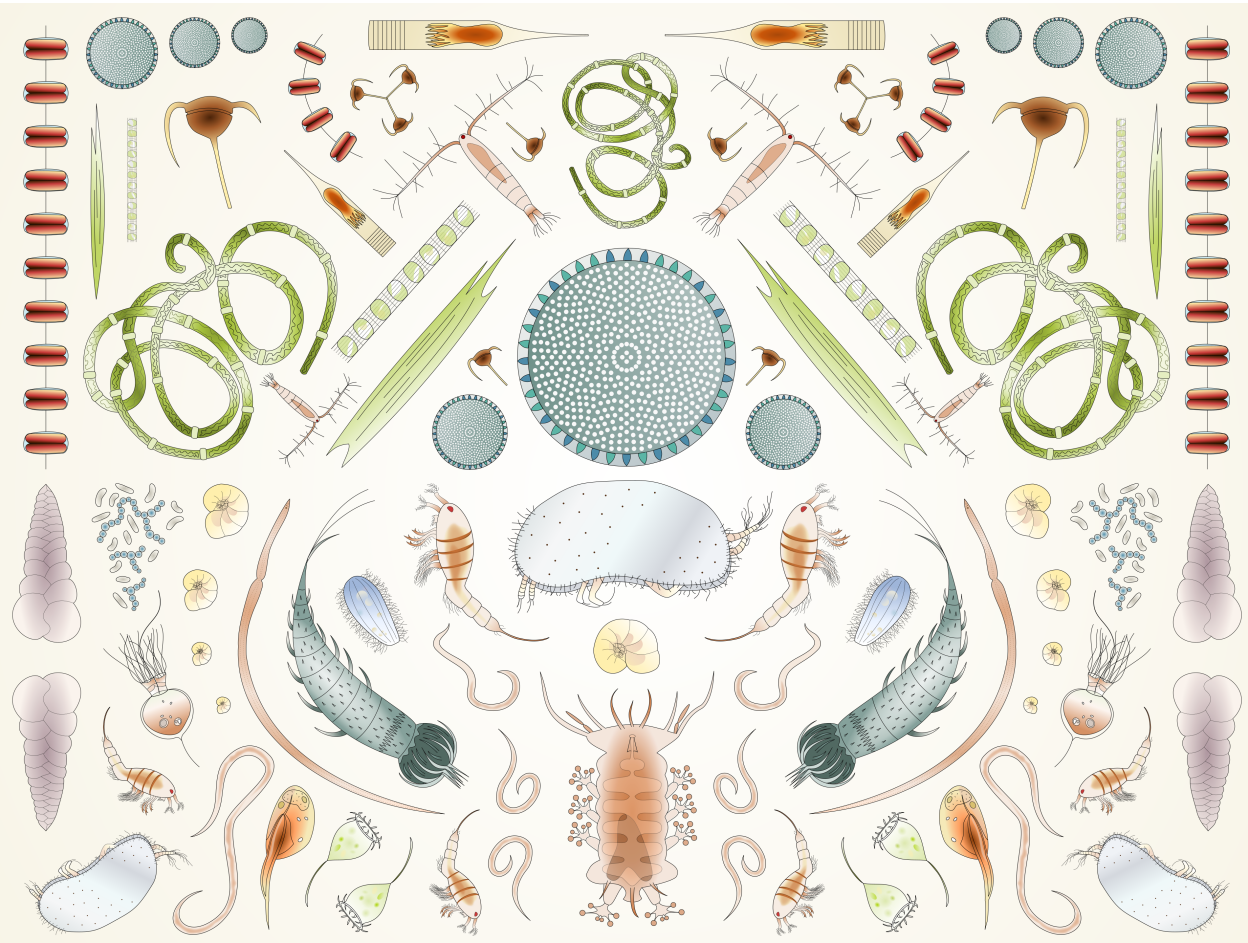
Stockholm University

Benthic-pelagic coupling in a changing world

Structural and functional responses of microbenthic communities to organic matter settling

Séréna Albert



Doctoral Thesis in Marine Ecology at Stockholm University, Sweden 2021

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Séréna Albert

Academic dissertation for the Degree of Doctor of Philosophy in Marine Ecology at Stockholm University to be publicly defended on Friday 17 September 2021 at 09.30 in Vivi Täckholmsalen (Q-salen), NPQ-huset, Svante Arrhenius väg 20.

Abstract

Marine soft sediments form the second largest habitat on the planet. Organisms residing in this environment represent a vast reservoir of biodiversity, and play key roles in ecosystem processes. Most benthic organisms depend on organic matter (OM) inputs from phytoplankton in the overlying water column as food supply, but human impacts such as eutrophication and climate change are profoundly altering natural ecosystem dynamics. The consequences of changes in benthic-pelagic coupling for the biodiversity and functioning of soft-sediment communities have yet to be resolved.

The aim of this thesis is to assess the role of OM settling on soft-sediments microeukaryotic (small organisms < 1 mm) and bacterial communities. The intents are two-fold, to investigate impacts on (1) community structure and diversity (**chapters I**, **II** and **IV**); and (2) ecosystem functioning, notably in relation to nitrogen (N) cycling (**chapters I** and **III**).

Our results show that settling OM quantity and quality both had a significant impact on microeukaryotic alpha-diversity. We observed a decrease in alpha-diversity following settling of diatom-derived spring bloom OM, possibly as a result of competitive exclusion, while cyanobacteria-derived summer bloom OM did not affect alpha-diversity (**chapters I** and **IV**). We also found that high biomass of diatoms and others fast sinking phytoplankton groups in the water column led to lower microeukaryotic alpha diversity after this material settled on the seafloor (**chapter IV**). Presumably, following this large sedimentation event, sediment oxygen (O_2) demand was strongly stimulated, excluding O_2-sensitive taxa. Overall, we propose that the assembly of microeukaryotic communities was primarily mediated by OM settling quantity (**chapter IV**), while differences in OM quality led to significant but more subtle changes, occurring at fine taxonomic level (**chapter I**). The response of bacterial communities to OM settling was less pronounced, and probably restricted to the uppermost sediment layer (**chapters I** and **IV**). We did, however, observe a significant effect of OM quality on bacterial communities assembly at the sediment-water interface, with taxa favored either by diatom- or by cyanobacteria-derived OM (**chapter II**). This study also showed that feedback mechanisms from nutrient recycling in the sediment could play a role in this response. Finally, our results indicated a substantial influence of OM quality on N cycling at the sediment-water interface. We found that settling of fresh OM (i.e. low C:N ratio) stimulated denitrification activity (**chapters I** and **III**), while simultaneously promoting more N recycling to the water column than settling of degraded OM (i.e. high C:N ratio) did (**chapter III**).

Altogether, our results indicate that current changes in OM settling dynamics in marine systems will likely impact microeukaryotic and, to some extent, bacterial biodiversity in soft sediments. Alterations in settling OM quality, in particular, may also affect crucial microbial processes involved in N cycling. This thesis highlights the importance of considering benthic-pelagic coupling mechanisms to better understand likely future changes in marine ecosystems.

Keywords: *Soft sediments, benthic-pelagic coupling, organic matter export, meiofauna, nitrogen cycle, metabarcoding, Baltic Sea.*

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To my grand-father,
To my parents,

À papi,
À mes parents,
pour m'avoir toujours
soutenue dans mon
choix de faire des études
courtes. Quel succès!

Abstract

Marine soft sediments form the second largest habitat on the planet. Organisms residing in this environment represent a vast reservoir of biodiversity, and play key roles in ecosystem processes. Most benthic organisms depend on organic matter (OM) inputs from phytoplankton in the overlying water column as food supply, but human impacts such as eutrophication and climate change are profoundly altering natural ecosystem dynamics. The consequences of changes in benthic-pelagic coupling for the biodiversity and functioning of soft-sediment communities have yet to be resolved.

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Keywords: soft sediments, benthic-pelagic coupling, organic matter export, meiofauna, nitrogen cycle, metabarcoding, Baltic Sea

List of papers

This thesis is based on the following papers, referred to in the text by their Roman numerals (**I-IV**):

I. **Albert S.**, Hedberg P., Motwani N.H., Sjöling S., Winder M., Nascimento F.J.A. (Manuscript submitted for publication in Scientific Reports) Phytoplankton settling quality has a subtle but significant effect on sediment microeukaryotic and bacterial communities.

II. Izabel-Shen D.*, **Albert S**.*, Winder M., Farnelid H., Nascimento F.J.A. (2021) Quality of phytoplankton deposition structures bacterial communities at the water-sediment interface. Mol. Ecol., 30: 3515-3529

III. **Albert S**., Bonaglia S., Stjärnkvist N., Winder M., Thamdrup B., Nascimento F.J.A. (2021) Influence of settling organic matter quantity and quality on benthic nitrogen cycling. *Limnol. Oceanogr.,* 66: 1882-1895

IV. **Albert S**., Liénart C., Winder M., Nascimento F.J.A. (Manuscript) Seasonal patterns of microeukaryotic and bacterial communities in Baltic Sea soft sediments.

*Shared first authorship

My contributions to the papers: Paper I – experiment design and execution, laboratory and data analyses, main responsibility in manuscript writing. Paper II – experiment design and execution, laboratory analyses, writing. Paper III – experiment design and execution, laboratory and data analyses, main responsibility in manuscript writing. Paper IV – sampling design and execution, laboratory and data analyses, main responsibility in manuscript writing.

Additional work completed during the PhD studies:

- Hedberg P., **Albert S.**, Nascimento F.J.A., Winder M. (2021) Effects of changing phytoplankton species composition on carbon and nitrogen uptake in benthic invertebrates. *Limnol. Oceanogr.*, 66: 469-480

Contents

Abbreviations

16S rRNA	16S ribosomal RNA
18S rRNA	18S ribosomal RNA
ACE	Abundance-based coverage estimator
ASV	Amplicon sequence variant
C	Carbon
CO_2	Carbon dioxide
COI	Mitochondrial cytochrome oxidase subunit 1
DIN	Dissolved inorganic nitrogen
DNA	Deoxyribonucleic acid
DNRA	Dissimilatory nitrate reduction to ammonium
eDNA	environmental DNA
eRNA	environmental RNA
H_2SiO_4	Silicate
IPT	Isotope-pairing technique
N	Nitrogen
N_2	Dinitrogen
N_2O	Nitrous oxide
NH_4^+	Ammonium
NO_2^-	Nitrite
NO_3^-	Nitrate
NO_x^-	Nitrite/nitrate
O_2	Oxygen
OM	Organic matter
OTU	Operational taxonomic unit
P	Phosphorus
PCR	Polymerase chain reaction
PO_4^{3-}	Phosphate
RNA	Ribonucleic acid
RT-qPCR	Reverse transcription quantitative real-time PCR
SWI	Sediment-water interface

Introduction

Benthic-pelagic coupling

Marine ecosystems are traditionally separated in two realms: the water column (pelagos) and the seafloor (benthos). These two habitats host different life forms and are constrained by different factors, which has naturally prompted scientists to focus their attention on one or the other. Yet, benthic and pelagic habitats are in constant interaction through exchange of matter, energy, nutrients, gases and organisms (Griffiths et al. 2017). As a whole, these processes are referred to as benthic-pelagic coupling, and constitute a central piece in marine ecosystem functioning (Rowe et al. 1975; Graf 1992). Examples of passive and active coupling across the two habitats include suspension-feeding by benthic organisms, resting stages or eggs deposition, fish predation, nutrient regeneration or organic matter (OM) settling to the seafloor (Griffiths et al. 2017). Extensive research efforts have been devoted to quantify and characterize settling OM fluxes (McCave 1975; Lochte et al. 1993; Blomqvist and Heiskanen 2001), as well as to investigate their impact on the benthos (Graf et al. 1982; Pfannkuche 1993; Josefson and Conley 1997). However, many of these questions remain to be resolved, in particular how such OM fluxes determine benthic biodiversity and function in a context of rapid change within marine ecosystems.

Organic matter settling to the seafloor

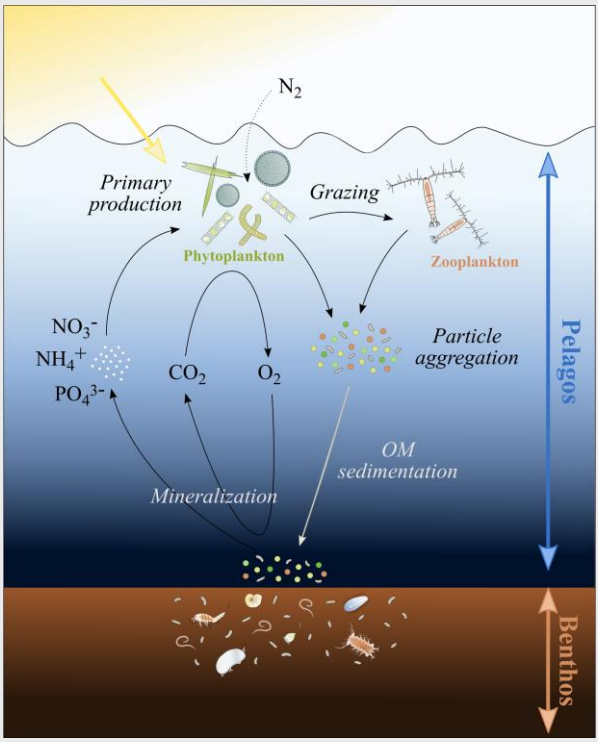
In marine systems, the biological pump plays a central role in regulating the global carbon (C) cycle by fixing inorganic carbon (i.e. CO_2) from the atmosphere and exporting it to the seafloor as particulate or dissolved OM (Box 1; Ducklow et al. 2001). Deposition of OM to the seafloor constitutes the main fuel for benthic food webs (Thrush et al. 2021) and in aphotic sediments, OM inputs primarily originate from pelagic production (Graf 1992; Griffiths et al. 2017). Phytoplankton growing in the photic zone, but also pelagic consumers and decomposers (e.g. zooplankton and particle-associated bacteria) all contribute to OM inputs to the sediment in the form of sinking aggregates, fecal pellets or carcasses (Turner 2015). As a result, the quantity and quality of OM settling varies temporally and spatially depending on pelagic dynamics.

Organic matter quantity and quality both have an impact on benthic biodiversity and functioning, and are equally relevant to consider (Graf 1992;

Campanyà-llovet et al. 2017). Organic matter quantity can be objectively assessed on a specific scale (e.g. g of C), along which OM fluxes can be compared through space and time (Buesseler et al. 2007). Organic matter quality, however, is a more elusive concept, since it encompasses a multiplicity of parameters such as shape, stoichiometry, biochemical composition or toxicity. Furthermore, the purpose of OM may determine its objective quality: OM as a food source will differ for primary consumers or decomposers (Campanyà-llovet et al. 2017; Burian et al. 2020).

