

1 **Reviews and syntheses: Benthic foraminifera and gromiids**
2 **from oxygen depleted environments - Survival strategies,**
3 **biogeochemistry and trophic interactions**

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The oceans are losing oxygen (O₂) and oxygen minimum zones are expanding, due to climate warming (lower O₂ solubility) and eutrophication related to agriculture. This trend is challenging for most marine taxa that are not well adapted to O₂ depletion. For other taxa this trend might be advantageous, because they can withstand low O₂ concentrations or thrive under O₂ depleted or even anoxic conditions. Benthic foraminifera are a group of protists that include taxa with adaptations to partly extreme environmental conditions. Several species possess adaptations to O₂ depletion that are rare amongst eukaryotes and these species might benefit from ongoing ocean deoxygenation. In addition, since some foraminifera can calcify even under anoxic conditions they are important archives for paleoceanographic reconstruction in O₂ depleted environments. This paper reviews the current state of knowledge about foraminifera from low O₂ environments. Recent advances to understand specific survival strategies of foraminifera to withstand O₂ depletion are summarized and discussed. These adaptations include an anaerobic metabolism, heterotrophic denitrification, symbiosis with bacteria, kleptoplasty and dormancy and have a strong impact on their preferred microhabitat in the sediments, especially the ability to denitrify by some benthic foraminiferal species. Benthic foraminifera also differ regarding their trophic strategies which has additional impact on the selection of their microhabitat. For example, some species are strict herbivores that feed exclusively on fresh phytodetritus and live close to the sediment surface, while some species are non-selective detritivores that occupy intermediate to deep infaunal habitats. There is evidence that foraminifera have the capacity of phagocytosis, even under anoxia, and some foraminiferal species, which can withstand low O₂ conditions, seem to prey on meiofauna. Also, due to their high abundances in O₂ depleted environments and their metabolic adaptations, benthic foraminifera are key players in marine nutrient cycling, especially within the marine N and P cycles. This review summarizes the denitrification rates for the species that are known to denitrify and the intracellular nitrate concentrations of the species that are known to intracellularly store nitrate. Finally, equations are provided that can be used to estimate the intracellular nutrient storage and denitrification rates of foraminifera and might be integrated into biogeochemical models.

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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 O₂ depleted environments. About a decade later, Koho and Piña-Ochoa (2012) published another overview about benthic foraminifera as inhabitants in low-O₂ 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, advances in methods to analyze the metabolic rates, intracellular nitrate storage and molecular genetics of foraminifera have changed our understanding of strategies such as an anaerobic metabolism that help them to withstand O₂ depletion. This paper aims to summarize these developments, mainly focusing on benthic foraminifera. For the discussion about life in habitats, where O₂ is scarce or absent it is important to define the range of O₂ concentration for terms such as anoxia, hypoxia, suboxic or oxic conditions. The concentration range for these terms varies with literature. To avoid confusion, this review will only use the following definitions from literature:

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Anoxia usually indicate the complete absence of O₂ ([O₂] = 0 μM; Diaz, 2016)

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Suboxic conditions indicate habitats, where O₂ is low enough that denitrification and Mn- and Fe-reduction but sulfide concentrations are still low, due to the absence of sulfate reduction ([O₂] ~ 1-10 μM; Oakley et al., 2007)

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Hypoxia in aquatic environments indicate habitats where O₂ is present but the O₂ saturation is less than 30%, since most fish cannot survive below 30% saturation ([O₂] < 62.5 μM Levin et al., 2009).

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Low O₂ or O₂ depleted habitats will summarize all environments that fulfil one of the above definitions (i.e., every environment where [O₂] is < 62.5 μM)

54

Knowledge about planktic foraminifera from O₂ depleted habitats is scarce compared to the 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). As a result, *G. hexagonus* has proven to be a valuable paleo-indicator for the presence of pelagic OMZs during the Pliocene (Davis et al., 2023). Benthic foraminifera from low O₂ environments have also been established as an invaluable archive for paleoceanography. However, this review will touch on summarizing redox proxies based on benthic foraminifera only briefly, since there is work in progress to give a comprehensive review about proxies for O₂

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61 concentrations in paleoceanography (Hoogakker et al., in prep). Due to their ability to precipitate their calcitic tests
62 even under anoxic conditions, fossil benthic foraminifera became routine tools in paleoceanography to reconstruct
63 past redox conditions (Nardelli et al., 2014; Orsi et al., 2020). Some morphological adaptations are very common
64 for benthic foraminifera that thrive in O₂ depleted habitats. Small, more elongated and flattened morphologies are
65 often characteristic for O₂ depletion, while more spherical forms can indicate oxygenated conditions (Bernhard,
66 1986; Bernhard et al., 1997). In addition, high porosity and thin test walls seem to be characteristic for foraminifera
67 that live in low O₂ environments (Kaiho, 1994). The porosity, including pore size and pore density, of foraminiferal
68 tests recently received more attention as possible paleoceanographic tool. Different foraminiferal species seem to
69 adapt their pore characteristics in a different way to environmental conditions. *Cibicides* spp. for example mainly
70 thrive in well oxygenated environments (Mackensen et al., 1995) and the porosity in epifaunal *Cibicides* spp. and
71 *Planulina* spp. is significantly negatively correlated to the O₂ concentrations in the bottom water (Rathburn et al.,
72 2018; Glock et al., 2022). If O₂ is too depleted, these foraminifers increase their porosity to optimize the O₂ uptake.
73 Furthermore, the mechanism of biomineralisation in foraminifera can preserve the chemical signature of ambient
74 seawater in their test calcite. These species precipitate their test calcite directly from vacuolized seawater (Erez,
75 2003; de Nooijer et al., 2014; Toyofuku et al., 2017) and thus the chemical composition of the test calcite reflects
76 the chemical composition of the surrounding water in their habitats. Different element/Ca ratios are used as proxy
77 for various parameters. Over the past decades several redox sensitive element/Ca ratios in foraminiferal calcite
78 were identified as potential O₂ proxies, where Mn/Ca (Reichert et al., 2003; Barras et al., 2018; Brinkmann et al.,
79 2021) and I/Ca (e.g., Zhou et al., 2014, 2022; Lu et al., 2016; Glock et al., 2019d; Winkelbauer et al., 2021; Cook
80 et al., 2022) are amongst the most prominent examples. The offset of the stable carbon isotope fractionation ($\delta^{13}\text{C}$)
81 between the tests of epifaunal and deep infaunal benthic foraminifera can also be used as a quantitative [O₂]_{BW}
82 proxy (e.g., McCorkle and Emerson, 1988; Schmiedl and Mackensen, 2006; Hoogakker et al., 2014, 2018). Finally,
83 species compositions of benthic foraminifera assemblages are used to reconstruct past environmental conditions.
84 Kaiho et al. (1994) developed the first benthic foraminifera O₂ index (BFOI). Further development of this index is
85 still going on with recent developments by Tetard et al., 2021 and Kranner et al., 2022.

86 The first part of the present paper reviews recent advances in our understanding of the diverse strategies
87 that foraminifera use to withstand O₂ depletion, focusing mainly on denitrification, dormancy and kleptoplasty.
88 The part about foraminiferal denitrification also incorporates denitrification into the conceptual TROX model of
89 Jorissen et al. (1995). The TROX model explains the sediment microhabitats of benthic foraminifera in terms of
90 an interplay in the supply of O₂ and non-refractory organic matter that can be used as food. The next section briefly
91 summarizes the knowledge about ecological and trophic interactions of foraminifera from O₂ depleted
92 environments. Finally, the role of foraminifera in marine biogeochemical cycling will be discussed, with a focus
93 on nitrogen and phosphorous cycling.

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95

2.1 Survival strategies

96 Some benthic foraminiferal species have very specific adaptations that provide the opportunity either to
97 thrive in anoxia or at least to survive periods of O₂ depletion (see examples in fig. 1).

98 2.1.1 Foraminiferal denitrification

99 More than a decade ago first evidence emerged that some foraminifera from O₂ depleted environments
100 are able to perform complete denitrification (Risgaard-Petersen et al., 2006). Heterotrophic denitrification
101 describes the step-by-step reduction of nitrate (NO₃⁻) to inert N₂ gas (Eq. 1 according to Jorgensen, 2006 & Fig.
102 2).



104 ,where [CH₂O] symbolizes organic matter of unspecified composition.

105 Heterotrophic denitrification provides energy to an organism for oxidative phosphorylation in a similar
106 way as O₂ respiration. The ΔG^0 for heterotrophic denitrification per mol carbon at a pH of 7 is -453 kJ mol⁻¹,
107 which is slightly less efficient O₂ respiration ($\Delta G^0 = -479$ kJ mol⁻¹ according to Jorgensen, 2006).

108 The discovery of foraminiferal denitrification by Risgaard-Petersen et al. (2006) was also the first
109 evidence for complete denitrification in eukaryotic cells in general and it showed that they likely take up NO₃⁻
110 from the surrounding pore water and store it within intracellular seawater vacuoles. Nevertheless, no later study

111 could actually proof a bonafide “complete” denitrification pathway in foraminifera and the eukaryotic
112 foraminiferal denitrification pathway is today considered to be incomplete (Woehle et al., 2018; Orsi et al, 2020;
113 Gomaa et al., 2021; see discussion below). Other eukaryotes that are known to perform incomplete denitrification
114 are the primitive eukaryote *Loxodes* (Finlay et al., 1983) and two species of fungi (Usuda et al., 1995).

115 Four years after the study by Risgaard-Petersen et al. (2006), Pina-Ochoa et al. (2010b)
116 documented that intracellular NO_3^- storage and denitrification are not an exception, limited to a few specialized
117 foraminiferal species, but actually a widespread phenomenon. Within a couple of years more studies either
118 quantified denitrification rates or the intracellular NO_3^- storage of various foraminifera and gromiid species
119 (Høgslund et al., 2008; Glud et al., 2009; Piña-Ochoa et al., 2010b, a; Koho et al., 2011; Bernhard et al., 2012b).
120 The intracellular NO_3^- storage can reach concentrations up to 567 mM in gromiids (Piña-Ochoa et al., 2010b) and
121 experiments with isotopically labeled NO_3^- showed that *Globobulimina turgida* takes up NO_3^- in a similar rate,
122 independently of the presence or magnitude of the intracellular NO_3^- pool (Koho et al., 2011). It has been
123 hypothesized that at least some denitrifying foraminifera seem to take up NO_3^- through the pores in their tests and
124 the pore-density (# of pores per area) of some denitrifying species, such as *Bolivina spissa* turned out to be a
125 promising proxy for quantitative NO_3^- reconstructions (Glock et al., 2011, 2018). However, not all benthic
126 foraminifera are able to denitrify, even if they live in environments that are periodically exposed to anoxia such as
127 representatives of the intertidal species morphogroup *Ammonia tepida* (either *Ammonia venata*, *Ammonia*
128 *aberdoveyensis* or *Ammonia confertitesta* according to Hayward et al., 2021), which neither store NO_3^- nor show
129 any denitrification activities (Piña-Ochoa et al., 2010b). Some foraminifera from the Bering Sea have been shown
130 to store NO_3^- but did not denitrify in incubation experiments (Langlet et al., 2020). These species include
131 *Nonionella pulchella*, *Uvigerina peregrina* and *Bolivinelina pseudopunctata*. Also, the NO_3^- storage in *U.*
132 *peregrina* shows a high variability, depending on the environment. Individuals of *U. peregrina* from the Bay of
133 Biscay lack a significant NO_3^- storage, while *U. peregrina* from the North Sea and the Bering Sea both show
134 intracellular NO_3^- enrichments (Piña-Ochoa et al., 2010b, Langlet et al., 2021). Other *Uvigerina* and *Nonionella*
135 species have been shown to denitrify (Risgaard-Petersen et al., 2006; Høgslund et al., 2008; Piña-Ochoa et al.,
136 2010b; Glock et al., 2019b; Gomaa et al., 2021). Many miliolids and allogromiids, several intertidal rotaliid
137 species but also some other rotaliids and textulariids completely lack an intracellular NO_3^- storage (Piña-Ochoa et
138 al., 2010b).

