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## Abstract

For the first time, we have documented the Arctic benthic faunal structure in the Kveithola Trough (NW Barents Sea), to improve knowledge gaps existing in this area. The Kveithola is characterized by peculiar morpho-depositional and hydrographic conditions, which allow to distinguish three main areas (the outer, the inner area and Northern channel). In the outer area, high hydrodynamic does not favour the accumulation of the organic matter and low sediment organic carbon bioavailability supports a poorly sediment community oxygen consumption. The inner part and Northern channel represent an eutrophic area, dominated by a detritivores community (subsurface-feeding polychaeta *Maldane sarsi*, the surface-feeding polychaeta *Lenisenia gracilis*, the subsurface lamellibranch bivalve *Mendicula cf. pigmea*, the subsurface protobranch bivalve genus *Yoldiella*), predators belonging to Nemertea and foraminifera as calcareous *Nonionellina labradorica*, *Globobulimina auriculata* and agglutinated *Lagenammia difflugiformis*. These taxa indicate the presence of an organic-rich sediment and oxygen-depleted environment possibly linked to a cold seep system and are also responsible for the bioturbation activity. Interestingly, delicate foraminifera monothalamous morphotypes (*Micrometula* and *Cylindrogullmia*) were reported from all sites with high abundance percentage, they inhabit typically the detritus layer of Arctic fjords and live in an extremely oxygen-deficient environment. Meanwhile, megafauna results suggest the possibility of the methane emission creating a biomass and diversity hotspot on the site 21 seafloor, characterized by heterogeneous environment with carbonate structures, microbial mats and chemosynthetic worm tufts.

To conclude, the distinct geomorphological and environmental feature, supply of organic matter and seep activity of this area, are key drivers of benthic faunal structure and their heterogeneity distribution.

## Riassunto

Per la prima volta, abbiamo documentato la struttura della comunità bentonica artica nel Kveithola Trough (NW Mare di Barents), per migliorare i gaps conoscitivi esistenti. Il Kveithola è caratterizzato da particolari condizioni morfo-deposizionali e idrografiche che permettono di distinguere tre aree principali (esterna, interna e il canale settentrionale). Nell'area esterna, l'elevato idrodinamismo contrasta l'accumulo di materia organica e la bassa biodisponibilità di carbonio organico nei sedimenti supporta una comunità con bassa richiesta di ossigeno. L'area interna e il canale settentrionale sono ambienti eutrofici, dominati da una comunità di detritivori (policheti subsurface-feeding *Maldane sarsi* e surface-feeding *Lenisenia gracilis*, bivalvi lamellibranchia subsurface *Mendicula* cf. *pigmea*, protobranchia subsurface del genere *Yoldiella*), predatori appartenenti al phylum Nemertea, foraminiferi calcarei *Nonionellina labradorica* e *Globobulimina auriculata*, e agglutinanti *Lagenammia difflugiformis*. Questi taxa, delineano un ambiente con elevate concentrazioni di materia organica nel sedimento e impoverito di ossigeno (probabilmente legati alla presenza di cold seep) inoltre, sono anche responsabili di attività di bioturbazione. Interessante notare, in tutti i siti, l'elevata densità di morfotipi di foraminiferi monotalamici (*Micrometula* e *Cylindrogullmia*) che popolano tipicamente lo strato detritico dei fiordi artici e ambienti estremi poveri di ossigeno. Inoltre, i risultati della megafauna mostrano come nel sito 21, caratterizzato da un ambiente eterogeneo con strutture carbonatiche, tappeti microbici e vermi chemiosintetici, le emissioni di metano possano creare un hotspot di biomassa e diversità.

Per concludere, le diverse caratteristiche geomorfologiche e ambientali, l'apporto di materia organica e la presenza di cold seep in questa area, rappresentano i fattori chiave della struttura della fauna bentonica e della loro distribuzione eterogenea.

# Chapter 1

## 1. General introduction

### 1.1. Climate change and methane release in Arctic ocean

Climate warming has accelerated over the past 30 y, according to the most recent studies, human activities are estimated to have caused approximately 1.0 °C of global warming above pre-industrial levels, with a likely range of 0.8 °C to 1.2°C (IPCC, 2018). The greatest changes have been recorded in the Arctic, that offers valuable insights into the degree and pace of climate change. Arctic responses very sensitively to and amplifies the effects of global climate change (Stein et al., 2008), playing a key role in the global climate system (Carbonara et al., 2016). Sea ice coverage in the Arctic Ocean has been facing a considerable reduction and the extreme retreats of summer sea ice since 2007 are well documented (National Snow and Ice Data Center, 2007). The declines in Arctic sea ice cover have been attributed to different factors, including increased advection of warm water into the Arctic Ocean (Steele and Boyd, 1998; Dickson et al., 2000; Maslowski et al., 2001; Shimada et al., 2006), atmospheric circulation patterns that favour advection of sea ice out of the Arctic Ocean through the Fram Strait (Rigor and Wallace, 2004; Maslanik et al., 2007; Serreze et al., 2007), and increased Arctic temperatures (Rothrock and Zhang, 2005; Lindsay and Zhang, 2005). Therefore, this would influence Arctic ecology and climate, enhancing available solar irradiance, increasing mixing, and radically the albedo during the boreal summer (James et al., 2016). Moreover the increase of the fall and winter temperatures undergoes stronger wave activity intensifying the coastal erosion (Serreze et al., 2007), disrupts the thermohaline circulation (Peterson et al., 2006), and improves navigation and anthropogenic impact. At the same time, a loss of Arctic sea ice might be expected to increase the area favourable for phytoplankton growth and enhance the productivity of the Arctic Ocean. Statistically, significant increasing trends of primary productivity during the 2003-2015 occurred in the eastern (Eurasian) Arctic, Barents Sea, Greenland Sea, and North Atlantic with particularly high increases in the eastern Arctic (19.26 g C/m<sup>2</sup>/yr/dec, 41.9% increase) and the Barents Sea (17.98 g C/m<sup>2</sup>/yr/dec, 30.2% increase) (Arctic Report Card, 2015). Along the shallow-water areas of the Arctic continental shelf, due to change in glacier extent and ocean warming, a large part of the seabed in the depth range 350–600 m could be prone to the release of methane over the next 100 years (Biastoch et al., 2011). Post-glacial warming and the resulting release of the previously sequestered methane has been linked to formation of the numerous pockmarks in this Arctic region. Methane is the most abundant greenhouse gas on Earth and is produced in oceanic sediments either by methanogens at temperatures typically below ~80 °C, or through the

breakdown of organic molecules at higher temperatures (Wilhelms et al., 2001; Stolper et al., 2014). Buoyancy and pressure gradients can drive gas advection to shallower sediments where methane can be consumed via anaerobic oxidation of methane (AOM) (Barnes et al., 1976) at the sulphate-methane transition zone and aerobic methane oxidation at the sediment surface (Murrell et al., 2010). A vast amount of methane is stored in sediment as gas hydrate (Kretschmer et al., 2015) or trapped in submerged permafrost as hydrate or free gas (McGuire et al., 2009). Gas hydrates are ice-like solid of a lattice of hydrogen-bonded water molecules forming cage-like structures or clathrates, that form under high pressure and low temperature conditions in the pore space of marine sediments (McGuire et al., 2009). High gas hydrate saturations can lower the permeability of the host sediment and prevent diffusive migration of gas resulting in its accumulation beneath the base of the gas hydrate stability zone (BGHSZ) (Nimblett et al., 2003). Such gas accumulations result in the build-up of high pore-overpressure, which can lead to the formation or reactivation of focused fluid conduits (Clayton et al., 1994). Pressurized fluids are released by natural blowout events and create sea floor craters known as pockmarks (Judd et al., 2007). Enhanced methane concentrations measured in the water column on western Svalbard are likely related to the melting of marine hydrate and sub emerged permafrost (James et al., 2016) therefore, this methane release could affect the Arctic carbon cycle (McGuire et al., 2009) and contributes to further global warming (Westbrook et al., 2009; Thatcher et al., 2013).

These changes can modify Arctic marine ecosystems and impact local biological communities, particularly benthic assemblage (foraminifera, macrofauna and megafauna). Conceptual and ecosystem models suggest dramatic changes in environmental conditions, which will affect species distributions, interactions, and functioning (ACIA, 2004). In fact, marine benthic communities are considered a good indicator of subtle environmental long-term changes in an ecosystem (Kroncke, 1995). In particular, benthic organisms play a major ecological role in trophic interactions, are excellent indicators for assessing the exported productivity on the ocean floor, for energy transfer to the higher trophic levels (Fontanier et al., 2006; Langezaal et al., 2006) and for recycling the organic matter, decomposed in the sediment or bottom water (Gooday et al., 1992; Cusson and Bourget, 2005). Moreover, they are also widely used in marine environments as bioindicators of environmental quality (e.g., Alve, 1995; Armynot du Châtelet and Debenay, 2010; Frontalini and Coccioni, 2011; Martins et al., 2016).

In the Arctic well-documented examples of changes of benthic fauna in relation to environmental patterns are still scarce. Meiofauna and megafauna studies in the last decade or two have concentrated on the Svalbard area (e.g., Urban-Malinga et al., 2005; Åström et al., 2018; Sabbatini et al., in preparation) and the deep-sea (e.g., Soltwedel et al., 2009; Sen et al., 2018), while macrobenthic studies have been part of all larger recent research programs across the Arctic. Of the single-celled benthos, foraminifera appear to be the prominent taxon of interest, and more so by palaeontologists than biologists (e.g., Sabbatini et al., 2007; Panieri et al., 2014).

The recent International Polar Year and related initiatives have helped Arctic researchers to improve knowledge gaps existing in these areas. In this context, aim of this thesis is to investigate patterns in the abundance and composition of benthic faunal assemblage in the Kveithola Trough, an abrupt and narrow trough formed during the Late Pliocene, when the Barents Sea Ice reached the continental shelf edge. At present the trough is influenced by strong dense bottom currents, but its inner part, where active seepage activity has been recently recognized (Lucchi et al., 2016, Mau et al., 2017), appears as a stagnant and possibly chemosynthetic environment.

These distinct geomorphological and environmental features (e.g., currents, temperature, oxygenation, grain size, organic carbon content and cold seep) which characterize the Kveithola Trough, seems to exert an important role on the distribution, abundance and diversity of benthic assemblage, which appears stressed and affected by low-oxygen conditions and high organic matter content (Hanebuth et al., 2013, Caridi et al., 2019).

Few or no data about the biotic component of this area documented up to date and our study, for the first time, has begun a systematic census of Kveithola Trough benthic fauna. The study of megafaunal communities, which could be threatened by climate-change-induced ecological disturbances, are important to understand the response of a changing Barents Sea (Barry et al., 2013; Jørgensen et al., 2015). Furthermore, today's Arctic fauna reflect the aggregated effects of millions of years of exchange across ocean basins and subsequent ecological and evolutionary change and relatively few time-series exist with which to evaluate the nature of biodiversity changes already occurring. Therefore, it would be also important to compare our results with paleoecology study to answer the question: *“What is the biodiversity status of Kveithola Trough benthos today, and the historical context that has steered its development?”*

In order to obtain a clear picture of the area in terms of active environmental factors: oceanography, sediment, organic matter sink and accumulation and seep activities this



thesis work concerned the analyses of three different benthic component which represent different ecological and dimensional categories:

- Foraminifera that are single-celled organism, ascribed to meiofauna group for tiny dimension (63-500  $\mu\text{m}$ )
- Macrofauna and megafauna, pluricellular organism sized  $>500 \mu\text{m}$ .

## **2. Dissertation structure**

This thesis is organized in four case studies, corresponding to as many research articles, of which one has already been published (Caridi et al., 2019) and three are in preparation for submission:

Chapter 2 points to the assemblage analysis of living (stained) benthic foraminifera along the Kveithola Trough. Assemblage were analysed using two different labelling methods (Rose Bengal Vs Cell Tracker Green - CTG) and the results shows that foraminiferal fauna is affected by quality and distribution of organic matter. In this frame, results show also considerable differences in the density and taxonomy composition of living foraminifera between the two methods, suggesting that CTG allows a real discrimination between viable and recently dead organisms especially in low oxygen environment.

Chapter 3 documents, for the first time, the Arctic benthic macrofaunal communities in Kveithola Trough. Three main areas can be described (the outer, the inner area and shallowest site 07) characterized by different morphological, sedimentological and oceanographical patterns that are reflected in the faunal community and organic matter distribution. Our results suggest that peculiar environmental conditions such as those of the Kveithola Trough are key drivers shaping the macrofaunal diversity and assemblage composition.

Chapter 4 investigates megafaunal communities in the shallow transect of Kveithola Trough by means of high-resolution images acquired with the Ocean Floor Observation System (OFOS). Our faunal results underline the differences between the site 21, where active methane seepage strongly influences megafaunal community compared to outside (site 02 and 06). The principal driver is the bottom substrate that in the outside is relatively homogeneous, dominated by soft bottom substrate and organisms, while the site 21 is characterized by carbonate structure, microbial mats and chemosynthetic worm tufts and created a biomass and diversity hotspot on the seafloor.

Our results serve as a first step towards addressing some of the existing gaps in our knowledge about Kveithola and its associated community and highlight the presence of cold seep.

Chapter 5 presents data on the benthic fauna community (foraminifera, macro and megafauna) from one site on the Main Drift of the Kveithola trough. Recently collected geochemical and geophysical evidences indicate the occurrence of cold seep events inside the Kveithola, most likely associated to the vertical migration of thermogenic gas. Our findings suggest that episodic seepage activity with high methane fluxes could affect on the distribution and composition of megafauna community, while foraminifera and macrofauna are influenced by organic matter patterns.

In the chapter 6 general conclusion are drawn.

## References

- ACIA Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press (2004).
- Intergovernmental Panel on Climate Change. (2018). Global Warming of 1.5° C: An IPCC Special Report on the Impacts of Global Warming of 1.5° C Above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. Intergovernmental Panel on Climate Change.
- Alve, E. (1995). Benthic foraminiferal responses to estuarine pollution: a review. *Journal of Foraminiferal Research*, 25(3), 190-203.
- Barnes, R. O., and Goldberg, E. D. (1976). Methane production and consumption in anoxic marine sediments. *Geology*, 4(5), 297-300. [https://doi.org/10.1130/0091-7613\(1976\)4](https://doi.org/10.1130/0091-7613(1976)4)
- Barry, J. P., Buck, K. R., Lovera, C., Brewer, P. G., Seibel, B. A., Drazen, J. C., Tamburri M.N., Whaling P.J., and Pane, E. F. (2013). The response of abyssal organisms to low pH conditions during a series of CO<sub>2</sub>-release experiments simulating deep-sea carbon sequestration. *Deep Sea Research Part II: Topical Studies in Oceanography*, 92, 249-260. <https://doi.org/10.1016/j.dsr2.2013.03.037>
- Biaostoch, A., Treude, T., Rüpke, L. H., Riebesell, U., Roth, C., Burwicz, E. B., Park, W., Latif, M., Boning, C.W., Madec, G., and Wallmann, K. (2011). Rising Arctic Ocean temperatures cause gas hydrate destabilization and ocean acidification. *Geophysical Research Letters*, 38(8). <https://doi.org/10.1029/2011GL047222>
- Bjarnadóttir, L.R., Rüther, D.C, Winsborrow, C.M., and Andreassen, K. (2013). "Grounding-Line Dynamics during the Last Deglaciation of Kveithola, W Barents Sea, as Revealed by Seabed Geomorphology and Shallow Seismic Stratigraphy." *Boreas* 42 (1): 84–107. <https://doi.org/10.1111/j.1502-3885.2012.00273.x>.
- Carbonara, K., Mezgec, K., Varagona, G., Musco, M. E., Lucchi, R. G., Villa, G., Melis, R., and Morigi, C. (2016). Late Quaternary deglaciation in the Arctic Ocean: evidences from microfossils. In *PAST Gateways conference* (Vol. 2016, pp. 24-25). Geological Survey of Norway (NGU).
- Caridi, F., Sabbatini, A., Morigi, C., Dell'Anno, A., Negri, A., and Lucchi, R.G. (2019). "Patterns and Environmental Drivers of Diversity and Community Composition of Macrofauna in the Kveithola Trough (NW Barents Sea)." *Journal of Sea Research* 153 (June): 101780. <https://doi.org/10.1016/j.seares.2019.101780>.
- Clayton, C. J., and Hay, S. J. (1994). Gas migration mechanisms from accumulation to surface. *Bulletin of the Geological Society of Denmark*, 41(1), 12-23.

- Cusson, M., and Bourget, E. (2005). Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series*, 297, 1-14. <https://doi.org/10.3354/meps297001>
- Data, I. E. (2007). National Snow and Ice Data Center.
- Dickson, R. R., Osborn, T. J., Hurrell, J. W., Meincke, J., Blindheim, J., Adlandsvik, B., Vigne, T., Alekseev, G., and Maslowski, W. (2000). The Arctic ocean response to the North Atlantic oscillation. *Journal of Climate*, 13(15), 2671-2696. [https://doi.org/10.1175/1520-0442\(2000\)013](https://doi.org/10.1175/1520-0442(2000)013)
- Du Châtelet, É. A., and Debenay, J. P. (2010). The anthropogenic impact on the western French coasts as revealed by foraminifera: a review. *Revue de micropaléontologie*, 53(3), 129-137. <https://doi.org/10.1016/j.revmic.2009.11.002>
- Fontanier, C., MacKensen, A., Jorissen, F. J., Anschutz, P., Licari, L., and Griveaud, C. (2006). "Stable Oxygen and Carbon Isotopes of Live Benthic Foraminifera from the Bay of Biscay: Microhabitat Impact and Seasonal Variability." *Marine Micropaleontology* 58 (3): 159–83. <https://doi.org/10.1016/j.marmicro.2005.09.004>.
- Frontalini, F., and Coccioni, R. (2011). Benthic foraminifera as bioindicators of pollution: a review of Italian research over the last three decades. *Revue de micropaléontologie*, 54(2), 115-127. <https://doi.org/10.1016/j.revmic.2011.03.001>
- Gooday, A. J., Levin, L. A., Linke, P., and Heeger, T. (1992). The role of benthic foraminifera in deep-sea food webs and carbon cycling. In *Deep-sea food chains and the global carbon cycle* (pp. 63-91). Springer, Dordrecht. [https://doi.org/10.1007/978-94-011-2452-2\\_5](https://doi.org/10.1007/978-94-011-2452-2_5)
- Hanebuth, T.J., M. Bergenthal, A. Caburlotto, S. Dippold, R. Düßmann, T. Freudenthal, T. Hörner, K. Kaszemeik, S. Klar, H. Lantzsch, J. Llopart, R.G. Lucchi, L.S. Nicolaisen, K. Noorlander, G. Osti, A. Özmaral, M. Rebesco, U. Rosiak, A. Sabbatini, W. Schmidt, A. Stachowski, R. Urgeles (2013). CORIBAR – Ice Dynamics and Meltwater Deposits: Coring in the Kveithola Trough, NW Barents Sea. Cruise MSM30
- James, R. H., Bousquet, P., Bussmann, I., Haeckel, M., Kipfer, R., Leifer, I., Niemann, H., Ostrovsky, I., Piskozub, J., Rehder, G., Treude, T., Vielstädte, L., and Greinert, J. (2016). Effects of climate change on methane emissions from seafloor sediments in the Arctic Ocean: A review. *Limnology and oceanography*, 61(S1), S283-S299. <https://doi.org/10.1002/lno.10307>
- Jeffries, M. O., Richter-Menge, J., and Overland, J. E. (2015). Arctic report card 2015.

- Jørgensen, L. L., Planque, B., Thangstad, T. H., and Certain, G. (2015). Vulnerability of megabenthic species to trawling in the Barents Sea. *ICES Journal of Marine Science*, 73(suppl\_1), i84-i97. <https://doi.org/10.1093/icesjms/fsv107>
- Judd, A. G. (2000). Geological sources of methane. In *Atmospheric Methane* (pp. 280-303). Springer, Berlin, Heidelberg. [https://doi.org/10.1007/978-3-662-04145-1\\_15](https://doi.org/10.1007/978-3-662-04145-1_15)
- Kretschmer, K., Biastoch, A., Rüpke, L., and Burwicz, E. (2015). Modeling the fate of methane hydrates under global warming. *Global Biogeochemical Cycles*, 29(5), 610-625. <https://doi.org/10.1002/2014GB005011>
- Kröncke, I. (1995). Long term changes in North Sea benthos. *Senckenbergiana maritima*, 26.
- Langezaal, A. M., Jorissen, F. J., Braun, B., Chaillou, G., Fontanier, C., Anschutz, P., and Van der Zwaan, G. J. (2006). The influence of seasonal processes on geochemical profiles and foraminiferal assemblage on the outer shelf of the Bay of Biscay. *Continental Shelf Research*, 26(15), 1730-1755. <https://doi.org/10.1016/j.csr.2006.05.005>
- Lindsay, R. W., and Zhang, J. (2005). The thinning of Arctic sea ice, 1988–2003: Have we passed a tipping point? *Journal of Climate*, 18(22), 4879-4894. <https://doi.org/10.1175/JCLI3587.1>
- Lucchi, R. G., Bazzaro, M., Biebow, N., Carbonara, K., Caridi, F., De Vittor, C., ... and Krueger, M. (2016). BURSTER-Bottom Currents in a Stagnant Environment. EUROFLEETS-2 Cruise Summary Report.
- Martins, M.V.A., Helali, M.A., Zaaboub, N., Boukef-BenOmrane, I., Frontalini, M., Reis, D., Portela, H., Clemente I.M.M., Nogueira, L., Pereira, E., Aleya, L., Frontalini, F., and El Bour, M. (2016). "Organic Matter Quantity and Quality, Metals Availability and Foraminiferal Assemblage as Environmental Proxy Applied to the Bizerte Lagoon (Tunisia)." *Marine Pollution Bulletin* 105 (1): 161–79. <https://doi.org/10.1016/j.marpolbul.2016.02.032>.
- Maslanik, J., Drobot, S., Fowler, C., Emery, W., and Barry, R. (2007). On the Arctic climate paradox and the continuing role of atmospheric circulation in affecting sea ice conditions. *Geophysical Research Letters*, 34(3). <https://doi.org/10.1029/2006GL028269>
- Maslowski, W., Marble, D. C., Walczowski, W., and Semtner, A. J. (2001). On large-scale shifts in the Arctic Ocean and sea-ice conditions during 1979–98. *Annals of Glaciology*, 33, 545-550. <https://doi.org/10.3189/172756401781818978>
- Mau, S., M. Römer, M. E. Torres, I. Bussmann, T. Pape, E. Damm, P. Geprägs, Wintersteller, P., Hsu, C.W., Loher, M., and Bohrmann, G. (2017). "Widespread Methane Seepage along the Continental Margin off Svalbard—from Bjørnøya to Kongsfjorden." *Scientific Reports*. <https://doi.org/10.1038/srep42997>.

- Murrell, J. C. (2010). In *Handbook of Hydrocarbon and Lipid Microbiology* (ed Timmis, K. N.) Springer. Ch. 26, 1953–1966
- Nimblett, J., and Ruppel, C. (2003). Permeability evolution during the formation of gas hydrates in marine sediments, *J. Geophys. Res.*, 108(B9) 2420. doi: 10.1029/2001JB001650
- Panieri, G., Rachael, H.J., Camerlenghi, A., Westbrook, G.K., Consolaro, C., Cacho, I., Cesari, V., and Sanchez Cervera, C. (2014). “Record of Methane Emissions from the West Svalbard Continental Margin during the Last 23.500yrs Revealed by  $\Delta^{13}\text{C}$  of Benthic Foraminifera.” *Global and Planetary Change* 122: 151–60. <https://doi.org/10.1016/j.gloplacha.2014.08.014>.
- Peterson, B. J., McClelland, J., Curry, R., Holmes, R. M., Walsh, J. E., and Aagaard, K. (2006). Trajectory shifts in the Arctic and subarctic freshwater cycle. *Science*, 313(5790), 1061-1066. <https://doi.org/10.1126/science.1122593>
- Rebesco, M., Liu, Y., Camerlenghi, A., Winsborrow, M., Laberg, J.S., Caburlotto, A., Diviacco, P., Accettella, D., Sauli, C., Wardell, N., and Tomini, I. (2011). “Deglaciation of the Western Margin of the Barents Sea Ice Sheet - A Swath Bathymetric and Sub-Bottom Seismic Study from the Kveithola Trough.” *Marine Geology* 279 (1–4): 141–47. <https://doi.org/10.1016/j.margeo.2010.10.018>.
- Rigor, I. G., and Wallace, J. M. (2004). Variations in the age of Arctic sea-ice and summer sea-ice extent. *Geophysical Research Letters*, 31(9). <https://doi.org/10.1029/2004GL019492>
- Rothrock, D. A., and Zhang, J. (2005). Arctic Ocean sea ice volume: What explains its recent depletion?. *Journal of Geophysical Research: Oceans*, 110(C1) <https://doi.org/10.1029/2004JC002282>
- Sabbatini, A., Morigi, C., Negri, A., and Gooday, A.J. (2007). “Distribution and Biodiversity of Stained Monothalamous Foraminifera from Tempelfjord, Svalbard Anoxic Environments in Arctic Sediment Drifts-AXED View Project Towards a Better Understanding of Hydrocarbon Potential at the Cross-Road of Europe, Middle-East and Asia (The Eastern Greater Caucasus) View Project.” *Article in The Journal of Foraminiferal Research*. <https://doi.org/10.2113/gsjfr.37.2.93>.
- Sen, A., Aström, E.K.L., Li Hong, W., Portnov, A., Waage, M., Serov, P., Carroll, M.L., and Carroll, J.L. (2018). “Geophysical and Geochemical Controls on the Megafaunal Community of a High Arctic Cold Seep.” *Biogeosciences* 15 (14): 4533–59. <https://doi.org/10.5194/bg-15-4533-2018>.
- Serreze, M. C., Holland, M. M., and Stroeve, J. (2007). Perspectives on the Arctic's shrinking sea-ice cover. *science*, 315(5818), 1533-1536. <https://doi.org/10.1126/science.1139426>

- Schulte-Rüther, M., Mainz, V., Fink, G. R., Herpertz-Dahlmann, B., and Konrad, K. (2012). Theory of mind and the brain in anorexia nervosa: Relation to treatment outcome. *Journal of the American Academy of Child and Adolescent Psychiatry*. <https://doi.org/10.1016/j.jaac.2012.06.007>
- Shimada, K., Kamoshida, T., Itoh, M., Nishino, S., Carmack, E., McLaughlin, F., Zimmermann, S., and Proshutinsky, A. (2006). Pacific Ocean inflow: Influence on catastrophic reduction of sea ice cover in the Arctic Ocean. *Geophysical Research Letters*, 33(8). <https://doi.org/10.1029/2005GL025624>
- Sloan, E. D. (2003). Clathrate hydrate measurements: microscopic, mesoscopic, and macroscopic. *The Journal of Chemical Thermodynamics*, 35(1), 41-53. [https://doi.org/10.1016/S0021-9614\(02\)00302-6](https://doi.org/10.1016/S0021-9614(02)00302-6)
- Soltwedel, T., Jaeckisch, N., Ritter, N., Hasemann, C., Bergmann, M., and Klages., M. (2009). "Bathymetric Patterns of Megafaunal Assemblage from the Arctic Deep-Sea Observatory HAUSGARTEN." *Deep-Sea Research Part I: Oceanographic Research Papers*. <https://doi.org/10.1016/j.dsr.2009.05.012>.
- Steele, M., and Boyd, T. (1998). Retreat of the cold halocline layer in the Arctic Ocean. *Journal of Geophysical Research: Oceans*, 103(C5), 10419-10435. <https://doi.org/10.1029/98JC00580>
- Stein, R. (2008). *Arctic Ocean sediments: processes, proxies, and paleoenvironment* (Vol. 2). Elsevier
- Stolper, D. A., Lawson, M., Davis, C. L., Ferreira, A. A., Neto, E. S., Ellis, G. S., Lewan, M.D., Martini, A.M., Tang, Y., Schoell, M., Sessions, A.L., and Eiler, J.M. (2014). Formation temperatures of thermogenic and biogenic methane. *Science*, 344(6191), 1500-1503. <https://doi.org/10.1126/science.1254509>
- Thatcher, K. E., Westbrook, G. K., Sarkar, S., and Minshull, T. A. (2013). "Methane Release from Warming-Induced Hydrate Dissociation in the West Svalbard Continental Margin: Timing, Rates, and Geological Controls." *Journal of Geophysical Research: Solid Earth* 118 (1): 22–38. <https://doi.org/10.1029/2012JB009605>.
- Urban-Malinga, B., Wiktor, J., Jabłońska, A., and Moens, T. (2005). Intertidal meiofauna of a high-latitude glacial Arctic fjord (Kongsfjorden, Svalbard) with emphasis on the structure of free-living nematode communities. *Polar Biology*, 28(12), 940-950. <https://doi.org/10.1007/s00300-005-0022-4>
- Westbrook, G. K., Thatcher, K. E., Rohling, E. J., Piotrowski, A. M., Pälike, H., Osborne, A. O., Nisbet, E. G., Minshull, T. A., Lanoisellé, M., James, R. H., Hühnerbach, V., Green, D., Fisher, R. E., Crocker, A. J., Chabert, A., Bolton, C., Beszczynska-Möller, A., Berndt, C., and Aquilina, A. (2009), Escape of methane gas from the seabed along the West Spitsbergen continental margin, *Geophys. Res. Lett.*, 36, L15608, doi:10.1029/2009GL039191.

Wilhelms, A., Larter, S. R., Head, I., Farrimond, P., Di-Primio, R., and Zwach, C. (2001). Biodegradation of oil in uplifted basins prevented by deep-burial sterilization. *Nature*, 411(6841), 1034. <https://doi.org/10.1038/35082535>



## Chapter 2

### Abstract

#### **Foraminiferal assemblage along the shallow transect on the Kveithola Trough (NW Barents Sea)**

This work analyses the distribution of living benthic foraminiferal assemblage along the shallow transect on the Kveithola Trough. We report the quantitative data of the living benthic foraminiferal density, biodiversity and vertical distribution in relation to environmental features (e.g. currents, oxygenation, grain size and organic carbon content). Kveithola Trough located in the NW of Barents Sea, is characterized by peculiar geo-morphological and environmental conditions, which between high regional primary and secondary production are key drivers of foraminiferal assemblage distribution. Faunal distribution varied significantly (in term of abundance and diversity, in relation to their size) along the transect and statistical tests indicated significant differences in the composition of foraminifera community between the sites group 02 and 03 (outer Kveithola Trough), and group 04, 05, 21, 06 and 07 located in inner part (from Drift to Northern channel). Particularly, the species distribution is consistent with depositional settings and with data of quantity and biochemical composition of the organic matter. The inner part appears as a stressed environment and living benthic foraminiferal assemblage is dominated by species associated with organic-rich sediment and oxygen-depleted environments as *Nonionellina labradorica*, *Globobulimina auriculata*, *Leptohalysis scottii* and *Reophax scorpiurus*. Instead, the site corresponding to the outer shelf is characterized by the presence of diverse and abundant benthic foraminiferal assemblage suggesting an oxygenated and oligotrophic environment. We notice in all sites the presence of delicate monothalamous taxa (organic-walled allogromiids, agglutinated saccamminids, psammosphaerids and tubular forms).

Moreover, we use two different labelled methods and results suggest that Cell Tracker Green (CTG) technique well distinguished living from dead organisms and is a suitable staining method to document the response of selected meiofauna groups to short-term disturbances. Considering that this is the first study of foraminifera assemblage CTG labelled in the Kveithola, the discussions will be addressed including only a CTG results, while Rose Bengal (RB) data will be used for comparison to other studies.

To conclude, the Kveithola Trough is characterized by high primary production and high nutrient rates that reach the benthic community, suggesting a close relationship between the pelagic and benthic compartments. These conditions allow us to describe the Kveithola Trough as an eutrophic hot-spot in an oligotrophic Arctic ocean, characterized by peculiar environmental conditions which shapes the living benthic faunal structure.

## 1. Introduction

Living benthic foraminifera from the Kveithola Trough, in the NW Berents sea, are undocumented in the published literature, except by Sabbatini et al., (submitted to BOREAS). Foraminifera are unicellular eukaryotes that occur ubiquitously in all the world oceans and in all marine habitats, including both aquatic and benthic environments. Benthic foraminifera are an important component of oceanic systems and may even account for 50% of eukaryotic biomass (Gooday et al., 1992). These organisms are excellent indicators for assessing the exported productivity on the ocean floor (van der Zwaan et al., 1999) for energy transfer to the higher trophic levels (Fontanier et al., 2006; Langezaal et al., 2006) and for cycling the organic matter, decomposing in the sediment or bottom water (Cusson and Bourget, 2005; Gooday et al., 1992). They are characterised by a short life cycle (compared to macrofaunal metazoans) and react rather quickly to changes in marine environments. For these reasons, foraminifera are used to evaluate the environmental status of marine coastal systems impacted by pollution and eutrophication (Armynot du Châtelet and Debenay, 2010, Frontalini and Coccioni, 2011; Martins et al., 2013). Moreover, as they can fossilise, they are also reliable descriptors of environmental change over historical and geological time scales (Gooday et al., 2009). The distribution, abundance and diversity of benthic foraminifera are mostly controlled by physicochemical properties of water and sediment (Gupta, 1999). Currents, temperature, pH, oxygenation, grain size and organic carbon content represent the main factors regulating the foraminiferal assemblage and distribution (Murray, 2006; Martins et al., 2016; Fontanier et al., 2002). Early studies (Diz et al., 2004; Riera et al., 2011) report the effect of sediment grain-size on foraminiferal density and diversity; show how the quantity and quality of the organic matter and low oxygen content is considered crucial for benthic foraminifera ecological inference (Martins et al., 2016; Sabbatini et al., 2012; Haller et al., 2019). Altenbach et al., (1999) suggest an optimum range of organic input (1 to 10 g [C org. m<sup>-2</sup> yr<sup>-1</sup>]) within which they reproduce, are competitive and attain their maximum abundance. At the same time, some species show a strong tolerance to hypoxia and proliferate in oxygen-depleted environments (Bernhard and Gupta, 1999; Cardich et al., 2012; Caille et al., 2015). Various mechanisms could explain how foraminifera survive in these adverse conditions and these include anaerobic metabolic pathways, bacterial symbionts, chloroplasts sequestration or proliferation of peroxisomes and mitochondria (Koho and Piña-Ochoa, 2012, and references therein) up to the ability of some calcareous foraminifera to use nitrate for respiration instead of oxygen (Risgaard-Petersen et al., 2006; Pina-Ochoa et al., 2010).

