Coastal signals of environmental changes: foraminifera as benthic monitors

Brinkmann, Inda

2022

Citation for published version (APA):
Brinkmann, I. (2022). *Coastal signals of environmental changes: foraminifera as benthic monitors*. [Doctoral Thesis (compilation), Quaternary Sciences]. Lund University.

Total number of authors:
1

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LUNDQUA THESIS 93

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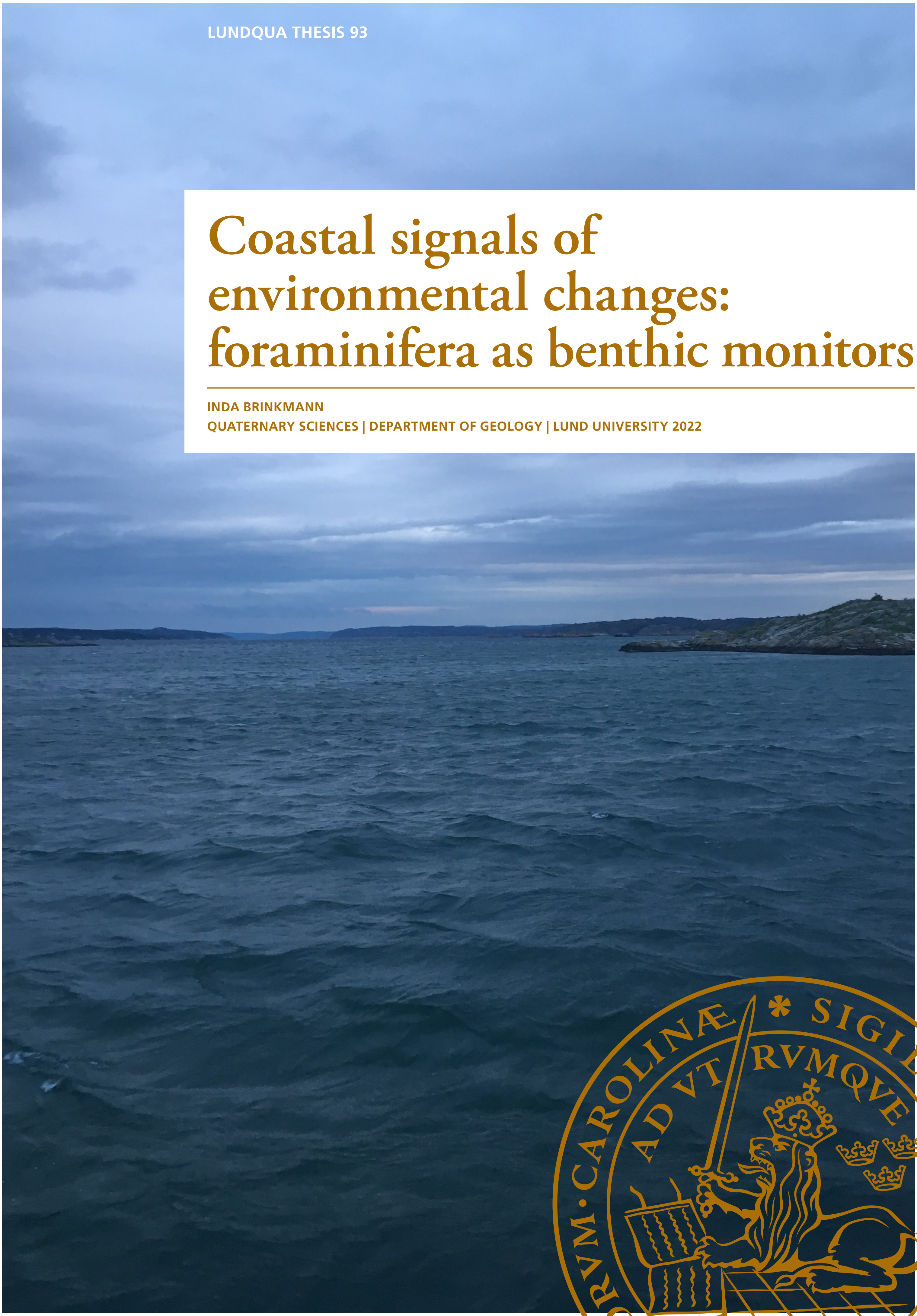
INDA BRINKMANN

QUATERNARY SCIENCES | DEPARTMENT OF GEOLOGY | LUND UNIVERSITY 2022



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Coastal signals of environmental changes: foraminifera as benthic monitors

Inda Brinkmann

Quaternary Sciences
Department of Geology

DOCTORAL DISSERTATION
by due permission of the Faculty of Science, Lund University, Sweden.
To be defended on October 21, 2022, at 09:15 a.m.
in Pangea, Geocentrum II, Sölvegatan 12, Lund, .

Faculty opponent
Prof. Michal Kucera
MARUM, University of Bremen, Germany

Funding information: This PhD project has been funded by the Swedish Research Council (grant no. 2017-04190), the Crafoord Foundation, the Royal Physiographic Society of Lund, and Lund University.

Cover image, front: Inda Brinkmann; back: Jonas Donnenfield; illustrations: Inda Brinkmann

Quaternary Sciences
Department of Geology
Faculty of Science

ISBN 978-91-87847-66-0 (print)

ISBN 978-91-87847-67-7 (pdf)

ISSN 0281-3033

Printed in Sweden by Media-Tryck, Lund University, Lund 2022

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Printed matter
3041 0903

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MADE IN SWEDEN

Organization

LUND UNIVERSITY
Department of Geology
Sölvegatan 12
SE-223 62 Lund
Sweden

Document name

DOCTORAL DISSERTATION

Date of issue: 21 Oct 2022

Author: Inda Brinkmann

Sponsoring organization

Title: Coastal signals of environmental changes: foraminifera as benthic monitors

Abstract

Climate changes, tightly linked to anthropogenic activities, are significantly altering environments and ecosystems globally, such as by increasing marine and coastal deoxygenation or occurrences of extreme weather events. The significance of paleoenvironmental and -climate reconstructions, as well as monitoring of current conditions, for unravelling baseline natural variation, today's changes and potential future impacts, has been recognised by the Intergovernmental Panel on Climate Change (IPCC) reports. However, to access past records of physical and chemical environmental variables, and comprehensively assess ecosystem reactions, reliable and sensitive proxies are critical.

This thesis' focus lies on benthic foraminifera—unicellular protists with mineralised or organic test, abundantly inhabiting ocean and coastal sediments—and their calibration as indicator for a variety of environmental conditions in field-sampling approaches. The research projects follow two general strategic tracks: (I) a biogeochemical assessment of trace-elemental ratios in foraminiferal calcium-carbonate tests using high-resolution, micro-analytical techniques; (II) a molecular approach investigating foraminiferal environmental DNA derived from coastal sediments.

Papers I and II concern the calibration of the benthic foraminiferal Mn/Ca proxy for marine oxygenation conditions in modern field studies. Trace-element concentrations and distributions were measured by plasma-, laser- and synchrotron-based analyses in a high-resolution, individual-foraminifera approach, and interpreted in the context of ambient physical and chemical conditions of the water column, pore-waters and sediments (including oxygen and manganese concentrations). Investigating two coastal systems with almost permanently severely oxygen-deficient bottom-waters (Santa Barbara Basin, Paper I), and undergoing a seasonal oxygenation cycle across the low- to well-oxygenated range (Gullmar Fjord, Paper II), respectively, demonstrated the utility of the Mn/Ca proxy for indicating low-oxygen conditions specifically. Continued calibration efforts under consideration of ambient oxygenation and redox regimes may open further possibilities of quantitative oxygen reconstructions. Paper III explores the use of coastal, benthic Ba/Ca records as indicator of riverine runoff and drought on land across the years 2018 and 2019, characterised by severe heat and drought, and warm and wet conditions, respectively. Benthic Ba/Ca correlated significantly with the hydroclimate conditions, as inferred from extensive meteorological and hydrological data sets of the region, highlighting qualitative proxy potential for paleo-drought reconstructions. Based on ambient sediment and pore-water geochemistry, we discuss mediation of water-column transport and pore-water Ba cycling by Fe and Mn oxides. All three investigations of these geochemical proxies (Paper I–III) highlighted the significance of biological controls on foraminiferal TE/Ca, which are species-specific and, thus, should be a deciding factor in choosing proxy candidate species. In particular the influences of micro-habitat distribution and utilised metabolic pathways by foraminifera are discussed in detail.

In Paper IV foraminiferal biodiversity and assemblage responses to natural and anthropogenic environmental trends in a fjord system (Swedish west coast) are documented in a metabarcoding approach. Environmental DNA successfully tracked biodiversity and community composition changes associated with contrasting ecosystems but showed damped sensitivity to environmental variability on sub-annual time-scales. Overlaps and discrepancies between molecular and traditional, observation-based assessment techniques, as well as future trajectories to resolve uncertainties are discussed.

Overall, this thesis solidifies and expands the currently available proxy toolbox for reconstructions of both coastal low-oxygen, as well as terrestrial hydroclimate conditions. The findings contribute towards filling current knowledge gaps pertaining to biotic impacts on foraminifera-derived biogeochemical signals and methodological uncertainties in metabarcoding approaches and highlight the significance of implementing molecular techniques in conventional foraminiferal assemblage studies.

Key words: benthic foraminifera, proxy calibration, trace element geochemistry, environmental DNA, deoxygenation, drought, coastal environments

Classification system and/or index terms (if any)

Supplementary bibliographical information

Language: English

ISSN and key title: 0281-3033 LUNDQUA THESIS

ISBN: 978-91-87847-66-0

Recipient's notes

Number of pages: 184

Price

Security classification

Signature: I. Bri

Date: 16. Sept. 2022

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Acknowledgements

First of all, Helena L. Filipsson: You provided foundation and room for my progress, and I'm thankful for having had you as my main supervisor. I appreciate your positive mindset, and you always having my back throughout the years. Thank you for the endless encouragement, many opportunities, and ideas you shared with me.

No less, I thank my co-supervisors. Joan M. Bernhard, working with you was an inspiration, and your devotion to giving thorough feedback, often at short notice, did not go unnoticed. Christine Barras, the discussions I had with you and your advice were extremely appreciated; thank you for believing in me. Magali Schweizer, thank you for welcoming me to the molecular world of foraminiferal research; I highly value the new perspectives and your patient support.

I'm grateful to the many people who contributed to my research, for being so generous with their time and sharing their knowledge and experience with me. I learned so much from you:
All my co-authors, and especially: Tom Jilbert, and workgroup, for discussions and explanations of coastal geochemistry. Tomas Næraa, for figuring out the best way to laser-ablate my samples, and advice on data processing. Andrea Somogyi and Kadda Medjoubi at NANOSCOPIUM, for their support before, during and after the analyses. The same goes for Martin Whitehouse, Kerstin Lindén and Heejin Jeon at Nordsim. Sha Ni and Constance Choquel, for answering so many of my foraminifera questions, and David Singer, for guiding me through the eDNA and R code jungle. Thanks to the senior members of the LPG in Angers, for constructively and critically discussing my data, and thanks to the PhD students, for welcoming me during my several stays. Dirk Müter, for the 3D scans of *Nonionella stella*, Carl Alwmark, for assisting with the SEM, and Ezgi Vardar and Gioele Pappalardo, who picked foraminifera for me. Thanks also to the Captains and crews of R/V 'Oscar von Sydow' and R/V 'Skagerak', the staff of the Kristineberg Center for Marine Research and Innovation, as well as Hanna Nilsson, Sami Jokinen, and everyone else who helped out during the sampling campaigns.

Gratitude also goes to all the funders of my projects and travels, especially the Swedish Research Council, the Crafoord Foundation, the Royal Physiographic Society of Lund and the Carl Swartz Memorial Fund, without who's support my work would not have been possible.

I thank all current and former colleagues at the Department of Geology, for making the department a pleasant place to work at, and particularly Gert Pettersson, Åsa Wallin, Git Ahlberg, Isa Doverbratt, members of kansliet, the library and administration for helping out with everyday work difficulties.

An added thank-you goes to all the PhD students and post-docs, for the company and commiseration. Especially those whom I shared an office with: Constance, Jonas, Maria, Minjie, Nisha, and have become my friends: Josefin, Lena, Megan, Miriam.

Finally, I thank those in my personal life who offered comfort, encouragement or distraction along the way or parts thereof. You being there made a difference.

Lund, September 2022

Inda

1 Introduction

Today's environment has been and still is fundamentally changing in its physical, chemical and biological conditions, forced by global warming and human impacts, as recognised by the 5th and 6th assessment report of the Intergovernmental Panel on Climate Change (IPCC) (Cooley *et al.*, 2022; Parmesan *et al.*, 2022; Rhein *et al.*, 2013). In coastal marine environments, deoxygenation is one of the most ecologically challenging symptoms, evoked by anthropogenic warming and eutrophication (e.g., Breitburg *et al.*, 2018; Laffoley & Baxter, 2019; Limburg *et al.*, 2020; Zhang *et al.*, 2010), and demanding active monitoring and adaptations (e.g., Gilbert *et al.*, 2010; Harley *et al.*, 2006; Rhein *et al.*, 2013; Toimil *et al.*, 2020). The terrestrial realm is challenged by an unprecedented frequency, duration, and intensity of extreme weather events, stressing ecosystems as well as society, agriculture, and economy (e.g., Kron *et al.*, 2019; Toreti *et al.*, 2019). Predictions show further accelerations in the near future of both deoxygenation and extreme weather patterns (e.g., Cook *et al.*, 2020; Rabalais *et al.*, 2010; Tetard *et al.*, 2021; Zhang *et al.*, 2010). These present-day environmental transitions, as well as their underlying forcing mechanisms, urge a contextual understanding of natural variability in order to better understand severity and implications.

Observations of current and past changes are vital to explore climate and ecosystem dynamics and interactions, and can provide a baseline for future comparisons, as well as support management strategies (e.g., Heinze *et al.*, 2021). Records of past variability are especially valuable for inferences on temporal development and responses of ecosystems, and vital for calibrating and testing climate models more effectively. Direct (instrumental) observations of climate factors are inherently limited temporally, spatially, as well as for practical reasons. In contrast, indirect measures by substitute variables, such as bioindicators and biogeochemical proxies, allow comprehensive understanding of environmental dynamics and consequences in the past and current, including biotic changes and ecosystem reactions (e.g., Holt & Miller, 2011; Markert *et al.*, 2003). However, to exploit the full potential of proxies, reliable calibrations specific to the used indicator and environmental variable in question are imperative. In particular quantitative proxies for bottom-water oxygenation are not fully constrained (e.g., Gooday *et al.*, 2009; Koho *et al.*, 2017), and most previous reconstructions are only qualitative (e.g., Erdem *et al.*, 2020; McKay *et al.*, 2015).

