Foraminiferal metabolism and its role in geochemical processes

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Les foraminifères sont des eucaryotes de petite taille pouvant être, cependant, très abondants dans les fonds marins y compris dans les environnements peu oxygénés voire anoxiques. Leur rôle dans les processus géochimiques a été longtemps négligé laissant place à de nombreuses études sur le rôle des bactéries d'un côté et de la macrofaune de l'autre. Les études menées récemment au laboratoire montrent en effet que leur contribution à la minéralisation aérobie de la matière organique sur la plate-forme continentale est relativement faible (0.5 à 2.5 %) mais cependant pas négligeable. Par contre, dans certains milieux sous-oxygénés, où l'abondance d'autres compartiments de la faune benthique est relativement plus faible, leur rôle devient important. Certaines espèces de foraminifères sont capables, en absence d'oxygène, de respirer des nitrates. Ces espèces vivent préférentiellement dans des milieux faiblement oxygénés et riches en matière organique. Dans ces milieux, les foraminifères peuvent contribuer jusqu'à 80% à la dénitrification benthique faisant d'eux des acteurs importants du cycle de l'azote océanique. Dans les milieux côtiers tels que les vasières intertidales, les foraminifères sont capables de vivre sans oxygène libre, mais pour l'instant aucune preuve de dénitrification n'a été établie indiquant probablement l'existence d'autres voies métaboliques. Des techniques innovantes couplant l'analyse cytologique à la spectrométrie de masse haute résolution (NanoSIMS) sont en cours de développement pour essayer de percer les zones d'ombre entourant les mécanismes de survie à l'anoxie des foraminifères. Ces recherches originales montrent la diversité des stratégies de vie des foraminifères benthiques et leur rôle dans les écosystèmes extrêmes où ils sont les rares eucaryotes à pouvoir vivre.

1: Aerobic respiration of benthic foraminifera

A new protocol using microelectrodes was used to measure the respiration rates (RR) of benthic foraminifera [2]. Numerous analyses performed on different species show a relation between respiration rate (R) and the foraminiferal biovolume (BioVol) ($R=3.9810^{-3}$ $BioVol^{0.88}$ (n=44, R2=0.72) [2]. The RR of foraminifera are lower than those of other groups of meiofauna.

2: Foraminiferal ability to survive under hypoxia and anoxia

Experiments were conducted to test survival rates, growth (Fig. 1), and reproduction capacities of benthic foraminifera under hypoxia and anoxia. Innovative techniques were used 1) to follow oxygen concentrations in the aquaria, 2) to distinguish live foraminifera, and 3) to determine foraminiferal growth [1-3].

A first experiment (hypoxic conditions over 56 days) showed high survival and growth rates suggesting that survival and growth are not negatively impacted by hypoxia [1]. According to the previous results on aerobic respiration, we suggest that foraminifera are not affected by hypoxia because their oxygen demand is very low.

A second series of experiments test the effect of complete anoxia on survival and growth rates. Survival rates are not affected by anoxia after 56 days of incubation. However, growth is inhibited probably because anaerobic metabolism is less energy efficient and induces limitation of biological processes.

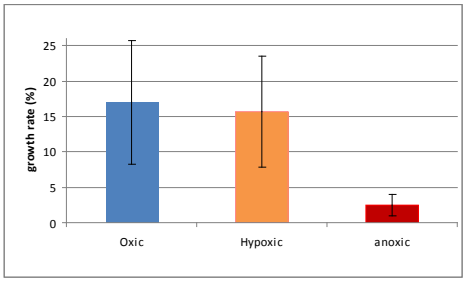

Fig. 1: Growth rate of *Ammonia tepida*

A recent set of experiments has shown that foraminifera are able to calcify under anoxia, contradicting the idea of dormancy during anoxia [5]. This observation has several implications on the implication of the geochemical composition of foraminiferal tests as paleoxygenation proxies. In future, trace elements of the newly built chambers under anoxia/hypoxia will be performed to refine their potential as paleoproxies.

3: Anaerobic metabolism

Complete denitrification by foraminifera was shown (Risgaard-Petersen et al., 2006, Nature).
It is now accepted that anaerobic metabolism such as denitrification are used by foraminifera to survive under anoxia [4], but not all foraminiferal species are able to respire nitrate. We have shown that some species living in coastal and intertidal zones were able to survive under anoxia but were not able to denitrify. They probably used other anaerobic metabolic pathways.
New experiments are performed to understand these alternative anaerobic metabolic pathways. Cytological observations using TEM combined with a NanoSIMS will help us to better understand the various strategies that foraminifera adopt to live in extreme environments.

4: Foraminiferal role in geochemical processes

The role of foraminifera in low-oxygen environments may be higher, and may contribute up to 80 % of the total benthic denitrification.
Other types of anaerobic metabolism remain to be identified to explain how foraminifera survive anoxia without using nitrate as electron acceptors. This may change our knowledge of geochemical processes in low-oxygen environments where foraminifera are dominant.

Collaborations

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Associated publications

[1] **Geslin E**., **Barras C., Langlet D., Nardelli M.P**., Kim J.H., Bonnin J., **Metzger E., Jorissen** F., 2014, Survival, reproduction and calcification of three benthic foraminiferal species in response to experimentally induced hypoxia. In: Kitazato, H.,. Bernhard, J. (Eds.). *"Experim. Approaches in Foraminifera: Collection, Maintenance and Experiments",* Springer, pp. 163-195.

[2] **Geslin, E**., Risgaard-Petersen, N., Lombard, F., **Metzger, E., Langlet, D., Jorissen, F**.J., 2011, Respiration rates of benthic foraminifera using oxygen microsensors. *Journal of Experimental Marine Biology Ecology*, 396, 108-114.

[3] Heinz, P., **Geslin, E.**, 2012, Ecological and biological response of benthic foraminifera under oxygen-depleted conditions In Altenbach A., Berhnard J., (eds.), "*Anoxia: evidence for Eukaryote Survival and paleontological Strategie"s*, Springer, pp. 289-303.

[4] Koho, K., Pina-Ochoa, E., **Geslin, E.,** Risgaard-Petersen, N., 2011, Survival and nitrate uptake mechanisms of foraminifers (*Globobulimina turgida*): laboratory experiments. *FEMS Microbiology Ecology* 75: 273–283

[5] Nardelli, M.P., Barras, C. , Metzger, E. , Mouret, A. , Filipsson H.L., **Jorissen, F. , Geslin, E.,** 2014, Experimental evidence for foraminiferal calcification under anoxia. *Biogeoscience Discussion.*.