To conduct an ecological study, it is therefore necessary the identification of live vs dead benthic fauna. In order to do this, we use two different method: Cell Tracker Green and Rose Bengal. Cell tracker green method is more accurate in abundance assessment because exclusively labels surviving cells/organisms (Bernhard et al., 2006). When living cells are incubated with fluorogenic probes such as CTG, the probe passes through the cellular membrane and reaches the cytoplasm, where hydrolysis with nonspecific esterase causes the fluorogenic reaction (Bernhard et al.,2006; Pucci et al., 2009). Once in the cell, the CTG probe is converted to cell-impermeant reaction products (Peperzak and Brussaard, 2011). CTG is applied in many fields, such as medicine e.g. human tissue cultures (Boleti et al., 2000); parasitology e.g. drug–multicellular parasites relation (Trejo-Ch´avez et al., 2011), phytoplankton ecology (Peperzak and Brussaard, 2011); and microbenthology – e.g. benthic microalgae, ciliates, flagellates and foraminifera (Bernhard et al., 2006; Pucci et al., 2009; Figueira et al., 2012). Instead, Rose Bengal is the standard method to benthic foraminifera. Rose Bengal is a typical bulk stain which adheres to (cytoplasmatic) proteins and is applied into formalin-fixed samples (Higgins and Thiel, 1988; Somerfield et al., 2005). As a stain it has various advantages (cheap, simple to apply, animals are easily visible under light microscope because producing a magenta coloration of the specimen), but there are several negative aspects regarding the use of Rose Bengal. For example, the reaction of Rose Bengal with protein defines it as a non-vital stain; that is, it will adhere to dead as well as living cytoplasm (Bernhard et al., 2006) in fact, the cytoplasm of Foraminifera stays in the shell for a long period after death, particularly in anoxic conditions, and it still stains well with RB (Bernhard et al., 2006; Pucci et al., 2009). In addition, the protein can stain the organic lining of foraminiferal tests (Walker et al., 1974) or bacteria attached to or located inside the test (Martin and Steinker, 1973). Despite these aspects, this remain the most used method and because of this, it is also used in this work in order to compare this research to previous studies on living foraminiferal assemblage.

The main objectives of this study are to describe the patterns of distribution, density and diversity of living foraminiferal fauna in the arctic Kveithola Trough (NW Barents Sea) and to test the CTG labelling method, comparing with Rose Bengal results. Moreover, to define the total assemblage (live and dead) a study will be conducted to compare living benthic foraminiferal assemblage (results of this thesis) to benthic foraminiferal thanatocoenoses (Sojo Gamboa, PhD thesis).

## 1.1. Study Area

The Kveithola Trough (Fig.1) is an abrupt and narrow glacial sedimentary system located in the NW Barents Sea. The trough extends in E-W direction over 100 km, less than 13 km wide and shows an average water depth of 200-400 m along its axis (Schulte-Rüther et al., 2012). Along with the larger Storfjorden glacial system, the Kveithola Trough hosted during the last glaciation ice streams draining ice from the southern Svalbard in the north and Bear Island in the south (Pedrosa et al., 2011; Bjarnadóttir et al., 2013). The seafloor in the Kveithola Trough is characterized by a series of E–W trending mega-scale glacial lineation that record a fast-flowing ice stream draining the Barents Sea ice sheets during the Last Glacial Maximum. Glacial lineation are overprinted by transverse Grounding-Zone Wedges (GZW) generated during episodic retreat of the last glacial ice sheet, giving rise to a staircase bathymetric axial profile of the trough (Rebesco et al., 2011; Bjarnadóttir et al., 2013). The Kveithola Trough is intersected with N-S direction by the Hornsund and Knølegga fault systems related to the phases of crustal extension associated with the opening of the Norwegian - Greenland Sea since the Cretaceous (Gabrielsen et al., 1990; Bergh and Grogan, 2003). The innermost Knølegga fault is responsible for an elongated bathymetric depression indicated by Rebesco et al., (2016) as the “northern channel”. The inner part of the trough hosts a complex sediment drift characterized by two main depocentres (Main and Minor Drifts; Rebesco et al., 2016), with internal acoustic reflectors on the sub-bottom record indicating persistent bottom currents that were active in the area since at least 13 cal ka BP (Bjarnadóttir et al., 2013; Rebesco et al., 2016). Beside of the highly dynamic depositional environment depicted from the morphological and structural characteristics of the sediment drift (Rebesco et al., 2016), the lithofacies characteristics of surface sediments indicate low-energy and/or low-oxygen conditions with black sediments having a strong smell of hydrogen sulphide (Hanebuth et al., 2013), whereas on the outer trough, at only a few tens of km distance, the sediments appear fully oxygenated. Furthermore, the sedimentological settings be influenced by the particular oceanographic patterns: in the outer part of the trough, the North Atlantic Current sweeps the outer seafloor and remove the fine sediment fraction leaving a coarse lag of pebbly sands (Caricchi et al., 2018); instead, the inner part is is subject to continuous fine-grained sediment deposition due to cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow (Rebesco et al., 2016; Lantzsich et al., 2017).

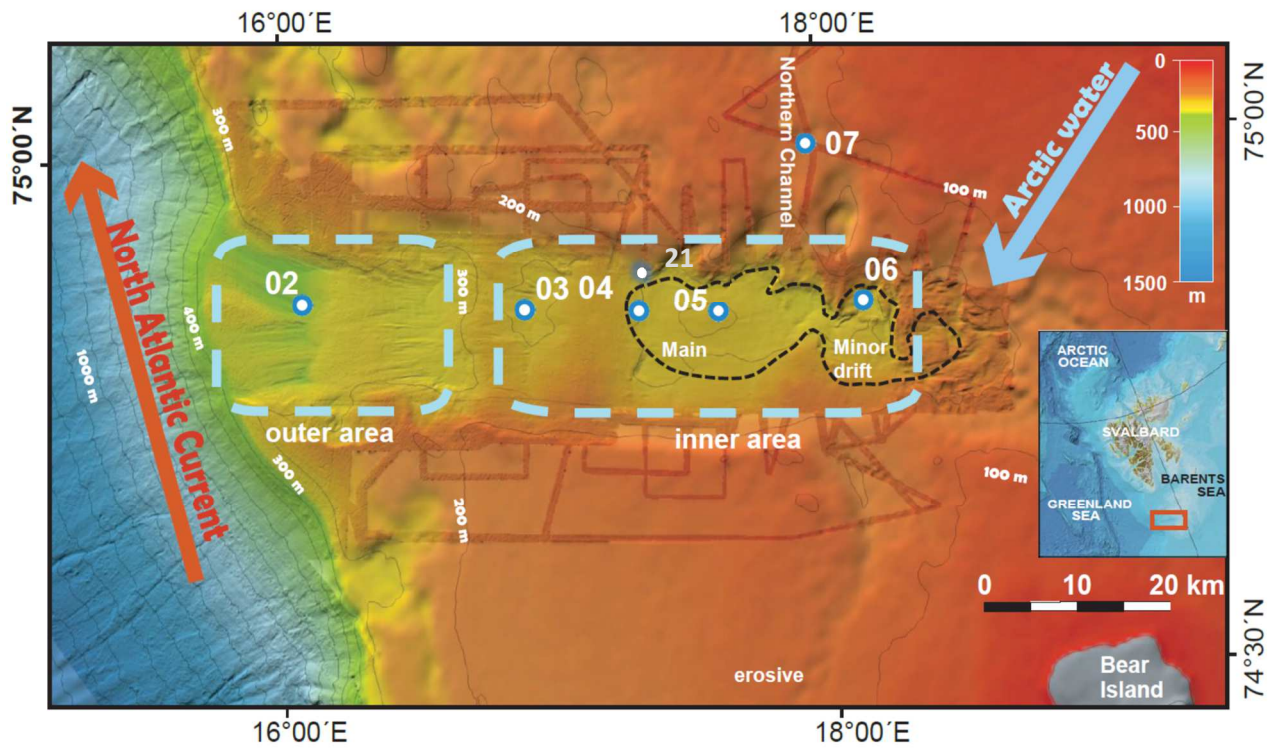


Fig. 1 Study area and location of the studied sites. The arrows indicate surface currents.

Station	Latitude	Longitude	Depth(m)	Site location
02	74° 51,53' N	16° 05,93' E	376	Outern Kveithola Trough
03	74° 51,00' N	16° 54,52' E	317	Grounding-Zone Wedges
04	74° 50,75' N	17° 20,86' E	304	Kveithola Main Drift
21	74° 52,40' N	17° 21,64' E	306	Kveithola Main Drift
05	74° 50,53' N	17° 38,37' E	293	Kveithola Main Drift
06	74° 50,75' N	18° 10,55' E	335	Kveithola Minor Drift
07	74° 59,69' N	17° 59,72' E	159	Northern Channel (Knølegga Fault Zone)

Tab. 1 TV-multi-corer sampling sites location.

## 2. Materials and Methods

Sediment samples were collected using a video-guided multicorer (TV-MUC) in June 13–23, 2016 during Eurofleets 2- BURSTER cruise that was conducted onboard the German icebreaker RV Polarstern (Expedition PS99-1a; Lucchi et al., 2016). At each studied site a water column profile was performed with a SBE911plus CTD system.

Sediment samples were collected at five sites (CTG) and seven sites for Rose Bengal (Fig. 1 and Tab. 1) using a video-guided multi-corer (TV-MUC) that was assembled with 8 tubes in polycarbonate having 60 cm length, 10 cm outer diameter, and 2.5 mm of thickness. 1 (CTG) and 2 (RB) replicate subsamples for living foraminiferal analysis were obtained using Plexiglas corers, inner diameter 3.6 (surface area 10.18 cm<sup>2</sup>), inserted manually at each site from the first TV-MUC deployment. The replicate for each site was opened on board and sliced at every 0.5 cm for the first 2 cm and at every 1 cm between 2–10 cm depths. Each slice was incubated in a refrigerator for 12-15 hours in Cell Tracker Green CMFDA (CTG) following the staining procedure as indicated in Pucci et al., (2009). After incubation, samples were fixed in 10% formalin buffered with sodium borate solution. For Rose Bengal the samples were stained and preserved in 10% buffered formalin. In the laboratory, the fixed sediment samples were sieved through 63, 150 and 500 µm mesh (in order to evaluate the size structure of foraminiferal assemblage) and the residues were kept wet and hand-sorted in water for all CTG-stained benthic foraminifera e macrofauna using a fluorescence binocular microscope and binocular microscope for Rose-Bengal-stained benthic foraminifera. Hard-shelled polythalamous foraminifera (agglutinated and calcareous species) were stored in micro-palaeontological slides. Soft-shelled monothalamous taxa were placed in cavity slides in glycerol and photographed under a compound microscope (Nikon Eclipse E 600 POL). The Rose Bengal technique is an inexpensive and easy method to recognise foraminifera that were alive (or recently alive) when they were collected (Walton, 1952; Murray and Bowser, 2000). However, especially in low oxygen settings, the cell material may persist long after death, resulting in false positives (Corliss and Emerson, 1990; Bernhard, 2000). In order to minimise overestimation in the live foraminifera counts, strict staining criteria were always applied. Specimens were considered “alive” only when all chambers, except for the last one or two, were well stained. Furthermore, doubtful specimens were compared with perfectly stained specimens of the same species and non-transparent agglutinated and miliolid taxa were broken to inspect their contents. A special effort was made to recognize soft-shelled monothalamous taxa, which are largely undescribed, and they are included

in this data analyses. Few fragments of branching and tubular foraminifera (i.e. *Hyperammina*, *Rhizammina*) were not included in the data analyses because of their easily breakable tests, which makes it very difficult to quantify them correctly. Species identification followed previous studies from the high latitude environments and for the hard-shelled polythalamous foraminifera (agglutinated and calcareous taxa) taxonomy we followed papers and atlas by Loeblich and Tappan (1953), Seidenkrantz (1995), Majewski and Zajaczkowski (2007), Sabbatini et al., (2007). For the soft-shelled monothalamous foraminiferal taxonomy we followed papers by Gooday et al. (2010), Majewski et al., (2005) and Sabbatini et al., (2013).

All the specimens were counted, and their numbers standardised per 10 cm<sup>2</sup> and the taxonomic composition of the main taxa was calculated. Also, the gromiid morphotypes are included in the total abundance. *Gromia* is a widespread genus of marine and freshwater amoeboid, closely resembling some foraminifera.

In order to describe the vertical distribution of the total faunas or individual taxa, we used the average living depth (ALD, Jorissen et al., 1995), which allows a rapid description of the microhabitat patterns. The ALD is calculated according to the following equation:

$$ALD_x = \sum_{i=0,x} (n_i D_i) / N,$$

where  $x$  is the lower boundary of deepest sample,  $n_i$  the number of individuals in interval  $i$ ;  $D_i$  the midpoint of sample interval  $i$ ;  $N$  the total number of individuals for all levels.

Faunal biodiversity was estimated using different diversity indices: species richness ( $S$ ) measured as the number of species, species diversity ( $H \log_e$ ) measured by the Shannon–Wiener ( $H$ ) information function and species evenness ( $J$ ) measured using the Pielou (1975) index. All indices were calculated using the statistical PAST software (Paleontological Statistics; Version 3.12'; Hammer et al., 2009) for level and for the total 0-10 cm.

## **2.1. Quantity and biochemical composition of sedimentary organic matter**

Chlorophyll-a and phaeopigment determinations of the top 2 cm of the sediment were carried out fluorometrically according to Lorenzen and Jeffrey, 1980. Pigments were extracted with 90% acetone (12 h in the dark at 4 °C). After the extraction the pigments were analysed to estimate the quantity of chlorophyll-a and, after acidification with 0.1 N HCl, to estimate the amount of phaeopigments. The sum of the chlorophyll-a and phaeopigment concentrations were assumed to



represent the total phytopigment concentrations which were converted to carbon equivalents by using the conversion factor of 40  $\mu\text{g}$  of C  $\mu\text{g}^{-1}$  (Pusceddu et al., 1999; Pusceddu et al., 2009). Such a conversion factor was used to allow a proper comparison with previous investigations (Pusceddu et al., 1999; 2000; 2009).

Protein, carbohydrate and lipid concentrations of the top 2 cm of the sediment were determined spectrophotometrically (Pusceddu et al., 2009, 2010). Protein concentration was obtained according to Hartree (1972) as modified by Danovaro (2010). Concentrations are reported as mg albumin equivalents per dry weight g of sediment. Carbohydrate were analysed according to Gerchakov and Hatcher (1972) and expressed as mg glucose equivalents per dry weight g of sediment. Lipids were extracted with methanol and chloroform (2:1 vol/vol) according to Bligh and Dyer (1959) and then analysed according to Marsh and Weinstein (1966). Lipid concentrations are reported as mg tripalmitin equivalents per dry weight g of sediment. Protein, carbohydrate and lipid concentrations were converted into carbon equivalents by using the following conversion factors: 0.49, 0.40 and 0.75 g C  $\text{g}^{-1}$ , respectively (Fabiano et al., 1995). The sum of protein, carbohydrate and lipid carbon was referred as biopolymeric C (BPC), while bioavailable carbon (BAC) concentration was calculated as the sum of digestible proteins and carbohydrates converted into carbon equivalents by using the same factors as for their total pools (Danovaro et al., 2001). The contribution of chlorophyll-a concentrations converted into C equivalent to biopolymeric C concentrations was used as descriptors of the ageing of sediment organic matter (Pusceddu et al., 2010; Pusceddu et al., 2011). For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). All the analyses were performed as three pseudo-replicates, with about 1 g of sediment per sample.

## **2.2. Statistical analysis: Cell Tracker Green method**

To test differences in communities composition among sites one-way ANOSIM was applied for both benthic communities. SIMPER analysis was applied to assess the dissimilarity percentage between foraminiferal assemblage and biochemical compounds and to identify which species contributed most to the observed dissimilarities between sites. Pearson's correlation coefficient ( $r$ ) was calculated to determine individual pairwise relationship between environmental variables and univariate faunal community data. The forward selection of explanatory variables was carried out under a linear regression model using 999 permutations. To identify the potential relationships between environmental variables and macrofaunal species composition a canonical

correspondence analysis (CCA) was performed. All statistical analyses were carried out using the software Past 3'12 (Hammer et al., 2009).

### **2.3. Statistical analyses: Rose Bengal method**

To test spatial variations in the composition of the benthic foraminiferal assemblage, a non-parametric test (One-way ANOSIM; Clarke 1993) based on Bray–Curtis similarity matrix, was applied. The non-metric multi-dimensional scaling plot (nMDS) based on a Bray-Curtis matrix for similarity assembled on taxon abundances from standardized and transformed (single square-root) data, was conducted. Single square-root transformation and standardization were carried out to balance the community effect of the highly abundant and rarer taxa and to control the high variability between replicate samples. SIMPER analyses were applied to assess the dissimilarity percentage between foraminiferal assemblage in the different sampling sites and to identify which species contributed most to the observed dissimilarities between sampling sites. All statistical analyses were carried out using the software Past 3'12 (Hammer et al., 2009).

### 3. Results

#### 3.1. Food quantity and quality at the seafloor

The concentrations of all investigated biochemical compounds as well as the contribution of the C of the algal fraction to biopolymeric C are summarized in Tab. 2.

Station	Depth	PRT mg/g	CHO mg/g	LIP mg/g	Chl-a µg/g	Phaeo µg/g	BPC mg/g	BAC mg/g	Algal fraction of BPC(%)
02	376	3,24	2,34	0,49	0,27	7,56	2,89	2,52	10.45
03	317	4,69	4,22	0,87	0,69	18,94	4,64	3,99	16.34
04	305	8,50	5,89	1,20	1,48	33,35	7,43	6,52	17.96
05	294	7,22	6,71	1,37	1,34	30,98	7,48	6,23	17.27
06	336	6,45	7,02	1,72	4,13	61,92	7,09	6,07	17.47
07	159	3,01	5,09	1,14	1,22	26,42	7,25	5,97	34.13

Tab. 2 Concentration of all investigating biochemical compounds by sites: protein (PRT), carbohydrates (CHO), lipid (LIP), chlorophyll-a (Chl-a), phaeopigments (Phaeo), biopolymeric C (BPC), bioavailable carbon (BAC) and algal fraction of BPC.

The total phytopigment content varied significantly among sites of the Kveithola Trough, with values ranging from  $7.33 \pm 0.55 \mu\text{g/g}$  in the site 02 (Grounding-Zone Wedges) to  $66.1 \pm 4.4 \mu\text{g/g}$  in the site 07 out of the Kveithola Trough. Total carbohydrate concentrations were characterized by a wide variability with the lowest value at site 02 ( $2.34 \pm 0.27 \text{ mg/g}$ ) and highest value in site 07 ( $7.01 \pm 0.79 \text{ mg/g}$ ). Similar patterns were generally observed also for lipid and protein concentrations. Bioavailable carbon was lower at GZW sites (02 and 03), where the values were  $2,52 \pm 0.82$  and  $3,99 \pm 0.40 \text{ mg/g}$ , respectively. Conversely, at the other out sites decreased from  $6,52 \pm 1.92 \text{ mg/g}$  in the site 04 to  $5,97 \pm 0.39 \text{ mg/g}$  in the site 07. The contribution of the C associated to the algal fraction to the biopolymeric C changed significantly across the sampling sites, ranging from 10% in the site 02 to 34% in the site 07.

### 3.2. Cell Tracker Green

All sites and their benthic communities are themselves quite different. ANOSIM test for foraminifera  $R:0.14$  and  $p<0.05$ , shows all pairwise comparisons significant except for the sites 02,05Vs21 with the others.

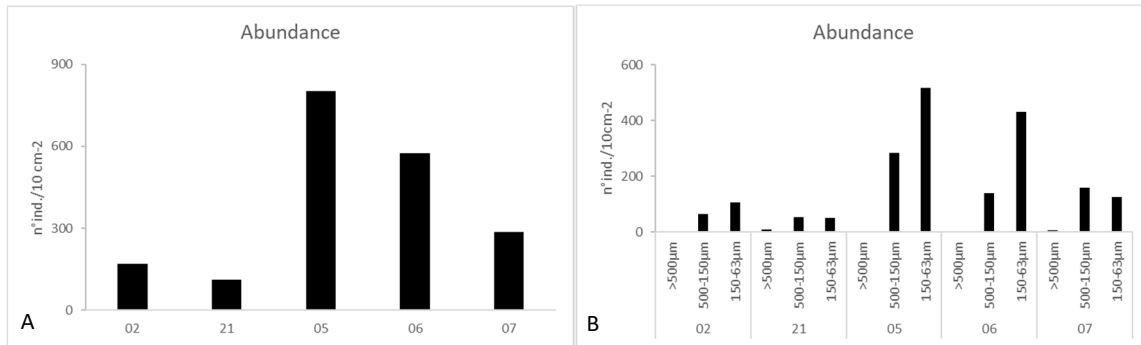


Fig. 2 Abundance of living foraminiferal assemblage (0-10 cm). A) represents the fraction >63 µm and B) represents the abundance in the three fractions

Living foraminiferal abundance for the fraction >63 µm (0-10 cm) decreased from 803 ind./ 10cm<sup>2</sup> at the site 05 to 112 ind./10 cm<sup>2</sup> at the site 21. Comparing the three different fractions, the smaller fraction (150-63 µm) is the most abundant fraction at all sites, except at the site 21. The highest density is observed at the sites 05 and 06 (518 and 432 ind./ 10 cm<sup>2</sup>, respectively), while lowest density is presented at the site 21 with 49 ind./ 10cm<sup>2</sup>. The fraction 500-150 µm showed high density value at the site at the end of the transect, the value varies from 285 ind./ 10 cm<sup>2</sup> at the site 05 to 139 ind./ 10 cm<sup>2</sup> at the site 06, while the lowest density is observed at the site 21 (54 ind./ 10 cm<sup>2</sup>). The fraction >500 µm represents only a minor contribution at all sites (Fig.2).

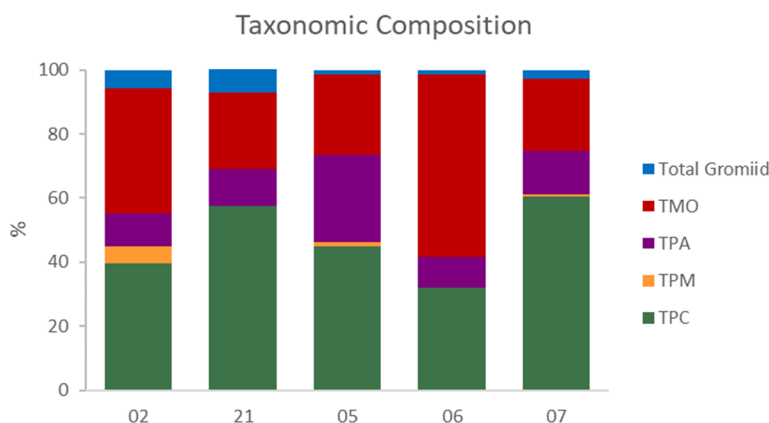


Fig. 3 Taxonomic composition of foraminiferal assemblage. The figure shows the values in the fraction >63 µm (0-10 cm). TMO= Total Monothalamous Organic, TPA= Total Polythalamous Agglutinated, TPM= Total Monothalamous Miliolids and TPC= Total Polythalamous Calcareous

Taxa composition for the foraminiferal assemblage in the fraction >63  $\mu\text{m}$  (total assemblage 0-10 cm) shows that the calcareous species represent in all sites the most abundant group, except at the site 06, where monothalamous group is the most abundant. Agglutinated species are present at all sites with percentages that varies from 9 at site 06 to 27 at the site 05. Miliolid group is rare at all sites, always less than 6% and totally absent in the sites 06 and 21. The gromiid morphotype are present in all sites with less important percentage, no more 8%. In the fraction >500 calcareous group is the most abundant group with a percentage of 100 % at the site 07 e 88% at the site 21 but disappear in the other sites. Agglutinated and monothalamous species are presented only at the site 06 with a percentage of 67% and 33% respectively. The gromiid group dominates at the site 02 (100%), with a less important percentages at site 21 (11%) (Fig.3).

	<b>02</b>	<b>21</b>	<b>05</b>	<b>06</b>	<b>07</b>
Taxa_S	37	26	41	36	41
Dominance_D	0,06	0,09	0,15	0,25	0,10
Shannon_H	3,14	2,72	2,46	2,10	2,81
Equitability_J	0,87	0,83	0,66	0,58	0,75
ALD10	1,06	1,09	1,14	2,58	2,80

Tab. 3 Diversity index and ALD<sub>10</sub> (Average Living Depth), for the fraction >63  $\mu\text{m}$ , of foraminiferal assemblage along the transect.

Considering the total foraminiferal assemblage from 0-10 cm for the fraction >63  $\mu\text{m}$ , the highest species richness occurs at the sites 05 and 07 with 41 identified species, followed by the sites 02 and 06 with 37 and 36 identified species, respectively. The lowest value is observed at the site 21 (26 species). The dominance is very low at the site 02 and 21 (0,06 and 0,09 respectively) while in the other sites increases (>0,1). The Shannon index is very high at all sites (2,1). The equitability value decreases from 0,87 at the site 02 to 0,58 at the site 06. The average living depth (ALD<sub>10</sub>) shows that the living depth of benthic foraminifera in the outer Kveithola trough (site 02,05 and 21) is located between 0-1 cm depth in the sediment, while a deeper ALD is found in the inner part, site 06 and 07 (Tab. 3).

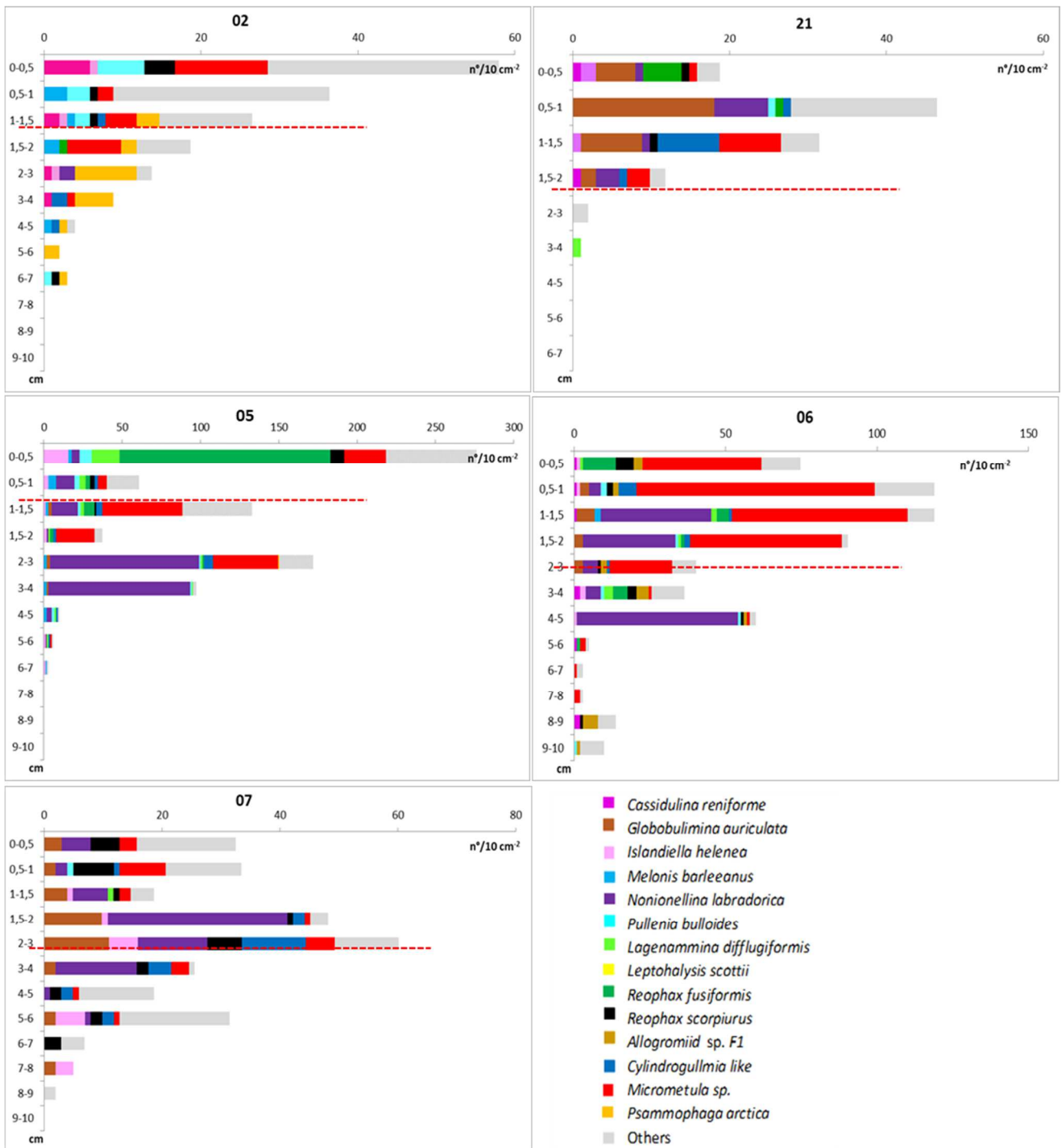


Fig.4 Vertical Distribution of the most representative species (> 10 ind./10 cm<sup>2</sup>) along the Kveithola. The red dashed line is the Avarege Living Depth (ALD).

In the vertical distribution (Fig. 4) are represented the species with a density > 10 ind./10 cm<sup>2</sup> only, while the species with lowest density have been include on the “others” group. The vertical distribution at the site 02 shows a low density compared to the other sites, there is a clear trend in relation to depth, down to the sediment. Difference (88%) between site 02 and site 05 is due to *N. labradorica* that occurs at each level at site 05 showing a high density, while appears only at 2-3 cm

interval at the site 02. *Micrometula* sp. is well represented at both sites, at the site 02 dominates the assemblage up to 3-4 cm, while at the site 05 up to 5-6 with higher density. *Psammophaga arctica* is the exclusive and important species from the 1-1,5 cm to 6-7 cm at the site 02. *Reophax fusiformis* occurs with high density only at the site 05 and is distributed up to 3-4 cm. *Melonis barleanus* is observed at both sites and is well distributed up to 6-7 cm at the site 05 and up to 4-5 at the site 02. *Lagenamma diffflugiformis*, *Bolivinellina pseudopunctata* and *Islandiella helene* appear in the first three centimetres. Difference (93,6%) between site 02 and 06 is due to *Micrometula* sp. that occurs at each level with high density at the site 06, *N. labradorica* occurs from the level 0,5-1 to 5-6 cm with high density and *Allogromiid* sp. F1 that is observed only at the site 06 at each level. *G. auriculata* and *L. diffflugiformis* is distributed at first centimetres. Difference (91%) between site 02 and 07 is due to *N. labradorica* and *Micrometula* sp. occurred, with high density, at each level up to 5-6 cm. *G. auriculata* occurs up to 3-4 cm and *Buccella frigida* was exclusive of this site and is distributed only in a 0-0,5, 4-5 and 5-6 cm. Difference (87%) between site 02 and 21 is due to *G. auriculata*, *N. labradorica*, *Micrometula* sp. and *Cylindrogullmia like*, well distributed at each level up to 1,5-2 and with high density. Difference (87%) between 05 and 06 is due to *Micrometula* sp., *N. labradorica* and *R. fusiformis* which occur at both site but with higher density at the site 05. Difference (89%) between sites 05 and 07 is due to *Micrometula* sp., *N. labradorica*, *R. scorpiurus* and *Cylindrogullmia like* observe at both sites but with higher density at the site 05. *R. fusiformis* occurs only at the site 05 and is distributed up to 2-3 cm., while *G. auriculata* appears only at the site 07 and is well distributed up to 7-8 cm. Difference (86%) between 05 and 21 is due to *Micrometula* sp., *N. labradorica* and *Cylindrogullmia like* appear at both site with different density, while the other simpler species are exclusive of one site es. *G.auriculata* ( site 05), *L. diffflugiformis*, *I. helene* and *M. barleanus* ( site 21). Difference (88%) between sites 06 and 07 and 06 vs 21 (93%) were due to density distribution at each level. Difference (87%) between sites 07 and 21 is due to *Micrometula* sp., *N. labradorica*, *G. auriculata* and *Cylindrogullmia like* which appeared at both sites, while *R. scorpiurus* and *I. helene* are exclusive of 07 site. At the site 21 the gromiid morphotype *Gromia ovale* is significant in the first centimetres.

	02		21		05		06		07	
	Dens	D	Dens	D	Dens	D	Dens	D	Dens	D
<i>Bolivinelina pseudopunctata</i> (TPC)	0	0	5	4.4	28	3.4	1	0.1	8	3.0
<i>Cassidulina reniforme</i> (TPC)	10	6.0	2	2.0	3	0.3	8	1.3	4	1.3
<i>Globobulimina auriculata</i> (TPC)	0	0	22	19.4	5	1.0	15	2.5	28	9.5
<i>Islandiella helene</i> (TPC)	3	2.0	3	3.0	24	3.0	5	1.0	15	5.1
<i>Melonis baleanus</i> (TPC)	7	4.0	0	0	16	2.0	2	0.3	0	0
<i>Nonionellina labradorica</i> (TPC)	2	1.1	12	11.0	224	28.0	134	23.2	71	25.0
<i>Pullenia bulloides</i> (TPC)	12	7.0	1	1.0	17	2.1	6	1.0	1	0.3
<i>Lagenammina difflugiformis</i> (TPA)	0	0	1	1.0	28	3.5	7	1.1	1	0.3
<i>Leptohalysis scottii</i> (TPA)	4	2.2	3	3.0	5	1.0	12	2.0	7	2.3
<i>Reophax fusiforme</i> (TPA)	1	0.5	6	5.3	147	18.3	22	4.0	0	0
<i>Reophax scorpiurus</i> (TPA)	7	4.0	2	2.0	13	1.5	14	2.3	28	10.0
<i>Cylindrogullmia</i> like (TPO)	4	2.2	10	9.0	16	2.0	10	2.0	22	7.5
<i>Micrometula</i> sp. (TPO)	26	15.0	12	11.0	150	19.0	253	44.1	24	8.2
<i>Psammophaga arctica</i> (TPO)	22	13.0	0	0	15	0.1	8	0.1	0	0

Tab. 4 Densities (Dens, ind. 10cm<sup>2</sup>) and dominance (D%) of the most abundant species (>10 ind./ 10 cm<sup>2</sup> at least at one site). TMO= Total Monothalamous Organic, TPA= Total Polythalamous Agglutinated, TPM= Total Monothalamous Miliolids and TPC= Total Polythalamous Calcareous

At the site 02 the monothalamous morphotype *Micrometula* sp. is the most represented species, followed by calcareous species *Pullenia bulloides*, *Trifarina angulosa* and *Cassidulina reniformis* (12, 11 and 10 ind./ 10 cm<sup>2</sup>, respectively). At site 21 calcareous perforate and monothalamous group are dominant, the most representative species are *G. auriculata*, *N. labradorica*, *Micrometula* sp. and *Cylindrogullmia* like (22,12,20 and 12 ind./ 10 cm<sup>2</sup>, respectively). At the site 05 the calcareous perforated group is mainly represented by *N. labradorica* with 224 ind./ 10 cm<sup>2</sup>, followed by *R. fusiformis* that is the most represented species among agglutinated group (147 ind./ 10 cm<sup>2</sup>), and Monathalamus group is mostly represented by *Micrometula* sp. with 150 ind./ 10 cm<sup>2</sup>. The fauna of the site 06 is dominated by monothalamus morphotype *Micrometula* sp. with 253 ind./ 10 cm<sup>2</sup> and calcareous perforate species *N. labradorica* (71 ind./10 cm<sup>2</sup>). At the site 07, *N. labradorica* (71 ind./10 cm<sup>2</sup>) is the most abundant among calcareous perforated group, followed by *G. auriculata* (28 ind./ 10 cm<sup>2</sup>), the agglutinated species *R. scorpiurus* (28 ind./ 10 cm<sup>2</sup>) and the Monothalamous morphotype *Micrometula* sp. (24 ind./ 10 cm<sup>2</sup>)(Tab. 4); SIMPER analyses, shows that these species also give the greatest dissimilarity (more than 85%) contribution between the sites. Pearson's correlation coefficient, that results from environmental variables and faunal parameters, for foraminiferal assemblage shows only a significantly (p <0.05) positive correlation between BAC and Density (r=0.67) (Tab. 5).