The study of benthic responses to pelagic OM settling has a long history in marine research (Gooday and Turley 1990; Graf 1992; Josefson and Conley 1997). Studies have, however, tended to be focused either on the effect of OM quantity (Sloth et al. 1995; Witte et al. 2003; Vanaverbeke et al. 2004), or evaluated from field studies, where multiple environmental factor vary concomitantly (Albertelli et al. 1999; Ingels et al. 2011; Tait et al. 2015). In comparison, the specific influence of OM quality on benthic communities and ecosystem functions remains underexplored, despite indications that it may be equally as important as OM quantity (Arnosti and Holmer 2003; Campanyà-llovet et al. 2017). In this thesis, **chapters I** and **II** address the effects of OM quality, and **chapters III** and **IV** cover both the effects of quantity and quality of OM on the biodiversity and functioning of benthic communities.

Box 1: Benthic-Pelagic coupling



Box Figure 1. Conceptualization of some of the benthic-pelagic coupling processes investigated in this thesis.

The cycle of production and degradation of OM is a prime example of how pelagic and benthic processes are tightly connected and interdependent (Box Fig. 1; Griffiths et al. 2017). **Primary production** mainly occurs through photosynthesis. Phytoplankton use solar energy to produce OM from CO_2 and inorganic nutrients (NH_4^+, NO_3^-, PO_4^{3-}). Nitrogen (N) and phosphorus (P) are key in this process, although other elements like silicate (Si) or iron (Fe) are also required. Specialized diazotrophic cyanobacteria have the ability to fix N_2, present in vast quantities in the atmosphere and dissolved in seawater. Phytoplankton production fuels pelagic food webs in the upper water column, and all organisms eventually sink to the seafloor, which constitutes the main input of OM to the benthos. During its descent and upon reaching the sediment, OM is decomposed in a process called **mineralization**. This is mainly carried out by microorganisms that break down the organic compounds, simultaneously releasing inorganic nutrients and CO_2 back into the system (Rowe et al. 1975). Eventually, these elements make their way back to the upper water column, where they may fuel primary production again.

Soft sediment communities

Soft sediments cover approximately 70.8 % of the Earth's surface, making it the second largest habitat on the planet, behind only the open ocean when taking into account the 3-dimensional habitat (Snelgrove 1999). Soft sediments as a whole thus represent a tremendous amount of biodiversity, and the ecosystem processes that take place here are of vital importance for the planet's functioning (Snelgrove 1997; Thrush et al. 2021).

Microeukaryotes

Benthic communities are often classified according to their size in relation to sieve mesh characteristics used during sampling (Somerfield and Warwick 2013). As such, we discriminate between macrofauna (> 0.5 or 1 mm), meiofauna (40 or 63 µm – 0.5 or 1 mm) and microfauna (< 40 µm) (Fig. 1; Thrush et al. 2021). Beyond practical sampling considerations, these size boundaries also distinguish ecological units, governed by distinct community assembly processes (Somerfield et al. 2018; Luan et al. 2020). Meiofauna are particularly abundant in soft sediment habitats, where they have adapted to live in the interstitial space (Giere 2009). The term "meiofauna" originally designates multicellular metazoans, including groups such as nematodes, ostracods, copepods, kinorhynchs or platyhelminths (McIntyre 1969; Vincx 1996). This definition *sensu stricto* is still commonly used today, although numerous studies recognize the importance of unicellular protists such as ciliates or foraminifers in benthic habitats, and consider them as integral members of meiofauna (Giere 2009). In this thesis, we use the term "microeukaryotes" to collectively refer to small metazoans (i.e. meiofauna *sensu stricto*) and unicellular protists (Fig. 1). Due to technical challenges having to do with their small size and large taxonomic diversity, research on microeukaryotes has been neglected compared to other groups (Giere 2009; Bik 2019). However, their ubiquity and the central role that they play in sedimentary habitats should act as strong motives to expand our knowledge on microeukaryotes (Schratzberger and Ingels 2018).

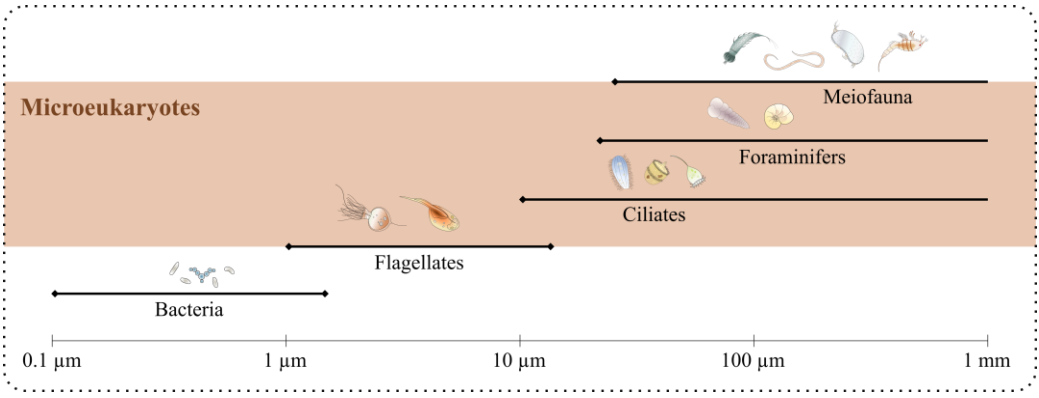


Figure 1. Size range of the benthic meio- and microorganisms investigated in this thesis.

Microeukaryotes are ubiquitous in soft sediment habitats (Giere 2009). They also constitute one of the most diverse communities on Earth, including representatives from most metazoan phyla, some of which are exclusively microeukaryotic (Vincx 1996; Giere 2009). Within soft sediment habitats, microeukaryotes play a key role in ecosystem processes through their interactions with the macro- and microfauna (Coull 1999; Schratzberger and Ingels 2018). They may affect sediment stability through their bioturbating activity, and, by grazing on sediment bacteria, influence microbial processes such as OM mineralization or denitrification (Nascimento et al. 2012; Bonaglia et al. 2014b). They also serve as important food for secondary consumers (Coull 1999; Schratzberger and Ingels 2018).

Many microeukaryotic taxa rely directly or indirectly on OM settling to the seafloor as food supply (Fenchel 1968; Giere 2009). Consequently, positive effects of OM settling on microeukaryotic biomass and abundance have often been reported (Gooday and Turley 1990; Graf 1992; Pfannkuche 1993; Ólafsson and Elmgren 1997), although there are disparities in the response of different trophic groups and species (Vanaverbeke et al. 2004; Schratzberger et al. 2008). For example, Ólafsson and Elmgren (1997) found that spring bloom sedimentation was followed by an increase in nematodes classified as epistrate-feeders (i.e. feeding on microalgae) and selective deposit-feeders (i.e. feeding on bacteria and small detritus), benefiting from freshly deposited microalgae and potential stimulation in bacterial production. Yet, these patterns are not always consistent, and it has been demonstrated that many microeukaryotes exhibit a large plasticity in resource utilization (Moens and Vincx 1997; Schuelke et al. 2018). Current knowledge on the response of microeukaryotes to OM settling is strongly biased in favor of a few specific groups such as nematodes and copepods (Nascimento et al. 2008; Rzeznik-

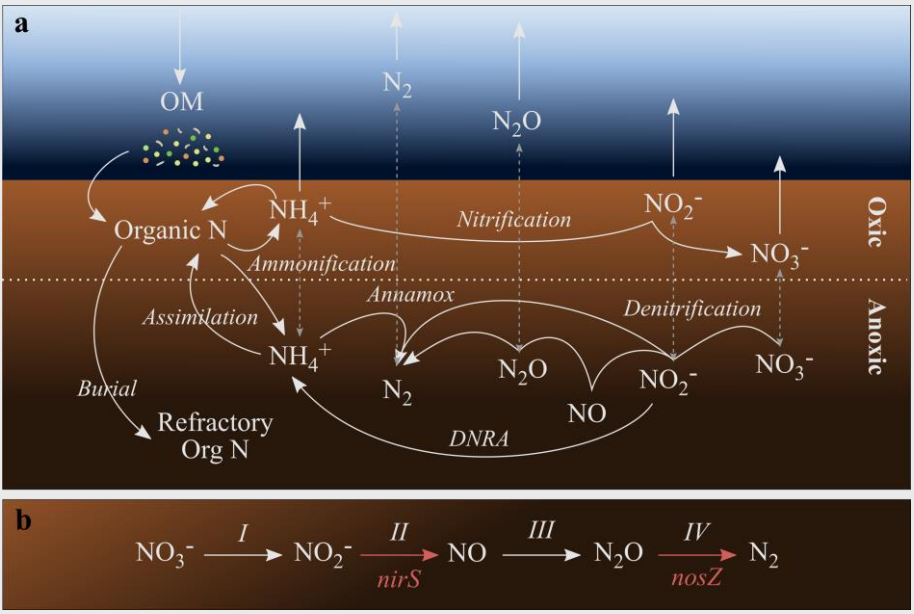
Orignac and Fichet 2012). As such, potential effects of OM settling at the community level deserves further attention. In **chapters I** and **IV**, we aimed to address this gap by adopting a DNA-based approach in the context of a controlled experiment and a field monitoring study.

Bacteria

Bacteria account for the largest biomass and abundance of organisms in soft sediments (Nealson 1997; Dietrich and Arndt 2000). Recent advances in molecular ecology have also shed light upon the tremendous diversity in bacterial communities, although estimates of total richness are still widely uncertain (Ojaveer et al. 2010; Hoshino et al. 2020). Benthic bacterial communities, in particular, appear to be more diverse than pelagic communities (Zinger et al. 2011). Benthic bacteria play key roles in ecosystem functioning. They largely mediate OM mineralization in sediments (Billen et al. 1990; Middelburg et al. 1993) and are involved in several biochemical pathways that ultimately control element cycling in marine systems (Azam et al. 1993; Thamdrup and Dalsgaard 2008). The N cycle notably involves many microbial processes, carried out by more or less specialized bacterial taxa (Box 2; Canfield et al. 2005). For example, the process of nitrification is only mediated by a limited number of taxa (e.g. *Nitrosomonas*, *Nitrospira*, *Nitrobacter*; Canfield et al. 2005), while the ability to denitrify is widespread among bacteria (Box 2; Zumft 1997). Altogether, this suggests that potential structural changes in benthic bacterial communities may have important repercussions on ecosystem functioning as a whole (Nagata 2008).

Box 2: Marine nitrogen cycle at the sediment-water interface

Nitrogen is a central element for OM production, and often the principal limiting factor for primary production in marine systems (Tyrrell 1999). The marine N cycle is complex, involving several forms of dissolved N and transformation reactions, principally mediated by bacteria (Canfield et al. 2005; Thamdrup and Dalsgaard 2008). Since many of these processes are tied to oxygen (O_2) conditions, the sharp oxic/anoxic gradient in upper sediment layers represents a zone of notable importance for N cycling (Box Fig. 2a; Canfield et al. 2005; Thrush et al. 2021).



Box Figure 2. Schematic representation of the marine nitrogen cycle at the sediment-water interface. (a) Overview of the main transformation pathways occurring in oxic and anoxic conditions; (b) details of the denitrification process, converting nitrate (NO_3^-) to dinitrogen (N_2) in four steps (numbered I to IV). Genes coding for the enzymes involved in steps II and IV – investigated in this thesis – are shown in red. OM = organic matter, Org N = organic nitrogen, DNRA = dissimilatory nitrate reduction to ammonium. Modified from Bonaglia (2015)

Organic matter decomposition occurs in conjunction with **ammonification**, a process through which organic N is mineralized and released in the form of ammonium (NH_4^+). The NH_4^+ pool in sediment pore waters at any given time is generally small, but it has a dynamic cycle. NH_4^+ may be **assimilated** (mainly by bacteria in aphotic sediments), or oxidized to nitrite (NO_2^-) and nitrate (NO_3^-) in a strictly aerobic process called **nitrification**. The N compounds produced during these reactions may diffuse upwards to the water column or downwards into deeper sediment layers, depending on concentration gradients. In anoxic sediments, oxidized forms of N (NO_3^- and NO_2^-) either enter the **dissimilatory nitrate reduction to ammonium (DNRA)** pathway, where they are recycled back into NH_4^+, or are semi-permanently removed from the environment as dinitrogen gas (N_2) (Canfield et al. 2005; Thamdrup and Dalsgaard 2008). The latter path constitutes a major sink in the marine N cycle (Codispoti 2007; Voss et al. 2011). The conversion of N-oxides to N_2 is carried out through **denitrification** and **anaerobic ammonia oxidation (anammox)**, with nitrous oxide gas (N_2O) as an intermediate product. The process of anammox was discovered more recently than denitrification, and

can locally contribute significantly to N_2 production (Dalsgaard et al. 2005), but only to a limited extent in Baltic Sea sediments (Bonaglia et al. 2014a). Denitrification accounts for most N_2 production in marine systems (Box Fig. 2b; Devol 2015). It consists of 4 steps, carried out by a highly diverse range of bacteria, and catalyzed by a set of different enzymes, namely: NO_3^- reductase, NO_2^- reductase (coded for by **nirS** genes), NO reductase, and N_2O reductase (coded for by **nosZ** genes; Zumft 1997; Canfield et al. 2005). Finally, a fraction of the organic N that reaches the sediment does not enter any of the aforementioned pathways, but is permanently **buried**, accounting for a small part of total N loss in the system (Canfield et al. 2005; Thamdrup and Dalsgaard 2008; Voss et al. 2011).

As primary agents of OM mineralization, benthic bacteria often react rapidly to settling OM (Meyer-Reil 1987; Witte et al. 2003). As for microeukaryotes, pelagic inputs of OM represent their main source of energy in aphotic sediments (Thamdrup and Dalsgaard 2008). Previous research has documented that OM settling events often stimulate microbial enzymatic activity and respiration, leading to increased O_2 demand by the sediment (Kelly and Nixon 1984; Bühring et al. 2006; Glud 2008). This can in turn affect important microbially-mediated processes such as nutrient recycling or denitrification at the sediment-water interface (SWI) (Box 2; Tuominen et al. 1996; Zilius et al. 2016). At the same time, certain microbial taxa (e.g. Bacteroidetes, Gammaproteobacteria, Verrumicrobia) appear to be preferentially associated with OM degradation in marine environments (Gihring et al. 2009; Vetterli et al. 2015), which may partly explain shifts in bacterial community composition following sedimentation events (Franco et al. 2007; Fagervold et al. 2014; Hoffmann et al. 2017). Yet, many aspects of such responses of benthic bacteria to OM settling remain to be investigated. Particularly, the role of OM quality has been underexplored, despite strong evidence that it is an important driver of bacterial biodiversity and activity (Arnosti and Holmer 2003; Aspetsberger et al. 2007; Mayor et al. 2012; Hoffmann et al. 2017). In **chapters I**, **II** and **IV**, we address the effects of settling OM, notably from a qualitative perspective, on bacterial community biodiversity in the sediment and at the SWI. In **chapter III** (and part of **chapter I**) we focus on effects on ecosystem function, and N cycling in particular.

