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Reviews and syntheses: Foraminifera from anaerobic environments - Survival strategies, biogeochemistry, ecology and applications for paleoceanography

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Abstract

The oceans are losing oxygen (O_2) and oxygen minimum zones are expanding, due to climate warming (lower O_2 solubility) and artificial fertilization related to agriculture. This ongoing trend is challenging for most marine taxa that are not well adapted to O_2 depletion. For other taxa this trend might be advantageous, because they can withstand low O_2 concentrations or thrive under anaerobic or even anoxic conditions. Benthic foraminifera are a group of protists that might benefit from ongoing ocean deoxygenation, since several foraminifera species possess adaptations to O_2 depletion that are unique amongst eukaryotes. This paper reviews the current state of knowledge about foraminifera from low O_2 environments. The specific survival strategies of foraminifera to withstand O_2 depletion include an anaerobic metabolism, heterotrophic denitrification, symbiosis with bacteria, kleptoplasty and dormancy. These adaptations, especially the ability to denitrify by some benthic foraminiferal species, have a strong impact on their preferred microhabitat in the sediments, which will be discussed in detail. In addition, due to their high abundances in O_2 depleted environments and their metabolic adaptations, benthic foraminifera are key players in marine nutrient cycling, especially within the marine N and P cycles. Studies about the ecology of benthic foraminifera are scarce but there is evidence that foraminifers have the capacity of phagocytosis, even under anoxia, and some foraminiferal species, which can withstand low O_2 conditions, even seem to prey on meiofauna. Finally, the fact that foraminifera can calcify even under anaerobic conditions makes them important archives for paleoceanographic applications. So this review will briefly summarize O_2 proxies based on foraminiferal morphology, shell geochemistry and composition of foraminiferal assemblages.

1 Introduction

More than two decades have passed since Bernhard and Sen Gupta (1999) provided a comprehensive review about the history of research on foraminifera from O_2 depleted environments. About a decade later, Koho and Piña-Ochoa (2012) provided another overview about benthic foraminifera as inhabitants in low-O_2 habitats, mainly focusing on the species distribution in different environments and the different depth layers in the sediment. They also summarized the early work on foraminiferal denitrification, kleptoplasty and evidence for bacterial symbiosis. Nevertheless, a lot has changed in our point of view about the anaerobic metabolism of benthic foraminifera and other survival strategies that help them to withstand O_2 depletion, due to advances in methods that can analyze metabolic rates, intracellular nutrient storage and even DNA and RNA of microeukaryotes such as foraminifera. This paper aims to summarize these developments, mainly focusing on benthic foraminifera.

Our knowledge about planktic foraminifera from O_2 depleted habitats is scarce compared to our knowledge about benthic foraminifera. Nonetheless, at least two species *Globorotaloides hexagonus* and *Hastigerina parapelagica* are known to live in pelagic oxygen minimum zones (OMZs) (Davis et al., 2021) and therefore, *G. hexagonus* has proven to be a valuable paleo-indicator for the presence of pelagic OMZs during the Pliocene (Davis et al., 2023). In general, also benthic foraminifera from low O_2 environments have been established as an invaluable archive for paleoceanography. I will only briefly summarize some redox proxies based on benthic foraminifera, since there is work in progress to give a comprehensive review about proxies for O_2 concentrations in paleoceanography (Hoogakker et al., in prep).

Within this paper, I will summarize recent advances to understand diverse survival strategies of benthic foraminifera to withstand O_2 depletion. This part will mainly focus on foraminiferal denitrification, dormancy and kleptoplasty. In the chapter 1.3.1 about denitrification, I will also utilize our current knowledge about foraminiferal denitrification to complement the conceptual TROX model by Jorissen et al. (1995), which explains the microhabitat of benthic foraminifera by an interplay in the supply of O_2 and organic matter (i.e. food). Afterwards, I will briefly discuss our scarce knowledge about ecological and trophic interactions of foraminifera from O_2 depleted environments. Finally, I will review the role of foraminifera for marine biogeochemical cycling, focusing on nitrogen and phosphorous and, as mentioned above, provide a brief overview about applications of benthic foraminifera from O_2 depleted environments in paleoceanography.

2.1 Survival strategies

Some benthic foraminiferal species have very specific adaptations that provide the opportunity either to thrive in anaerobic conditions or at least to survive periods of O_2 depletion (examples see in fig. 1). This chapter will discuss the recent advances in knowledge about these survival strategies. Contemporary improvements in

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molecular biological methods resulted in a strong increase of our understanding about the anaerobic metabolism in benthic foraminifera.

2.1.1 Foraminiferal denitrification

More than a decade ago first evidence came up that some foraminifera from O_2 depleted environments are able to perform complete denitrification (Risgaard-Petersen et al., 2006). Complete heterotrophic denitrification describes the step-by-step reduction of nitrate (NO_3^-) to inert N_2 gas (Fig. 2&3). Heterotrophic denitrification provides energy to an organism for oxidative phosphorylation in a similar way as O_2 respiration. The discovery by Risgaard-Petersen et al. (2006) was also the first evidence for complete denitrification in eukaryotic cells in general. Furthermore, this study showed that denitrifying foraminifera can have a substantial intracellular NO_3^- storage. They likely take up NO_3^- from the surrounding pore water and store it within intracellular seawater vacuoles.

Four years after the study by Risgaard-Petersen et al. (2006), Pina-Ochoa et al. (2010b) documented that intracellular NO_3^- storage and denitrification are not an exception, limited to a few specialized foraminiferal species, but actually a widespread phenomenon. Within a couple of years more studies either quantified denitrification rates or the intracellular NO_3^- storage of various foraminiferal species (Høgslund et al., 2008; Glud et al., 2009; Piña-Ochoa et al., 2010b, a; Koho et al., 2011; Bernhard et al., 2012b). The intracellular NO_3^- storage can reach concentrations up to 567 mM in gromiids (Piña-Ochoa et al., 2010b) and experiments with isotopically labeled NO_3^- showed that *Globobulimina turgida* takes up NO_3^- in a similar rate, independently of presence or size of the intracellular NO_3^- pool (Koho et al., 2011). However, not all benthic foraminifera are able to denitrify, even if they live in environments that are periodically exposed to anoxia such as the intertidal species *Ammonia tepida*, which neither stores NO_3^- nor shows any denitrification activities (Piña-Ochoa et al., 2010b). Some foraminifera from the Bering Sea have been shown to store NO_3^- but did not denitrify in incubation experiments (Langlet et al., 2020). These species include *Nonionella pulchella*, *Uvigerina peregrina* and *Bolivinellina pseudopunctata*. Also, the NO_3^- storage in *U. peregrina* shows a high variability, depending on the environment. Individuals of *U. peregrina* from the Bay of Biscay lack a significant NO_3^- storage, while *U. peregrina* from the North Sea and the Bering Sea both show intracellular NO_3^- enrichments (Piña-Ochoa et al., 2010b, Langlet et al., 2021). Other *Uvigerina* and *Nonionella* species have been shown to denitrify (Risgaard-Petersen et al., 2006; Høgslund et al., 2008; Piña-Ochoa et al., 2010b; Glock et al., 2019b; Gomaa et al., 2021). Many milliolids and allogromiids, several intertidal rotaliid species but also some other rotaliids and textulariids completely lack an intracellular NO_3^- storage (Piña-Ochoa et al., 2010b).

For about a decade after the first discovery of foraminiferal denitrification it remained unclear if foraminifera indeed denitrify themselves, or if they host bacterial symbionts that are responsible for the denitrification. Evidence came up for both hypotheses. Bernhard et al. (2012a) showed that *Bolvina argentaea* was able to denitrify, even after a very harsh treatment with antibiotics, which indicates that this species can denitrify even, when potential bacterial symbionts are killed. Other studies showed that bacterial endobionts likely perform denitrification in some gromiid and allogromiid species (Bernhard et al., 2012a; Høgslund et al., 2017). With the recent advances in molecular biology, however, it became possible to analyze the transcriptome of denitrifying foraminifera and Woehle & Roy et al. (2018) showed that the enzymes responsible for denitrification in *Globobulimina spp.* from a Swedish hypoxic Fjord basin are indeed transcribed by eukaryotic RNA. These enzymes are homologues of enzymes that are also used by bacteria for denitrification, which indicates an ancient prokaryotic origin of denitrification in foraminifera. Nevertheless, the homologues of the enzymes that catalyze the first and the last step of foraminiferal denitrification (Reduction of NO_3^- to nitrite (NO_2^-) and reduction of nitrous oxide (N_2O) to N_2 gas; fig. 3) have not been identified, yet. This indicates either that foraminifera use other enzymes to catalyze these steps, that they rely on bacterial symbionts for these steps or that they use an alternative denitrification pathway in general. One hypothesis, brought up by Woehle & Roy et al. (2018) is that the homologue of the nitric oxide reductase (Nor) is indeed a nitric oxide dismutase that has been proposed to catalyze the enzymatic reaction $2\ NO \rightarrow N_2 + O_2$ (alternative pathway in fig. 3) (Ettwig et al., 2012). The presence of the eukaryotic denitrification pathway found in foraminifera (Woehle et al., 2018) has been confirmed through other analyses of foraminiferal genomes (Orsi et al., 2020; Gomaa et al., 2021). Gomaa et al. (2021) also identified an enzyme of yet unknown functionality that might be responsible for the first step in the foraminiferal denitrification pathway. Recent metagenomics and transcriptomics results of denitrifying foraminifera indicate that bacterial symbionts might perform the missing steps in the foraminiferal denitrification pathway or that they at least partly contribute to the amount of NO_3^- that is denitrified within foraminiferal cells (Woehle et al., 2022). The study by Woehle & Roy et al. (2022) also reconstructed that the last common ancestor of denitrifying foraminifera likely has its origin during the Cretaceous, likely related to the occurrence of the Cretaceous Anoxic Events. The fact

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that the foraminiferal denitrification pathway is incomplete and the first and last steps are likely performed by Desulfobacteraceae in their microbiome suggests that the acquisition of denitrification ability in foraminifera occurred in multiple stages (starting during the Cretaceous) but is not yet complete (Woehle et al., 2022).