Foraminifera, single-celled microorganisms in the group Rhizaria residing in either the water-column (planktonic life habitat) or sea-floor (benthic life habitat, in focus of this thesis) of dominantly the marine realm, are important palaeo-recorders of past environmental variability (e.g., Katz *et al.*, 2010; Kucera, 2007; Murray, 2006). Palaeoenvironmental reconstructions are based both on diversity and composition of assemblages, as well as the chemical composition of foraminiferal calcium-carbonates. Benthic foraminifera, living in or on the sediment, inform both about bottom-water conditions as well as in-sediment geochemical cycling. In coastal settings benthic records have the potential to link marine and terrestrial climate records. In recent decades, efforts have been made to establish extant foraminifera for bioindication and biomonitoring purposes (e.g., Alve *et al.*, 2016; Barras *et al.*, 2014; Bouchet *et al.*, 2012), partially relying on new molecular methods (e.g., Cavaliere *et al.*, 2021; Laroche *et al.*, 2016; Pawlowski *et al.*, 2018). Foraminifera-based records have the potential to link past and present environmental variability, thus, presenting a powerful tool informing baselines, ecosystem responses and recovery, and current environmental changes. However, persistent challenges associated with biological controls on foraminifers' proxy potential (e.g., Barras *et al.*, 2018; Koho *et al.*, 2017; van Dijk *et al.*, 2019; Zeebe *et al.*, 2008), as well as methodological uncertainties of molecular approaches (e.g., O'Brien *et al.*, 2021), call for the expansion and further calibration of proxies in modern settings. Here we use *in situ* approaches investigating living foraminifera assemblages and biogeochemical signals in context of measured physical and chemical environmental factors, to calibrate proxies and elucidate biological biases.

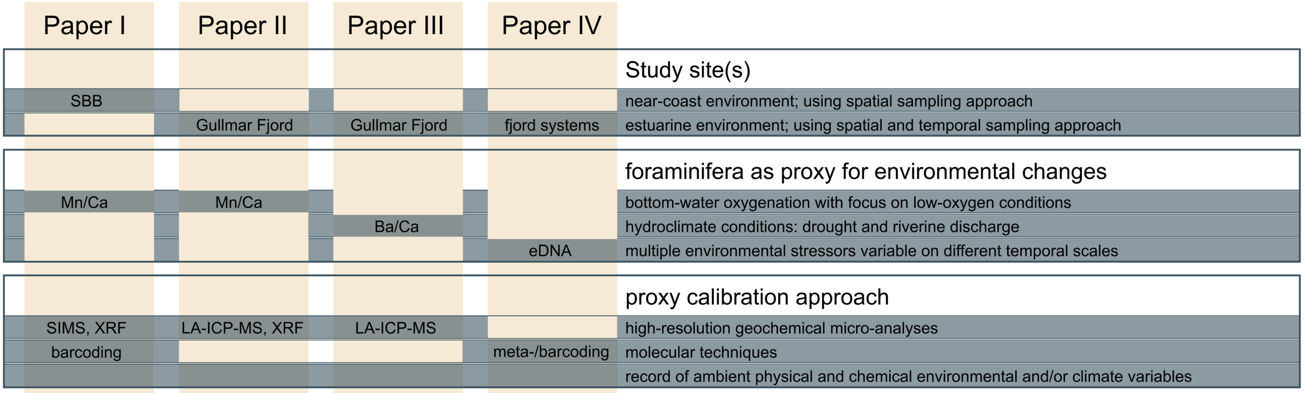
2 Scope of thesis

The aim of my thesis is to improve foraminifera-based proxies for the investigation of climatic and environmental changes affecting coasts and transitional marine settings, constrain associated (biological) uncertainties, and contribute to a better understanding of modern foraminiferal ecology and biomineralization.

The overarching objectives of this thesis can be summarised as:

- Develop and improve foraminiferal proxies by analysing modern field-sampled foraminifera over temporal and spatial environmental gradients
- Investigate abiotic and biotic controls on trace-element incorporation in foraminifera using high-resolution micro-analytical techniques and comparing species of contrasting lifestyles
- Assess the reliability of foraminifera-based environmental inferences by comparing records of ambient physical and chemical conditions, and/or established foraminiferal indicators

To achieve these aims, my thesis work comprises both geochemical and molecular approaches (Fig. 1).



Paper I	Paper II	Paper III	Paper IV	
				Study site(s)
SBB				near-coast environment; using spatial sampling approach
	Gullmar Fjord	Gullmar Fjord	fjord systems	estuarine environment; using spatial and temporal sampling approach
				foraminifera as proxy for environmental changes
Mn/Ca	Mn/Ca			bottom-water oxygenation with focus on low-oxygen conditions
		Ba/Ca		hydroclimate conditions: drought and riverine discharge
			eDNA	multiple environmental stressors variable on different temporal scales
				proxy calibration approach
SIMS, XRF	LA-ICP-MS, XRF	LA-ICP-MS		high-resolution geochemical micro-analyses
barcoding			meta-/barcoding	molecular techniques
▨	▨	▨	▨	record of ambient physical and chemical environmental and/or climate variables

Fig. 1 Display of projects and approaches dealt with in this thesis.

3 Background

3.1 Oxygen depletion in coastal waters

The oceans' oxygen inventory globally has decreased by more than 2% within the last century (e.g., Schmidtko *et al.*, 2017), and this decrease in dissolved oxygen concentrations is most prevalent and severe in coastal waters (e.g., Gilbert *et al.*, 2010). The phenomenon of coastal deoxygenation is generally a seasonal feature, with only ca. 8 % of coastal settings being permanently depleted of oxygen (Diaz & Rosenberg, 2008). Deoxygenation is often associated with the term 'hypoxia', referring to a condition where oxygen depletion becomes harmful for marine life. For instance, oxygen thresholds below which mortality of macro-organisms, such as fishes, increases significantly (e.g., Rosenberg *et al.*, 1991; Vaquer-Sunyer & Duarte, 2008). However, the definition of oxygen concentration limits for hypoxia is arbitrary, and further inconsistency stems from the variety of units currently in use to express oxygen concentrations. Commonly used are the units ml/l, mg/l and µmol/l—with the following conversions: 1.0 ml/l = 1.4 mg/l = 44.66 µmol/l O_2—as well as the equivalents with kg as denominator. Definitions of hypoxia frequently centre around an upper limit of 2 mg/l or 2 ml/l (e.g., Diaz & Rosenberg, 1995; Rabalais *et al.*, 2010), which correspond to a value of 63 and 89 µmol/l, respectively. Naturally, tolerance to oxygen-depletion varies between, or even within, groups of organisms (Vaquer-Sunyer & Duarte, 2008), as well as in correlation with other environmental factors such as temperature (Vaquer-Sunyer

& Duarte, 2011). Based on oxygen tolerances of benthic foraminifera Kranner *et al.* (2022) defined ranges as follows: oxic > 1.5 ml/l, suboxic = 1.5–0.3 ml/l, dysoxic = 0.3–0.1 ml/l (corresponding to 67, 67–13 and 13–5 µmol/l O_2). In summary, depending on research object or objective, different definitions of hypoxia are relevant, hindering the universal implementation of generic values.

In aquatic systems, dissolved oxygen concentrations are dictated by physical and biogeochemical mechanisms representing sources (mainly chemical or physical transport) and sinks of oxygen (mainly consumption via respiration, organic matter degradation, oxidation pathways) (Fig. 2). A system imbalance favouring oxygen sinks causes deoxygenation (e.g., Oschlies *et al.*, 2018; Pena *et al.*, 2010; Pitcher *et al.*, 2021). In bottom-waters, the oxidation of organic matter by aerobic remineralisation is the main sink of oxygen. This consumption mechanism is driven by upper ocean primary productivity and associated downward fluxes of nutrients, as well as warming, which increases respiration rates of biota (e.g., Carstensen *et al.*, 2014; Gilbert *et al.*, 2010; Rabalais *et al.*, 2002; Vázquez-Domínguez *et al.*, 2007). In turn, oxygen is dominantly supplied to deep waters by vertical mixing and diffusion. These processes experience negative feedbacks from warming: reduction of ventilation rates and intensification of stratification (e.g., Gilbert *et al.*, 2005; Monteiro & van der Plas, 2006). Increasing temperatures further reduce the solubility of gases (i.e., oxygen storage capacity). In coastal settings, geomorphological features such as sills may affect water circulation and stratification through the isolation of water masses from the open ocean. Additionally, the close proximity to the continent associates coastal waters with increased anthropogenic influences, of which nutrient input by agriculture and industry can play a significant role in driving deoxygenation (i.e., eutrophication; e.g., Conley *et al.*, 2011; Kemp *et al.*, 2005; Rabalais *et al.*, 2010).

3.2 Drought and heatwaves

Extreme weather events have been increasing globally over the last decades (e.g., Bastos *et al.*, 2020; Russo *et al.*, 2015). The frequency, intensity, and extent of heatwaves and droughts is predicted to further accelerate in the near future (e.g., Diffenbaugh *et al.*, 2017; Field *et al.*, 2012; Lehner *et al.*, 2017), with negative effects on imporant sectors of the global economy, (agriculture and energy) (e.g., Brás *et al.*, 2021; Freire-González *et al.*, 2017; Naumann *et al.*, 2015) and human health (e.g., review by Weilnhammer *et al.*, 2021). In recent years, northern and central Europe experienced a series of extremely hot and dry conditions in short succession—2003, 2006, 2012, 2015, 2018, and most recently 2022 (e.g., Bastos *et al.*, 2020; Kornhuber *et al.*, 2019b; Peters *et al.*, 2020; Toreti *et al.*, 2022). Such conditions are unprecedented in the past c. 2000 years (Büntgen *et al.*, 2021), and tightly connected to anthropogenic, global warming (e.g., Kornhuber *et al.*, 2019a; Vogel *et al.*, 2019). The consequences can be devastating, particularly in regions not accustomed to seasonally high temperatures and low precipitation rates such as northern Europe.

Drought is a complex phenomenon, influenced by both physical and biological processes and interactions thereof, specifically precipitation, evaporation, and transpiration. The definition of drought (Fig. 3) differs by the affected compartments of the hydrological cycle (or ecology, socioeconomy), and describes a deviation from normal conditions on local scale: meteorological drought refers to the lack of precipitation; agricultural drought is the deficit in soil moisture; and hydrological drought is the deficiency in streamflow and/or water storages,, and a comprehensive measure representing accumulated responses after propagation through the hydrological cycle (e.g., Tallaksen & Van Lanen, 2004).

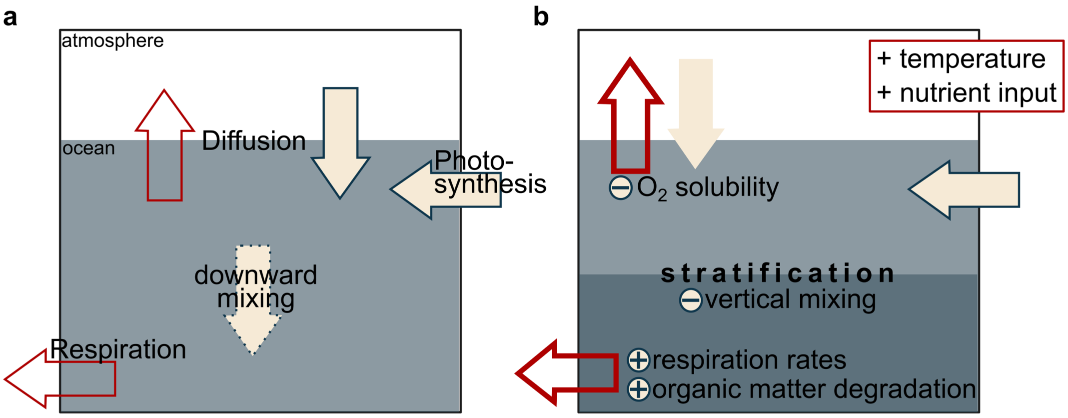


Fig. 2a Simplified schematic of sinks and sources of oxygen to the ocean, and **2b** changes to these mechanisms under warming and eutrophication.

Currently, the ability of Earth system models to accurately render pre- and post-industrial drought patterns and forcing mechanisms appear insufficient (e.g., Büntgen *et al.*, 2021; Gómez-Navarro *et al.*, 2013, 2015). Palaeo-reconstructions of drought events, extending the temporal and spatial scale of instrumental records, are vital to assess the natural variability and reoccurrence patterns of droughts, understand underlying forcing mechanisms and put the severity of current droughts into context. The majority of palaeo-drought records derive from terrestrial records, relying in particular on dendrochronology (e.g., Cook *et al.*, 2015; Steiger *et al.*, 2018). Marine proxies are in use as well, albeit largely restricted to applications in tropical environments (e.g., D'Olivo & McCulloch, 2022; McCulloch *et al.*, 2003; Saha *et al.*, 2018). Annual series with alternations between extreme and 'normal' weather conditions provide ideal conditions for the exploration of new potential proxies based on modern data over annual scales.

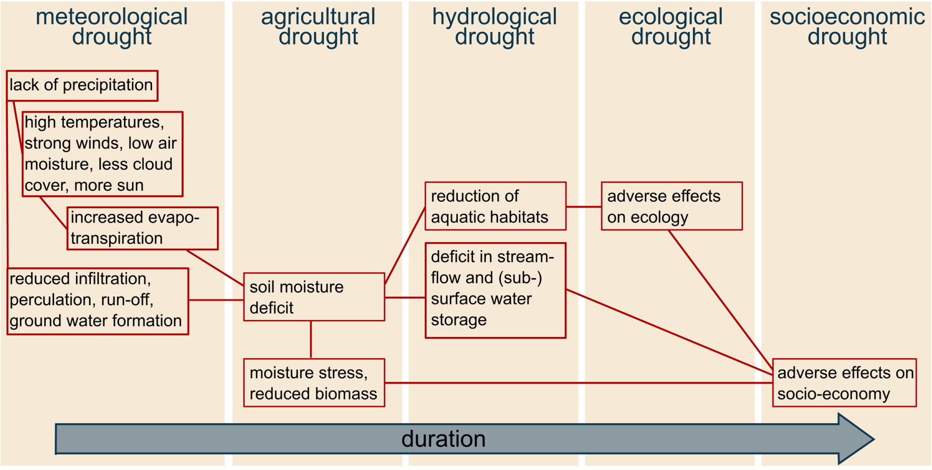


Fig. 3 Interplay between different types of drought (adapted from the Swedish Meteorological and Hydrological Institute, SMHI, 2022).

3.2 Foraminifera as indicators of past and current environmental changes

Foraminifera (Rhizaria) are defined by unicellularity, the possession of a shell (referred to as test), as well as pseudopodia (i.e., protrusions of ectoplasm, largely used for locomotion and feeding) (Adl *et al.*, 2005). The group is primarily known from those representatives that produce a mineralised test (by precipitation of calcium-carbonate or agglutination of foreign particles)—due to their interest for micropalaeontology—, although a wide diversity of foraminifera exists that in fact do not produce a hard structure surrounding their cell (i.e., organic-walled). Conventionally, the taxonomic classification of foraminifera is based on the morphology and composition of the tests (e.g., Cushman, 2013; Tappan & Loeblich, 1988), which were the only observable features of fossil material and extant specimens before the advent of molecular techniques. Molecular phylogenetic studies ranked foraminifera into the classes of Globothalamea (globular, multi-chambered, mineralised tests)—including Textulariida (agglutinated tests) and Rotaliida (calcitic, hyaline tests)—and Tubothalamea (tubular, multi-chambered mineralised tests)—including Miliolida (porcelaneous tests)—, on the one hand, and a paraphyletic group comprising all single-chambered, organic-walled foraminifera ('monothalamids') (Pawlowski *et al.*, 2013). In particular the group of monothalamids has long received little attention in research, due to their low preservation potential in the geologic record and, thus, limited interest to micropalaeontologists. Nevertheless, monothalamids are highly abundant and diverse with long evolutionary history, predating that of mineralised, multi-chambered groups, and putatively include taxa highly relevant as bioindicators (e.g., Pawlowski *et al.*, 2002, 2003, 2008; Sierra *et al.*, 2022; Tsuchiya *et al.*, 2013).