139 The observations that some species store NO_3^- and denitrify in some environments and in others not might
140 have two reasons. One reason could be that these species belong to an opportunistic group of foraminifera that can
141 well adapt to both oxygenated environments where they respire O_2 and do not denitrify and O_2 depleted
142 environments where they switch to denitrification. The other reason could be that some of these foraminifera
143 belong to morphogroups that are identified as a single species but indeed are a mixture of cryptic and pseudocryptic
144 species that include denitrifying and non-denitrifying species. An example for such a morphogroup that has
145 recently had a revision is *A. tepida*. This morphogroup includes three species (*A. venata*, *A. aberdoveyensis* or *A.*
146 *confertitesta*) that now can be morphologically distinguished (Richirt et al., 2019; Hayward et al., 2021). A similar
147 case concerns the morphogroup *Nonionella stella*, where representatives have been found to denitrify (Høgslund
148 et al., 2008; Choquel et al., 2021). The morphogroup *N. stella* also consists out of several cryptic to pseudocryptic
149 species (Deldicq et al., 2019). The situation might be similar with other *Nonionella* species and the widespread
150 species *U. peregrina*.

151 There is strong evidence for symbiosis between foraminifera and prokaryotes in many hosts from O_2
152 depleted environments, which most likely are an adaptation to survive within the steep geochemical gradients close
153 to the oxic/anoxic boundary (Bernhard et al., 2000; Bernhard, 2003; Bernhard et al., 2006; Nomaki et al., 2014;
154 Bernhard et al., 2018). Most of the observed prokaryotic associates are endobionts within the foraminiferal
155 cytoplasm but some are ectobionts that often are observed close to the pores in the foraminiferal shell (Bernhard
156 et al., 2001, 2010a, 2018). For about a decade after the first discovery of foraminiferal denitrification it remained
157 unclear if foraminifera indeed denitrify themselves, or if the bacterial symbionts are responsible for the
158 denitrification. Evidence came up for both hypotheses. Bernhard et al. (2012b) showed that *Bolvina argentea*
159 consumed its intracellular NO_3^- storage in O_2 free incubations even after a very harsh treatment with antibiotics,
160 which indicates that this species can denitrify even, when the activity of potential bacterial symbionts would be
161 inhibited. Other studies showed that bacterial endobionts likely perform denitrification in some allogromiid
162 foraminifera and gromiid species (Bernhard et al., 2012a; Høgslund et al., 2017). Gromiida are a separate group
163 of protists within the Rhizaria and closely related to foraminifera. With the recent advances in molecular biology,
164 however, it became possible to analyze the transcriptome of denitrifying foraminifera and Woehle & Roy et al.
165 (2018) showed that the enzymes responsible for denitrification in *Globobulimina spp.* from a Swedish O_2 depleted

166 Fjord basin are indeed transcribed by eukaryotic RNA. These enzymes are homologues of enzymes that are also
167 used by bacteria for denitrification, which indicates an ancient prokaryotic origin of denitrification in foraminifera.
168 Nevertheless, the homologues of the enzymes that catalyze the first and the last step of foraminiferal denitrification
169 (Reduction of NO_3^- to nitrite (NO_2^-) and reduction of nitrous oxide (N_2O) to N_2 gas; fig. 2) have not been identified,
170 yet. This indicates that foraminifera use other enzymes to catalyze these steps, or that they rely on bacterial
171 symbionts for these steps, or that they use an alternative denitrification pathway in general.

172 One hypothesis, brought up by Woehle & Roy et al. (2018) is that the homologue of the nitric oxide
173 reductase (Nor) is indeed a nitric oxide dismutase that has been proposed to catalyze the enzymatic reaction 2NO
174 $\rightarrow \text{N}_2 + \text{O}_2$ (alternative pathway in fig. 2) (Ettwig et al., 2012). The presence of the eukaryotic denitrification
175 pathway found in foraminifera (Woehle & Roy et al., 2018) has been confirmed through other analyses of
176 foraminiferal transcriptomes (Orsi et al., 2020; Goma et al., 2021). Goma et al. (2021) also identified an enzyme
177 of yet unknown functionality that might be responsible for the first step in the foraminiferal denitrification
178 pathway. Recent metagenomics and transcriptomics results of denitrifying foraminifera indicate that bacterial
179 symbionts might perform the missing steps in the foraminiferal denitrification pathway or that they at least partly
180 contribute to the amount of NO_3^- that is denitrified within foraminiferal cells (Woehle & Roy et al., 2022). It has
181 already been hypothesized before that the ectobionts, found on *Bolivina pacifica* from the Santa Barbara Basin are
182 either sulfate reducing or sulfur oxidizing bacteria (Bernhard et al., 2010a). The possible complementation of the
183 foraminiferal denitrification with bacterial symbionts appears to be contradictory to the results by Bernhard et al.
184 (2012b) who showed that *B. argentea* consumed its intracellular NO_3^- storage (likely for denitrification) even
185 after the antibiotics treatment. Goma et al. (2021) confirmed that *B. argentea* also lacks the first and last
186 denitrification step in its transcriptome, although it lacks intracellular bacterial symbionts (Bernhard et al., 2012b).
187 Future studies might decipher, if indeed bacteria are responsible for the missing denitrification step and are immune
188 to such antibiotic treatment, if an oxygenic nitric oxide dismutase skips the last denitrification step as discussed
189 by Woehle & Roy et al. (2018) and/or if foraminifera have unknown enzymes that catalyze the missing steps as
190 suggested by Goma et al. (2021). The study by Woehle & Roy et al. (2022) also reconstructed that the last
191 common ancestor of denitrifying foraminifera likely has its origin during the Cretaceous, possibly related to the
192 occurrence of the Cretaceous Anoxic Events. Since the foraminiferal denitrification pathway is incomplete and the
193 first and last steps might be performed by Desulfobacteraceae in their microbiome the authors suggested that the
194 acquisition of denitrification ability in foraminifera occurred in multiple stages (starting during the Cretaceous)
195 but is not yet complete (Woehle & Roy et al., 2022).

196 It is noteworthy that denitrifying foraminifera from the Peruvian OMZ show a metabolic preference of
197 NO_3^- over O_2 as an electron acceptor (Glock et al., 2019b). These foraminifera show an increasing cell volume
198 with increasing ambient NO_3^- and decreasing O_2 concentrations. Similar observations have been made at the
199 California Borderlands, where some benthic foraminifera also increase their cell-volume with decreasing ambient
200 O_2 concentrations (Keating-Bitonti and Payne, 2017). Additional evidence for the metabolic NO_3^- preference came
201 from comparing denitrification and O_2 respiration rates and scaling them to their cell volume (Glock et al., 2019b).
202 The scaling is lower for O_2 respiration than for denitrification, indicating that the NO_3^- metabolism during
203 denitrification is more efficient than the O_2 metabolism during aerobic respiration in foraminifera from the
204 Peruvian OMZ. This might explain, why some infaunal denitrifying foraminifera follow the oxycline within
205 sediments (Linke and Lutze, 1993; Duijnste et al., 2003). We have to keep in mind that O_2 can be quite harmful
206 for organisms that are not adapted to higher O_2 concentrations, due to its strong reactivity. Even trace amounts of
207 O_2 can inhibit denitrification and O_2 can repress the denitrifying enzyme synthesis (Smith and Tiedje, 1979;
208 Knowles, 1981; Tiedje, 1988; Mckenney et al., 1994). Thus, if denitrifying foraminifera are exposed to small
209 amounts of O_2 they cannot denitrify but also do not have enough O_2 to supply their demands for electron acceptors.
210 Larger amounts of O_2 might supply this demand but also harm the cell. For example, O_2 can inhibit the growth of
211 some obligate anaerobes poison enzymes that are important for their metabolism (Lu and Imlay, 2021). Also for
212 aerobes O_2 can be harmful. “Hyperoxia”, an excess supply of O_2 , leads to damaging effects by highly-reactive
213 metabolic products of O_2 (free O_2 radicals) that inactivate enzymes in the cell, damage DNA and destroy lipid
214 membranes (Frank and Massaro, 1980). Furthermore, foraminifera are able to store NO_3^- within vacuoles, due to
215 its lower reactivity and still have an electron acceptor reservoir if NO_3^- is depleted in their microhabitat. This is
216 not possible for O_2 due to its high reactivity (Auten and Davis, 2009). Finally, a review by Zimorski et al. (2019)
217 addresses the common misconception that the presence of O_2 improves the overall energetic state of the cell. It is
218 a fact that the energy yield from remineralizing glucose or amino acids is higher in the presence of O_2 (“ O_2
219 respiration”) but it is also a fact that the synthesis of biomass consumes thirteen times more energy per cell,
220 if O_2 is present, compared to anoxic conditions. This is related to the chemical equilibrium between organic matter

221 and CO₂, which strongly shifts to the side of CO₂ in the presence of O₂ (Zimorski et al., 2019). All this might
222 explain, why the metabolism of at least some foraminifera is better adapted to denitrification than to O₂ respiration.

223 The circumstance that some foraminifera have a metabolic preference of NO₃⁻ over O₂ as electron
224 acceptor (Glock et al., 2019b) and that other species like *U. peregrina* denitrify in some environments but
225 completely lack an intracellular NO₃⁻ storage in others (Piña-Ochoa et al., 2010b) might partly explain the
226 microhabitat selectivity of benthic foraminifera in the sediment. According to the conceptual TROX model,
227 benthic foraminifera can be divided into groups, due to their microhabitat preference: epifauna, shallow infauna,
228 intermediate infauna and deep infauna (Jorissen et al., 1995). The presence of this species specific microhabitat
229 structure has first been documented by Corliss (1985). These microhabitats are mainly controlled by bottom water
230 O₂ concentrations and the supply of non-refractory organic matter (i.e., food, Jorissen et al., 1995). Due to our
231 increasing understanding about the anaerobic metabolism of foraminifera we can now assume that NO₃⁻
232 availability is another controlling factor (Fig.3). This is also indicated by a study coupled early diagenetic modeling
233 with foraminiferal ecology to model the microhabitats of benthic foraminifera (Jorissen et al., 2022). According
234 to their metabolic preference for NO₃⁻ or O₂ as electron acceptors many benthic foraminifera species that typically
235 occupy a certain microhabitat (epifauna, shallow infauna and deep infauna) might partly be assigned to three
236 different attributes (Aerobe, facultative anaerobe and facultative aerobe). Most likely there are exceptions to these
237 classifications that will be discussed below. Another controlling factor on the microhabitat can be the specific
238 trophic strategy of the foraminiferal species, which is further discussed in section 3.

239 **Deep infaunal** species can most likely be considered as **facultative aerobes** that have a metabolic
240 preference of NO₃⁻ over O₂ (Glock et al., 2019b) and try to avoid trace amounts of O₂. They cannot be accounted
241 as obligate anaerobes, though, since they can withstand periods of oxygenation. Many experiments show that
242 denitrifying foraminifera can switch to O₂ respiration, if they are exposed to O₂ (i.e., Piña-Ochoa et al., 2010b),
243 Still, they follow the oxycline in the sediments to avoid the inhibition of denitrification by trace amounts of O₂.
244 The δ¹³C signature of shells of deep infaunal globobuliminids indicates that they calcify in sediment depth where
245 the pore water O₂ level reaches zero or even deeper in the sediments. The offset between δ¹³C of *Globobulima*
246 spp. tests and δ¹³C of epifaunal foraminifera or of bottom water dissolved inorganic carbon (DIC) is nearly equal
247 to the offset between DIC at the zero O₂ layer and the bottom water (Schmiedl and Mackensen, 2006) and often
248 can be even higher (Costa et al., 2023), indicating that many globobuliminids live even below the oxycline. Even
249 though they can switch to O₂ respiration (Piña-Ochoa et al., 2010b), these species most likely would try to avoid
250 crossing the oxycline since denitrification would be already inhibited by nM O₂ concentrations (Dalsgaard et al.,
251 2014) and the O₂ concentration slightly above the oxycline is not high enough to fulfil their metabolic demands.
252 Indeed, the model by Jorissen et al. (2022) describes the distribution of deep infauna very well, by using the
253 presence of O₂ as an inhibiting factor, which also promotes that they can rather be considered facultative aerobes
254 instead of facultative anaerobes. Taxa belonging to the deep infaunal group that might be considered as facultative
255 aerobes that prefer NO₃⁻ over O₂ include for example *Valvulineria inflata* and *bradyana*, *Bolivina seminuda*,
256 *Globobulimina pyrula*, *Globobulimina affinis* and *Cancris carmenensis* (Jorissen et al., 1995; Schmiedl and
257 Mackensen, 2006; Mojtabid et al., 2010; Glock et al., 2019b).

