigation. **Paul E. Renaud:** Funding acquisition, Conceptualization, Formal analysis, Investigation, Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Andrew K. Sweetman and Paul E. Renaud reports financial support was provided by Research Council of Norway. Paul E. Renaud reports financial support was provided by The Fram Centre.

Acknowledgements

We would like to thank Anne-Katrin Enge, Hidetaka Nomaki, Alessio Gomiero, Petra Heinz and Bente Edvardsen for their help culturing the algae and foraminifera sample processing; Raul Primicerio and Mark Greenacre for their help with the statistical analyses; Dirk Linke for the use of his equipment; Raul Wolf, Boris Berkhout, Marco Brustolin, and Alexandr Lubin for their support in R-data programming; Mischa Seas for his mathematical support; Carl Ballantine, Hector Andrade, Katja Guilini, Hege Vågen and Marta Cecchetto for their assistance during the experiment; Peter van Breugel for performing the stable isotope analyses; Angelika Renner and Elizabeth Jones for sharing their hydrocast data; Captain Leif Arne Isaksen and crew of the Rolf-Tore; and the crew from Research and Innovation Station in Kraknes for technical support. We would like to thank the two anonymous reviewers and Editor-in-Chief Mike Elliot for their valuable comments on a previous version of the manuscript. This project was partly funded by the Research Council of Norway ('JellyFarm' project: RCN#244572), and the Fjord and Coast Flagship of Fram Centre for Climate and the Environment ('EFFECTS' project).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107535.

References

Aksnes, D.L., 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. https://doi.org/10.3354/meps08120.

Alve, E., 1991. Benthic foraminifera in sediment cores reflecting heavy metal pollution in Sorfjord , western Norway. J. Foraminifer. Res. 21, 1–19. https://doi.org/10.2113/gsjfr.21.1.1.

Alve, E., Bernhard, J.M., 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. Mar. Ecol. Prog. Ser. 116, 137–152. https://doi.org/10.3354/meps116137.

Alve, E., Nagy, J., 1990. Main features of foraminiferal distribution reflecting estuarine hydrography in Oslo Fjord. Mar. Micropaleontol. 16, 181–206. https://doi.org/10.1016/0377-8398(90)90003-5.

Austin, W.E.N., Sejrup, H.P., 1994. Recent shallow water benthic foraminifera from western Norway: ecology and palaeoecological significance. Cusman Found. Spec. Publ. 103–125.

Bernhard, J.M., Alve, E., 1996. Survival, ATP pool, and ultrastructural characterization of benthic foraminiferafrom Drammensfjord (Norway): response to anoxia. Mar. Micropaleontol. 28, 5–17. https://doi.org/10.1016/0377-8398(95)00036-4.

Billett, D.S.M., Bett, B.J., Jacobs, C.L., Rouse, I.P., Wigham, B.D., 2006. In the deep Arabian Sea Mass deposition of jellyfish. Limnol. Oceanogr. 51, 2077–2083.

Chelsky, A., Pitt, K.A., Ferguson, A.J.P., Bennett, W.W., Teasdale, P.R., Welsh, D.T., 2016. Decomposition of jellyfish carrion in situ: short-term impacts on infauna, benthic nutrient fluxes and sediment redox conditions. Sci. Total Environ. 566– 567, 929–937. https://doi.org/10.1016/j.scitotenv.2016.05.011.

Chelsky, A., Pitt, K.A., Welsh, D.T., 2015. Biogeochemical implications of decomposing jellyfish blooms in a changing climate. Estuar. Coast Shelf Sci. 154, 77–83. https://doi.org/10.1016/j.ecss.2014.12.022.

Chierici, M., Jones, E., Lødemel, H.H., 2019. Variability of the Marine CO2 System, Dissolved Inorganic Nutrients and Stable Oxygen Isotopic Ratio (δ18O) in Kaldfjorden in Northern Norway from 2016 to 2018. https://doi.org/10.21335/NMDC-646962623.

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.E., Purcell, J. E., Malej, A., Mianzan, H., Uye, S.I., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous Zooplankton in the world's oceans. Bioscience 62, 160–169. https://doi.org/10.1525/bio.2012.62.2.9.