	Density	Taxa_S	Shannon_H	Equitability_J
Depth	0.18	0.28	0.14	0.05
Clay	0.51	-0.19	-0.67	-0.6
Silt	0.95	-0.05	-0.64	-0.61
Sand	-0.57	0.09	0.65	0.6
BAC mg/g	0.67*	0.18	-0.71	-0.78
BPC mg/g	0.64	0.14	-0.69	-0.75

Tab. 5 Pearson's correlation coefficient from environmental variables and faunal parameters.

CCA was used to identify the influences of environmental variables at each site to assess the total site faunal abundance. Site taxon abundances was plotted along environmental variables: depth, grain size fraction, BAC, BPC and benthic pigments (Fig. 5). The output of CCA shows a clear separation between the sites: the site 02 was characterized by sand sediment size and calcareous foraminifera as *C. reniforme*, *P. bulloides* and *M. barleaanus*. The site 05 is correlated by the depth and high agglutinated species diversity such as the site 06. Moreover, in the site 05 there is a clear correlation between the most abundant species (e.g., *B. pseudopunctata*, *R. fusiformis*, *I. helene* and *L. difflugiformis*) and the quality parameters of organic matter (BPC and BAC). The sites 07 and 21 are defined by fine sediment, with high concentration of organic matter especially of benthic pigments and dominance of foraminifera species as *G. auriculata* and *N. labradorica*.

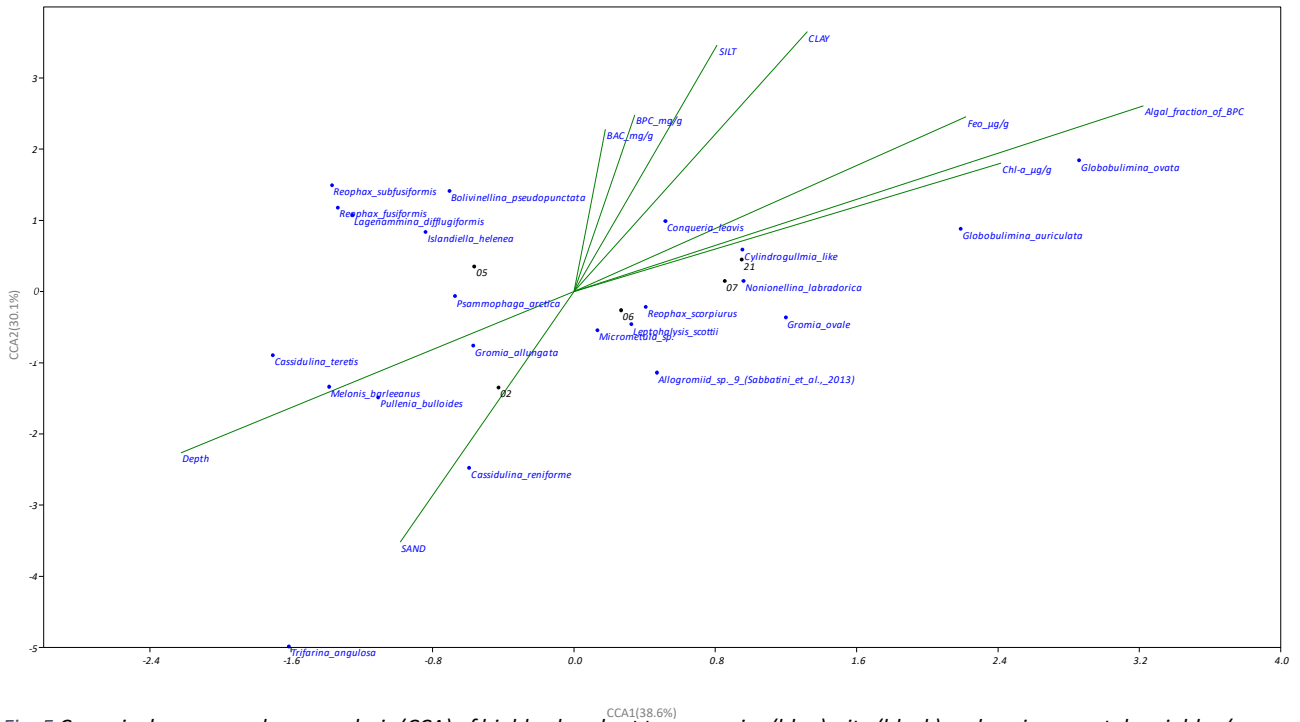


Fig. 5 Canonical correspondence analysis (CCA) of highly abundant taxa: species (blue), site (black) and environmental variables (green vectors). Most dominant species are indicated by labels names.

### 3.3. Rose Bengal

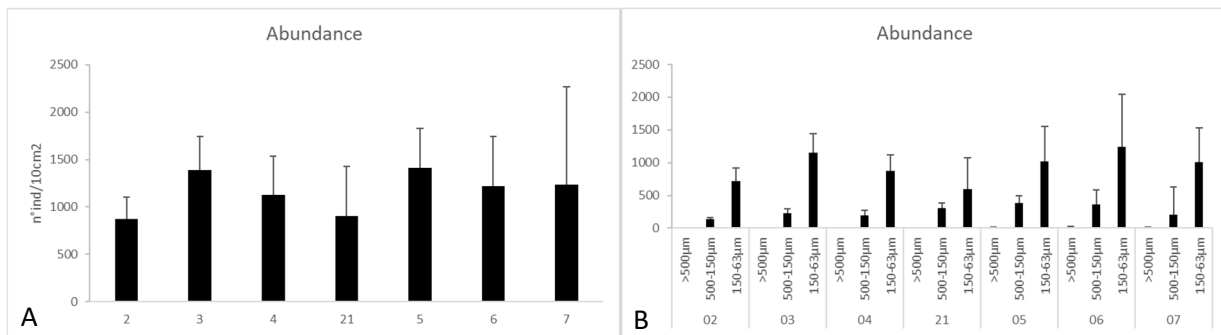


Fig.6 Abundance of living foraminiferal assemblage (0-10 cm). A) represents the fraction >63 μm and B) represents the abundance in the three fractions.

Living foraminiferal abundance for the fraction > 63 μm (0-10 cm) (Fig.6) increase from 872 ind./10 cm<sup>2</sup> at the site 02 to 1415 ind./10 cm<sup>2</sup> at the site 05. It is possible to observe 3 different cluster: the first cluster is represented by only 02 site, the second and the third ones include 3-4-21 sites and 5-6-7 respectively. The one-way ANOSIM (global R= 0.161, p<0.001) revealed significant differences in foraminiferal density between the sites with a dominance of small fraction foraminiferal populations in all studied sites. Regarding the three different fraction, total densities of live (Rose Bengal stained) foraminifera in the 0-10 cm interval shows that the fraction 63-150 was the most

abundant at all site, the lowest abundance was observed at the site 21 (593 ind./10 cm<sup>2</sup>) while the highest value was at the site 06(1243 ind./10 cm<sup>2</sup>). The fraction 150-500 µm showed high value at the sites 05 and 06 (384 and 366 ind./10 cm<sup>2</sup>, respectively) while lowest abundance was observed at the site 02 with 135 ind./10 cm<sup>2</sup>. The fraction >500 µm showed comparable value at all sites except for the site 07 that dominated with 19 ind./10 cm<sup>2</sup> (Fig.6).

A total of 116 morphospecies were identified (0-10 cm layers, > 63 µm), of which 45 were calcareous hyaline, 24 agglutinated and only 8 miliolids. We found 37 monothalamous organic taxa and 2 different gromiid species, the majority of which were undescribed, and they were included in the diversity analyses because most of them belong to well-known and widely spread genera of the polar environments, as *Cylindrogullmia*, *Gloiogullmia*, and *Micrometula*.

	02	03	04	21	05	06	07
Taxa_S	63	51	60	40	50	45	49
Dominance_D	0.05	0.05	0.08	0.08	0.11	0.10	0.08
Shannon_H	3.41	3.25	3.05	2.89	2.79	2.72	2.96
Equitability_J	0.82	0.83	0.75	0.78	0.71	0.72	0.76
ALD10	1.88	2.2	1.7	3.08	2.1	1.96	1.69

Tab.6 Diversity index of all analysed sites of the Kveithola Trough.

Considering the total living foraminiferal assemblage for the fraction >63-µm, species richness (S) varied from the site 02 (63 species) to the site 21(40 species). A total of 60 species was recognized in core 04, following by a total of 51 and 50 in the cores 03 and 05, respectively. Instead, in the Northern channel a total of 45 and 49 species was identified in cores 06 and 07, respectively. The dominance is very low at all sites, ranged from 0.05 at the sites 02 and 03, followed by the sites 04,21 and 07(0.08) and the sites 05 and 06 with value 0.11 and 0.10, respectively. The Shannon's index showed a trend along the transect, decreased from the site 02(3.41) to the site 07(2.96). The Equitability J showed a similar trend of Shannon's index, the value varied from the site 02 (0.82) to the site 07(0.76) (Tab. 6).

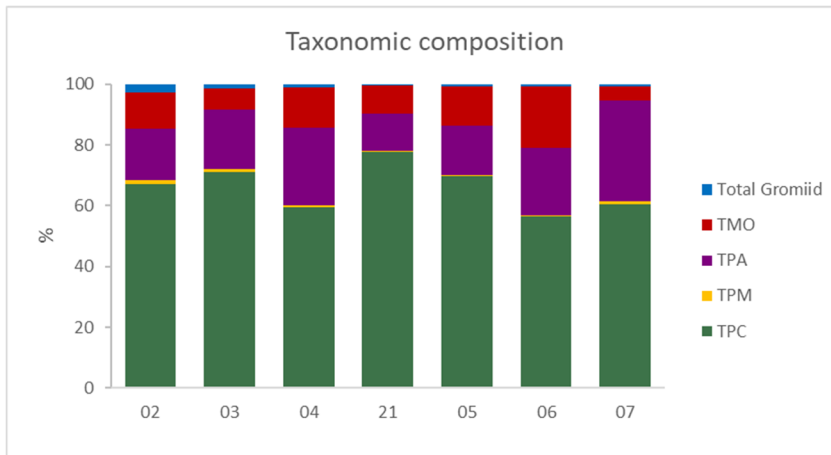


Fig. 7 Taxonomic composition of foraminiferal assemblage. The figure shows the values in the fraction  $>63 \mu\text{m}$  (0-10 cm). TMO= Total Monothalamous Organic, TPA= Total Polythalamous Agglutinated, TPM= Total Monothalamous Miliolids and TPC= Total Polythalamous Calcareous

Taxa composition for the fraction  $>63 \mu\text{m}$  (total assemblage 0-10 cm. Fig. 7) showed that faunas were dominated by polythalamous calcareous foraminifera, which represented between 56% (core 06) and 77 % (core 21) of total assemblage. Agglutinated group are well represented at all sites, the percentage varied from 12% at the site 21 to 33% at the site 07, while monothalamous species are present in all sites with less percentage, between 5 and 20%. Miliolid and Gromiid group sites are rare at all sites, always less than 2%. Soft-shelled monothalamous taxa were not abundant but they are qualitatively important because they represent the first record of the component in this area and most of taxa are undescribed. The polythalamous calcareous foraminifera dominated in all studied sites except in the finest fraction of core 22 (Northern Channel) where polythalamous agglutinated foraminifera were the most representative. *N. labradorica* and *Adercotryma glomerata* were typical of the size fraction  $>150 \mu\text{m}$  and they had an infaunal microhabitat in all sites except at GZW, where they did not occur. In this site the first centimetre of the sediment is colonized by a different and more diversified microfauna. In the finest fraction of all cores (63-150  $\mu\text{m}$ ) the species *N. labradorica* is replaced by the species *Nonionella iridea* while *A. glomerata* is always present. Moreover, tiny infaunal species as *Alabaminella weddellensis*, *Fursenkoina* sp., *L. scottii* occur. Monothalamous component is represented by taxa typical of polar foraminiferal assemblage. We noticed the presence of *Micrometula*, *Cylindrogullmia* and *Gloiogullmia* morphotypes among allogromiids; *Saccamminid* sp. 1 (silver), sp. 2 and sp. 4 (white) and *Psammophaga* morphotypes among the saccamminid component. They show an epifaunal and superficial infaunal microhabitat. The SIMPER test revealed also the presence of a large dissimilarity between depositional settings, with the largest dissimilarity observed between core 02 in the outer shelf corresponding to the

grounding-zone wedges and other cores in the inner drifts of the Kveithola Trough. SIMPER showed also that the species, which mostly contribute to the observed differences, are *A. weddellensis*, *B. pseudopunctata*, *N. auricula*, *N. labradorica*, *A. glomerata* and *Micrometula* sp..

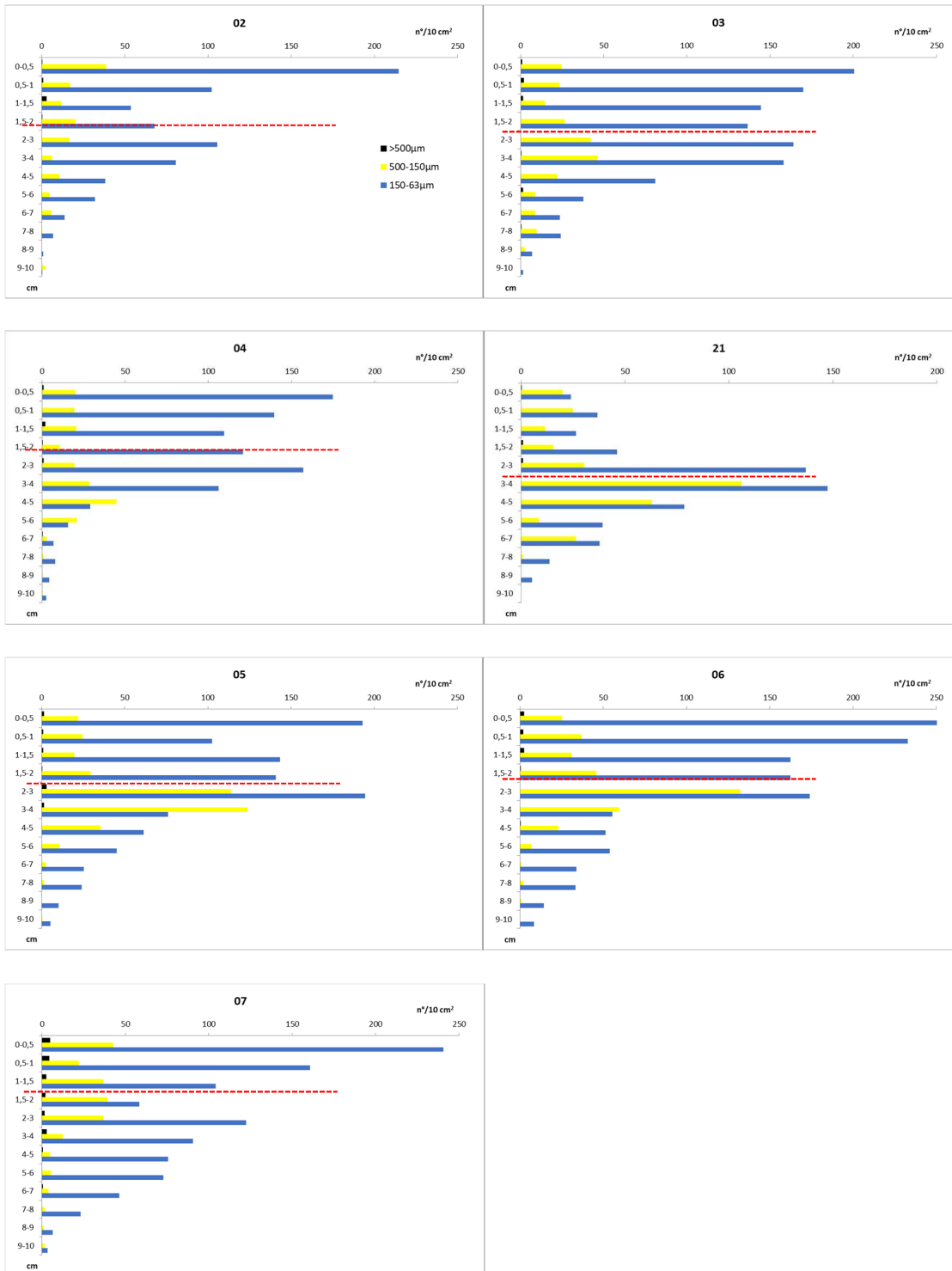


Fig. 8 Vertical distribution for the three fractions in all analysed sites. The red dashed line is the Average Living Depth (ALD).

Foraminiferal densities were normalised for each layer to a 10 cm<sup>2</sup> sediment area and represented separately for fraction: 63–150, 150-500 and >500-µm (Fig.8). In the cores collected from the inner trough sites, the 63-150 µm fraction presented a faunal assemblage that is strongly concentrated in the uppermost centimetres of the sediment(0-0.5 cm) varying from 257 live ind./10 cm<sup>2</sup> in the Minor

Drift (core 06), to 21 ind./10 cm<sup>2</sup> in the Main Drift, and in the level 2-4 cm varying from 319 live ind./10 cm<sup>2</sup>, at the GZW (core 07), to 238 ind./10 cm<sup>2</sup>, in the Minor Drift (core 06). Diversely, at GZW site and Northern channel (core 02 and 07) the highest foraminiferal density is recorded in the superficial sediment (0-0.5 cm) with values of 211 and 238 ind./10 cm<sup>2</sup>, respectively. The ALD<sub>10</sub> of the total live fauna of the 63-150 µm fraction varied from 1.65 to 3.1 cm in cores 07 and 21 respectively (Tab.4). The fauna from the drift area and Northern channel (cores 04, 05,21,06 and 07) was mainly dominated by *B. pseudopunctata* (ALD<sub>10</sub>=1.71 medium value), the agglutinated species *R. fusiformis* and *A. glomeratum* (ALD<sub>10</sub>=0.95 and 4.4 medium value). Monothalamous taxa as *Micrometula* sp. and squatter allogromiids had a superficial position in the sediment (ALD= 1.4 medium value). Core 02 and 03 showed a different biodiversity pattern along the vertical distribution and calcareous species *N. labradorica* was replaced by a diversified fauna from very deep epifaunal taxa (*A. weddellensis*) to a group of infaunal species (*P. bulloides* and *Micrometula* sp.). At all site the calcareous infaunal species *N. auricula* (ALD=2.53 medium value) was well represented, value varying from 58 ind./10 cm<sup>2</sup> (site 02) to 283 ind./10 cm<sup>2</sup> (site 05).

Faunal assemblage for the fraction 150-500 µm was strongly concentrated in the 2-5 cm of the sediment, varied from 272 live ind./10 cm<sup>2</sup> in the Main Drift (core 21) to 92 ind./10 cm<sup>2</sup> in the core 04. Conversely, at GZW site and Northern channel the highest foraminiferal density is recorded in the superficial sample (0-0.5 cm) with values of 47 ind./10 cm<sup>2</sup> and 41 ind./10 cm<sup>2</sup>. The ALD<sub>10</sub> of the total live fauna varied from 1.6 to 2.5 cm in cores 07 and 21 respectively and the most abundant species at all sites was the calcareous infaunal species *N. labradorica* (ALD= 2.93 medium value), the value varying from 282 ind./10 cm<sup>2</sup> (core 05) to 21 ind./10 cm<sup>2</sup> (core02).

The fraction >500 µm at all sites,was represented by few species as *N.labradorica*, *G.auriculata*, *R.scorpiurus* and morphotype belong to Gromiid group; these species had heterogeneous distribution up to 7 cm.



Fig. 9 nMDS plot depicting the foraminiferal community from the transects on the Kveithola trough. Colours highlight different clusters. A stress value of 0.12 indicates a good two-dimensional representation of the data.

Multivariate analysis of community structure by nMDS showed 4 main clusters of the replicate samples along the shallow Kveithola Trough. Sites (02 and 03) located in the outer Kveithola Trough are clearly separated from the other sites. At main drift, replicates were well clustered within sites and they formed a distinct group except for the site 21, where a replicate represent an outlier. While the separation between these sites and the site the site 06, located in the minor drift, is less visible. The site 07 in the Norther channel is well separated from the other sites but the two replicates were no closely resembled (Fig. 9).



## 4. Discussion

### 4.1. Trophic status and Foraminiferal distribution of Kveithola Trough

Kveithola Trough, located in the NW of Barents sea, is similar to other Barents Sea shallow area, where high nutrient rates reach the benthic community and high regional primary and secondary production exist (Piepenburg and Schmid, 1996; Piepenburg and Schmid, 1997; Grebmeier et al., 2006). The high productivity together to a distinct geomorphological and environmental feature of Kveithola trough, are key drivers of foraminiferal assemblage distribution. Spatial variability could respond to quantity or quality of organic matter (Alve and Murray, 2001; Fontanier et al., 2003; Sabbatini et al., 2012), substrate texture, water mass characteristics, temperature and dissolved oxygen content (Jennings and Helgadottir, 1994; Husum and Hald, 2004; Chatelet et al., 2009). Faunal distribution varied significantly along the transect of the Kveithola Trough and ANOSIM and NMDs tests (Fig.8) indicated significant differences in the composition of foraminiferal community between the sites group in the outer Kveithola Trough (site 02 and 03), minor drift ( site 04, 05 and 21) , main drift (site 06) and site located in Northern channel (site 07). Furthermore, the results show a different faunal distribution, in terms of abundance and diversity, in relation to their size with a dominance of small foraminiferal assemblage (63-150  $\mu\text{m}$ ) at all studied sites.

The outer part of the trough (sites 02 and 03, located on the GZW), the deepest studied area along the Kveithola Trough (400–450 m bsl), is under the influence of the North Atlantic Current (NAC, warm and saline, Slubowska-Woldengen et al., 2008); the NAC sweeps the outer seafloor and remove the fine sediment fraction leaving a coarse lag of pebbly sands (Caricchi et al., 2018). In fact, surface sediments are characterized by silty sand and fine-grained, clean sands with large scale ripple-like features, indicating the presence of moderately strong and persistent bottom currents. In contrast, the inner part which comprises the Main Drift and the Minor Drift, located between the Hornsund and Knølegga fracture zones (mean depth around 300 m bsl), is subject to continuous fine-grained sediment deposition due to cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow. These dense brine waters generate bottom currents that shape the Kveithola Drift moat (Rebesco et al., 2016; Lantzsch et al., 2017). This thesis results show that in the Drift and Northern channel of the Kveithola Trough the organic C load, considered as BPC concentration, is comparable to values typically encountered in eutrophic systems varying from 4.5 mg/g to 6.9 mg/g (Dell'Anno et al., 2002). Meanwhile, high supplies of organic matter and its breakdown, with strong water stratification, can lead to an oxygen depletion that might affect the

diversity and distribution of benthic foraminifera (Martins et al., 2016). These conditions can justify what Lucchi et al., (2016) described about bottom oxygen concentration in the Kveithola Trough. They show high value of oxygen concentration in the cores surface sediment (direct measurement of O<sub>2</sub> concentration in sediment is not available) becoming low oxic some millimetres below the sediment-water interface as indicated in black cores colour. So, it is possible to infer that strong water stratification is responsible for limited vertical exchange of dissolved gases leading to oxygen reduction conditions at the sea bottom; at the same time, it can contribute to organic matter preservation and accumulation, often associated with the absence of remineralization (Burdige, 2007).

The assessment of the trophic status needs to be extended to a more comprehensive description of the organic matter available for heterotrophic nutrition; Pusceddu et al., (2009) explain how the response of consumers to increased organic matter supply is mainly influenced by organic matter quality (i.e., bioavailability). For these reasons we analysed the BPC and BAC values, as well as the algal carbon contribution to BPC (Tab. 2). As already demonstrated by Pusceddu et al (2009), BAC is positively correlated with BPC, suggesting that eutrophic (e.g., enriched in BPC concentration) sediments are characterised also by high concentrations of rapidly digestible material. In the outer trough (sites 02 and 03) the BAC values indicate lower bioavailability of sediment organic carbon supporting a poorly sediment community oxygen consumption (Pusceddu et al., 2009) and high hydrodynamism resulting in enhanced sediment resuspension, cannot be excluded. This could inject more refractory organic matter pools (e.g., carbohydrates) in the bottom water column in nature (Pusceddu et al., 2016). At the same time, benthic microbes exposed to O<sub>2</sub>-rich waters caused by sediment disturbance could stimulate a faster mobilisation of organic C buried in the sediment, injecting more labile molecules into the system (Polymenakou et al., 2005). Furthermore, the BAC concentration in the inner trough (sites on the drift) is higher than other sites (Tab. 2), therefore enhancing the sediment community oxygen consumption. This suggests that the progressive accumulation of labile carbon could be an additional co-factor potentially responsible for transient hypoxic or anoxic conditions.

In the northern channel the high value of bioavailable organic matter is related to the dense cold Brine-shelf water presence which lead to the burial of organic matter rich sediment, while the superficial Arctic Water (AC) that guarantees the high productivity and the high nutritional quality organic matter input of to the seafloor (i.e., BAC and Chl-a). At site 21, the results show moderate

value of BPC but low BAC value (Tab. 2). Here, the presence of the Drift, associated with the water stratification, limit exchange with the surrounding areas and therefore is responsible for limited dissolved O<sub>2</sub> vertical exchange leading to suboxic condition at the sea bottom. Consequently, it is observed accumulation of large amount of organic matter in subsurface sediment, representing the refractory component that was less available to benthic communities (Pusceddu et al., 2009).

Within this context, foraminiferal density, species richness and composition show remarkable differences among the sites located on the Kveithola Trough according to Sabbatini et al., (submitted to BOREAS). The fauna in the outer trough is positively influenced by high productivity with strong influence from the Atlantic Water, with generally ice-free conditions throughout the year and a deep mixed layer. These parameters maintain a good oxygenated environment that reflect the high biodiversity of foraminiferal assemblage (Tab. 1). At the same time, high hydrodynamism, that not favour the accumulation of the organic matter, can enhance sediment resuspension injecting in the bottom water column organic matter pools more refractory in nature (e.g., carbohydrates). The low food availability can limit the number of foraminifera individuals (Fig. 2). Włodarska-Kowalczyk and Pearson, (2004) and Lesen, (2005), demonstrate how foraminifera, in arctic fjord, are sensitive to changing organic matter concentrations both in terms of species composition and standing stocks. Also, Wollemburg and Kuhnt, (2000) showed that in food-limited environments, such as Arctic Ocean sediments, the levels of primary production and food supply can shape the patterns of benthic foraminiferal density and species richness. Meanwhile, the inner part appears as a stressful, characterized by high concentration of organic matter that might lead to diversity decreased (Fig. 2) and a community structure dominated by fewer, specialized taxa. Many studies demonstrate that organic matter enrichment and oxygen depletion in the bottom water co-occur and have an adverse effect on the benthic faunas, favouring the development of some opportunistic taxa (e.g., Fontanier et al., 2003; Martins et al., 2016). Particularly, the case of site 21, where both abundance and diversity are low (Fig. 2 and Tab. 2). The peculiar conditions of this site (high organic matter content, low oxygen and intermittent methane flux) create a stressful environment where foraminifera are no able to inhabit.

Looking at the taxonomic composition, in the outer part of the study area the fauna is strongly dominated by monothalamous species *P. arctica* (Fig. 4), that displayed an opportunistic behaviour in response to the pulse of organic carbon of high nutritional quality in shallow waters (Sabbatini et al., 2012). The presence and dominance of *Psammophaga* morphotypes is consistently reported

from several authors, Sergeeva et al., (2010) report its presence from hypoxic and sulphidic settings near active methane seeps in the Black Sea. Larkin and Gooday, (2004) describe *Psammophaga* sp. from an intertidal site on the southern coast of England. Interestingly, the agglutinated foraminifera *L. scottii*, co-dominant with *Psammophaga* morphotype in the Portonovo organically enriched sediments in winter, is consistently observed in well oxygenated sediments enriched in labile compounds (Ernst, 2002; Diz et al., 2006). *C. reniforme*, that is abundant in cold-water areas of Barents Sea (Saher et al., 2012), together with *P. bulloides* are representative species of site 02 (Fig. 4). *C. reniforme* it is a small, opportunistic species that respond to pulsed organic matter supplies and can be resistant to oxygen deficiencies (Korsun et al., 1995; Wlodarska-Kowalczyk, 2012).

Instead, the inner part characterized by high concentration of metabolizable organic matter, is dominated by species associated with organic-rich sediment and oxygen-depleted environments as *N. labradorica* and *B. pseudopunctata* (Fig. 4). The calcareous species *N. labradorica*, typical of the size fraction >150  $\mu\text{m}$ , replaced by the species *N. auricula* in the finest fraction (63-150  $\mu\text{m}$ ) is a potential indicator of the highly productive conditions and it feeds on the buried organic matter or free phytodetritus (Corliss, 1991). *B. pseudopunctata* is an opportunistic species able to tolerate low oxygen condition (Gustafsson and Nordberg, 2001). Bouchet et al., (2018) reports this species along the Norwegian Skagerrak coast, in sediment with high TOC content and hypoxic or severe hypoxic condition. A higher percentage of agglutinated forms in this part of the Kveithola was also noted (Fig. 3). In the modern Arctic Ocean, abundance of agglutinants are on a regional scale related to carbon flux (Wollenburg et al., 2007). The most abundant species are *R. scorpiurus*, *A. glomeratum*, *L. difflugiformis* and *L. scottii*, which show an opportunistic behaviour in response to enhanced food conditions and are considered tolerant to hypoxic environment (Ernst and van der Zwaan, 2004; Caille et al. 2015). Furthermore, *L. scottii* is also considered as indicator of benthic eutrophication in shallow waters (Sabbatini et al., 2012) and together with *R. scorpiurus*, are representative of high sedimentation rate in canyon (Di Bella et al., 2017 and references therein). Meanwhile, the dominance of calcareous species *G. auriculata* was noticed only in two sites of the trough, 21 (main drift) and 07 (Northern channel). *Globobulimina* spp. have been found deeply in the sediments within or below the oxic-anoxic interface and referred to deep infauna in many meso-eutrophic settings (Fontanier et al., 2002; Licari et al., 2003; Koho et al., 2008). Our results disagree with Saidova, (1997) where *G. auriculata* assemblage was found in the surface sediments of the oligotrophic western Kurile Basin at water depths of 1808-3341 m that supports the probable existence of lateral transport of marine or terrestrial organic matter. In fact, in these sites, the

presence of *G. auriculata* in the first sediment centimetres, suggesting a eutrophic and anoxic environment.

Changes in-sediment distribution of these benthic fauna are often attributed to organic matter, oxygen availability, redox chemistry and/or the interaction between these parameters (Levin et al., 2000). In the outer trough the results of ALD<sub>10</sub> (average sites= 2. Tab. 1) show a deeper oxygen penetration in the sediment that support a high biodiversity with the occurrence of species adapted to poor food quality. Instead, in the inner part ALD<sub>10</sub> is 2.8 (Tab. 1) so, the high concentration of metabolizable organic matter deeper in the cores could represent an excellent food source for the benthic foraminiferal consumers but probably the population does not benefit totally from this organic stock because despite the food availability, the density shows a drastic fall from the first cm. In fact, infaunal species as *N. labradorica* and *B. pseudopunctata* react to these stressful conditions migrating to shallower microhabitats. Therefore, the relative increase of oxygen demand could simultaneously be the limiting factor to the benthic foraminiferal community in terms of biodiversity.

Interestingly, delicate foraminifera monothalamous taxa (organic-walled allogromiids, agglutinated saccamminids, psammosphaerids and tubular forms) were reported from all sites with high percentage (Fig.2), the dominance of *Micrometula* and *Cylindrogullmia* morphotypes is observed, inhabiting typically the detritus layer of Arctic fjords and they have elongated, and thread-like form tended to be more common in deeper sediment layers. *Micrometula* seems dependent on fresh phytodetritus (Alve, 2010) while *Cylindrogullmia* live in an extremely oxygen-deficient environment (Gooday, 2002).

#### **4.2. Cell Tracker Green Vs Rose Bengal**

At present the Kveithola Trough is characterized by peculiar geo-morphological and environmental features (e.g. currents, temperature, pH, oxygenation, grain size and organic carbon content) which are expected to exert an important role on the distribution, abundance and diversity of foraminiferal benthic assemblage. In most studies, foraminifera are recognized as living by staining with Rose Bengal that, unfortunately, is not a very critical method for its capacity to react with proteins, which persist in the cytoplasm for a long time after dead (Bernhard et al., 2006), especially in anoxic sediments, where protoplasm decay may be relatively slow. In the Kveithola Trough, that appeared stressed and affected by low-oxygen conditions and high organic matter content (Hanebuth et al., 2013; Caridi et al., 2019), the RB method is therefore inadequate to obtain information about

foraminiferal survival. On the contrary, the newly developed CTG method (Bernhard et al., 2000) should allow us to distinguish with much more precision between living and dead individuals. Despite these aspects, RB remains the most used method and for this reason, we also used it to compare our research with previous studies on living foraminiferal assemblage.

Comparing the CTG and RB methods, RB staining revealed a higher number of living foraminifera in all cores, especially in the first centimetres of the core (Fig. 8). The average living depth was different in the two methods (Tab. 4 and Tab.1), in RB results we notice a deepest distribution of species, probably do to inferences with increase of organic refractory matter and reduction of oxygen content. These kind of correlation between RB and oxygen-depletion was well documented by Grego et al., (2013). In our study the methods also gave different results for presence/absence of benthic species. The most abundant species for all cores was the same but, with RB method, other species were represented with high values (Fig. 8). In the outer trough, the results (RB labelling) show the abundance of species as the calcareous *A. weddellensis* and agglutinated *R. fusiformis*. Instead, in the inner sites the calcareous species *B. pseudopunctata* appears. These species show an opportunistic behaviour in response to enhanced food conditions and they are considered tolerant to hypoxic environment (Gooday, 2002; Ernst and van der Zwaan, 2004; Caille et al., 2015). This methodologic difference was most evident in the site 21, RB results showed a favourable niche inhabited by abundant foraminiferal fauna deep in the sediment as suggested by the total faunal ALD<sub>10</sub> (Fig. 8 and Tab.4). Instead, CTG results revealed the presence of a stressful environment, where benthic community reacts decreasing their abundance with the occurrence of few opportunistic species migrating at the sediment surface (Fig.4 and Tab.1). CTG results agree with Lucchi et al., (2016), which detect a stressful environment characterized by black-anoxic sediment below to the first centimetres.

In conclusion, we can infer that CTG technique well distinguished living from dead organisms and is a suitable staining method to document the response of selected meiofauna groups to short-term disturbances. Moreover, this is the first study of foraminiferal assemblage CTG labelled in the Kveithola so, the discussions will be addressed including only a CTG results. In the future, RB data will be used for comparison to other studies.