258 **Shallow infauna** can in many cases be considered as **facultative anaerobes** that are well adapted to the
259 presence of low O₂ concentrations but can switch to denitrification if they are exposed to anoxic conditions or need
260 to enter the deeper sediment parts to find food or avoid competitive stress. These species have the advantage that
261 they can utilize both fresh phytodetritus from the top of the sediments and organic matter of lower quality from
262 the deeper parts of the sediments. A good example for a shallow infaunal – facultative anaerobe species is *U.*
263 *peregrina*, that is well known for its shallow infaunal lifestyle (Schmiedl and Mackensen, 2006) and has been
264 found with or without intracellular NO₃⁻ storage in different environments (Piña-Ochoa et al., 2010b; Langlet et
265 al., 2020). Of course, it cannot be generalized that all foraminifera from a shallow infaunal habitat are indeed
266 facultative anaerobes. At least some species that can be considered shallow infaunal have been shown neither to
267 be able to store NO₃⁻ nor to denitrify. As mentioned above all specimens from the *Ammonia tepida* morphogroup
268 that have been analyzed so far lack an intracellular NO₃⁻ storage and cannot denitrify (Piña-Ochoa et al., 2010b).
269 Nevertheless, these taxa are often exposed to anoxia and can sometimes even be found alive in 4 to 26 cm sediment
270 depth (Alve and Murray, 2001; Thibault de Chanvalon et al., 2015). It is possible that these foraminifera indeed
271 only have an aerobe metabolism and just become dormant under exposure to anoxia (dormancy is discussed in
272 another section). Though, another possibility is that intertidal species such as *A. venata*, *A. aberdoveyensis* or *A.*
273 *confertitesta* have other adaptations to anoxia than denitrification. Recent studies revealed other possible anaerobic
274 metabolic pathways in foraminifera such as fermentation or dephosphorylation of creatine phosphate which are
275 discussed in section 2.1.3 (Orsi et al., 2020; Gomaa et al., 2021). Also, an *Ammonia* sp. has been shown to take up

276 nitrogen from ^{15}N labeled NO_3^- under O_2 depletion and to assimilate it within cell organelles known as electron
277 dense bodies (Nomaki et al., 2016). Eventually, studies on the transcriptome of non-denitrifying species from
278 infaunal environments might be able to show, if some of these species can switch an alternative anaerobe
279 metabolism under exposure to anoxia.

280 Many **epifaunal species** can most likely be considered as **aerobes** that typically occur at the sediment-
281 water interface or on elevated surfaces. Typical epifaunal – aerobe taxa include *Cibicides* spp. and *Planulina* spp.
282 (Corliss and Chen, 1988; Lutze and Thiel, 1989). These species have the advantage that they are well adapted to
283 collect fresh food supply from above (Wollenburg et al., 2021) but usually cannot withstand longer O_2 depleted
284 periods (Mackensen et al., 1995). Nevertheless, recent genetic data indicates that *Cibicidoides wuellerstorfi*
285 clusters very close to known denitrifying species in the phylogenetic tree, so it cannot be excluded that some
286 *Cibicides* spp. may denitrify under certain circumstances (Woehle & Roy et al., 2022). In the same way as for the
287 other microhabitats, not all species with an epifaunal lifestyle should be automatically considered as aerobes. There
288 are examples of epifaunal benthic foraminifera that have not been found in well oxygenated environments but
289 reach high abundances in O_2 depleted environments. One example is *Epistominella smithi*, which has been
290 described in low O_2 environments, such as the Santa Barbara Basin (Harman, 1964) or the Peruvian OMZ (Erdem
291 and Schönfeld, 2017). Nevertheless, the morphology of *E. smithi* strongly suggests an epifaunal lifestyle. Another
292 example is the epifaunal species *Planulina limbata*. This species is abundant only in O_2 depleted environments on
293 continental margins within the East Pacific (Natland, 1938; Erdem and Schönfeld, 2017; Glock et al., 2022).
294 Recent *P. limbata* specimens are present in severely O_2 depleted water masses within the Peruvian OMZ ($[\text{O}_2] =$
295 $3 - 12 \mu\text{mol/kg}$, Glock et al., 2022). Nevertheless, *P. limbata* also adapts its pore density to the availability of O_2
296 (Glock et al., 2022), which might indicate that it has an aerobic metabolism, despite that its presence appears to be
297 limited to low O_2 environments. Another possibility is that species such as *E. smithi* or *P. limbata* may denitrify
298 under certain circumstances and therefore can also be considered as facultative anaerobes. Hopefully,
299 measurements of metabolic rates, intracellular nutrient content and enzymatic activity might bring further evidence
300 in the future, if at least some epifaunal species can switch to an anaerobe metabolism, when O_2 is too depleted.

301 The **intermediate infauna** is somehow an exceptional case. Common representatives of intermediate
302 infaunal taxa are *Melonis barleeanus* or *Pullenia* spp. (Corliss, 1991). The typical example for intermediate
303 infaunal species *M. barleeanus* is interesting, since it either stores no or only very small amounts of NO_3^- (See
304 table 2 and 3). Still, several studies indicate that *M. barleeanus* lives deeper in the sediments than some *Uvigerina*
305 spp. (Corliss, 1991; Ní Fhlaithearta et al., 2018) although many *Uvigerina* species have been shown to store NO_3^-
306 and denitrify (Tab. 1&2). This might give room to speculate if *M. barleeanus* has other metabolic adaptations to
307 O_2 depletion than denitrification or if it simply does not store large amounts of NO_3^- but denitrifies NO_3^- directly
308 after the uptake from the seawater. Indeed, a recent study predicted the microhabitats of infaunal benthic
309 foraminifera using an early diagenetic model and showed that the intermediate infauna clusters around the NO_3^-
310 maximum in the pore water (Jorissen et al., 2022). Future perspectives on understanding the biology of
311 intermediate infauna might include transcriptome analyses to decipher other anaerobe metabolic pathways and
312 testing the denitrification capacity after incubation in NO_3^- -free and NO_3^- -containing seawater.

313 Note that the deep infauna can even migrate deeper into the sediments below the depth of NO_3^-
314 penetration, if they must, due to their ability to intracellularly store NO_3^- as a reservoir (Fig. 3). The deeper boundary
315 of the deep infauna might be controlled by the zone of sulfate reduction, where free sulfide is produced, which
316 could be toxic for the foraminifers. Research to measure denitrification rates in different benthic foraminiferal
317 species continues (Langlet et al., 2020; Choquel et al., 2021). This will add to the scarce available data and
318 contribute to estimates of the role of foraminifera in oceanic N-cycling. This topic is discussed a bit further in
319 section 4.

320 2.1.2 Kleptoplasty

321 Kleptoplasty describes a symbiosis between algal chloroplasts and a host organism that sequesters the
322 chloroplasts from algae (Clark et al., 1990). The word originates from the Greek word “Kleptes”, which means
323 “thief”. Kleptoplasty in foraminifera is most extensively studied for shallow *Elphidium* and *Haynesina* species that
324 often thrive within the photic zone and this research originated in the 1970s (Lopez, 1979; Lee et al., 1988; Correia
325 and Lee, 2000, 2002b, a; Goldstein et al., 2004; Pillet et al., 2011, 2013; Cevasco et al., 2015; Jauffrais et al., 2016,
326 2017, 2018; Cesbron et al., 2017; Goldstein and Richardson, 2018; Jesus et al., 2021). Several studies showed that
327 the sequestered chloroplasts in the intertidal species *Haynesina germanica* are still capable of photosynthesis under
328 light exposure (Lopez, 1979; Cesbron et al., 2017). *H. germanica* often shares the habitat with species from the
329 *Ammonia tepida* morphogroup (*Ammonia aberdoveyensis* or *Ammonia confertitesta* according to Hayward et al.,

330 2021) which also tend ingest chloroplasts but these chloroplasts do not show any photosynthetic activity anymore
331 (Jauffrais et al., 2016).

332 The kleptoplasts in foraminifera originate from diatoms, which has been confirmed on the basis of the
333 chloroplast shape in TEM-observations and by sequencing the chloroplasts using molecular biological methods
334 (Lopez, 1979; Lee et al., 1988; Cedhagen, 1991; Lee and Anderson, 1991; Bernhard and Bowser, 1999; Grzymiski
335 et al., 2002; Goldstein et al., 2004). Austin et al., (2005) hypothesized that the toothplates in *H. germanica* are
336 morphological adaptations to crack diatom frustules for access to their chloroplasts. Recently, LeKieffre et al.
337 (2018) showed in (aerated) incubation experiments with $\text{H}^{13}\text{CO}_3^-$ and $^{15}\text{NH}_4^+$ during a light/dark cycle that
338 *Haynesina germanica* is indeed able to fix inorganic carbon and nitrogen under light exposure. Intertidal
339 foraminifera are often exposed to O_2 depleted or even anoxic conditions, when water stagnates during low tide or
340 if they are transported to deeper anoxic sediment layers by bioturbation (Rybarczyk et al., 1996; Cesbron et al.,
341 2017). Oxygen penetration depths in tidal flats can vary between a few mm during low tide to several cm during
342 high tide (Jansen et al., 2009). Thus, intertidal foraminifera are often exposed to anoxia, even within the first cm
343 of the sediment column. *H. germanica* is also supposed to occur in black sediments of the British salt marsh tide
344 pools (Bernhard and Bowser, 1999), which likely become anoxic during a tidal cycle (Rybarczyk et al., 1996) and
345 it was among the first recolonizers of a Fjord suffering of organic pollution (Cato et al., 1980; Bernhard and
346 Bowser, 1999). Kleptoplasty might thus be an additional adaptation of foraminifera from photic environments to
347 stay active during periods of O_2 depletion, which already has been hypothesized by Cesbron et al., 2017.

348 Less well understood is the phenomenon of kleptoplasty, observed in the benthic foraminifers *Nonionella*
349 *stella*, *Virgulina fragilis* and *Nonionellina labradorica* that can thrive below the photic zone and often inhabit O_2
350 -depleted sediments (Cedhagen, 1991; Bernhard and Bowser, 1999; Grzymiski et al., 2002; Bernhard, 2003;
351 Tsuchiya et al., 2015; Jauffrais et al., 2019; Gomaa et al., 2021; Powers et al., 2022). Experiments to test if *N.*
352 *labradorica* is able to photosynthesize with its sequestered chloroplasts have been inconclusive. While Cedhagen
353 (1991) found active photosynthesis in *N. labradorica* specimens incubated with ^{14}C , Jauffrais et al. (2019) showed
354 an increased O_2 respiration rate instead of O_2 production and chloroplast degradation in specimens exposed to
355 light. Recently, Gomaa et al. (2021) found chloroplast encoded in transcripts of *N. stella*, indicating that the
356 kleptoplasts in this species are still active. Genetic analyses revealed that the kleptoplasts in *N. stella* and *N.*
357 *labradorica* are also mainly sequestered from diatoms, most likely after ingestion and selective digestion of
358 phytodetritus (Grzymiski et al., 2002; Jauffrais et al., 2019; Gomaa et al., 2021). Grzymiski et al. (2002) calculated
359 that the required amount of light for *N. stella* specimens collected from aphotic depths at the Santa Barbara Basin
360 is too low to sustain active photosynthesis. Instead, they suggested that the kleptoplasts in foraminifera from
361 aphotic environments provide the ability to fix inorganic nitrogen via the glutamine synthetase and glutamate 2-
362 oxo-glutarate amidotransferase (GOGAT) pathway. Indeed, Jauffrais et al. (2019) showed that kleptoplastic *N.*
363 *labradorica* are able to fix inorganic nitrogen but coupled TEM/Nano-SIMS revealed that the assimilated nitrogen
364 is associated with electron opaque bodies instead of sequestered chloroplasts. Analyses of the transcriptome of *N.*
365 *stella* by Gomaa et al. (2021) support the observations by Grzymiski et al. (2002), since *N. stella* appears to be able
366 to fix ammonia by itself. They also found that the fucoxanthin-chlorophyll binding protein (FCP) was expressed
367 in the transcriptome of *N. stella* and speculated that the ability to synthesize FCP was derived from the kleptoplasts
368 by horizontal gene-transfer. FCP is a pigment, commonly found in chloroplasts of brown algae and allows a more
369 efficient photosynthesis with a light absorption bandwidth especially useful in aquatic environments
370 (Papagiannakis et al., 2005; Premvardhan et al., 2008). The true function of the kleptoplasts in deep-sea benthic
371 foraminifera from aphotic, often O_2 depleted, environments still remains enigmatic, though.