It is noteworthy that denitrifying foraminifera from the Peruvian OMZ show a metabolic preference of NO_3^- over O_2 as an electron acceptor (Glock et al., 2019c). This might explain, why some infaunal denitrifying foraminifera follow the oxycline within sediments (Linke and Lutze, 1993; Duijnstee et al., 2003). We have to keep in mind that O_2 can be quite harmful for organisms that are not adapted to higher O_2 concentrations, due to its strong reactivity. In addition, even trace amounts of O_2 can inhibit denitrification and O_2 can repress the denitrifying enzyme synthesis (Smith and Tiedje, 1979; Knowles, 1981; Tiedje, 1988; Mckenney et al., 1994). Thus, if denitrifying foraminifera are exposed to small amounts of O_2 they cannot denitrify but also do not have enough O_2 to supply their demands for electron acceptors. Larger amounts of O_2 might supply this demand but also harm the cell. Furthermore, foraminifera can store NO_3^- within vacuoles, due to its lower reactivity and still have an electron acceptor reservoir if NO_3^- is depleted in their microhabitat. This is not possible for O_2 due to its high reactivity. Finally, a review by Zimorski et al. (2019) addresses the common misconception that the presence of O_2 improves the overall energetic state of the cell. It is a fact that the energy yield from remineralizing glucose or amino acids is higher in the presence of O_2 ("O_2 respiration") but it is also a fact that that the synthesis of biomass consumes thirteen times more energy per cell, if oxygen is present, compared to anoxic conditions. This is related to the chemical equilibrium between organic matter and CO_2, which strongly shifts to the side of CO_2 in the presence of O_2 (Zimorski et al., 2019). All this might explain, why the metabolism of at least some denitrifying foraminifera is better adapted to denitrification than to O_2 respiration.

Furthermore, the fact that some foraminifera prefer NO_3^- over O_2 as electron acceptor (Glock et al., 2019c) and other species like *U. peregrina* denitrify in some environments but completely lack an intracellular NO_3^- storage in others (Piña-Ochoa et al., 2010b) might explain the microhabitat selection of benthic foraminifera in the sediment. According to the conceptual TROX model, benthic foraminifera can be divided into three groups, due to their microhabitat preference: Epifauna, shallow infauna and deep infauna (Jorissen et al., 1995). These microhabitats are mainly controlled by bottom water O_2 concentrations $[O_2]_{BW}$ and the supply of organic matter (i.e. food, Jorissen et al., 1995). Due to our increasing understanding about the anaerobic metabolism of foraminifera we can now assume that NO_3^- availability is another controlling factor and according to their preference for NO_3^- or O_2 as electron acceptors the different microhabitat preferences (Epifauna, shallow infauna and deep infauna) might be assigned to three different attributes (Aerobe, facultative anaerobe and facultative aerobe; see also fig. 4).

Deep infauna can be considered as **facultative aerobes** that prefer NO_3^- over O_2 and try to avoid trace amounts of O_2 but can withstand periods of oxygenation, since they are also able to respire O_2. They follow the oxycline in the sediments to avoid the inhibition of denitrification by trace amounts of O_2. Taxa belonging to the deep infaunal – facultative aerobe group that prefers NO_3^- over O_2 include for example *Valvulineria* spp., *Bolivina* spp., *Globobulimina* and *Cassidulina* spp. (Jorissen et al., 1995; Mojtahid et al., 2010; Glock et al., 2019c).

Shallow infauna can be considered as **facultative anaerobes** that basically are well adapted to the presence of low O_2 concentrations but can switch to denitrification if they are exposed to anaerobic conditions or need to enter the deeper sediment parts to find food or avoid competitional stress. These species have the advantage that they can utilize both fresh phytodetritus from the top of the sediments and organic matter of lower quality from the deeper parts of the sediments. A good example for a shallow infaunal – facultative anaerobe species is *U. peregrina*, that is well known for their shallow infaunal lifestyle and has been found with or without intracellular NO_3^- storage in different environments (Schmiedl and Mackensen, 2006; Piña-Ochoa et al., 2010b; Langlet et al., 2020).

Epifauna can be considered as **aerobes** that are used to thrive on top of the sediments or even on elevated substrates. Typical epifaunal – aerobe taxa include *Cibicides* spp. and *Planulina* spp. (Corliss and Chen, 1988; Lutze and Thiel, 1989). These species have the advantage that they are well adapted to collect fresh food supply from above (Wollenburg et al., 2021) but usually cannot withstand longer anaerobic periods (Mackensen et al., 1995). Nevertheless, recent genetic data indicates that *Cibicidoides wuellerstorfi* clusters very close to known denitrifying species in the phylogenetic tree, so it cannot be excluded that some *Cibicides* spp. can denitrify under certain prerequisites (Woehle et al., 2022).

Note that the deep infauna can even migrate deeper into the sediments below the depth of NO_3^- penetration, if they have to, due to their ability to intracellulary store NO_3^- as a reservoir (Fig. 4). The deeper

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boundary of the elevated infauna might be controlled by the zone of sulfate reduction, where free sulfide is produced, which might be toxic for the foraminifers. In conclusion to this chapter it is worth to mention that research still continuous to measure denitrification rates for different benthic foraminiferal species (Langlet et al., 2020; Choquel et al., 2021). This is important since data for such rates is scarce for foraminifera but needed to estimate their contribution to oceanic N-cycling. This topic is discussed a bit further in chapter 1.5.

2.1.2 Dormancy

Dormancy is another strategy to survive anoxia or extreme O_2 depletion for some benthic foraminifera that cannot denitrify. Dormancy is defined as the reduced or suspended metabolic activity in response to exogenous factors (Ross and Hallock, 2016). Observations that indicate the potential of dormancy in foraminifera have been documented since the 1950s and are extensively reviewed by Ross & Hallock (2016). Nevertheless, many aspects of foraminiferal dormancy, such as role in foraminiferal life cycle or its role in structuring foraminiferal assemblages remained unexplored (Ross and Hallock, 2016).

In the 1990s some studies hypothesized about potential dormancy of foraminifera, when exposed to anoxia. Bernhard and Alve (1996) observed that the ATP concentration ([ATP]) of the benthic foraminiferal species *Bulimina marginata*, *Stainforthia fusiformis* and *Adercotryma glomerata* flushed with N_2 gas to drive out O_2 was significantly lower than in specimens from well aerated conditions. They already interpreted this observation as an indication that dormancy is a survival strategy for some foraminiferal species when they are exposed to periods of anoxia. Linke & Lutze (1993) observed cysts of *Elphidium incertum* from putative anoxia that might be interpreted as a sign for dormancy and Hannah and Rogerson (1997) hypothesized that foraminifera transported to an anoxic sediment layer might become dormant until they return to aerated conditions by transport through bioturbation.

Recently, dormancy of foraminifera exposed to anoxia has gained more attention again. LeKieffre et al. (2017) did a feeding experiment with *Ammonia tepida* (*Ammonia sp.* phylotype T6 according to Koho et al., 2018) using a ^{13}C-labeled diatom film as food source. They compared the metabolic differences of *Ammonia sp.* between oxic and anoxic conditions by mapping the distribution of ^{13}C within the cells using coupled TEM/Nano-SIMS and by analyzing the carbon concentration and stable carbon isotopic composition of the total organic matter and individual fatty acids in the foraminifer. Nearly the complete diatom biofilm was consumed and the foraminiferal cytoplasm was strongly enriched in ^{13}C under oxic conditions. Specimens from the anoxic incubation ingested only few of the diatoms and those were neither assimilated nor metabolized further. In addition, the specimens from the oxic incubation produced a significant amount of specific polyunsaturated fatty acids, which has not been the case under anoxic conditions. *Ammonia sp.* (T6) reacted to the induced anoxia with a severely reduced metabolic rate within less than 24 hours. All these observations provide solid evidence that dormancy is a survival strategy of *Ammonia sp.* (T6) under anoxia.

Koho et al. (2018) further analyzed cell structural changes in *Ammonia spp.* under exposure to anoxia collected from the field as well as from incubations. The specimens from anoxia showed an increase in lipid droplets and electron dense bodies within their cytoplasm. The cytoplasm itself was thinned out, which was interpreted as metabolization of the own cytosol. In addition, while absent within the specimens from oxic environments, various bacteria were present within the cytoplasm of the specimens from anoxia. These were interpreted as endobionts but might also be parasites that could not be fend off, due to the drastically reduced metabolism under anoxia. Considering all these studies, it is likely that dormancy is a common survival strategy under anoxia for foraminiferal species that don´t have an anaerobic metabolism and likely also to periods of other extreme environmental conditions.

2.1.3 Kleptoplasty

Kleptoplasty describes a symbiosis between algal chloroplasts and a host organism that sequesters the chloroplasts from algae (Clark et al., 1990). The word originates from the Greek word “Kleptes”, which means “thief”. Kleptoplasty in foraminifera is most extensively studied for shallow *Elphidium* and *Haynesina* species that often thrive within the photic zone and this research goes back until the 1970s (Lopez, 1979; Lee et al., 1988; Correia and Lee, 2000, 2002b, a; Goldstein et al., 2004; Pillet et al., 2011, 2013; Cevasco et al., 2015; Jauffrais et al., 2016, 2017, 2018; Cesbron et al., 2017; Goldstein and Richardson, 2018; Jesus et al., 2021). Several studies showed that the sequestered chloroplasts in the intertidal species *Haynesina germanica* are still capable of photosynthesis under light exposure (Lopez, 1979; Cesbron et al., 2017). In 2011 there came first proof using molecular biological methods, that the kleptoplasts in foraminifera orginate from diatoms (Pillet et al., 2011) but this had been hypothesized before on the basis of the chloroplast shape in TEM-observations (Lopez, 1979; Lee

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et al., 1988; Cedhagen, 1991; Lee and Anderson, 1991; Bernhard and Bowser, 1999; Goldstein et al., 2004). Austin et al., (2005) hypothesized that the toothplates in *H. germanica* are morphological adaptations to crack diatom frustules for access to their chloroplasts. Recently, LeKieffre et al. (2018) showed in incubation experiments with $H^{13}CO_3^-$ and $^{15}NH_4^+$ during a light/dark cycle that *Haynesina germanica* is indeed able to fix inorganic carbon and nitrogen under light exposure. Intertidal foraminifera are often exposed to hypoxic or even anoxic conditions, when water stagnates during low tide or if they are transported to deeper anoxic sediment layers by bioturbation (Rybarczyk et al., 1996; Cesbron et al., 2017). *H. germanica* is also supposed to occur in black sediments of the British salt marsh tide pools (Bernhard and Bowser, 1999) which likely become anoxic during a tidal cycle (Rybarczyk et al., 1996) and it was among the first recolonizers of a Fjord suffering of organic pollution (Cato et al., 1980; Bernhard and Bowser, 1999). Kleptoplasty might thus be an additional adaptation of foraminifera from photic environments to stay active during periods of O_2 depletion (Cesbron et al., 2017).