Study area: the Baltic Sea

Physical and chemical characteristics

The semi-enclosed Baltic Sea is one of the world's largest brackish water systems. It is subdivided into several basins (Fig. 2a), and characterized by pronounced environmental gradients from subarctic, nearly freshwater conditions in the north, to temperate, fully marine waters in the south-west (Snoeijs-Leijonmalm and Andrén 2017). This ~ 2000 km-long gradient in abiotic parameters largely constrains species distribution, and most major organisms groups in the Baltic Sea naturally exhibit a low biodiversity (e.g. benthic macro- and meiofauna; Elmgren and Hill 1997; Ojaveer et al. 2010). Despite being on average a rather shallow sea (~ 57 m; Snoeijs-Leijonmalm and Andrén 2017), most of the Baltic seafloor is located below the photic one. One important consequence of this is that benthic primary production is limited, hence strengthening the role of benthic-pelagic coupling (Griffiths et al. 2017). All experimental and field work of this thesis has been carried out in the Askö area, in the Stockholm archipelago, north-western Baltic Sea proper (Fig. 2b). Research on soft sediment communities has taken place around Askö since the 1960's, providing a good knowledge base for further research.

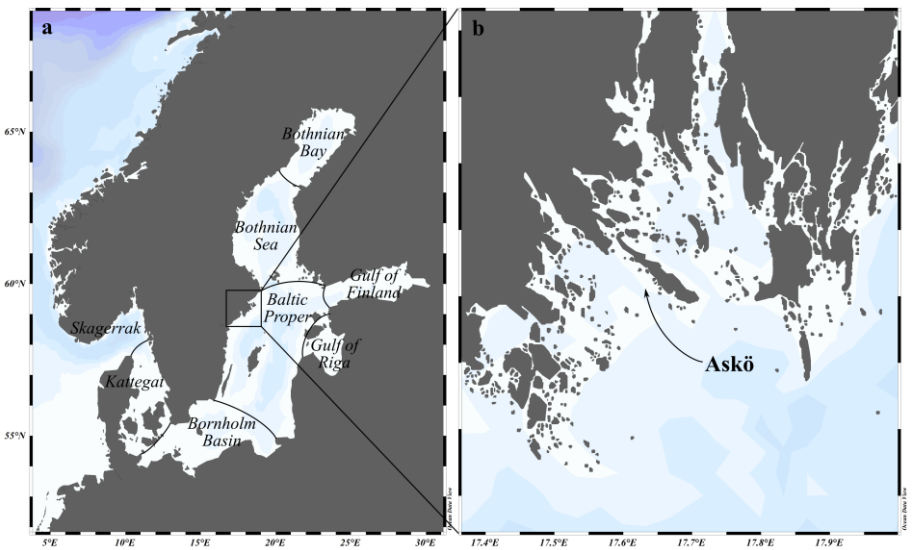


Figure 2. Map of the Baltic Sea, showing (a) the different sub regions, from the Skagerrak and Kattegat where marine water from the North Sea flows into the Baltic Sea and passes a series of shallow sills. Salinity drops from the Bornholm Basin northward, and the Bothnian Bay is essentially freshwater in nature. (b) Map of the study area (Askö) in the Stockholm archipelago. Maps created with Ocean Data View (Schlitzer 2021).

Seasonal cycles in pelagic production and export to the seafloor

The seasonal cycle of pelagic production in the Baltic Sea follows a similar pattern as other temperate marine systems (Winder and Cloern 2010). It is characterized by a pronounced spring bloom, dominated by diatoms and dinoflagellates, and followed by a summer bloom, usually dominated by filamentous cyanobacteria (Fig. 3; Wasmund et al. 2011; Andersson et al. 2017). Due to their ability to fix N_2 gas, the latter have a competitive advantage when other N sources are limiting for most phytoplankton groups (Paerl and Huisman 2009). Finally, a diatom-dominated bloom of smaller amplitude typically occurs in the autumn and ends the phytoplankton growth season (Andersson et al. 2017). Zooplankton temporal dynamics are partially synchronized with phytoplankton availability, but also constrained by water temperature (Möllmann et al. 2000). As such, there is only limited grazing activity during the early spring bloom, and zooplankton tend to peak during the summer months (Andersson et al. 2017). These seasonal patterns in phytoplankton and zooplankton production translate to important variations in OM sedimentation over the year, both in terms of quantity and quality (Blomqvist and Heiskanen 2001). Diatoms, as large, fast-sinking cells, contribute largely to the downward flux of OM during the spring bloom, and typically reach the sediment in a relatively fresh state (Blomqvist and Heiskanen 2001). In addition, they are rich in essential lipids and amino acids, and are hence considered nutritionally favourable to consumers (Brown 1991; Dunstan et al. 1994). Sedimentation from the summer cyanobacterial bloom, however, is more variable (Heiskanen and Kononen 1994). Indeed, cyanobacteria are particularly buoyant in the water due to their gas vacuoles (Walsby 1975). They tend to reach the seafloor in smaller quantities and in a more degraded state than spring bloom plankton (Blomqvist and Heiskanen 2001; Bianchi et al. 2002). Cyanobacteria are also considered of low nutritional quality and certain species produce toxic compounds (Engström et al. 2000; Nascimento et al. 2009). The grazing pressure from zooplankton is higher during the summer, which may reduce phytoplankton sedimentation, but also contribute to the overall settling of OM from fecal pellets and carcasses (Tang and Elliott 2014; Turner 2015). Altogether, the quantity and quality of plankton-derived OM that reaches the seafloor differs markedly along the year.

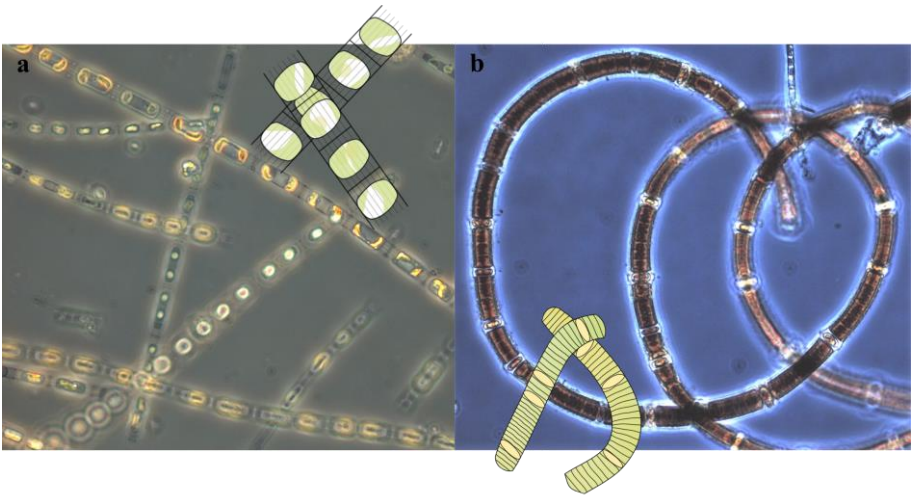


Figure 3. Phytoplankton species of (a) diatoms (*Skeletonema marinoi*) and (b) cyanobacteria (*Nodularia spumigena*), common in the Baltic Sea and used in some of the work of this thesis. Photo credits Helena Höglander.

Anthropogenic pressures are changing Baltic Sea ecosystems

Global climate change and anthropogenic activities are profoundly changing marine ecosystems around the world (IPCC 2014). Current changes in Baltic Sea ecosystems are happening at a fast pace, and may provide a glimpse of what the future holds for other coastal areas (Reusch et al. 2018). Over the last 30 years, there has been an increase in annual mean sea surface temperature by up to 1°C per decade, which is projected to continue in the future, reaching up to an additional 4°C by the end of the century (Andersson et al. 2015; BACC II Author Team 2015). In addition, the Baltic Sea experiences strong local anthropogenic pressure from the 85 million inhabitants living in its catchment area. It has notably a long history of eutrophication, with nutrient loads in the environment contributing to increased primary production and expansion of bottom water hypoxia (Carstensen et al. 2014; Snoeijs-Leijonmalm and Andrén 2017). Today, about 70,000 km^2 of the seafloor is permanently hypoxic and mostly devoid of fauna (Carstensen and Conley 2019). Due to important management actions, nutrient loads to the Baltic Sea have substantially decreased since the 1990s, but eutrophication effects persist to this day, and the ecosystem will probably need many more decades to fully recover (Elmgren et al. 2015; Reusch et al. 2018).

These anthropogenic disturbances are creating an imbalance in Baltic Sea ecosystems (Cloern et al. 2016). We are currently witnessing important changes in phytoplankton primary production, as well as other pelagic processes, which ultimately affect OM settling to the seafloor (Griffiths et al.

2017; Tamelander et al. 2017; Spilling et al. 2018). Current research indicates a decrease in diatoms biomass during spring blooms, with a dominance shift in favor of dinoflagellates (Wasmund et al. 2011; Spilling et al. 2018). In parallel, the frequency and spatial distribution of N_2-fixing cyanobacteria summer blooms is increasing in the area (Kahru and Elmgren 2014). Changes in pelagic food web dynamics also affect OM sedimentation to the seafloor. For example, warmer temperatures are projected to reduce the time lag between phytoplankton and zooplankton, as well as to increase the mineralization activity by water column bacteria (Aberle et al. 2015; Andersson et al. 2015; Tamelander et al. 2017). This ultimately suggests that less OM will settle to the seafloor in the future. Dominance by phytoplankton that are buoyant or swim (i.e. cyanobacteria and dinoflagellates), coupled to increased bacterial decomposition will also lead to OM reaching the seafloor in a more degraded state (Tamelander et al. 2017). Considering the primary importance of settling OM quantity and quality as drivers of the biodiversity and functioning of benthic communities, it is essential to evaluate how benthic-pelagic coupling might be affected by such rapid environmental change (Griffiths et al. 2017). As a model system for the future evolution of coastal areas, the Baltic Sea is a suitable environment in which to address these questions (Reusch et al. 2018).

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Aims of the thesis

In a context of rapid environmental change in the Baltic Sea, the overarching goal of the thesis was to investigate the importance of the quality and quantity of settling OM for microbenthic community structure and functioning (Fig. 4). More specifically, the different chapters focused on the following aspects:

In **chapter I**, we used an experimental approach to study the effect of two sources of OM, a common spring bloom diatom and a summer bloom cyanobacteria species, on the diversity and community structure of benthic microeukaryotes and bacteria, as well as on denitrification gene expression in the sediment.

In **chapter II**, we focused on the effects of settling diatoms and cyanobacteria on bacterial communities at the sediment-water interface.

In **chapter III**, we used a two factorial experiment to simultaneously explore the effects of OM quantity and quality on N cycling at the sediment-water interface.

In **chapter IV**, we conducted a year-long monitoring study to evaluate the seasonal dynamics of microeukaryotic and bacterial communities in response to pelagic environmental factors, particularly OM settling.

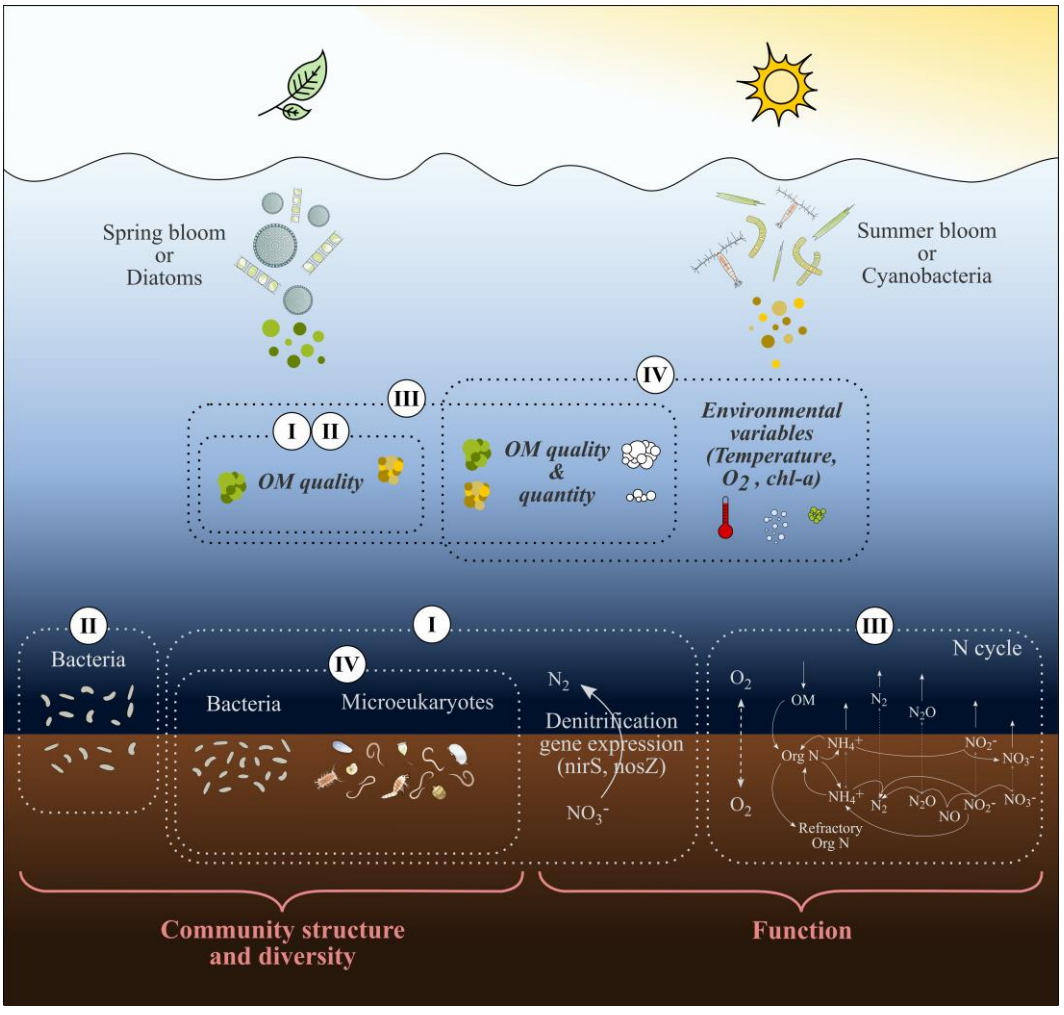


Figure 4. Conceptualization of the thesis framework, highlighting the focus of the different chapters (**I** to **IV**). The upper and lower boxes show the variables and responses studied in each chapter, respectively.