372 2.1.3 Other strategies: Fermentation, utilization of high energy phosphates and peroxisome proliferation

373 Several recent publications based on advances in molecular biological methods (e.g., next generation
374 sequencing) have revealed some other metabolic adaptations of foraminifera that thrive under O_2 depletion
375 (examples see fig. 4) (Woehle & Roy et al., 2018, 2022; Orsi et al., 2020; Gomaa et al., 2021). In *N. stella* and
376 *Bolivina argentea*, Gomaa et al. (2021) found evidence for the expression of proteins, including pyruvate -
377 ferredoxin oxidoreductase (PFOR) and [FeFe]-hydrogenase, that are characteristic of anaerobic metabolism. These
378 PFOR sequences were indeed eukaryotic and closely related to those of the facultative anaerobe polychaete
379 *Capitella teleta* and the anaerobic protistan parasite *Blastocystis*. The [FeFe]-hydrogenase is very similar to those
380 in the amoeba/flagellate *Naegleria gruberi*, which has experimentally been shown to be active and to produce
381 molecular hydrogen even under aerobic conditions (Tsaousis et al., 2014). Due to these observations Gomaa et al.
382 (2021) suggested that *N. stella* and *B. argentea* might be able to produce H_2 gas and have the capacity for an
383 anaerobic energy metabolism.

384 Another important observation was made by Orsi et al. (2020). They used metatranscriptomics on
385 sediments from the Namibian shelf, where the foraminiferal community is dominated by *Bolivina* and *Stainforthia*
386 species. Presumably living foraminifera were present in the sediment column up to 28 cm depth in an anoxic
387 habitat with high sulfide concentrations. The gene expression of those foraminifera increased under sulfidic
388 conditions, which indicates that they not only survive but thrive under anoxic conditions. The anaerobic energy
389 metabolism of these foraminifera seems to be sufficient enough to support calcification and phagocytosis even
390 under anoxic conditions. Evidence for foraminiferal calcification under anoxia already came up by a study by
391 Nardelli et al. (2014). Orsi et al. (2020) suggested that the Namibian foraminifera use phagocytosis (vacuolic
392 ingestion of food particles) to ingest prey cells even under anoxic conditions. These processes (calcification and
393 the ingestion of prey cells by phagocytosis) require bursts of high energy, which the authors suggest is generated
394 by dephosphorylation of an intracellular creatine phosphate storage to regenerate ATP from ADP. Evidence for
395 the capacity for the dephosphorylation of creatine phosphate under anoxia was indicated by the
396 metatranscriptomes. In addition, a high intracellular dissolved inorganic phosphate storage has been found in
397 benthic foraminifera from the Peruvian OMZ, which might serve as a reservoir to synthesize creatine phosphate
398 and/or to synthesize polyphosphates that might be broken down to harvest energy (Glock et al., 2020). Orsi et al.
399 (2020) and Gomaa et al. 2021 also found evidence for another anaerobic metabolism. Their data indicates that the
400 foraminifera metabolize hydrolyzed organics to produce ATP using fermentation and fumarate reduction.

401 Most foraminifera species from O₂ depleted habitats possess numerous peroxisomes that are usually
402 associated with mitochondria and the endoplasmic reticulum (Bernhard and Bowser, 2008). Bernhard and
403 Bowser (2008) hypothesized that these peroxisome proliferations might be used to either metabolize H₂O₂ and
404 other highly reactive oxygen species that are produced within the chemocline close to the oxic/anoxic boundary
405 or to reduce the oxidative stress by these compounds. Indeed, they showed in an experiment that ATP
406 concentrations in foraminifera increased proportional to ambient H₂O₂ concentrations. A recent study on
407 transcriptome and metatranscriptome of *N. stella* and *B. argentea* from the Santa Barbara Basin revealed that
408 these species utilize an adaptable mitochondrial and peroxisomal metabolism, depending on the chemical treatment
409 in the experiment (Powers et al., 2022). The high plasticity of their peroxisomal and mitochondrial metabolism
410 might be substantial for survival at the highly variable conditions at the chemocline in the sediments. The results
411 by Powers et al. (2022) indicate that at least some processes that are involved in foraminiferal denitrification are
412 associated with mitochondria. Interestingly, the expression of denitrification related genes in both species was
413 upregulated after incubation with elevated H₂O₂ but without NO₃⁻ and downregulated, if they were incubated
414 without H₂O₂ but with NO₃⁻, compared to a control treatment with both H₂O₂ and NO₃⁻. In the same way several
415 peroxisomal processes were upregulated in the H₂O₂ only treatment. In addition, despite that both species are able
416 to denitrify, Powers et al. (2022) found distinct metabolic adaptations to anoxia in both species. For example, a
417 quinol:fumarate oxidoreductase, which is considered as an adaptive mechanism for anaerobic respiration in
418 eukaryotic organisms, was present in *N. stella* but not in *B. argentea*. Vice versa, *B. argentea* has the capacity
419 to digest food vacuole contents under O₂ depletion, while *N. stella* was lacking food vacuoles (Powers et al., 2022).

420 2.1.4 Dormancy

421 Dormancy is another strategy to survive anoxia or extreme O₂ depletion for some benthic foraminifera
422 that cannot denitrify. Dormancy is defined as the reduced or suspended metabolic activity in response to exogenous
423 factors (Ross and Hallock, 2016). Observations that indicate the potential of dormancy in foraminifera have been
424 documented since the 1950s and are extensively reviewed by Ross & Hallock (2016). Nevertheless, many aspects
425 of foraminiferal dormancy, such as role in foraminiferal life cycle or its role in structuring foraminiferal
426 assemblages remained unexplored (Ross and Hallock, 2016).

427 In the 1990s some studies suggested that some foraminifera may become dormant when exposed to
428 anoxia. Bernhard and Alve (1996) observed that the ATP concentration ([ATP]) of the benthic foraminiferal
429 species *Bulimina marginata*, *Stainforthia fusiformis* and *Adercotryma glomerata* flushed with N₂ gas to drive out
430 O₂ was significantly lower than in specimens from well-aerated conditions. They interpreted this observation as
431 an indication that dormancy is a survival strategy for some foraminiferal species when they are exposed to periods
432 of anoxia. Linke & Lutze (1993) observed cysts of *Elphidium incertum* from putative anoxic habitats that might
433 be interpreted as a sign for dormancy and Hannah and Rogerson (1997) hypothesized that foraminifera transported
434 to an anoxic sediment layer might become dormant until they return to aerated conditions by transport through
435 bioturbation.

436 Recently, dormancy of foraminifera exposed to anoxia had gained more attention again. LeKieffre et al.
437 (2017) did a feeding experiment with specimens from the *Ammonia tepida* morphogroup (*A. confertitesta*

438 according to Koho et al., 2018 and Hayward et al., 2021) using a ^{13}C -labeled diatom film as food source. They
439 compared the metabolic differences of *Ammonia* sp. between oxic and anoxic conditions by mapping the
440 distribution of ^{13}C within the cells using coupled TEM/Nano-SIMS and by analyzing the carbon concentration and
441 stable carbon isotopic composition of the total organic matter and individual fatty acids in the foraminifer. Nearly
442 the complete diatom biofilm was consumed and the foraminiferal cytoplasm was strongly enriched in ^{13}C under
443 oxic conditions. Specimens from the anoxic incubation ingested only few of the diatoms and those were neither
444 assimilated nor metabolized further. In addition, the specimens from the oxic incubation produced a significant
445 amount of specific polyunsaturated fatty acids, which was not the case under anoxic conditions. *A. confertitesta*
446 reacted to the induced anoxia with a severely reduced metabolic rate within less than 24 hours. All these
447 observations provide solid evidence that dormancy is a survival strategy of *A. confertitesta* under anoxia.

448 Koho et al. (2018) further analyzed cell structural changes in *Ammonia* spp. under exposure to anoxia
449 collected from the field as well as from incubations. The specimens from anoxia showed an increase in lipid
450 droplets and electron dense bodies within their cytoplasm. The cytoplasm itself was thinned out, which was
451 interpreted as metabolization of the cytosol. In addition, while absent within the specimens from oxic
452 environments, various bacteria were present within the cytoplasm of the specimens from anoxia. These were
453 interpreted as endobionts but might also be parasites that could not be fended off, due to the drastically reduced
454 metabolism during dormancy under anoxia. A continuum of intracellular bacteria including prey in food vacuoles,
455 endobionts, parasites and necrophages has been documented before in benthic foraminifera from cold seeps
456 (Bernhard et al., 2010b). It already has been hypothesized by the authors that bacteria switched their function from
457 endobionts to predators, depending on the vitality of the host cell. Considering all the studies about dormancy, it
458 is likely that dormancy is a common survival strategy for foraminiferal species that either get exhausted of suitable
459 electron acceptors (i.e., O_2 or NO_3^-) or are exposed to periods of extreme environmental conditions. Since there is
460 evidence for dormancy in both *S. fusiformis* and *B. marginata* (Bernhard and Alve, 1996), it is likely that even
461 denitrifying species can get dormant under unfavorable conditions. Another *Stainforthia* sp. has been shown to
462 denitrify and *B. marginata* stores NO_3^- in some environments (Piña-Ochoa et al., 2010b).

463 **3 Trophic interactions in O_2 depleted environments**

464 In general, benthic foraminifera show a wide range of trophic strategies. Gooday et al. (2008) suggested
465 that they can be separated according to their main trophic types (examples see fig. 5): A: Selective herbivores,
466 which include phytophagous species that consume only phytodetritus; B: Seasonal herbivores, which feed on fresh
467 phytodetritus, when available and consume sedimentary organic matter at other times; C: Detrivores that non-
468 selectively ingest sediment and consume the present degraded organic matter, bacteria and/or other organisms; D:
469 Selective bacterivores, that consume only bacteria; and E: Suspension feeders, that either erect from the sediments
470 or occur on elevated substrates. The latter two are not discussed in detail, since they mainly apply to abyssal species
471 that inhabit more oxygenated environments. Nevertheless, some *Cibicides* and *Planulina* species, can also inhabit
472 environments with relatively low O_2 concentrations (Erdem and Schönfeld, 2017; Rathburn et al., 2018;
473 Hoogakker et al., 2018b; Glock et al., 2022) and at least some of these *Cibicides* species are certainly suspension
474 feeders (Wollenburg et al., 2018, 2021). The trophic types that have been introduced above suggest that
475 foraminifera mainly feed on a low trophic level and it has been suggested that they constitute a trophic link to
476 higher levels in the food chain (Lipps and Valentine, 1970; Gooday et al., 1992; Nomaki et al., 2008).

477 There are a few studies that specifically focused on trophic interactions of foraminifera in environments
478 where O_2 is scarce or absent. Early observations have been documented by Nomaki et al. (2006), who conducted
479 an *in situ* feeding experiment at central Sagami Bay (1450 m), Japan, using ^{13}C labeled algae and bacteria. Bottom
480 water O_2 concentration at this location is usually less than $60\ \mu\text{M}$ and O_2 penetration depth into sediments varies
481 between 3 and 10 mm indicating that infaunal foraminifera in this habitat are regularly exposed to hypoxia and
482 anoxia (Glud et al., 2005). Nomaki et al. (2006) described three different feeding strategies by benthic foraminifera
483 in this environment. Since the bottom water O_2 concentrations at central Sagami Bay are fluctuating and not strictly
484 hypoxic, these observations likely apply to more oxygenated environments as well, especially for the shallow
485 infaunal species. *Uvigerina akitaensis*, *Bolivina spissa* and *Bolivina pacifica* selectively ingest fresh phytodetritus
486 and thus can be described as phytophagous species (selective herbivores). *Bulimina aculeata*, *Textularia*
487 *kattgatensis* and *Globobulimina affinis* ingest fresh phytodetritus selectively but feed on sedimentary organic
488 matter instead, when fresh phytodetritus is unavailable (seasonal herbivores). The species *Cyclammina cancellata*
489 and *Chilostomella ovoidea* ingest sedimentary organic matter at random and can thus be described as detrivores.
490 A later study confirmed these trophic types for most of the species at Sagami Bay by measuring the nitrogen
491 isotope fractionation ($\delta^{15}\text{N}$) of their amino acids, which is commonly used to trace the trophic position of an