Condon, R.H., Steinberg, D.K., Del Giorgio, P.A., Bouvier, T.C., Bronk, D.A., Graham, W. M., Ducklow, H.W., 2011. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc. Natl. Acad. Sci. U.S.A. 108, 10225–10230. https://doi.org/10.1073/pnas.1015782108.

Das, M., Gupta, A.K., Anderson, D.M., 2006. Deep-sea paleoceanographic and surface productivity changes in the northwestern Arabian Sea driven by the Indian southwest monsoon during the last millennium. J. Geol. Soc. India 68, 387–394.

Duffield, C., Alve, E., Andersen, N., Andersen, T., Hess, S., Strohmeier, T., 2017. Spatial and temporal organic carbon burial along a fjord to coast transect: a case study from Western Norway. The Holocene 095968361769058. https://doi.org/10.1177/0959683617690588.

Duffield, C.J., Hess, S., Norling, K., Alve, E., 2015. The response of Nonionella iridea and other benthic foraminifera to "fresh" organic matter enrichment and physical disturbance. Mar. Micropaleontol. 120, 20–30. https://doi.org/10.1016/j.marmicro.2015.08.002.

Dunlop, K.M., Jones, D.O.B., Sweetman, A.K., 2018. Scavenging processes on jellyfish carcasses across a fjord depth gradient. Limnol. Oceanogr. 63, 1146–1155. https://doi.org/10.1002/lno.10760.

Elmgren, R., 1973. Methods of sampling sublittoral soft bottom meiofauna. Oikos Suppl 15, 112–120.

Enge, A.J., Nomaki, H., Ogawa, N.O., Witte, U., Moeseneder, M.M., Lavik, G., Ohkouchi, N., Kitazato, H., Kučera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Mar. Ecol. Prog. Ser. 438, 129–142. https://doi.org/10.3354/meps09298.

Enge, A.J., Witte, U., Kucera, M., Heinz, P., 2014. Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian margin (Arabian Sea). Biogeosciences 11. https://doi.org/10.5194/bg-11-2017-2014, 2017–2026.

Enge, A.J., Wukovits, J., Wanek, W., Watzka, M., Witte, U.F.M., Hunter, W.R., Heinz, P., 2016. Carbon and nitrogen uptake of calcareous benthic foraminifera along a depth-related oxygen gradient in the OMZ of the Arabian Sea. Front. Microbiol. 7, 1–12. https://doi.org/10.3389/fmicb.2016.00071.

Eppley, R.W., Holmes, R.W., Strickland, J.D.H., 1967. Sinking rates of marine phytoplankton measured with a fluorometer. J. Exp. Mar. Biol. Ecol. 1, 191–208. https://doi.org/10.1016/0022-0981(67)90014-7.

Faust, J.C., Knies, J., 2019. Organic matter sources in north atlantic fjord sediments. G-cubed 20, 2872–2885. https://doi.org/10.1029/2019GC008382.

Frigstad, H., Kaste, Ø., Deininger, A., Kvalsund, K., Christensen, G., Bellerby, R.G.J., Sørensen, K., Norli, M., King, A.L., 2020. Influence of riverine input on Norwegian coastal systems. Front. Mar. Sci. 7, 1–14. https://doi.org/10.3389/fmars.2020.00332.

Glud, R.N., 2008. Oxygen dynamics of marine sediments. Mar. Biol. Res. 4, 243–289. https://doi.org/10.1080/17451000801888726.

Glud, R.N., Gundersen, J.K., Barker Jørgensen, B., Revsbech, N.P., Schulz, H.D., 1994. Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: in situ and laboratory measurements. Deep. Res. Part I 41, 1767–1788. https://doi.org/10.1016/0967-0637(94)90072-8.

Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. Mar. Micropaleontol. 46, 83–110. https://doi.org/10.1016/S0377-8398(02)00050-6.

Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., 1992. The role of benthic foraminifera in deep-sea food webs and carbon cycling. Deep-Sea Foodchains and the Global Carbon Cycle, pp. 63–91. https://doi.org/10.1007/978-94-011-2452-2.

Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Mar. Chem. 49, 81–115. https://doi.org/10.1016/0304-4203(95)00008-F.

Heiskanen, A.S., Tallberg, P., 1999. Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. Hydrobiologia 393, 127–140. https://doi.org/10.1023/A:1003539230715.