## 5. Conclusions

Benthic foraminiferal assemblage is studied in the Kveithola Trough (NW Barents Sea), with environmental features as grain size, currents and organic matter content. One of the main determining factors of spatial distribution, density and species composition of benthic foraminiferal community is the supply of organic matter and its quality. In the outer sites, a low bioavailability of sediment organic carbon supports a poorly sediment community oxygen consumption and high hydrodynamic can enhance sediment resuspension injecting in the bottom water column organic matter pools more refractory in nature (e.g., carbohydrates). The inner trough represents an eutrophic high metabolizable organic matter area dominated by species associated with organic-rich sediment and oxygen-depleted environments. Meanwhile, morpho-depositional and oceanographical patterns still influence composition and accumulation of organic matter content. High hydro-dynamism due to NAC, that characterize the outer part of the Kveithola trough, does not favour the accumulation of the organic matter, which presence is mainly related to the settlement of organic rich fine-grained sediments; instead, the cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow, driving the rapid burial of fine-grained organic-rich sediments promoting a better preservation and quality of organic matter.

Moreover, the Kveithola Trough is characterized by high primary production and high nutrient rates that reach the benthic community, suggesting a close relationship between the pelagic and benthic compartments. These conditions allow us to describe the Kveithola Trough as an eutrophic hot-spot in an oligotrophic Arctic ocean, characterized by peculiar environmental conditions which shapes the living benthic faunal structure.

## References

- Altenbach, A. V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S., and Trauth, M. (1999). Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon. *The Journal of Foraminiferal Research*, 29(3), 173-185.
- Alve, E., and Murray, J. W. (2001). Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England. *The Journal of Foraminiferal Research*, 31(1), 12-24. <https://doi.org/10.2113/0310012>
- Alve, E. (2010). Benthic foraminiferal responses to absence of fresh phytodetritus: A two-year experiment. *Marine Micropaleontology*, 76(3-4), 67-75. <https://doi.org/10.1016/j.marmicro.2010.05.003>
- Bergh, S. G., and Grogan, P. (2003). Tertiary structure of the Sørkapp-Hornsund Region, South Spitsbergen, and implications for the offshore southern extension of the fold-thrust Belt. *Norsk Geologisk Tidsskrift*.
- Bernhard, J. M., and Sen Gupta, B. K. (1999). Foraminifera of oxygen-depleted environments, in: Modern Foraminifera, edited by: Sen Gupta, B. K., Kluwer Academic Press, Dordrecht, 201–216. [https://doi.org/10.1007/0-306-48104-9\\_12](https://doi.org/10.1007/0-306-48104-9_12)
- Bernhard, J. M. (2000). Distinguishing live from dead foraminifera: methods review and proper applications. *Micropaleontology*, 46, 38-46.
- Bernhard, J. M., Ostermann, D. R., Williams, D. S., and Blanks, J. K. (2006). Comparison of two methods to identify live benthic foraminifera: A test between Rose Bengal and CellTracker Green with implications for stable isotope paleo reconstructions. *Paleoceanography*, 21(4). <https://doi.org/10.1029/2006PA001290>
- Bjarnadóttir, L. R., Rüther, D. C., Winsborrow, M. C. M., and Andreassen, K. (2013). Grounding-line dynamics during the last deglaciation of Kveithola, W Barents Sea, as revealed by seabed geomorphology and shallow seismic stratigraphy. *Boreas*. <https://doi.org/10.1111/j.1502-3885.2012.00273>
- Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Biochemistry and Cell Biology*. <https://doi.org/10.1139/o59-099>
- Bouchet, V. M., Telford, R. J., Rygg, B., Oug, E., and Alve, E. (2018). Can benthic foraminifera serve as proxies for changes in benthic macrofaunal community structure? Implications for the definition of reference conditions. *Marine environmental research*, 137, 24-36. <https://doi.org/10.1016/j.marenvres.2018.02.023>



- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*.  
<https://doi.org/10.1021/cr050347q>
- Cardich, J., Morales, M., Quipúzcoa, L., Sifeddine, A., and Gutiérrez, D. (2012). Benthic foraminiferal communities and microhabitat selection on the continental shelf off central Peru. In *Anoxia* (pp. 323-340). Springer, Dordrecht. [https://doi.org/10.1007/978-94-007-1896-8\\_17](https://doi.org/10.1007/978-94-007-1896-8_17)
- Caricchi, C., Lucchi, R. G., Sagnotti, L., Macrì, P., Morigi, C., Melis, R., Caffau, M., Rebesco, M., and Hanebuth, T. J. J. (2018). Paleomagnetism and rock magnetism from sediments along a continental shelf-to-slope transect in the NW Barents Sea: Implications for geomagnetic and depositional changes during the past 15 thousand years. *Global and Planetary Change*.  
<https://doi.org/10.1016/j.gloplacha.2017.11.007>
- Caridi, F., Sabbatini, A., Morigi, C., Dell'Anno, A., Negri, A., and Lucchi, R. G. (2019). Patterns and environmental drivers of diversity and community composition of macrofauna in the Kveithola Trough (NW Barents Sea). *Journal of Sea Research*, 153, 101780.  
<https://doi.org/10.1016/j.seares.2019.101780>
- Caulle, C., Mojtahid, M., Gooday, A. J., Jorissen, F. J., and Kitazato, H. (2015). Living (Rose-Bengal-stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea). *Biogeosciences*, 12(16), 5005-5019. <https://doi.org/10.5194/bg-12-5005-2015>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian journal of ecology*, 18(1), 117-143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Corliss, B. H., and Emerson, S. (1990). Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. *Deep Sea Research Part A. Oceanographic Research Papers*, 37(3), 381-400. [https://doi.org/10.1016/0198-0149\(90\)90015-N](https://doi.org/10.1016/0198-0149(90)90015-N)
- Corliss, B. H. (1991). Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. *Marine Micropaleontology*, 17(3-4), 195-236. [https://doi.org/10.1016/0377-8398\(91\)90014-W](https://doi.org/10.1016/0377-8398(91)90014-W)
- Cusson, M., and Bourget, E. (2005). Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series*, 297, 1-14. <https://doi.org/10.3354/meps297001>
- Danovaro, R., Dell'Anno, A., and Fabiano, M. (2001). Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, northeastern Atlantic. *Marine Ecology Progress Series*, 220, 25-32. <https://doi.org/10.3354/meps220025>

- Danovaro, R. (2010). *Methods for the Study of Deep-Sea Sediments, Their Functioning and Biodiversity*. BocaRaton, FL: CRC Press. <https://doi.org/10.1201/9781439811382>
- Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R. (2002). Assessing the trophic state and eutrophication of coastal marine systems: A new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin*. [https://doi.org/10.1016/S0025-326X\(01\)00302-2](https://doi.org/10.1016/S0025-326X(01)00302-2)
- Di Bella, L., Pierdomenico, M., Porretta, R., Chiocci, F. L., and Martorelli, E. (2017). Living and dead foraminiferal assemblages from an active submarine canyon and surrounding sectors: the Gioia Canyon system (Tyrrhenian Sea, Southern Italy). *Deep Sea Research Part I: Oceanographic Research Papers*, 123, 129-146. <https://doi.org/10.1016/j.dsr.2017.04.005>
- Diz, P., Francés, G., Costas, S., Souto, C., and Alejo, I. (2004). Distribution of benthic foraminifera in coarse sediment, Ría de Vigo, NW Iberian margin. *Journal of Foraminiferal Research* 34, 258–275. <https://doi.org/10.2113/34.4.258>
- Diz, P., Francés, G., and Rosón, G. (2006). Effects of contrasting upwelling–downwelling on benthic foraminiferal distribution in the Ría de Vigo (NW Spain). *Journal of Marine Systems*, 60(1-2), 1-18. <https://doi.org/10.1016/j.jmarsys.2005.11.001>
- Du Châtelet, É. A., and Debenay, J. P. (2010). The anthropogenic impact on the western French coasts as revealed by foraminifera: a review. *Revue de micropaléontologie*, 53(3), 129-137. <https://doi.org/10.1016/j.revmic.2009.11.002>
- Ernst, S., Duijnste, I., and van der Zwaan, B. (2002). The dynamics of the benthic foraminiferal microhabitat: recovery after experimental disturbance. *Marine Micropaleontology*, 46(3-4), 343-361. [https://doi.org/10.1016/S0377-8398\(02\)00080-4](https://doi.org/10.1016/S0377-8398(02)00080-4)
- Ernst, S., and van der Zwaan, B. (2004). Effects of experimentally induced raised levels of organic flux and oxygen depletion on a continental slope benthic foraminiferal community. *Deep Sea Research Part I: Oceanographic Research Papers*, 51(11), 1709-1739. <https://doi.org/10.1016/j.dsr.2004.06.003>
- Fabiano, M., Danovaro, R., and Frascchetti, S. (1995). A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (northwestern Mediterranean). *Continental Shelf Research*. [https://doi.org/10.1016/0278-4343\(94\)00088-5](https://doi.org/10.1016/0278-4343(94)00088-5)
- Figueira, B. O., Grenfell, H. R., Hayward, B. W., and Alfaro, A. C. (2012). Comparison of Rose Bengal and CellTracker Green staining for identification of live salt-marsh foraminifera. *The Journal of Foraminiferal Research*, 42(3), 206-215. <https://doi.org/10.2113/gsjfr.42.3.206>
- Fontanier, C., Jorissen, F. J., Licari, L., Alexandre, A., Anschutz, P., and Carbonel, P. (2002). Live benthic

foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. *Deep Sea Research Part I: Oceanographic Research Papers*, 49(4), 751-785. [https://doi.org/10.1016/S0967-0637\(01\)00078-4](https://doi.org/10.1016/S0967-0637(01)00078-4)

Fontanier, C., Jorissen, F. J., Chaillou, G., David, C., Anschutz, P., and Lafon, V. (2003). Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay. *Deep Sea Research Part I: Oceanographic Research Papers*, 50(4), 457-494. [https://doi.org/10.1016/S0967-0637\(02\)00167-X](https://doi.org/10.1016/S0967-0637(02)00167-X)

Fontanier, C., A. MacKensen, F. J. Jorissen, P. Anschutz, L. Licari, and C. Griveaud. (2006). "Stable Oxygen and Carbon Isotopes of Live Benthic Foraminifera from the Bay of Biscay: Microhabitat Impact and Seasonal Variability." *Marine Micropaleontology* 58 (3): 159–83. <https://doi.org/10.1016/j.marmicro.2005.09.004>.

Frontalini, F., and Coccioni, R. (2011). Benthic foraminifera as bioindicators of pollution: a review of Italian research over the last three decades. *Revue de micropaléontologie*, 54(2), 115-127. <https://doi.org/10.1016/j.revmic.2011.03.001>

Gabrielsen, R. H., Faerseth, R. B., Jensen, L. N., Kalheim, J. E., and Riis, F. (1990). Structural Elements of the Norwegian Continental Shelf Part I: The Barents Sea Region. *Norwegian Petroleum Directorate Bulletin*.

Gerchakov, S. M., and Hatcher, P. G. (1972). Improved technique for analysis of carbohydrates in sediments. *Limnology and Oceanography*. <https://doi.org/10.4319/lo.1972.17.6.0938>

Gooday, A. J., Levin, L. A., Linke, P., and Heeger, T. (1992). The role of benthic foraminifera in deep-sea food webs and carbon cycling. In *Deep-sea food chains and the global carbon cycle* (pp. 63-91). Springer, Dordrecht. [https://doi.org/10.1007/978-94-011-2452-2\\_5](https://doi.org/10.1007/978-94-011-2452-2_5)

Gooday, A. J. (2002). Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography*, 58(2), 305-332. <https://doi.org/10.1023/A:1015865826379>

Gooday, A. J., Kamenskaya, O. E., and Soltwedel, T. (2010). The organic-walled genera *Resigella* and *Conicotheca* (Protista, Foraminifera) at two Arctic deep-sea sites (North Pole and Barents Sea), including the description of a new species of *Resigella*. *Marine Biodiversity*, 40(1), 33-44. <https://doi.org/10.1007/s12526-009-0031-6>

Grebmeier, J. M., Overland, J. E., Moore, S. E., Farley, E. V., Carmack, E. C., Cooper, L. W., Frey, K.E., Helle, J.H., McLaughlin, F.A., and McNutt, S. L. (2006). A major ecosystem shift in the northern Bering Sea. *Science*, 311(5766), 1461-1464. <https://doi.org/10.1126/science.1121365>

- Grego, M., Stachowitsch, M., De Troch, M., and Riedel, B. (2013). CellTracker Green labelling vs. rose bengal staining: CTG wins by points in distinguishing living from dead anoxia-impacted copepods and nematodes. *Biogeosciences*, 10(7), 4565-4575. <https://doi.org/10.5194/bg-10-4565-2013>
- Grémare, A., Medernach, L., DeBovee, F., Amouroux, J. M., Vétion, G., and Albert, P. (2002). Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Marine Ecology Progress Series*, 234, 85-94. <https://doi.org/10.3354/meps234085>
- Gupta, B. K. S. (1999). *Modern foraminifera* (pp. 7-36). B. K. S. Gupta (Ed.). Dordrecht: Kluwer Academic Publishers.
- Gustafsson, M., and Nordberg, K. (2001). Living (stained) benthic foraminiferal response to primary production and hydrography in the deepest part of the Gullmar Fjord, Swedish West Coast, with comparisons to Høglund's 1927 material. *The Journal of Foraminiferal Research*, 31(1), 2-11. <https://doi.org/10.2113/0310002>
- Haller, C., Smith, C. G., Hallock, P., Hine, A. C., Osterman, L. E., and McCloskey, T. (2019). Distribution of Modern Salt-marsh Foraminifera from the Eastern Mississippi Sound, Usa. *Journal of Foraminiferal Research*, 49(1), 29-47. <https://doi.org/10.2113/gsjfr.49.1.29>
- Hammer, Ø., Webb, K., and Depreiter, D. (2009). Numerical simulation of upwelling currents in pockmarks, and data from the Inner Oslofjord, Norway. *Geo Mar. Lett.* 29: 269–275. <https://doi.org/10.1007/s00367-009-0140-z>
- Hartree, E. F. (1972). Determination of protein: A modification of the lowry method that gives a linear photometric response. *Analytical Biochemistry*. [https://doi.org/10.1016/0003-2697\(72\)90094-2](https://doi.org/10.1016/0003-2697(72)90094-2)
- Hanebuth, T.J., M. Bergenthal, A. Caburlotto, S. Dippold, R. Düßmann, T. Freudenthal, T. Hörner, K. Kaszemeik, S. Klar, H. Lantzsch, J. Llopart, R.G. Lucchi, L.S. Nicolaisen, K. Noorlander, G. Osti, A. Özmaral, M. Rebesco, U. Rosiak, A. Sabbatini, W. Schmidt, A. Stachowski, R. Urgeles (2013). CORIBAR – Ice Dynamics and Meltwater Deposits: Coring in the Kveithola Trough, NW Barents Sea. Cruise MSM30
- Husum, K., and Hald, M. (2004). Modern foraminiferal distribution in the subarctic Malangen fjord and adjoining shelf, northern Norway. *The Journal of Foraminiferal Research*, 34(1), 34-48. <https://doi.org/10.2113/0340034>
- Jennings, A. E., and Helgadottir, G. (1994). Foraminiferal assemblage from the fjords and shelf of eastern Greenland. *The Journal of Foraminiferal Research*, 24(2), 123-144.

- Jorissen, F. J., de Stigter, H. C., and Widmark, J. G. (1995). A conceptual model explaining benthic foraminiferal microhabitats. *Marine micropaleontology*, 26(1-4), 3-15. [https://doi.org/10.1016/0377-8398\(95\)00047-X](https://doi.org/10.1016/0377-8398(95)00047-X)
- Koho, K. A., García, R. D., De Stigter, H. C., Epping, E., Koning, E., Kouwenhoven, T. J., and Van der Zwaan, G. J. (2008). Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon–Setúbal Canyon (southern Portugal). *Progress in Oceanography*, 79(1), 55-82. <https://doi.org/10.1016/j.pocean.2008.07.004>
- Koho, K. A., and Piña-Ochoa, E. (2012). Benthic foraminifera: inhabitants of low-oxygen environments. In *Anoxia* (pp. 249-285). Springer, Dordrecht. [https://doi.org/10.1007/978-94-007-1896-8\\_14](https://doi.org/10.1007/978-94-007-1896-8_14)
- Korsun, S. A., Pogodina, I. A., Forman, S. L., and Lubinski, D. J. (1995). Recent foraminifera in glaciomarine sediments from three arctic fjords of Novaja Zemlja and Svalbard. *Polar Research*, 14(1), 15-32. <https://doi.org/10.3402/polar.v14i1.6648>
- Krantz, M. S. (1995). *Cassidulina teretis* Tappan and *Cassidulina neoteretis* new species (Foraminifera): stratigraphic markers for deep sea and outer shelf areas. *Journal of Micropalaeontology*, 14(2), 145-157. <https://doi.org/10.1144/jm.14.2.145>
- Langezaal, A. M., Jorissen, F. J., Braun, B., Chaillou, G., Fontanier, C., Anschutz, P., and Van der Zwaan, G. J. (2006). The influence of seasonal processes on geochemical profiles and foraminiferal assemblage on the outer shelf of the Bay of Biscay. *Continental Shelf Research*, 26(15), 1730-1755. <https://doi.org/10.1016/j.csr.2006.05.005>
- Lantsch, H., Hanebuth, T. J. J., Horry, J., Grave, M., Rebesco, M., and Schwenk, T. (2017). Deglacial to Holocene history of ice-sheet retreat and bottom current strength on the western Barents Sea shelf. *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2017.08.016>
- Larkin, K. E., and Gooday, A. J. (2004). Soft-shelled monothalamous foraminifera at an intertidal site on the south coast of England. *Journal of Micropalaeontology*, 23(2), 135-137. <https://doi.org/10.1144/jm.23.2.135>
- Lesen, A. E. (2005). Relationship between benthic foraminifera and food resources in South San Francisco Bay, California, USA. *Marine Ecology Progress Series*, 297, 131-145. <https://doi.org/10.3354/meps297131>
- Licari, L. N., Schumacher, S., Wenzhofer, F., Zabel, M., and Mackensen, A. (2003). Communities and microhabitats of living benthic foraminifera from the tropical east Atlantic: impact of different productivity regimes. *The Journal of Foraminiferal Research*, 33(1), 10-31. <https://doi.org/10.2113/0330010>

- Loeblich, A. R., and Tappan, H. N. (1953). Studies of Arctic foraminifera. *Smithsonian Miscellaneous Collections*.
- Lorenzen, C. J., and Jeffrey, S. W. (1980). Determination of chlorophyll in seawater. *Unesco Technical Papers in Marine Science*.
- Lucchi, R. G., Bazzaro, M., Biebow, N., Carbonara, K., Caridi, F., De Vittor, C., ... and Krueger, M. (2016). BURSTER-Bottom Currents in a Stagnant Environment. EUROFLEETS-2 Cruise Summary Report.
- Majewski, W., Pawłowski, J., and Zajączkowski, M. (2005). Monothalamous foraminifera from West Spitsbergen fjords, Svalbard: a brief overview. *Polish Polar Research*, 26(4), 269-285.
- Majewski, W., and Zajaczkowski, M. (2007). Benthic foraminifera in Adventfjorden, Svalbard: Last 50 years of local hydrographic changes. *The Journal of Foraminiferal Research*, 37(2), 107-124. <https://doi.org/10.2113/gsjfr.37.2.107>
- Marsh, J. B., & Weinstein, D. B. (1966). Simple charring method for determination of lipids. *Journal of Lipid Research*.
- Martin, R. E., and Steinker, D. C. (1973). Evaluation of techniques for recognition of living foraminifera. In *Compass* (Vol. 50, No. 4, pp. 26-30).
- Martins, M. V. A., Pinto, A. F. S., Frontalini, F., da Fonseca, M. C. M., Terroso, D. L., Laut, L. L. M., Zaaboub, N., Rodriguez, M.A.C., and Rocha, F. (2016). Can benthic foraminifera be used as bio-indicators of pollution in areas with a wide range of physicochemical variability?. *Estuarine, Coastal and Shelf Science*, 182, 211-225. <https://doi.org/10.1016/j.ecss.2016.10.011>
- Murray, J. W. (2006). *Ecology and applications of benthic foraminifera*. Cambridge University Press.
- Pedrosa, M. T., Camerlenghi, A., De Mol, B., Urgeles, R., Rebesco, M., and Lucchi, R. G. (2011). Seabed morphology and shallow sedimentary structure of the Storfjorden and Kveithola trough-mouth fans (North West Barents Sea). *Marine Geology*, 286(1-4), 65-81. <https://doi.org/10.1016/j.margeo.2011.05.009>
- Peperzak, L., and Brussaard, C. P. (2011). Flow cytometric applicability of fluorescent vitality probes on phytoplankton 1. *Journal of phycology*, 47(3), 692-702. <https://doi.org/10.1111/j.1529-8817.2011.00991.x>
- Pielou, E. C. (1975). *Ecological diversity* (No. 574.524018 P5).
- Piepenburg, D., and Schmid, M. K. (1996). Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. *Marine Biology*, 125(2), 321-332.

<https://doi.org/10.1007/BF00346313>

- Piepenburg, D., and Schmid, M. K. (1997). A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance, and estimates of biomass and organic carbon demand. *Marine Ecology Progress Series*, 147, 63-75. <https://doi.org/10.3354/meps147063>
- Piña-Ochoa, E., Høglund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., Schweize, M., Jorissen, F., Rysgaard, S., and Risgaard-Petersen, N. (2010). Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida. *Proceedings of the National Academy of Sciences*, 107(3), 1148-1153. <https://doi.org/10.1073/pnas.0908440107>
- Polymenakou, P., Pusceddu, A., Tselepides, A., Polychronaki, T., Giannakourou, A., Fiordelmondo, C., Hatziyanni, E. and Danovaro, R. (2005). Benthic microbial abundance, enzymatic activities, bacterial production, C mineralization and oxygen consumption rates in a highly trawled ecosystem (Thermaikos Gulf, Aegean Sea).
- Pucci, F., Geslin, E., Barras, C., Morigi, C., Sabbatini, A., Negri, A., and Jorissen, F. J. (2009). Survival of benthic foraminifera under hypoxic conditions: Results of an experimental study using the CellTracker Green method. *Marine Pollution Bulletin*, 59(8-12), 336-351. <https://doi.org/10.1016/j.marpolbul.2009.08.015>
- Pusceddu, A., Sarà, G., Armeni, M., Fabiano, M., and Mazzola, A. (1999). Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea). *Hydrobiologia*. <https://doi.org/10.1023/A:1003690313842>
- Pusceddu, A., Dell'Anno, A., and Fabiano, M. (2000). Organic matter composition in coastal sediments at Terra Nova Bay (Ross Sea) during summer 1995. *Polar Biology*. <https://doi.org/10.1007/s003000050446>
- Pusceddu, Antonio, Dell'Anno, A., Fabiano, M., and Danovaro, R. (2009). Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps07735>
- Pusceddu, Antonio, Bianchelli, S., Canals, M., Sanchez-Vidal, A., Durrieu De Madron, X., Heussner, S., Lykousis, V., de Stigter, H., Trincardi, F., and Danovaro, R. (2010). Organic matter in sediments of canyons and open slopes of the Portuguese, Catalan, Southern Adriatic and Cretan Sea margins. *Deep-Sea Research Part I: Oceanographic Research Papers*.
- Pusceddu, Antonio, Bianchelli, S., Gambi, C., and Danovaro, R. (2011). Assessment of benthic trophic status of marine coastal ecosystems: Significance of meiofaunal rare taxa. *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1016/j.ecss.2011.05.012>

- Pusceddu, A., Carugati, L., Gambi, C., Mienert, J., Petani, B., Sanchez-Vidal, A., Canals, M., Heussener, S., and Danovaro, R. (2016). Organic matter pools, C turnover and meiofaunal biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard Archipelago. *Deep Sea Research Part I: Oceanographic Research Papers*, 107, 48-58. <https://doi.org/10.1016/j.dsr.2015.11.004>
- Rebesco, M., Liu, Y., Camerlenghi, A., Winsborrow, M., Laberg, J. S., Caburlotto, A., Diviacco, P., Accettella, D., Sauli, C., Wardell, N., and Tomini, I. (2011). Deglaciation of the western margin of the Barents Sea Ice Sheet - A swath bathymetric and sub-bottom seismic study from the Kveithola Trough. *Marine Geology*. <https://doi.org/10.1016/j.margeo.2010.10.018>
- Rebesco, M., Özmaral, A., Urgeles, R., Accettella, D., Lucchi, R. G., Rütther, D., Winsborrow, M., Liopart, J., Carbulotto, A., Lantzsch, H., and Hanebuth, T. J. J. (2016). Evolution of a high-latitude sediment drift inside a glacially-carved trough based on high-resolution seismic stratigraphy (Kveithola, NW Barents Sea). *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2016.02.007>
- Risgaard-Petersen, N., Langezaal, A. M., Ingvarlsen, S., Schmid, M. C., Jetten, M. S., den Camp, H. J. O., Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., and Revsbech, N. P. (2006). Evidence for complete denitrification in a benthic foraminifer. *Nature*, 443(7107), 93. <https://doi.org/10.1038/nature05070>
- Sabbatini, M. E., Rodriguez, M. R., Dabas, P., Vatta, M. S., and Bianciotti, L. G. (2007). C-type natriuretic peptide stimulates pancreatic exocrine secretion in the rat: role of vagal afferent and efferent pathways. *European journal of pharmacology*, 577(1-3), 192-202. <https://doi.org/10.1016/j.ejphar.2007.08.043>
- Sabbatini, A., Bonatto, S., Bianchelli, S., Pusceddu, A., Danovaro, R., and Negri, A. (2012). Foraminiferal assemblage and trophic state in coastal sediments of the Adriatic Sea. *Journal of Marine Systems*, 105, 163-174. <https://doi.org/10.1016/j.jmarsys.2012.07.009>
- Sabbatini, A., Nardelli, M. P., Morigi, C., and Negri, A. (2013). Contribution of soft-shelled monothalamous taxa to foraminiferal assemblage in the Adriatic Sea. *Acta Protozoologica*, 52(3).
- Saher, M., Kristensen, D. K., Hald, M., Pavlova, O., and Jørgensen, L. L. (2012). Changes in distribution of calcareous benthic foraminifera in the central Barents Sea between the periods 1965–1992 and 2005–2006. *Global and Planetary Change*, 98, 81-96. <https://doi.org/10.1016/j.gloplacha.2012.08.006>
- Saidova, K. M. (1997). Communities of benthic Foraminifera in the Bering Sea and the Sea of Okhotsk. *Oceanology*, 37, 105-112.



- Schulte-Rüther, M., Mainz, V., Fink, G. R., Herpertz-Dahlmann, B., and Konrad, K. (2012). Theory of mind and the brain in anorexia nervosa: Relation to treatment outcome. *Journal of the American Academy of Child and Adolescent Psychiatry*. <https://doi.org/10.1016/j.jaac.2012.06.007>
- Sergeeva, N. G., Anikeeva, O. V., and Gooday, A. J. (2010). Soft-shelled, monothalamous foraminifera from the oxic/anoxic interface (NW Black Sea). *Micropaleontology*, 393-407.
- Somerfield, P. J., Warwick, R. M., and Moens, T. (2005). Meiofauna techniques. *Methods for the study of marine benthos*, 3, 229-272.
- Thiel, H., and Higgins, R. P. (1988). Introduction to the study of meiofauna. *Smithsonian*.
- Walker, D.A., Linton, A.E., and Schafer, C.T. (1974). Sudan black B: a superior stain to rose Bengal for distinguishing living from non-living foraminifera. *J. Foraminiferal Res.* 4, 205–215.
- Włodarska-Kowalczyk, M., Renaud, P. E., Węśławski, J. M., Cochrane, S. K., and Denisenko, S. G. (2012). Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. *Marine Ecology Progress Series*, 463, 73-87. <https://doi.org/10.3354/meps09858>
- Wollenburg, J. E., Mackensen, A., and Kuhnt, W. (2007). Benthic foraminiferal biodiversity response to a changing Arctic palaeoclimate in the last 24.000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 255(3-4), 195-222. <https://doi.org/10.1016/j.palaeo.2007.05.007>

## Chapter 3

### Abstract

#### **Patterns and environmental drivers of diversity and community composition of macrofauna in the Kveithola Trough (NW Barents Sea)**

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The Kveithola Trough located in the NW Barents Sea is a peculiar system characterized by distinct geomorphological and environmental features which are expected to exert an important role on the distribution of benthic assemblage. In the present study we investigated for the first time the distribution of macrofaunal abundance, biomass and diversity along the Kveithola Trough. Our analysis reveals major differences of the macrofaunal assemblage along the Kveithola Trough related not only to the different morpho-depositional features but also to differences in trophic conditions. The inner part of the Kveithola Trough was characterized by the presence of opportunistic species such as *Levinsenia gracilis* and *Maldane sarsi* among polychaetas, *Mendicula* cf. *pygmaea* and *Yoldiella* sp. among bivalves, which are known to inhabit oxygen-depleted environments and organic-enriched sediments. Results reported in this study suggest that the peculiar environmental conditions of the Kveithola Trough along with the occurrence of methane seepage in the neighbouring Storfjorden Trough in association to the Knølegga fault may exert a major selective effect on macrofaunal organisms.

Keywords: Kveithola Trough - Arctic - Benthic ecology - Macrofauna - Biodiversity - Eutrophic

## 1. Introduction

Macrofauna is an important component of the benthic food web in marine ecosystems, playing a key role in C cycling and energy transfer to the higher trophic levels (Cusson and Bourget, 2005). Macrofaunal invertebrates (in particular infaunal organisms) through bioturbation greatly influence sediment biogeochemistry with cascade effects on the abundance, biomass and diversity of other benthic components (Christensen et al., 2000; Welsh, 2003; Mermillod-Blondin et al., 2005; Birchenough et al., 2012). Bioturbation intensity can be quantitatively estimated using different approaches including the community bioturbation potential (BPc), which combines abundance and biomass data with information about the life traits of individual species or taxonomic group (Solan et al., 2004; Birchenough et al., 2012; Queirós et al., 2013). Abundance, biomass and biodiversity of benthic macrofauna are controlled by an interplay of biotic factors such as competition and predation and abiotic factors such as grain size, hydrodynamic regimes and food availability (Peterson 1979; Snelgrove and Butman 1994; Kendall 1996; Piepenburg et al., 2001; Włodarska-Kowalczyk et al., 2004). Therefore the benthic macrofauna through their feeding, bioturbation, burrow construction and burrow irrigation activities influence rates of organic matter inputs to the sediment, the vertical distribution of this organic matter, the rates and pathways of organic matter mineralization within the sediment compartment and the fluxes of the regenerated dissolved nutrients back to the overlying water, which in turn, ultimately represents the organic matter input to the sediment and the food source for the benthic community (Graf and Rosenberg, 1997; Christensen et al., 2000; Welsh, 2003). In the arctic ecosystem, the primary production is highly variable in time and space, and benthic food supply is often in the form of episodic pulses of pelagic- and ice-related organic carbon (i.e. the spring bloom; Carmack and Wassmann 2006a).

For example, in the Barents Sea a large fraction of the organic C produced by photosynthesis (range: 60-80 g C m<sup>-2</sup> yr<sup>-1</sup> for the whole Barents Sea) occurs during the spring bloom (Loeng, 1991). In the Barents Sea, 48-96% of organic C produced by photosynthesis can reach the seafloor (Wassmann, 1991; Carmack and Wassmann, 2006b), thus contributing to support abundant and diverse benthic communities (Wassmann et al., 1996). However, in some areas of the NW Barents Sea such as the Kveithola Trough, the organic enrichment of the sediment along with water column stratification can cause bottom hypoxia with cascade detrimental consequences on macrobenthic assemblage as documented in other eutrophic coastal systems throughout the world (Hyland et al., 2005; Diaz and Rosenberg, 2008; Magni et al., 2008). The Kveithola Trough (Fig. 1) is an abrupt and narrow glacial sedimentary system located in the NW Barents Sea. The trough extends in E-W direction over 100

km, less than 13 km wide and shows an average water depth of 300-350 m along its axis (Schulte-Rüther et al., 2012). Along with the larger Storfjorden glacial system, the Kveithola Trough hosted during the last glaciation ice streams draining ice from the southern Svalbard in the north and Bear Island in the south (Pedrosa et al., 2011; Bjarnadóttir et al., 2013). The seafloor in the Kveithola Trough is characterized by a series of E–W trending mega-scale glacial lineations that record a fast-flowing ice stream draining the Barents Sea ice sheets during the Last Glacial Maximum. Glacial lineation are overprinted by transverse Grounding-Zone Wedges (GZW) generated during episodic retreat of the last glacial ice sheet, giving rise to a staircase bathymetric axial profile of the trough (Rebesco et al., 2011; Bjarnadóttir et al., 2013).

The Kveithola Trough is intersected with N-S direction by the Hornsund and Knølegga fault systems related to the phases of crustal extension associated with the opening of the Norwegian - Greenland Sea since the Cretaceous (Gabrielsen et al., 1990; Bergh and Grogan, 2003). The innermost Knølegga fault is responsible for an elongated bathymetric depression indicated by Rebesco et al., (2016) as the “northern channel”.

The inner area of the Kveithola Trough hosts a sediment drift (the Kveithola Drift of Rebesco et al., 2016) that is associated to a field of pockmarks (Bjarnadóttir et al., 2013). This drift has a very articulated morphology (Main and Minor drift, Fig. 1) and it is inferred to have been formed by sediments supplied by dense bottom currents reaching the trough via a large channel that is connected to the innermost Kveithola Trough from the northern area (Thomas et al., 2004; Bjarnadóttir et al., 2013).