492 organism in the food chain (Nomaki et al., 2015). Another feeding experiment at Sagami Bay by Nomaki et al.
493 (2011) revealed that all of the analyzed benthic species assimilated carbon from ^{13}C labeled glucose and thus can
494 effectively utilize also dissolved organic carbon. The same study indicated that even the deep infaunal detritivores
495 can be selective regarding their food source. Four of the five analyzed species, except *C. cancellata*, incorporated
496 proportionally more ^{13}C -labeled organic matter from the green algae *Dunaliella* sp. than from other carbon sources,
497 while *C. cancellata* preferentially incorporated carbon from *Chlorella* sp. (Nomaki et al., 2005, 2006, 2011).
498 Additional feeding experiments have been conducted at the Arabian Sea OMZ, where benthic foraminifera from
499 locations with different bottom water O_2 concentrations have been supplied with ^{13}C and ^{15}N labeled algae (Enge
500 et al., 2014, 2016). Nine out of nine analyzed species took up labeled phytodetritus during the four days
501 experimental phase (Enge et al., 2014). The foraminifera took up the highest amount of labeled carbon in the OMZ
502 center and the uptake decreased with distance from the OMZ (Enge et al., 2016). The authors hypothesized that
503 either the foraminifera from the core OMZ have a higher carbon demand or that there was less food competition
504 with macrofauna at the O_2 depleted locations. Similar to the studies by Nomaki et al. at Sagami Bay, the
505 experiments by Enge et al. (2014 & 2016) showed a more or less selective ingestion at the Arabian Sea OMZ
506 depending on the foraminiferal species. For example, several several *Uvigerina* species took up large amounts of
507 carbon from the labeled algae and are thus either selective or seasonal herbivores, while *Globobulimina* spp. took
508 up either no or only small amounts of the labeled carbon indicating their detritivore behavior (Enge et al., 2016).
509 Further examples for selective herbivores, opportunistic omnivores, which include seasonal herbivores, and
510 sediment detritivores are discussed by Gooday et al. (2008). It appears that many of the species that are considered
511 to be selective herbivores (e.g., *B. spissa*, *U. akitaensis*, *Eponides pusillus* or *Cassidulina carinata*) are living
512 epifaunal or shallow infaunal, although the selective herbivore *B. pacifica* can be also considered as intermediate
513 infauna (Gooday et al., 2008). The seasonal herbivores (or opportunistic omnivores; e.g., *U. peregrina*, *G. affinis*
514 or *G. pacifica*) can be found in a relatively wide range of microhabitats from shallow to deep infauna (Gooday et
515 al., 2008). Species that are considered to be sediment deposit feeders (or detritivores, e.g., *C. ovoidea* or *M.*
516 *barleanum*) are usually found in the deeper habitats and belong to intermediate to deep infauna (Gooday et al.,
517 2008). This indicates that the selective herbivores must live closer to the source of fresh food supply, while the
518 less selective species can also feed on degraded organic matter or bacteria deeper in the sediments. Thus, the
519 specific trophic type is another control on the microhabitat of benthic foraminifera in addition to the availability
520 of O_2 , NO_3^- and the metabolic adaptations discussed in section 2. Indeed, the coupled diagenetic and ecologic
521 model of Jorissen et al. (2022) successfully uses different types of food particles as a controlling factor to simulate
522 the microhabitats of benthic foraminifera.

523 Although benthic foraminifera feed mainly on detritus and minute organisms there is also (less common)
524 evidence for carnivorous behavior when foraminifera prey on meiofauna (e.g., Lee, 1980; Bowser et al., 1986,
525 1992; Hallock and Talge, 1994). These observations have mainly been done on species that usually live in
526 oxygenated environments. Dupuy et al. (2010) documented carnivorous behavior in a laboratory experiment also
527 for the *Ammonia tepida* morphogroup (*A. aberdoveyensis* or *A. confertitesta* according to Hayward et al., 2021),
528 which is not uncommon in anoxic layers of tidal mudflats. A study on the trophic behavior of intertidal
529 foraminifera, using metabarcoding brought up evidence that *A. confertitesta* is actively preying on small
530 eukaryotes (e.g., nematodes) even in their natural environment (Panagiota-Chronopoulou et al., 2019). The
531 intracellular eukaryotic community in *A. confertitesta* varies with sediment depth but even up to 10 cm depth the
532 metabarcoding indicates freshly ingested eukaryotic prey in this species (Panagiota-Chronopoulou et al., 2019).
533 Still, the main eukaryotic prey of *A. confertitesta* appear to be diatoms (Panagiota-Chronopoulou et al., 2019).
534 Similar results have been documented by Schweizer et al. (2022). Recently, new evidence came up indicating
535 ingestion of nematodes by *Globobulimina auriculata* from the O_2 depleted Alsbäck Deep in Gullmar Fjord,
536 Sweden (Glock et al., 2019a). The species *G. auriculata* denitrifies and lives under O_2 depleted conditions (Woehle
537 & Roy et al., 2018). It is inconclusive, though, if the foraminifer preys on the nematode or vice versa but the
538 nematodes have most likely been ingested in the natural O_2 depleted habitat (Glock et al., 2019a). Although
539 predation is the main type of interaction in aerobic communities, it usually plays a much smaller role in anoxic
540 communities (Fenchel and Finlay, 1995). This is related to the low growth yields associated with the anaerobic
541 metabolism, which results in very short food chains. Thus, the decrease in energy flow along the anaerobic food
542 chains is higher than along the aerobic food chain (Fenchel and Finlay, 1995). The predatory isopod *Saduria*
543 *entomon* for example strongly reduces its predatory activity under hypoxia in comparison to aerobic conditions
544 (Sandberg, 1994) and the predator/prey biomass ratio has been shown to be 4 times lower in anoxic environments
545 compared to oxic environments (Fenchel and Finlay, 1995). There is evidence that foraminifera from the Namibian
546 shelf can perform phagocytosis (vacuolic ingestion of food particles) even under anoxic conditions, which usually
547 requires bursts of energy (Orsi et al., 2020). This study provides further evidence that the Namibian foraminifera

548 express enzymes for lysing digested prey cells inside food vacuoles after phagocytosis (schematic representations
549 for phagocytosis and predation on meiofauna shown in fig. 5). The evidence for phagotrophy and predation on or
550 by benthic foraminifera under O₂ depleted conditions, although it is rare, is thought-provoking and future studies
551 might shed more light on predator-prey interactions of benthic foraminifera in O₂ depleted environments. In
552 general, future metabarcoding studies to identify food sources of deep infauna or foraminifera that inhabit anoxia
553 might shed more light on trophic strategies in O₂ depleted environments.

554 **4 The role of foraminifera in benthic nutrient cycling and biogeochemistry**

555 Pina-Ochoa et al. (2010b) also suggested the possible importance of denitrifying foraminifera for the
556 benthic N-cycle, due partly to their high abundances in O₂ depleted environments. In some environments, such as
557 certain habitats in the Peruvian OMZ, foraminifera even seem to be the key players in benthic denitrification (Glud
558 et al., 2009; Glock et al., 2013, 2019b; Choquel et al., 2021). Complete heterotrophic denitrification produces non-
559 reactive (i.e., not bioavailable) N₂ gas. Denitrifying benthic foraminifera can thus be considered a sink for
560 bioavailable N. The recent genetic studies on denitrifying benthic foraminifera did not find transcripts for
561 homologues of enzymes that catalyze the last step of denitrification – the reduction of N₂O to N₂ (Woehle & Roy
562 et al., 2018, 2022; Orsi et al., 2020; Gomaa et al., 2021). Some Globobuliminids from the O₂ depleted Alsbäck
563 Deep in the Swedish Gullmar Fjord have been shown to produce N₂O gas as product of denitrification, although
564 the rates were lower than their rates for complete denitrification (Piña-Ochoa et al., 2010a). The NO₃⁻ storage in
565 denitrifying foraminifera, but also in some sulfur bacteria, such as *Beggiatoa*, is of greater importance for benthic
566 biogeochemical cycling, due to the potential of biological transport of these intracellular reservoirs (Dale et al.,
567 2016). Most of the other diagenetic models that describe and calculate benthic N-cycling are based on (and limited
568 to) diffusive transport of the different N-species in bottom and pore water. Active biological transport of different
569 N-species can thus efficiently influence the benthic fluxes of different N-species (Dale et al., 2016).

570 The estimates of total benthic foraminiferal denitrification rates are mainly based on upscaling individual
571 species specific denitrification rates by the living abundances of benthic foraminifera in different environments
572 (Piña-Ochoa et al., 2010b; Glock et al., 2013, 2019b). This approach is limited by the availability of species
573 specific denitrification rates, although, various approximations can be used to calculate estimated denitrification
574 rates for species with unknown denitrification rates (Glock et al., 2013). A summary of all published benthic
575 foraminiferal denitrification rates can be found in tab. 1. Further data about species specific foraminiferal
576 denitrification rates will improve our estimates about the role of foraminifera in benthic N-cycling and, thus, also
577 models for benthic biogeochemical cycling.

578 Recently, it has been found that some benthic foraminifera are not only storing NO₃⁻ for denitrification
579 but also store larger amounts phosphate (Glock et al., 2020). The intracellular phosphate concentration can exceed
580 the concentration in the surrounding pore waters by a factor of 10 to 100. The use of this intracellular phosphate
581 storage is still under debate. Hypotheses include the synthesis of polyphosphates or a reservoir for the synthesis of
582 phospholipids for the cell membranes (Glock et al., 2020). In addition, there is evidence that the intracellular
583 phosphate storage in foraminifera facilitates phosphogenesis in some environments, similar to the intracellular
584 polyphosphate enrichments in some sulfur bacteria (Schulz and Schulz, 2005). The release of phosphate after
585 breakdown of these polyphosphates to harvest energy in times of electron acceptor depletion results in apatite
586 supersaturation and initiates phosphogenesis (Schulz and Schulz, 2005). Sediments at the lower boundary of the
587 Peruvian OMZ contain many small phosphorite grains with similar size and shape of foraminifera (Manheim et
588 al., 1975; Glock et al., 2020). The sand fraction of the surface sediments in this region is a mixture of pristine
589 living foraminifer shells with dead tests that show a transition from shells that are filled with phosphorites until
590 small phosphorite grains that only retain the size and coarse shape of a foraminifer. It is likely that a *post mortem*
591 release of the intracellular phosphate storage results in a supersaturated microenvironment within the shells that
592 initiates apatite formation (Glock et al., 2020) in a similar way as it has been suggested for other organisms
593 (Kulakovskaya, 2014). The recent evidence for the potential of benthic foraminifera to use dephosphorylation of
594 an intracellular creatine phosphate storage to regenerate ATP under anoxic conditions might be another
595 explanation for the high intracellular phosphate storage (Orsi et al., 2020). It might be that this is an adaptation of
596 foraminifera to enable phagocytosis even under anoxic conditions.

597 4.1 Estimating the contribution of foraminifera to benthic nutrient budgets and fluxes

598 The intracellular NO₃⁻ storage in benthic foraminifera from different environments shows a relatively
599 wide concentration range (Tab.2). In addition, species that lack intracellular NO₃⁻ storage are relatively widespread
600 and there are species that, depending on the environment, either have or lack intracellular NO₃⁻ (Tabs.2&3). Most

601 of the species that have been found both with and without intracellular NO_3^- in different environments (bold species
602 in Tab.3) are species that are typically shallow infaunal. They belong to the group of foraminifera that might partly
603 be considered facultative anaerobe and likely are opportunistic species that are well adapted to transitional
604 environments with periodic O_2 depletion, since they apparently can handle oxygenated and anoxic environments
605 (see 2.1.1). In addition, the NO_3^- is most likely stored in seawater vacuoles and the vacuole volume of foraminifera
606 can have a large variability (LeKieffre et al., 2018).

607 Given this variation in NO_3^- storage capability, the reliability of estimates for the foraminiferal
608 contribution to NO_3^- budgets depends crucially on the availability of data. The more data there is, the better we are
609 able to calculate foraminiferal NO_3^- budgets. Nevertheless, there are thousands of benthic foraminiferal species
610 and a considerable amount of these species inhabit O_2 depleted environments and potentially store NO_3^- and
611 denitrify. It will be unrealistic to measure the intracellular nutrient content and metabolic rates for all foraminifera.
612 Thus, functions to estimate the contribution of species with unknown denitrification rates or intracellular NO_3^- will
613 provide more data for better estimates of total foraminiferal budgets within the nitrogen cycle. Of course, it is not
614 possible to strictly define, which foraminiferal species are able to denitrify or to store NO_3^- without real
615 measurements. If a foraminiferal species inhabits O_2 depleted environments and belongs to a genus of the species,
616 listed in tab.1 or tab.2, as a rule of thumb, they are good candidates for potential denitrifiers. In addition, if a
617 species is known to inhabit well oxygenated environments and/or belongs to a genus of the species shown in tab.3
618 it should be avoided to use equations presented below to estimate NO_3^- storage or denitrification rates. Considering
619 this, an analysis of published data about intracellular NO_3^- content reveals a highly significant correlation between
620 the intracellular NO_3^- and the cell volume of denitrifying benthic foraminifera (Fig. 6; power regression; $R^2 = 0.59$;
621 $F = 86$; $P = 3\text{E-}13$).