Hard-shelled foraminifera have an extensive, well described fossil record, well resolved evolutionary history, and are used both for biostratigraphy and as indicators of palaeoenvironmental and -ecological conditions (e.g., Katz *et al.*, 2010; Murray, 2006). Palaeo-reconstructions focus, on the one hand, on the diversity of foraminiferal assemblages and presence, absence and/or abundance of taxa, which can be indicative of specific physicochemical environments. On the other hand, the geochemical composition of calcium-carbonate tests can shed light on physical and chemical conditions ambient during the precipitation of the tests. Alongside calcium (Ca) and carbonate (CO_3), other elements (e.g., Mg, Sr, Mn, Ba) are incorporated into the tests during precipitation in relation to availability in the surroundings and/or guided by thermodynamics. Both the concentration of certain trace elements, as well as the ratio of an element's isotopes, can be useful as indicators of environmental conditions (see review by Katz *et al.*, 2010; also e.g., Epstein *et al.*, 1951; McCrea, 1950; Nürnberg *et al.*, 1996; Pearson, 2012). One of the most prominent examples is the use of foraminiferal biogeochemistry as a palaeothermometer—by the tests' oxygen isotope ratio ($\delta^{18}O$) (e.g., Bemis *et al.*, 1998; Shackleton, 1967), or Mg/Ca (e.g., Lear *et al.*, 2000; Nürnberg *et al.*, 1996).

Foraminifera are still abundant in the benthic and pelagic zone of oceans and coastal marine settings today (e.g., Pawlowski *et al.*, 2003; Sen Gupta, 1999). Some taxa occupy even the freshwater and terrestrial realm (e.g., review by Holzmann *et al.*, 2021; see also e.g., Siemensma *et al.*, 2021; Thakur *et al.*, 2022). Interest in extant foraminifera mainly derives from the aim to improve proxy calibrations through modern analogue studies and by gaining a better understanding of biology and biomineralisation mechanisms. Several biological processes ('vital effects') have been shown to potentially influence the precipitation and/or composition of test calcium-carbonates (e.g., Angell, 1980; Bé *et al.*, 1979; Bentov *et al.*, 2009; de Nooijer *et al.*, 2009; 2014b), introducing uncertainties in the relationship between geochemical signals of seawater and test (e.g. Epstein *et al.*, 1951; Nürnberg *et al.*, 1996; Urey *et al.*, 1951; Zeebe *et al.*, 2008). The biomineralisation process of foraminifera is still not fully understood (e.g. Erez, 2003), and several conceptual models have been proposed (e.g., Bentov *et al.*, 2009; Borrelli *et al.*, 2018b; Elderfield *et al.*, 1996; Nehrke *et al.*, 2013), which may differ between species (e.g., de Nooijer *et al.*, 2014b; ter Kuile *et al.*, 1989). A detailed review of calcification strategies is given in de Noojer *et al.* (2014b), as well as Barras *et al.* (2018).

Furthermore, within the last two decades, efforts were made to develop foraminifera-based biotic indices for modern environmental studies and eventually integrate foraminifera into ecological and environmental monitoring programs (e.g., Barras *et al.*, 2014; Bouchet *et al.*, 2021; Jorissen *et al.*, 2018; Parent *et al.*, 2021; Schönfeld *et al.*, 2012). With the advancement and increased accessibility of molecular tools the integration of metabarcoding into biological assessments has become more commonplace (e.g., Cavaliere *et al.*, 2021; Frontalini *et al.*, 2018, 2020; Pawlowski *et al.*, 2018).

3.3 Geochemical cycling

Manganese cycling at the sediment-water interface

Manganese (Mn) is a redox-sensitive element that has received increasing attention as proxy for low oxygen conditions, such as by the manganese-to-calcium ratio (Mn/Ca) in biogenic calcium-carbonates (e.g., Barras et al., 2018; Glock et al., 2012; Groeneveld & Filipsson, 2013; Groeneveld et al., 2018; Guo et al., 2019, 2021; Koho et al., 2015; McKay et al., 2015; Ní Fhlaithearta et al., 2010, 2018; Petersen et al., 2019; Reichart et al., 2003). The trace element is actively involved in biogeochemical cycling and biological processes, including (de-)nitrification (e.g., Aller et al., 1990; Mortimer et al., 2002, 2004). In marine surface sediments, Mn cycling is controlled by oxidation and reduction reactions during bacterial organic matter decomposition, for which bottom- and pore-water oxygen concentrations are a major variable (e.g., Burdige, 1993; Slomp et al., 1997; Sundby & Silverberg, 1985; Thamdrup et al., 1994) (Fig. 4). Organic matter degradation turns to anaerobic pathways after the depletion of oxygen, causing steep vertical redox gradients in pore-waters, including Mn (e.g., Froelich et al., 1979; Soetaert et al., 1996; Sundby, 2006; Wijsman et al., 2001). Manganese (oxyhydr-)oxides (IV)

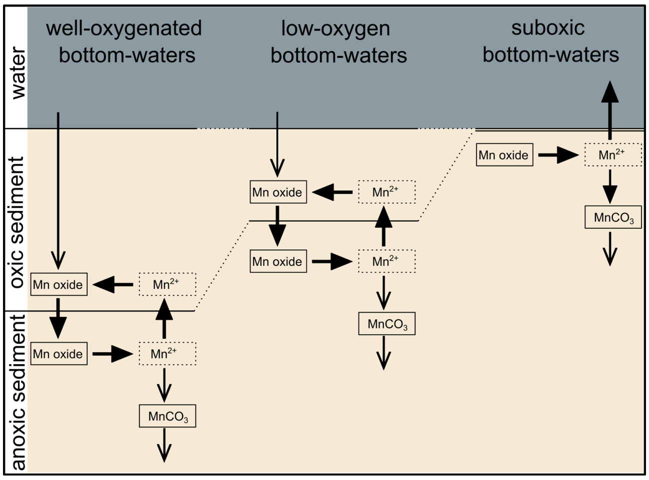


Fig. 4 Schematic representations of the sedimentary manganese cycle under various bottom-water oxygenation conditions (adapted from Slomp et al., 1997).

are reduced to soluble Mn (II, III) under oxygen depletion, which may diffuse upwards until re-oxidisation under oxic conditions (e.g. Burdige et al., 2016; Froelich et al., 1979; Mouret et al., 2009; Thamdrup, 2000; Tribovillard et al., 2006). To a small extent also downward diffusion occurs, and Mn carbonates form under supersaturation in deeper anoxic layers (e.g., Froelich et al., 1979; Tribovillard et al., 2006). Hence, under low-oxygen conditions, dissolved Mn concentrations will be elevated in pore-waters, as dissolved Mn is released but no re-oxidation can take place (Havig et al., 2015; Koho et al., 2015; Middelburg et al., 1987; Scholz et al., 2013; Slomp et al., 1997). In the case of bottom-water anoxia, diffusion of Mn^{2+} into the water-column interrupts sedimentary recycling, leading to low benthic Mn availability (e.g., Koho et al., 2015; Konovalov et al., 2007; Law et al., 2009; Slomp et al., 1997; Sundby & Silverberg, 1985). While both dissolved Mn(II) and Mn(III) are potentially bioavailable (e.g., Madison et al., 2011; Oldham et al., 2015, 2017), only Mn(II) is incorporated in biogenic calcium-carbonates as foraminifera tests (van Dijk et al., 2019). Hence, as the Mn redoxcline varies with the oxygenation state of pore- (and bottom-) waters (Fig. 4), Mn/Ca of foraminifera of specific in-sediment habitats can reflect the system's oxygenation state.

(Coastal) marine barium cycling

Barium (Ba) in seawater is dominantly sourced terrestrially from the dissolved load of rivers, land runoff and groundwater, as well as riverine sediments, where barium occurs as solid (e.g., Wolgemuth & Broecker, 1970). To a much lesser degree, hydrothermal vents also contribute Ba (e.g., Elderfield & Schultz, 1996). Estuarine mixing behaviour modulates dissolved Ba availability in seawater at the transition between fluvial and marine environments, where low to medium salinities drive desorption of Ba^{2+} from fluvial suspended matter by cation exchanges (e.g., Coffey et al., 1997; Hanor & Chan, 1977) (Fig. 5). This close relationship between dissolved barium availability and terrestrial freshwater input has motivated the use of Ba/Ca in planktonic foraminifera (e.g., Bahr et al., 2013; Lea & Boyle, 1991; Mojtahid et al., 2019)—and less commonly also benthic foraminifera (Groeneveld et al., 2018; Ni et al., 2020)—as a freshwater or salinity proxy in coastal settings.

Marine Ba is associated with various solid phases, including carbonates, clays, organic matter, oxyhydroxides, and barite (BaSO4) (e.g., Coffey et al., 1997; Dehairs et al., 1980; McManus et al., 1998). Barite formation is controlled by biologic activity—dissolved Ba is adsorbed or bound to primary producers and forms biogenic barite upon organic matter degradation in the water column (e.g., Dehairs et al., 1980; Martinez-Ruiz et al., 2019)—although the exact mechanisms are still under discussion (see review by Carter et al., 2020; also e.g., Griffith & Paytan, 2012; Paytan & Griffith, 2007; Paytan & Kastner, 1996). The process of adsorption and particulate Ba formation is a function of depth as the material sinks through the water column (e.g., Von Breymann et al., 1992). At depth, the majority of barite dissolves due to undersaturation in bottom-waters and surface sediments (e.g., Chow & Goldberg, 1960; McManus et al., 1998; Paytan & Kastner, 1996). The coupling between benthic barium (e.g., sedimentary barite or biogenic Ba/Ca) and primary productivity is frequently used to estimate palaeo-productivty in open-ocean records (e.g., Carter et al., 2020; Dymond et al., 1992; Mojtahid et al., 2019; Ní Fhlaithearta et al., 2010). The main barium fluxes in coastal and open-ocean settings are summarised in Fig. 5.

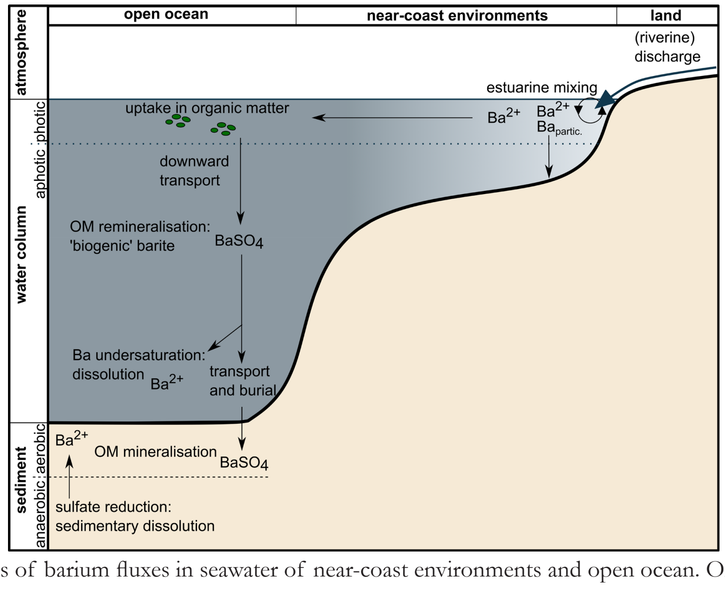


Fig. 5 Schematic representations of barium fluxes in seawater of near-coast environments and open ocean. OM = organic matter.

4 Study sites

Near-coast settings are the focus of this thesis, as those are especially vulnerable in both an ecological, societal and economic sense, and represented by the Santa Barbara Basin off Southern California and three fjords along the Swedish west coast (Gullmar, Havstens and Koljö Fjord). While all coastal, the study areas differ distinctly in their hydrography, bathymetry, geochemistry, marine influences, and timescale of environmental variability. Hence, a wide spectrum of chemical and physical conditions is represented, favourable to the calibration of environmental proxies, and offering insights into potential beneficial or adverse factors to proxy applications by comparison.

Both regions have a long history of palaeoceanographic research, and are monitored contemporarily, providing context of environmental variability on short and long timescales. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) Program has routinely collected quarterly hydrographic data over the past five decades in the Santa Barbara Basin. For the Swedish west coast, detailed hydrographic data sets are offered by the Water Quality Association of the Bohus Coast (Bohuskustens vattenvårdsförbund) and Swedish Meteorological and Hydrological Institute (SMHI; Sveriges meteorologiska och hydrologiska institut).

4.1 Santa Barbara Basin

The Santa Barbara Basin (Fig. 6), continental Southern California Borderland, USA, Eastern Pacific, is a shallow underwater plane of max. 627 m water depth. It is confined by the Santa Barbara coastline northwards, Channel Islands southwards, as well as two tectonic sills towards the open ocean in the East and West (475 m and 200 m water depth, respectively; Hülsemann & Emery, 1961). The sills restrict the exchange of deep basin waters with the open ocean. Water exchanges occur predominantly during spring, when waters of the California Current System (i.e., eastern boundary current of North Pacific) switch from a poleward to equatorward directionality (Harms & Winant, 1998; Huyer, 1983; Lynn & Simpson, 1987) and flush the basin through the western sill (e.g., Bograd *et al.*, 2002; Reimers *et al.*, 1990; Sholkovitz & Gieskes, 1971). Water renewal events are documented and exchange mechanisms discussed in detail by e.g., Bograd *et al.* (2002), Goericke *et al.* (2015), Harms & Winant (1998) and Reimers *et al.* (1990). Below sill level, dissolved oxygen concentrations decrease distinctly (to below 45 µmol/l; e.g., Bograd *et al.*, 2002; Komada *et al.*, 2016). Both, restricted water circulation and high oxygen consumption rates, promote the low-oxygen conditions (e.g., Emmer & Thunell, 2000; Kienast *et al.*, 2002; Reimers *et al.*, 1996; van Geen *et al.*, 2003). Further, water masses introduced during water renewal events originate from the eastern North Pacific oxygen minimum zone, where oxygen concentrations are generally low with 18–45 µmol/l O_2 (e.g., Bograd *et al.*, 2002; Helly & Levin, 2004; Reimers *et al.*, 1990). The deep-basin waters of the Santa Barbara Basin are almost consistently characterised by $[O_2] < 3$ µmol/l (e.g., Bernhard *et al.*, 1997, 2006a). Predicted reductions in frequencies and rates of water exchanges in the future may lead to permanently anoxic bottom-waters (Goericke *et al.*, 2015).

Due to the low oxygen conditions, and consequently shallow oxygen penetration depth, pore-water Mn concentrations are low in surface sediments of the Santa Barbara Basin (Ivanochko & Pedersen, 2004; Reimers *et al.*, 1996). Manganese concentrations are comparable to such in sediments within or underlying oxygen minimum zones (< 20 µmol/l Mn^{2+}; e.g., Koho *et al.*, 2017; Law *et al.*, 2009; van der Weijden *et al.*, 1999), and significantly lower

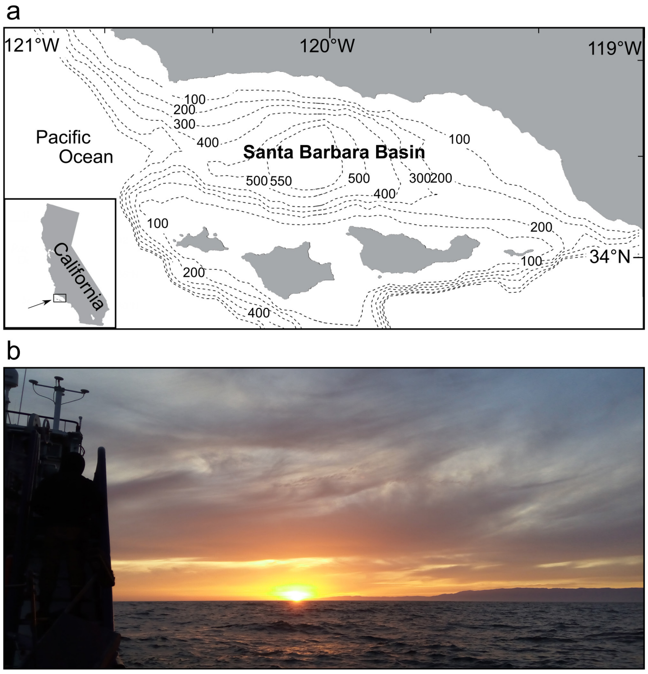


Fig. 6a Geographical location and bathymetry of the Santa Barbara Basin. **6b** Evening view of the Santa Barbara Basin from R/V Robert Gordon Sproul (foto credit: Sha Ni).

than in sediments of estuarine settings (up to 500 μmol/l Mn^{2+}; e.g., Goldberg *et al.*, 2012; Sulu-Gambari *et al.*, 2017).