Comments on the methods

In this doctoral project, I combined experimental and field approaches to investigate the role of settling OM on benthic community structure and functioning. **Chapters I** and **II** were based on the same experimental set-up, in which we mimicked an OM quality gradient from 100 % diatoms to 100 % cyanobacteria input to the sediment (Fig. 5). Considering a scenario where the contribution of diatoms and cyanobacteria to total phytoplanktonic production is progressively shifting (Klais et al. 2011; Suikkanen et al. 2013; Hjerne et al. 2019), the goal was to assess potential effects on microeukaryotic and bacterial community structure and functioning. The latter was also addressed in **chapter III**, where the aim was to simultaneously explore the role of settling OM quantity (high vs. low) and quality (spring vs. summer plankton OM) on N cycling at the SWI (Fig. 5). Finally, in **chapter IV**, we carried out a year-long monitoring study in the Stockholm archipelago, Askö area, during which surface sediment was sampled on a monthly basis (Fig. 5). Results from this last study were paired with environmental data gathered by the Swedish National Marine Monitoring Program at the same site, in order to distinguish potential effects of OM settling and other pelagic environmental variables on benthic communities under natural conditions. In order to evaluate the impact of OM settling on benthic microeukaryotes and bacteria at a community level, we opted for a molecular approach – metabarcoding. The second goal was to assess the functional response of sediment communities, more specifically around the N cycle. This was addressed by combining a molecular approach of reverse transcription quantitative real-time PCR (RT-qPCR) on denitrification gene expression, with sediment core incubations, designed to measure fluxes and rates at the SWI. In the following section, we will cover in more details our approach on molecular methods and sediment core incubations.

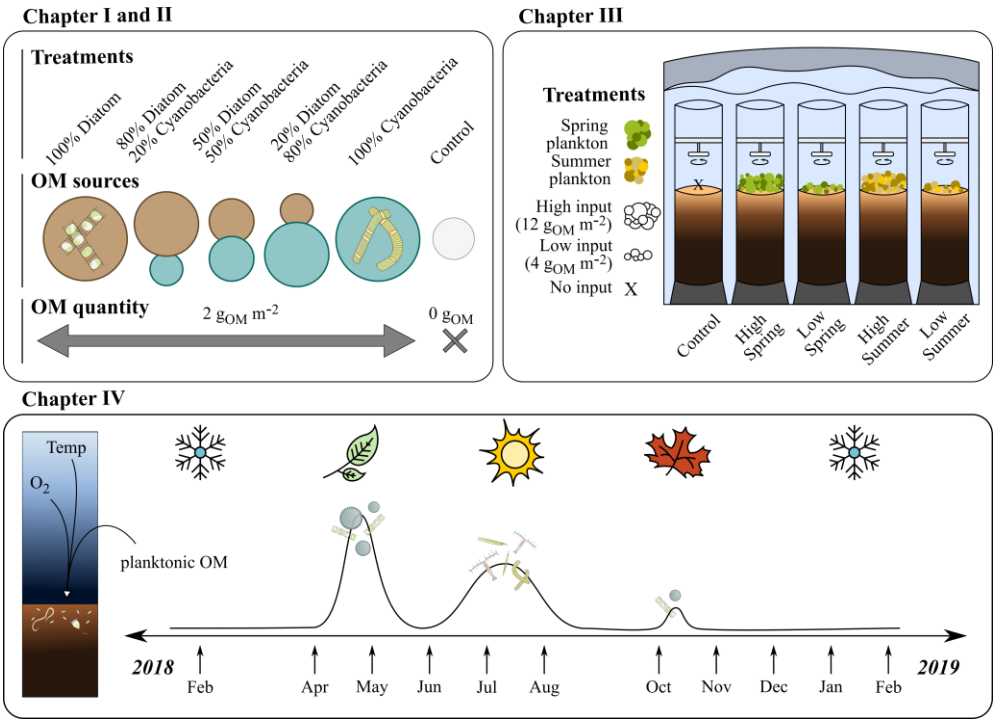


Figure 5. Schematic representation of the experimental (**chapters I** to **III**) and field work (**chapter IV**) designs conducted in this thesis.

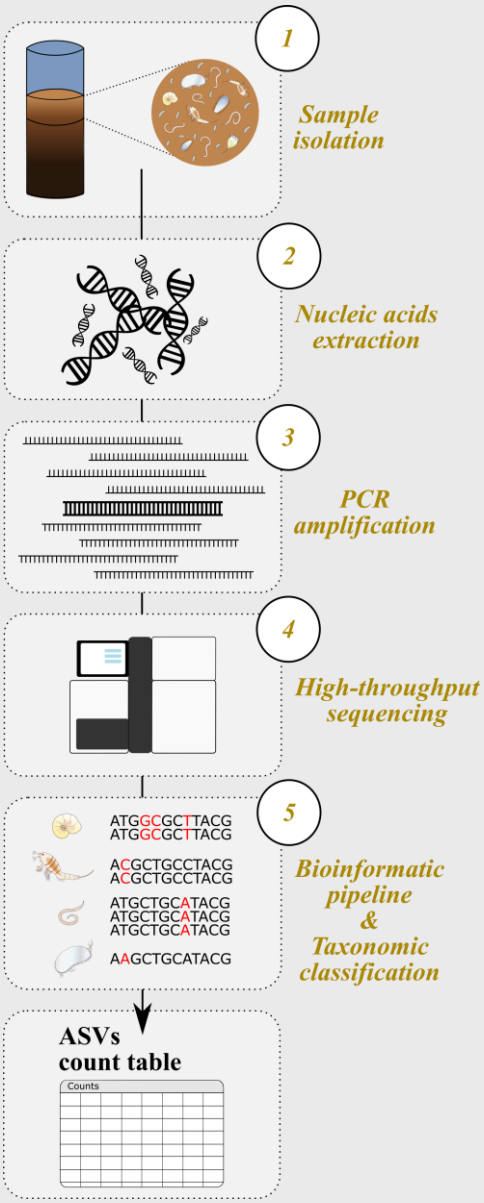
Molecular approaches

Over the last decades, the use of molecular approaches has boomed in environmental research (Taberlet et al. 2018). Initially developed within the realm of microbiology, molecular methods have quickly expanded to investigate biodiversity of larger organisms, including microeukaryotes (Creer et al. 2016; Fonseca et al. 2017), macrofauna (Leray and Knowlton 2015), fish (Fraija-Fernández et al. 2020), and even sharks (Boussarie et al. 2018). Targeting eukaryotes through molecular approaches faces a number of challenges (Bik et al. 2012; van der Loos and Nijland 2021), but altogether, has proven remarkably valuable, particularly among taxonomically challenging groups such as microeukaryotes (Fonseca et al. 2017). In parallel, molecular methods are commonly applied to access functional information within natural communities (Taberlet et al. 2018). In this thesis, we have relied on metabarcoding to characterize effects of OM settling on both microeukaryotic and bacterial communities (**chapters I, II** and **IV**), and applied RT-qPCR to quantify the expression of genes involved in N cycling (**chapter I**).

Uncovering benthic communities using metabarcoding

Metabarcoding is one of the most popular molecular approach to examine species composition in the environment (Leray and Knowlton 2016; Porter and Hajibabaei 2018). This technique is based on the analysis of short, standard DNA markers called barcodes, which carry taxonomic information about the organisms they are isolated from (Taberlet et al. 2018). Metabarcoding is a versatile tool that can be applied to profile almost all natural communities. Combined with high-throughput sequencing platforms, it provides a rapid and cost-efficient method to simultaneously assess the composition of entire communities from a single sample (Box 3; Ruppert et al. (2019)). In the following sections, we will cover the main steps involved in metabarcoding, and discuss some of the methodological choices made in the thesis chapters.

Box 3: Metabarcoding workflow



The **starting material (1)** for metabarcoding may come from isolated organisms (bulk samples) or environmental samples (e.g. water or sediment). In this thesis, we have used the second option, which allowed to simultaneously investigate bacterial, protist and metazoan communities. The next step consists in **(2) extracting nucleic acids (DNA or RNA)** from the samples, using standard kits or protocols. Once a barcode region is selected, the DNA or RNA fragments are then used as template for **(3) amplification** *via* **Polymerase Chain Reaction (PCR)**. During this reaction, specific primers, attaching to either sides of the barcode region, are used to simultaneously obtain billions of DNA fragments referred to as **amplicons**. The amplicons are processed on a **(4) high-throughput sequencing platform** – in our case, Illumina MiSeq – and DNA sequences are filtered and analyzed through a **(5) bioinformatic pipeline**. Ultimately, the DNA sequences are compared to a reference database, allowing for the taxonomic classification of the organisms or DNA fragments present in the original sample (Taberlet et al. 2018).

Box Figure 3. General metabarcoding workflow, showing the main steps of the process from sample isolation to taxonomic classification of the DNA sequences (1 to 5).

Nucleic acids: DNA or RNA?

Environmental samples (e.g. sediment, water) typically contain a complex mixture of genetic material composed of intracellular and extracellular DNA and RNA molecules (Taberlet et al. 2018; Eble et al. 2020). Intracellular DNA/RNA from the organisms present in the sample contribute a large part to the total pool of genetic material, but extracellular fragments originating from past and distant communities may also persists in significant amounts (Taberlet et al. 2018). The fact that short DNA fragments in particular may long be detected in the environment (e.g. 10,000 years; Corinaldesi et al. (2008)) is an interesting feature for a number of applications, including the reconstruction of past communities (Pawłowska et al. 2014). However, this may hinder our ability to resolve changes on a shorter time frame (e.g. weeks) from DNA samples. Conversely, RNA molecules are less stable than DNA, at least under laboratory conditions (Yates et al. 2021), and RNA-based analyses could therefore provide a more accurate representation of metabolically active organisms at the time of sampling (Blazewicz et al. 2013; Pochon et al. 2017; Cristescu 2019). The experiment conducted in **chapter I** spanned over 4 weeks. In order to maximize our chances to detect changes in living communities of microeukaryotes and bacteria in the sediment, we used metabarcoding on environmental RNA (eRNA). The analyses of bacterial communities in the water column presented in **chapter II** were based on the same experiment, but due to methodological constraints, we targeted environmental DNA (eDNA) instead of eRNA. Interestingly, we were still able to detect changes within 4 weeks based on eDNA analyses. Finally, in the field monitoring project, both eRNA and eDNA were extracted from the sediment. The results presented in **chapter IV** are based entirely on the eDNA dataset. Again, we were able to detect significant changes from one month to the next. Altogether, it seems that the persistence of DNA and RNA in the environment is more complex than theory would predict (Blazewicz et al. 2013; Cristescu 2019). In a recent experiment, Wood et al. (2020) even found similar decay rates for eRNA and eDNA in aquatic environments. Nevertheless, a few studies have compared eRNA and eDNA-based community analyses, and highlighted the benefits of using a combined approach (Guardiola et al. 2016; Pochon et al. 2017; Nawaz et al. 2019; Marshall et al. 2021).

Regions of interest: 18S and 16S rRNA genes

The choice of barcode region is of crucial importance in metabarcoding, as it will inevitably affect the output of the analysis (Box 3; Bik et al. 2012; Alberdi et al. 2017; Taberlet et al. 2018). Ideally, a barcode region needs to be short (i.e. < 300-400 bp), sufficiently variable to distinguish between species, flanked by highly conserved regions which primers can anchor to, and with extensive documentation in reference databases (Taberlet et al. 2018; Ruppert

et al. 2019; van der Loos and Nijland 2021). In practice, DNA barcodes rarely fulfill all these criteria perfectly, meaning that a compromise has to be made between taxonomic coverage (i.e. how broadly it will amplify across target groups) and resolution (i.e. how accurately will species be delineated) provided by a particular region (Alberdi et al. 2017; Taberlet et al. 2018). For example, the mitochondrial cytochrome c oxidase 1 (COI) gene is widely used for metabarcoding of animal communities (Radulovici et al. 2010; Leray and Knowlton 2015), and is one of the standard barcodes recommended by the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007). However, the COI gene is not optimal for resolving nematode taxonomy (Creer et al. 2010; Carugati et al. 2015; Fontaneto et al. 2015). Instead, other markers such as the 18S ribosomal RNA (rRNA) gene may be more appropriate for microeukaryote metabarcoding (Creer et al. 2010; Deagle et al. 2014), although it may underestimate the overall diversity (Tang et al. 2012). In our case, since we wanted to recover information on the whole microeukaryotic community, we based our metabarcoding analyses in **chapters I** and **IV** on the 18S rRNA gene, targeting the hypervariable region v4, previously used for community analyses of microeukaryotes (Stoeck et al. 2010; Lejzerowicz et al. 2015; Brandt et al. 2020). For bacterial community analyses, the 16S rRNA gene is the most commonly used barcode. Studies have sequenced different hypervariable regions, but in our case, we targeted v3-v4 for **chapters I**, **II** and **IV**, as it has been shown to work well to recover community scale information of bacteria both in the sediment and in the water (Herlemann et al. 2011; Klier et al. 2018; Broman et al. 2019).

Library preparation and sequencing

Once nucleic acids are extracted from the sample(s), regions of interest are targeted and amplified *via* PCR (Box 3). In the case of eRNA, RNA fragments were first converted to cDNA and we also carried out a DNase degradation procedure in order to remove all traces of DNA that could interfere with the signals from the RNA pool. All downstream applications from this step onwards were the same for eDNA and cDNA. PCR amplification protocols may vary across studies but always follow the same general principle (Box 3; (Alberdi et al. 2017; Taberlet et al. 2018; van der Loos and Nijland 2021)). In all our community analyses (**chapters I**, **II** and **IV**), we followed a dual-index protocol, involving two sequential rounds of PCR amplification and cleaning steps (Taberlet et al. 2018). During this procedure, DNA amplicons from the same sample were identified by a unique combination of reverse and forward index tags. In addition, adapter sequences were included in order for the DNA fragments to attach to the sequencing flow cell. All amplicons were sequenced on the Illumina MiSeq platform (2 x 300 bp paired-end reads) at the Science for Life Laboratory, Stockholm.

Bioinformatic pipeline

High-throughput sequencing of natural communities yield billions of DNA sequences that require bioinformatic handling in order to ensure the quality and reliability of the data (Deiner et al. 2017; Taberlet et al. 2018). For our community analyses, we processed 18S and 16S rRNA sequences using the DADA2 bioinformatic pipeline, implemented in R (Box 3; Callahan et al. (2016)). During data processing, our DNA sequences were merged into amplicon sequence variants (ASVs). This method aims to discriminate biologically meaningful information from sequencing errors, and does not rely on a fixed dissimilarity threshold to cluster sequences (Callahan et al. 2016). Usually, DNA sequences are clustered into operational taxonomic units (OTUs) based on how much they differ from each other, typically using a cut-off at 97 % (Taberlet et al. 2018; Ruppert et al. 2019). The ASV approach has been described as more sensitive and reproducible than OTU clustering (Callahan et al. 2017), although it does not resolve all the pitfalls associated with metabarcoding. Finally, sequences were assigned taxonomic classification with the help of reference databases (Taberlet et al. 2018). For microeukaryotes analyzed using the 18S rRNA barcode, sequences were compared simultaneously against two databases. In **chapter I**, we used the NCBI *nt* (Benson et al. 2013) and SILVA databases (Quast et al. 2013). The former, as one of the largest DNA sequence repositories available, retrieved taxonomic information on a good portion of the dataset (e.g. 73.3 % of sequences identified at phylum level in **chapter I**), but did not provide fine taxonomic resolution on unicellular eukaryotes. This limitation was partly alleviated by simultaneously comparing our data against the SILVA database. In **chapter IV**, we also identified DNA sequences using the NCBI *nt* database, but in combination with the PR2 database, specifically designed for protists (Guillou et al. 2013). For taxonomic assignment of bacteria, analyzed using the 16S rRNA barcode, we compared our DNA sequences to the SILVA database in all our studies (**chapters I**, **II** and **IV**). It is both well-documented for prokaryotes, and provided an acceptable level of taxonomic resolution (Quast et al. 2013; Creer et al. 2016).