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

624
$$\text{Eq.2: } \ln(\text{NO}_3^-)_i = 1.07(\pm 0.11) \times \ln(V_{\text{cell}}) - 11.5(\pm 1.9)$$

625 where $\text{NO}_3^-_i$ is the intracellular NO_3^- content in pmol ind^{-1} and V_{cell} is the cell volume in μm^3 . Note that
626 only species from table 2 with an intracellular $[\text{NO}_3^-] \geq 1 \text{ mM}$ were considered for the power regression. In
627 addition, two extreme datapoints were discarded as outliers (see supplementary note). Similar equations have been
628 published to estimate foraminiferal denitrification rates (Glock et al., 2019b; here Eq.3) and intracellular dissolved
629 inorganic phosphorous content (Glock et al., 2020, here Eq.4).

630
$$\text{Eq.3: } \ln(R_{\text{den(ind)}}) = 0.68(\pm 0.12) \times \ln(V_{\text{cell}}) - 5.57(\pm 1.9)$$

631
$$\text{Eq.4: } \ln(\text{DIP}_i) = 0.82(\pm 0.03) \times \ln(V_{\text{cell}}) - 7.65(\pm 0.52)$$

632 where $R_{\text{den(ind)}}$ is the individual denitrification rate in $\text{pmol ind}^{-1} \text{ day}^{-1}$ and DIP_i is the intracellular dissolved
633 inorganic phosphorous content in pmol ind^{-1} .

634 Further equations and principles for upscaling foraminiferal nitrogen- and phosphorous-budgets from
635 abundances of living foraminifera can be found in Glock et al. (2013, 2019b and 2020) and (Xu et al., 2021).
636 Formulae to estimate the biovolume of many different common shapes of foraminifera have recently been
637 published (de Freitas et al., 2021). Due to the high uncertainties related to the natural variability in metabolic rates
638 and nutrient storage, a thorough error estimation is recommended (see Appendix B in Glock et al. 2020). With an
639 increasing amount of data about metabolic rates and intracellular nutrient storage more accurate models and
640 equations might become available in the future that describe the role of benthic foraminifera within marine
641 biogeochemistry. Similar models and equations might be also very helpful for exploring the role of planktonic
642 foraminifera in pelagic biogeochemistry.

643 **6 Author contribution**

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

645 **7 Competing interests**

646 The author declare that they have no conflict of interest.

647 **8 Acknowledgements**

648 I would like to thank Gerhard Schmiedl for providing constructive feedback on an early draft of this
649 manuscript. In addition, I acknowledge the extensive and constructive feedback Andrew Gooday, Frans Jorissen,
650 another anonymous reviewer and the editor Lisa Levin, which significantly improved this manuscript. Funding
651 was provided by the Deutsche Forschungsgemeinschaft (DFG) through Heisenberg grant GL 999/3-1 to N.G.
652 Finally, I would like to thank all the authors and co-authors that are cited in this review, because of their pioneering
653 research on benthic foraminifera from O₂ depleted environments.

654

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Figure captions:

1116 Figure 1: Schematic representations for three survival strategy examples performed by benthic foraminifera under
1117 O₂ depleted conditions.

1118 Figure 2: Schematic view of two alternative pathways suggested for foraminiferal denitrification. Abbreviations
1119 above the reaction arrows indicate the enzymes that are catalyzing the respective step (see legend). Enzymes in
1120 black have been found transcribed by eukaryotic (foraminiferal) RNA (Woehle & Roy et al., 2018). Enzymes in
1121 grey are missing in the foraminiferal denitrification pathway and are likely performed by bacterial symbionts
1122 (Woehle & Roy et al., 2022). The straight pathway above describes the normal heterotrophic denitrification
1123 pathway. The junction, catalyzed by the Nod, which produces O₂, has been suggested as an alternative pathway
1124 for foraminiferal denitrification (Woehle & Roy et al., 2018).

1125 Figure 3: TROX model modified after Jorissen et al. (1995) and Xu et al. (2021). The supply of organic matter
1126 and bottom water O₂ and NO₃⁻ concentrations in different environments control the penetration depth of O₂ and
1127 NO₃⁻ into the sediment. Benthic foraminifera choose their microhabitat according to their metabolic preferences
1128 for O₂ or NO₃⁻ as an electron acceptor and the availability of food. Intermediate infauna is not specifically
1129 schematized in the figure but peak between the shallow and deep infauna with an overlap to both directions. Note
1130 that denitrifying foraminifera can actively transport intracellular NO₃⁻ below the NO₃⁻-penetration depth in the
1131 sediments. The deeper regions where production of free sulfide occurs will mainly be avoided. For further details
1132 see text.

1133 Figure 4: Examples for molecules and processes that are relevant in the anaerobic metabolism of foraminifera. A:
1134 Structural formula of creatine phosphate. B: The role of creatine kinase (Ck) and creatine phosphate in the
1135 anaerobic metabolism. High energy creatine phosphate is produced by phosphorylation of creatine. Creatine
1136 phosphate can rapidly recycle ADP to ATP to provide resources for rapid energy bursts. This pathway has been
1137 described by Orsi et al.(2020). C: Fermentation has been found to be relevant in the anaerobic metabolism of
1138 foraminifera by both Orsi et al.(2020) and Gomaa et al. (2021). The possibility of a H₂ producing fermentation
1139 pathway, catalyzed by Fe-hydrogenase has been described by Gomaa et al. (2021).

1140 Figure 5: A: Schematic representation of a *boliviniid* ingesting bacterial cells. Recent studies showed that benthic
1141 foraminifera from O₂ depleted habitats have the capacity of phagocytosis even under anoxia (Orsi et al., 2020). B:
1142 Schematic representation of *Ammonia* sp. preying on a nematode. Some benthic foraminifera are known to prey
1143 on meiofauna (Dupuy et al., 2010) and there is evidence, that even some *globobuliminids* that usually thrive under
1144 O₂ depleted conditions might prey on nematodes (Glock et al., 2019a).

1145 Figure 6: Log-log plot and power regression of intracellular NO₃⁻ content (NO₃⁻_i) against the biovolume (V_{cell}) of
1146 benthic foraminifera from diverse environments (Tab. 2). Only species with an intracellular [NO₃⁻] ≥ 1 mM, where
1147 both NO₃⁻_i and V_{cell} were published were considered for the power regression.

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Tables

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1157 Table 1: Summary of foraminiferal denitrification rates (individual and volume specific), where Ind. refers to the
 1158 number of individuals used for one incubation. Individual denitrification rates refer to average rates per
 1159 individual while specific denitrification rates refer to rates normalized to the biovolume of the foraminifers.
 1160 Errors are given as standard deviations (1sd) ^(a): Data from Piña-Ochoa et al. (2010b); ^(b): Data from Bernhard et
 1161 al. (2012b); ^(c): Data from Glock et al. (2019b); ^(d): Data from Langlet et al. (2020); ^(e): Data from Woehle & Roy
 1162 et al. (2018); ^(f): Data from Risgaard-Petersen et al. (2006); ^(g): Data from Choquel et al (2021); ^(h): Data from
 1163 Høgslund et al. (2008). *: *Ammonia tepida* is a morphogroup of pseudocryptic species that recently had a
 1164 revision. Specimens earlier identified as *A. tepida* are likely either *A. aberdoveyensis* or *A. confertitesta*
 1165 according to Hayward et al. (2021).

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

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Table 2: Summary of intracellular nitrate (NO_3^-) storage in benthic foraminifera and gromiids from different environments. Only species where intracellular $[\text{NO}_3^-]$ was at least 0.1 mM are listed. Species with intracellular $[\text{NO}_3^-] < 0.1$ mM are listed in Tab.3. Errors are given as standard error of the mean (SEM) ^(a): Data from Piña-Ochoa et al. (2010b); ^(b): Data from Bernhard et al. (2012b); ^(d): Data from Langlet et al. (2020); ^(f): Data from Risgaard-Petersen et al. (2006); ^(h): Data from Høgslund et al. (2008); ⁽ⁱ⁾: Data from Bernhard et al. (2012a); ^(j): Data from Xu et al. (2017); ^(k): Data from Glock et al. (2020); ^(l): Data from Xu et al. (2021); ^(m): Data from Nomaki et al. (2015).

Species	Location	NO_3^- (pmol per cell)	1SEM	Volume ($\mu\text{m}^3 \cdot 10^{-6}$)	1SEM	$[\text{NO}_3^-]$ (mM)	1SEM
Foraminifera							
<i>Allogromia</i> sp. ⁽ⁱ⁾	Santa Barbara Basin	570	354	n.a.	n.a.	70.0	49.0
<i>Ammonia</i> sp. ^(m)	Sagami Bay	80	4	n.a.	n.a.	n.a.	n.a.
<i>Bolivina alata</i> ^(a)	Bay of Biscay	615	154	17.0	1.1	37.0	12.0
<i>Bolivina argentea</i> ^(b)	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	195.1	160.3
<i>Bolivina</i> cf. <i>abbreviata</i> ^(a)	OMZ-Peru	1081	368	12.0	2.7	153.0	49.0
<i>Bolivina</i> cf. <i>skagerrakensis</i> ^(a)	North Sea	83	n.a.	17.0	0.0	5.0	n.a.
<i>Bolivina costata</i> ^(k)	OMZ-Peru	34	4	0.8	0.0	43.1	4.3
<i>Bolivina interjuncta</i> ^(k)	OMZ-Peru	1239	267	15.6	0.5	80.2	18.9
<i>Bolivina plicata</i> ^(a)	OMZ-Peru	478	72	7.5	1.0	79.0	15.0
<i>Bolivina robusta</i> ^(j)	Yellow Sea	212	46	6.1	0.4	35.0	6.0
<i>Bolivina seminuda</i> ^(k)	OMZ-Peru	140	45	1.6	0.1	88.6	29.8
<i>Bolivina seminuda</i> ^(a)	OMZ-Peru	564	135	5.2	1.8	118.0	18.0
<i>Bolivina spathulata</i> ^(d)	Bering Sea	154	n.a.	10.3	n.a.	14.9	n.a.
<i>Bolivina spissa</i> ^(m)	Sagami Bay	190	72	n.a.	n.a.	n.a.	n.a.
<i>Bolivina subaenariensis</i> ^(a)	Bay of Biscay	285	46	25.0	4.3	44.0	9.0
<i>Bolivinellina pseudopunctata</i> ^(d)	Bering Sea	133	n.a.	0.9	n.a.	148.1	n.a.
<i>Bulimina aculeata</i> ^(a)	Bay of Biscay	19	12	7.4	0.4	3.0	2.0
<i>Bulimina</i> cf. <i>elongata</i> ^(a)	OMZ-Peru	817	287	7.9	1.2	116.0	43.0
<i>Bulimina marginata</i> ^(l)	Yellow Sea	70	11	2.7	0.3	26.0	1.0
<i>Bulimina marginata</i> ^(a)	Skagerrak	5	n.a.	1.1	11.0	0.5	0.2
<i>Bulimina marginata</i> ^(a)	Bay of Biscay	40	4	32.0	1.1	4.0	1.0
<i>Bulimina subula</i> ^(l)	Yellow Sea	79	8	1.7	0.3	51.0	5.0
<i>Buliminella tenuata</i> ^(b)	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	217.4	150.5
<i>Cancris auriculus</i> ^(j)	East China Sea	3211	1046	28.0	5.1	114.0	23.0
<i>Cancris inflatus</i> ^(a)	OMZ-Peru	263877	4253	120.0	24.0	262.0	37.0
<i>Cassidulina carinata</i> ^(a)	Rhône Delta	3	1	4.1	0.2	1.0	0.5
<i>Cassidulina</i> cf. <i>laevigata</i> ^(a)	North Sea	21	n.a.	4.1	0.0	5.0	5.0
<i>Cassidulina</i> cf. <i>laevigata</i> ^(a)	OMZ-Peru	523	289	12.0	3.6	41.0	12.0
<i>Cassidulina limbata</i> ^(k)	OMZ-Peru	1408	710	16.8	2.9	72.9	37.8
<i>Chilostomella oolina</i> ^(a)	Bay of Biscay	1124	520	20.0	2.0	65.0	36.0
<i>Chilostomella ovoidea</i> ^(m)	Sagami Bay	50	13	n.a.	n.a.	n.a.	n.a.
<i>Clavulina cylindrica</i> ^(a)	Rhône Delta	2202	480	35.0	1.0	48.0	13.0
<i>Clavulina cylindrica</i> ^(a)	Bay of Biscay	1941	314	37.0	5.8	61.0	12.0
<i>Cyclammina cancellata</i> ^(a)	OMZ-Peru	45563	45563	380.0	3.1	119.0	118.0
<i>Fursenkoina cornuta</i> ^(b)	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	125.2	68.9