Less well understood is the phenomenon of kleptoplasty, observed in the benthic foraminifers *Nonionelle stella* and *Nonionella labradorica* that can thrive below the photic zone and often inhabit O_2 -depleted sediments (Cedhagen, 1991; Bernhard and Bowser, 1999; Grzymski et al., 2002; Jauffrais et al., 2019; Gomaa et al., 2021). Experiments to test, if *N. labradorica* is able to photosynthesize with its sequestered chloroplasts have been inconclusive. While Cedhagen (1991) found active photosynthesis in *N. labradorica* specimens incubated with ^{14}C, Jauffrais et al. (2019) showed an increased O_2 respiration rate instead of O_2 production and chloroplast degradation in specimens exposed to light. Recently, Gomaa et al. (2021) found chloroplast encoded transcripts in *N. stella*, indicating that the kleptoplasts in this species are still active. Genetic analyses revealed that the kleptoplasts in *N. stella* and *N. labradorica* are also mainly sequestered from diatoms, most likely after ingestion and selective digestion of phytodetritus (Grzymski et al., 2002; Jauffrais et al., 2019; Gomaa et al., 2021). Grymzky et al. (2002) calculated that the rest amount of light for *N. stella* specimens collected from aphotic depths at the Santa Barbara Basin is too low to sustain active photosynthesis. Instead, they suggested that the kleptoplasts in foraminifera from aphotic environments provide the ability to fix inorganic nitrogen via the glutamine synthetase and glutamate 2-oxo-glutarate amidotransferase (GOGAT) pathway. Indeed, Jauffrais et al. (2019) showed that kleptoplastic *N. labradorica* are able to fix inorganic nitrogen but coupled TEM/Nano-SIMS revealed that the assimilated nitrogen is associated with electron opaque bodies instead of sequestered chloroplasts. Analyses of the transcriptome of *N. stella* by Gomaa et al. (2021) support these observations, since *N. stella* appears to be able to fix ammonia by itself. They also found that the fucoxanthin-chlorophyll binding protein (FCP) was expressed in the transcriptome of *N. stella* and speculated that the ability to synthesize FCP was derived from the kleptoplasts by horizontal gene-transfer. FCP is a pigment, commonly found in chloroplasts of brown algae and allows a more efficient photosynthesis with a light absorption bandwidth especially useful in aquatic environments (Papagiannakis et al., 2005; Premvardhan et al., 2008). The true function of the kleptoplasts in deep-sea benthic foraminifera from aphotic, often O_2 depleted, environments still remains enigmatic, though.

2.1.4 Other recent developments due to advances in molecular biological methods

The recent advances in molecular biological methods (e.g. next generation sequencing) lead to several contemporary publications about metabolic adaptions of foraminifera to O_2 depletion (examples see fig. 5) (Woehle et al., 2018, 2022; Orsi et al., 2020; Gomaa et al., 2021). These studies mainly focused on denitrification but also brought attention to some other metabolic features of foraminifera that can thrive under anaerobic conditions. Gomaa et al. (2021) found the expression of characteristic proteins for an anaerobic metabolism in *N. stella* and *B. argentaea*. These proteins include pyruvate-ferredoxin oxidoreductase (PFOR) and [FeFe]-hydrogenase. These PFOR sequences were indeed eukaryotic and closely related to those of the facultative anaerobe polychaete *Capitella teleta* and the anaerobic protistan parasite *Blastocystis*. The [FeFe]-hydrogenase is very similar to those in the amoeba/flagellate *Naegleria gruberi*, which has experimentally been shown to be active and to produce molecular hydrogen even under aerobic conditions (Tsaousis et al., 2014). Due to these observations Gomaa et al. (2021) suggested that *N. stella* and *B. argentaea* might be able to produce H_2 gas and have the capacity for an anaerobic energy metabolism.

Another important observation has been made by Orsi et al. (2020). They used metatranscriptomics on sediments from the Namibian shelf, where the foraminiferal community is dominated by *Bolivina* and *Stainforthia* species. Living foraminifera were present in the sediment column up to 28 cm depth in an anoxic habitat with high sulfide concentrations. The gene expression of those foraminifers increased under sulfidic conditions, which indicates that they not only survive but thrive under anoxic conditions. The anaerobic energy metabolism of these foraminifers seems to be sufficient enough to support calcification and phagocytosis even under anoxic conditions. Evidence for foraminiferal calcification under anoxia already came up by a study from Nardelli et al. (2014). Orsi

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et al. (2020) suggested that the Namibian foraminifera use phagocytosis to ingest prey cells even under anoxic conditions. Though, this requires high bursts of energy. The authors suggested that the foraminifera use dephosphorylation of an intracellular creatine phosphate storage to regenerate ATP for these energy bursts. Evidence for the capacity for the dephosphorylation of creatine phosphate under anoxia was indicated by the metatranskriptomes. In addition, a high intracellular dissolved inorganic phosphate storage has been found in benthic foraminifera from the Peruvian OMZ, which might serve a reservoir to synthesize creatine phosphate (Glock et al., 2020). Orsi et al. (2020) also found evidence for an anaerobic metabolism in foraminifera from the Namibian shelf. Their data indicates that the foraminifers metabolize hydrolyzed organics to produce ATP using fermentation and fumarate reduction.

3 Ecology

Studies about ecological and trophic interactions of foraminifera from O_2 depleted environments are scarce. Nomaki et al. (2006) made an *in situ* feeding experiment at central Sagami Bay (1450 m), Japan, using ^{13}C labeled algae and bacteria. Bottom water O_2 concentration at this location is less than 60 µM (Glud et al., 2005). Nomaki et al. (2006) described three different feeding strategies by benthic foraminifera in this environment. *Uvigerina akitaensis*, *Bolivina spissa* and *Bolivina pacifica* selectively ingest fresh phytodetritus and thus can be described as phytophagous species. The seasonal phytophagous species *Bulimina aculeata*, *Textularia kattegatensis* and *Globobulimina affinis* ingest fresh phytodetritus selectively but feed on sedimentary organic matter instead, when fresh phytodetritus is unavailable. The species *Cyclammina cancellata*, *Chilostomella ovoidea* ingest sedimentary organic matter at random and can thus be described as deposit feeders.

Several studies describe carnivorous behavior of benthic foraminifera (Goldstein, 1999; Lee, 1980; Lipps, 1983; Hallock and Talge, 1994; Dupuy et al., 2010). These observations have mainly been done on species that usually live in oxygenated environments. Recently, new evidence came up indicating ingestion of nematodes by *Globobulimina auriculata* from the hypoxic Alsbäck Deep in Gullmar Fjord, Sweden (Glock et al., 2019a). The species *G. auriculata* denitrifies and thrives under anaerobic conditions (Woehle et al., 2018). It is inconclusive, though, if the foraminifer preys on the nematode or vice versa (Glock et al., 2019a). Although predation (phagotrophy) is the main type of interaction in aerobic communities, it usually plays a much smaller role in anaerobic communities (Fenchel and Finlay, 1995). This is related to the low growth yields associated with the anaerobic metabolism, which results in very short food chains. Thus, the decrease in energy flow along the anaerobic food chains is higher than along the aerobic food chain (Fenchel and Finlay, 1995). The predatory isopod *Saduria entomon* for example strongly reduces its predatory activity under hypoxia in comparison to aerobic conditions (Sandberg, 1994) and the predator/prey biomass ratio has been shown to be 4 times lower in anaerobic environments compared to aerobic environments (Fenchel and Finlay, 1995). Still, there is further evidence by Orsi et al. (2020) that foraminifera from the Namibian shelf perform phagocytosis even under anoxic conditions (schematic representations for phagocytosis and predation on meiofauna shown in fig. 6). It is remarkable that there is so much evidence for phagotrophy on or by benthic foraminifera under anaerobic conditions and future studies might shed more light on predator prey interactions of benthic foraminifera in O_2 depleted environments.

4 The role of foraminifera in benthic nutrient cycling and biogeochemistry

Some benthic foraminifera from O_2 depleted environments are rare examples for eukaryotes that can perform complete denitrification (Risgaard-Petersen et al., 2006). In 2010, Pina-Ochoa et al. (2010b) showed that NO_3^- storage in foraminifera as reservoir for heterotrophic denitrification is not exotic and related to some foraminifera from a Swedish fjord but actually a widespread phenomenenon. Pina-Ochoa et al. (2010b) also pointed out the possible importance of denitrifying foraminifera for the benthic N-cycle, due to their partly high abundances in O_2-depleted environments. In some environments, such as some habitats in the Peruvian OMZ, foraminifera even seem to be the keyplayers in benthic denitrification (Glock et al., 2013, 2019b). Complete heterotrophic denitrification produces non-reactive (i.e. not bioavailable) N_2 gas. Denitrifying benthic foraminifera can thus be considered a sink for bioavailable N. The recent genetic studies on denitrifying benthic foraminifera did not find transcripts for homologues of enzymes that catalyze the last step of denitrification – the reduction of N_2O to N_2 (Woehle et al., 2018, 2022; Orsi et al., 2020; Gomaa et al., 2021). Some *Globobuliminids* from the hypoxic Alsbäck Deep in the Swedish Gullmar Fjord have been shown to produce N_2O gas as product of denitrification, although the rates were lower than their rates for complete denitrification (Piña-Ochoa et al., 2010a). The NO_3^- storage in denitrifying foraminifera but also in some sulfur bacteria, such as *Beggiatoa*, is of greater importance for benthic biogeochemical cycling, due to the potential of biological transport of these intracellular reservoirs (Dale et al., 2016). Most of the diagenetic models that describe and calculate benthic N-cycling are based on (and limited to) diffusive transport of the different N-species in bottom and pore water. Active

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biological transport of different N-species can thus efficiently influence the benthic fluxes of different N-species (Dale et al., 2016).