Box 4: Traditional versus molecular approaches in community studies

Resolving community biodiversity is a central objective in most ecological studies. At a time when marine ecosystems are facing intense anthropogenic pressure and biodiversity is declining at unprecedented rates (Sala and Knowlton 2006; Ceballos et al. 2015), this objective has become even more pressing (Costello et al. 2010). The emergence of molecular approaches offers a remarkable opportunity to address some of these knowledge gaps (Taberlet et al. 2012; Cristescu 2014), although it still faces important challenges (Leray and Knowlton 2016; van der Loos and Nijland 2021). In this context, numerous studies have explored biodiversity through the lens of traditional and molecular methods in order to compare the taxonomic information derived from each (Ruppert et al. 2019 and references therein). To our knowledge, comparison studies of traditional and molecular methods for biodiversity assessment have been mostly performed for eukaryotes, as the pros of molecular approaches vastly outweigh the cons for prokaryote biodiversity determination. The leap of knowledge that microbial ecology experienced as molecular methods developed is a prime illustration of how limited traditional techniques (i.e. based on morphology and cultivation) were in resolving bacterial communities (Taberlet et al. 2018). For larger organisms, however (e.g. macrofauna, meiofauna), morphological identification has a long history, and is often still the standard approach in research studies and monitoring programs. There, benchmarking studies are essential to evaluate the suitability of molecular-based community assessments as alternative or complementary approaches (Aylagas et al. 2016; Cahill et al. 2018; Leasi et al. 2018). Traditional and molecular approaches both have advantages and disadvantages which will ultimately generate biases in the analysis (summarized in Box Table 1, (Leasi et al. 2018)).

Box Table 1. Discussion of the advantages (green symbols) and disadvantages (red symbols) from traditional (i.e. morphology-based) and molecular approaches to monitor eukaryotic communities. Based on Carugati et al. (2015) & Goodwin et al. (2017).

	Traditional
	Information on species abundance
⊕	Greater taxonomic resolution (genus or species level) for certain taxonomic groups
	Continuity and comparability with previous work
	Limited information from challenging groups (e.g. juveniles, soft-bodied organisms, cryptic species, damaged specimens)
⊖	Requires taxonomic expertise
	Time-consuming and costly

Molecular	
	Resolves taxonomic information on some of the groups overlooked by traditional approaches Allows for simultaneous investigations of multiple communities from the same samples Does not require taxonomic expertise High sample throughput and time-efficient Declining costs
	Not quantitative Biases in taxa detection (PCR amplification, barcode region) Poorer taxonomic resolution for certain taxonomic groups

Molecular-based community analyses have unveiled new horizons in biodiversity studies (Fonseca et al. 2010; Leray and Knowlton 2016; Deiner et al. 2017). However, the challenges of relating DNA read abundances to species counts and obtaining a good taxonomic resolution for certain groups still limits the broader implementation of molecular approaches for monitoring purposes (Mathieu et al. 2020; van der Loos and Nijland 2021). Despite these limitations, molecular methods can perform just as well as traditional inventories for ecological status and impact assessments (Pawlowski et al. 2014; Lejzerowicz et al. 2015; Aylagas et al. 2016, 2018; Stoeck et al. 2018). Ultimately, both approaches are highly relevant, and methodological choices should be tailored to the research question(s).

Estimating functional gene activity using reverse transcription quantitative real-time PCR

Community composition assessments only provide limited information on the functional role of organisms in the ecosystem. Bacteria, in particular, may be involved in a wide array of element cycling processes, and a particular process may be carried out by many different bacterial groups (Thamdrup and Dalsgaard 2008). The development of molecular approaches represent a great opportunity to bypass this issue and directly assess functional processes in the ecosystem (Taberlet et al. 2018). In **chapter I**, we used the technique of RT-qPCR to quantify gene expression in the sediment at the end of our experiment. Unlike standard qPCR, used to quantify gene abundances, RT-qPCR quantifies RNA transcripts to provide an estimate of the community's activity related to a particular function at the time of sampling. In our case, we assessed the expression of genes *nirS* and *nosZ*, coding for NO_2^- reductase and N_2O reductase enzymes, respectively, both involved in the denitrification process (Box 2; Zumft 1997). Although gene expression quantification (RNA) gives a more accurate picture of how active the community is compared to gene quantification (DNA), the link to enzymatic activity and rate measurements is not always straightforward (Wallenstein et al. 2006; Bowen et al. 2014). Until these links are fully resolved, it can be a good idea to complement molecular approaches with other techniques to investigate functional responses.

Sediment core incubations

One goal of this thesis was to assess the impact of OM settling on functional processes, in particular related to N cycling, taking place at the SWI. In the preceding section, we reviewed the approach implemented in **chapter I**, based on RT-qPCR of denitrification gene expression. In **chapter III**, we measured rates of solute exchange using whole-core incubations, combined with the isotope-pairing technique (IPT), which we will cover in the following sections.

Solute exchange at the sediment-water interface

The SWI is a site of dynamic exchanges of solutes (i.e. liquid, gas or solid substance dissolved in a solution) between benthic and pelagic environments (Thrush et al. 2021). Implementing standardized methods is crucial to achieve accurate elemental budgets across different systems and in response to different factors (Dalsgaard (ed.) et al. 2000). In that regard, core incubation techniques constitute a cornerstone in biogeochemistry studies (Dalsgaard (ed.) et al. 2000). The general principle involves enclosed containers – in our case,

sediment cores – which are incubated for a set amount of time. By measuring the concentration of solute in the water at the beginning and end of the incubation period, we can reliably determine the direction and strength of flux(es) across the SWI. An increase in solute concentration in the water over time indicates a net release from the sediment, while a decrease indicates a net uptake from the sediment. In **chapter III**, we simulated different OM settling scenarios to intact sediment cores collected in the Stockholm archipelago. Using whole-core incubations, we assessed how OM settling quantity and quality impacted fluxes of O_2 and nutrients (NH_4^+, NO_x^-, PO_4^{3-}, H_2SiO_4) across the SWI (Fig. 6).

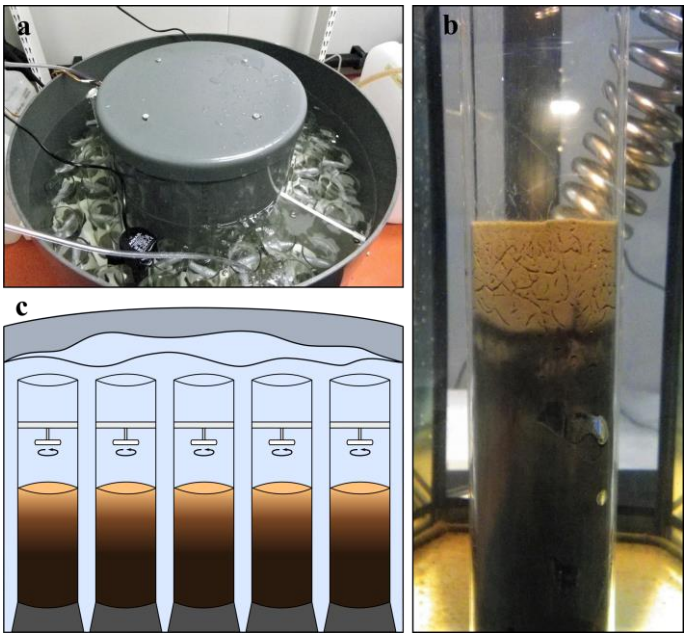


Figure 6. Experimental set-up used in **chapter III**. (a) Incubation tank containing all the sediment cores, the water was constantly oxygenated and circulated to ensure homogeneous conditions; (b) sediment core collected around Askö and used for the experiment; (c) cross-section schematic of the tank and cores, showing the rotating magnets that circulated water in each core. Photo credits Séréna Albert.

More specifically, one of the aims of **chapter III** was to evaluate the effect of OM settling on N cycling, including NO_3^- reduction rates. To this end, we combined whole core incubations (Fig. 6) with the widely used IPT. The IPT method was developed 30 years ago by Nielsen (1992) to measure denitrification in sediments through the addition of labelled ^{15}N-nitrate ($^{15}NO_3^-$). It has

since been applied extensively, resulting in a large body of literature documenting NO_3^- reduction rates and controlling factors in a diverse range of ecosystems (Seitzinger et al. 2006 and references therein). The IPT involves the addition of ^{15}N-labelled NO_3^- to overlying water, which eventually diffuses into the sediment, and reaches an equilibrium with the NO_3^- naturally present (99.64 % ^{14}N and 0.36 % ^{15}N; Steingruber et al. 2001). By tracking the production of ^{15}N-N_2 gas ($^{30}N_2$ and $^{29}N_2$), it is possible to measure denitrification rates through a set of simple equations (Nielsen 1992; Steingruber et al. 2001). The IPT further enables the differentiation between denitrification fueled by NO_3^- from the overlying water column (D_w) and by NO_3^- produced through nitrification in the sediment (D_n; Nielsen 1992). Over the years, some of the inherent limitations to the IPT, as well as knowledge expansion on N cycling have prompted a number of methodological revisions to this approach (Robertson et al. 2019 and references therein). It is notably possible to calculate the contribution of anammox to N_2 production (Risgaard-petersen et al. 2003) and measure DNRA through the production of $^{15}NH_4^+$ (Robertson et al. 2019). In **chapter III**, we measured the release of ^{15}N-N_2 and $^{15}NH_4^+$ following $^{15}NO_3^-$ addition in order to simultaneously evaluate denitrification and DNRA rates, respectively (Box 2).

Main results and discussion

Effects of organic matter sedimentation on benthic community structure and diversity

Microeukaryotes

Our results confirm that OM settling acts as an important structuring factor for benthic microeukaryotic communities (Graf 1992; Pfannkuche 1993; Ólafsson and Elmgren 1997; Schratzberger et al. 2008). In **chapter IV**, we notably observed that microeukaryotic alpha diversity decreased substantially following spring bloom sedimentation (Fig. 7a). Negative impacts of OM settling on community diversity are not uncommon in soft sediments, especially after large OM pulses (Quijón et al. 2008; Soltwedel et al. 2018; Stoeck et al. 2018). For example, at a coastal site in the English Channel, the settling of a particularly large phytoplankton bloom triggered a decline in macrofauna richness and community evenness (Zhang et al. 2015). However, these effects are poorly documented for microeukaryotic communities as a whole (Stoeck et al. 2018; Salonen et al. 2019). Changes in environmental conditions (e.g. O_2 concentration) caused by OM settling can mediate responses by the microeukaryotic community (Modig and Ólafsson 1998; Levin 2003). In the case of our seasonal monitoring study (**chapter IV**), we suggest that the negative effect on alpha diversity was partially caused by a decrease in O_2 concentration at the SWI following mineralization of spring bloom OM (Pfannkuche 1993; Zhang et al. 2015). This could explain the decreased proportion of taxa sensitive to low O_2 conditions such as harpacticoid copepods (Modig and Ólafsson 1998; Levin 2003)

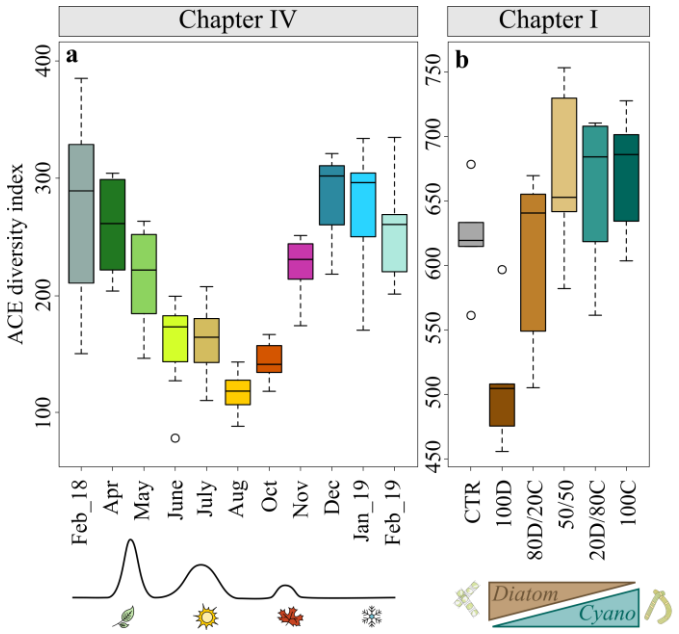


Figure 7. Changes in microeukaryotic alpha diversity based on the abundance coverage estimator (ACE). (a) Results from **chapter IV**, showing the seasonal dynamics from February 2018 (Feb_18) to February 2019 (Feb_19), the schematic below illustrates the general pattern of phytoplankton production throughout the year. (b) Results from **chapter I**, four weeks after organic matter addition, the experimental treatments are on the x-axis, including control (CTR) and the organic matter quality gradient from 100 % diatoms (100D) to 100 % cyanobacteria (100C) inputs.

In **chapter I,** we also observed a decrease in microeukaryotic alpha diversity following addition of diatoms, but not cyanobacteria (Fig. 7b). However, the processes that led to this decrease were probably not connected to poor O_2 conditions. Indeed, the water column was oxygenated throughout the entire duration of the experiment. In addition, sediment O_2 demand seems primarily linked to differences in OM quantities, as evidenced in **chapter III** (Sloth et al. 1995; Zilius et al. 2016), and in **chapter I,** OM amounts were standardized across all treatments. This suggests that specific characteristics linked to OM quality can also play a key role in triggering changes in microeukaryotic diversity (Ingels et al. 2011; Campanyà-llovet et al. 2017). Decline in alpha diversity following the provision of a new food resource can occur as a result of competitive exclusion by specialized taxa (Paine 1966; Peterson 1979). In both **chapters I** and **IV**, it is worth pointing out that our molecular approach enabled us to investigate microeukaryotic community diversity in a broad sense, not only encompassing species diversity, but also intraspecific diversity linked to the presence of multiple genotypes (Stoeck et al. 2010; Taberlet et

al. 2018). In **chapter I**, the negative impact of settling diatom material on alpha diversity was not tied to the exclusion of broad taxonomic nor functional microeukaryotic groups. Instead, we hypothesize that particular genotypes displayed a competitive advantage in their utilization of diatom-derived OM. For instance, resource partitioning among cryptic species has been documented for a bacterivorous nematode species complex (Derycke et al. 2016; Guden et al. 2018). Selection of a few genotypes through competitive exclusion would in turn decrease the overall genetic diversity of the microeukaryotic community, without necessarily inducing marked changes at high taxonomic level. It is possible that competitive exclusion was also partly responsible for the decrease in alpha diversity following spring bloom settling in our field study (**chapter IV)**. Conversely, settling cyanobacteria did not trigger pronounced changes in microeukaryotic diversity, either positively or negatively, in our experimental study (**chapter I**) and seasonal survey (**chapter IV**) (Fig. 7).