<i>Globobulimina affinis</i> ^(m)	Sagami Bay	480	116	n.a.	n.a.	n.a.	n.a.
<i>Globobulimina auriculata</i> cf. <i>arctica</i> ^(a)	Greenland	10624	3555	100.0	17.0	113.0	43.0
<i>Globobulimina cf. ovula</i> ^(a)	OMZ-Peru	3,369	1602	1.0	2.3	375.0	174.0
<i>Globobulimina pacifica</i> ^(j)	East China Sea	1167	455	75.0	7.0	16.0	5.0
<i>Globobulimina pacifica</i> ^(d)	Bering Sea	6530	5563	34.2	8.9	243.9	203.6
<i>Globobulimina turgida</i> ^(f)	Gullmar fjord	18000	4852	500.0	360.0	10.0	2.0
<i>Globobulimina turgida</i> ^(a)	Skagerrak	8192	1497	100.0	17.0	71.0	13.0
<i>Goesella flintii</i> ^(a)	OMZ-Peru	459	424	100.0	27.0	24.0	23.0
<i>Gyroidina neosoldanii</i> ^(a)	OMZ-Peru	13190	480	27.0	12.0	241.0	46.0
<i>Hanzawaia nipponica</i> ⁽ⁱ⁾	Yellow Sea	316	73	30.0	0.5	11.0	3.0
<i>Hanzawaia nipponica</i> ^(l)	Yellow Sea	296	49	16.2	4.9	25.0	9.0
<i>Hyalinea balthica</i> ^(a)	North Sea	8	2	8.0	120.0	1.0	0.3
<i>Labrospira cf. kosterensis</i> ^(a)	OMZ-Peru	3139	845	51.0	12.0	57.0	12.0
<i>Melonis barleeanus</i> ^(a)	North Sea	9	3	14.0	20.0	0.6	0.2
<i>Nonionella cf. stella</i> ^(h)	OMZ-Chile	186	24	5.2	0.7	35.0	5.0
<i>Nonionella pulchella</i> ^(d)	Bering Sea	31	7	6.7	2.0	7.6	2.2
<i>Nonionella stella</i> ⁽ⁱ⁾	Yellow Sea	162	27	53.0	3.9	3.0	0.6
<i>Nonionella stella</i> ^(l)	Yellow Sea	178	28	5.5	0.9	34.0	3.0
<i>Nonionella stella</i> ^(b)	Santa Barbara Basin	n.a.	n.a.	n.a.	n.a.	11.6	15.7
<i>Protelphidium tuberculatum</i> ^(l)	Yellow Sea	232	26	3.7	0.5	68.0	9.0
<i>Pyrgo elongata</i> ^(a)	Rhône Delta	43	14	47.0	5.8	0.8	0.2
<i>Pyrgo williamsoni</i> ^(a)	North Sea	5	n.a.	47.0	0.0	0.1	n.a.
<i>Pyrgoella sphaera</i> ^(a)	North Sea	6	1	47.0	5.8	0.1	0.0
<i>Stainforthia</i> sp. var. I ^(a)	OMZ-Chile	60	46	0.3	0.0	180.0	29.0
<i>Textularia cf. tenuissima</i> ^(a)	OMZ-Peru	450	432	11.0	2.9	43.0	7.0
<i>Uvigerina akitaensis</i> ^(m)	Sagami Bay	210	73	n.a.	n.a.	n.a.	n.a.
<i>Uvigerina elongatastriata</i> ^(a)	Bay of Biscay	274	244	5.1	0.6	60.0	55.0
<i>Uvigerina mediterranea</i> ^(a)	Bay of Biscay	101	66	20.0	6.6	6.0	4.0
<i>Uvigerina peregrina</i> ^(d)	Bering Sea	74	20	9.9	4.1	10.0	4.7
<i>Uvigerina peregrina</i> ^(a)	North Sea	332	184	20.0	6.6	16.0	9.0
<i>Uvigerina phlegeri</i> ^(a)	Rhône Delta	444	44	8.4	0.2	209.0	48.0
<i>Valvulineria bradyana</i> ^(a)	Rhône Delta	1268	164	15.0	1.4	95.0	15.0
<i>Valvulineria cf. laevigata</i> ^(a)	OMZ-Peru	865	640	19.0	3.7	25.0	12.0
<i>Valvulineria inflata</i> ^(k)	OMZ-Peru	17666	5319	135.4	16.4	120.1	34.1
<i>Verneuillinella advena</i> ^(l)	Yellow Sea	86	15	2.5	0.3	34.0	3.0
Gromiids							
<i>Gromia</i> sp. ^(a)	Bay of Biscay	2846	1275	93.0	20.0	35.0	21.0
<i>Gromia</i> sp. ^(a)	Skagerrak	35277	16546	510.0	110.0	53.0	19.0
<i>Gromia</i> sp. ^(a)	Rhône Delta	3889	1024	160.0	110.0	91.0	26.0
<i>Gromia</i> sp. ^(a)	North Sea	14682	4649	160.0	3500.0	140.0	46.0
<i>Gromia</i> sp. ^(a)	Greenland	12997	2954	80.0	23.0	163.0	n.a.
<i>Gromia</i> spp. ^(d)	Bering Sea	367	85	11.3	6.1	40.2	14.1

Table 3: Summary of benthic foraminifera from different environments that lack intracellular nitrate (NO₃⁻) storage. Only species with intracellular [NO₃⁻] < 0.1 mM are listed. Species in **bold** letters have been found to store NO₃⁻ in other environments (see table 2). ^(a): Data from Piña-Ochoa et al. (2010b); ^(j): Data from Xu et al. (2017); ^(m): Data from Nomaki et al. (2015). *: *Ammonia tepida* is a morphogroup of pseudocryptic species that recently had a revision. Specimens earlier identified as *A. tepida* are likely either *A. aberdoveyensis* or *A. confertitesta* according to Hayward et al. (2021).

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

Figures

Figure 1:

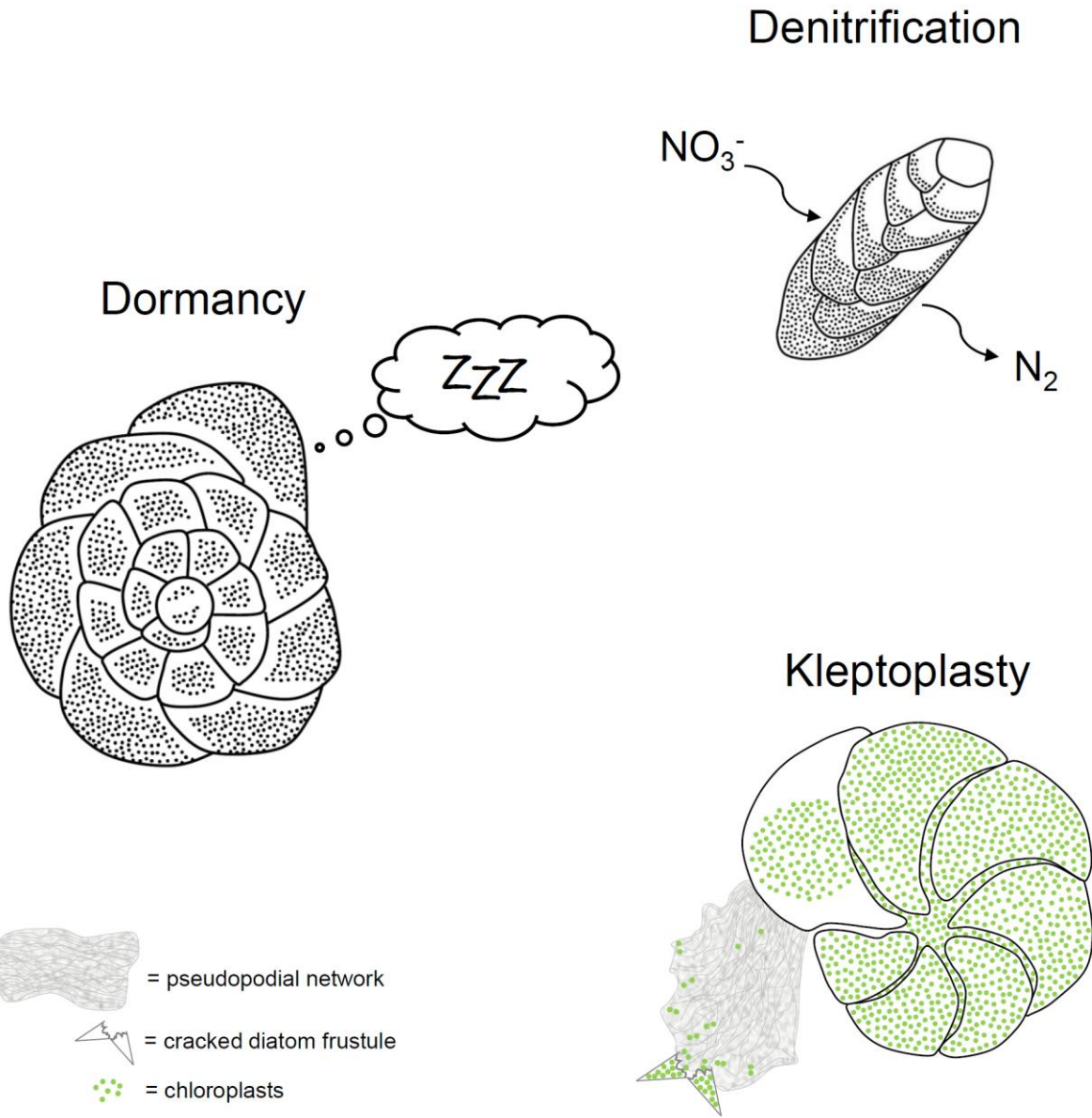


Fig. 1: Schematic representations for three survival strategy examples performed by benthic foraminifera under O_2 depleted conditions.

Figure 2:

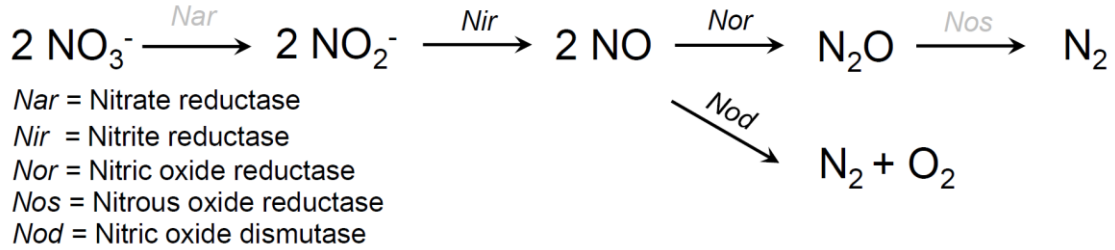


Fig. 3: Schematic view of two alternative pathways suggested for foraminiferal denitrification. Abbreviations indicate the enzymes that are catalyzing the respective step (see legend). Enzymes in black have been found transcribed by eukaryotic (foraminiferal) RNA (Woehle & Roy et al., 2018, Orsi et al., 2020; Goma et al., 2021). Enzymes in grey are missing in the foraminiferal denitrification pathway and are likely performed by bacterial symbionts (Woehle & Roy 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 & Roy et al., 2018).