4.2 Gullmar Fjord, Havstens Fjord, Koljö Fjord

Gullmar-, Havstens- and Koljö Fjord (Fig. 7), Swedish west coast, are silled fjords whose hydrography is determined by influences of marine waters of the Skagerrak, brackish waters of the Baltic Sea and freshwaters deriving from the adjacent land (i.e., land runoff and river input). In Gullmar Fjord, freshwater is dominantly supplied by the river Örekilsälven (Fig. 7c). The fjords' water-columns are strongly salinity stratified, with halocline depths being governed by topography and particularly sill depth. Stratification and limited water exchanges with the open sea create conditions benefitting the development of (seasonal) bottom-water oxygen deficiency.

Water exchange events are largely determined by seasonal water circulation and wind patterns, associated with the North Atlantic Oscillation (NAO), which is the main factor of influence on Scandinavian climate (Chen & Hellström, 1999; Hurrell, 1995). Negative phases of the NAO—defined as the normalised sea-level pressure difference between the Azores islands (high) and Iceland (low)—favour upwelling and deep-water exchanges in the fjords (west- and eastward, respectively). Conversely, prolonged positive phases are associated with severe seasonal hypoxia (Filipsson & Nordberg, 2004a; Nordberg *et al.*, 2000). Previous studies suggested not only a causal relationship between the NAO pattern and the frequency and intensity of water exchange events (Polovodova Asteman & Nordberg, 2013), but also the distribution of phytoplankton biomass and occurrences of blooming events (Belgrano *et al.*, 1999; Lindahl *et al.*, 1998). Both, restricted ventilation and increased primary production, with associated organic matter degradation rates, constitute oxygen sinks.

The first documentation of hypoxic bottom-waters in Gullmar Fjord dates back to February 1890 (Pettersson & Ekman, 1891), followed by more frequent hypoxic episodes during the 20th and early 21st century (e.g., Filipsson & Nordberg, 2004a; Polovodova Asteman & Nordberg, 2013) (Fig. 5b). Most recently hypoxic conditions persisted for several months in the end of 2017. Choquel *et al.* (2021) recorded non-detectable oxygen in bottom-waters in Nov. 2017. In Havstens Fjord low-oxygen conditions occur more frequently, and the bottom-waters of Koljö Fjord are almost permanently sub- or anoxic (e.g.,

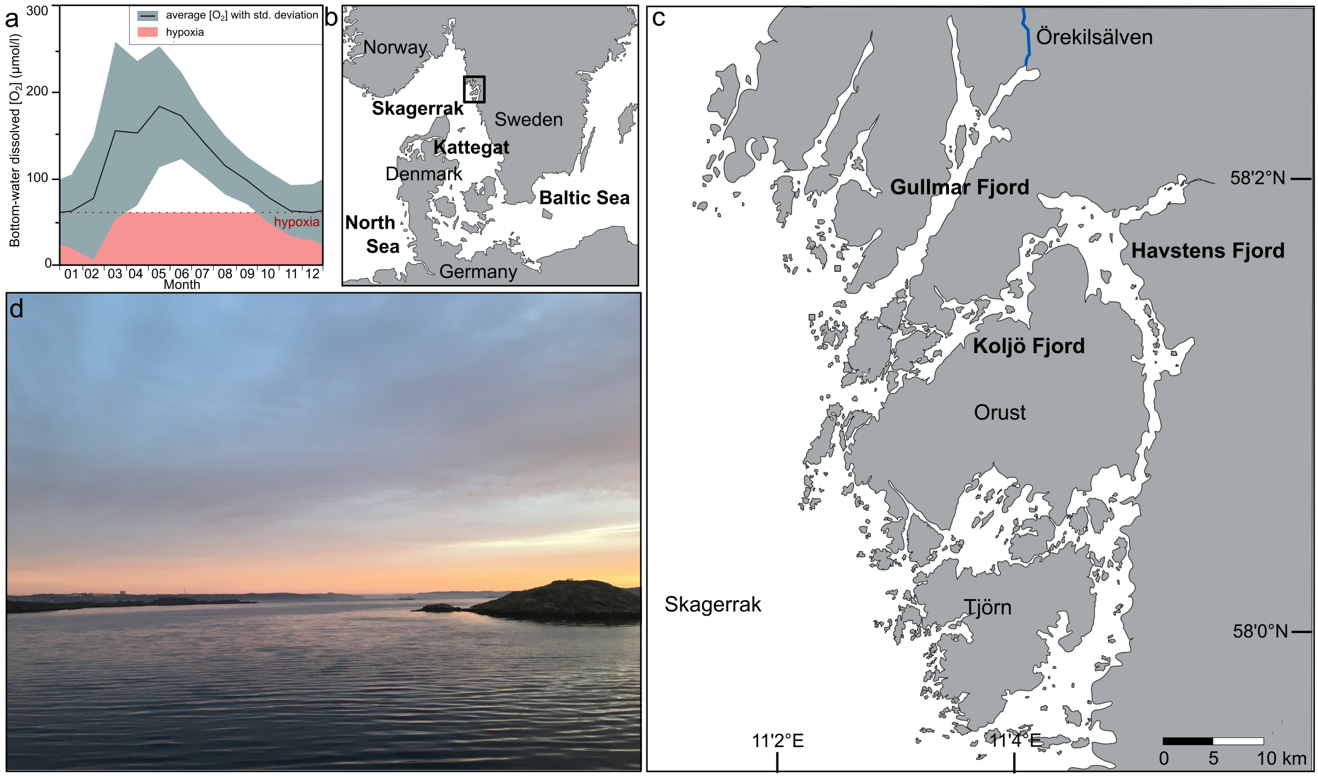


Fig. 7a Compiled average bottom-water oxygen concentration in Gullmar Fjord (Alsbäck site) across a year, based on monitoring data from 1980 to 2014 (SMHI, 2022). **7b** Geographic location of the study area in the context of northern Europe (rectangle marks area of 7c). **7c** Location of the studied fjords on the west coast of Sweden. **7d** Evening view of Gullmar Fjord.

Gustafsson & Nordberg, 1999, 2000; Nordberg *et al.*, 2001).

Foraminiferal studies of Gullmar Fjord date back as early as the end of the 19th Century, with Goës (1894) documenting for instance the occurrence of *Bulimina marginata*, one of the candidate species of this thesis. More recent assemblage assessments of the three fjords in focus here recorded communities of distinct diversity and composition each (e.g., Choquel *et al.*, 2021; Gustafsson & Nordberg, 1999, 2000, 2001), in adaptation to the respective conditions. The highest diversity and abundance were found in Gullmar Fjord, whereas sediments of the deep basin in Koljö Fjord typically only contain few specimens representing a single genus (*Elphidium*).

5 Methods

5.1 Field data collection

The four projects conducted within this thesis rely on the field collection of surface-sediment samples in a spatial and/or temporal sampling approach, in order to survey responses in modern foraminiferal geochemistry or communities to a range of environmental conditions.

Sediment cores were collected with an Ocean Instruments MC800 multicorer or GEMAX® twinbarrel corer (Oy Kart AB, Finland). This method of sampling allows the collection of cores of up to 70 cm length preserving the original sediment position and keeping the sediment-water interface undisturbed. Accordingly, sub-samples can be taken with confidence of their original positioning in the sediment column, and environmental conditions of surface-sediment pore-waters can be measured practically *in situ*.

Several replicate cores were taken—in multiple deployments in case of the twinbarrel corer—to provide sufficient material for the analytical purposes within the scope of the individual projects: (I) foraminiferal analyses (geochemistry, metabarcoding), (II) solid- and dissolved phase trace-element geochemistry, (III) recording of physicochemical parameters. As benthic foraminifera typically inhabit the first few cm of the sediment, and only currently living foraminifera were of interest to this project, the focus of all analyses lay on the top 1–2 cm of the sediment. Nevertheless, dissolved and solid trace-elemental profiles were collected down-core in some cases (Paul *et al.*, in prep.; Papers II–III). Environmental parameters—salinity, temperature, dissolved oxygen concentrations—of the water-column and bottom-waters at the time of sampling were recorded by CTDO$_2$, and allowed to assess, among others, the current state of the water exchange cycles in the study regions.

(I) To retrieve sediments for foraminiferal analyses core-tops were subsampled using a core-splitting device (top 1–2 cm in 0.5–1 cm intervals). Sediment samples intended for biogeochemistry were treated with CellHunt Green (CHG; Saterah Biotech, Oregon, USA) or Cell Tracker^{TM} Green (CTG) with CMFDA (5-Chloromethylfluorescein Diacetate) and dimethyl sulfoxide (DMSO), incubated and finally preserved by adding approximately the samples' volume ethanol—a method for the assessment of foraminifera viability (e.g., Bernhard *et al.*, 2003, 2006b). Both, CHG and CTG, are compounds that are modified to be fluorescent by active hydrolytic enzymes in cells (i.e., non-specific esterases). As the involved enzymes degrade rapidly after cell death, the method is highly precise as live-dead assay. A bright green fluorescence in specimens during later observation under a fluorescence-stereomicroscope is interpreted as the specimens having been alive at the time of sampling (Fig. 8). 'Living' foraminifera of interest were wet-picked from the >100 µm fraction of the sediment samples, and stored dried for further analyses. Sediment samples intended for analyses of environmental DNA were taken using sterile equipment, which was cleaned with ethanol after each use to avoid potential cross-contamination between samples. The material was stored in sterile plastic containers and kept frozen until proceeding to the next processing steps (i.e., DNA extraction, amplification, sequencing).

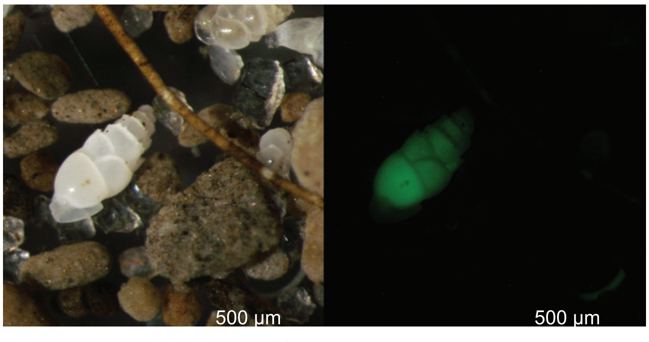


Fig. 8 Microscope view of CTG-labelled *Bulimina marginata* specimen under normal (left) and fluorescent (right) light.

(II) Samples for sediment geochemistry were acquired by sectioning, and for pore-water geochemical analyses by either sectioning and centrifuging, or using Rhizons^{TM} (method described in Jokinen *et al.*, 2020). Measuring of trace-element availability in solid and dissolved state in the environment of the studied foraminifera aids linking biogenic and environmental trace-element signals, and, thus, validating empirical geochemical proxy relationships. Under the assumption of trace-element concentrations during the time of sampling representing conditions ambient during foraminiferal chamber calcification, the distribution dynamics between pore-water and calcium carbonate of the trace element in question can be established by the following formula (i.e., partition coefficient; e.g., Henderson & Kracek, 1927; Morse & Bender, 1990):

$$D_{\mathrm{Mn}} = (\mathrm{Mn/Ca})_{\mathrm{foram}}/(\mathrm{Mn/Ca})_{\mathrm{pore\text{-}water}}$$

(III) Profiles of dissolved oxygen concentration and pH in bottom- and pore-waters were recorded at sub-millimetre resolution using clark-type micro-electrodes, connected to a motor and multi-meter (Unisense; Fig. 9). The measurements were performed directly in the sediment cores to a depth of up to 2 cm, within a temperature-controlled room set to *in situ* bottom-water conditions as inferred from CTDO$_2$ data. The oxygen penetration depth is of particular interest for the understanding of the Mn/Ca proxy relationship. The indirect coupling between bottom-water oxygenation and foraminiferal Mn/Ca is linked by the direct control of bottom-water oxygen availability on the penetration depth of oxygen into the sediment, in turn determining pore-water reduction-oxidation (redox) chemistry. On the other hand, pH is a factor of interest for its role in the sea-waters calcium carbonate saturation state (Zeebe & Wolf-Gladrow, 2001), which, if decreasing, may be detrimental to calcifying organisms such as foraminifera (e.g., Berkeley *et al.*, 2007; Kroeker *et al.*, 2010; Uthicke *et al.*, 2013). Thus, pore-water pH should be considered when assessing changes in foraminiferal abundances.

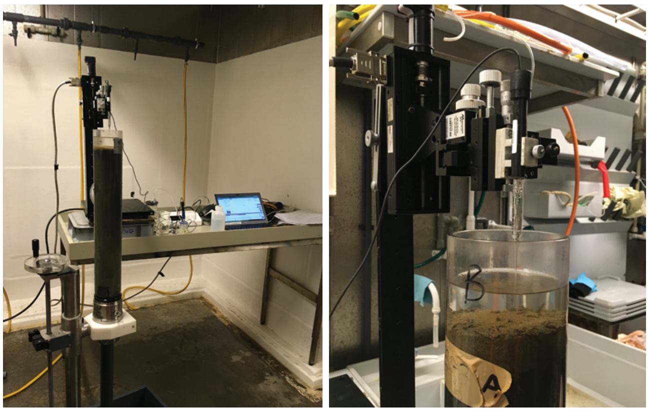


Fig. 9 Fotos showing set-up of micro-profiling equipment and sediment core in overview (left) and zoom-in showing the oxygen sensor and core-top (right).

5.2 Foraminifera species of special interest

Nonionella stella (T6)

Nonionella stella Cushman & Moyer, 1930 (Fig. 10a) is a typical morphospecies of the Santa Barbara Basin, representing one of the most abundant taxa there (e.g., Bernhard *et al.*, 1997). It has been described to be cosmopolitan in distribution (Asteman & Schönfeld, 2016). However, molecular studies highlighted that several taxa, identified as *N. stella* by morphological criteria, are representing distinct phylotypes (Deldicq *et al.*, 2019), necessitating re-evaluations of previous occurrence records. *Nonionella stella* is tolerant to hypoxia and anoxia, and used as indicator of such in the Santa Barbara Basin (e.g., Bernhard *et al.*, 1997), but may also occur in well-oxygenated conditions (see Asteman & Schönfeld, 2016 and references therein). This tolerance is conceivably explained by the active use of kleptoplasts in trophic pathways proposed for *N. stella* (e.g., Bernhard & Bowser, 1999; Grzymski *et al.*, 2002) and demonstrated by transcriptomics (Gomaa *et al.*, 2021), possibly aiding inorganic nitrogen and sulfate assimilation (Grzymski *et al.*, 2002). Kleptoplasty refers to the ability to ingest and maintain chloroplasts in 'husbandry' (see e.g., Bernhard, 2003; Bernhard & Bowser, 1999; Clark *et al.*, 1990; Grzymski *et al.*, 2002; Jauffrais *et al.*, 2018). Further, other representatives of the same genus have been shown to use denitrification as alternative, anaerobic respiratory pathway (Piña-Ochoa *et al.*, 2010; Risgaard-Petersen *et al.*, 2006). The project of this thesis presents the first study exploring the species' trace-elemental composition (Paper I), but it has been used in isotope-based palaeoceanographic reconstructions previously (Altenbach *et al.*, 2012; Kawahata, 2019).