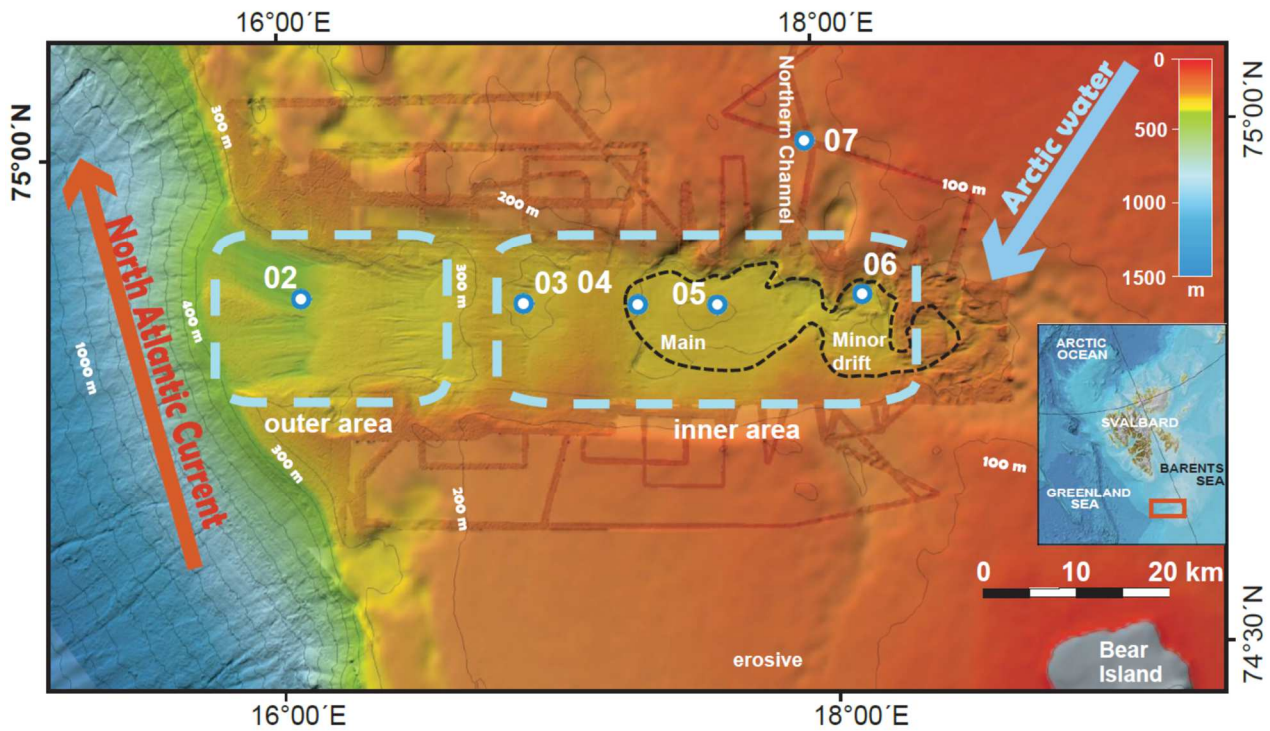


Fig.1 Study area and location of the studied sites. The arrows indicate surface currents.

Station	Latitude	Longitude	Depth(m)	Site location
02	74° 51,53' N	16° 05,93' E	376	Outern Kveithola Trough
03	74° 51,00' N	16° 54,52' E	317	Grounding-Zone Wedges
04	74° 50,75' N	17° 20,86' E	304	Kveithola Main Drift
05	74° 50,53' N	17° 38,37' E	293	Kveithola Main Drift
06	74° 50,75' N	18° 10,55' E	335	Kveithola Minor Drift
07	74° 59,69' N	17° 59,72' E	159	Northern Channel (Knølegga Fault Zone)

Tab.1 TV-multi-corer sampling sites location.

The Kveithola Drift has been surveyed during several cruises (oceanographic expeditions of the RV OGS-Explora 2008; RV Jan Mayer 2009; RV Maria S. Merian 2013, and RV Polarstern 2016) focusing mainly on the glacial history of the area associated to climate changes. The dataset recovered during the cruises outlined a highly dynamic depositional environment with strong bottom currents responsible for sediment drifts formation, but also the existence of a stressed benthic environment

affected by low-oxygen conditions (Hanebuth et al., 2013) with likely ongoing seep activity (Lucchi et al., 2016). Very limited information is available on benthic assemblage inhabiting this area (Caridi et al., 2017) and data about benthic macrofauna have not been published yet. To fill this gap, in this study we investigated, for the first time, the abundance, biomass and diversity of benthic macrofauna in the Kveithola Trough (NW Barents Sea) and the potential environmental factors shaping their distribution.

## 2. Materials and methods

### 2.1. Benthic sampling strategy

Sediment samples were collected using a video-guided multicorer (TV-MUC) in June 13–23, 2016 during Eurofleets 2- BURSTER cruise that was conducted onboard the German icebreaker RV Polarstern (Expedition PS99-1a; Lucchi et al., 2016). Videos and photos were acquired at each site using a high-definition benthic camera (Ocean Floor Observatory System). At each studied site a water column profile was performed with a SBE911plus CTD system.

Sediment samples were collected at six sites (Fig. 1, Tab. 1) using a video-guided multi-corer (TV-MUC) that was assembled with 8 tubes in polycarbonate having 60 cm length, 10 cm outer diameter, and 2.5 mm of thickness. In each site, 4 replicate cores were collected dedicated only to the macrofaunal analyses except for site 04 where only 3 replicates were collected due to fail in sediment recovery during the last deployment. From each core, three levels were analysed (0–2, 2–5, and 5–10 cm) and quantitative samples were treated in accordance with ISO 16665: 2014 fieldwork protocols and sieved on-board with a mesh size of 500  $\mu\text{m}$ . The material retained on the sieve was stored at  $-20^{\circ}\text{C}$ . Additional sediment sub-samples of the top 2 cm of the sediment were collected for the analysis of the quantity and biochemical composition of organic matter.

In the laboratory, samples were sorted and counted, and the living individuals were extracted, recognized at the lowest taxonomic level and stored in Eppendorfs filled with 70% alcohol. All individuals were counted, weighed and the data standardized at 1  $\text{m}^2$  for comparison with the macrofaunal data obtained from the literature. The abundance counts were expressed as individuals per area ( $\text{ind.m}^{-2}$ ) and the average density and the taxonomic composition of the main taxa was calculated.

The biomass was determined as blotted wet weight (ww) per higher taxon after drying the specimens on absorbent paper for a few minutes applying the method described by Dermott and Paterson, 1974. The molluscs were weighed with their shells, and the polychaetes without tubes.

Phyletic groups were distinguished into Crustacea, Echinodermata, Mollusca, Polychaeta, Nemertea, Sipuncula and Bryozoan.

## 2.2. Quantity and biochemical composition of sedimentary organic matter

Chlorophyll-a and phaeopigment determinations of the top 2 cm of the sediment were carried out fluorometrically according to Lorenzen and Jeffrey, 1980. Pigments were extracted with 90% acetone (12 h in the dark at 4 °C). After the extraction the pigments were analysed to estimate the quantity of chlorophyll-a and, after acidification with 0.1 N HCl, to estimate the amount of phaeopigments. The sum of the chlorophyll-a and phaeopigment concentrations were assumed to represent the total phytopigment concentrations which were converted to carbon equivalents by using the conversion factor of 40  $\mu\text{g}$  of C  $\mu\text{g}^{-1}$  (Pusceddu et al., 1999; Pusceddu et al., 2009). Such a conversion factor was used to allow a proper comparison with previous investigations (Pusceddu et al., 1999; 2000; 2009).

Protein, carbohydrate and lipid concentrations of the top 2 cm of the sediment were determined spectrophotometrically (Pusceddu et al., 2009, 2010). Protein concentration was obtained according to Hartree (1972) as modified by Danovaro (2010). Concentrations are reported as mg albumin equivalents per dry weight g of sediment. Carbohydrate were analysed according to Gerchakov and Hatcher (1972) and expressed as mg glucose equivalents per dry weight g of sediment. Lipids were extracted with methanol and chloroform (2:1 vol/vol) according to Bligh and Dyer (1959) and then analysed according to Marsh and Weinstein (1966). Lipid concentrations are reported as mg tripalmitin equivalents per dry weight g of sediment. Protein, carbohydrate and lipid concentrations were converted into carbon equivalents by using the following conversion factors: 0.49, 0.40 and 0.75 g C  $\text{g}^{-1}$ , respectively (Fabiano et al., 1995). The sum of protein, carbohydrate and lipid carbon was referred as biopolymeric C (BPC), while bioavailable carbon (BAC) concentration was calculated as the sum of digestible proteins and carbohydrates converted into carbon equivalents by using the same factors as for their total pools

(Danovaro et al., 2001). The contribution of chlorophyll-a concentrations converted into C equivalent to biopolymeric C concentrations was used as descriptors of the ageing of sediment organic matter (Pusceddu et al., 2010; Pusceddu et al., 2011).

For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). All of the analyses were performed as three pseudo-replicates, with about 1 g of sediment per sample.



### 2.3. Estimate of the community bioturbation potential BPc

The bioturbation classification of all identified macrofaunal taxa were derived according to the standardised scores for mobility and sediment reworking mode listed in Queirós et al., (2013). These data were used to estimate community bioturbation potential (BPc), using the equation in Solan et al. (2004a):

$$\sum_{i=1}^n \sqrt{Bi/Ai} * Ai * Mi * Ri$$

Bi and Ai are the biomass and abundance of a taxon (i) in a sample; Mi is their standardised score for mobility; and Ri is their standardised score for sediment re-working mode.

### 2.4. Statistical analysis

All statistical analyses were carried out using the software Past 3'12 (Hammer et al., 1999) and Primer 6 (Clarke and Gorley, 2006) (Tab.2). Faunal diversity was calculated using species richness (S) (Warwick and Clarke, 1995), the Shannon-Wiener index (H', log10) (Shannon and Weaver, 1963) and Pielou's Evenness (equitability) index (J) (Peet, 1974).

To test the temporal variations in the composition of the benthic macrofaunal assemblage and the biochemical composition of sediment organic matter, multivariate permutational analysis of variance (PERMANOVA; McArdle and Anderson, 2001) based on Euclidean (organic matter) and Bray–Curtis distances (macrofaunal community), were applied. For the biochemical compounds concentration (i.e., protein, carbohydrate) and the macrofaunal assemblage we used 999 permutations.

SIMPER analysis was applied to assess the dissimilarity percentage between macrofaunal assemblage and biochemical compounds and to identify which species contributed most to the observed dissimilarities between sites. To assess whether, and how much, the benthic trophic resources (i.e., quantity and biochemical composition of the organic matter) explained changes in the composition of the macrofaunal assemblage, non-parametric multivariate multiple regression analyses based on Bray–Curtis distances were carried out using the routine DISTLM forward (McArdle and Anderson, 2001). The forward selection of explanatory variables was carried out under a linear regression model using 999 permutations.

Pearson's correlation coefficient ( $r$ ) was calculated to determine individual pairwise relationship between environmental variables and univariate faunal community data. To identify the potential relationships between environmental variables and macrofaunal species composition a canonical correspondence analysis (CCA) was performed.

### 3. Results

#### 3.1. Food quantity and quality at the seafloor

The concentrations of all investigated biochemical compounds as well as the contribution of the C of the algal fraction to biopolymeric C are summarized in Table 2.

Station	Depth	PRT mg/g	CHO mg/g	LIP mg/g	Chl-a µg/g	Phaeo µg/g	BPC mg/g	BAC mg/g	Algal fraction of BPC(%)
02	376	3,24	2,34	0,49	0,27	7,56	2,89	2,52	10.45
03	317	4,69	4,22	0,87	0,69	18,94	4,64	3,99	16.34
04	305	8,50	5,89	1,20	1,48	33,35	7,43	6,52	17.96
05	294	7,22	6,71	1,37	1,34	30,98	7,48	6,23	17.27
06	336	6,45	7,02	1,72	4,13	61,92	7,09	6,07	17.47
07	159	3,01	5,09	1,14	1,22	26,42	7,25	5,97	34.13

Tab. 2 Concentration of all investigating biochemical compounds by site: protein (PRT), carbohydrates (CHO), lipid (LIP), chlorophyll-a (Chl-a), phaeopigments (Phaeo), biopolymeric C (BPC), bioavailable carbon (BAC) and algal fraction of BPC.

The total phytopigment content varied significantly among sites of the Kveithola Trough, with values ranging from  $7.33 \pm 0.55 \mu\text{g/g}$  in the site 02 (Grounding-Zone Wedges) to  $66.1 \pm 4.4 \mu\text{g/g}$  in the site 07 out of the Kveithola Trough. Total carbohydrate concentrations were characterized by a wide variability with the lowest value at site 02 ( $2.34 \pm 0.27 \text{ mg/g}$ ) and highest value in site 07 ( $7.01 \pm 0.79 \text{ mg/g}$ ). Similar patterns were generally observed also for lipid and protein concentrations. Bioavailable carbon was lower at GZW sites (02 and 03), where the value were  $2,52 \pm 0.82$  and  $3,99 \pm 0.40 \text{ mg/g}$ , respectively. Conversely, at the other out sites decreased from  $6,52 \pm 1.92 \text{ mg/g}$  in the site 04 to  $5,97 \pm 0.39 \text{ mg/g}$  in the site 07. The contribution of the C associated to the algal fraction to the biopolymeric C changed significantly across the sampling sites, ranging from 10% in the site 02 to 34% in the site 07.

#### 3.2. Sites variation of BPC

BPC calculations were conducted at all sites for each replicate. Fig.2 shows the four replicates averages for each site, and the value reported were log transformed. The highest BPC value were observed at the site 06 (2.69) in the inner area, followed by the site 02 (2.53) in the outer area and the sites 03 and 07, located in the inner area and Northern channel respectively, both showing a

value of 2.46. Finally, the sites 04 and 05 in the inner area of Kveithola Trough both show the lowest value of BPc (1.94).

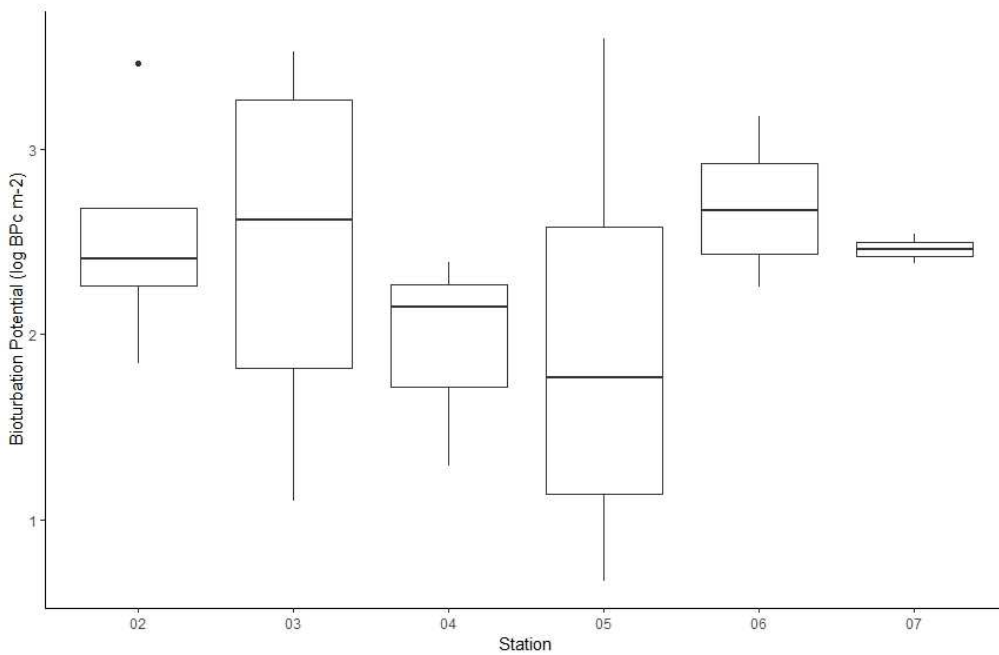


Fig. 2 Boxplots showing the sites variability of BPc

### 3.3. Faunal communities

In 23 replicates made among 6 sites, a total of 6459 macrofaunal individuals were identified (0-10 cm layers, > 500  $\mu\text{m}$ ) belonging to 27 taxa and 6 phyletic groups. The phylum showing the highest abundance is the Mollusca, with 1924 individuals divided among 9 taxa, representing the 29% of the total faunal sample. The second largest group is the Annelida (class Polychaeta) with 1847 individuals distributed among 12 taxa and representing the 28% of the total faunal sample.

Macrofaunal abundance ranged from 841 to 1350 ind.  $\text{m}^{-2}$  at sites 06 and 04, respectively (Fig.3).

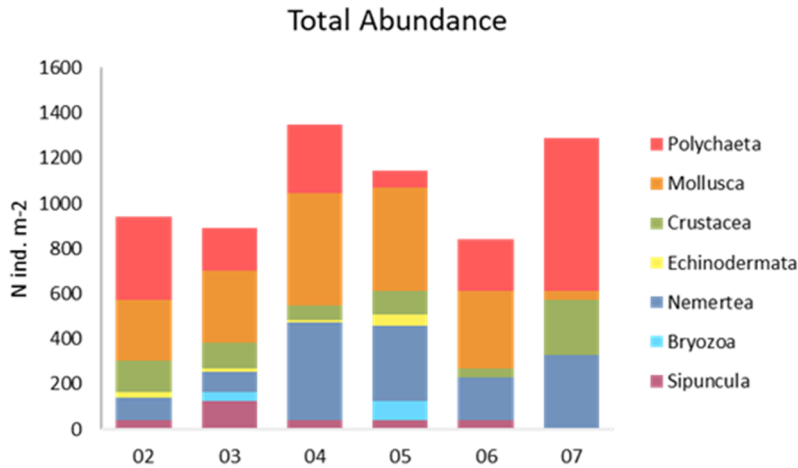


Fig. 3 Macrofaunal Abundances (ind.m<sup>-2</sup>) in the different sites investigated

The total macrofaunal biomass is dominated by polychaets, representing 180.6 g wet weight (ww) m<sup>-2</sup> and contributing to 40% of total biomass. Crustacea and mollusca have a weight of 126.7 and 102.7 g ww m<sup>-2</sup>, corresponding to the 28 and 23 %, respectively, of the total sample weight. The highest biomass per site increases from 36.6 g ww m<sup>-2</sup> at site 03 (outer area of Kveithola) to 120.5 g ww m<sup>-2</sup> at site 06, located in the inner part of the Kveithola (Fig.4).

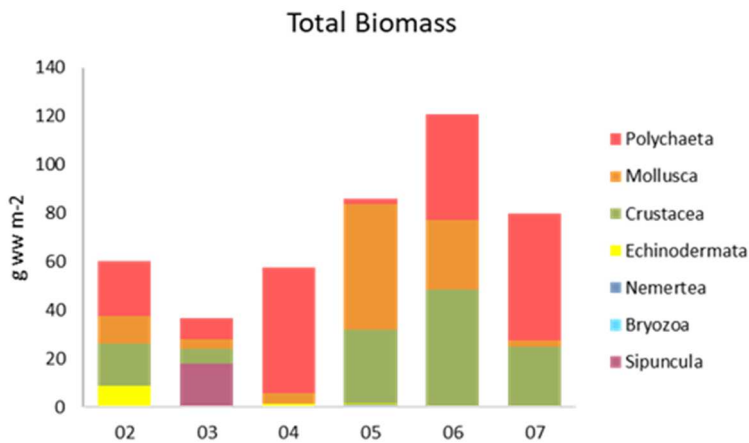


Fig. 4 Biomass (g ww m<sup>-2</sup>) aggregated by site

Pearson's correlation coefficient, that results from environmental variables and faunal parameters, shows a significantly (\*p > 0.05) positive correlation between biomass and Chl-a (r= 0.76), and biomass with Feo (r= 0.76). Shannon index have a positive correlation with water depth (r= 0.50),

whereas taxon density and diversity such as S and J indexes, have no significant correlation with the other parameters (Tab.3).

	Taxon density (ind. m <sup>-2</sup> )	Biomass (ww g m <sup>-2</sup> )	Species richness	Shannon (H')	Equitability (J')
Depth	0.26	-0.25	0.16	<b>0.50*</b>	0.14
Chl-a µg/g	-0.16	<b>0.76*</b>	0.18	0.06	-0.24
Feo µg/g	-0.23	<b>0.66*</b>	0.16	0.15	-0.25
BPC mg/g	-0.18	0.02	-0.20	-0.05	-0.15

Tab. 3 Pearson's correlation coefficient (r-values) relating environmental variables to benthic community structure. Significant relationships are shown in **bold**; \*p < 0.05

At all sites, the majority of organisms were encountered in the top 2 cm of the sediment (overall 4242 ind.m<sup>-2</sup> accounting for 65% of the total faunal abundance; Fig. 5).

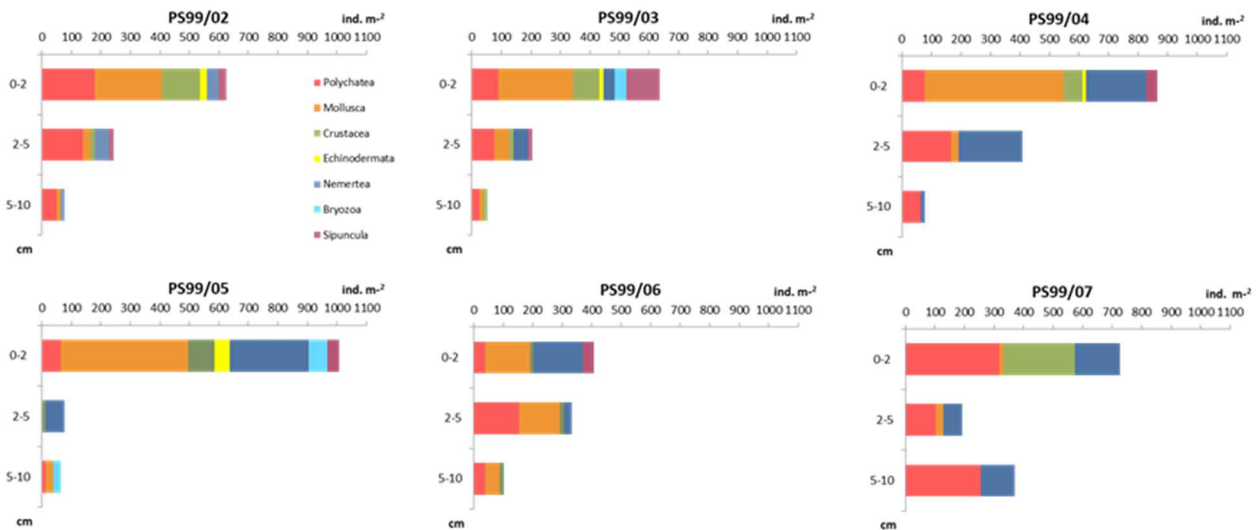


Fig. 5 Macrofaunal abundances along the vertical profile of sediment collected in the different sites investigated

However, whereas all macrofaunal groups were well represented in the first 2 cm of the sediments of sites located in the Grounding Zone Wedge and Main drift, Echinodermata, Bryozoan and Sipuncula were absent in the sites 06 and 07 located in the inner Kveithola Trough. The highest species richness (S) occurs in the site 03, with 20 identified species, decreasing to 19, 18, 13 and 10 species in the site 04 and 05, site 02, site 06, and site 07 respectively (Tab. 4). The Shannon's Index

values are higher in the most outer sites 02 and 03 ( $H'=2.0$ ), with respect to the site 04, 05 and 06 ( $H'=1.7$ ) located in the middle-inner area, and site 07 ( $H'=1.5$ ) along the Northern Channel. The highest Pielou's evenness occurs in the site 02 (0.68) and the lowest in the site 04 (0.54) (Tab. 4).

Station	Depth	Taxon density (ind. m <sup>-2</sup> )	Biomass (wwg m <sup>-2</sup> )	Species richness	Shannon (H')	Equitability (J')
02	376	943	60.2	18	2.0	0.69
03	317	892	63.6	20	2.0	0.67
04	305	1350	57.7	19	1.7	0.59
05	294	1146	85.8	13	1,7	0.68
06	336	841	120.5	10	1.6	0.68
07	159	1287	79.6	9	1.4	0.62

Tab.4 Diversity and faunal characteristics by site.

### 3.4. Taxonomic composition

Mollusca are the most abundant faunal group in all sites, accounting for 9 out of the 27 taxa observed (Fig. 4). Among them, the overall most abundant taxon, is the bivalve *Mendicula* cf. *pygmaea* (Verrill and Bush 1898) occurring in 19 out of 24 faunal replicates, with the highest value of 1095 ind.m<sup>-2</sup>. The second most abundant taxon is the polychaeta *Maldane sarsi*, representing 675 ind/m<sup>2</sup> occurring in 8 out of 24 faunal replicates, and the third most abundant taxon is the polychaeta *Levinsenia gracilis* contributing with 280 ind/m<sup>2</sup> of the entire assemblage. Also, the morphotype assigned to the phylum Nemertea occurs in all replicates, with 1643 ind.m<sup>-2</sup>.

At the site 02, the polychaeta *M. sarsi* is the dominant species, representing 16% of the total sample, followed by the bivalves *M. cf. pygmaea* (12 %) and *Yoldiella* sp. (10%). At the site 03, the fauna is dominated by the bivalves *M. cf. pygmaea* with 14% of the total number of individuals, followed by the polychaeta *Syllides* spp. (10% of the total abundance).

*M. cf. pygmaea* is the dominant species also in the sites 03 and 04, representing 30% and 28% respectively, of the total faunal assemblage. At 06, *Yoldiella* sp. is the most abundant species, representing 25% of the total samples, followed by *M. cf. pygmaea* (13%) and *L. gracilis* (7%). *M. cf. pygmaea* does not occur at site 07, where *M. sarsi* is the dominant species, contributing to 36% of

the total number of individuals, followed by the crustacea *Diastylis* sp. and *L. gracilis*, representing 12% and 8%, respectively, of the total sample abundance (Tab.5).

	02		03		04		05		06		07	
	AvDens	D	AvDens	D	AvDens	D	AvDens	D	AvDens	D	AvDens	D
<i>Levinsenia gracilis</i> (P)	0	0.0	38	4.3	51	3.8	13	1.1	64	7.6	115	8.9
<i>Maldane sarsi</i> (P)	153	16.2	0	0.0	0	0.0	0	0.0	51	6.1	471	36.6
<i>Syllides</i> sp. (P)	64	6.8	89	10.0	89	6.6	13	1.1	0	0.0	0	0.0
<i>Diastylis</i> spp. (C)	76	8.1	64	7.1	25	1.9	25	2.2	25	3.0	166	12.9
<i>Yoldella</i> sp. (M)	102	10.8	13	1.4	0	0.0	13	1.1	217	25.8	38	3.0
<i>Mendicula</i> <i>cf. pygmaea</i> (M)	115	10.2	127	14.3	408	30.2	331	28.9	115	16.6	0	0.0
Nemertea	102	10.8	89	10.0	433	32.1	331	28.9	191	22.7	331	25.7

Tab.5 Average densities (AvDens, ind.m<sup>-2</sup>) and dominance (D, %) of the most numerous species in the core samples. Faunal group abbreviations are given in parentheses: P-Polychaeta, M-Mollusca, C-Crustacea

Significant regional differences among macrofaunal assemblage are detected between sites (ANOVA \*\*\*P> 0.001), in particular pairwise comparison shows that site 07 (Northern Channel) is significantly different from all the other sites. The SIMPER test reveals also the presence of dissimilarity between sampling sites and shows the most important species, which contribute to this dissimilarity. Those contributing to the observed differences are polychaeta and in particular the species *L. gracilis*, and *M. sarsi*, bivalve as *M. cf. pygmaea* e *Yoldiella* sp. and the organisms belonging to the taxon Nemertea.

To identify relationships between environmental variables such as water depth, food quantity (as BPC concentrations and quality as the contribution of algal fraction to BPC) and macrofaunal species composition, DistML and CCA analysis were carried out. DistML shows that the principal food resources that influence the distribution and taxonomic composition of benthic community are chlorophyll a and phaeopigment (Tab. 6).



Variable	SS(trace)	Pseudo-F	P
Chl-a µg/g	6203.7	3.4795	<b>0.001***</b>
Phaeo µg/g	5260.7	2.8562	<b>0.006**</b>
PRT mg/g	3177.7	1.6114	0.125
CHO mg/g	3412.1	1.7432	0.088
LIP mg/g	2226.8	1.0962	0.363

Tab. 6 Results of distance based linear models (DistML) for biochemical compound: chlorophyll-a (Chl-a), phaeopigments (Phaeo), protein (PRT), carbohydrates (CHO) and lipid (LIP). Significant differences are shown in **bold**; \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

The output of CCA allowed us to identify three different cluster, the figure shows a clear separation of the sites 02 (out of the Kveithola Trough) and 07 (shallower site in the inner Kveithola Trough) from all the other sites located along the Trough (Fig. 6).

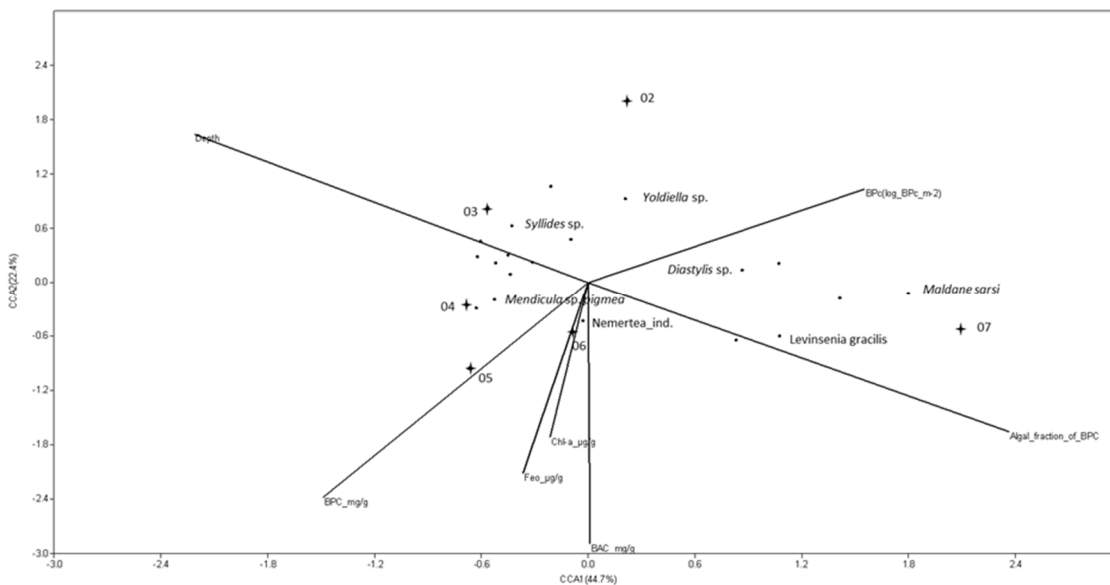


Fig.6 Canonical correspondence analysis (CCA) of highly abundant taxa: species (dots), site (crosses) and environmental variables (vectors). Most dominant species are indicated by labels names.

Macrofaunal species composition of site 07 was related with the contribution of the algal fraction to BPC, the site 03 was related with water depth, the site 5 with the concentration of biopolymeric carbon, while the site 06 was related with chloroplastic pigment. As far as the species distribution is concerned, the cumacea *Diastylis* sp. was related with the bioturbation potential, the polychaetas as *L. gracilis* and *M. sarsi* were related with the contribution of the algal fraction to BPC and, whereas

taxa such as the bivalve *M. cf. pygmaea* and organisms belonging to the taxon Nemertea were related with chloroplastic pigment, BAC and BPC concentrations.

## 4. Discussion

### 4.1. Environmental drivers

The macrofauna and organic matter results allow us to identify three different areas in the Kveithola Trough: the outer and the inner part of the trough; the latter identified as Main and Minor drifts areas. A third area is represented by site 07 located in the Northern channel (namely the Knølegga fracture zones, Fig 1). Different morphological and sedimentological features lead also Rebesco et al., (2016) to observe this subdivision.

As such, our data will be discussed in relation with the existing literature, focussing in particular on the possible relationship among trophic conditions, seabottom morphology and oceanographic features.

The outer part of the trough is the deepest studied area along the Kveithola Trough (400–450 m bsl) and is directly influenced by the North Atlantic Current (NAC, warm and saline ,Slubowska-Woldengen et al., 2008); the NAC sweeps the outer seafloor and remove the fine sediment fraction leaving a coarse lag of pebbly sands (Caricchi et al., 2018). Instead, the inner part which comprises the Main Drift and the Minor Drift, located between the Hornsund and Knølegga fracture zones (mean depth around 300 m bsl), is subject to continuous fine-grained sediment deposition due to cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow. These dense brine waters generate bottom currents that shape the Kveithola Drift moat (Rebesco et al., 2016; Lantzsch et al., 2017).

The distribution of the macrofaunal assemblage, in term of density and biomass, reflects this morpho-depositional subdivision and we infer there is a close relationship between benthic fauna structure and water-column characteristics. The outer trough (site 02), shows highly diversified species composition, high species richness ( $S=18$ ) and *Shannon* index ( $H'=2.0$ ) while biomass and taxon density are low ( $60.2 \text{ g ww m}^{-2}$  and  $943 \text{ ind. m}^{-2}$ , respectively). This faunal overview might be related to the exposure to the NAC hydrodynamic conditions that represents the main water mass of the studied area with negligible influence from other type of water masses (little or any water masses stratification). The high species diversity suggests that the influence of the NAC contribute to maintain a well-oxygenated environment and on the other hand, the high intensity current makes the substrate instable preventing the possibility to increase the number of specimens (Picard, 1965; Marques, 1987).

Instead, in the inner areas (sites 03, 04, 05, 06) both S and H' indexes are low (Tab. 4), while density and biomass are high (Tab. 4). In this area the oceanographic pattern, evidences a progressive vertical stratification of the water column from West to East (i.e. from the outer to the inner area of the trough), in which water density increases with depth. We can recognize in this area three main water masses: the Atlantic Water, the Arctic Water and the BSW (Lucchi et al., 2016). Strong water stratification is responsible for limited dissolved gasses vertical exchange leading to oxygen reduction conditions at the sea bottom.

In the Kveithola Trough, these hydrographic and morpho-depositional features not only determine the different macrofaunal assemblage ecological distribution but are also crucial for the expression of benthic-pelagic coupling and consequently on trophic resource distribution (Mauna et al., 2011). In fact, shallow marine environments are often considered to be nutrient limited and primary production depend on inorganic nutrient regenerated in the sediment by benthic fauna (i.e. bioturbation). On the other hand, high primary production characterizes the Kveithola Trough, this meaning that high nutrient rates reach the benthic community, suggesting a close relationship between the pelagic and benthic compartments.

The relationship between primary productivity, or proxy of productivity (i.e. benthic pigments), and benthic community structure has been documented across the Arctic. The amount of food reaching the seafloor of Arctic system is positively related with benthic abundance and biomass, with richer benthic communities supported by more food (Ambrose and Renaud, 1995; Carroll et al., 2008; Cochrane et al., 2009). Our results show that in the Kveithola Trough the organic C load, considered as BPC concentration, is comparable to values typically encountered in eutrophic systems varying from 4.5 mg/g to 6.9 mg/g (Dell'Anno et al., 2002). In the sites of the Kveithola Trough, the biochemical compound concentration increases from the site 02 (2.89 mg/g) to the site 06 (7.26 mg/g), showing more eutrophic conditions to the inner part of the trough and also the quality of organic matter follows the same trend (Tab 2). DistLM analysis highlights that the freshness of organic matter (in terms of phytopigment concentrations), influence the distribution and taxonomic composition of benthic community in the Kveithola Trough (Tab. 2). Consistently, in the Barents Sea, Cochrane et al., (2009) found a positive correlation between benthic pigments and faunal abundance, reporting a lower faunal abundance and higher evenness in the food-limited northern sites of the Barents Sea in contrast to the more productive southern sites, which generally had higher abundances, but also higher dominance.