The estimates of total benthic foraminiferal denitrification rates are mainly based on upscaling individual species specific denitrification rates by the living abundances of benthic foraminifera in different environments (Piña-Ochoa et al., 2010b; Glock et al., 2013, 2019b). This approach is limited by the availability of species specific denitrification rates, although, various approximations can be used to estimate denitrification rates for species with unknown denitrification rates (Glock et al., 2013). In addition, Glock et al. (2019b) provided an equation to calculate an estimate for the denitrification rate, using the cell volume of the species of interest. A summary of all published benthic foraminiferal denitrification rates can be found in tab. 1. Further Data about species specific foraminiferal denitrification rates will improve our estimates about the role of foraminifera in benthic N-cycling and, thus, also models for benthic biogeochemical cycling.

Recently, it has been found that some benthic foraminifera are not only storing NO_3^- for denitrification but also store larger amounts phosphate (Glock et al., 2020). The intracellular phosphate concentration can exceed the concentration in the surrounding pore waters by a factor of 10 to 100. The use of this intracellular phosphate storage is still under debate. Hypotheses about the use of the stored phosphate include the synthesis of polyphosphates or a reservoir for the synthesis of phospholipids for the cell membranes (Glock et al., 2020). In addition, there is evidence that the intracellular phosphate storage in foraminifera facilitates phosphogenesis in some environments, similar to the intracellular polyphosphate enrichments in some sulfur bacteria (Schulz and Schulz, 2005). Sediments at the lower boundary of the Peruvian OMZ bear small phosphorite grains that show a step by step transition from pristine foraminifer shells via shells that are filled with phosphorites until small phosphorite grains that only retain the size and coarse shape of a foraminifer. The recent evidence for the potential of benthic foraminifera to use dephosphorylation of an intracellular creatine phosphate storage to regenerate ATP under anoxic conditions might be another explanation for the high intracellular phosphate storage (Orsi et al., 2020). It might be that this is an adaptation of foraminifera to enable phagocytosis even under anaerobic conditions.

4.1 Estimating the contribution of foraminifera to benthic nutrient budgets and fluxes

The intracellular NO_3^- storage in benthic foraminifera from different environments shows a relatively wide concentration range (Tab.2). In addition, species that lack intracellular NO_3^- storage are relatively widespread and there are species that, depending on the environment, either have or lack intracellular NO_3^- (Tabs.2&3). Most of the species that have been found both with and without intracellular NO_3^- in different environments (bold species in Tab.3) are species that are typically found to live shallow infaunal and belong to the group of foraminifera that can be considered facultative anaerobe and likely are opportunistic species that are well adapted to transitional environments with periodic O_2 depletion, since they apparently can handle oxygenated and anaerobic environments (see 1.3.1).

Due to the strong natural variability in NO_3^- storage, it strongly depends on the data basis to estimate the contribution of foraminifera to benthic NO_3^- budgets with a relative robust certainty. Nevertheless, the more data is available, the better we are able to calculate foraminiferal NO_3^- budgets including species with unknown denitrification rates or intracellular NO_3^-. Considering this, an analysis of published data about intracellular NO_3^- content reveals a highly significant correlation between the intracellular NO_3^- and the cell volume of denitrifying benthic foraminifera (Fig. 7; power regression; $R^2 = 0.59$; $F = 86$; $P = 3E\text{-}13$).

Thus, the intracellular NO_3^- content of a potentially denitrifying foraminifer can be estimated from its biovolume according to the following equation:

$$\text{Eq.1: } \ln(NO_{3\,i}^-) = 1.07(\pm0.11) \times \ln(V_{cell}) - 11.5(\pm1.9)$$

,where $NO_{3\,i}^-$ is the intracellular NO_3^- content in pmol ind^{-1} and V_{cell} is the cell volume in μm^3. Note that only species from table 2 with an intracellular $[NO_3^-] \geq 1$ mM were considered for the power regression. In addition, two extreme datapoints were discarded as outliers (see supplementary note). Similar equations have been published to estimate foraminiferal denitrification rates (Glock et al., 2019b; here Eq.2) and intracellular dissolved inorganic phosphorous content (Glock et al., 2020, here Eq.3).

$$\text{Eq.2: } \ln(R_{den(ind)}) = 0.68(\pm0.12) \times \ln(V_{cell}) - 5.57(\pm1.9)$$

$$\text{Eq.3: } \ln(DIP_i) = 0.82(\pm0.03) \times \ln(V_{cell}) - 7.65(\pm0.52)$$

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,where $R_{den(ind)}$ is the individual denitrification rate in pmol ind^{-1} day^{-1} and DIP_i is the intracellular dissolved inorganic phosphorous content in pmol ind^{-1}. Further equations and principles for upscaling foraminiferal nitrogen- and phosphorous-budgets from abundances of living foraminifera can be found in Glock et al. (2013, 2019b and 2020) and (Xu et al., 2021). Formulae to estimate the biovolume of many different common shapes of foraminifera have recently been published (de Freitas et al., 2021). Due to the high uncertainties related to the natural variability in metabolic rates and nutrient storage, a thorough error estimation is recommended (see Appendix B in Glock et al. 2020).

5 Applications for paleoceanography

Due to their ability to precipitate their calcitic tests even under anoxic conditions, fossil benthic foraminifera became routine tools in paleoceanography to reconstruct past redox conditions (Nardelli et al., 2014; Orsi et al., 2020). This chapter will discuss briefly that morphological features and geochemistry of benthic foraminiferal tests and the species composition of benthic foraminiferal communities can be used to reconstruct redox conditions in the bottom water. Nevertheless, this chapter will be short, since a larger review paper is in progress that will summarize modern O_2 proxies in general (Hoogakker et al., in prep).

5.1 Morphological adaptations and test porosity

Some morphological adaptations are very common for benthic foraminifera that thrive in O_2 depleted habitats. Small, more elongated and flattened morphologies are often characteristic for O_2 depletion, while more spherical forms can indicate oxygenated conditions (Bernhard, 1986; Bernhard et al., 1997). This generalization has to be taken with care, though, because there are larger spherical species that live deep infaunal below or at the oxycline. *Globobulimina spp.* for example are well known to thrive deep in the sediments and are model organisms to study foraminiferal denitrification (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010b; Woehle et al., 2018). Though, *Golobobuliminidae* are relatively large and have a strongly spherical shape. Also, the individual size within some species can be completely decoupled from O_2 availability. The size of *Bolivina seminuda* from the Peruvian OMZ is directly proportional to the $[NO_3^-]_{BW}$ concentration in their habitats, even though the analyzed specimens were all from O_2 depleted conditions (Glock et al., 2019c). An inverse correlation between size and $[O_2]$ has also been shown for other benthic foraminifera (Keating-Bitonti and Payne, 2017). Nevertheless, small size, high porosity and thin test walls seem to be characteristic for foraminifera that live in low O_2 environments (Kaiho, 1994). Most of these characteristics are already quantified and summarized by Kaiho (1994) and won´t be further discussed here.

One morphological feature that recently got more attention as a possible paleoceanography tool is the porosity that includes pore size and pore density of the foraminiferal tests. Research regarding foraminiferal pore characteristics already ranges back till the 1950s (Arnold, 1954). Then, in the 1960s, first attempts have been made to use the porosity of foraminifera as an index for (paleo-)climate (Bé, 1968). This chapter will mainly focus on the latest studies on the porosity of benthic foraminifera and its potential as a paleo proxy. Different foraminiferal species seem to adapt their pore characteristics in a different way to different environmental conditions. *Cibicides* spp. for example mainly thrive in well oxygenated environments (Mackensen et al., 1995). Recent studies, however, observed living *Cibicidoides* spp. thriving in environments of < 2 µmol/kg O_2 (Rathburn et al., 2018) and fossil specimens in the paleorecord during periods of severe O_2 depletion (Hoogakker et al., 2018). It is not known, if any *C.* spp. are able to denitrify but recent genetic data indicates that *Cibicidoides wuellerstorfi* clusters very close to known denitrifying species in the phylogenetic tree (Woehle et al., 2022). Rathburn et al., (2018) also showed that the porosity in *C.* spp. and *Planulina* spp. is significantly negatively correlated to the O_2 concentrations in the bottom water ($[O_2]_{BW}$). If O_2 is too depleted, the foraminifers increase their porosity to optimize the O_2 uptake. A recent study tested several approaches to determine the correlation between the pore density of *Planulina limbata* and bottom water oxygenation and used the pore density of *P. limbata* from the Peruvian margin to quantitatively reconstruct $[O_2]_{BW}$ at the Peruvian OMZ during the Late Holocene and the Last Glacial Maximum (Glock et al., 2022). More comprehensive reviews about the history of studies on the porosity of foraminifera and the use of morphological features as O_2 proxy can be found in other recent review papers (Glock et al., 2012; Hoogakker et al., *in prep.*).