Figure 3:

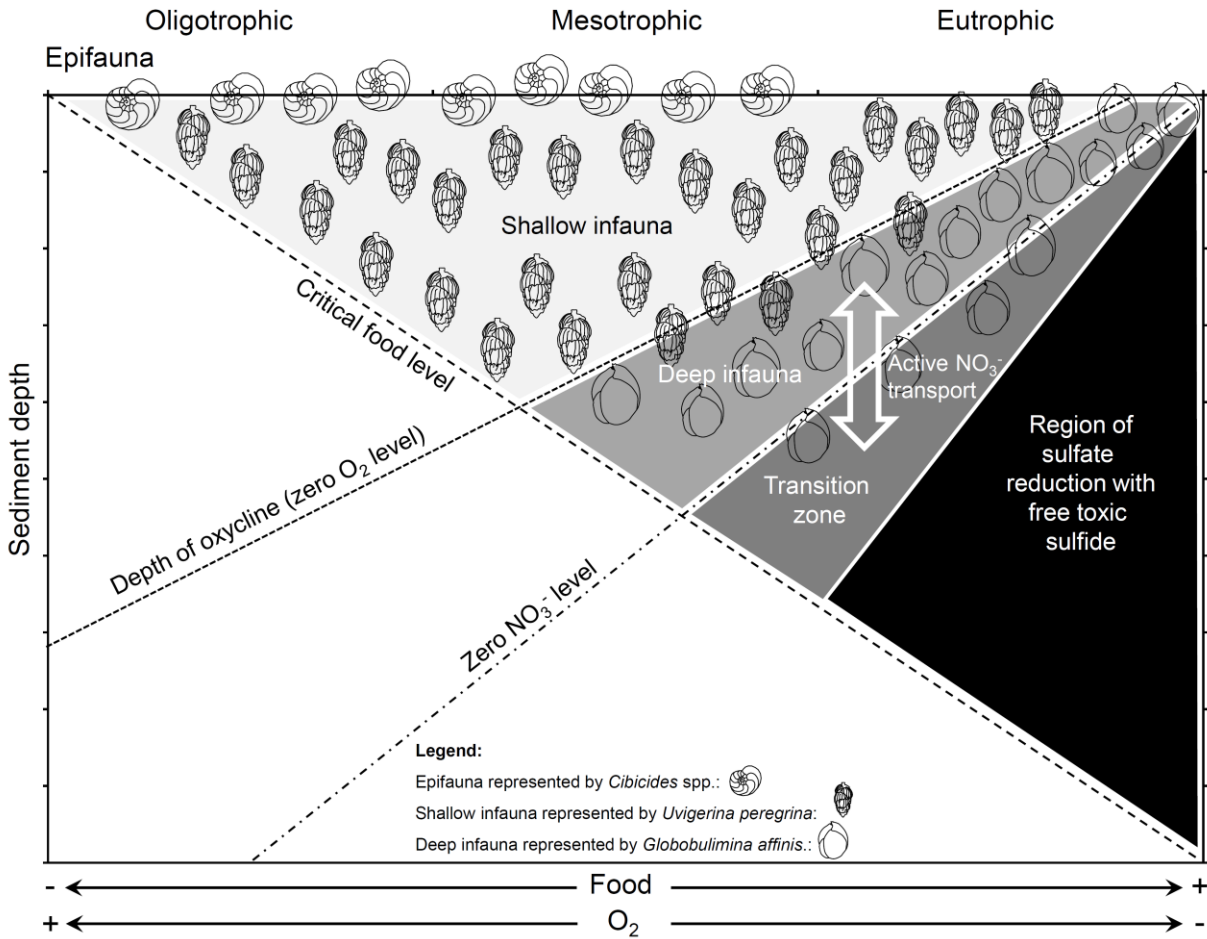


Fig.4: TROX model modified after Jorissen et al. (1995) and Xu et al. (2021). The supply of organic matter and bottom water O₂ and NO₃⁻ concentrations in different environments control the penetration depth of O₂ and NO₃⁻ into the sediment. Benthic foraminifera choose their microhabitat according to their metabolic preferences for O₂ or NO₃⁻ as an electron acceptor and the availability of food. Intermediate infauna is not specifically schematized in the figure but peak between the shallow and deep infauna with an overlap to both directions and often peak within the NO₃⁻ maximum (Jorissen et al., 2022). Note that denitrifying foraminifera can actively transport intracellular NO₃⁻ below the NO₃⁻-penetration depth in the sediments. The deeper regions where production of free sulfide occurs will mainly be avoided. For further details see text.

Figure 4:

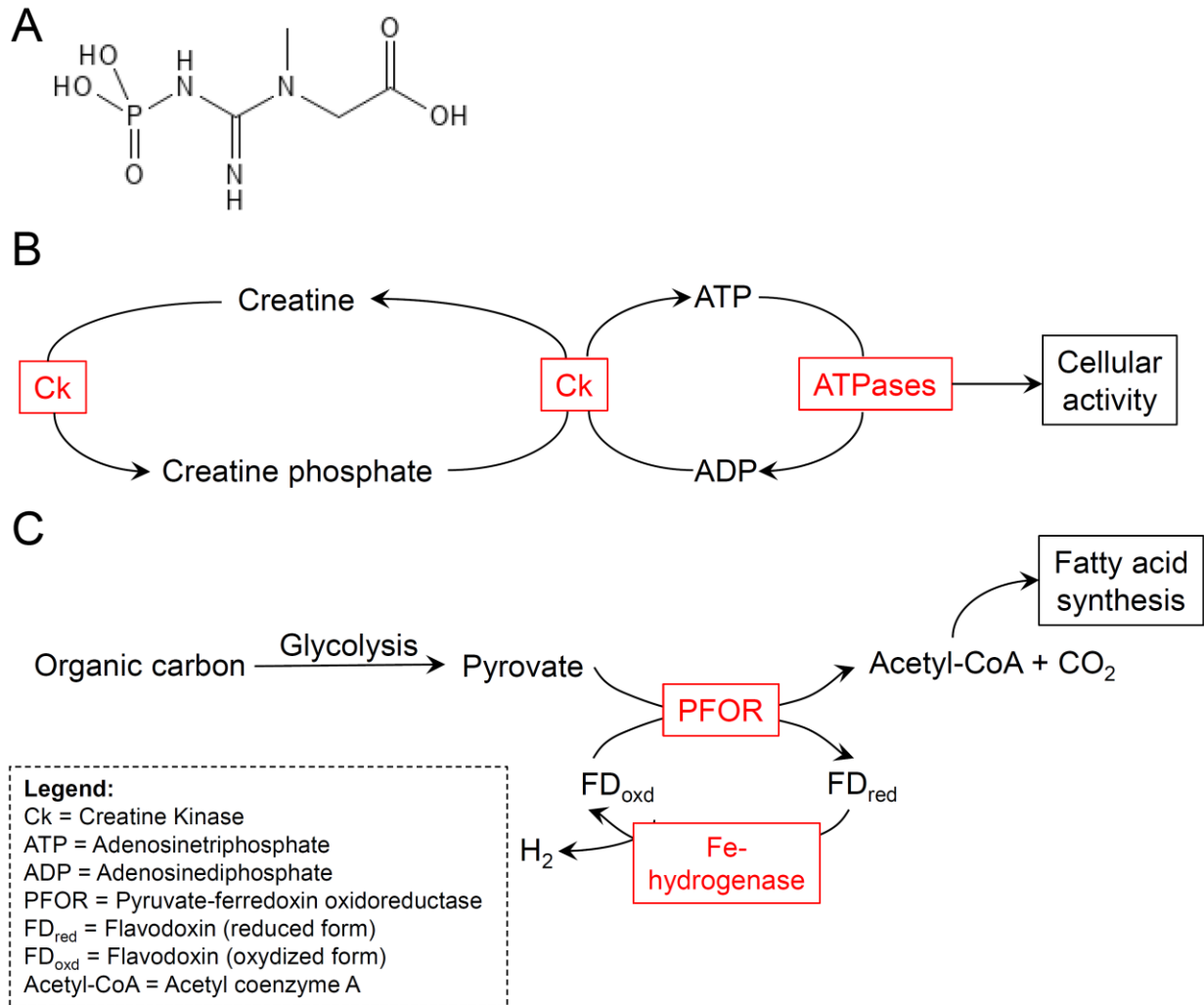


Fig. 5: Examples for molecules and processes that are relevant in the anaerobic metabolism of foraminifera. A: Structural formula of creatine phosphate. B: The role of creatine kinase (Ck) and creatine phosphate in the anaerobic metabolism. High energy creatine phosphate is produced by phosphorylation 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 H₂ producing fermentation pathway, catalyzed by Fe-hydrogenase has been described by Gomaa et al. (2021).

Figure 5:

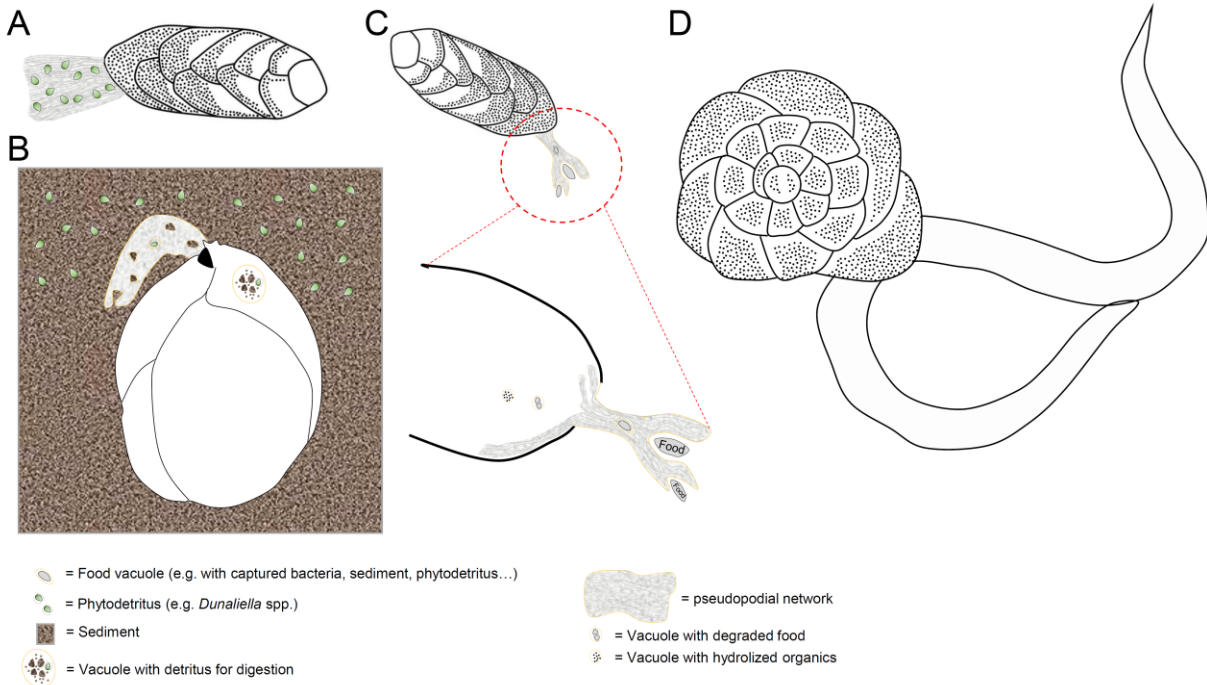


Fig. 6: Schematic representation of different trophic strategies by foraminifera: A: Strict herbivore species only ingest fresh phytodetritus. B: Non selective detritivores and seasonal herbivores ingest and partly digest detritus from the surrounding sediment (omnivores). C: Schematic representation of phagocytosis. Recent studies showed that benthic foraminifera from O₂ depleted habitats have the capacity of phagocytosis even under anoxia (Orsi et al., 2020). D: Schematic representation of *Ammonia* sp. preying on a nematode. Some omnivoric benthic foraminifera are known to prey on meiofauna (e.g., Dupuy et al., 2010) and there is first evidence, that some species can be carnivores even under O₂ depleted conditions (Glock et al., 2019a; Panagiota-Chronopoulou et al., 2019; Schweizer et al., 2022).

Figure 6:

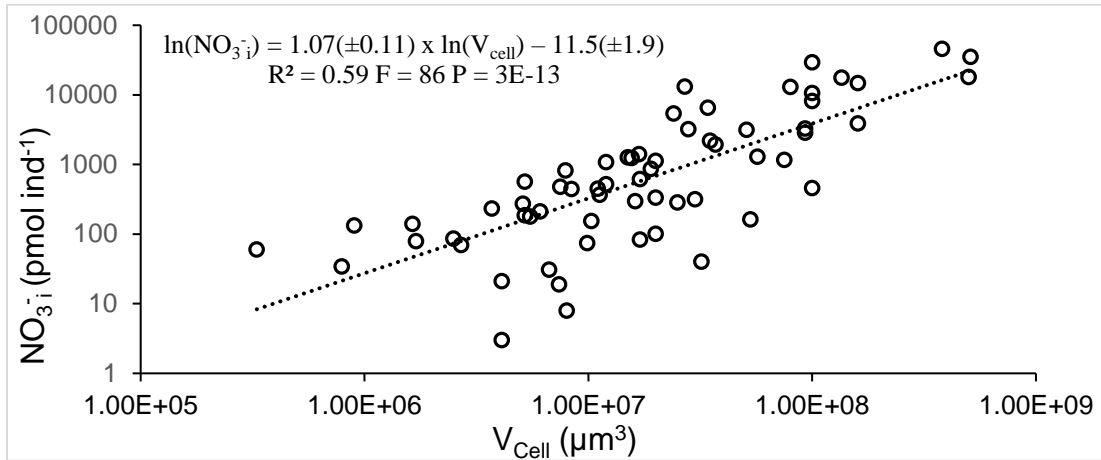


Figure 7: Log-log plot and power regression of intracellular NO_3^- content (NO_3^-) against the biovolume (V_{cell}) of benthic foraminifera from diverse environments (Tab. 2). Only species with an intracellular $[\text{NO}_3^-] \geq 1 \text{ mM}$ were considered for the power regression.