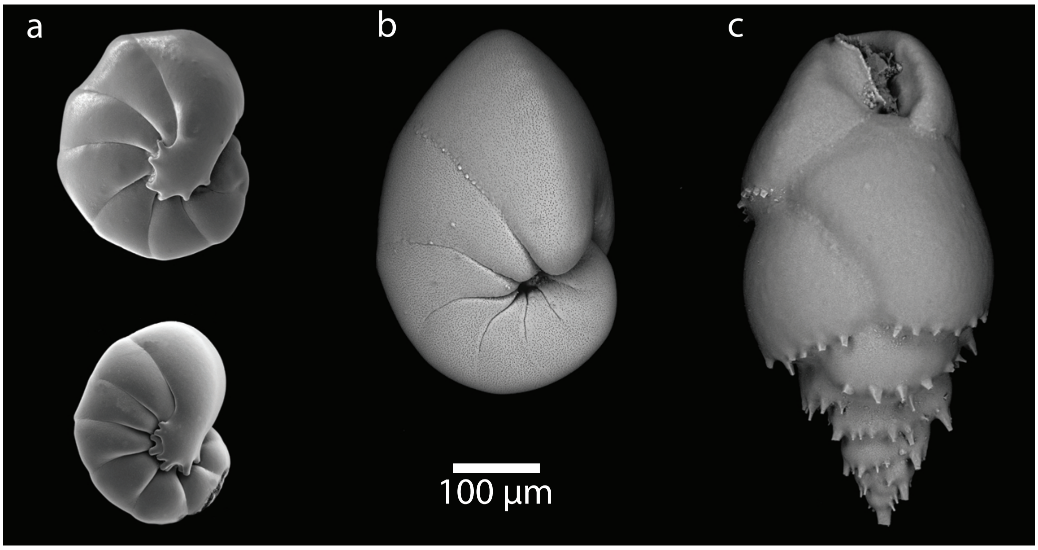


Fig. 10 Scanning electron microscope images of benthic foraminifera species studied in this thesis. **10a** *Nonionella stella* from the Santa Barbara Basin. **10b** *Nonionellina labradorica* from Gullmar Fjord. **10c** *Bulimina marginata* from Gullmar Fjord.

Nonionellina labradorica (T5)

Nonionellina labradorica (Dawson, 1960) (Fig. 10b) is a fully-marine, cold-temperature species common in sublittoral environments of the Arctic and North Atlantic. It has a deep infaunal in-sediment distribution, with an estimated average living depth of 4 cm (e.g., Alve & Bernhard, 1995; Corliss, 1991; Koho *et al.*, 2017), although it is found shallower in Gullmar Fjord (c. 2 cm depth; Choquel *et al.*, 2021). Generally, *N. labradorica* is common in Gullmar Fjord, although its abundance has been decreasing since the early 1980s (Filipsson & Nordberg, 2004b). As *N. stella*, *N. labradorica* was shown to harbour diatom-derived kleptoplasts in its cytoplasm (Jauffrais *et al.*, 2019). Although initially the involvement of photosynthetic pathways has been suggested (Cedhagen, 1991), more recently this hypothesis was challenged and instead a possible role of the kleptoplasts in ammonium or sulfate assimilation proposed (Jauffrais *et al.*, 2019). The species is frequently used as environmental indicator in palaeo-reconstructions (e.g., Perner *et al.*, 2015; Seidenkrantz *et al.*, 2013), and considered indicative of oxic conditions (e.g., Fontanier *et al.*, 2014) and high organic matter availability (e.g., Corliss, 1991), as well as geochemical proxy for salinity and temperature (based on δ^{18}O, e.g., Shetye *et al.*, 2011; or Mg/Ca, e.g., Skirbekk *et al.*, 2016).

Bulimina marginata

Bulimina marginata d'Orbigny, 1826 (Fig. 10c) is an open-marine benthic species that occurs in deep-sea environments as well as on the continental shelf. Next to having a wide distribution, the species is easily cultured in laboratory conditions and therefore considered to be a good candidate for (trace-element-based) proxy calibrations (e.g., Barras *et al.*, 2009, 2018; Bernhard *et al.*, 2004; Havach *et al.*, 2001; Hintz *et al.*, 2006a, 2006b; McCorkle *et al.*, 2008; Wit *et al.*, 2012). Besides trace-element concentrations, also the distribution of trace elements in test walls of individual specimens have previously been investigated (van Dijk *et al.*, 2019). Abundance of *B. marginata* is typically highest under well-oxygenated conditions, although the species does tolerate hypoxia and even anoxia (e.g., Alve, 2003; Alve & Bernhard, 1995; Bouchet *et al.*, 2018; Ernst *et al.*, 2005; Filipsson *et al.*, 2010). Specifically, it has been observed to both reproduce (Alve & Bernhard, 1995) and calcify new chambers (Nardelli *et al.*, 2014) under anoxic conditions.

5.3 Geochemical micro-analyses

Geochemical micro-analysis techniques enable high spatial resolution *in situ* measurements of trace-elements (and isotope compositions) in individual foraminifera specimens. The increased accessibility and use of micro-analytical techniques enabled important advances in the understanding of foraminiferal trace-element incorporation, as well as highlighted current short-comings in our knowledge of such mechanisms including the role of vital effects (e.g., de Nooijer *et al.*, 2014a; Evans *et al.*, 2018; Hathorne *et al.*, 2009, 2018). In projects of this thesis, we made use of several micro-analytical techniques to infer trace-element ratios in individual chambers: (I) Laser-ablation Inductively Coupled Mass Spectrometry (LA-ICP-MS) and (II) Secondary Ion Mass Spectrometry SIMS); and distributions across specimen cross-sections: (III) synchrotron-based X-ray Fluorescence (XRF). Further examples of such techniques, not used here, include Electron Microprobe, Electron Backscatter Diffraction, or Raman spectroscopy.

Micro-analytical methods—as opposed to traditional whole-shell and several-specimen analyses—are crucial when only a limited number of specimens is available and/or only specific test regions are of interest. For the investigation and calibration of foraminiferal trace-element proxies we were interested in chambers precipitated under specific conditions (i.e., in close temporal proximity to the conditions measured during sampling), as well as signals from a succession of chambers for assessing biogeochemical variability on a temporal scale. Further advantages of the used methods include the possibility of assessing chemical heterogeneity on an inter- and intra-specimen level (e.g., Glock *et al.*, 2019; van Dijk *et al.*, 2019), and identifying potential contaminations, such as coatings on the inner or outer wall surface or even within pore spaces (e.g., Ni *et al.*, 2020; Pena *et al.*, 2008). Finally, some micro-analytical methods are non- or less destructive, allowing analyses of fragile samples, or re-analysis for other purposes.

All here named techniques, except for LA-ICP-MS, require the embedding of samples in epoxy, and exposure of the areas of interest on the mount surface (i.e., foraminifera test cross-section). The quality of embedding can hamper the precision of analytical results significantly. To date no standardised embedding protocol has been published describing reliable embedding procedures for chambered micro-organisms such as foraminifera.

Epoxy embedding

The main challenge of embedding foraminifera is the filling of the specimens' chamber cavities, as epoxy is viscous, the chambers typically air-filled after being stored dry, and the only opening in tests through which epoxy can penetrate efficiently the aperture. Complete filling of tests is, however, crucial to achieve a smooth sample surface when exposing the specimens to cross-section for analyses (particularly important for SIMS), to avoid breakage of chamber walls during polishing and the adherence of contamination in unfilled (micro-)spaces.

We developed a step-wise embedding protocol, which achieves complete filling of foraminifera chambers. Two essential components of this procedure are (I) the pre-treatment of tests to remove dried cell material on the inside of chambers, and (II) a step-wise filling of specimens by epoxy of increasing viscosity.

In specimens sampled living, the removal of cell material is essential as it can hinder the successful distribution of epoxy throughout the chamber cavities. Furthermore, the influence trace elemental signals deriving from organic material on the measurements can be avoided. For our 'live' specimens we chose bleaching with 5% NaOCl (e.g., Lea *et al.*, 1999; Mashiotta *et al.*, 1999). Subsequently we submerged the tests in acetone, and used vacuum treatment to drive out the air within chambers and aid the replacement with the solvent. The acetone is then replaced by an epoxy-acetone mixture in two steps (ratios 1:2 and 2:1, respectively), and finally by pure epoxy. Mixing acetone with epoxy serves the purpose of decreasing the liquid's viscosity to a degree that facilitates penetration into foraminiferal tests. The advantages of using acetone as a solvent are its dehydration capabilities (water hinders the polymerization of epoxy resin), and it lowering the epoxies' viscosity without being detrimental to its chemical structure (if removed prior to curing; Loos *et al.*, 2008). Finally, the epoxy-filled specimens can be fully embedded in a mold fitting the machines' specifications planned to be used for analyses. A comparison of embedding results without and with these two steps is shown in Fig. 11, highlighting the improved filling capacity and reduction in sample surface relief.

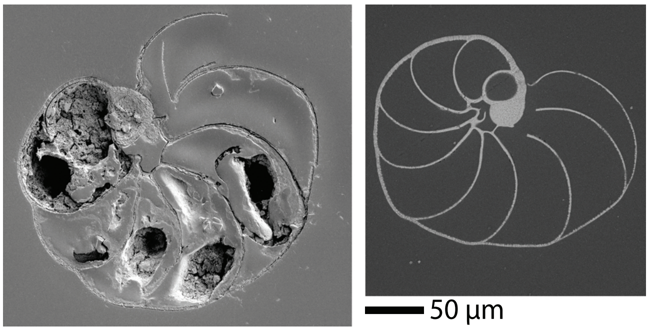


Fig. 11 SEM images of two specimens of *Nonionella stella* in cross-section, embedded in epoxy without (left) and with (right) prior bleaching and step-wise filling procedure.

Laser-ablation Inductively Coupled Plasma Mass Spectrometry

Laser-ablation Inductively Coupled Plasma Mass Spectrometry is nowadays a standard technique for measuring trace-element ratios in foraminifera. Briefly, a short-pulsed high-power laser beam is focused on a sample region of interest (e.g., chamber wall), ablating sample material and transforming it into an aerosol, which is transported from the airtight sampling chamber through a transport line to the ICP-MS detector, where the elemental composition is measured. Several trace elements can be measured simultaneously. Quantification relies on reference material analysed under the same conditions as the sample itself.

Measurements are acquired by ablating chamber walls from the outside to the inside, providing a 2D signal with the possibility of excluding specific profile segments during data processing (i.e., contamination-associated signal parts; e.g., Guo *et al.*, 2019; Koho *et al.*, 2017). Laser-ablation is a destructive process, leaving a hole in the targeted chamber wall, or, in some cases, causing the entire chamber to break. Hence, re-analysis of the same chamber is not possible.

Samples require minimal preparation, as only fixing on a flat surface fitting into the sample chamber is technically required for analyses. Furthermore, LA-ICP-MS systems are widely available and accessible, and analysis costs are comparatively low. This method was used for the majority of our trace-elemental analyses (Papers II–III).

Secondary Ion Mass Spectrometry

Secondary Ion Mass Spectrometry is an alternate method for measuring element compositions of calcite tests (e.g., Allison & Austin, 2003; Bice *et al.*, 2005; Glock *et al.*, 2012; Glock *et al.*, 2016; Livsey *et al.*, 2020; McKay *et al.*, 2015; Sano *et al.*, 2005). Briefly, a focused primary ion beam is directed onto the surface of a sample mount, transforming the targeted material into secondary ions. For measuring ions of positive charges, such as Mn, Mg or Sr, a negative primary beam from a $^{16}O^-$ source ("duo-plasmatron") is used. The secondary ions are extracted by applying voltage in an electrostatic analyser or mass filter, magnetically separated by their mass and eventually introduced into an ion counting system (mono- or multicollector). Changing the source to one of positive charge enables the measurement of stable isotope compositions, such as oxygen or carbon (e.g., Balestra *et al.*, 2020; Kasemann *et al.*, 2009; Kozdon *et al.*, 2013; Livsey *et al.*, 2020)—a distinct advantage of SIMS compared to other micro-analytical techniques. Individual elements (or isotopes) of interest are measured in succession. Like for LA-ICP-MS, reference material is needed to quantify the geochemical signals.

Compared to LA-ICP-MS, SIMS is less frequently used for trace-element analyses of foraminifera, being a more complex system, costly in acquisition, maintenance, and operation, and time-consuming in use, both pre- and during analyses. One time-consuming but important aspect is the need for epoxy-embedding the samples, as SIMS analyses require a smooth and even samples surface (< 100 nm roughness) in order to reach high precision in the measurement of element concentrations, as well as avoid distortion, shadowing or charging (e.g., Kita *et al.*, 2009). As parts of our sample material was very fragile and not able to withstand the ablation by laser long enough to produce a quantifiable signal (i.e., *N. stella*; Paper I), epoxy-embedding for structural support and analyses by SIMS were a good alternative. To guide analyses, scanning electron microscope imaging (SEM) of the to-be-investigated specimens is essential.

Synchrotron-based X-ray Fluorescence mapping

Synchrotron-based XRF analyses are a state-of-the-art technique in foraminiferal geochemical analyses, allowing the micro- and nano-scale mapping of trace-element concentrations (e.g., De Giudici *et al.*, 2018; Munsel *et al.*, 2010; Ni *et al.*, 2020; van Dijk *et al.*, 2019). It is an imaging technique based on X-ray excitation and fluorescence emission of elements. The relative intensity ratios can be converted to semi-quantitative concentration ratios (percentage mass and molar mass) by taking the measurement geometry, the XRF yields and detection efficiencies of the XRF spectral lines into account (Jenkins, 1995). Samples require embedding in mounts, and polishing to cross-section. Elemental concentrations and distributions are mapped on the mount surface with several tens of μm information depth.

We used synchrotron-light based XRF to investigate biomineralization patterns in foraminifera, by imaging the micro- and nano-scale distribution of Mn in foraminiferal chamber walls (Paper I and II). The method allows inferences on the co-location of trace-elements, important for the understanding of trace element incorporation by foraminifera. For instance, one of the assumptions trace-element-based proxies rely on is the active incorporation of elements of interest in the calcite lattice, as opposed to the adsorption and secondary precipitation in distinct phases on the test surfaces. In Fig. 12 the co-localisation of Mn within the high-Ca intensity area, representing the foraminiferal chamber wall, is highlighted. Further, information of elemental distribution patterns can be drawn (e.g., heterogeneity, banding), which may shed light on biomineralization processes and/or environmental variability throughout the growth of tests.