5.2 Geochemistry of benthic foraminiferal tests

The unique mechanism of biomineralisation in rotaliid foraminifera preserves the chemical signature of ambient seawater in their test calcite. These species precipitate their test calcite directly from vacuolized seawater (Erez, 2003) and thus the chemical composition of the test calcite reflects the chemical composition of the surrounding water in their habitats. Different element/Ca ratios are used as proxy for various parameters. Over the

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past decades several redox sensitive element/Ca ratios in foraminiferal calcite were focused as potential O_2 proxies, for example V/Ca (Hastings et al., 1996b, a, c), Fe/Ca (Glock et al., 2012a), Mn/Ca (Reichart et al., 2003; Hathorne et al., 2003; Munsel et al., 2010; Glock et al., 2012a; Groeneveld and Filipsson, 2013; Koho et al., 2015; Petersen et al., 2018; Barras et al., 2018; van Dijk et al., 2019; Ni et al., 2021; Brinkmann et al., 2021) and I/Ca (Glock et al., 2014, 2016, 2019d; Zhou et al., 2014, 2022; Lu et al., 2016, 2020; Winkelbauer et al., 2021; Cook et al., 2022). All these proxies have their individual advantages and disadvantages, which are discussed in detail in Hoogakker et al., in prep. In addition, the offset of the stable carbon isotope fractionation ($\delta^{13}C$) between the tests of epifaunal and deep infaunal benthic foraminifera can be used as a quantitative $[O_2]_{BW}$ proxy (McCorkle and Emerson, 1988; Hoogakker et al., 2014, 2018). This offset is now referred to as $\Delta\delta^{13}C$. While epifaunal benthic foraminifera incorporate the $\delta^{13}C$-signature of dissolved inorganic carbon (DIC) in the bottom water, deep infaunal foraminifera incorporate the $\delta^{13}C$-signature of DIC in the pore water (Schmiedl and Mackensen, 2006; Hoogakker et al., 2014). This offset increases with the height difference in the sediment column (McCorkle and Emerson, 1988). With increasing $[O_2]_{BW}$, deep infaunal foraminifera migrate deeper into the sediment to avoid the oxycline (Duijnstee et al., 2003) and $\Delta\delta^{13}C$ increases (Hoogakker et al., 2014). Thus, there is a significant correlation between $[O_2]_{BW}$ and $\Delta\delta^{13}C$ at the lower $[O_2]$ range. The $\Delta\delta^{13}C$ proxy is also discussed in detail in Hoogakker et al., in prep.

5.3 Foraminifera assemblage compositions

Species compositions of benthic foraminifera assemblages are routinely used to reconstruct past environmental conditions and it is not the focus of this review to summarize the history of this approach. Since some benthic foraminifera species are especially well adapted to O_2 depleted conditions (see chapter 2), the use of benthic foraminifera assemblages to reconstruct past $[O_2]$ appears obvious and has a relatively long history (e.g. Sen Gupta and Machain-Castillo, 1993; Kaiho, 1994; Alve and Bernhard, 1995; Bernhard et al., 1997; Baas et al., 1998; Nordberg et al., 2000; Leiter and Altenbach, 2010; Erdem et al., 2020; Ovsepyan et al., 2021). Kaiho et al. (1994) developed the first benthic foraminifera O_2 index (BFOI), to quantitatively reconstruct past $[O_2]_{BW}$. Further development of this index is still going on with recent developments by Tetard et al., 2021 and Kranner et al., 2022. Nevertheless, according to the conceptual TROX model (Jorissen et al., 1995), microhabitats and assemblage composition of benthic foraminifera are not only controlled by $[O_2]_{BW}$, but the supply of organic carbon to the sediments is another major controlling factor, which hampers the straightforward interpretation of assemblage compositions as a pure $[O_2]_{BW}$ proxy. History, applications and different approaches to use benthic foraminifera assemblage compositions as qualitative and quantitative O_2 proxy are all summarized in Hoogakker et al., in prep.

6 Author contribution

NG wrote the manuscript and did the data compilation and statistical analyses.

7 Competing interests

The authors declare that they have no conflict of interest.

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Figure captions:

Figure 1: Schematic representations for three survival strategy examples performed by benthic foraminifera under O_2 depleted conditions.

Figure 2: Stoichiometry for heterotrophic denitrification. Organic matter is oxidized using nitrate (NO_3^-) as an electron acceptor in a similar way O_2 is used for O_2 respiration. This process provides energy for the organism for oxidative phosphorylation. [CH_2O) symbolizes organic matter of unspecified composition. ΔG0 value relates to PH of 7. Taken from (Jorgensen, 2006).

Figure 3: Schematic view of two alternative pathways suggested for foraminiferal denitrification. Abbreviations above the reaction arrows indicate the enzymes that are catalyzing the respective step (see legend). Enzymes in black have been found transcribed by eukaryotic (foraminiferal) RNA (Woehle et al., 2018). Enzymes in grey are missing in the foraminiferal denitrification pathway and are likely performed by bacterial symbionts (Woehle et al., 2022). The straight pathway above describes the normal heterotrophic denitrification pathway. The junction, catalyzed by the Nod, which produces O_2, has been suggested as an alternative pathway for foraminiferal denitrification (Woehle et al., 2018).

Figure 4: TROX model modified after Jorissen et al. (1995) and Xu et al. (2021). The supply of organic matter in different environments controls the penetration depth of O_2 and NO_3^- into the sediment. Benthic foraminifera choose their microhabitat according to their metabolic preferences for O_2 or NO_3^- as an electron acceptor and the availability of food. **Epifaunal** – **aerobic** species depend purely on O_2 and live on top the sediment or elevated substrate. They are well adapted to collect fresh food supply and survive even in oligotrophic environments. **Shallow infaunal – facultative anaerobic** species are well adapted to switch between O_2 and NO_3^- respiration. If they store NO_3^- for denitrification they can even migrate and survive below the oxycline, when they have to. Though, if food supply is getting critical they can migrate close to the sediment surface and easily withstand exposure to O_2. **Deep infaunal – facultative aerobes** prefer NO_3^- over O_2 and try to avoid O_2, because even trace amounts of O_2 inhibit denitrification. Thus, they thrive below the oxycline, when there is still enough supply of NO_3^- and usually migrate upwards, when the oxycline shallows. They are able to survive short periods in the transition zone below the NO_3^- penetration depth, due to their high intracellular NO_3^- storage but are likely limited in depth by the region of sulfate reduction due to the presence of free toxic sulfide. Note that they also can actively transport intracellular NO_3^- below the NO_3^--penetration depth in the sediments. For further details see text.

Figure 5: Examples for molecules and processes that are relevant in the anaerobic metabolism of foraminifera. A: Structural formula of creatine phosphate. B: The role of creatine kinase (Ck) and creatine phosphate in the anaerobic metabolism. High energy creatine phosphate is produced by phosphorylation of creatine. Creatine phosphate can rapidly recycle ADP to ATP to provide resources for rapid energy bursts. This pathway has been described by Orsi et al.(2020). C: Fermentation has been found to be relevant in the anaerobic metabolism of foraminifera by both Orsi et al.(2020) and Gomaa et al. (2021). The possibility of a H_2 producing fermentation pathway, catalyzed by Fe-hydrogenase has been described by Gomaa et al. (2021).

Figure 6: A: Schematic representation of a *bolivinid* ingesting bacterial cells. Recent studies showed that benthic foraminifera from O_2 depleted habitats have the capacity of phagocytosis even under anoxia (Orsi et al., 2020). B: Schematic representation of *Ammonia* sp. preying on a nematode. Some benthic foraminifera are known to prey on meiofauna (Dupuy et al., 2010) and there is evidence, that even some *globobuliminids* that usually thrive under anaerobic conditions might prey on nematodes (Glock et al., 2019a).

Figure 7: Log-log plot and power regression of intracellular NO_3^- content ($NO_3^-{}_i$) against the biovolume (V_{cell}) of benthic foraminifera from from diverse environments (Tab. 2). Only species with an intracellular [NO_3^-] ≥ 1 mM, where both $NO_3^-{}_i$ and V_{cell} were published were considered for the power regression.

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892 **Tables**

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894 Table 1: Summary of foraminiferal denitrification rates (individual and volume specific), where Ind. refers to the
895 number of individuals used for one incubation. Errors are given as standard deviations (1sd) ৸: Data from Glock
896 et al. 2019b ¥: Data from (Piña-Ochoa et al., 2010b); ł: Data from (Risgaard-Petersen et al., 2006); ɨ: Data from
897 (Høgslund et al., 2008) ʒ: Data from (Bernhard et al., 2012b); Ɵ: Data from (Woehle et al., 2018) ɣ: Data from
898 Choquel et al (2021) ɮ: Data from Langlet et al. (2020).

Species	Ind.	Denitrification (pmol nitrogen individual^{-1} d^{-1})	Specific Denitrification (pmol nitrogen µm^{-3} d^{-1})
Bolivina costata (OMZ, Peru)৸	13-14	21 ± 8 (n = 3)	3.42E-5 ± 1.53E-5 (n = 3)
Bolivina plicata (OMZ, Perú)৸	5-8	105 ± 33 (n = 2)	2.49E-5 ± 3.27E-6 (n = 2)
Bolivina seminuda (OMZ, Peru)৸	6-13	86 ± 57 (n = 11)	5.73E-5 ± 2.53E-5 (n = 10)
Bolivina spissa (OMZ, Peru)৸	4-7	373 ± 205 (n = 5)	9.12E-5 ± 3.66E-5 (n = 5)
Cancris carmenensis (OMZ, Peru)৸	3-4	765 ± 306 (n = 3)	1.86E-5 ± 4.25E-6 (n = 3)
Cassidulina limbata (OMZ, Peru)৸	4-6	45 ± 16 (n = 4)	7.62E-6 ± 9.25E-6 (n = 3)
Nonionella auris (OMZ, Peru)৸	10	7 ± 1 (n = 1)	2.70E-6 (n = 1)
Uvigerina striata (OMZ, Peru)৸	6-13	244 ± 35 (n = 3)	9.26E-6 ± 1.50E-6 (n = 3)
Valvulineria inflata (OMZ, Peru)৸	2-3	2241 ± 1825 (n = 2)	3.50E-5 ± 2.49 E-5 (n = 2)
Ammonia tepida (Aiguillon Bay)¥	2	0 (n = 1)	0 (n = 1)
Bolivina subaenariensis (B. Biscay)¥	10–12	78 ± 2 (n = 2)	3.12E-6 ± 5.43E-7 (n = 2)
Uvigerina phlegeri (Rhône)¥	10	46 ± 2 (n = 1)	5.48E-6 (n = 1)
Valvulineria bradyana (Rhône)¥	10	183 ± 10 (n = 2)	1.22E-5 ± 1.32E-6 (n = 2)
Nonionella cf. *stella* (OMZ, Chile)ł,ɨ	3–5	84 ± 33 (n = 3)	1.62E-5 ± 6.72E-6 (n = 3)
Globobulimina turgida (Gullmar fjord)ł	3	565 ± 339 (n = 10)	1.13E-6 (n = 1)
Bolivina plicata (OMZ, Perú)¥	3	79 (n = 1)	1.05E-5 (n = 1)
Valvulineria cf. *laevigata* (OMZ, Perú)¥	10	248 ± 180 (n = 2)	1.31E-5 + 9.81E-6 (n = 2)
Bolivina seminuda (OMZ, Perú)¥	3	216 (n = 1)	4.15E-5 (n = 1)
Stainforthia sp. (OMZ, Perú)¥	4	70 (n = 1)	n.a.
Globobulimina turgida (Gullmar fjord)¥	2-3	358 ± 134 (n = 2)	7.16E-7 + 5.16E-6 (n = 2)
Bolivina argentea (Santa Barbara)ʒ	10	1976 ± 1103 (n = 8)	n.a.
Fursenkoina cornuta (Santa Barbara)ʒ	10	1386 ± 320 (n = 2)	n.a.
Globobulimina turgida (Gullmar fjord)Ɵ	3-5	310 ± 573 (n = 8)	9.34E-6 ± 1.34E-5 (n = 8)
Globobulimina auriculata (Gullmar fjord)Ɵ	4-5	75 ± 44 (n = 4)	2.39E-6 ± 1.50E-6 (n = 4)
Nonionella T1 (Gullmar Fjord)ɣ	5	38 (n = 1)	n.a.
Bolivina spathulata (Bering Sea)ɮ	19	11 (n = 1)	9.17E-7 (n = 1)
Globobulimina pacifica (Bering Sea)ɮ	4-5	378 ± 471 (n = 2)	1.63E-5 ± 2.07 E-5 (n = 2)