Heløø, G., Lejon, R., 2009. Hovedplan Avløp Og Vannmiljø 2009-2018 Sak 113/09 1–156.

Husum, K., Hald, M., 2004. Modern foraminiferal distribution in the subarctic malangen fjord and adjoining shelf, northern Norway. J. Foraminifer. Res. 34, 34–48. https://doi.org/10.2113/0340034.

Jones, E.M., Renner, A.H.H., Chierici, M., Wiedmann, I., Lødemel, H.H., Biuw, M., 2020. Seasonal dynamics of carbonate chemistry, nutrients and CO_2 uptake in a sub-Arctic fjord. Elem Sci Anth 8, 41. https://doi.org/10.1525/elementa.438.

Kennedy, M.J., Pevear, D.R., Hill, R.J., 2002. Mineral surface control in organic black shale. Science (80-.) 295, 657–660.

Klootwijk, A.T., Alve, E., Hess, S., Renaud, P.E., Sørlie, C., Dolven, J.K., 2020. Monitoring environmental impacts of fish farms : comparing reference conditions of sediment geochemistry and benthic foraminifera with the present. Ecol. Indicat. 120, 106818 https://doi.org/10.1016/j.ecolind.2020.106818.

Kokarev, V., Tachon, M., Austad, M., McGovern, M., Reiss, H., 2021. Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales. Estuar. Coast Shelf Sci. 252, 107271 https://doi.org/10.1016/j.ecss.2021.107271.

Korsun, S., Hald, M., 2000. Seasonal dynamics of benthic foraminifera in a glacially fed fjord of svalbard, european arctic. J. Foraminifer. Res. 30, 251–271. https://doi.org/10.2113/0300251.

Lalande, C., Dunlop, K., Renaud, P.E., Nadaï, G., Sweetman, A.K., 2020. Seasonal variations in downward particle fluxes in Norwegian fjords. Estuar. Coast Shelf Sci. 241, 106811 https://doi.org/10.1016/j.ecss.2020.106811.

Lamb, A.L., Wilson, G.P., Leng, M.J., 2006. A review of coastal palaeoclimate and relative sea-level reconstructions using δ13C and C/N ratios in organic material. Earth Sci. Rev. 75, 29–57. https://doi.org/10.1016/j.earscirev.2005.10.003.

Lebrato, M., de Jesus Mendes, P., Steinberg, D.K., Cartes, J.E., Jones, B.M., Birsa, L.M., Benavides, R., Oschlies, A., 2013. Jelly biomass sinking speed reveals a fast carbon export mechanism. Limnol. Oceanogr. 58, 1113–1122. https://doi.org/10.4319/lo.2013.58.3.1113.

Linshy, V.N., Ravjiv, N., Heinz, P., 2014. Approaches to Study Living Foraminifera. https://doi.org/10.1007/978-4-431-54388-6_8. Springer 238.

Lintner, M., Biedrawa, B., Wukovits, J., Wanek, W., Heinz, P., 2020. Reviews and syntheses: salinity-dependent algae uptake and subsequent carbon and nitrogen metabolisms of two intertidal foraminifera (Ammonia tepida and Haynesina germanica). Biogeosciences 17, 3723–3732. https://doi.org/10.5194/bg-17-3723-2020.

McGovern, M., Poste, A.E., Oug, E., Renaud, P.E., Trannum, H.C., 2020. Riverine impacts on benthic biodiversity and functional traits: a comparison of two sub-Arctic fjords. Estuar. Coast Shelf Sci. 240, 106774 https://doi.org/10.1016/j.ecss.2020.106774.

McKee, B.A., Aller, R.C., Allison, M.A., Bianchi, T.S., Kineke, G.C., 2004. Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: benthic boundary layer and seabed processes. Continent. Shelf Res. 24, 899–926. https://doi.org/10.1016/j.csr.2004.02.009.

McMahon, K.W., Ambrose, W.G., Reynolds, M.J., Johnson, B.J., Whiting, A., Clough, L. M., 2021. Arctic lagoon and nearshore food webs: relative contributions of terrestrial organic matter, phytoplankton, and phytobenthos vary with consumer foraging dynamics. Estuar. Coast Shelf Sci. 257, 107388 https://doi.org/10.1016/j.ecss.2021.107388.

Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chem. Geol. 114, 289–302. https://doi.org/10.1016/0009-2541(94)90059-0.

Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H. R., 2000. The fate of intertidal microphytobenthos carbon: an in situ 13C-labeling study. Limnol. Oceanogr. 45, 1224–1234. https://doi.org/10.4319/lo.2000.45.6.1224.

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68. https://doi.org/10.1023/A:1011888006302.

Mojtahid, M., Jorissen, F., Lansard, B., Fontanier, C., Bombled, B., Rabouille, C., 2009. Spatial distribution of live benthic foraminifera in the Rhône prodelta: faunal response to a continental-marine organic matter gradient. Mar. Micropaleontol. 70, 177–200. https://doi.org/10.1016/j.marmicro.2008.12.006.

Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P.M. J., Heip, C.H.R., 2002. Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Mar. Ecol. Prog. Ser. 236, 23–29. https://doi.org/10.3354/meps236023.

Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., Heip, C.H. R., 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. J. Mar. Res. 63, 457–469. https://doi.org/10.1357/0022240053693662.

Murray, J.W., Alve, E., 2016. Benthic foraminiferal biogeography in NW European fjords: a baseline for assessing future change. Estuar. Coast Shelf Sci. 181, 218–230. https://doi.org/10.1016/j.ecss.2016.08.014.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: in situ tracer experiments. Limnol. Oceanogr. 50, 134–146. https://doi.org/10.4319/lo.2005.50.1.0134.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N.O., Kogure, K., Ikemoto, E., Kitazato, H., 2006. Different ingestion patterns of 13C-