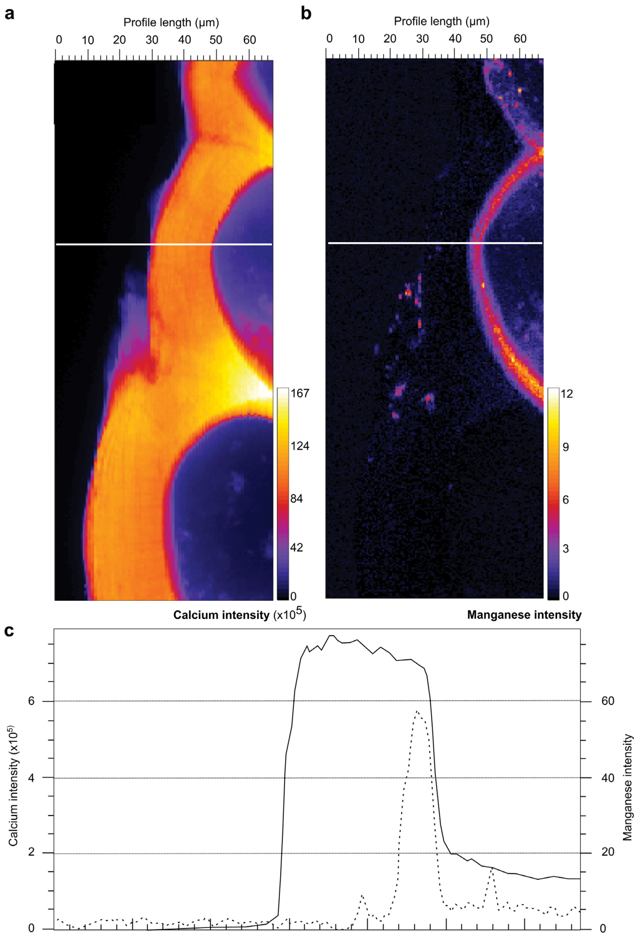


Fig. 12 Exemplary profile selection from XRF maps. **12a–b** XRF 'zoom-in' maps of chamber wall portions showing distribution of Ca (a) and Mn (b). **12c** Plotted intensity profiles of Ca (straight line) and Mn (dashed line) along selected profile (indicated by vertical white line in a and b).

5.4 Molecular techniques: Metabarcoding and barcoding

Metabarcoding is a molecular tool for the assessment of communities based on amplification and high-throughput sequencing of DNA in mixed samples, followed by bioinformatic data processing. Taxonomically informative DNA barcodes are used for the identification of sequences; for foraminifera these are fragments of the hypervariable region of the small subunit (SSU) rDNA, which is known to have rapidly evolving ribosomal genes (e.g., Cordier *et al.*, 2019; Pawlowski & Lecroq, 2010; Thakur *et al.*, 2022).

We extracted the total DNA of our sediment samples with two different extraction kits, respectively, using manufacturer's instructions: DNeasy PowerMax Soil Kit (Qiagen) and NucleoSpin Soil Minikit (Macheret Nagel). Currently several commercial kits for the extraction of DNA from sediment and soil samples are available, utilizing a variety of sediment volumes (0.25–10 g) and presenting different material and chemical properties (review by Lear *et al.*, 2018). It is well established that extraction kit type can affect quantity and quality of extracted DNA, as well as inferred alpha- and beta diversity (e.g., Carrigg *et al.*, 2007; Hestetun *et al.*, 2021; Pearman *et al.*, 2020). However, to date extraction kit use has not been standardised (Pawlowski *et al.*, 2022), and is often guided by availability and/or costs. In all commercial kits, extraction comprises the following general steps: sample homogenisation (chemical and/or physical), cell lysis, inhibitor removal, DNA binding and washing, elution. The success of the extraction process, indicated by nucleic acid concentrations, can be tested by NanoDrop microvolume spectrophotometry.

Environmental DNA refers to the total DNA pool found in the environment, deriving from whole individuals (if specimen size is small or sample volume large) and extracellular DNA, of living and potentially (recently) dead organisms (Corinaldesi *et al.*, 2018). Still, specific organisms can be targeted using primers during the DNA amplification step. Here we used the foraminifera-specific primers s14F1 (AAGGGCACCACAAGAACGC; Pawlowski, 2000) and s15r (CCACCTATCACAYAATCATG; Lejzerowicz *et al.*, 2014). Amplification results were tested by gel electrophoresis. Following the first, the second amplification, library constructions and Illumina MiSeq sequencing were performed externally at the ANAN platform (SFR QUASAV, INRAE Beaucouzé, France), which delivered demultiplexed, paired-end sequencing data.

Data derived from high-throughput sequencing requires stringent processing with bioinformatical tools: Reads were trimmed to remove forward and reverse primers, and following processed following the 'dada2' protocol (adapted from https://benjjneb.github.io/dada2/tutorial.html). This pipeline comprises the filtering of reads for length and quality, denoising by merging paired reads, construction of a sequence table clustering variants, and removal of chimeras. It delivers a sequence table of so called 'amplicon sequence variants' (ASV), which present a reliable and comprehensive representation of biological variation of single DNA sequences, albeit not necessarily corresponding to species (e.g., Callahan *et al.*, 2017; Eren *et al.*, 2013). The ASVs were taxonomically assigned using VSEARCH v. 2.18.0 (Rognes *et al.*, 2016) and a partially self-generated reference database (courtesy of David Singer and Magali Schweizer) comprising sequences of specimens collected from the studied fjords and other regions, as well as barcodes from GenBank. As molecular- and morphological species concepts do differ (e.g., review by Pawlowski *et al.*, 2014), we verified taxonomic assignment of each ASV manually by sequence alignment and comparisons with reference databases. The reads of ASVs that could be confidently assigned to the same taxon were pooled.

Reference databases comprise sequences acquired by barcoding, which refers to the taxonomic identification of species by sequencing of diagnostic markers in individual specimens (Hebert *et al.*, 2003). The pool of published reference sequences for the taxonomic identification of foraminiferal DNA is growing, albeit still lacking behind those available for animals, plants and fungi (Pawlowski & Holzmann, 2014). Ideally, single-cell barcoding is combined with morphological characterisations (such as image documentation and/or descriptions) of the species, in an effort to ultimately unite morphological and molecular species concepts. (e.g., Bird *et al.*, 2020; Pawlowski & Holzmann, 2014; Schweizer *et al.*, 2005).

6. Summary of Papers: Results

My thesis comprises four papers, summarised below and appended later. The distribution of work contributing towards each paper is given in Table 1 (positioned after the concluding section).

Paper I

Foraminiferal Mn/Ca as Bottom-Water Hypoxia Proxy: An Assessment of ***Nonionella stella*** **in the Santa Barbara Basin, USA.**
Brinkmann, I., Ni, S., Schweizer, M., Oldham, V. E., Quintana Krupinski, N. B., Medjoubi, K., Somogyi, A., Whitehouse, M. J., Hansel, C. M., Barras, C., Bernhard, J. M., & Filipsson, H. L. (2021) Paleoceanography and Paleoclimatology, 36, e2020PA004167.

This paper presents a comprehensive in-field investigation of Mn incorporation by foraminifera under low-oxygen conditions, on the example of the low-oxygen tolerant species *N. stella*. Three suboxic (bottom-water oxygen concentrations < 10 µmol/l) sites within the Santa Barbara Basin, USA, were studied to explore the relationship between foraminiferal Mn/Ca and bottom-water oxygenation at the lower end of 'low-oxygen' conditions.

Foraminiferal Mn/Ca was measured by SIMS in a micro-analytical approach focusing on the most recently formed chambers of *N. stella* specimens, and ambient geochemical conditions were constrained by measurements of bottom- and pore-water Mn concentrations. The analysis was complemented with synchrotron-based XRF nano-imaging of the distribution of Mn and Ca in *N. stella* specimens (Fig. 13).

Our results confirmed that the trend between bottom-water oxygenation and foraminiferal Mn/Ca is of opposite directionality under dominantly suboxic vs. hypoxic conditions (< 10 µmol/l and < 60 µmol/l [O_2], respectively), making an understanding of oxygenation and sedimentary Mn redox regime essential. While we could show that *N. stella* incorporated Mn directly into its calcium-carbonate chamber walls, incorporation was low and heterogeneous, suggesting restricted proxy potential for this species. Regardless of investigated species, reliable interpretations of proxy-signals with respect to environmental variability will require the consideration of uncertainties pertaining to trace-element responses on intra- and inter-specimen level in foraminifera.

Lastly, the study entailed a taxonomic part, in which the studied species' affinity was molecularly (DNA barcoding) and morphologically (SEM imaging) validated and its phylogenetic position within the nonionids established. We defined a new phylotype 'T6' for *N. stella* from the Santa Barbara Basin, confirming its distinct status from genetically close specimens from Namibia (Deldicq *et al.*, 2019).

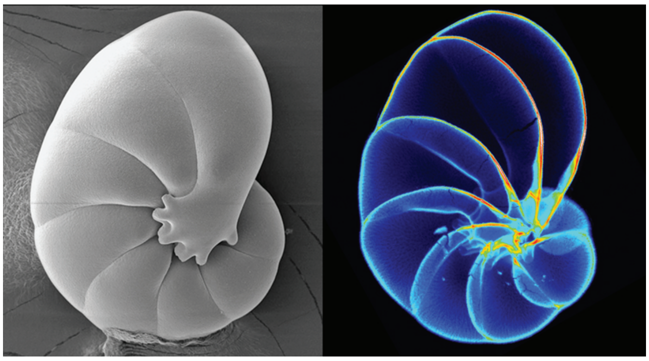


Fig. 13 Two specimens of the benthic foraminifer *Nonionella stella* from the Santa Barbara Basin imaged by scanning electron microscope (entire test; left) and X-ray fluorescence (calcium distribution in test cross-section; right). XRF photo credit: Dr. Andrea Somogyi.

Paper II

Benthic foraminiferal Mn/Ca as low-oxygen proxy in fjord sediments.
Brinkmann, I., Barras, C., Jilbert, T., Paul, K. M., Somogyi, A., Ni, S., Schweizer, M., Bernhard, J. M., & Filipsson, H. L. (manuscript)

In this contribution we continue the investigation of the foraminiferal Mn/Ca proxy for bottom-water oxygenation conditions, now focussing on Mn/Ca responses to a wide gradient of oxygen concentrations, ranging from low- to well-oxygenated, in a setting characterised by high Mn availability (Gullmar Fjord, Sweden).

We approach this following the concept of the previous study, utilising a two-fold micro-analytical approach to acquire data on trace-element concentrations and distribution in foraminiferal tests (here: LA-ICP-MS and XRF), and documenting ambient environmental conditions at the time of sampling (here: bottom- and pore-water oxygen, bottom- and pore-water dissolved Mn, sedimentary Mn concentrations).

Our results highlight the potential of the foraminiferal Mn/Ca proxy, however, only under low to moderate oxygen availability (approx. < 130 µmol/l O_2). The data indicate that the correlation curve likely flattens at well-oxygenated conditions, and this may be universal to Mn/Ca from coastal settings on a global scale. Accordingly, and in complement to our first study, we propose that the proxy possesses both a lower and upper oxygen limit of utility.

The response of foraminiferal Mn/Ca to ambient [Mn] and [O_2] was specific to the two investigated species, *B. marginata* and *N. labradorica*, with only the former showing proxy potential. For the selection of proxy candidate species, the biogeochemical effects of kleptoplasts, denitrification and formation of cysts require further attention. In proxy applications, it is imperative to consider a species' life-style, such as micro-habitat preferences and reproduction timing, in order to constrain uncertainties of biological origin in Mn/Ca signals.

Paper III

Drought recorded by Ba/Ca in coastal benthic foraminifera.
Brinkmann, I., Barras, C., Jilbert, T., Næraa, T., Paul, K. M., Schweizer, M., & Filipsson, H. L. (2022) Biogeosciences, 19, 2523–2535.

In this study we investigated modern benthic foraminiferal barium incorporation in response to opposing continental hydroclimate conditions, adding a new coastal marine proxy to the toolbox for reconstructing past drought events. Foraminiferal Ba/Ca data derived from the LA-ICP-MS analyses carried out for the project of Paper II, and covered the year 2018, characterised by exceptionally hot and dry conditions across Northern and Central Europe, as well as the following wet and warm year 2019.

We found that prolonged drought imprints with exceptionally low Ba/Ca in coastal benthic foraminifera. This resulted in a record of strongly contrasting Ba/Ca between 2018 and 2019 in direct relation to runoff and discharge conditions. By using extensive meteorological and hydrological data sets, as well as sediment- and pore-water geochemical profiles, we could link physical and chemical processes across the continent-sea transition zone. Resting upon these observations we propose a concept for Ba transport and cycling in the fjord's water and sediment, explaining availability to foraminifera.

Limitations of the proposed proxy pertain to both environmental Ba availability—a function of distance to terrestrial Ba source, water depth and pore-water geochemical regime—, and foraminiferal Ba incorporation—a function of a species' micro-habitat and/or ontogenetic stage. Hence, these factors require consideration in (palaeo)applications.

This study offers new perspectives on the interpretation of benthic Ba/Ca, as well as implications for barium proxy applications in palaeo-studies of near-continent sediment records.

Paper IV

Through the eDNA looking glass: Responses of fjord benthic foraminiferal communities to contrasting environmental conditions.
Brinkmann, I., Schweizer, M., Singer, D., Quinchard, S., Barras, C., Bernhard, J. M., & Filipsson, H. L. (manuscript in review at The Journal of Eukaryotic Microbiology)

This study explores the metabarcoding approach for identifying foraminiferal biodiversity and assemblage changes across environmental gradients. The material comprised sediment sampled on a temporal scale from several sites in the interconnected fjord system of Gullmar, Havstens and Koljö Fjord, Sweden, as well as foraminifera specimens from the study area. The latter served the construction of a taxonomic reference database of local species by single-cell barcoding and image documentation, paramount to the identification of sequences derived from metabarcoding.

We focused both on methodological aspects—comparing the output of two commercial DNA extraction kits of different sample volume—and the capacity of foraminiferal eDNA as bioindicator tool.

The DNA extraction procedure significantly influenced metabarcoding outputs with respect to both diversity and species composition, with indications of only one of the extract types representing present foraminiferal diversity reliably. In those extracts, foraminiferal communities were specific to settings contrasting strongly in their environmental conditions (e.g., brackish vs. fully-marine salinity), matching prior morphological assessments of the study areas' foraminiferal assemblages. Sensitivity to environmental factors variable on shorter scales (i.e., sub-annual), on the other hand, was damped on community level, and correlations of individual taxon abundance with various environmental parameters could not be confirmed by known species ecology.

Our work showcases current abilities and limitations of molecular techniques for tracing microbial biodiversity changes and species abundance, and advocate for homogeneity in the DNA extraction procedure within and between studies.

7 Discussion and perspectives

7.1 Inferences facilitated by in-field investigations for the calibration of proxies

The focal point of my thesis was the development of benthic foraminifera-based indicators for a variety of environmental conditions in a field-sampling approach. The investigations focused on the one hand on biogeochemical signals derived from several high-resolution micro-analytical approaches, and assemblage trends using a metabarcoding approach. The outcomes highlighted both opportunities and pitfalls of field-based calibration attempts, and can serve as reference for future studies devoted to refinements of the here dealt with proxies, as well as other trace-elemental proxies.