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Table 2: Summary of intracellular nitrate (NO_3^-) storage in benthic foraminifera and gromiida from different environments. Only species where intracellular [NO_3^-] was at least 0.1 mM are listed. Species with intracellular [NO_3^-] < 0.1 mM are listed in Tab.3. Errors are given as standard error of the mean (SEM) ¥: Data from (Piña-Ochoa et al., 2010b); ł: Data from (Risgaard-Petersen et al., 2006); ɿ: Data from (Høgslund et al., 2008) ʒ: Data from (Bernhard et al., 2012b); ο: Data from (Bernhard et al., 2012a); ʑ: Data from (Xu et al., 2017); ж: Data from (Glock et al., 2020); ƪ: Data from Langlet et al. (2020); ц: Data from (Xu et al., 2021).

Species	Location	NO_3^- (pmol per cell)	1SEM	Volume ($\mu m^3 \cdot 10^{-6}$)	1SEM	[NO_3^-] (mM)	1SEM
Allogromia sp. ο	Santa Barbara Basin	570	354	n.a.	n.a.	70.0	49.0
Bolivina alata ¥	Bay of Biscay	615	154	17.0	1.1	37.0	12.0
Bolivina argentea ʒ	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	195.1	160.3
Bolivina cf. *abbreviata* ¥	OMZ-Peru	1081	368	12.0	2.7	153.0	49.0
Bolivina cf. *skagerrakensis* ¥	North Sea	83	n.a.	17.0	0.0	5.0	n.a.
Bolivina costata ж	OMZ-Peru	34	4	0.8	0.0	43.1	4.3
Bolivina interjuncta ж	OMZ-Peru	1239	267	15.6	0.5	80.2	18.9
Bolivina plicata ¥	OMZ-Peru	478	72	7.5	1.0	79.0	15.0
Bolivina robusta ʑ	Yellow Sea	212	46	6.1	0.4	35.0	6.0
Bolivina seminuda ж	OMZ-Peru	140	45	1.6	0.1	88.6	29.8
Bolivina seminuda ¥	OMZ-Peru	564	135	5.2	1.8	118.0	18.0
Bolivina spathulata ƪ	Bering Sea	154	n.a.	10.3	n.a.	14.9	n.a.
Bolivina subaenariensis ¥	Bay of Biscay	285	46	25.0	4.3	44.0	9.0
Bolivinellina pseudopunctata ƪ	Bering Sea	133	n.a.	0.9	n.a.	148.1	n.a.
Bulimina aculeata ¥	Bay of Biscay	19	12	7.4	0.4	3.0	2.0
Bulimina cf. *elongata* ¥	OMZ-Peru	817	287	7.9	1.2	116.0	43.0
Bulimina marginata ц	Yellow Sea	70	11	2.7	0.3	26.0	1.0
Bulimina marginata ¥	Skagerrak	5	n.a.	1.1	11.0	0.5	0.2
Bulimina marginata ¥	Bay of Biscay	40	4	32.0	1.1	4.0	1.0
Bulimina subula ц	Yellow Sea	79	8	1.7	0.3	51.0	5.0
Buliminella tenuata ʒ	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	217.4	150.5
Cancris auriculus ʑ	East China Sea	3211	1046	28.0	5.1	114.0	23.0
Cancris inflatus ¥	OMZ-Peru	263877	4253	120.0	24.0	262.0	37.0
Cassidulina carinata ¥	Rhône Delta	3	1	4.1	0.2	1.0	0.5
Cassidulina cf. *laevigata* ¥	North Sea	21	n.a.	4.1	0.0	5.0	5.0
Cassidulina cf. *laevigata* ¥	OMZ-Peru	523	289	12.0	3.6	41.0	12.0
Cassidulina limbata ж	OMZ-Peru	1408	710	16.8	2.9	72.9	37.8
Chilostomella oolina ¥	Bay of Biscay	1124	520	20.0	2.0	65.0	36.0
Clavulina cylindrica ¥	Rhône Delta	2202	480	35.0	1.0	48.0	13.0
Clavulina cylindrica ¥	Bay of Biscay	1941	314	37.0	5.8	61.0	12.0
Cyclammina cancellata ¥	OMZ-Peru	45563	45563	380.0	3.1	119.0	118.0
Fursenkoina cornuta ʒ	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	125.2	68.9
Globobulimina auriculata cf. *arctica* ¥	Greenland	10624	3555	100.0	17.0	113.0	43.0
Globobulimina cf. ovula ¥	OMZ-Peru	3,369	1602	1.0	2.3	375.0	174.0

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Globobulimina pacifica ʖ	East China Sea	1167	455	75.0	7.0	16.0	5.0
Globobulimina pacifica ɮ	Bering Sea	6530	5563	34.2	8.9	243.9	203.6
Globobulimina turgida ɬ	Gullmar fjord	18000	4852	500.0	360.0	10.0	2.0
Globobulimina turgida ¥	Skagerrak	8192	1497	100.0	17.0	71.0	13.0
Goesella flintii ¥	OMZ-Peru	459	424	100.0	27.0	24.0	23.0
Gromia sp. ¥	Bay of Biscay	2846	1275	93.0	20.0	35.0	21.0
Gromia sp. ¥	Skagerrak	35277	16546	510.0	110.0	53.0	19.0
Gromia sp. ¥	Rhône Delta	3889	1024	160.0	110.0	91.0	26.0
Gromia sp. ¥	North Sea	14682	4649	160.0	3500.0	140.0	46.0
Gromia sp. ¥	Greenland	12997	2954	80.0	23.0	163.0	n.a.
Gromia spp ɮ	Bering Sea	367	85	11.3	6.1	40.2	14.1
Gyroidina neosoldanii ¥	OMZ-Peru	13190	480	27.0	12.0	241.0	46.0
Hanzawaia nipponica ʖ	Yellow Sea	316	73	30.0	0.5	11.0	3.0
Hanzawaia nipponica ц	Yellow Sea	296	49	16.2	4.9	25.0	9.0
Hyalinea balthica ¥	North Sea	8	2	8.0	120.0	1.0	0.3
Labrospira cf. *kosterensis* ¥	OMZ-Peru	3139	845	51.0	12.0	57.0	12.0
Melonis barleeanus ¥	North Sea	9	3	14.0	20.0	0.6	0.2
Nonionella cf. *stella* ɬ	OMZ-Chile	186	24	5.2	0.7	35.0	5.0
Nonionella pulchella ɮ	Bering Sea	31	7	6.7	2.0	7.6	2.2
Nonionella stella ʖ	Yellow Sea	162	27	53.0	3.9	3.0	0.6
Nonionella stella ц	Yellow Sea	178	28	5.5	0.9	34.0	3.0
Nonionella stella ʒ	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	11.6	15.7
Protelphidium tuberculatum ц	Yellow Sea	232	26	3.7	0.5	68.0	9.0
Pyrgo elongata ¥	Rhône Delta	43	14	47.0	5.8	0.8	0.2
Pyrgo williamsoni ¥	North Sea	5	n.a.	47.0	0.0	0.1	n.a.
Pyrgoella sphaera ¥	North Sea	6	1	47.0	5.8	0.1	0.0
Stainforthia sp. var. I ¥	OMZ-Chile	60	46	0.3	0.0	180.0	29.0
Textularia cf. *tenuissima* ¥	OMZ-Peru	450	432	11.0	2.9	43.0	7.0
Uvigerina elongatastriata ¥	Bay of Biscay	274	244	5.1	0.6	60.0	55.0
Uvigerina mediterranea ¥	Bay of Biscay	101	66	20.0	6.6	6.0	4.0
Uvigerina peregrina ɮ	Bering Sea	74	20	9.9	4.1	10.0	4.7
Uvigerina peregrina ¥	North Sea	332	184	20.0	6.6	16.0	9.0
Uvigerina phlegeri ¥	Rhône Delta	444	44	8.4	0.2	209.0	48.0
Valvulineria bradyana ¥	Rhône Delta	1268	164	15.0	1.4	95.0	15.0
Valvulineria cf. *laevigata* ¥	OMZ-Peru	865	640	19.0	3.7	25.0	12.0
Valvulineria inflata ж	OMZ-Peru	17666	5319	135.4	16.4	120.1	34.1
Verneuilinulla advena ц	Yellow Sea	86	15	2.5	0.3	34.0	3.0

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Table 3: Summary of benthic foraminifer from different environments that lack intracellular nitrate (NO_3^-) storage. Only species with intracellular [NO_3^-] < 0.1 mM are listed. Species in **bold** letters have been found to store NO_3^- in other environments (see table 2). ¥: Data from (Piña-Ochoa et al., 2010b); ʒ: Data from (Xu et al., 2017).