Beyond these effects on diversity, our results further confirm the importance of OM settling as a driver of microeukaryotic community structure. We noticed the most striking changes in community structure in our field monitoring study following spring bloom sedimentation (Fig. 8a, **chapter IV**). Some groups (e.g. alveolates, nematodes) responded positively to spring OM input, while others responded negatively (e.g. metazoans, harpacticoid copepods, acoels). These results are in line with previous studies conducted at this site (Ólafsson and Elmgren 1997), and in other coastal areas (Schratzberger et al. 2008; Lampadariou and Eleftheriou 2018), regarding the importance of spring bloom sedimentation as a structuring factor for microeukaryotic communities. Yet, there are also some discrepancies between our results and those described in the literature. For example, in **chapter I**, we did not observe significant changes in relative abundance of nematode feeding groups in response to OM settling, whilst previous work found that deposit-feeding and epistrate-feeding nematodes often increase after the sedimentation of phytodetritus (Ólafsson and Elmgren 1997; Vanaverbeke et al. 2004; Lampadariou and Eleftheriou 2018). We think that these divergent observations stem partially from methodological choices (Leasi et al. 2018). Our molecular approach was not ideally suited to resolve nematode taxonomy at species level, which limited our ability to detect changes within this taxonomic group (Box 4). On the other hand, morphology-based studies rarely investigate changes in metazoan meiofauna, unicellular eukaryotes and soft-bodied organisms (e.g. acoels) simultaneously. Yet, the two last groups appeared as important drivers of microeukaryotic community variation after spring bloom settling in **chapter IV**. Using combinations of molecular and traditional approaches will undeniably contribute to broaden our knowledge on the response of microeukaryotic communities to environmental drivers, and OM settling in particular (Leray and Knowlton 2016; Deiner et al. 2017).

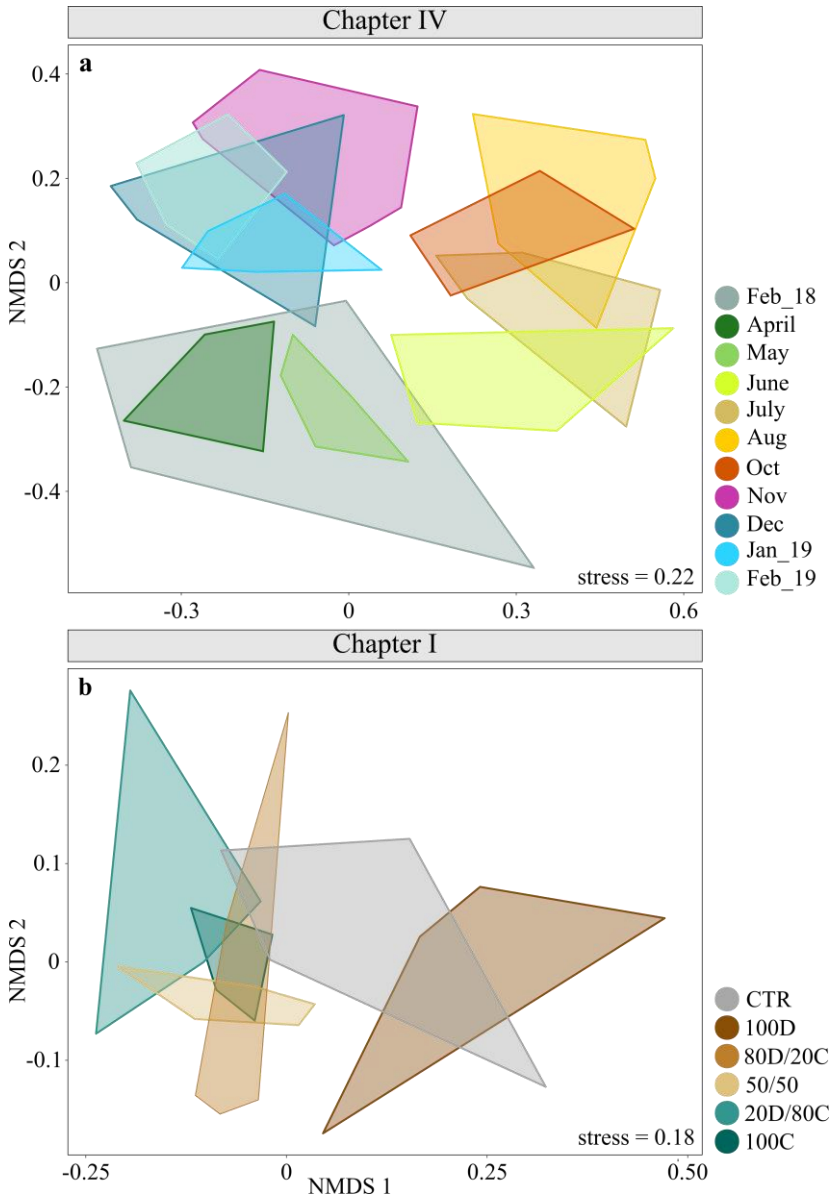


Figure 8. Non-metric multidimensional scaling plots of microeukaryotic communities based on the Sørensen distance metric. (a) Results from **chapter IV**, showing the seasonal dynamics from February 2018 (Feb_18) to February 2019 (Feb_19). The stress value for each plot is displayed in the bottom right corner. (b) Results from **chapter I**, four weeks after organic matter addition, experimental treatments are displayed on the right-hand side, including control (CTR) and the organic matter quality gradient from 100 % diatoms (100D) to 100 % cyanobacteria (100C) inputs.

The effect of OM quality on microeukaryotic community structure was significant but more subtle than on alpha diversity. This is particularly evident in the results presented in **chapter I** (Fig. 8b), where we observed that the community responded differently to inputs of cyanobacteria OM, even in small proportions, compared to inputs of diatoms. However, we did not see a change at high taxonomic levels, but shifts in the lower taxonomic levels, as previously discussed. On the one hand, microeukaryotic organisms, in particular meiofauna, have been shown to assimilate cyanobacteria in substantial quantities (Nascimento et al. 2008), although with reduced growth benefits compared to a diatom diet (Nascimento et al. 2009). On the other hand, cyanobacteria can represent a favorable nutritional resource for certain invertebrate consumers, notably when used to complement other food sources (Engströmöst et al. 2002; Groendahl and Fink 2017). Cyanobacterial blooms have naturally occurred in the Baltic Sea for thousands of years (Bianchi et al. 2000). Despite somewhat unpredictable export to the seafloor (Blomqvist and Heiskanen 2001; Tamelander et al. 2017), it is possible that some microeukaryotic taxa or genotypes have adapted to utilize this resource when available (Nascimento et al. 2009; Karlson et al. 2015; Gorokhova et al. 2021). The importance of settling OM quality for microeukaryotic communities is also supported to some extent by the results in **chapter IV**. There, we found both diatom and cyanobacteria biomass in the water column as significant drivers of microeukaryotic community structure throughout the year, but the clearest changes in community composition occurred after the large pulse of spring bloom settling. This indicates that although seasonal changes in OM quality played a role, it was probably overwhelmed by variations in OM quantity. In parallel, we found that seasonal variations in temperature and O_2 concentration in bottom waters were also significant drivers of microeukaryotic communities during the study year (Schratzberger et al. 2008; Grego et al. 2014; Salonen et al. 2019).

Bacteria

Based on the different studies, we found few distinct changes in bacterial communities in response to OM settling. As for microeukaryotes, the most pronounced response occurred following the spring bloom settling in our field survey (**chapter IV**). After the spring bloom, we observed a stimulation of mineralization activity at our study site, as indicated by low O_2 concentration in bottom waters. In parallel, we detected a shift in bacterial community structure. However, we were not able to connect this shift to changes in relative abundance at a high taxonomic level, which indicates a more subtle reorganization of the community at intermediate or low taxonomic levels (Landa et al. 2014). Similarly, we did not detect marked differences in bacterial communities in our experimental set-up testing the influence of OM quality amendments from diatoms and cyanobacteria (**chapter I**). There was no evidence that particular bacterial taxonomic groups or ASVs were favored by either source of OM in the sediment. These observations are somewhat unexpected since previous studies have demonstrated that the relative abundance of certain groups (e.g. Bacteroidetes, Alpha- and Gammaproteobacteria, Verrumicrobia) tended to increase with OM availability (Riemann et al. 2000; Andersson et al. 2010; Vetterli et al. 2015; Hoffmann et al. 2017). In the Gulf of Finland, it has been shown that different sediment bacterial taxa were favored at different times of the year, notably in relation to the availability and origin of settling OM (Vetterli et al. 2015). We must, however, point out that our sampling strategy differed from most other studies in the literature. While these studies on benthic bacteria usually target the upper sediment layer (i.e. 0-0.5 or 1 cm; (Franco et al. 2007; Tait et al. 2015; Vetterli et al. 2015)), we sampled the sediment over a greater depth spectrum (0-3 cm) in both field and experimental studies (**chapters I** and **IV**). Although this depth layer was appropriate to recover most microeukaryotes (Giere 2009), it represents a much broader zonation for bacteria (Hoshino et al. 2020), and most of the community that we picked up comprised bacteria present in anoxic layers. Based on our results, the bulk of the community, as integrated over 0-3 cm, remains stable during the year (**chapter IV**). Although some changes were induced by spring bloom settling, bacterial communities did not respond markedly to different OM quality from diatoms and cyanobacteria (**chapter I**). It is likely that the upper sediment layer displayed stronger changes in bacterial community structure and diversity, but that these effects were masked by the stability of the community in deeper sediment layers.

The hypothesis that bacterial communities close to the sediment surface responded more markedly to OM sedimentation is partially supported by our results from **chapter II**. This study is based on the same experimental set-up as that described in **chapter I**, where we mimicked a gradient in OM quality

deposition to the sediment, ranging from 100 % diatoms to 100 % cyanobacteria. In **chapter II**, we focused on the assembly of bacterial communities at the SWI. We hypothesized that upon OM settling to the seafloor, the release of dissolved organic compounds and potential alterations on benthic communities might in turn affect bacterial assemblages in the overlying water column (Sarmento et al. 2013; Landa et al. 2014; Dang and Lovell 2016). Even though there was an overlap in pelagic bacterial communities across treatments, we found that ~ 20 % of community variations were explained by the input of diatom or cyanobacteria OM. Community reorganization occurred at low rather than high taxonomic levels, as observed in **chapter I** and **IV** for benthic bacterial communities. Additionally, we found that certain pelagic bacterial taxa increased in relative abundance in response to diatom- or cyanobacteria-derived OM (e.g. *Methylophagaceae* favored by diatom input; Fig. 9; Landa et al. 2018). Finally, we wanted to investigate the extent to which bacteria in the overlying water were recruited from sediment bacteria. Indeed, dormant bacteria present in the sediment might represent an important seed bank, which could be reactived in response to OM settling (Luna et al. 2002). We found limited overlap between bacterial communities in the sediment and overlying water, indicating that direct recruitment from sediment represented a minor process in our experiment. However, our results highlighted significant correlations between specific bacterial taxa and nutrient concentrations in the water column. This supports the idea that benthic communities can have an influence on the assembly of bacterial communities in overlying waters by acting on nutrient recycling. Indeed, the activity of surface-associated bacteria can directly influence the dynamics of free-living bacteria, and these two compartments are in constant exchange and cooperation (Dang and Lovell 2016). Feedback effects from the benthos to the pelagos are likely to be exacerbated upon OM settling to the seafloor, when metabolic activity is stimulated and large quantities of dissolved compounds are released to surrounding waters (Jensen et al. 1990; Hansen and Blackburn 1992; Sarmento et al. 2013). For example, in **chapter III**, we observed that OM settling, and in particular OM quality, had a strong influence on dissolved inorganic nitrogen (DIN) recycling to the water column (Fig. 10). Based on the results presented in **chapter II**, we can hypothesize that these impacts on ecosystem functioning may further affect bacterial communities at the SWI.

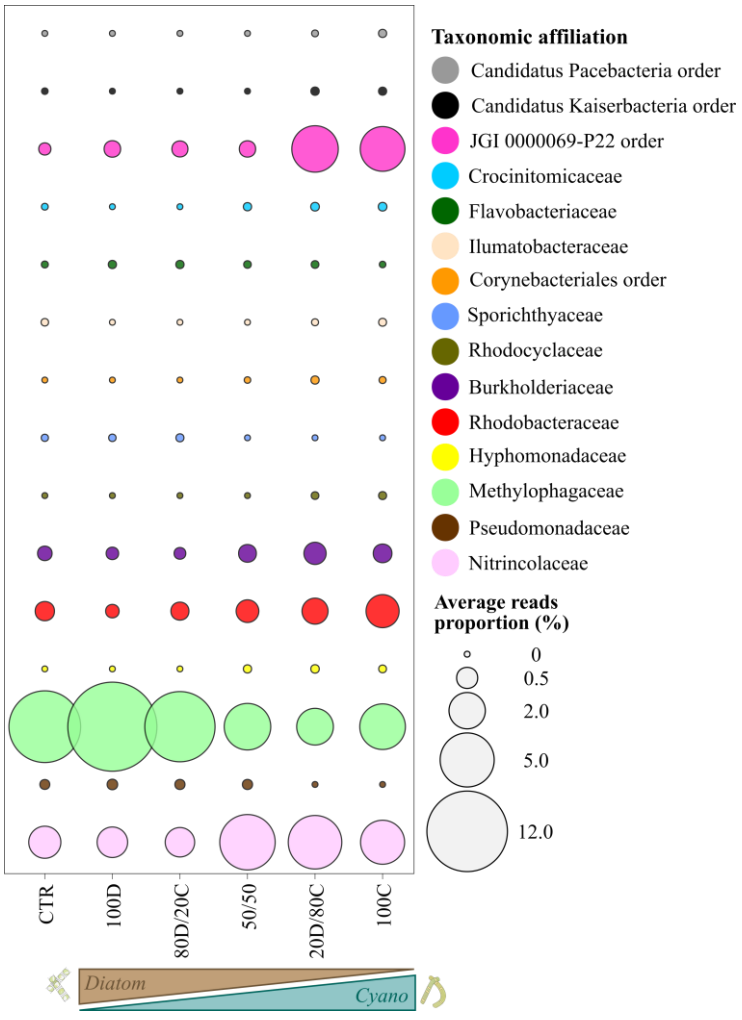


Figure 9. Change in bacterioplankton relative abundance observed in **chapter II** four weeks after organic matter addition. Experimental treatments included control (CTR) and an organic matter quality gradient from 100 % diatoms (100D) to 100 % cyanobacteria (100C) inputs. The size of the bubbles is proportional to the relative abundance of each taxa.