Generally, calibrations can be set up either as laboratory experiments or field-studies. The main advantage of laboratory studies is that all chemical and physical parameters involved in the experimental environment can be externally controlled. Hence, eliminating uncertainties introduced by environmental and/or geochemical interactions. This is especially valuable for inferences of direct relationships describing a proxy, such as trace-element partition coefficients (e.g., Barras *et al.*, 2018; Munsel *et al.*, 2010), or the relationship between DNA sequence abundance and specimen biomass (e.g., Lacoursière-Roussel *et al.*, 2016). Indeed, in all of our studies on geochemistry-based proxies (Papers I–III) it proved difficult to link environmental chemical and biogenic signals directly. Specifically, foraminiferal TE/Ca did not correlate positively with ambient availability in pore-waters (which we measured at the time of sampling), for either Mn/Ca or Ba/Ca. This contrasts the foraminiferal incorporation of trace-elements being proportional to ambient availability, as has been shown in laboratory studies for both Mn and Ba (e.g., Barras *et al.*, 2018; de Nooijer *et al.*, 2017). Generally, the extent to which relationships established under laboratory conditions can be extrapolated to natural environments and interactions are questionable, and in principle call for field-based validations of empirical relations. Despite the lacking direct correlations, in our field-studies the overall proxy relationships did work as expected—at least for some species and conditions. Accordingly, the underlying lab-supported assumptions imperative for the functioning of the proxy relations must have been given. We therefore inferred that our pore-water measurements did not reflect accurately on the trace-element availability during foraminiferal test precipitation, due to insufficient spatial and/or temporal resolution (Paper I–III). Such may be improved in future geochemical proxy calibration studies, such as by extended sampling efforts and/or use of analytical methods allowing for higher resolution measurements of pore-water and sedimentary geochemistry. Nevertheless, our records of solid and dissolved trace-element concentrations did aid reconstructing potential trace-elemental pathways and cycling of the studied environment (specifically transport and fluxes of Ba; Paper III), and reinforced the relevance of in-field proxy calibration studies.

Complex associations, as between terrestrial trace-element input and water-column transport to the sediment, or individual- and community-level behaviour of foraminiferal assemblages in response to natural environmental variability, are difficult to re-create in experimental setups. Here our field-sampling approach and associated findings could make important contributions, in particular with regards to the environment-specific utility of proxies and proxy sensitivity limits under natural conditions. The implications of these are briefly discussed below.

Fjords as field-laboratories

The utility of trace-elemental proxies being specific to the environment they are applied to is well established, particularly over large gradients such as comparing open-ocean versus coastal settings. For instance, biogenic Ba signals reflect on (palaeo-)productivity of the overlying water-column and surface waters in open ocean settings but are controlled by terrestrial input and estuarine mixing processes in coastal environments (see discussion in Paper III). Hence, consideration of regional environmental factors is important both in the development of proxies, as well as the interpretation of proxy signals in applications.

Based on our investigations of Gullmar Fjord, we infer that fjords present settings of high potential for the calibration of proxies, particularly such based on relationships relating directly or indirectly to redox cycling such as Mn/Ca and Ba/Ca. In the specific cases dealt with in my thesis, the fjord setting proofed ideal particularly due to its transitional position at the land-sea interface, facilitating significant inputs of terrestrial-derived trace elements (and associated high availability for foraminiferal incorporation), and the seasonal oxygenation cycle driving active redox cycling in surface sediments. Specifically, proxy signals derived from samples of the deep basin located in the inner Gullmar Fjord captured geochemical and associated environmental variability with high sensitivity (Papers II, III). It is typical for fjords, albeit not universal, to exhibit greatest depths in the inner (land-ward) part (e.g., Sars, 1872). There, sediment accumulation rates are highest (also in comparison to the open shelf and deep-sea), and sediment records span far back in time (e.g., Howe *et al.*, 2010). Hence, it is sensible to focus both continued calibration efforts and following applications on the deep basin of fjords.

Both Mn/Ca and Ba/Ca proxies deal with the indication of environmental and/or climate factors that are very timely—the decline of oxygen in coastal marine environments (e.g., Breitburg *et al.*, 2018) and the increase of drought and heatwaves (e.g., Bastos *et al.*, 2020). Thus, settings that can provide sensitive, high-resolution records of past developments of these variables are of high interest. Having been recently defined as 'Aquatic Critical Zones', this is particularly true for fjords (Bianchi *et al.*, 2020). Palaeo-reconstructions could put ongoing physical and chemical changes of fjords and the adjacent continent into a historical perspective and aid the plea for investigative efforts of these vulnerable systems.

From a practical point of view, also the relatively high accessibility for sample acquisitions is an advantage of fjords as study regions—particularly when compared to offshore areas. Fjord foraminiferal assemblages have been shown to often comprise deep-sea species occurring in shallower depths than their typical ranges in open ocean settings (bathyal to abyssal depths) (e.g., Alve *et al.*, 2011; Buhl-Mortensen & Buhl-Mortensen, 2014). With the deep basin often being stagnant in its environmental conditions (e.g., temperature, salinity) and generally not affected by short-term meteorological changes such as coastal waters, it in many ways mimics deep-sea conditions, facilitating its use as 'inland deep sea' laboratory (Buhl-Mortensen *et al.*, 2020). Besides that, the variety of habitats along a fjord's depth gradient, as well as contrasting influences of environmental conditions from land, sea and atmosphere, support the study of a diverse range of environmental and ecological research questions (for reviews see e.g., Brattegard, 1980; Howe *et al.*, 2010).

Scope of the Mn/Ca proxy for bottom-water oxygenation

Proxy relationships do not necessarily have a universal sensitivity independent of the range of physical and chemical factor of interest. For example, the Mg/Ca palaeothermometer loses its sensitivity at cold temperatures, as the exponential correlation curves flattens (e.g., Lear *et al.*, 2002). Similarly, our and previous field-calibration attempts of the Mn/Ca-oxygenation proxy revealed Mn/Ca trends indicating that, once established, a correlation curve will likely flatten at well-oxygenated conditions (Paper II; Guo *et al.*, 2019). The data from the Yangtze River Estuary indicated a potential maximum of 3–4 mg/l O_2 (approx. 94–125 µmol/l), which matched our observations in Gullmar Fjord, although studies measuring Mn/Ca precipitated under a gradient of oxygen concentration in higher resolution (i.e., concentration steps) will be necessary to define an exact limit. Similarly, such studies may have success in quantifying the relationship between Mn/Ca and oxygen concentrations under low-oxygen conditions. While the empirical, direct relationship between ambient Mn availability and biogenic incorporation has been shown to cover a wide gradient of Mn concentrations in linear correlation (e.g., 2.4–595 µmol/l Mn in Barras *et al.*, 2018), in practice the proxy is limited by the in-sediment positioning of the Mn redox-cline and foraminiferal in-sediment depth distribution (e.g., Koho et al., 2017). As bottom-water oxygen concentrations increase, allowing oxygen to penetrate deeply into the sediment, microbes will default to anaerobic respiration pathways, including reduction of Mn, only beyond the main micro-habitat of foraminifera. Accordingly, deep-infaunal foraminifera may show a wider sensitivity range even at higher bottom-water oxygenation than shallow or epifaunal taxa—if their depth-distribution is not coupled to the oxic-anoxic boundary and thus shifts with the redox-cline. However, we could not proof the latter with the deep-infaunal species investigated in this thesis (i.e., *Nonionellina labradorica*). Conceivable could also be the use of Mn/Ca signals of foraminifera of different depth habitats specifically, following the approach of the 'interspecies $\delta^{13}C$ gradient' suggested by Hoogakker et al. (2015). These authors proposed that the difference in normalised carbon isotope signal between epifaunal (*Cibicidoides wuellerstorfi* (Schwager, 1866)) and deep-infaunal foraminifera (*Globobulimina affinis* (d'Orbigny, 1839), living at the dysoxic/anoxic boundary) represents the same isotope gradient between pore- and bottom-waters across the anoxic boundary (i.e., oxygen penetration depth). In turn, this gradient is guided by bottom-water oxygen concentrations and, thus, can be used as proxy of such. Theoretically, such a concept can circumvent uncertainties associated with regional trace element availability and redox regimes, as the values are normalised. However, the utility is governed by the same limitations as the Mn/Ca proxy itself: at well-oxygenated conditions the signal of foraminifera from both shallow and deep micro-habitats will converge, and the same is true for suboxic states.

A second mechanism limiting the Mn/Ca proxy utility range is the diffusive loss of Mn to the water column under oxygen-depleted conditions in bottom-waters. This was previously highlighted by Glock *et al.* (2012) in studies of foraminiferal Mn/Ca from the Peruvian oxygen minimum zone, and confirmed by the Mn/Ca trends of our samples from the Santa Barbara Basin (Paper I). As this phenomenon causes low pore-water Mn availability, equivalent to under well oxygenated conditions, independent proxies are necessary to put Mn/Ca signals into perspective and allow a correct interpretation of observed Mn/Ca shifts. Even rough assessments of the foraminiferal assemblage may be sufficient, focussing on the presence or absence of indicator species of well- and low-oxygenated conditions, respectively.

Finally, it is noteworthy that our studies were based on 'clean' Mn/Ca signals of the primary calcium-carbonate in foraminifera tests. The presence of Mn diagenetic overgrowths on the out- and inside of foraminiferal tests, as common in fossil material, can limit the proxy's information value for bottom-water oxygen conditions (e.g., Edgar et al., 2013; Hasenfratz et al., 2017; Ni et al., 2020). The influence of such should, therefore, be considered in palaeo-applications, particularly if using bulk-analysis techniques.

7.2 Biological uncertainties of biogeochemical proxies and implications for palaeo-applications

In foraminiferal geochemical proxies, substantial uncertainty still surrounds how and to what degree intrinsic (i.e., between and within individuals) and extrinsic (i.e., environmental) processes affect the incorporation of trace elements into test walls. This uncertainty narrows the application of proxies to species for which biomineralization processes and lifestyle parameters potentially influencing trace-elemental signals can be constrained. Further, it can limit the quantification of (palaeo-)proxy signals especially when few data points are available, as individual-level differences cannot be distinguished from environmental drivers. One example of intrinsic effects with direct control on trace-elemental incorporation are ontogenetic trends, most often explained by changing calcium-carbonate precipitation rates and associated ability to discriminate against specific trace elements during foraminifers' growth (e.g., Diz *et al.*, 2012; Elderfield *et al.*, 2002). Examples of intrinsic effects indirectly causing variable trace element uptake are micro-habitat-specific trace-element availability. For instance, in-sediment depth preferences may expose respective species to different geochemical gradients, for example documented by the TROXCHEM[3] model by Koho *et al.* (2015) (see also e.g., Koho *et al.*, 2017; Ní Fhlaithearta *et al.*, 2018). Alternatively, the geochemistry of a foraminifer's calcification micro-habitat may be biologically altered, such as by the aggregation of organic matter (in planktonic species e.g., Fehrenbacher *et al.*, 2018). Interpretations of palaeo trace-elemental signals, therefore, relies heavily on a thorough understanding of biology and ecology of foraminifera.

Albeit not having investigated biomineralization processes directly or from a mechanistic viewpoint, our observations of foraminiferal trace-element incorporation through time (i.e., comparing successively precipitated chambers) and space (i.e., different environmental settings, specimen in-sediment depth) provided important insights into potential biological contributions to proxy signals. The most distinct observations comprise, on the one hand, changing trace-element concentrations through successively precipitated chambers, and, on the other hand, significantly different signals between the investigated species. To explain these patterns, we proposed the influence of potential ontogeny-driven lifestyle changes, micro-habitat preferences, as well as a variety of biological mechanisms conceivably modifying geochemical conditions in the foraminifers' (micro-) environment (Papers I–III). All of these processes describe a bio-environmental regulation of foraminiferal TE/Ca that acts independently of the proxy-environment relationship.

Our comparisons of different benthic species highlighted that established calibrations should not be transferred between taxa, and the need for careful considerations of biological uncertainties when deciding on candidate proxy species.

Proxy potential of *Bulimina marginata*

In both of our studies dealing with the development of trace-elemental proxies based on *B. marginata* in Gullmar Fjord (Papers II–III), this species stood out for its potential to indicate the variables in question (i.e., Mn/Ca for bottom-water oxygenation and Ba/Ca for hydroclimate conditions). Generally, representatives of *Bulimina* are considered as reliable environmental indicators based on a variety of TE/Ca, such as Mg/Ca for palaeotemperature reconstructions (e.g., Grunert *et al.*, 2018). Nevertheless, inter-individual variability due to vital effects have been highlighted (e.g., for Mg/Ca in Wit *et al.*, 2012). Similarly, our studies gave insights into intrinsic trace-element variability, both on intra- and inter-specimen level. Most notably, we documented elevated signals and abrupt differences in trace-element ratios between proloculus and initial chambers versus successive 'adult' chambers (Papers II–III), which led to the development of several hypotheses explaining this contrast. These include growth spanning a sequence of oxygen-deficiency to well-oxygenated conditions (going from high to low pore-water Mn availability), and the potential biological regulation of TE/Ca (in detail discussed in Paper II, with regards to Mn).

However, proxy signals of ambient environmental conditions were not overprinted by these intrinsic effects. In the case of Ba/Ca a distinct shift in ratios from 'dry' to 'wet' weather situations was noted even in measurements from solely the proloculus area, as well as when averaging over all measured chambers, despite proloculus signals ranging significantly higher than those of the more recently precipitated chambers. This implies that even bulk-analysis techniques pooling entire (and several) specimens likely will provide reliable proxy signals. The proloculus area constitutes a relatively small percentage of the calcium-carbonate material, compared to the entire test, particularly in adult specimens. Furthermore, the primary wall of the proloculus is secondarily covered by additional calcium-carbonate layers with each chamber addition. Hence, the proloculus contributes to a minor degree to the overall 'entire-specimen' TE/Ca. A complete mechanistic understanding of the biological trends is, therefore, not a strict requirement for the application of *B. marginata*-based trace-element proxies for palaeo-reconstructions, albeit desirable.

Our investigations clearly benefitted from the XRF trace-element mapping across entire specimens' cross-sections, particularly with regards to allowing more thorough considerations of mechanistic factors of influence (Paper II). However, comparable observations could be made by individual-chamber analyses using more widely available and easily accessible instruments, such as LA-ICP MS (Papers II–III) or SIMS. Theoretically, although time-intensive, even bulk techniques could be an option when separating either young and old specimens, or breaking individual tests, and measuring both fractions separately.

Proxy potential of *Nonionella stella* and *Nonionellina labradorica*

In contrast to *B. marginata*, both nonionids showed little potential as candidates for the here tested proxies and investigated settings, albeit for different reasons respectively.

Nonionella stella is not recommendable as trace-elemental proxy mainly for practical purposes. Due to its test fragility, time-intensive sample preparation was needed to allow micro-analytical measurements of trace-elemental signals (by SIMS; Paper I). While SIMS analyses theoretically allow for isotopic measurements as well, such in this case prevented by the thinness of the species' test walls (pers. comm. Martin Whitehouse). Bulk-analyses are conceivable, but samples comprising of many specimens would be required to reach the technically required weight limit. Hence, the use of this species as geochemical proxy would be limited to samples with high abundances, rare in particular in palaeo-applications. However, test fragility may be a factor of the ambient environmental conditions and, thus, the use of *N. stella*—or related, morphologically similar species such as *Nonionella* sp. T1—may be relevant in different setting than studied here.

Conversely, *N. labradorica* presents properties beneficial to geochemical studies, producing tests (and chamber walls) of comparatively large size, that can easily withstand laser-ablation and thereby provide long and stable measurement signals. The species' Mg/Ca signals have been proposed to be useful for relative or even semi-quantitative inferences of temperatures (Barrientos *et al.*, 2018). However, its Ba and Mn uptake, as investigated in my thesis, appeared to be not controlled solely or dominantly by environmental availability and we consider the proxy calibration attempts as unsuccessful. Nevertheless, our findings highlighted several biogeochemical features of this species that should be followed-up on in future explorations. Specifically, investigations of potential biogeochemical pathways contributing to the apparent insensitivity of *N. labradoricas*' Ba/Ca and Mn/Ca to ambient trace-element availability have the potential to make important contributions to the understanding of foraminiferal biology. In Paper II we proposed and discussed the influence of denitrification (albeit so far only shown for other nonionids), kleptoplasty and cyst formation as conceivable factors determining the elevated Mn/Ca signals of this species, whereas micro-habitat distribution was the most conclusive explanation of the lacking response to hydroclimate-driven Ba availability changes (Paper III). High-resolution, *in situ* geochemical studies of *N. labradorica* are a conceivable research pathway that may shed light on the potential biogenic alterations of sedimentary or pore-water trace-element availability and/or speciation in the specimens' (calcification) micro-environments. Conceivable are also culturing studies investigating foraminiferal metabolism and biogeochemistry, or combined molecular-geochemical approaches (discussed below).