In order to highlight some functional traits influencing the benthic ecosystem processes, and in particular the capacity of benthic organisms to control water column fluxes we estimated the community bioturbation potential (BPC). This index could be used as a proxy of organic matter mineralization because provides an indirect information on the oxygen penetration within the sediment. In this way, the BPC contributes to explain how the environmental parameters drive the benthic macrofauna distribution in the morpho-depositional setting of the Kveithola Trough. The index shows high value in the outer Kveithola Trough (site 02) where bioturbation activity is expected to be high as a function low quality and quantity of organic matter and of the high oxygen characterizing the NAC (Lucchi et al., 2016) (Tab. 2). Consequently, high BPC relates to higher diversity of trophic groups and a deeper distribution of infauna (Gutierrez et al., 2000). Moreover, the BAC values indicate a low bioavailability of sediment organic carbon supporting a poorly sediment community oxygen consumption (Pusceddu et al., 2009). We cannot exclude that high hydrodynamism can enhance sediment resuspension injecting in the bottom water column organic matter pools more refractory in nature (e.g., carbohydrates) (Pusceddu et al., 2015) and in particular, benthic microbes exposed to O<sub>2</sub>-rich waters caused by sediment disturbance could, at the same time, stimulate a faster mobilisation of organic C buried in the sediment, injecting more labile molecules into the system (Polymenakou et al., 2005).

If we consider the transect of sites 03, 04, 05, we observe that at site 03 BPC is high as well (although showing high variability in the replicates), and this can be explained by the presence of Grounding Zone Wedges which, is bathymetric staircase transverse to the axial profile of the trough and acts separating two areas characterized by different oceanic current behaviour. In fact, it allows the site 03 to be exposed to NAC influence with respect to the near sites located in the inner part of the channel (sites 04, 05) (Fig.1). We thus interpret the lower BPC at the sites 04 and 05 as the result of a confined depositional condition of Kveithola trough, where the presence of the Drift, associated with the water stratification, limit exchange with the surrounding areas and therefore is responsible for limited dissolved O<sub>2</sub> vertical exchange leading to suboxic condition at the sea bottom. Although direct measurement of O<sub>2</sub> concentration in sediment is not available, evidences of burrowing structures in sub-surface sediments (Lucchi et al., 2016) can be referred to dysoxic conditions typically occurring in deeper environments (Wetzel and Uchman, 2012) which can contribute to organic matter preservation and accumulation, often associated with the absence of remineralization (Burdige, 2007). Furthermore, the BAC concentrations at sites 04 and 05 (Tab.2) are higher than other sites and they could enhance the sediment community oxygen consumption,

suggesting that the progressive accumulation of labile carbon could be an additional co-factor potentially responsible for transient hypoxic or anoxic conditions. In such microhabitat the macrofaunal species are represented by suspension- and surface-deposit feeders as polychaeta and molluscs (Pearson and Rosemberg 1978), that in fact, are the most representative groups in our study, followed by Nemertea (Fig. 2).

Finally, particular are the cases of sites 06 and 07 showing both high BPc values.

At these sites the high BPc values are related by the dense cold Brine-shelf water presence which lead to the burial of organic matter rich sediment, while the superficial Arctic Water (AC) guarantees the high productivity and the input of organic matter with a high nutritional quality to the seafloor (i.e., BAC and Chl-a). This trophic situation can stimulate infaunal feeding and bioturbation activities (Gutierrez et al., 2000); moreover, the enzymatically digestible and algal fractions of biopolymeric carbon decreased in sediments with increasing biopolymeric carbon content (i.e. eutrophic systems), suggesting that organic carbon in eutrophic sediments is mostly refractory in nature. In this context of rapid organic matter burial, the macrofauna is dominated by opportunistic species as polychaeta *M. sarsi*, bivalve as *M. cf. pygmaea* e *Yoldiella* sp. and the organisms belonging to the taxon Nemertea.

## 4.2. Macrofauna community

Despite the high quantity and good quality of food resources, a lower macrofaunal abundance occur in area object of the present study, ranging from 943 ind. m<sup>-2</sup> in the outer site to an average of 1057 ind. m<sup>-2</sup> in the inner sites. These value are definitively lower than those previously reported at similar depths in high latitude ecosystems such as those surrounding the Svalbard (up to 6000 ind. m<sup>-2</sup>, Wlodarska-Kowalczyk and Pearson, 2004; Cochrane et al., 2009; Åström et al., 2016). Also, in the southern part of the Barents Sea, Cochrane et al., (2009) show a high faunal abundance (average of 2400 ind. 0.5 m<sup>-2</sup> for site) positively influenced by the environmental conditions. In fact, this area is characterized by high productivity with strong influence from the Atlantic Water, with generally ice-free conditions throughout the year and a deep mixed layer. Aström et al., (2016) also show a high faunal abundance (average of 6624 ind. m<sup>-2</sup> for site) in the Storfjorden Trough area, but their sites are influenced by the Polar Front system and they are characterised by the presence of active seepages. However, the environmental stressors typically seen at fluid vents and seeps (i.e. strong chemical gradients), might lead to diversity decreased and a community structure dominated by fewer, specialized taxa. Therefore, the density bias between our samples and the surrounding area might depend on several factors and in particular by the high sediment and nutrient supply transported by the bottom currents to the drift area.

As Mau et al., (2017) reported methane seepages in the inner Kveithola Trough, and Lucchi et al., (2016) observed the presence of spotty high nekton activity in the area object of our study we infer that such seepage activity plays a role in the remobilization of buried organic matter that generates local food web oasis. High nekton activity would be, in turn, responsible for high organic matter accumulation generating the favourable conditions for the development of the eutrophic benthic community observed in the sediments.

Looking at the taxonomic composition, the structure of the faunal groups shown in this study, are in agreement with the previously identified “northern” and “central” biocoenoses in the Barents Sea (Cochrane et al., 2009). The outer site (02) shows polychaeta, mollusks, crustaceans and echinoderms in equal proportions whereas the inner sites (03-04-05-06) are dominated by polychaeta, followed by mollusks and crustacean. Therefore, in the Kveithola Trough many of the taxa commonly found at the outer site also occur at the inner sites, with different relative abundances. In particular, the macrozoobenthic communities exhibit similar species composition and a great abundance of small, opportunistic species; among these, the paraonids *L. gracilis*

(Tauber, 1879), a surface deposit feeder typical of muddy bottom, and the tubicolous *M. sarsi*, a sub-surface deposit feeder common in shelf environment worldwide (Fauchald and Jumars, 1979). We also find the presence of sub-surface detritivorous lamellibranch *M. cf. pygmaea*, and the small bivalve, sub-surface detritivorous protobranch *Yoldiella* spp. that is typical of Arctic area (Holte and Gulliksen, 1998; Włodarska-Kowalczyk and Pearson, 2004; Carroll et al., 2008; Cochrane et al., 2009; Åström et al., 2016). Such species are known to inhabit oxygen reduced environments and organic-enriched sediments (Włodarska-Kowalczyk et al., 2004; Sweetman et al., 2014; Smith et al., 2015). We also observe several individuals belonging to Nemertea which are predators that can exert a significant impact on the populations of their preferred prey organisms (McDermott and Roe, 1985; McDermott, 1988; Nordhausen, 1988; Rowell and Woo, 1990; Thiel and Reise, 1993; Kruse and Buhs, 2000). This group is indicated by previous authors (e.g., Holte and Gulliksen, 1998; Cochrane et al., 2009, Carroll et al., 2008; Riedel et al., 2012, among others) to populate eutrophic benthic ecosystems of the Barents Sea as well as the Mediterranean Sea. Summarising, the taxonomic composition suggests that eutrophic condition prevail in the inner part of the Kveithola Trough.

Finally, separate considerations must be made for the site 07. This site located along the Knølegga fault zone (Northern channel 150 m water depth) (see Fig. 1) differs from all the others for the higher macrofaunal biomass (79.6 g ww m<sup>-2</sup>), density (1287 ind.m<sup>-2</sup>) and organic matter quantity (Tab. 2). We related such characteristics to the dominance of fewer, specialized species as *M. sarsi* and *L. gracilis* that are known to inhabit oxygen reduced environments as well as cold seeps (Włodarska-Kowalczyk and Pearson, 2004; Carroll et al., 2008; Cochrane et al., 2009; Smith et al., 2015; Aström et al., 2016). We therefore hypothesize a relation of the faunal assemblage observed at the site 07 with possible local methane emissions associated to the Knølegga fault zone in analogy with methane seepage observed in the neighbouring Storfjorden Trough (Mau et al., 2017).



## 5. Conclusions

For the first time, we have documented the Arctic benthic macrofaunal communities in Kveithola Trough Located in the NW Barents Sea. Three main areas can be described (the outer, the inner area and shallowest 07) characterized by different morphological, sedimentological and oceanographical patterns that are reflected in the faunal community and organic matter distribution.

The Kveithola Trough is dominated by a detritivorous community (small subsurface-feeding polychaeta *M. sarsi*, the surface-feeding polychaeta *L. gracilis*, the subsurface lamellibranch bivalve *M. cf. pigmea*, the subsurface protobranch bivalve genus *Yoldiella*), and predators belonging to Nemertea. These taxa indicate the presence of a low oxygen bottom water possibly linked to a cold seep system; they are also responsible for the organic matter mineralization due to bioturbation activity. At the Kveithola Trough the high primary production and the high nutrient rates that reach the benthic community, suggest a close relationship between the pelagic and benthic compartments.

The site 07, located along the Knølegga fault zone, is associated with the methane seepage in the neighbouring Strofjorden Trough. This lead us to hypothesize a possible selective effect on macrofaunal organisms adapted to such extreme environments, due to the high BPC, high productivity and the input of high nutritional quality organic matter to the seafloor (i.e. BAC and Chl-a) which are related to the cold BSW and AW. These drivers stimulate the presence of polychaetas *M. sarsi*, *L. gracilis* and the bivalve *M.cf pigmea*, which typically also occur in oxygen reduced environments and cold seeps.

Overall, our findings suggest that peculiar environmental conditions such as those of the inner Kveithola Trough are key drivers shaping the macrofaunal diversity and assemblage composition.

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## References

- Ambrose, W. G., and Renaud, P. E. (1995). Benthic response to water column productivity patterns: evidence for benthic-pelagic coupling in the Northeast Water Polynya. *Journal of Geophysical Research*. <https://doi.org/10.1029/94JC01982>
- Åström, E. K. L., Carroll, M. L., Ambrose, W. G., and Carroll, J. (2016). Arctic cold seeps in marine methane hydrate environments: Impacts on shelf macrobenthic community structure offshore Svalbard. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps11773>
- Bergh, S. G., and Grogan, P. (2003). Tertiary structure of the Sørkapp-Hornsund Region, South Spitsbergen, and implications for the offshore southern extension of the fold-thrust Belt. *Norsk Geologisk Tidsskrift*.
- Birchough, S. N. R., Parker, R. E., McManus, E., and Barry, J. (2012). Combining bioturbation and redox metrics: Potential tools for assessing seabed function. *Ecological Indicators*. <https://doi.org/10.1016/j.ecolind.2011.03.015>
- Bjarnadóttir, L. R., Rütther, D. C., Winsborrow, M. C. M., and Andreassen, K. (2013). Grounding-line dynamics during the last deglaciation of Kveithola, W Barents Sea, as revealed by seabed geomorphology and shallow seismic stratigraphy. *Boreas*. <https://doi.org/10.1111/j.1502-3885.2012.00273.x>
- Bligh, E. G., and Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Biochemistry and Cell Biology*. <https://doi.org/10.1139/o59-099>
- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*. <https://doi.org/10.1021/cr050347q>
- Caricchi, C., Lucchi, R. G., Sagnotti, L., Macrì, P., Morigi, C., Melis, R., ... Hanebuth, T. J. J. (2018). Paleomagnetism and rock magnetism from sediments along a continental shelf-to-slope transect in the NW Barents Sea: Implications for geomagnetic and depositional changes during the past 15 thousand years. *Global and Planetary Change*. <https://doi.org/10.1016/j.gloplacha.2017.11.007>
- Carmack, E., and Wassmann, P. (2006a). Food webs and physical-biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography*. <https://doi.org/10.1016/j.pocean.2006.10.004>
- Carmack, E., and Wassmann, P. (2006b). Food webs and physical-biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography*. <https://doi.org/10.1016/j.pocean.2006.10.004>

- Carroll, M. L., Denisenko, S. G., Renaud, P. E., and Ambrose, W. G. (2008). Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing. *Deep-Sea Research Part II: Topical Studies in Oceanography*. <https://doi.org/10.1016/j.dsr2.2008.05.022>
- Christensen, B., Vedel, A., and Kristensen, E. (2000). Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps192203>
- Clarke, K. R., and Gorley, R. N. (2006). PRIMER v6: User Manual/Tutorial. *PRIMER-E, Plymouth UK*. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Cochrane, S. K. J., Denisenko, S. G., Renaud, P. E., Emblow, C. S., Ambrose, W. G., Ellingsen, I. H., and Skardhamar, J. (2009). Benthic macrofauna and productivity regimes in the Barents Sea - Ecological implications in a changing Arctic. *Journal of Sea Research*. <https://doi.org/10.1016/j.seares.2009.01.003>
- Cusson, M., and Bourget, E. (2005). Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps297001>
- Danovaro, R. (2010). *Methods for the Study of Deep-Sea Sediments, Their Functioning and Biodiversity*. BocaRaton, FL: CRC Press. <https://doi.org/10.1201/9781439811382>
- Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R. (2002). Assessing the trophic state and eutrophication of coastal marine systems: A new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin*. [https://doi.org/10.1016/S0025-326X\(01\)00302-2](https://doi.org/10.1016/S0025-326X(01)00302-2)
- Dermott, R. M., and Paterson, C. G. (1974). Determining dry weight and percentage dry matter of chironomid larvae. *Canadian Journal of Zoology*. <https://doi.org/10.1139/z74-165>
- Diaz, R. J., and Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*. <https://doi.org/10.1126/science.1156401>
- Fabiano, M., Danovaro, R., and Fraschetti, S. (1995). A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (northwestern Mediterranean). *Continental Shelf Research*. [https://doi.org/10.1016/0278-4343\(94\)00088-5](https://doi.org/10.1016/0278-4343(94)00088-5)
- Fauchald, K., and Jumars, P. a. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology. An Annual Review*. <https://doi.org/10.12691/marine-1-1-6>
- Gabrielsen, R. H., Faerseth, R. B., Jensen, L. N., Kalheim, J. E., and Riis, F. (1990). Structural Elements of the Norwegian Continental Shelf Part I: The Barents Sea Region. *Norwegian Petroleum Directorate Bulletin*.

- Gerchakov, S. M., and Hatcher, P. G. (1972). Improved technique for analysis of carbohydrates in sediments. *Limnology and Oceanography*. <https://doi.org/10.4319/lo.1972.17.6.0938>
- Gooday, A. J., Jorissen, F., Levin, L. A., Middelburg, J. J., Naqvi, S. W. A., Rabalais, N. N., ... & Zhang, J. (2009). Historical records of coastal eutrophication-induced hypoxia. *Biogeosciences*, 6(8), 1707-1745.
- Graf, G., and Rosenberg, R. (1997). Bioresuspension and biodeposition: a review. *Journal of Marine Systems*, 11(3-4), 269-278. [https://doi.org/10.1016/S0924-7963\(96\)00126-1](https://doi.org/10.1016/S0924-7963(96)00126-1)
- Gutierrez, D., Gallardo, V. A., Mayor, S., Neira, C., Vasquez, C., Sellanes, J., ... Baltazar, M. (2000). Effects of dissolved oxygen and fresh organic matter on the bioturbation potential of macrofauna in sublittoral sediments off Central Chile during the 1997/1998 El Nino. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps202081>
- Hammer, B., Hansen, L. B., and Nørskov, J. K. (1999). Improved adsorption energetics within density-functional theory using revised Perdew-Burke-Ernzerhof functionals. *Physical Review B*. <https://doi.org/10.1103/PhysRevB.59.7413>
- Hartree, E. F. (1972). Determination of protein: A modification of the lowry method that gives a linear photometric response. *Analytical Biochemistry*. [https://doi.org/10.1016/0003-2697\(72\)90094-2](https://doi.org/10.1016/0003-2697(72)90094-2)
- Holte, B., and Gulliksen, B. (1998). Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar Biology*. <https://doi.org/10.1007/s003000050262>
- Hyland, J., Balthis, L., Karakassis, I., Magni, P., Petrov, A., Shine, J., ... Warwick, R. (2005). Organic carbon content of sediments as an indicator of stress in the marine benthos. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps295091>
- Kendall, M. A. (1996). Are Arctic soft-sediment macrobenthic communities impoverished? *Polar Biology*. <https://doi.org/10.1007/BF02390421>
- Kruse, I., and Buhs, F. (2000). Preying at the edge of the sea: The nemertine *Tetrastemma melanocephalum* and its amphipod prey on high intertidal sandflats. *Hydrobiologia*. <https://doi.org/10.1023/A:1003955523468>
- Lantzsch, H., Hanebuth, T. J. J., Horry, J., Grave, M., Rebesco, M., and Schwenk, T. (2017). Deglacial to Holocene history of ice-sheet retreat and bottom current strength on the western Barents Sea shelf. *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2017.08.016>
- Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*. <https://doi.org/10.1111/j.1751-8369.1991.tb00630.x>
- Lorenzen, C. J., and Jeffrey, S. W. (1980). Determination of chlorophyll in seawater. *Unesco Technical Papers*

*in Marine Science.*

- Magni, P., De Falco, G., Como, S., Casu, D., Floris, A., Petrov, A. N., ... Perilli, A. (2008). Distribution and ecological relevance of fine sediments in organic-enriched lagoons: The case study of the Cabras lagoon (Sardinia, Italy). *Marine Pollution Bulletin*. <https://doi.org/10.1016/j.marpolbul.2007.12.004>
- Marsh, J. B., and Weinstein, D. B. (1966). Simple charring method for determination of lipids. *Journal of Lipid Research*.
- Mau, S., Römer, M., Torres, M. E., Bussmann, I., Pape, T., Damm, E., ... Bohrmann, G. (2017). Widespread methane seepage along the continental margin off Svalbard-from Bjørnøya to Kongsfjorden. *Scientific Reports*. <https://doi.org/10.1038/srep42997>
- Mauna, A. C., Acha, E. M., Lasta, M. L., and Iribarne, O. O. (2011). The influence of a large SW Atlantic shelf-break frontal system on epibenthic community composition, trophic guilds, and diversity. *Journal of Sea Research*. <https://doi.org/10.1016/j.seares.2011.04.014>
- McArdle, B. H., and Anderson, M. J. (2001). Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology*. [https://doi.org/10.1890/0012-9658\(2001\)082\[0290:FMMTCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2)
- McDermott, J J, and Roe, P. (1985). Food, Feeding Behavior and Feeding Ecology of Nemertean. *American Zoologist*. <https://doi.org/10.1093/icb/25.1.113>
- McDermott, John J. (1988). The role of hoplonemertean in the ecology of seagrass communities. *Hydrobiologia*. <https://doi.org/10.1007/BF00027972>
- Mermillod-Blondin, F., François-Carcaillet, F., and Rosenberg, R. (2005). Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: An experimental study. *Journal of Experimental Marine Biology and Ecology*. <https://doi.org/10.1016/j.jembe.2004.09.013>
- Nordhausen, W. (1988). Impact of the nemertean *Lineus viridis* on its polychaete prey on an intertidal sandflat. *Hydrobiologia*. <https://doi.org/10.1007/BF00027976>
- Pedrosa, M. T., Camerlenghi, A., De Mol, B., Urgeles, R., Rebesco, M., and Lucchi, R. G. (2011). Seabed morphology and shallow sedimentary structure of the storfjorden and kveithola trough-mouth fans (north west barents sea). *Marine Geology*. <https://doi.org/10.1016/j.margeo.2011.05.009>
- Peet, R. K. (1974). The Measurement of Species Diversity. *Annual Review of Ecology and Systematics*. <https://doi.org/10.1146/annurev.es.05.110174.001441>
- Pearson T., Rosenberg R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of

the marine environment. *Oceanography and Marine Biology Annual Review*.

Pusceddu, A., Dell'Anno, A., and Fabiano, M. (2000). Organic matter composition in coastal sediments at Terra Nova Bay (Ross Sea) during summer 1995. *Polar Biology*.

<https://doi.org/10.1007/s003000050446>

Pusceddu, A., Sarà, G., Armeni, M., Fabiano, M., and Mazzola, A. (1999). Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea). *Hydrobiologia*.

<https://doi.org/10.1023/A:1003690313842>

Pusceddu, Antonio, Bianchelli, S., Canals, M., Sanchez-Vidal, A., Durrieu De Madron, X., Heussner, S., ... Danovaro, R. (2010). Organic matter in sediments of canyons and open slopes of the Portuguese, Catalan, Southern Adriatic and Cretan Sea margins. *Deep-Sea Research Part I: Oceanographic Research Papers*.

<https://doi.org/10.1016/j.dsr.2009.11.008>

Pusceddu, Antonio, Bianchelli, S., Gambi, C., and Danovaro, R. (2011). Assessment of benthic trophic status of marine coastal ecosystems: Significance of meiofaunal rare taxa. *Estuarine, Coastal and Shelf Science*.

<https://doi.org/10.1016/j.ecss.2011.05.012>

Pusceddu, Antonio, Dell'Anno, A., Fabiano, M., and Danovaro, R. (2009). Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Marine Ecology Progress Series*.

<https://doi.org/10.3354/meps07735>

Queirós, A. M., Birchenough, S. N. R., Bremner, J., Godbold, J. A., Parker, R. E., Romero-Ramirez, A., ... Widdicombe, S. (2013). A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution*.

<https://doi.org/10.1002/ece3.769>

Rebesco, M., Liu, Y., Camerlenghi, A., Winsborrow, M., Laberg, J. S., Caburlotto, A., ... Tomini, I. (2011). Deglaciation of the western margin of the Barents Sea Ice Sheet - A swath bathymetric and sub-bottom seismic study from the Kveithola Trough. *Marine Geology*.

<https://doi.org/10.1016/j.margeo.2010.10.018>

Rebesco, M., Özmaral, A., Urgeles, R., Accettella, D., Lucchi, R. G., Rütther, D., ... Hanebuth, T. J. J. (2016). Evolution of a high-latitude sediment drift inside a glacially-carved trough based on high-resolution seismic stratigraphy (Kveithola, NW Barents Sea). *Quaternary Science Reviews*.

<https://doi.org/10.1016/j.quascirev.2016.02.007>

Riedel, B., Zuschin, M., and Stachowitsch, M. (2012). Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: A realistic scenario. *Marine Ecology Progress Series*.

<https://doi.org/10.3354/meps09724>

- Rowell, T. W., and Woo, P. (1990). Predation by the Nemertean Worm *Cerebratulus-Lacteus* Verrill on the Soft-Shell Clam *Mya-Arenaria* Linnaeus 1758 and Its Apparent Role in the Destruction of a Clam Flat. *Journal of Shellfish Research*.
- Schulte-Rüther, M., Mainz, V., Fink, G. R., Herpertz-Dahlmann, B., and Konrad, K. (2012). Theory of mind and the brain in anorexia nervosa: Relation to treatment outcome. *Journal of the American Academy of Child and Adolescent Psychiatry*. <https://doi.org/10.1016/j.jaac.2012.06.007>
- Shannon, C. E., and Weaver, W. (1963). The mathematical theory of communication. *The University of Illinois Press*. <https://doi.org/10.1145/584091.584093>
- Ślubowska-Woldengen, M., Koç, N., Rasmussen, T. L., Klitgaard-Kristensen, D., Hald, M., and Jennings, A. E. (2008). Time-slice reconstructions of ocean circulation changes on the continental shelf in the Nordic and Barents Seas during the last 16,000 cal yr BP. *Quaternary Science Reviews*, 27(15-16), 1476-1492. <https://doi.org/10.1016/j.quascirev.2008.04.015>
- Smith, C.R., Glover, A.G., Treude, T., Higgs, N.D., Amon, D.J. (2015). Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*. <https://doi.org/10.1146/annurev-marine-010213-135144>
- Snelgrove, P. V. R., and Butman, C. A. (1994). Animal Sediment Relationships Revisited - Cause Versus Effect. *Oceanography and Marine Biology*.
- Solan, M., Cardinale, B. J., Downing, A. L., Engelhardt, K. A. M., Ruesink, J. L., and Srivastava, D. S. (2004). Extinction and ecosystem function in the marine benthos. *Science*. <https://doi.org/10.1126/science.1103960>
- Sweetman, A.K., Norling, K., Gunderstad, C., Haugland, B.T., Dale, T. (2014) Benthic ecosystem functioning beneath fish farms in different hydrodynamic environments. *Limnology and Oceanography*. <https://doi.org/10.4319/lo.2014.59.4.1139>
- Tauber, P. (1879) *Annulata Danica*. En kritisk revision af de in Danmark fundne Annulata Chaetognatha, Gephyrea, Balanoglossi, Discophoreae, Oligochaeta, Gymnocopa og Polychaeta. Copenhagen: Reitzel.
- Thiel, M., and Reise, K. (1993). Interaction of nemertines and their prey on tidal flats. *Netherlands Journal of Sea Research*. [https://doi.org/10.1016/0077-7579\(93\)90006-E](https://doi.org/10.1016/0077-7579(93)90006-E)
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*. <http://www.nature.com/nature/journal/v427/n6970/full/nature02121.html#close>
- Warwick, R. M., and Clarke, K. R. (1993). Increased variability as a symptom of stress in marine

communities. *Journal of Experimental Marine Biology and Ecology*. [https://doi.org/10.1016/0022-0981\(93\)90098-9](https://doi.org/10.1016/0022-0981(93)90098-9)

Warwick, R. M., and Clarke, K. R. (1995). New “biodiversity” measures reveal a decrease in taxonomic distinctness with increasing stress.” *Marine Ecology Progress Series*.  
<https://doi.org/10.3354/meps129301>

Wassmann, P. (1991). Dynamics of primary production and sedimentation in shallow fjords and polls of western Norway. *Oceanography and Marine Biology*.

Wassmann, Paul, Andreassen, I., Reigstad, M., and Slagstad, D. (1996). Pelagic-Benthic Coupling in the Nordic Seas: The Role of Episodic Events. *Marine Ecology*. <https://doi.org/10.1111/j.1439-0485.1996.tb00520.x>

Welsh, D. T. (2003). It’s a dirty job but someone has to do it: The role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chemistry and Ecology*.  
<https://doi.org/10.1080/0275754031000155474>

Wetzel, A., and Uchman, A. (2012). Hemipelagic and pelagic basin plains. In *Developments in Sedimentology* . Elsevier. <https://doi.org/10.1016/B978-0-444-53813-0.00022-8>

Wlodarska-Kowalczyk, M., and Pearson, T. H. (2004). Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology*.  
<https://doi.org/10.1007/s00300-003-0568-y>



## Chapter 4

### **Abstract**

#### **Image analyses for the assessment of megafaunal community along the Kveithola Trough (NW Barents Sea)**

Megabenthic community plays an important role in benthic ecosystems and contributes significantly to benthic biomass in the Arctic. The distribution is mostly studied using towed cameras. We compare the megafauna from three sites located in the Kveithola Trough (NW Barents Sea): one site in the outer part, one in the Minor Drift and one in the Main Drift. We observed significant differences in their species composition, particularly the Minor Drift area, where the occurrence of cold seep was demonstrated. We conclude that the principal driver is the bottom substrate that in the outside is relatively homogeneous, dominated by soft bottom substrate and organisms, while the site 21 is characterized by methane emissions and consequently heterogeneous environment with carbonate structure, microbial mats and chemosynthetic worm tufts. Moreover, various epifaunal taxa including sponges, hard-bottom anemones, bryozoans and commercial species are distributed on or near the carbonate structures, we hypothesize that they provide hard substrate to colonize, protection and high food supply.

We suggest that methane emissions provide an alternative food source for heterotrophic consumers and carbonate outcrops, providing 3D-structure and hard substrate at an otherwise relatively featureless and homogenous soft-bottom seafloor. Therefore, the study of megabenthic communities, which could be threatened by climate-change-induced ecological disturbances, may be important to understand the response of a changing Barents Sea.

## 1. Introduction

The knowledge of Arctic benthic ecosystems, their functioning and drivers has strongly increased in the past two decades (Piepenburg, 2005), especially for the regions off Svalbard and the northern Barents Sea (Piepenburg et al., 2011). Most biological study have focused on the structure of benthic communities in the west coast of Svalbard (Blacker 1957, 1965), in the western fjords (Włodarska-Kowalczyk and Pearson, 2004; Renaud et al., 2007) and across the shelf break in Fram Strait (Weslawski et al., 2003; Włodarska-Kowalczyk et al. 2004). Also, many studies have been concentrated on the HAUSGARTEN observatory, located in the Fram Strait (Soltwedel et al. 2005, 2009; Hoste et al., 2007; Bergmann et al., 2009, 2011a; van Oevelen et al., 2011). Other benthic studies have concentrated on the Barents Sea (Carroll et al., 2008; Cochrane et al., 2009) or on megafaunal community structure at methane seeps (Tunnicliffe et al., 2003; Sen et al., 2018). In comparison, the area of Svalbard, as the Kveithola Trough have been much less investigated. Megafauna is defined as the size group of organisms  $\geq 1$  cm (Grassle et al., 1975; Rex, 1981) that constitute seafloor communities and are critical components of the marine ecosystem. Megabenthic organisms often contribute considerably to the total benthic biomass (Lampitt et al., 1986) and to remineralization processes (Piepenburg et al., 1995), and have a strong impact on the physical and biogeochemical micro-scale environment (e.g., Hüttel and Gust, 1992; Guillén et al., 2008). For example, they provide three-dimensional habitat which can be protective or supportive to other organisms (Soltwedel and Vopel, 2001; Hasemann, 2006; Queric and Soltwedel, 2007). Furthermore, they are food for other organisms, and can play important roles as ecosystem engineers, functioning to redistribute and remineralise carbon (Renaud et al., 2007) Therefore, the composition, diversity, abundance and biomass of megabenthic communities have often been used as sensitive indicators of natural decadal-scale environmental change (e.g., Reise and Schubert, 1987; Kroncke, 2001; Groger and Rumohr, 2006) and of the ecological impacts of human activities like fishing and eutrophication (e.g., Pearson and Rosenberg, 1978; Underwood, 1996; Pearson and Mannvik, 1998; Kaiser et al., 2006). Despite their importance, knowledge about arctic megabenthic assemblage is scarce because of limitations in adequate quantitative sampling gear available and the effort required for analyses. Traditionally, bottom trawls have been employed to sample megafauna (e.g., Frauenheim et al., 1989; van Leeuwen, 1994), also in polar waters (Piepenburg et al., 1996). However, they have low and variable catch efficiencies for different biota (e.g., Lindeboom and de Groot 1998; Reiss et al., 2006). Generally, trawls are invasive, destructive and provide limited data about habitat characteristics. In recent years, towed images by underwater

camera systems have become the principal method to investigate megafauna abundance and distribution (e.g., Hecker, 1994; Bluhm et al., 2005; Jones et al., 2007a; Ruhl 2007). They enable us to study the seafloor at the scale of kilometres without causing disturbance or altering habitat structure (Solan et al., 2003), which is particularly important as megafauna can be characterized by a rare or aggregated occurrence (Gutt and Starman, 2003; Thistle, 2003; Soltwedel et al., 2009). Camera footage still allows us to discern spatial patterns at a high resolution and shows the organisms in situ, providing information about habitat features such as sediment properties, geological and biogenic structures, tracks, detrital aggregations or to infer biotic interactions.

Cold seeps are environments where emissions of methane, sulphide, or other reduced chemicals occur at the seafloor and contain a variety of geomorphic and biological features that are sources of heterogeneity (Cordes et al., 2010). They are commonly associated with seafloor features like pockmarks, craters, carbonate mounds, or underwater pingos, and provide a highly diverse suite of potential habitats for both endemic seep organisms and more opportunistic colonists (Hovland and Svensen, 2006; Zeppilli et al., 2012). Cold seeps, in general, exhibit a wide range of seep fauna, as chemo-obligate species (Cordes et al., 2010; Levin et al., 2016), and usually support faunal communities with high abundances and biomass but low diversity compared to surrounding non-seep habitats (Levin, 2005; Tarasov et al., 2005). However, several sites of cold seep have been discovered in the northwestern Barents Sea (Sahling et al., 2014; Åström et al., 2016; Lucchi et al., 2016; Andreassen et al., 2017). Arctic seep research has expanded recently (Gebruk et al., 2003; Lösekann et al., 2008; Åström et al., 2016, 2017b, Sen et al., 2018), but many gaps still remain. In particular, the Kveithola trough, where recently gas seep activity was recognized (Lucchi et al., 2016; Mau et al., 2017), has been less investigated.

For all these reasons, the aims of this study are to characterize the abundance and distribution of the megafaunal community along the shallow water transect of Kveithola Trough (NW Barents Sea), and to compare different habitat types, site 21 where the occurrence of cold seep was demonstrated, and site 02 (Grounding-Zone Wedges) and 06 (Minor Drift), which will be called “outside”. Our results serve as a first step towards addressing some of the existing gaps in our knowledge about Kveithola and its associated community.

## 2. Materials and methods

### 2.1. Kveithola Through

The Kveithola Trough (Fig. 1) is an abrupt and narrow glacial sedimentary system located in the NW Barents Sea. The trough extends in E-W direction over 100 km, less than 13 km wide and shows an average water depth of 300-350 m along its axis (Schulte-Rüther et al., 2012). The seafloor in the Kveithola Trough is characterized by a series of E–W trending mega-scale glacial lineations that record a fast-flowing ice stream draining the Barents Sea ice sheets during the Last Glacial Maximum. Glacial lineation are overprinted by transverse Grounding-Zone Wedges (GZW) generated during episodic retreat of the last glacial ice sheet, giving rise to a staircase bathymetric axial profile of the trough (Rebesco et al., 2011; Bjarnadóttir et al., 2013). The Kveithola Trough is intersected with N-S direction by the Hornsund and Knølegga fault systems related to the phases of crustal extension associated with the opening of the Norwegian - Greenland Sea since the Cretaceous (Gabrielsen et al., 1990; Bergh and Grogan, 2003). The innermost Knølegga fault is responsible for an elongated bathymetric depression indicated by Rebesco et al., (2016) as the “northern channel”. The inner area of the Kveithola Trough hosts a sediment drift (the Kveithola Drift of Rebesco et al., 2016) that is associated to a field of pockmarks (Bjarnadóttir et al., 2013). This drift has a very articulated morphology (Main and Minor drift, Fig.1, chapter 3) and it is inferred to have been formed by sediments supplied by dense bottom currents reaching the trough via a large channel that is connected to the innermost Kveithola Trough from the northern area (Thomas et al., 2004; Bjarnadóttir et al., 2013). The sedimentation and particle distribution in the Kveithola Trough are mainly controlled by the hydrodynamic pattern. The outer part of the trough is directly influenced by the North Atlantic Current (NAC, warm and saline, Slubowska-Woldengen et al., 2008); the NAC sweeps the outer seafloor and remove the fine sediment fraction leaving a coarse lag of pebbly sands (Caricchi et al., 2018). Instead, the inner part which comprises the Main Drift and the Minor Drift, located between the Hornsund and Knølegga fracture zones is subject to continuous fine-grained sediment deposition due to cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow. These dense brine waters generate bottom currents that shape the Kveithola Drift moat (Rebesco et al., 2016; Lantzsch et al., 2017). Here, the oceanographic pattern, evidences a progressive vertical stratification of the water column from West to East (i.e. from the outer to the inner area of the trough), in which water density increases with depth. Strong water stratification and confined depositional condition of the Drift is

responsible for limited dissolved gasses vertical exchange leading to oxygen reduction conditions at the sea bottom. At the same time, the organic C load, considered as BPC concentration, is comparable to values typically encountered in eutrophic systems varying from 4.5 mg/g to 6.9 mg/g (Dell'Anno et al., 2002). Therefore, preliminary faunal and sedimentological data allow to describe sediments of the Kveithola Drift as an apparently stagnant environment strongly affected by low-oxygen concentration, possibly chemosynthetic conditions.