Effects of organic matter settling on nitrogen cycling at the sediment-water interface

The SWI is a key compartment for ecosystem functioning, where many of the microbial processes that drive element cycling take place (Thrush et al. 2021). A lot of these processes, including N cycling, are tightly linked to OM inputs to the sediment (Thamdrup and Dalsgaard 2008). Upon OM settling, the N contained in organic molecules may enter one of 4 pathways: (1) assimilation by benthic consumers; (2) mineralization and recycling as inorganic nutrients (i.e. NH_4^+ and NO_x^-) (3) transformation to N_2 via denitrification and anammox and (4) permanent burial in the sediment (Box 2; Thamdrup and Dalsgaard 2008). The balance between these 4 mechanisms determines the proportion of N that remains in the system in a bioavailable form (1 and 2) or is removed as an inert form of N, not available to most primary producers (3 and 4). By estimating the fluxes of permanent N removal, and comparing them to the amount of N that enters the system in bioavailable forms (i.e. through N_2 fixation or human effluents), we can ultimately evaluate if the system is a source or sink for N (Voss et al. 2011). Considering the changes currently at hand in marine ecosystems worldwide and in the Baltic Sea (BACC II Author Team 2015), it is of prime importance to expand our understanding of how changes in OM settling could affect the fate of organic N in soft sediments (Griffiths et al. 2017; Tamelander et al. 2017).

The results in **chapter III** highlight the importance of OM quality in controlling N cycling processes upon settling on the seafloor. In this experiment, we observed that denitrification rates were stimulated by OM settling from the summer bloom, but not the spring bloom. In parallel, DIN fluxes (NH_4^+ and NO_x^-) were also stimulated in the summer bloom treatments, but decreased substantially in the spring bloom treatments (Fig. 10). Overall, by calculating the proportion of total inorganic N released as N_2 (i.e. denitrification efficiency; (Eyre and Ferguson 2002)), we showed that spring bloom material was more efficiently denitrified upon settling to the seafloor than summer bloom material (Fig. 10). Accordingly, settling OM quality has been identified as an important regulating factor for benthic microbial metabolism (Tuominen et al. 1996; Arnosti and Holmer 2003; Aspetsberger et al. 2007; Oakes et al. 2011; Carlson et al. 2020). However, most of these observations originate from field-based studies, which do not allow the influence of settling OM quality to be disentangled from quantity or other abiotic factors (Tuominen et al. 1996; Oakes et al. 2011), a difficulty also encountered in **chapter IV** of this thesis. Using a full factorial experimental design, we were able to demonstrate in **chapter III** that OM quantity (high vs. low input of OM) only played a minor role in driving N cycling processes at the SWI compared to OM qual-

ity. Mineralization activity was more stimulated by high than by low OM inputs, leading to a stronger decline in O_2 concentration in the sediment. In spite of O_2 concentration acting as an important control over N cycling processes (Box 2; Canfield et al. 2005; Thamdrup and Dalsgaard 2008), the effect of OM quantity was overwhelmed by OM quality, as previously discussed.

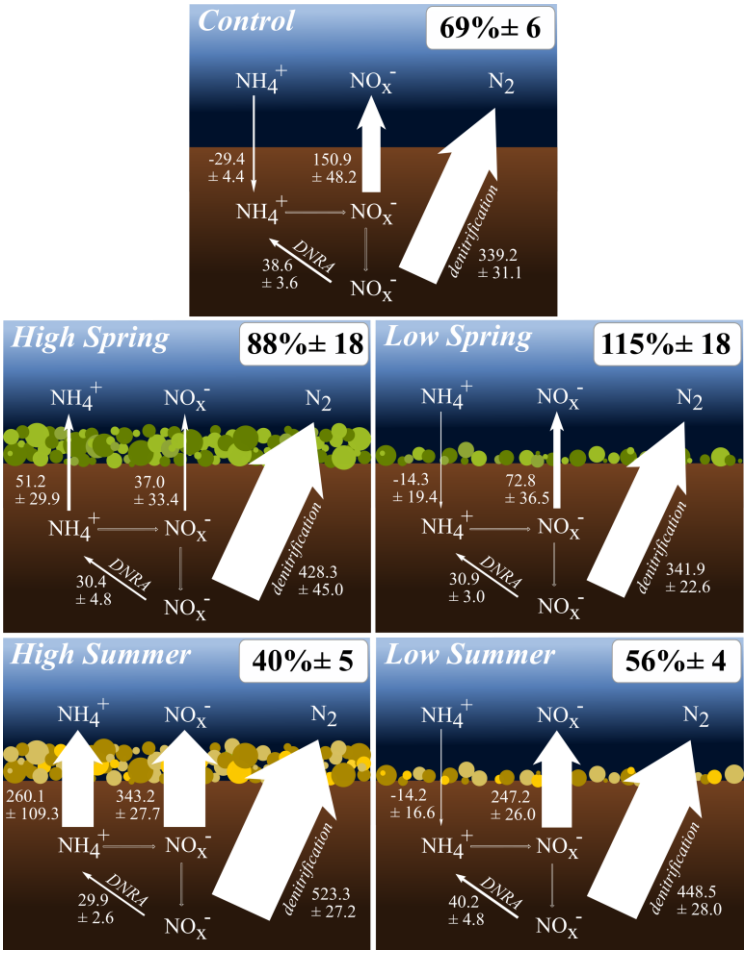


Figure 10. Nitrogen budget at the sediment-water interface observed in **chapter III**, ten days after organic matter addition. Fluxes and rates expressed as mean ± SE ($\mu mol\ N.m^{-2}.d^{-1}$), arrow width reflects the strength of the fluxes. Denitrification efficiency integrated over the duration of the experiment is displayed in the upper right corner (mean ± SE, %). Experimental treatments consisted in two OM quantities: high and low; and two OM qualities: spring and summer plankton bloom material; as well as control with no OM addition.

The results on denitrification gene expression obtained in our other experimental study (**chapter I**) support the findings on the importance of OM quality for functional processes. Indeed, we found that denitrification gene expression (*nirS* and *nosZ*, Box 2) varied by a factor of four along the OM quality gradient that we tested, from 100 % diatom to 100 % cyanobacteria input (Fig. 11). Similarly as in **chapter III**, higher denitrification gene expression was recorded in sediment cores that received cyanobacteria input. Zilius et al. (2016) also reported high denitrification rates and DIN fluxes to the water column following cyanobacteria amendments to the seafloor.

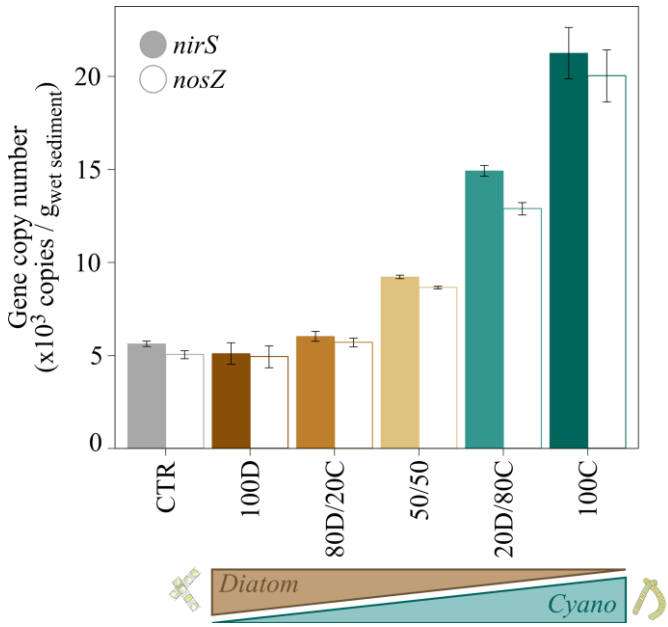


Figure 11. Transcript abundance of the denitrification genes *nirS* and *nosZ* (mean ± SE) observed in **chapter I**, four weeks after organic matter addition. Experimental treatments included control (CTR) and an organic matter quality gradient from 100 % diatoms (100D) to 100 % cyanobacteria (100C) inputs.

It is likely that in both experiments (**chapters I** and **III**), the overall stimulation of N recycling and denitrification processes in response to summer bloom or cyanobacteria settling was prompted by a higher N content in the settling OM. In both cases, the summer bloom and cyanobacteria-derived OM was in a less degraded state than the spring bloom and diatoms-derived OM that we tested (i.e. lower C:N; Jiao et al. 2010). Additionally, cyanobacteria and zooplankton carcasses (which constituted an important part of our summer bloom material in **chapter III**) are naturally richer in N than most spring bloom diatoms (Walve and Larsson 2010; Zilius et al. 2016). Heterotrophic

bacteria assimilate relatively high quantities of N (Van Den Meersche et al. 2004; Canfield et al. 2005). Hence, the availability of an OM source with low C:N ratio (in our case, summer bloom or cyanobacteria) could sustain bacterial metabolic needs, as well as fuel ecosystem processes such as DIN recycling and denitrification. Conversely, upon settling of OM with a high C:N ratio (i.e. spring bloom or diatoms), the limited N pool available was immobilized to a larger extent by bacteria to fulfill their metabolic needs. Dissolved inorganic N fluxes to the water column were reduced (Fig. 10, **chapter III**), and denitrification was not stimulated compared to control conditions (Fig. 11, **chapter I**). Similar conclusions were drawn from laboratory experiments testing the response of bacteria to a range of artificial organic substrates with different C:N ratios (Goldman et al. 1987; Tezuka 1990) but this is the first time that the importance of stoichiometric ratios for N cycling is shown in more ecologically realistic scenarios. Further evidence of competition for N resources between benthic heterotrophic bacteria and nitrifiers/denitrifiers was also found in a field-manipulative experiment (Oakes et al. 2011)

It is interesting to note that in both studies (**chapters I** and **III**) the results on denitrification gene expression obtained via RT-qPCR and the rates measurements showed the same patterns. Rate measurements and genetic information do not always correlate, even within the same experimental set-up (Bowen et al. 2014; Babbin et al. 2016). Presumably, this may be because each method captures processes occurring at different time scales. On the one hand, gene expression can vary substantially within minutes (Härtig and Zumft 1999), such that the information obtained from RT-qPCR represents only a snapshot of transcriptional activity. On the other hand, rates measurements obtained from whole-core incubations such as that described in **chapter III** capture ecosystem processes over a longer time period (e.g. several hours). With this in mind, that we found coherent patterns between our two studies is encouraging in regard to the validity of the conclusions, that settling of OM with low C:N ratios tends to promote both DIN recycling and denitrification processes.

Synthesis

Marine ecosystems across the globe are subject to cumulative anthropogenic pressures from global and local sources that severely affect community dynamics and functioning (Walther 2010; IPCC 2014; Ceballos et al. 2015; Cavicchioli et al. 2019). Mitigating these changes in the future demands strong policies, backed with solid science, and a substantial reduction of our greenhouse gas emissions. Yet, even under the best scenario, full ecosystems recovery will be slow, if at all possible (Heiskanen et al. 2019; IPCC 2019). In the Baltic Sea, substantial recent nutrient load reductions, combined with increased heterotrophic processes in the water column due to global warming are projected to reduce OM settling to the seafloor (Tamelander et al. 2017). Furthermore, climate-driven changes of phytoplankton communities, resulting in a shift from a diatom-dominated to a cyanobacteria-dominated system, will exacerbate this reduction in settling OM fluxes (Griffiths et al. 2017; Hjerne et al. 2019). In parallel, the quality of OM reaching the seafloor will change substantially, leading to inputs of material in a more advanced state of degradation due to longer residence time and higher mineralization in the water column (Blomqvist and Heiskanen 2001; Andersson et al. 2015; Hjerne et al. 2019). Considering the strong coupling between pelagic and benthic processes in the Baltic Sea, it is essential to improve our knowledge on how changes in OM settling could influence soft sediment community structure and functioning (Griffiths et al. 2017; Ehrnsten et al. 2020). In this thesis, the role of OM quality was addressed (**chapters I** to **IV**), as well as OM quantity (**chapters III** and **IV**) as drivers of change on benthic communities and processes. We targeted more specifically the smallest organisms that inhabit soft sediments, namely microeukaryotes and bacteria, which have been largely overlooked, despite their prominent role in the ecosystem.

Overall, our results support existing literature indicating an important influence of OM settling on benthic microeukaryotes (Graf 1992; Ólafsson and Elmgren 1997). We report new evidence on community response in terms of structure and diversity. We also show that OM quality plays a role in mediating this response. Based on the results presented in **chapter I**, the effects of settling OM quality led to a subtle reorganization of the community at low rather than high taxonomic levels. In parallel, we observed a clear effect of

diatom-derived vs. cyanobacteria-derived OM on microeukaryotic alpha diversity. The former triggered a decrease in diversity after four weeks, whilst the latter did not induce significant change. The results from our field monitoring study (**chapter IV**) are in accordance with these findings regarding the negative effect of diatom-derived OM settling on microeukaryotic alpha diversity. However, simultaneous seasonal changes in OM quantity and quality, correlated with other abiotic factors (e.g. temperature, O_2 concentration) is not allowing for the role of each variable to be completely disentangled and quantified. In **chapter IV**, we propose that the reduction in alpha diversity was primarily linked to settling of OM in large quantities after the spring bloom, which stimulated mineralization activity and caused a decrease in O_2 concentrations (Pfannkuche 1993; Levin 2003). Competitive exclusion from taxa or genotypes adapted to assimilate diatom-derived OM could have also contributed to the negative impact on microeukaryotic alpha diversity observed both in **chapters I** and **IV** (Paine 1966; Peterson 1979; Guden et al. 2018). Conversely, cyanobacteria settling did not induce clear negative or positive effects on microeukaryotic alpha diversity. Considering future projections for the Baltic Sea (Tamelander et al. 2017; Spilling et al. 2018; Hjerne et al. 2019), it appears that a general decrease in OM fluxes to the seafloor, as well as a shift from diatoms- to cyanobacteria-dominated primary production would have a positive impact on microeukaryotic biodiversity. A reduction in settling from spring bloom diatoms could alleviate some of the negative consequences on microeukaryotic diversity as a result of hypoxic conditions (Grego et al. 2014), while maintaining the general structure of the community. Other organisms, both in the pelagic and benthic systems, have been shown to assimilate cyanobacteria-derived OM (Nascimento et al. 2008; Gorokhova et al. 2021). Despite adverse effects documented on the growth of a few meiofauna taxa (Nascimento et al. 2009), we did not observe that they translated to important changes at the scale of the community. In the future, we should nevertheless consider potential impacts of reduced OM settling on benthic microeukaryotic biomass, as model projections suggest a negative effect on macrofauna biomass (Ehrnsten et al. 2020).