7.3 Integration of molecular techniques in foraminiferal studies

Biodiversity assessments and bioindication

Metabarcoding is often referred to as a 'quick and easy' alternative to conventional assemblage studies, by circumventing the time-intensive microscopic observations and morphology-based taxonomic identification requiring expert knowledge, which is becoming rare. However, especially the processing of metabarcoding data does require time and specialised knowledge—albeit of different nature than traditional approaches—in particular before efficient and reliable protocols are developed to partially automate the (bioinformatic) protocols. Further, while theoretically taxonomy-free approaches are possible, the identification of recorded taxonomic units is preferential in order to align and validate the molecular output with established (morpho-)species concepts. This calls both for expertise in foraminiferal genomics, and sequence reference databases of wide coverage.

In the metabarcoding project of my thesis (Paper IV), the taxonomic identification of the molecular units proved crucial in appropriately interpreting responses to environmental variability on species-level. Observed sequence abundance shifts with environmental changes were not congruent with known species' ecology, highlighting both reliable calibrations of molecular species responses to environmental factors of interest being still outstanding, and shortcomings in methodological understanding of the metabarcoding approach. Furthermore, several issues that are currently associated with the metabarcoding approach also became evident in our study, such as biases related to the DNA extraction methods and the seemingly variable influence of propagules, questions regarding DNA preservation through time, the relationship between read- and specimen abundance, and lacking reference data base coverage preventing assignments of taxonomic units (see discussion in Paper IV).

Continued efforts should be directed at systematic comparisons of assemblages derived from molecular and morphological studies, as well as their respective responses to environmental stressors, in order to eventually establish metabarcoding as standalone method in diversity and ecological assessments. Complementation of our metabarcoding study with single-cell barcoding was able to bridge some gaps between previously observation-based assemblage data and the metabarcoding output. Specifically creating a local database of species diversity eased comparisons between morpho- and molecular species composition and allowed to constrain potential sources of (methodological) uncertainties, such as the contribution of propagule sequences to the extracted DNA pool.

Barcoding can further inform about species-level genomic variability (e.g., Borrelli *et al.*, 2018a; Pillet *et al.*, 2012), knowledge of which is essential to correctly estimate biodiversity, as well as taxon abundance (e.g., Weber & Pawlowski, 2014). In the project presented in Paper IV we corrected the taxonomic assignment of amplicon sequence variants (ASV) manually, by cross-checking sequences with reference barcodes. Accordingly, variants that could with confidence assigned to the same species were pooled. The most prominent example was the reassignment of 17 ASVs to *Ammonia confertitesta* (phylotype T6), a representative of one of the molecularly best studied foraminifera genera (e.g., Bird *et al.*, 2020; Hayward *et al.*, 2004, 2021; Holzmann, 2000; Holzmann & Pawlowski, 2000; Richirt *et al.*, 2019, 2021; Schweizer *et al.*, 2011). Naturally, if only a single specimen was barcoded to represent a species, no information on potential polymorphisms could be inferred. Still, overall environmental trends were approximately equivalent for unpooled and pooled assemblages, although strength and significance of environmental correlations improved distinctly with pooling (Brinkmann *et al.*, unpublished data).

Taxonomic certainty is also an important factor in foraminifera-based bioindication. Benthic foraminifera species can be morphologically similar and difficult to separate taxonomically, requiring detailed taxonomical descriptions and illustrations for confident species identification (e.g., Cage *et al.*, 2021). In some cases, morphological criteria are not sufficient and molecular analyses required to elucidate different genetic types categorised under one morphospecies (e.g., Deldicq *et al.*, 2019; Pawlowski & Holzmann, 2014). Additionally, genetic types may have distinct distribution patterns and/or be ecologically distinct (e.g., Gooday & Jorissen, 2012; Richirt *et al.*, 2021). Thus, observations of species' responses to environmental factors may not be transferable between phylotypes and grouping of morphologically similar taxa may lead to loss of modern and past environmental information. Phylogenetically informed species identification based on foraminiferal barcodes can resolve taxonomic uncertainties and is particularly informative if combined with morphological and ecological assessments (e.g., Bird *et al.*, 2020; Darling *et al.*, 2016; Hayward *et al.*, 2004; Roberts *et al.*, 2016). In Papers I and IV we could confirm several (pseudo-) cryptic species within the nonionids (Papers I, IV), with several clades representing taxa previously morphologically recognised as *Nonionella stella* (see also Deldicq *et al.*, 2019), and *Nonionella turgida*, respectively. *Nonionella* species, in particular *N. stella*, are frequently used as indicators of oxygen-depleted conditions. Hence, correct taxonomic identifications are of significance if the phylotypes' bioindicator qualities differ. In turn, once genetically characterised and included in reference databases, distribution patterns and ecologies of distinct phylotypes can be efficiently tracked by large-scale metabarcoding efforts.

Geochemical proxy calibrations and applications

Species-specific effects were also a common source of uncertainty in our geochemical proxy calibration attempts (Papers I–III) and have the potential to introduce significant errors in environmental interpretations if not constrained. By genetically characterising proxy candidate species, such as implemented by Groeneveld *et al.* (2018) and Paper I, taxonomic uncertainties can be circumvented, and unaccounted-for variability by potentially geochemically distinct genotypes avoided. While we identified several (pseudo-)cryptic species (see previous section; Papers I, IV), it was beyond the scope of our studies to investigate the geochemical signals of the respective clades and assess potential differences in trace-elemental incorporation.

While not addressed within this thesis, metabarcoding and other molecular approaches are viable options to identify metabolic interactions and trophic pathways in foraminifera (e.g., denitrification, kleptoplasty). Foraminifera single-cell or high-throughput sequencing of microbial DNA within foraminifera have the potential to reveal symbioses or interactions with bacteria (e.g., Bird *et al.*, 2018; Greco *et al.*, 2021). (Meta)transcriptome data of foraminifera has been used to investigate active genes with potential links to metabolic strategies, such as denitrification (e.g., Gomaa *et al.*, 2021; Orsi *et al.*, 2020), or differential (metabolic) gene expression in response to exposure to environmental stressors (e.g., Titelboim *et al.*, 2021). Metabolic strategies of foraminifera, or their symbionts, may directly or indirectly affect incorporation of trace-elements, as hypothesised in Paper II—or foraminiferal stable isotopes signals, as recently hypothesised by e.g., Schmidt *et al.* (2022). However, to date no molecular studies linked metabolic and biogeochemical investigations specifically.

8. Conclusions

- Benthic foraminiferal Mn/Ca has potential as indicator of low-oxygen conditions in bottom-waters. With continued calibration efforts quantitative reconstructions of bottom-water oxygenation might be feasible for oxygen concentrations within the low-oxygen range

- In near-coast areas with relevant terrestrial Ba input benthic foraminiferal Ba/Ca may present a powerful tool for palaeo-drought reconstructions. The case study of Ba/Ca trends in response to contrasting coastal hydroclimate conditions and associated riverine input demonstrated strong qualitative trends in trace-elemental signals of shallow-dwelling foraminifera.

- Quantitative interpretations of trace-element proxy signals are aided by an understanding of ambient geochemical conditions—Mn availability, oxygenation and redox regime in the case of Mn/Ca, and riverine concentrations, water-column shuttling mechanisms and sedimentary fluxes of Ba in the case of Ba/Ca.

- The relative contributions of abiotic and biotic factors controlling TE/Ca of benthic foraminifera are species- and trace-element specific and affect biogeochemical proxy relationships to various degrees. Chamber-specific micro-analyses of trace element concentrations and distributions are of high value for investigating intra-specimen geochemical trends of both extrinsic and intrinsic nature. Micro-habitat distribution and utilised metabolic pathways, such as by denitrification or kleptoplasty, appear to be the most significant factors in determining a species' proxy potential. Further studies are required to constrain the possible contributions of these biological factors to biogeochemical cycling in benthic environments.

- Metabarcoding is a useful tool for surveying differentiation of foraminiferal communities of strongly contrasting environments (e.g., brackish vs. marine), in dependence of DNA extraction methodology. Despite foraminiferal morpho- and molecular communities differing in composition, perceived diversity trends in response to environmental variability are congruent between conventional and metabarcoding assemblage assessments. Lacking sensitivity of sequence abundance data to short-term environmental perturbations limits stand-alone applications in bioindication at this point in time.

Table 1. Author contributions to papers included in this thesis. Non-author contributions marked by italics.

	Paper I	**Paper II**	**Paper III**	**Paper IV**
Study design	I. Brinkmann S. Ni H. L. Filipsson N. B. Quintana Krupinski	I. Brinkmann H. L. Filipsson C. Barras	I. Brinkmann H. L. Filipsson	I. Brinkmann H. L. Filipsson M. Schweizer C. Barras J. M. Bernhard
Data collection				
Field sampling	S. Ni H. L. Filipsson J. M. Bernhard V. E. Oldham N. B. Quintana Krupinski C. M. Hansel	I. Brinkmann H. L. Filipsson T. Jilbert K. M. Paul M. Schweizer *S. Jokinen* *H. Nilsson*	I. Brinkmann H. L. Filipsson T. Jilbert K. M. Paul M. Schweizer *S. Jokinen* *H. Nilsson*	I. Brinkmann H. L. Filipsson M. Schweizer *H. Nilsson* *E. Vardar*
Foraminifera Sample Preparation	I. Brinkmann S. Ni *K. Lindén*	I. Brinkmann	I. Brinkmann *G. Pappalardo*	I. Brinkmann S. Quinchard M. Schweizer
Biogeochemistry: SIMS	I. Brinkmann M. J. Whitehouse *H. Jeon*			
Biogeochemistry: Laser-Ablation ICP-MS		I. Brinkmann *T. Næraa*	I. Brinkmann T. Næraa	
Biogeochemical imaging (XRF)	I. Brinkmann S. Ni H. L. Filipsson K. Medjoubi A. Somogyi C. Barras	I. Brinkmann A. Somogyi H. L. Filipsson S. Ni C. Barras		
SEM imaging	I. Brinkmann *R. Mallet*			M. Schweizer *R. Mallet*
Barcoding and Metabarcoding	M. Schweizer			I. Brinkmann M. Schweizer S. Quinchard
Sediment Geochemistry	V. E. Oldham C. M. Hansel	T. Jilbert K. M. Paul	T. Jilbert K. M. Paul	
Statistical Analyses	I. Brinkmann S. Ni	I. Brinkmann	I. Brinkmann	I. Brinkmann D. Singer
Writing of Original Manuscript Draft	I. Brinkmann M. Schweizer	I. Brinkmann	I. Brinkmann	I. Brinkmann M. Schweizer
Preparation of Figures	I. Brinkmann M. Schweizer A. Somogyi	I. Brinkmann	I. Brinkmann	I. Brinkmann M. Schweizer
Review of Manuscript	All authors	All authors	All authors	All authors

Populärvetenskaplig sammanfattning

FN:s mellanstatliga klimatpanel, IPCC (Intergovernmental Panel on Climate Change) har under en längre tid belyst konsekvenserna av långsiktiga förändringar i vårt klimatsystem och varnat för hur dessa kan komma att påverka ekosystem och samhället i stort. En sådan långsiktig förändring är minskande syrgashalter i världshaven. Detta är en av många allvarliga konsekvenser till följd av klimatförändringarna, och orsakas bland annat av uppvärmning och övergödning. Minskningen i syrgashalt har en negativ påverkan på både djur och andra organismer som är beroende av syre för sin respiration, vilket kan driva hela ekosystem i obalans.

De senaste decennierna har även andra effekter av klimatförändringarna blivit märkbara, t ex den ökande förekomsten av extrema väderhändelser, såsom torka och värmeböljor. Utdragen och svår torka har förödande effekter för jordbruk, samhälle och ekonomi samt ekosystem. Prognoser från klimatmodeller visar dessutom att vi kan vänta oss en förvärrad situation inom en snar framtid, både med avseende på minskad syrgashalt i världshaven och extrema vädermönster. En ökad förståelse för ingående processer och vilka ”naturliga” variationer det finns i olika ekosystem kan hjälpa till för att förstå framtida effekter, och kan i slutändan hjälpa till att informera om potentiella lösningar för ekologiska och mänskliga anpassningar.

En metod för att lära sig mer om variationer i miljö- och klimatfaktorer, ekosystemreaktioner och -återhämtning är att studera det förflutna. För att ta fram miljödata som går längre tillbaka i tiden än traditionell miljöövervakning krävs miljöindikatorer som bevarar sådan information. Marina sediment utgör i många fall ett unikt miljöarkiv, och kan ge indirekt information om forna tiders hav and dess miljöförhållanden eller om närliggande landområden, till exempel i form av olika rester av mikroorganismer, växter eller djur. Vi brukar kalla dessa indirekta miljövariabler för proxyvariabler eller proxies. Dessa proxyvariabaler behöver dock ’översättas’ och ordboken utgörs av kunskap om förhållanden mellan miljö- och klimatförhållanden och samtida marina biologiska indikatorer.

Min avhandling består av fyra olika forskningsprojekt, alla med det övergripande syftet att vidareutveckla foraminifer-baserade proxies för miljö- och klimatvariabilitet. Foraminiferer är mikroskopiskt små encelliga mikroorganismer som ofta har ett skal av kalk. Kalkskalen har flera stora fördelar, t. ex de bevaras oftast i marina sediment, och olika isotoper och grundämnen från havsvattnet byggs in i kalkskalen. Projekten baseras på en mängd nya biogeokemiska och molekylära tillvägagångssätt för att studera biologiska markörer av pågående miljöförändringar i kustområden – fjordar på den svenska västkusten och Santa Barbara Basin utanför Kalifornien; USA. Först undersöktes halten av olika spårelement (mangan och barium) i foraminiferers skal för att öka kunskapen om kopplingen mellan dels mangan och syrebrist i havet (Artikel I–II), dels barium och torka på land (Artikel III). Jag har använt mig av en rad olika högupplösta plasma-, laser- och synkrotronbaserad tekniker. Resultaten belyser potentialen hos mangan- och barium-proxies som miljöindikatorer, men lyfter även fram betydelsen av artspecifika kalibreringar och olika biologiska funktioners inverkan på skalsammansättningen. Slutligen studerades sammansättningen av foraminiferer genom deras DNA-fotavtryck i marina sediment i olika miljöer (Artikel IV). Här lyfter vi fram hur och var denna nya metod skulle kunna ge viktiga bidrag i moderna miljöbedömningar, samt diskuterar metodologiska osäkerheter som kräver ytterligare uppmärksamhet.

Avhandlingen bidrar till en mer detaljerad förståelse av de biologiska processer som påverkar foraminifer-baserade miljöindikatorer, och föreslår framtida forskningsinriktningar som är nödvändiga för att befästa en framgångsrik tillämpning av de föreslagna proxyvariablerna i olika miljöhistoriska studier och modern övervakning.

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Printed by Media-Tryck, Lund 2022 NORDIC SWAN ECOLABEL 3041 0903

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ISSN 0281-3033
ISBN 978-91-87847-66-0

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