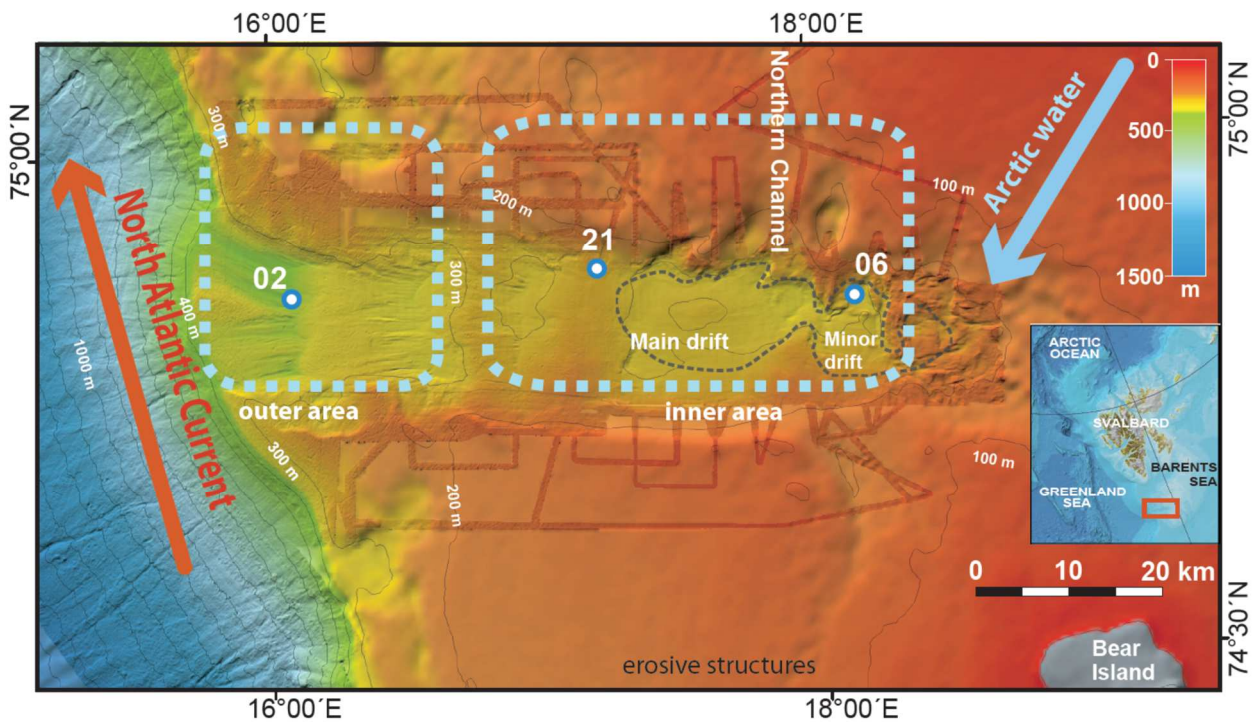


Fig. 1 Study area and location of the studied sites. The arrows indicate surface currents.

## 2.2 Images sampling

The seafloor imagery was collected in 2016 during Eurofleets 2- BURSTER cruise, onboard the German icebreaker RV Polarstern, using the Ocean Floor Observation System (OFOS).

The OFOS system available onboard consisted of a metal frame equipped with a fixed downwards looking Canon camera (EOS 5D Mark III, 22 Mpixel), a HD digital videocamera (Sony FCB-H11), an underwater Flash (SeaandSea YS-250PRO), four LED lights (DeepSea PowerandLight, SeaLite Sphere 3150) and three laser-pointer (Oktopus) at a distance of 50 cm to each others. The images via the digital still camera, automatically triggered every 30 seconds, were collected. The system was maintained approximately 1.5 m above the seafloor. One transects was taken over each of the sites (02, 06 and 21). Navigation files from transects were inadequate for georeferencing purposes, and therefore the images associated with these transects were only used qualitatively to ascertain species' presence or absence by ImageJ (National Institute of Health, USA).

Visible fauna was identified to the lowest possible taxonomic division and each individual was marked manually in imageJ (Tab. 1 and Fig. 2). Though single individuals were visible of the small solitary Caryophyllia coral, it was not always feasible to mark every individual of this taxon in the images either due to aggregations containing large numbers of individuals. Another exception to the standard methodology of marking every visible taxon was a type of encrusting animal, possibly a bryozoan, porifera, etc.. All morphotypes of this organism were seen but given the difficulty in identifying them or even visualizing them sufficiently, these animals were marked in the image transects as "unknown".

### **2.3. Data analysis**

Faunal biodiversity was estimated using different diversity indices: species richness (S) measured as the number of species, species diversity ( $H \log_e$ ) measured by the Shannon–Wiener (H) information function and species evenness (J) measured using the Pielou (1975) index. All indices were calculated using the statistical PAST software (Paleontological Statistics; Version 3.12'; Hammer et al., 2009). To test differences in community composition among transects one-way ANOSIM was applied. SIMPER analysis was applied to assess the dissimilarity percentage between the sites and to identify which species contributed most to the observed dissimilarities between sites. The similarities of different images and transects were depicted in an ordination biplot (MDS, non-metric multidimensional scaling). The analysis were performed using the statistical PAST software (Paleontological Statistics; Version 3.12'; Hammer et al., 2009).

### 3. Results

Phylum and taxon	02	06	21
<b>Nonanamals</b>			
Bacterial mats	249(0.01)	431.37(0.01)	82682(3.5)
Carbonates	1798722(86.4)	311750(13.42)	8449979(361.1)
<b>Porifera</b>			
Thenea sp.	0(0)	0(0)	559(0.02)
Unknown species 1 (white)	863(0.04)	0(0)	182(0.007)
Unknown species 2 (opaque)	434(0.02)	379(0.01)	0(0)
Unknown species 3 (yellow)	0(0)	761(0.03)	0(0)
Unknown species 4 (encrusting,blue)	109(0.005)	0(0)	0(0)
Unknown species 5 (encrusting, green)	537(0.02)	0(0)	0(0)
Unknown species 6 (encrusting,opaque)	2817(0.13)	610(0.02)	9426(0.4)
Unknown species 7 (encrusting, orange)	489(0.02)	0(0)	0(0)
Unknown species 8 (encrusting, white)	254(0.01)	0(0)	14347(0.6)
Unknown species 9 (encrusting,yellow)	9794(0.47)	0(0)	62510(2.6)
<b>Bryozoa</b>			
Retepora sp.	48(0.002)	0(0)	672(0.02)
Securiflustra securifrons	0(0)	3098(0.13)	732(0.03)
Unknown bryozoan	511(0.02)	19754(0.8)	20691(0.8)
<b>Cnidaria</b>			
Bolocera sp.	0(0)	5(0.0002)	128(0.05)
Caryophyllia sp.	21(0.001)	0(0)	22164(0.9)
Ceranthius sp.	30(0.001)	0(0)	1(4.2E-05)
Ceranthius sp. (red)	1(4.8E-05)	17(0.0007)	0(0)
Gersemia sp. (white)	1(4.8E-05)	2(8.6E-05)	2(8.5E-05)
Hormathia sp.	5(0.00024)	1(2.0E-05)	57(0.002)
Juvenile anemones	0(0)	1(4.3E-05)	0(0)
Liponema multicornis	0(0)	1(4.3E-05)	0(0)
Unknown anemones	0(0)	1(4.3E-05)	0(0)
Unknown medusa	3(0.0001)	2(8.6E-05)	0(0)
<b>Anellida</b>			
Siboglinids	3973(0.19)	0(0)	240626(10.2)
Unknown species	3(0.0001)	2(8.6E-05)	0(0)
<b>Arthropoda</b>			
Euphasiacea (krill)	Few	Few	A lot
Pandalus borealis (northern shrimp)	Few	Few	A lot
Pycnogonids	2(9.6E-05)	18(0.0007)	6(0.0002)
<b>Mollusca</b>			
Gastropods and hermit crabs	4(0.0002)	19(0.0008)	4(0.0001)
Unknown scaphopod	0(0)	1(4.3E-05)	0(0)
Unknown clam	0(0)	4(0.0001)	0(0)
<b>Echinodermata</b>			
Icasterias planopla	0(0)	2(8.6E-05)	1(4.2E-05)
Molpadia borealis	0(0)	1(4.3E-05)	0(0)
Ophiuroids	A lot	A lot	A lot
Sea urchin	0(0)	0(0)	1(4.7E-05)
Unknown crinoids	3(0.0001)	(0)	0(0)
Unknown starfish	0(0)	1(2.0E-05)	1(4.2E-05)
<b>Chordata</b>			
Anarhichas minor (spotted wolffish)	0(0)	0(0)	1(4.2E-05)
Gadus morhua (Atlantic cod)	5(0.0002)	0(0)	1(4.2E-05)
Hippoglossoides platessoides (A. plaice)	2(9.6E-05)	1(4.3E-05)	1(4.2E-05)
Leptagonus sp. (snake blenny)	0(0)	0(0)	1(4.2E-05)
Rockfish	0(0)	0(0)	6(0.0002)
Possible tunicates	41(0.002)	243(0.01)	1093(0.04)



*Tab. 1. Total numbers of individuals, aggregations and densities of fauna seen, listed by transect. For each taxon, the first number represents the number of individuals, or the number of aggregations in the case of fauna where counting and marking each individual was not possible. The number in parentheses refers to the density, calculated based on the area of each mosaic or transect.*

On the seafloor of the site 02 there were a lot of rounded holes, which could be burrows and holes (5-10 cm) half-rimmed by remobilized sediments possibly deriving from organisms excavation. There were also diffuse crusts, Ice Rafted Debris (IRD) pebbles, and few small carbonates (Fig. 2). The seafloor of the site 06 contained many holes of the same types described at site 02. The large number of holes gives a general hummocky/mounded aspect to the seafloor, with presence of abundant IRD and many traces of locomotion (Fig. 3). The seafloor of the site 21 was characterized mostly by abundant large holes, bacterial mats and carbonates (Fig. 4). These bacterial mats could confirm the presence of reduced chemical in the sediment or seepage activity. Fewer bacterial mats were seen on sites 02 and 06 in comparison to the site 21 (Tab. 1). For hard substrates, most of them could be methanogenic carbonates indicative of long-term gas seepage, especially in the site 21. Therefore, in the sites 02 and 06, some of the hard features could possibly be drop stones or other substrates not formed as a result of seepage activity.

A total of 43 taxa were identified and marked in the image transect (Tab. 1). In the site 21, the community was composed by hard bottom living organisms as Porifera, Bryozoa, Cnidaria and Echinodermata, which represent the most abundant taxon. Tufts of chemosymbiotic Siboglinid worms, were also seen at this site. Pycnogonids were often seen among these tufts. Together with Siboglinid, the most numerous taxa were *Hormathia* and *Caryophyllia* corals, *Thenea* sponges and ophiuroids. Moreover, among the various taxa, several hold economic value such as Atlantic cod (*Gadus morhua*), northern shrimp (*Pandalus borealis*) and American plaice (*Hippoglossoides platessoides*).

Instead, in the sites 02 and 06, the most abundant taxa were represented by soft bottom organisms, sporadically distributed like as *Cerianthus* corals, the pom pom anemone (*Liponema multicornis*), unknown encrusting sponges, ophiuroids which cover the seafloor. Siboglinid tufts and hard-substrate were nonetheless observed at both these sites as well, however, they were present in much lower numbers, particularly at Site 02.



Fig. 2. Examples of images labelled of site 21



Fig. 3 Site 2: The seafloor presents diffuse burrows in the form of small rounded holes and holes half-rimmed by remobilized sediments possibly deriving from organisms excavation. The seafloor presents also less crusts, Ice Rafted Debris (IRD) pebbles and small carbonates.

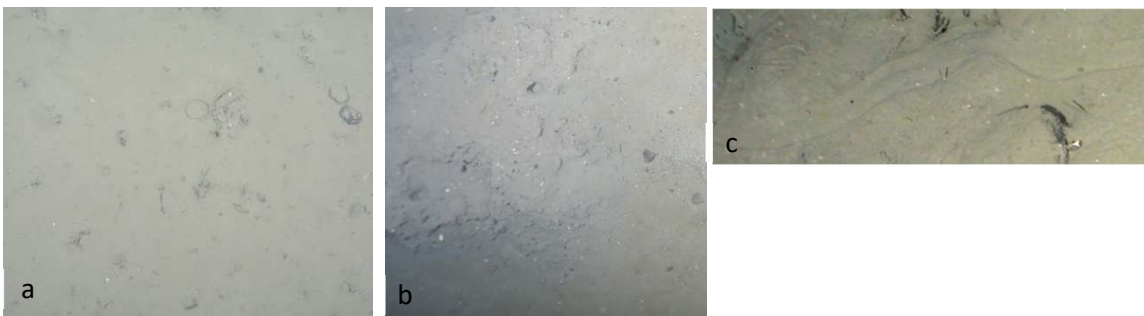
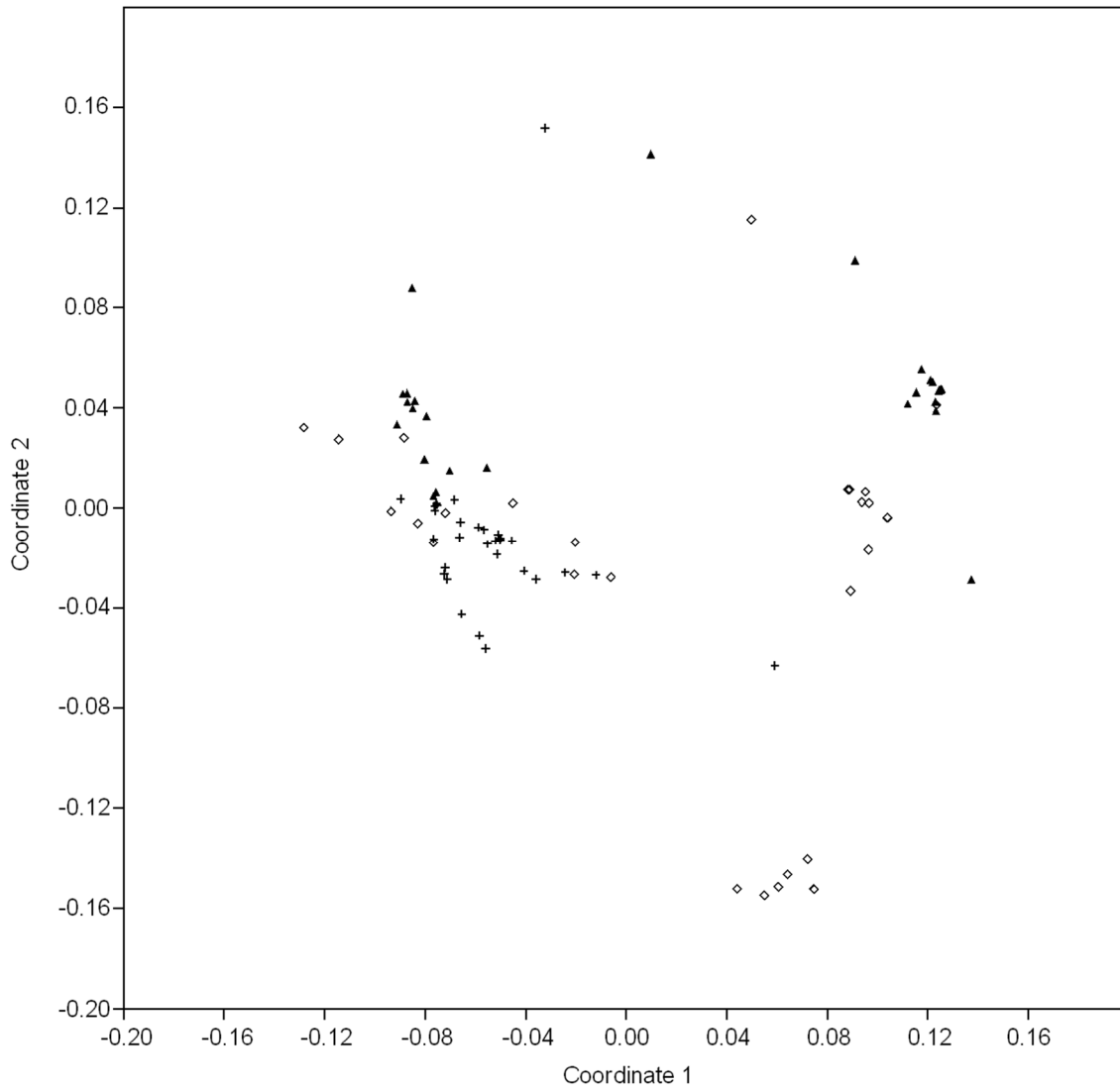


Fig. 4 Site 6: The seafloor contained many holes of the same types described at site 02. The large number of holes gives a general hummocky/mounded aspect to the seafloor (a), with presence of abundant IRD (b) and many traces of locomotion (c).

ANOSIM analysis confirmed that there was a clear difference between transects (21 Vs 02 and 06) ( $p < 0.001$ ). The SIMPER analysis of megafaunal taxa identified from the seafloor images demonstrate that average dissimilarity between the site 21 and the sites 02 and 06 was more than 90%, where bacterial mats and bryozoan organisms represented the largest dissimilarities. These differences were also reflected in the grouping of the nMDS plot (Fig. 5).

Fig. 5 Non-metric multidimensional scaling plot based on Bray-Curtis similarities of faunal abundances for the three transect. The red crosses represent the site 06, the rhombus green the site 02 and yellow triangles the site 21. A stress value of 0.17 indicates a good two-dimensional representation of the data.



## 4. Discussion

The inventory of the glacial depression Kveithola Trough epibenthic megafauna here presented extends the knowledge on the distribution and composition of the benthos in this area, which never was described. For this study, three transect (<400 m) within a 2.5 km<sup>2</sup> area were examined. As reported by Caridi et al., (2019), important differences in morpho-depositional, hydrographic, grain size and organic matter patterns characterizes these transects. Site 02 was influenced by NAC and has coarse sediment, site 06 was exposed to AW and BSW and has fine sediment. Instead, on site 21, located between sites 02 and 06, carbonate formation and bacterial mats were seen, suggestive of long-term seepage (Berndt et al., 2014, Cremiere et al., 2016, Seabrook et al., 2018).

In fact, recently geophysical and geochemical evidence collected in occasion of two surveys conducted along the north-western Barents Sea margin by Lucchi et al., (2016) and Mau et al., (2017), indicated the presence of a few single methane flares along the northern edge of the Trough. Furthermore, these emitted gases were associated to the vertical migration of thermogenic gas, as reported by Weniger et al., (2019).

So, the trough represents a small area where natural variation allows you to test for how bottom fauna is affected by, or correlates to these different environmental parameters, or, habitat types.

### 4.1. Megafauna community

A total of 43 megafaunal taxa were identified and most of the faunal community were observed at all sites. Despite that, there were few taxa exclusively restricted to the site 21 compared to sites 02 and 06, and vice versa (Tab. 1). At the site 21 the most important species, belonging to the phylum cnidarians, were *Bolocera* sp., *Hormatia* sp. and *Ceranthius* sp., which together with hard-substrate-dwelling animals like sponge or corals, provide a hard substrate to shelter and protection (Astrom et al., 2017b). Interestingly, the exclusive presence of spherical *Thenea* sp. sponge. This species not appeared associate with any seep-specific habitats but, Vacelet and Donadey, (1977), described it into soft sediment, where used fascicles of spicules to anchor itself. The only obligate chemosynthetic faunal taxa found in the present study was siboglinid worms, which hosts microbial endosymbionts known to utilize methane and sulphur sources (Pleijel et al., 2009). In addition, numerous bacterial mats were observed, which between the siboglinid worms constitute the base of local food chain in the seep habitat. Regarding bacteria, Bazzaro et al., (submitted) demonstrated

the presence of high microbial community activity due to AOM linked sulphate flux rates, which ensured high availability of carbon compound (either organic or inorganic, or both) and a good sustenance of benthic community. Therefore, seep environment provides food, substrate to colonize, protection and the benthic faunal community appear to take advantage of and utilize the seep environment and its inherent characteristics. One of the snow crabs, for example, was seen grazing among the bacterial mats and importantly, Sen et al., (2018) reported the first record of such behaviour in snow crabs, since they are not normally associated with cold seeps. Other crabs in the Majidae family have been seen at cold seeps (Martin and Haney, 2005) and are considered to either be grazers of filamentous bacteria or predators of vesicomid clams (Barry et al., 1996). Moreover, the increase of food available due to chemosynthetic source, supported a diverse community of commercial species as Atlantic cod (*Gadus morhua*), northern shrimp (*Pandalus borealis*) and halibut *American place*. *P. borealis* individuals were often present among bacterial mats and around carbonate concretions.

Therefore, it is possible that, despite the cold-seep setting, the entire visible megafaunal at this site consists solely of background benthic species, regardless of whether community members are chemosynthesis based or conventionally heterotrophic.

Meanwhile, outside sites were characterized by soft bottom species, sporadically distributed as anemones *Cerianthus* sp., crustacean “hermit crab” and species belonging to the phylum Echinodermata as crinoid and starfish. At all sites the densities of ophiuroids (we were unable to count) were high and several authors reported similar densities in arctic area (Soltwedel et al., 2009, Meyer et al., 2013; Galkin et al., 2013). Thistle, (2003) considered that one of the possible reasons for the success of echinoderms in polar environments is that many species are highly mobile, which allows them to respond quickly to spatially and seasonally patchy food input. For these reasons, the presence of ophiuroids at the outside site could be related to high productivity of the area and the high amount of organic matter (Caridi et al., 2019). Also, Pycnogonida were present in all transects; they were largely associated with frenulate worms, but the images transect of outside sites contained a high number of these organisms maybe due their capacity to feed on a wide variety of prey, mostly on sessile animals (Dietz et al., 2018).

## 4.2. Methane site

Based on what reported above, it is evident that the seafloor recorded significant changes in megafaunal composition along transect from the outside (02 and 06) to the site 21 ( $p < 0.001$ ). Visible benthic faunal differences between the sites may be attributed either to strong gradients in physical and environmental drivers such as currents, sedimentation, substrate and geochemistry (Levin 2005). In fact, the sites 02 and 06 are relatively homogeneous, dominated by soft bottom substrate. Meanwhile, at the site 21 the presence of seepage that creates a heterogeneous environment and leads to 1) carbonates, which provides a hard substrate for hard-substrate animals (e.g., sponges, anemones). Correspondingly, we observed microbial mats, lying on the seafloor in softer sediments between carbonate outcrops and motile megafauna was frequently observed in association with mats, either adjacent to them or sitting directly within them. 2) local primary production that leads to enhanced food availability and therefore also, new predators. Moreover, habitat complexity, the physical substrate and shelter to avoid predation, are all believed to be important factors in attracting organisms to such structures (Stone et al., 1979; Ashley et al. 2014). Pockmarks from shelves and slopes worldwide are known to attract aggregations of motile megafauna regardless of seepage activity, where local heterogeneity attracts “background” (conventional) fauna even when there is no gas seepage (MacDonald et al., 2010; Zeppilli et al., 2012). Organisms occupying peripheral habitats may also benefit from increased productivity close to the seep because advection from seafloor emissions may influence the amount of particulate organic matter in adjacent areas. Increased vertical mixing can enhance water column productivity, supporting nearby benthos and suspension feeders in the periphery of a seep or vent (Levin et al., 2016). The presence of methane at the site 21, combined with the dissimilarity in all environmental parameters at the three transects, strongly suggests that methane emissions provide an alternative food source for conventional heterotrophic consumers and carbonate outcrops, providing 3D-structure and hard substrate at an otherwise relatively featureless and homogenous soft-bottom seafloor.

Few studies have been conducted at other seep sites around the Arctic area using imagery to characterize megafaunal communities (Astrom et al., 2017). These studies reported the same background fauna and seep-obligate siboglinid, despite the study area vary considerably in term of water depth and Gebruk et al., (2003) and Astrom et al., (2017b), also found higher species richness, biomass and diversity at seep site in comparison to non-seep sites. However, they confirmed that the high diversity at the seep site is not completely unexpected, given the shallow

(less than 400 m) water depth at which it is located. In general, diversity and species richness at cold seeps tend to decrease with increasing water depths (Sibuet and Olu, 1998).

## **5. Conclusions**

The Kveithola Trough is characterized by differences in morpho-depositional, hydrographic, grain size and organic matter patterns and the presence of cold seep activity at drift area is demonstrated. Our faunal results underline these differences, particularly active methane seepage strongly influences megafaunal community resulting in enhanced abundance, diversity and biomass compared to outside. The principal driver is the bottom substrate that in the outside is relatively homogeneous, dominated by soft bottom substrate, while the site 21 is characterized by methane emissions and consequently heterogeneous environment with carbonate structure, microbial mats and chemosynthetic worm tufts due to intermittent methane emissions. Then we can conclude that, despite cold seep systems exhibiting strong chemical gradients are usually known to have high faunal abundance and high biomass but low diversity due to chemical stress (Vismann, 1991; Warwick and Clarke, 1995; Bernardino et al., 2012), our results suggest the possibility of the methane emission creating a biomass and diversity hotspot on the seafloor, that Levin et al., (2016) called "oasi effect".



## References

- Andreassen, K., Hubbard, A., Winsborrow, M., Patton, H., Vadakkepuliambatta, S., Plaza-Faverola, A., Gudlaugsson, E., Serov, P., Deryabin, A., Mattingsdal, R., Mienert, J., and Bünz, S. (2017). Massive blow-out craters formed by hydrate-controlled methane expulsion from the Arctic seafloor, *Science*, 356, 948–953. <https://doi.org/10.1126/science.aal4500>
- Ashley, M. C., S. C. Mangi, and L. D. Rodwell. (2014). The potential of offshore windfarms to act as marine protected areas - a systematic review of current evidence. *Mar. Policy* 45: 301–309. <https://doi.org/10.1016/j.marpol.2013.09.002>
- Åström, E. K. L., Carroll, M. L., Ambrose, W. G., and Carroll, J. (2016). Arctic cold seeps in marine methane hydrate environments: Impacts on shelf macrobenthic community structure offshore Svalbard. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps11773>
- Åström, E. K. L., Carroll, M. L., Ambrose, W. G., Sen, A., Silyakova, A., and Carroll, J. (2017b). Methane cold seeps as biological oases in the high-Arctic deep sea, *Limnol. Oceanogr.*, 23 pp. <https://doi.org/10.1002/lno.10732>
- Barry, J. P., Gary Greene, H., Orange, D. L., Baxter, C. H., Robison, B. H., Kochevar, R. E., Nybakken, J. W., Reed, D. L., and McHugh, C. M. (1996). Biologic and geologic characteristics of cold seeps in Monterey Bay, California, *Deep-Sea Res. Pt. I*, 43, 1739–1762, [https://doi.org/10.1016/S0967-0637\(96\)00075-1](https://doi.org/10.1016/S0967-0637(96)00075-1)
- Bjarnadóttir, L. R., Rüther, D. C., Winsborrow, M. C. M., and Andreassen, K. (2013). Grounding-line dynamics during the last deglaciation of Kveithola, W Barents Sea, as revealed by seabed geomorphology and shallow seismic stratigraphy. *Boreas*. <https://doi.org/10.1111/j.1502-3885.2012.00273>
- Bergh, S. G., and Grogan, P. (2003). Tertiary structure of the Sørkapp-Hornsund Region, South Spitsbergen, and implications for the offshore southern extension of the fold-thrust Belt. *Norsk Geologisk Tidsskrift*.
- Bergmann, M., Dannheim, J., Bauerfeind, E., and Klages, M. (2009). Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(3), 408-424. <https://doi.org/10.1016/j.dsr.2008.10.004>
- Bergmann, M., Soltwedel, T., and Klages, M. (2011). The interannual variability of megafaunal assemblages in the Arctic deep sea: Preliminary results from the HAUSGARTEN observatory (79°N). *Deep Sea Research Part I: Oceanographic Research Papers*, 58(6), 711-723. <https://doi.org/10.1016/j.dsr.2009.05.012>

- Bernardino, A. F., Levin, L. A., Thurber, A. R., and Smith, C. R. (2012). Comparative composition, diversity and trophic ecology of sediment macrofauna at vents, seeps and organic falls. *PLoS One* 7: 1–17. <https://doi.org/10.1371/journal.pone.0033515>
- Berndt, C., Feseker, T., Treude, T., Krastel, S., Liebetrau, V., Niemann, H., Bertics, V. J., Dumke, I., Dunnbier, K., Ferre, B., Graves, C., Gross, F., Hissmann, K., Huhnerbach, V., Krause, S., Lieser, K., Schauer, J., and Steinle, L. (2014): Temporal constraints on hydrate-controlled methane seepage off Svalbard, *Science*, 343. 284–287, <https://doi.org/10.1126/science.1246298>
- Blacker, R.W. (1957) Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fish Investig Ser* 2 20:1–49
- Blacker, R. (1965) Recent changes in the benthos of the West Spitsbergen fishing grounds. *Int Comm Northwest Atl Fish (Special Publication)* 6:791–794
- Bluhm, B. A., Iken, K., Hardy, S. M., Sirenko, B. I., and Holladay, B. A. (2009). Community structure of epibenthic megafauna in the Chukchi Sea. *Aquatic Biology*, 7(3), 269-293. <https://doi.org/10.1016/j.dsr2.2009.08.012>
- Caricchi, C., Lucchi, R. G., Sagnotti, L., Macrì, P., Morigi, C., Melis, R., Caffau, M., Rebesco, M., and Hanebuth, T. J. J. (2018). Paleomagnetism and rock magnetism from sediments along a continental shelf-to-slope transect in the NW Barents Sea: Implications for geomagnetic and depositional changes during the past 15 thousand years. *Global and Planetary Change*. <https://doi.org/10.1016/j.gloplacha.2017.11.007>
- Caridi, F., Sabbatini, A., Morigi, C., Dell'Anno, A., Negri, A., and Lucchi, R. G. (2019). Patterns and environmental drivers of diversity and community composition of macrofauna in the Kveithola Trough (NW Barents Sea). *Journal of Sea Research*, 153, 101780. <https://doi.org/10.1016/j.seares.2019.101780>
- Carroll, M. L., Denisenko, S. G., Renaud, P. E., and Ambrose Jr, W. G. (2008). Benthic infauna of the seasonally ice-covered western Barents Sea: patterns and relationships to environmental forcing. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(20-21), 2340-2351. <https://doi.org/10.1016/j.dsr2.2008.05.022>
- Cochrane, S. K., Denisenko, S. G., Renaud, P. E., Emblow, C. S., Ambrose Jr, W. G., Ellingsen, I. H., and Skarðhamar, J. (2009). Benthic macrofauna and productivity regimes in the Barents Sea—ecological implications in a changing Arctic. *Journal of Sea Research*, 61(4), 222-233. <https://doi.org/10.1016/j.seares.2009.01.003>

- Cordes, E. E., Cunha, M. R., Galéron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A., and Levin, L.A. (2010). The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity: Seep habitat heterogeneity, *Mar. Ecol.*, 31, 51–65, <https://doi.org/10.1111/j.1439-0485.2009.00334>
- Crémière, A., Lepland, A., Chand, S., Sahy, D., Condon, D. J., Noble, S. R., Martma, T., Thorsnes, T., Sauer, S., and Brunstad, H. (2016): Timescales of methane seepage on the Norwegian margin following collapse of the Scandinavian Ice Sheet, *Nat. Commun.*, 7, 11509 <https://doi.org/10.1038/ncomms11509>
- Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R. (2002). Assessing the trophic state and eutrophication of coastal marine systems: A new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin*. [https://doi.org/10.1016/S0025-326X\(01\)00302-2](https://doi.org/10.1016/S0025-326X(01)00302-2)
- Dietz, L., Dömel, J. S., Leese, F., Lehmann, T., and Melzer, R. R. (2018). Feeding ecology in sea spiders (Arthropoda: Pycnogonida): what do we know?. *Frontiers in zoology*, 15(1), 7. <https://doi.org/10.1186/s12983-018-0250-4>
- Frauenheim, K., Neumann, V., Thiel, H., and Türkay, M. (1989). The distribution of the larger epifauna during summer and winter in the North Sea and its suitability for environmental monitoring. *Senckenbergiana Maritima: wissenschaftliche Mitteilungen der Senckenbergischen naturforschenden Gesellschaft*, (3/4).
- Gabrielsen, R. H., Faerseth, R. B., Jensen, L. N., Kalheim, J. E., and Riis, F. (1990). Structural Elements of the Norwegian Continental Shelf Part I: The Barents Sea Region. *Norwegian Petroleum Directorate Bulletin*.
- Galkin, S., Bergmann, M., Soltwedel, T., and Gebruk, A. (2013). Density and distribution of megafauna at the Håkon Mosby mud volcano (the Barents Sea) based on image analysis. *Biogeosciences*, 10(5), 3359-3374. <https://doi.org/10.5194/bg-10-3359-2013>
- Gebruk, A. V., Krylova, E. M., Lein, A. Y., Vinogradov, G. M., Anderson, E., Pimenov, N. V., Cherkashev, G. A., and Crane, K. (2003). Methane seep community of the Håkon Mosby mud volcano (the Norwegian Sea): composition and trophic aspects, *Sarsia*, 88, 394–403. <https://doi.org/10.1080/00364820310003190>
- Grassle, J. F., Sanders, H. L., Hessler, R. R., Rowe, G. T., and McLellan, T. (1975). Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. In *Deep Sea Research and Oceanographic Abstracts* (Vol. 22, No. 7, pp. 457-481). Elsevier. [https://doi.org/10.1016/0011-7471\(75\)90020-0](https://doi.org/10.1016/0011-7471(75)90020-0)
- Gröger, J., and Rumohr, H. (2006). Modelling and forecasting long-term dynamics of Western Baltic macrobenthic fauna in relation to climate signals and environmental change. *Journal of Sea Research*, 55(4), 266-277. <https://doi.org/10.1016/j.seares.2005.11.005>

- Guillén, J., Soriano, S., Demestre, M., Falqués, A., Palanques, A., and Puig, P. (2008). Alteration of bottom roughness by benthic organisms in a sandy coastal environment. *Continental Shelf Research*, 28(17), 2382-2392. <https://doi.org/10.1016/j.csr.2008.05.003>
- Gutt, J., and Starvans, A. (2003). Patchiness of the megabenthos at small scales: ecological conclusions by examples from polar shelves. *Polar biology*, 26(4), 276-278. <https://doi.org/10.1007/s00300-002-0468-6>
- Hammer, B., Hansen, L. B., and Nørskov, J. K. (1999). Improved adsorption energetics within density-functional theory using revised Perdew-Burke-Ernzerhof functionals. *Physical Review B*. <https://doi.org/10.1103/PhysRevB.59.7413>
- Hammer, Ø., Webb, K., and Depreiter, D. (2009). Numerical simulation of upwelling currents in pockmarks, and data from the Inner Oslofjord, Norway. *Geo Mar. Lett.* 29: 269–275. <https://doi.org/10.1007/s00367-009-0140-z>
- Hasemann, C., and Soltwedel, T. (2006). Small-scale heterogeneity in the Arctic deep sea: impact of small cold-water sponges on the diversity of benthic nematode communities (Vortrag). <https://doi.org/10013/epic.25531>
- Hecker, B. (1994). Unusual megafaunal assemblage on the continental slope off Cape Hatteras. *Deep Sea Research Part II: Topical Studies in Oceanography*, 41(4-6), 809-834. [https://doi.org/10.1016/0967-0645\(94\)90050-7](https://doi.org/10.1016/0967-0645(94)90050-7)
- Hoste, E., Vanhove, S., Schewe, I., Soltwedel, T., and Vanreusel, A. (2007). Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(1), 109-129. <https://doi.org/10.1016/j.dsr.2006.09.007>
- Hovland, M., and Svensen, H. (2006): Submarine pingoes: Indicators of shallow gas hydrates in a pockmark at Nyegga, Norwegian Sea, *Mar. Geol.*, 228, 15–23. <https://doi.org/10.1016/j.margeo.2005.12.005>
- Huettel, M., and Gust, G. (1992). Impact of bioroughness on interfacial solute exchange in permeable sediments. *Marine ecology progress series*, 253-267.
- Jones, D. O., Bett, B. J., and Tyler, P. A. (2007). Megabenthic ecology of the deep Faroe–Shetland channel: a photographic study. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(7), 1111-1128. <https://doi.org/10.1016/j.dsr.2007.04.001>
- Kaiser, M. J., Clarke, K. R., Hinz, H., Austen, M. C., Somerfield, P. J., and Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311, 1-14. <https://doi.org/doi:10.3354/meps311001>

- Kröncke, I., Zeiss, B., and Rensing, C. (2001). Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. *Senckenbergiana maritima*, 31(1), 65-82. <https://doi.org/10.1007/BF03042837>
- Lampitt, R. S., Billett, D. S. M., and Rice, A. L. (1986). Biomass of the invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean. *Marine Biology*, 93(1), 69-81. <https://doi.org/10.1007/BF00428656>
- Lantsch, H., Hanebuth, T. J. J., Horry, J., Grave, M., Rebesco, M., and Schwenk, T. (2017). Deglacial to Holocene history of ice-sheet retreat and bottom current strength on the western Barents Sea shelf. *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2017.08.016>
- Levin, L. A. (2005). Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. In *Oceanography and Marine Biology* (pp. 11-56). CRC Press.
- Levin, L. A., Baco, A. R., Bowden, D. A., Colaco, A., Cordes, E. E., Cunha, M. R., Demopoulos, A. W. J., Gobin, J., Grupe, B. M., Le, J., Metaxas, A., Netburn, A. N., Rouse, G. W., Thurber, A. R., Tunnicliffe, V., Van Dover, C. L., Vanreusel, A., and Watling, L. (2016). Hydrothermal vents and methane seeps: rethinking the sphere of influence, *Front. Mar. Sci.*, 3, 72. <https://doi.org/10.3389/fmars.2016.00072>
- Lindeboom, H. J., and De Groot, S. J. (1998). IMPACT-II: the effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems.
- Lösekan, T., Robador, A., Niemann, H., Knittel, K., Boetius, A., and Dubilier, N. (2008): Endosymbioses between bacteria and deep-sea siboglinid tubeworms from an Arctic Cold Seep (Haakon Mosby Mud Volcano, Barents Sea), *Environ. Microbiol.*, 10, 3237–3254. <https://doi.org/10.1111/j.1462-2920.2008.01712>
- Lucchi, R. G., Bazzaro, M., Biebow, N., Carbonara, K., Caridi, F., De Vittor, C., ... and Krueger, M. (2016). BURSTER-Bottom Currents in a Stagnant Environment. EUROFLEETS-2 Cruise Summary Report.
- MacDonald, I. R., Bluhm, B. A., Iken, K., Gage, S., and Strong, S. (2010). Benthic macrofauna and megafauna assemblage in the Arctic deep-sea Canada Basin. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 57: 136–152. <https://doi.org/10.1016/j.dsr2.2009.08.012>
- Martin, J. W., and Haney, T. A. (2005). Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005, *Zool. J. Linn. Soc.*, 145, 445–522, <https://doi.org/10.1111/j.1096-3642.2005.00178>
- Mau, S., M. Römer, M. E. Torres, I. Bussmann, T. Pape, E. Damm, P. Geprägs, Wintersteller, P., Hsu, C.W., Loher, M., and Bohrmann, G. (2017). “Widespread Methane Seepage along the Continental Margin off

Svalbard-from Bjørnøya to Kongsfjorden." *Scientific Reports*. <https://doi.org/10.1038/srep42997>.