Organic matter settling effects on bacterial communities were generally less pronounced than for microeukaryotes. Aside from the shift in community structure observed after spring bloom sedimentation in our field study (**chapter IV**), we could not identify a coherent pattern of community response towards settling of diatoms or cyanobacteria, in terms neither of structure nor of diversity. Nevertheless, OM settling was a significant factor in driving variations in benthic bacterial communities in both **chapters I** and **IV**. The absence of a clear pattern was most likely caused by our sampling strategy, which targeted the upper 3 cm of sediment in both studies. It is probable that measurable changes occurred close to the sediment surface (e.g. 0-0.5 or 1 cm, as shown in other studies (Tait et al. 2015; Vetterli et al. 2015)), while subsurface

layers were less responsive to OM pulses to the seafloor. With this in mind, we strongly advise that future studies differentiate sediment depth layers at a finer scale when investigating bacterial community dynamics, in order to better resolve their response to future changes. This strategy would, on the other hand, make more difficult to obtain a representative sample for microeukaryotes, when simultaneously assessing multiple communities. In **chapter II**, we found that bacterial community structure in overlying waters was significantly affected by the OM quality gradient from 100 % diatoms to 100 % cyanobacteria OM. More specifically, certain bacterial ASVs were preferentially associated to each source of OM, suggesting the occurrence of a selection based on resource utilization (Landa et al. 2014). Furthermore, our results highlighted that modifications of nutrient fluxes triggered by OM settling could have an effect on the assembly of bacterial communities in overlying waters by favoring particular taxa or ASVs. As demonstrated in **chapter III**, OM quality is an important control of DIN recycling, and future changes in OM settling to the sediment may therefore have cascading effects on bacterial communities in the overlying water through feedback mechanisms (Dang and Lovell 2016).

Finally, while benthic bacterial communities remained largely stable in response to OM settling, their metabolic activity and some of the N cycling processes that they mediate were clearly affected. Results from **chapters I** and **III** indicate that summer bloom and cyanobacteria OM stimulated denitrification at a greater extent than spring bloom and diatom OM. Based on our observations, as well as evidence from the literature (Goldman et al. 1987; Tezuka 1990), we attributed this response to the bulk stoichiometry of the OM (i.e. C:N ratio). In more details, the higher N content (and corresponding low C:N ratio) of summer bloom and cyanobacteria OM presumably provided enough N substrate both for bacterial metabolic needs and N cycling processes, including denitrification and DIN recycling, resulting in a lower denitrification efficiency. Conversely, settling of OM with higher C:N ratio prompted a stronger immobilization of N by bacteria, and the N that entered microbial transformation pathways was largely denitrified. In a context where OM is projected to reach the sediment in a more degraded state (i.e. higher C:N, (Andersson et al. 2015; Tamelander et al. 2017)), our results suggest a positive influence on denitrification efficiency at the SWI. Yet, we should keep in mind that longer OM residence time in the water column would inevitably increase the time during which it is subjected to remineralization during its descent. As such, most organic N would be recycled as bioavailable DIN before reaching the sediment (Ducklow et al. 2001; Almroth-Rosell et al. 2016), and only a small fraction would be efficiently denitrified at the SWI. We therefore stress the need to consider the full cycle from production to decomposition of OM in order to evaluate accurately future changes in elemental fluxes in the ecosystem.

Future perspectives

As this project developed and results started to come together, a number of questions rose in regard to future investigations needed to improve our understanding of benthic-pelagic coupling. I want to highlight three research areas in particular that I believe deserve further attention: (1) estimation of OM fluxes to the seafloor, notably the contribution of zooplankton; (2) the role of biotic interactions in structuring benthic communities; and (3) deciphering the influence of various OM quality parameters on consumers and decomposers.

Organic matter settling to the seafloor has been at the center of our work. Nevertheless, estimating the quantity and quality of these OM fluxes remains, to this day, a challenging task. As we try to predict future evolutions of OM fluxes, the uncertainty is further exacerbated since a plethora of processes act all at once, inducing synergistic and antagonistic effects on those fluxes (Tamelander et al. 2017). Currently, most estimates of OM fluxes originate from sediment trap analyses, which suffer from significant limitations (Buesseler et al. 2007; Gustafsson et al. 2013). This is particularly true in shallow coastal systems, where sediment resuspension due to storm events may induce important biases in fluxes measurements (Heiskanen and Leppänen 1995). Additionally, some of our observations in **chapter III** raised the question of the contribution of material of zooplanktonic origin to total OM settling. Indeed, the field-collected summer plankton material used in this experiment contained a large amount of zooplankton material (e.g. ciliates, copepod carcasses, eggs, fecal pellets), while cyanobacteria accounted for a relatively minor portion of the total biomass. Mesozooplankton (e.g. copepods) are routinely removed from sediment traps analyzes in order to prevent the inclusion of active swimmers. However, this procedure can induce another bias by excluding carcasses which passively sediment into the traps (Buesseler et al. 2007; Turner 2015). Zooplankton may die from non-predatory causes such as parasitism or senescence (Tang and Elliott 2014; Tang et al. 2014), and it has been found that sedimentation of zooplankton carcasses can account for a significant portion of the annual OM export to the seafloor (Sampei et al. 2009; Turner 2015). To our knowledge, the contribution of zooplankton to total OM settling is not well-documented in the Baltic Sea. In a context where environmental change is affecting zooplankton communities (Aberle et al. 2015;

Mäkinen et al. 2017), I believe that this question deserves further attention in order to evaluate more accurately future changes in benthic-pelagic coupling processes.

In **chapter IV**, our main goal was to evaluate the role of pelagic environmental variables (e.g. OM settling, temperature, O_2 concentration) on the seasonal successions of benthic microeukaryotic and bacterial communities. We found that 10.4 and 5.3 % of total microeukaryotic and bacterial community variation were accounted for by the abiotic factors measured. Completing our model with additional abiotic variables such as pigment or macromolecule concentrations in the sediment (Danovaro et al. 1999; Schratzberger et al. 2008; Lampadariou and Eleftheriou 2018) might improve the explanatory power, but most likely, biotic factors played an important role in structuring these communities (Peterson 1979; Thrush et al. 2021). Species interactions such as competition, predation, parasitism or symbiosis are key drivers of community structure in soft sediments (Moodley et al. 2000; Walther 2010; Schratzberger and Ingels 2018; Vafeiadou et al. 2018; Forsblom et al. 2021). Yet, investigating organism interactions in such a heterogeneous habitat represents a challenge, and currently limits the scope of our understanding on biotic interactions, especially for the smallest organisms (i.e. microeukaryotes and bacteria). Rapid advances in molecular approaches open up promising new possibilities to address these questions, even down to the individual scale (Krabberød et al. 2017; Zamora-Terol et al. 2020). In an effort to discern spatial and functional patterns, Schuelke et al. (2018) analyzed nematode microbiomes associated to nearly 300 single specimens across the north-American coastline. It is also possible to combine several approaches (e.g. Scanning Electron Microscopy, Fluorescence *In Situ* Hybridization and DNA metabarcoding) to characterize and identify extracellular symbionts on nematode cuticles (Bellec et al. 2019). These are just a few of many examples highlighting the potential of molecular approaches for investigating biotic interactions that were previously much more challenging to study.

Finally, I want to stress the need to better evaluate the influence of specific parameter(s) related to OM quality on benthic community responses (Campanyà-llovet et al. 2017). As discussed earlier, characterizing OM quality is conceptually complex. In our two experimental studies (**chapters I** to **III**), the OM sources that we used differed on many levels, including origin, size, bulk stoichiometry, potential toxin concentration or biochemical composition. Although we laid out some hypotheses, disentangling the role of each of these qualitative parameters on the biodiversity and functioning of benthic communities was beyond the scope of our work. Yet, this information would be essential to predict future ecosystem dynamics in response to changes in benthic-pelagic coupling.

Sammanfattning (Svenska)

Marina mjukbottnar utgör planetens största habitat. Organismerna som bosätter sig i denna miljö utgör en enorm tillgång för biodiversitet och innehar en nyckelroll för ett flertal ekosystemprocesser. De flesta bentiska organismer är beroende av organiskt material (OM) från fytoplankton i den överliggande vattenkolumnen då detta utgör dess födokälla, men mänsklig påverkan såsom eutrofiering och *klimatförändringar har orsakat djupgående förändringar* i den naturliga ekosystemdynamiken. Konsekvenserna av dessa förändringar för den bentiska-pelagiska kopplingen och mjukbottensamhällets funktioner har ännu inte klarlagts.

Syftet med denna avhandling är att bedöma betydelsen av OM-tillförsel på mjukbottens mikroeukaryotiska (små organismer <1 mm) och bakteriella samhällen. Våra intressen var tvåfaldiga, då vi ämnat utreda påverkan på (1) samhällsstruktur och diversitet (**kapitel I**, **II** och **IV**) och (2) ekosystemfunktioner, främst i relation till kvävecykeln (**kapitel I** och **III**).

Kvalitet och kvantitet av det OM som tillkommer till sedimentet hade markant påverkan på mikroeukaryotisk alfa-diversitet. Vi såg en minskning av alfa-diversitet efter sedimentationen av OM kopplat till vårblomningen av kiselalger, möjligen ett resultat av kompetitiv exkludering, medan OM kopplat till sommarblomningen av cyanobakterier inte påverkade alfa-diversiteten (**kapitel I** och **IV**). Vi fann även att hög tillförsel av OM till sedimentet hade negativ påverkan på mikroeukaryotisk alfa-diversitet (**kapitel IV**). Troligtvis ledde en hög tillförsel av OM från vårblomningen till ett kraftigt ökat syrebehov, vilket slog ut taxa känsliga för minskad syrehalt. Samtidigt fann vi att sammansättningen av det mikroeukaryotiska samhället främst drevs av mängden sedimenterande OM (**kapitel IV**), medan skillnader i OM-kvalitet främst ledde till förändringar på lägre taxonomisk nivå (**kapitel I**).

Bakteriesamhällets reaktion på OM-sedimentation var mindre tydlig, och troligtvis begränsad till det ytligaste sedimentet (**kapitel I** och **IV**). Vi såg däremot en betydande effekt av OM-kvalitet på bakteriesamhällets struktur vid gränsen mellan sediment och vatten, där taxa antingen gynnades av OM från kiselalger eller cyanobakterier (**kapitel II**). Denna studie visade även att feedback-mekanismer av näringsomsättningen i sedimentet skulle kunna utgöra en roll i denna respons.

Slutligen tyder våra resultat på att OM-kvalitet har en stor betydelse för kvävets omsättning vid gränsen mellan sediment och vatten. Vi fann att sedimentation av nytt OM (med låg C:N-kvot) stimulerade denitrifikation (**kapitel I** och **III**), och att det samtidigt ledde till högre kvävetransport till vattenpelaren än sedimentation av nerbrutet OM (med hög C:N-kvot) (**kapitel III**).

Sammantaget visar våra resultat att nuvarande förändringar i OM-dynamiken i marina system troligtvis leder till inverkan på mikroeukaryotisk, och till viss del även bakteriell, biodiversitet i mjuka bottnar. Förändringar, särskilt i kvaliteten av sedimenterade OM, kan även påverka mikrobiella processer som är kritiska för kvävecykeln. Denna avhandling påvisar betydelsen i att överväga den bentiska-pelagiska kopplingens mekanismer för att bättre förstå troliga framtida förändringar i marina ekosystem.

Résumé (Français)

Les sédiments marins constituent le second habitat le plus large sur la planète. Les organismes qui y résident représentent un vaste réservoir de biodiversité et jouent des rôles clés dans le fonctionnement des écosystèmes. La plupart des organismes benthiques dépendent des apports pélagiques en matière organique (MO) issus du phytoplancton présent dans la colonne d'eau en tant que nourriture. Cependant, les pressions anthropiques telles que l'eutrophisation et le changement climatique altèrent profondément les dynamiques naturelles des écosystèmes. Les potentiels impacts des modifications du couplage bentho-pélagique en terme de biodiversité et de fonctionnement des communautés de fonds meubles sont encore largement incertains..

Le but de cette thèse est d'évaluer le rôle de la sédimentation de MO sur les communautés de fonds meubles microeukaryotiques (organismes < 1 mm) et bactériennes. L'ensemble de ce travail couvre deux aspects principaux, à savoir, estimer les impacts sur (1) la structure et la biodiversité des communautés (**chapitres I, II** et **IV**) et (2) sur le fonctionnement de l'écosystème, notamment en lien avec le cycle de l'azote (N) (**chapitres I** et **III**).

Nous avons démontré que la quantité et la qualité des apports en MO ont toutes deux des impacts significatifs sur la diversité alpha des communautés microeukaryotiques. Nous avons observé une diminution de la diversité alpha à la suite de la sédimentation de MO dérivée de diatomées issues du bloom printanier, possiblement du fait d'une exclusion par compétition, tandis que la MO dérivée de cyanobactéries issues du bloom estival ne tend pas à affecter la diversité alpha (**chapitres I** et **IV**). Nous avons également constaté que la sédimentation de MO en larges quantités avait un effet négatif sur la diversité alpha des microeukaryotes (**chapitre IV**). À la suite d'un important apport en MO issue du bloom printanier, la demande en oxygène (O_2) du sédiment peut être largement stimulée, entraînant l'exclusion des organismes les plus sensibles au manque d'oxygène. Dans l'ensemble, nous avons remarqué que l'assemblage des communautés microeukaryotiques étaient principalement lié à la quantité d'apport en MO (**chapitre IV**), tandis que les différences qualitatives de la MO entrainaient des changements significatifs mais plus subtils au sein des communautés, prenant place à des niveaux taxonomiques plus fins (**chapitre I**). La réponse des communautés bactériennes aux apports en MO semble moins prononcée, et est probablement restreinte à la couche supérieure

du sédiment (**chapitres I** et **IV**). Nous avons néanmoins observé un effet significatif de la qualité de MO sur l'assemblage des communautés bactériennes à l'interface eau-sédiment, certains taxons étant respectivement favorisés par la MO issue de diatomées ou de cyanobactéries. Nous avons également mis en évidence que les mécanismes de recyclage des nutriments dans le sédiment pouvaient jouer un rôle dans cette réponse (**chapitre II)**. Pour finir, nos résultats indiquent une influence significative de la qualité de MO sur le cycle de l'azote à l'interface eau-sédiment. Nous avons remarqué que l'apport de MO fraîche (i.e. ratio C:N bas) stimulait l'activité de dénitrification (**chapitres I** et **III**), tout en favorisant un recyclage plus important de N vers la colonne d'eau que l'apport de MO dégradée (i.e. ratio C:N élevé) (**chapitre III**).

De manière générale, nos résultats indiquent que les changements actuels en terme d'apports en MO au sein des systèmes marins impacteront probablement la biodiversité microeukaryotique et, en partie, bactérienne dans les sédiments marins. Les modifications de la qualité de MO, en particulier, peut également affecter des processus microbiens essentiels dans le cycle de l'azote. Cette thèse met en avant l'importance de considérer les mécanismes de couplage bentho-pélagique afin de mieux comprendre les futurs changements au sein des écosystèmes marins.

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