labeled bacteria and algae by deep-sea benthic foraminifera. Mar. Ecol. Prog. Ser. 310, 95–108. https://doi.org/10.3354/meps310095.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2010. Vegan: community ecology package.
Paassche, E., Erga, S.R., 1988. Phosphorus and Nitrogen Limitation of Phytoplankton in the Inner Oslofjord (Norway). https://doi.org/10.1080/00364827.1988.10413409.
Purcell, J.E., Uye, S.I., Lo, W.T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174. https://doi.org/10.3354/meps07093.
R Core Team, 2019. R: a Language and Environment for Statistical Computing.
Renaud, P.E., Morata, N., Carroll, M.L., Denisenko, S.G., Reigstad, M., 2008. Pelagic – benthic coupling in the western Barents Sea : processes and time scales. Deep. Res. II 55, 2372–2380. https://doi.org/10.1016/j.dsr2.2008.05.017.
Schlünz, B., Schneider, R.R., 2000. Transport of terrestrial organic carbon to the oceans by rivers: Re-estimating flux- and burial rates. Int. J. Earth Sci. 88, 599–606. https://doi.org/10.1007/s005310050290.
Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Abramovich, S., Almogi-Labin, A., du Chatelet, E.A., Barras, C., Bergamin, L., Bicchi, E., Bouchet, V., Cearreta, A., Di Bella, L., Dijkstra, N., Disaro, S.T., Ferraro, L., Frontalini, F., Gennari, G., Golikova, E., Haynert, K., Hess, S., Husum, K., Martins, V., McGann, M., Oron, S., Romano, E., Sousa, S.M., Tsujimoto, A., 2012. The FOBIMO (FOraminiferal BIo-MOnitoring) initiative-Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. Mar. Micropaleontol. 1–13. https://doi.org/10.1016/j.marmicro.2012.06.001, 94–95.
Sen Gupta, B.K., 1999. Modern Foraminifera. Kluwer Academic Publishers. https://doi.org/10.1007/0-306-48104-9.
Smart, C.W., Gooday, A.J., 1997. Recent benthic foraminifera in the abyssal Northeast Atlantic Ocean: relation to phytodetrital inputs. J. Foraminifer. Res. 27, 85–92. https://doi.org/10.2113/gsjfr.27.2.85.
Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23, 518–528. https://doi.org/10.1016/j.tree.2008.05.002.
Sørnes, T.A., Aksnes, D.L., Båmstedt, U., Youngbluth, M.J., 2007. Causes for mass occurrences of the jellyfish Periphylla periphylla: a hypothesis that involves optically conditioned retention. J. Plankton Res. 29, 157–167. https://doi.org/10.1093/plankt/fbm003.
Sweetman, A.K., Chapman, A., 2015. First assessment of flux rates of jellyfish carcasses (jelly-falls) to the benthos reveals the importance of gelatinous material for biological C-cycling in jellyfish-dominated ecosystems. Front. Mar. Sci. 2, 1–7. https://doi.org/10.3389/fmars.2015.00047.
Sweetman, A.K., Chapman, A., 2011. First observations of jelly-falls at the seafloor in a deep-sea fjord. Deep. Res. Part I Oceanogr. Res. Pap. 58, 1206–1211. https://doi.org/10.1016/j.dsr.2011.08.006.
Sweetman, A.K., Chelsky, A., Pitt, K.A., Andrade, H., van Oevelen, D., Renaud, P.E., 2016. Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. Limnol. Oceanogr. 61, 1449–1461. https://doi.org/10.1002/lno.10310.
Sweetman, A.K., Norling, K., Gunderstad, C., Haugland, B.T., Dale, T., 2014a. Benthic ecosystem functioning beneath fish farms in different hydrodynamic environments. Limnol. Oceanogr. 59, 1139–1151. https://doi.org/10.4319/lo.2014.59.4.1139.
Sweetman, A.K., Smith, C.R., Dale, T., Jones, D.O.B., 2014b. Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. Proc. R. Soc. B Biol. Sci. 281, 1–8. https://doi.org/10.1098/rspb.2014.2210.
Sweetman, A.K., Sommer, S., Pfannkuche, O., Witte, U., 2009. Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord. J. Foraminifer. Res. 39, 15–22. https://doi.org/10.2113/gsjfr.39.1.15.
Syvitski, P.M., Burrell, D.C., Skei, J.M., 1987. Fjords. Processes and Products, vol. 379. Springer-Verlag.
Tiller, R.G., Borgersen, Å.L., Knutsen, Ø., Bailey, J., Bjelland, H.V., Mork, J., Eisenhauer, L., Liu, Y., 2017. Coming soon to a fjord near you: future jellyfish scenarios in a changing climate. Coast. Manag. 45, 1–23. https://doi.org/10.1080/08920753.2017.1237239.
Underwood, A.J., 1996. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press. https://doi.org/10.1017/CBO9780511806407.
Vågen, H., 2018. Temporal changes of the benthic environmental conditions in a subarctic fjord with aquaculture activity A geochemical and micropaleontological study. Thesis, Master Sci. Nat.
van Nugteren, P., Moodley, L., Brummer, G.J., Heip, C.H.R., Herman, P.M.J., Middelburg, J.J., 2009. Seafloor ecosystem functioning: the importance of organic matter priming. Mar. Biol. 156, 2277–2287. https://doi.org/10.1007/s00227-009-1255-5.
Veileder, 2018. (02:2018), Klassifisering Av Miljøtilstand I Vann (Økologisk Og Kjemisk Klassifiseringssystem for Kystvann, Grunnvann, Innsjøer Og Elver.
West, E.J., Welsh, D.T., Pitt, K.A., 2009. Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. Hydrobiologia 616, 151–160. https://doi.org/10.1007/s10750-008-9586-7.
Woulds, C., Andersson, J.H., Cowie, G.L., Middelburg, J.J., Levin, L.A., 2009. The short-term fate of organic carbon in marine sediments: comparing the Pakistan margin to other regions. Deep. Res. Part II Top. Stud. Oceanogr. 56, 393–402. https://doi.org/10.1016/j.dsr2.2008.10.008.
Woulds, C., Bouillon, S., Cowie, G.L., Drake, E., Middelburg, J.J., Witte, U., 2016. Patterns of carbon processing at the seafloor: the role of faunal and microbial communities in moderating carbon flows. Biogeosciences 13, 4343–4357. https://doi.org/10.5194/bg-13-4343-2016.
Wukovits, J., Oberrauch, M., Enge, A.J., Heinz, P., 2018. The distinct roles of two intertidal foraminiferal species in phytodetrital carbon and nitrogen fluxes -results from laboratory feeding experiments. Biogeosciences 15, 6185–6198. https://doi.org/10.5194/bg-15-6185-2018.