Species	Location	Species	Location
Agglutinated sp. ¥	Rhône Delta	***Hyalinea balthica*** ¥	North Sea
Ammonia beccarii ¥	Rhône Delta	Komokiacea ¥	OMZ-Peru
Ammonia beccarii ¥	Bay of Biscay	*Labrospira* cf. *subglobosa* ¥	OMZ-Peru
Ammonia sp. ¥	Limfjorden	***Melonis barleeanus*** ¥	Rhône Delta
Ammonia tepida ¥	Aiguillon Bay	*Nonion scaphum* ¥	Rhône Delta
Arenoparella asiatica ʒ	Yellow Sea	*Nonion scaphum* ¥	Bay of Biscay
Bathysiphon cf. *argenteus* ¥	OMZ-Peru	*Nouria polymorphinoides* ¥	Bay of Biscay
Bathysiphon minutus ¥	Skagerrak	*Pelosina variabilis* ¥	Skagerrak
Biloculinella depressa ¥	North Sea	*Pseudoeponides falsobeccarii* ¥	Rhône Delta
Bolivinita quadrilatera ¥	Bay of Biscay	*Quinqueloculina seminulum* ¥	Skagerrak
Bulimina aculeata ¥	Rhône Delta	*Quinqueloculina seminulum* ¥	Bay of Biscay
Bulimina marginata ¥	Rhône Delta	*Quinqueloculina seminulum* ¥	Rhône Delta
Cibicidoides pachyderma ¥	Bay of Biscay	*Quinqueloculina* sp. ¥	OMZ-Perú
Crithionina hispida ¥	OMZ-Peru	*Reophax micaceus* ¥	Bay of Biscay
Cyclammina cancellata ¥	Bay of Biscay	*Reophax* sp. ¥	OMZ-Perú
Cypris subglobosus ¥	Bay of Biscay	*Rhabdammina inaequalis* ¥	North Sea
Dentalina sp. ¥	Rhône Delta	*Saccammina* sp. ¥	Bay of Biscay
Epistominella exigua ¥	OMZ-Peru	*Technitella legumen* ¥	Skagerrak
Gyroidina altiformis ¥	Bay of Biscay	*Triloculina tricarinata* ¥	North Sea
H*aynesina germanica* ¥	Aiguillon Bay	***Uvigerina peregrina*** ¥	Bay of Biscay
Hippocrepinella alba ¥	Skagerrak		

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Figures

Figure 1:

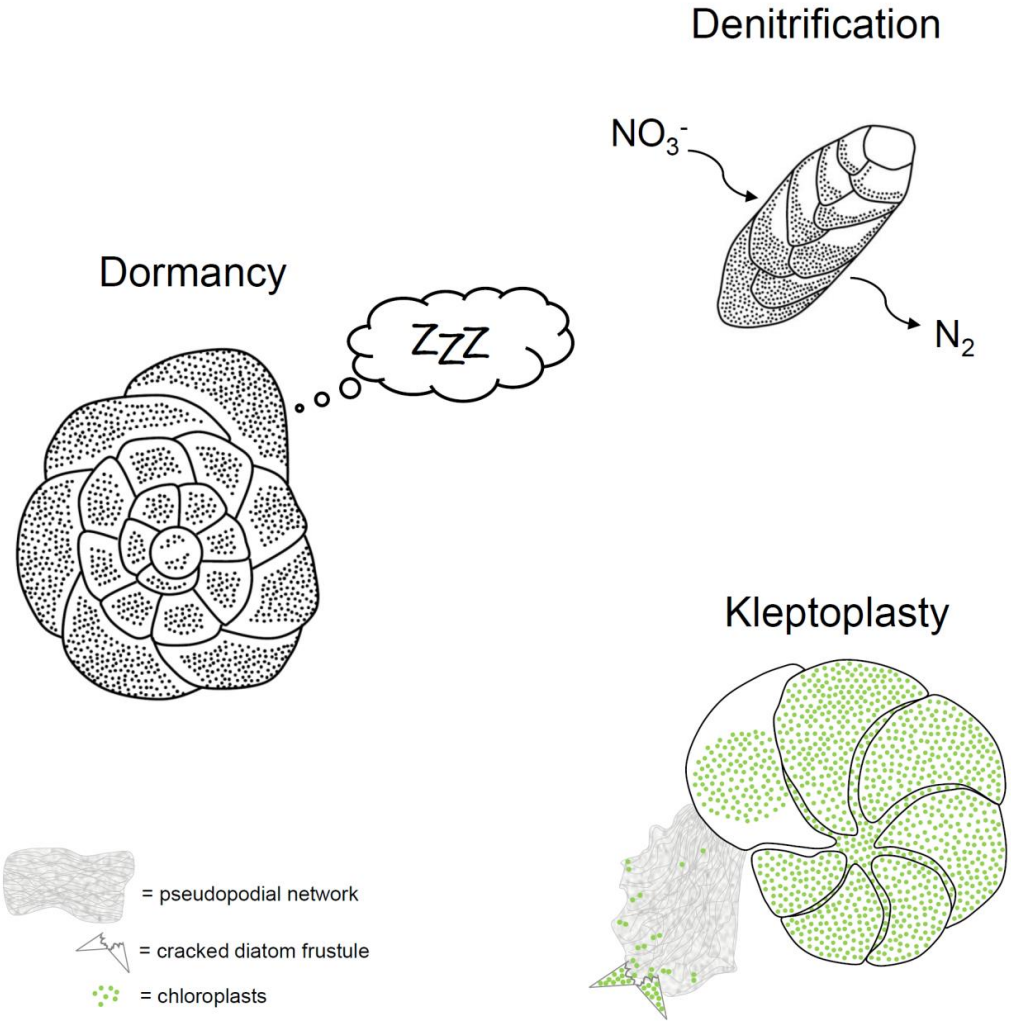

Fig. 1: Schematic representations for three survival strategy examples performed by benthic foraminifera under O_2 depleted conditions.

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Figure 2:

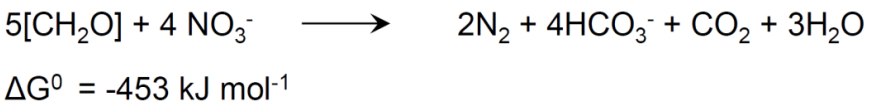

Fig. 2: Stoichiometry for heterotrophic denitrification. Organic matter is oxidized using nitrate (NO_3^-) as an electron acceptor in a similar way O_2 is used for O_2 respiration. This process provides energy for the organism for oxidative phosphorylation. [CH_2O) symbolizes organic matter of unspecified composition. ΔG^0 value relates to PH of 7. Taken from (Jorgensen, 2006).

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Figure 3:

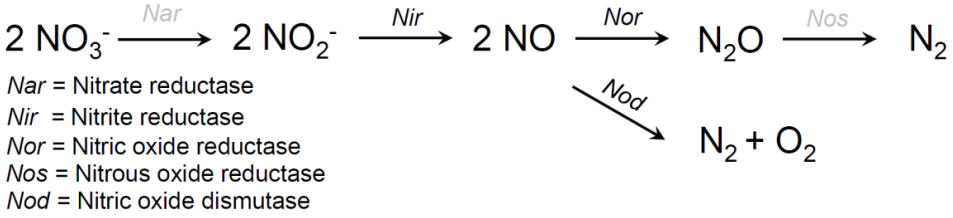

Fig. 3: Schematic view of two alternative pathways suggested for foraminiferal denitrification. Abbreviations above the reaction arrows indicate the enzymes that are catalyzing the respective step (see legend). Enzymes in black have been found transcribed by eukaryotic (foraminiferal) RNA (Woehle et al., 2018). Enzymes in grey are missing in the foraminiferal denitrification pathway and are likely performed by bacterial symbionts (Woehle et al., 2022). The straight pathway above describes the normal heterotrophic denitrification pathway. The junction, catalyzed by the Nod, which produces O_2, has been suggested as an alternative pathway for foraminiferal denitrification (Woehle et al., 2018).

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Figure 4:

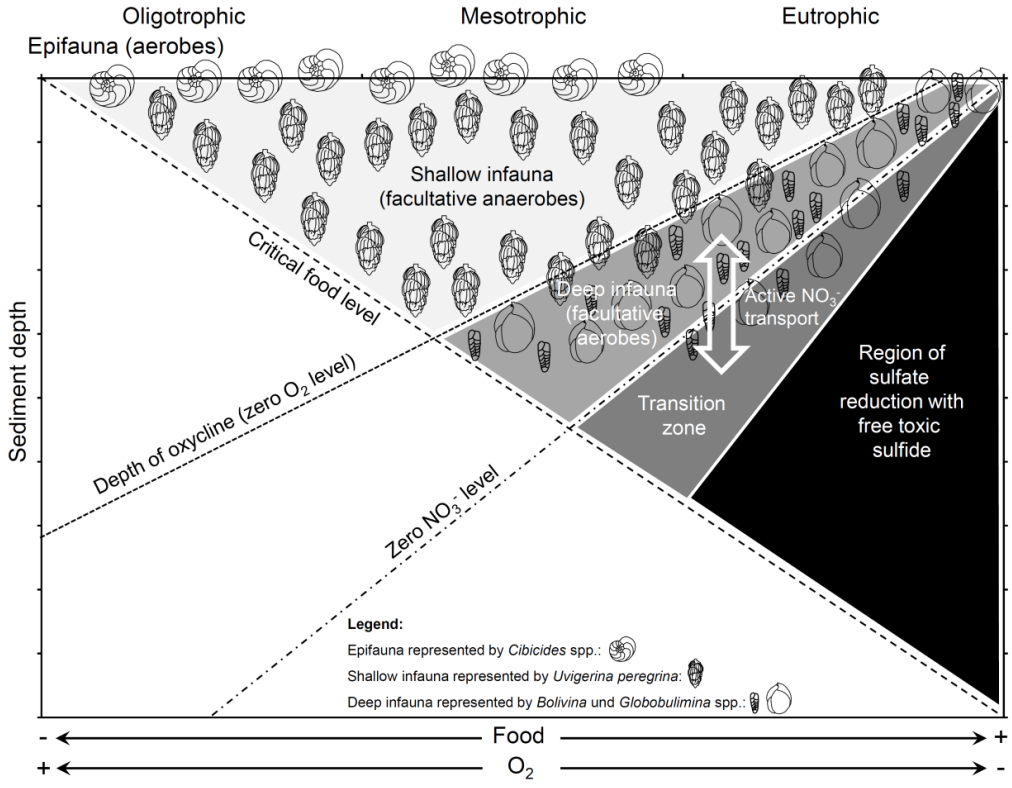

Fig.4: TROX model modified after Jorissen et al. (1995) and Xu et al. (2021). The supply of organic matter in different environments controls the penetration depth of O_2 and NO_3^- into the sediment. Benthic foraminifera choose their microhabitat according to their metabolic preferences for O_2 or NO_3^- as an electron acceptor and the availability of food. **Epifaunal** – **aerobic** species depend purely on O_2 and live on top the sediment or elevated substrate. They are well adapted to collect fresh food supply and survive even in oligotrophic environments. **Shallow infaunal – facultative anaerobic** species are well adapted to switch between O_2 and NO_3^- respiration. If they store NO_3^- for denitrification they can even migrate and survive below the oxycline, when they have to. Though, if food supply is getting critical they can migrate close to the sediment surface and easily withstand exposure to O_2. **Deep infaunal – facultative aerobes** prefer NO_3^- over O_2 and try to avoid O_2, because even trace amounts of O_2 inhibit denitrification. Thus, they thrive below the oxycline, when there is still enough supply of NO_3^- and usually migrate upwards, when the oxycline shallows. They are able to survive short periods in the transition zone below the NO_3^- penetration depth, due to their high intracellular NO_3^- storage but are likely limited in depth by the region of sulfate reduction due to the presence of free toxic sulfide. Note that they also can actively transport intracellular NO_3^- below the NO_3^--penetration depth in the sediments. For further details see text.

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Figure 5:

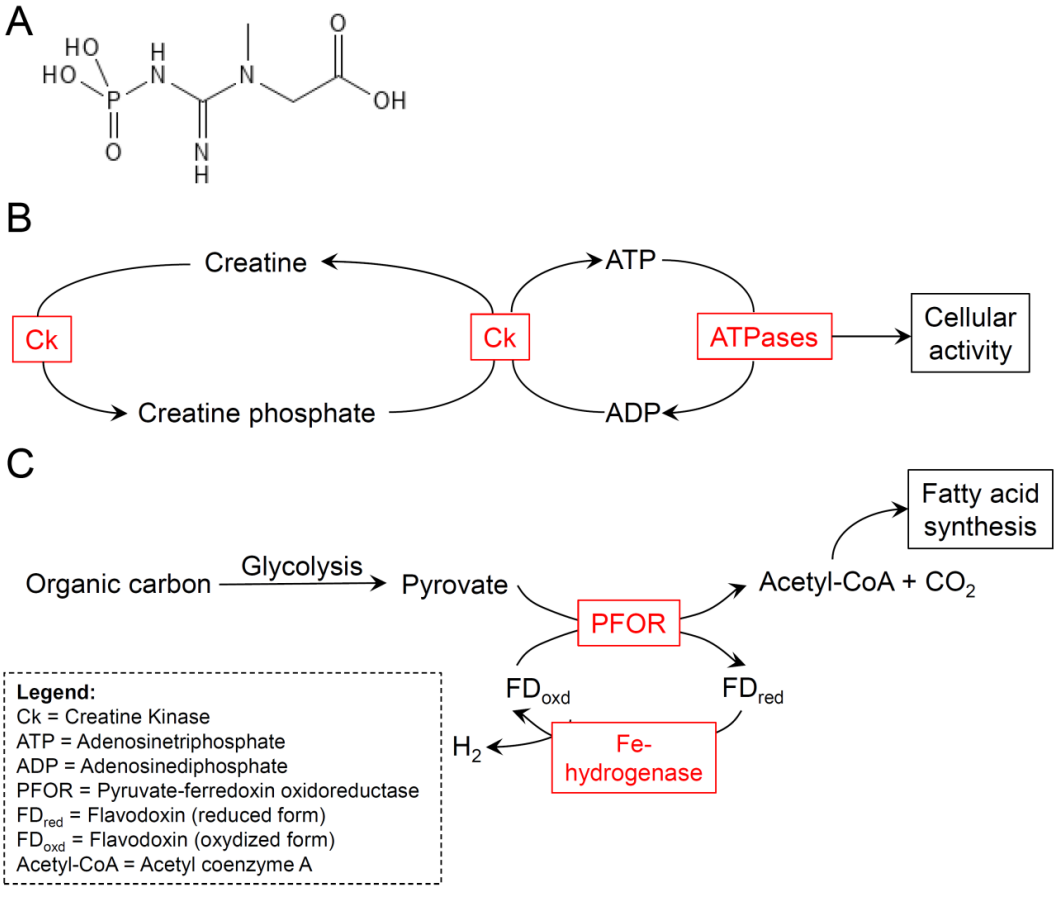

Fig. 5: Examples for molecules and processes that are relevant in the anaerobic metabolism of foraminifera. A: Structural formula of creatine phosphate. B: The role of creatine kinase (Ck) and creatine phosphate in the anaerobic metabolism. High energy creatine phosphate is produced by phosphorylation of creatine. Creatine phosphate can rapidly recycle ADP to ATP to provide resources for rapid energy bursts. This pathway has been described by Orsi et al.(2020). C: Fermentation has been found to be relevant in the anaerobic metabolism of foraminifera by both Orsi et al.(2020) and Gomaa et al. (2021). The possibility of a H_2 producing fermentation pathway, catalyzed by Fe-hydrogenase has been described by Gomaa et al. (2021).

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Figure 6:

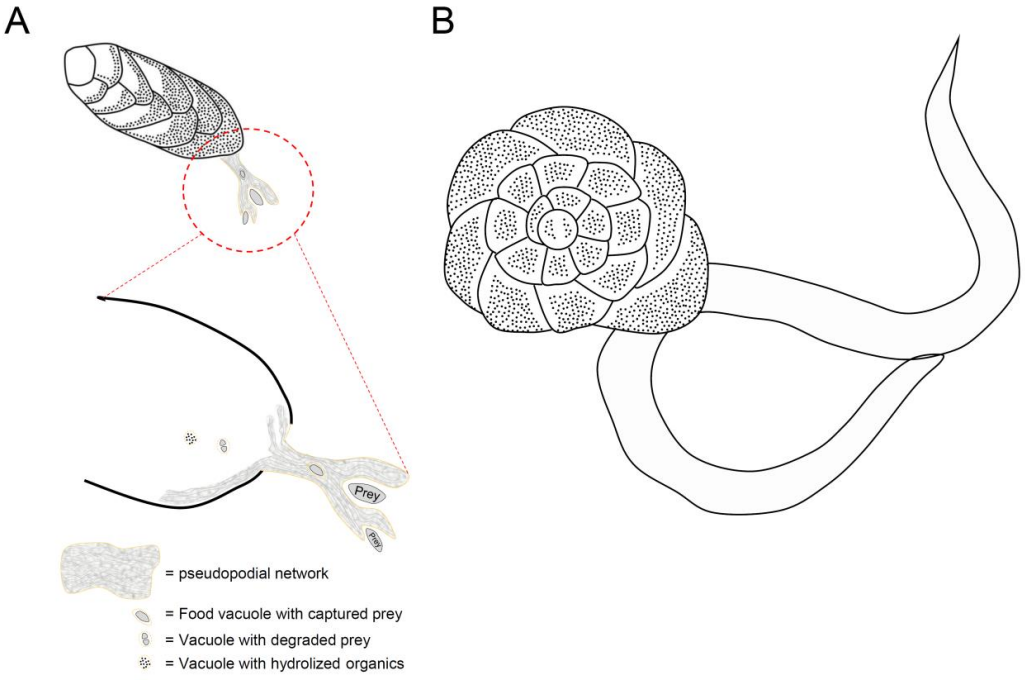

Fig. 6: A: Schematic representation of a *bolivinid* ingesting bacterial cells. Recent studies showed that benthic foraminifera from O_2 depleted habitats have the capacity of phagocytosis even under anoxia (Orsi et al., 2020). B: Schematic representation of *Ammonia* sp. preying on a nematode. Some benthic foraminifera are known to prey on meiofauna (Dupuy et al., 2010) and there is evidence, that even some *globobuliminids* that usually thrive under anaerobic conditions might prey on nematodes (Glock et al., 2019a).

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Figure 7:

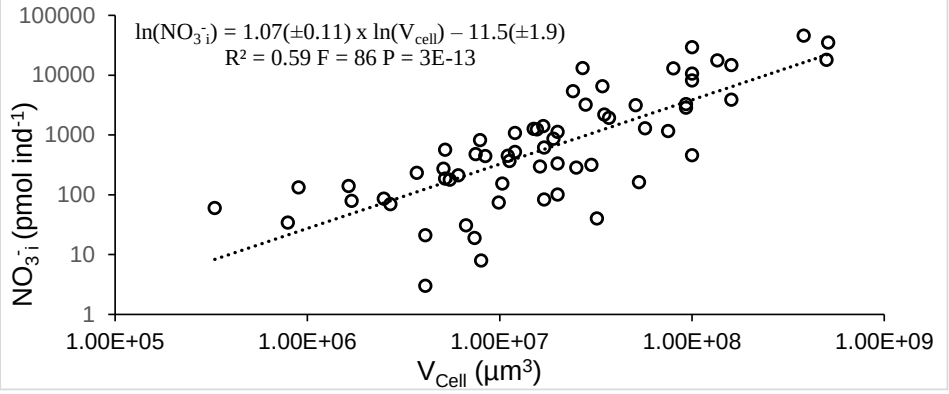

Figure 7: Log-log plot and power regression of intracellular NO_3^- content ($NO_{3\,i}^-$) against the biovolume (V_{cell}) of benthic foraminifera from from diverse environments (Tab. 2). Only species with an intracellular $[NO_3^-] \geq 1$ mM, where both $NO_{3\,i}^-$ and V_{cell} were published were considered for the power regression.