Meyer, K. S., Bergmann, M., and Soltwedel, T. (2013). Interannual variation in the epibenthic megafauna at the shallowest site of the HAUSGARTEN observatory (79 N, 6 E). *Biogeosciences* 10: 3479–3492. <https://doi.org/10.5194/bg-10-3479-2013>

Pearson, T. H., and Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 16, 229-311.

Pearson, T. H., and Mannvik, H. P. (1998). Long-term changes in the diversity and faunal structure of benthic communities in the northern North Sea: natural variability or induced instability?. In *Recruitment, Colonization and Physical-Chemical Forcing in Marine Biological Systems* (pp. 317-329). Springer, Dordrecht. [https://doi.org/10.1007/978-94-017-2864-5\\_26](https://doi.org/10.1007/978-94-017-2864-5_26)

Pielou, E. C. (1975). *Ecological diversity* (No. 574.524018 P5).

Piepenburg, D., Blackburn, T.H., vonDorrien, C.F., Gutt, J., Hall, P.O.J., Hulth, S., Kendall, M.L., Opalinski, K.L., Rachor, E. and Schmid, M. K. (1995). Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea) *Marine Ecology Progress Series*, 118 , pp. 199-213

Piepenburg, D., Chernova, N. V., Von Dorrien, C. F., Gutt, J., Neyelov, A. V., Rachor, E., Saldanha, L., and Schmid, M. K. (1996). Megabenthic communities in the waters around Svalbard. *Polar Biology*, 16(6), 431-446. <https://doi.org/10.1007/s003000050074>

Piepenburg, D. (2005). Recent research on Arctic benthos: common notions need to be revised. *Polar Biology*, 28(10), 733-755. <https://doi.org/10.1007/s00300-005-0013-5>

Piepenburg, D., Archambault, P., Ambrose, W. G., Blanchard, A. L., Bluhm, B. A., Carroll, M. L., Conlan, K. E., Cusson, M., Feder, H. M., Grebmeier, J. M., Jewett, S. C., Lévesque, M., Petryashev, V. V., Sejr, M. K., Sirenko, B. I., and Włodarska-Kowalczyk, M. (2011). Towards a pan-Arctic inventory of the species diversity of the macro-and megabenthic fauna of the Arctic shelf seas. *Marine Biodiversity*, 41(1), 51-70. <https://doi.org/10.1007/s12526-010-0059-7>

Pleijel, F., Dahlgren, T. G., and Rouse, G. W. (2009). Progress in systematics: From Siboglinidae to Pogonophora and Vestimentifera and back to Siboglinidae. *C. R. Biol.* 332:140–148. <https://doi.org/10.1016/j.crv.2008.10.007>

Quéric, N. V., and Soltwedel, T. (2007). Impact of small-scale biogenic sediment structures on bacterial distribution and activity in Arctic deep-sea sediments. *Marine Ecology*, 28, 66-74. <https://doi.org/10.1111/j.1439-0485.2007.00177.x>

- Rebesco, M., Liu, Y., Camerlenghi, A., Winsborrow, M., Laberg, J. S., Caburlotto, A., Diviacco, P., Accettella, D., Sauli, C., Wardell, N., and Tomini, I., (2011). Deglaciation of the western margin of the Barents Sea Ice Sheet - A swath bathymetric and sub-bottom seismic study from the Kveithola Trough. *Marine Geology*. <https://doi.org/10.1016/j.margeo.2010.10.018>
- Rebesco, M., Özmaral, A., Urgeles, R., Accettella, D., Lucchi, R. G., Rütther, D., Winsborrow, M., Liopart, J., Carbulotto, A., Lantzsch, H., and Hanebuth, T. J. J., (2016). Evolution of a high-latitude sediment drift inside a glacially-carved trough based on high-resolution seismic stratigraphy (Kveithola, NW Barents Sea). *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2016.02.007>
- Reise, K., and Schubert, A. (1987). Macrobenthic turnover in the subtidal Wadden Sea: the Norderaue revisited after 60 years. *Helgoländer Meeresuntersuchungen*, 41(1), 69. <https://doi.org/10.1007/BF02365100>
- Reiss, H., Kröncke, I., and Ehrich, S. (2006). Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. *ICES Journal of Marine Science*, 63(8), 1453-1464. <https://doi.org/10.1016/j.icesjms.2006.06.001>
- Renaud, P. E., Włodarska-Kowalczyk, M., Trannum, H., Holte, B., Węśławski, J. M., Cochrane, S., Dahle, S., and Gulliksen, B. (2007). Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). *Polar Biology*, 30(3), 295-305. <https://doi.org/10.1007/s00300-006-0183-9>
- Rex, M. A. (1981). Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics*, 12(1), 331-353. <https://doi.org/10.1146/annurev.es.12.110181.001555>
- Ruhl, H. A. (2007). Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology*, 88(5), 1250-1262. <https://doi.org/10.1890/06-0890>
- Sahling, H., Römer, M., Pape, T., Bergès, B., dos Santos Fereirra, C., Boelmann, J., Geprägs, P., Tomczyk, M., Nowald, N., Dimmler, W., Schroedter, L., Glockzin, M., and Bohrmann, G. (2014). Gas emissions at the continental margin west of Svalbard: mapping, sampling, and quantification. *Biogeosciences*, 11(21), 6029-6046. <https://doi.org/10.5194/bg-11-6029-2014>
- Schulte-Rütther, M., Mainz, V., Fink, G. R., Herpertz-Dahlmann, B., and Konrad, K. (2012). Theory of mind and the brain in anorexia nervosa: Relation to treatment outcome. *Journal of the American Academy of Child and Adolescent Psychiatry*. <https://doi.org/10.1016/j.jaac.2012.06.007>
- Seabrook, S., C. De Leo, F., Baumberger, T., Raineault, N., and Thurber, A. R. (2018): Heterogeneity of methane seep biomes in the Northeast Pacific, *Deep-Sea Res. Pt. II*, 150, 195–209, <https://doi.org/10.1016/j.dsr2.2017.10.016>, 2018.

- Sen, A., Aström, E.K.L., Li Hong, W., Portnov, A., Waage, M., Serov, P., Carroll, M.L., and Carroll, J.L. (2018). "Geophysical and Geochemical Controls on the Megafaunal Community of a High Arctic Cold Seep." *Biogeosciences* 15 (14): 4533–59. <https://doi.org/10.5194/bg-15-4533-2018>.
- Sibuet, M., and Olu, K. (1998). Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins, *Deep-Sea Res. Pt. II*, 45, 517–567. [https://doi.org/10.1016/S0967-0645\(97\)00074-X](https://doi.org/10.1016/S0967-0645(97)00074-X)
- Ślubowska-Woldengen, M., Koç, N., Rasmussen, T. L., Klitgaard-Kristensen, D., Hald, M., and Jennings, A. E. (2008). Time-slice reconstructions of ocean circulation changes on the continental shelf in the Nordic and Barents Seas during the last 16,000 cal yr BP. *Quaternary Science Reviews*, 27(15-16), 1476-1492. <https://doi.org/10.1016/j.quascirev.2008.04.015>
- Solan, M., Germano, J. D., Rhoads, D. C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L., Valente, R., Watson, J., and Rosenbergn, R. (2003). Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *Journal of experimental marine biology and ecology*, 285, 313-338. [https://doi.org/10.1016/S0022-0981\(02\)00535-X](https://doi.org/10.1016/S0022-0981(02)00535-X)
- Soltwedel, T., and Vopel, K. (2001). Bacterial abundance and biomass in response to organism-generated habitat heterogeneity in deep-sea sediments. *Marine Ecology Progress Series*, 219, 291-298. <https://doi.org/10.3354/meps219291>
- Soltwedel, T., Bauerfeind, E., Bergmann, M., Budaeva, N., Hoste, E., Jaeckisch, N., von Juterzenka, K., Matthiessen, K., Mokievsky, V., Nöthig, E. M., Quéric, N. V., Sablotny, B., Sauter, B.E., Schewe, I., Urban-Malinga, B., Wegner, J., Włodarska-Kowalczyk, M. and Klages, M. (2005). HAUSGARTEN: multidisciplinary investigations at a deep-sea, long-term observatory in the Arctic Ocean. *Oceanography*, (3).
- Soltwedel, T., Jaeckisch, N., Ritter, N., Hasemann, C., Bergmann, M., and Klages, M. (2009). Bathymetric patterns of megafaunal assemblage from the arctic deep-sea observatory HAUSGARTEN. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(10), 1856-1872. <https://doi.org/10.1016/j.dsr.2009.05.012>
- Stone, R. B., Pratt, H. L., Parker, R. O., and Davis, G. E. (1979). A comparison of fish populations on an artificial and natural reef in the Florida Keys. *Mar. Fish. Rev.* 41: 1–11.
- Tarasov, V. G., Gebruk, A. V., Mironov, A. N., and Moskalev, L. I. (2005). Deep-sea and shallow-water hydrothermal vent communities: two different phenomena? *Chemical Geology*, 224(1-3), 5-39. <https://doi.org/10.1016/j.chemgeo.2005.07.021>



- Thistle, D. (2003). THE DEEP-SEA FLOOR: AN OVERVIEW. *Ecosystems of the deep oceans*, 28, 5.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Barend, F. N. E., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., and Williams, S. E. (2004). Extinction risk from climate change. *Nature*.
- Tunnicliffe, V., Juniper, S. K., and Sibuet, M. (2003). Reducing environments of the deep-sea floor. *Ecosystems of the World*, 81-110.
- Vacelet, J. and Donadey, C. (1977): Electron microscope study of the association between some sponges and bacteria, *J. Exp. Mar. Biol. Ecol.*, 30, 301–314, [https://doi.org/10.1016/0022-0981\(77\)90038-7](https://doi.org/10.1016/0022-0981(77)90038-7)
- Van Leeuwen, P. I., Rijnsdorp, A. D., and Vingerhoed, B. (1994). Variations in abundance and distribution of demersal fish species in the coastal zone of the southeastern North Sea between 1980 and 1993. *CM Documents-ICES*, (G: 10).
- van Oevelen, D., Bergmann, M., Soetaert, K., Bauerfeind, E., Hasemann, C., Klages, M., Schewe, I., Soltwedel, T. and Budaeva, N. (2011). Carbon flows in the benthic food web at the deep-sea observatory HAUSGARTEN (Fram Strait). *Deep-Sea Res I* 58:1069–1083 <https://doi.org/10.1016/j.dsr.2011.08.002>
- Vismann, B. (1991). Sulfide tolerance: Physiological mechanisms and ecological implications. *Ophelia* 34: 1–27.
- Warwick, R. M., and K. R. Clarke. (1995). New “biodiversity” measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.* 129: 301–305. <https://doi.org/10.3354/meps129301>
- Weniger, P., Blumenberg, M., Berglar, K., Ehrhardt, A., Klitzke, P., Krüger, M., and Lutz, R. (2019). Origin of near-surface hydrocarbon gases bound in northern Barents Sea sediments. *Marine and Petroleum Geology*, 102, 455-476. <https://doi.org/10.1016/j.marpetgeo.2018.12.036>
- Weslawski J.M., Wlodarska-Kowalczyk M. and Legezynska J. (2003) The occurrence of soft bottom macrofauna along the depth gradient in the High Arctic, 79°N. *Pol Polar Res* 23:73–88
- Wlodarska-Kowalczyk, M., and Pearson, T. H. (2004). Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology*, 27(3), 155-167. <https://doi.org/10.1007/s00300-003-0568-y>
- Zeppilli, D., Canals, M., and Danovaro, R. (2012). Pockmarks enhance deep-sea benthic biodiversity: a case study in the western Mediterranean Sea. *Diversity and Distributions*, 18(8), 832-846. <https://doi.org/10.1111/j.1472-4642.2011.0085>

## Chapter 5

### Abstract

#### **New elemental geochemistry and Stable isotopic data on benthic foraminifera and comparison to the benthic fauna community data (foraminifera, macro and megafauna) from site 21 on the Main Drift of the Kveithola trough**

To investigate the possible influence of methane emission on benthic foraminifera communities, we analysed stable isotope and geochemical data on the shell of two different taxa: a shallow-infaunal *Nonionellina labradorica* and a deep-infaunal *Globobulimina auriculata*. A Core sample was collected from site 21, located at the northern boundary of the Kveithola Trough where the Main Drift developed thanks to strong bottom currents. This site represents peculiar environment, where seep activities, high sedimentation rate and strong bottom currents create a stagnant and possibly chemosynthetic environment. Stable isotope results show light negative  $\delta^{13}\text{C}$  value (  $-3.250 \text{ e } - 1.492\text{‰}$ ) and does not support the evidence of methane influence, perhaps due to the short-life of foraminifera species and/or the intermittent flair. In addition, trace element (i.e., Mn/Ca) results are highly variable within and between species, but support the idea that foraminifera migrate to their preferred microhabitat to respond to a stressful environment, due to high sedimentation rate and low oxygen penetration in the sediment. Therefore, the presented data are mainly related to the organic matter and does not support the evidence of methane influence.

Concluding, these results are in agreement with those of benthic communities particularly, foraminifera and macrofauna, which respond more to quality/quantity and distribution of organic matter as stress driver than methane emissions. Meanwhile, megafauna results suggest the possibility of the methane emission creating a biomass and diversity hotspot on the seafloor.

## 1. Introduction

Cold seeps are sites where hydrocarbons, sulphide and other reduced compounds emanate from the seabed, providing the setting to fuel chemoautotrophic production. Microbial assemblage convert these compounds to organic biomass, typically through anaerobic oxidation of methane and reduction of sulphur (Boetius and Suess, 2004; Lösekann et al., 2007). In Arctic significant quantities of methane are stored as hydrate, an ice-like compound which forms under high pressure and low temperature conditions from methane-saturated water in marine sediments (Dickens, 2011; Pinero et al., 2013). The zone where gas hydrates are stable is known as gas hydrate stability zone (GHSZ) (Khokhar, Gudmundsson and Sloan, 1998). An increase in ocean bottom temperature can cause gas hydrate to dissociate and might release free gas (gas bubbles) into the water column (Berndt et al., 2014). Several sites of methane seepage have been discovered on the continental shelf offshore Svalbard and in the north-western Barents Sea (Åström et al., 2016; Sahling et al., 2014; Andreassen et al., 2017). The Barents Sea is considered an ecological hotspot for the circumpolar Arctic and the interaction between cold Arctic and warm Atlantic water masses, seasonal sea ice cover and the interplay of pelagic–benthic coupling creates a highly productive region (Tamelander et al., 2006; Degen et al., 2016). Moreover, the Arctic and particularly the Barents Sea are predicted to experience amplified impacts of climate warming such as shrinking sea ice cover, changing oceanographic patterns and increasing ocean acidification (Haug et al., 2017; Onarheim and Årthun, 2017).

The growing evidence of gas seepages in Arctic indicates a widespread potential for a strong environmental driver affecting local seafloor conditions, including community structure and ecosystem function. Where enough seepage occurs, these processes can support large faunal communities directly via chemosynthetic symbiosis or through trophic interactions (Levin, 2005; Thurber et al., 2013; Zapata Hernández et al., 2014). Seafloor methane emissions may also generate the formation of carbonate outcrops, providing a 3-D hard substrate to colonize and add supplementary hard bottom substrate in otherwise soft-bottom-dominated environments (Bohrmann et al., 1998, Van Dover, 2000). Cold seeps host complex seep-adapted faunal assemblage, in addition to conventional heterotrophic sessile organisms and vagrant fauna, that directly or indirectly rely on the release of methane (Thurber et al., 2013; Zapata Hernández et al., 2014). Literature on Arctic seep macro and megafauna communities is limited to a few studies in the Barents and Beaufort seas (Gebruk et al., 2003; Lösekann et al., 2008; Åström et al., 2016, 2017b).

Instead, interest in Foraminifera stems largely from process of biologically controlled mineralization, they record chemical changes in their environment. For example, stable carbon isotopes ( $\delta^{13}\text{C}$ ) from foraminiferal calcite provide information about ocean circulation, productivity (Katz et al., 2010), and methane seepage (e.g., Rathburn et al., 2003; Panieri, 2006). Stable oxygen isotopes ( $\delta^{18}\text{O}$ ) are used to assess ice volume, chemostratigraphy, and most commonly, temperature (Ravelo and Hillaire-Marcel, 2007). In addition, several trace-element ratios analysed on foraminiferal tests have been developed as proxies in the last decades: Mg/Ca used to reconstruct of seawater temperature (Elderfield et al., 2006), Mn/Ca ratio as redox-sensitive element (Glock et al., 2012; Koho et al., 2015; Petersen et al., 2018), Mn/Ca and Mn/Al ratios as proxies of relative bottom-water oxygenation in the low-latitude NE Atlantic upwelling system (Mckay et al., 2015).

In this work, data regarding the benthic fauna community (foraminifera, macro and megafauna) are presented from site 21 on the Main Drift of the Kveithola trough, a glacial depression located in north-western Barents Sea. Recently geochemical and geophysical evidences indicated the occurrence of cold seep events inside the Kveithola, most likely associated to the vertical migration of gas with thermogenic origin (Mau et al., 2017; Weniger et al., 2019). Our findings would suggest that episodic seepage activity with high methane fluxes could affect on the distribution and composition of benthic community.

### **1.1. Study area**

The present study site is positioned in the inner drift area of the Kveithola trough (Fig.1), an East–West trending, glacially-carved depression located in northwestern Barents Sea between the Spitsbergenbanken (which topographically separates the Kveithola from the Storfjorden Trough) and Bjørnøya (Pedrosa et al., 2011; Lucchi et al., 2013; Rebesco et al., 2016). The trough extends in E-W direction over 100 km, less than 13 km wide and shows an average water depth of 200–400 m along its axis (Bjarnadóttir et al., 2013; Carbonara et al., 2016; Caricchi et al., 2018). Mega-scale lineations (MSL), specifically longitudinal seabed landforms made of grooves and ridges, testify that, during the Last Glacial Maximum (LGM), the trough hosted a fast-flowing paleo-icestream, most likely fed by a local ice sheet grounded on the southeastern part of Spitsbergenbanken. Five transverse sediment ridges composed of Grounding Zone Wedges (GZWs), superimposed on the MSL, indicate that the subsequent deglaciation was characterized by periods of rapid retreats interrupted by stillstands and re-advances of the ice stream (Bjarnadóttir et al., 2013; Rebesco et

al., 2011; Rebesco et al., 2016). The Kveithola Trough is intersected with N-S direction by the Hornsund and Knølegga fault systems related to the phases of crustal extension associated with the opening of the Norwegian - Greenland Sea since the Cretaceous (Gabrielsen et al., 1990; Bergh and Grogan, 2003). The innermost Knølegga fault is responsible for an elongated bathymetric depression indicated by Rebesco et al., (2016) as the “northern channel”. The inner part of the trough hosts a complex sediment drift characterized by two main depocenters (Main and Minor Drifts; Rebesco et al., 2016), with internal acoustic reflectors on the sub-bottom record indicating persistent bottom currents that were active in the area since at least 13 cal ka BP (Bjarnadóttir et al., 2013; Rebesco et al., 2016); these deposits in the innermost part of the trough are also associated to a field of pockmarks (Bjarnadóttir et al., 2013; Rebesco et al., 2016; Lantzsch et al., 2017). The Kveithola Drift formation is thought to be resulted from the combination, over the past 13 cal ka BP, of an off-bank wedge and a confined drift. Such a combination was most likely favoured by the interaction between two strong bottom currents, the brine-enriched shelf waters (BSW) and the Atlantic Waters. The former enters the Kveithola via a northern feeder channel, whereas the latter, as a branch of the West Spitsbergen Current (WSC), intrude from the west across the southern bank of the trough (Lantzsch et al., 2017). Very recently, geophysical and geochemical data acquired by Lucchi et al., 2016, Mau et al., (2017) when a survey conducted along the north western Barents Sea margin indicated the presence of a few single flares along the northern edge of the Kveithola trough. Furthermore, Weniger et al., (2019) reported high concentrations of bound gases with thermogenic origin in near-surface sediments collected at different sites inside the trough, thus suggesting that mature petroleum systems are likely to be present in the study area.

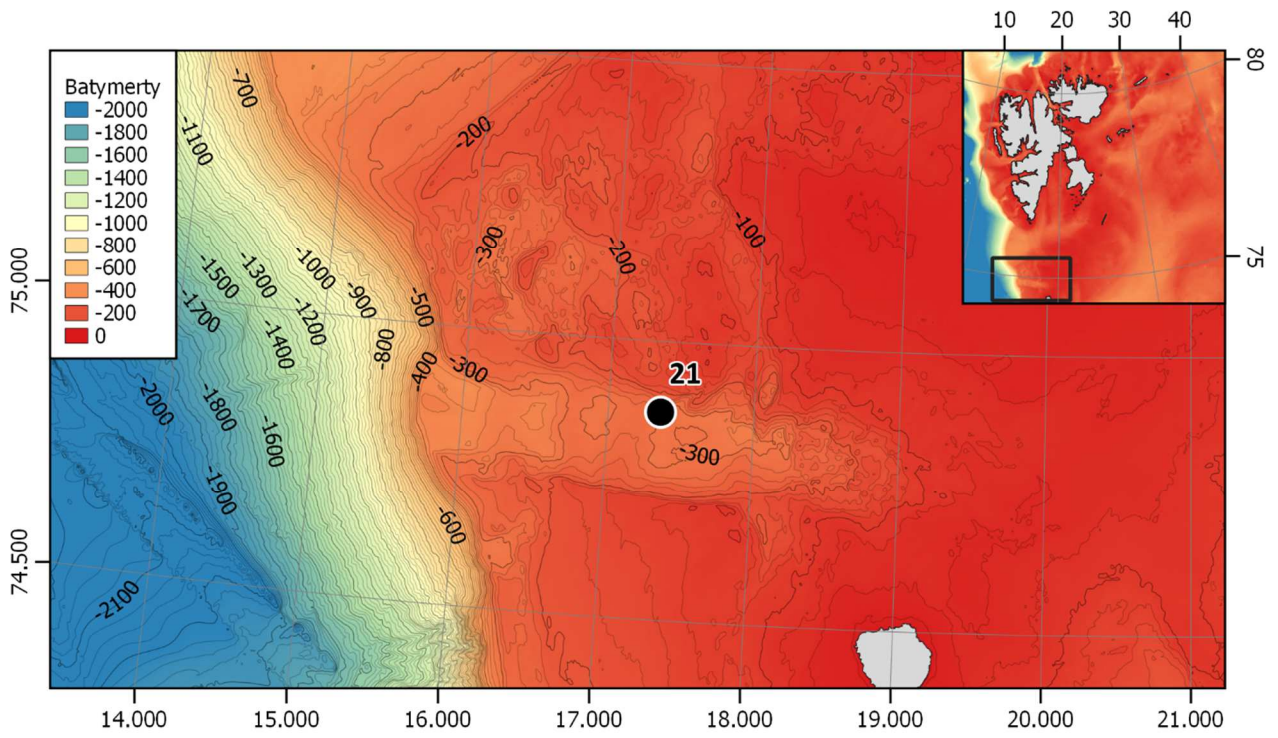


Fig. 1 Study area, black dot is the sample site.

## 2. Materials and methods

The samples were collected using a video-guided multicorer (TV-MUC) and a HD digital camera Ocean Floor Observation System (OFOS) in June 13–23, 2016 during Eurofleets 2- BURSTER cruise that was conducted onboard the German icebreaker RV Polarstern (Expedition PS99-1a; Lucchi et al., 2016). During the oceanographic survey, the presence of flare-like features observed on the echosounder profile forced a new re-modulation of the working programme in order to dedicate the necessary time for a deeper investigation of the revealed vents.

Sediment sample was collected at one site (Fig.1) using a video-guided multi-corer (TV-MUC) that was assembled with 8 tubes in polycarbonate having 60 cm length, 10 cm outer diameter, and 2.5 mm of thickness. 1 replicate sub-samples for analysis were obtained using Plexiglas corers, inner diameter 3.6 (surface area 10.18 cm<sup>2</sup>), inserted manually at each site from the first TV-MUC deployment. Core was opened on board and sliced at every 0.5 cm for the first 2 cm and at every 1 cm between 2–10 cm depths. Each slice was incubated in a refrigerator for 12-15 hours in CellTracker Green CMFDA (CTG) following the staining procedure as indicated in Pucci et al., (2006). After incubation, samples were fixed in 10% formalin buffered with sodium borate solution. In the laboratory, the fixed sediment samples were sieved through 63, 150 and 500 µm mesh.

For the fraction >500 µm also macrofaunal samples were sorted and counted, and the living individuals were extracted, recognized at the lowest taxonomic level and stored in Eppendorfs filled with 70% alcohol. All individuals were counted, weighed and the data standardized at 1 m<sup>2</sup> for comparison with the macrofaunal data obtained from the literature. The abundance counts were expressed as individuals per area (ind.m<sup>-2</sup>) and the density and the taxonomic composition of the main taxa was calculated. The biomass was determined as blotted wet weight (ww) per higher taxon after drying the specimens on absorbent paper for a few minutes applying the method described by Dermott and Paterson, (1974). The molluscs were weighed with their shells, and the polychaetes without tubes. Phyletic groups were distinguished into Crustacea, Echinodermata, Mollusca, Polychaeta, Nemertea, Sipuncula and Bryozoa.

For megafauna, the images were collected using the Ocean Floor Observation System (OFOS), that was a benthic camera system used for the investigation of the sea floor to assess environmental characteristics like sediment depositional structures, benthic organisms and/or other objects like

dropstones, litter, etc., present on the seafloor. The OFOS system available on the RV Polarstern consisted of a metal frame equipped with a fixed downwards looking Canon camera (EOS 5D Mark III, 22 Mpixel), a HD digital videocamera (Sony FCB-H11), an underwater Flash (SeaandSea YS-250PRO), four LED lights (DeepSea PowerandLight, Sealite Sphere 3150) and three laser-pointer (Oktopus) at a distance of 50 cm to each others useful to scale the collected images. The system was deployed offboard to approximately 1.5 m above the seafloor using a fibre optical cable for data, video and energy transfer. The camera allows to record a movie along the track and to collect pictures that are automatically triggered at every 30 seconds and additional pictures can be triggered manually if necessary. Visible fauna (at least a few centimetres across) were identified to the lowest possible taxonomic division and each individual was marked and the raw numbers were standardized to the different areas of the mosaics and transects by converting to densities based on the size of the mosaic or transect area. To processes the images was used the software image J (National Institute of Health, USA).

## **2.1. Geochemical analysis on foraminiferal test**

### **2.1.1. Trace element analysis**

From the >63- $\mu\text{m}$  size fraction (0-10 cm core depth), a total of 42 individuals belonging to foraminifera species *Globobulimina auriculata* and *Nonionellina labradorica* were hand-picked under binocular microscope for trace element analysis. Because foraminifera were presumed alive at collection, the rigorous cleaning procedure required for dead/fossil specimens was not necessary. Instead, the modified cleaning procedure described in Dissard et al., (2009, 2010a, b) was adopted. Organic matter was removed by soaking specimens for 30 min in a 3–7% NaOCl solution before analysis (Gaffey and Brönnimann, 1993). A stereomicroscope was used during the cleaning procedure to check optically for contamination and possible damage to the foraminiferal tests. Specimens were removed from the cleaning solution directly after complete bleaching. After cleaning, samples were thoroughly rinsed with deionized water to ensure complete removal of reagents.

Only the last chamber (n) and penultimate (n-1) were investigated. Single chambers were ablated using an Nd–YAG Laser (NWR-213, New Wave, ESI) inside an ablation chamber flushed with Helium



(0.7 L/min). Then the ablated sample with Helium was mixed with an Argon flow (0.6 L/min) and transported to an Inductively Coupled Plasma Mass Spectrometry (ICP-MS). Pulse repetition rate was set at 10 Hz, with an energy density at the sample surface of 30 J/cm<sup>2</sup>. Ablation craters were 50 µm in diameter and ablated material was analyzed with respect to time (and hence depth) using an ICP-MS (7500cx Agilent). Average ablations values of these measurements are presented in Tab. 1 and Tab. 2. Analyses were calibrated against NIST SRM 610 glass, using the concentration data of Pearce et al. (1997) with <sup>43</sup>Ca as an internal standard. Concentrations of Mg, Sr, Ba and Mn were calculated using <sup>24</sup>Mg, <sup>88</sup>Sr, <sup>138</sup>Ba and <sup>55</sup>Mn. An in-house matrix matched carbonate standard was used to verify potentially different ablation behavior for glass and carbonate. Simultaneously monitoring the Al allowed us to discard contaminated profiles, or part of the profiles, from further elemental concentration calculations. These analyses were conducted to ICP-MS Plateforme Alysés, Centre IRD France Nord, Bondy.

### **2.1.2. Stable Isotope measurements ( $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ )**

Stable oxygen and carbon isotope analyses were performed on individuals belonging to two dominant taxa *N.labradorica* and *G. auriculata*. Bulk foraminifera samples were reacted with orthophosphoric acid at 70 °C for <sup>18</sup>O s in individual vessels with an automated cryogenic distillation system (Kiel IV device), interfaced with a DeltaV Advantage Isotope Ratio Mass Spectrometry (IRMS). Over the period of analysis, 20 runs of our laboratory's internal carbonate standard (Marbre LM) gave an average  $\delta^{13}\text{C}$  value of 2.117‰ ± 0.022‰ (< 0.03‰) (k = 1) (theoretical value normalized to NBS 19 = 2.13‰) and an average  $\delta^{18}\text{O}$  value of - 1.865‰ ± ± 0.051‰ (< 0.06‰) (k = 1) (theoretical value normalized to NBS 19 = - 1.83‰). The analytical precision within each run, calculated from 1 to 20 measurements of the standard Marbre LM, varies from 2.079 to 2.162‰ for  $\delta^{13}\text{C}$  and from - 1.769 to - 1.949‰ for  $\delta^{18}\text{O}$ .

### 3. Results

#### 3.1. Trace element

Species	Depth interval (cm)	N°sample	Chamber	Li/Ca ( $\mu\text{mol/mol}$ )	Mg/Ca (mmol/mol)	Al/Ca (mmol/mol)	Sr/Ca ( $\mu\text{mol/mol}$ )	Ba/Ca ( $\mu\text{mol/mol}$ )	Mn/Ca ( $\mu\text{mol/mol}$ )
<i>Globobulimina auricula</i>	0-1	802	n	21.36319	3.96450	0.83671	1091.129	4.24613	65.32257
<i>Globobulimina auricula</i>	0-1	1003-1006	n	19.19078	3.57191	0.16810	1166.695	3.79744	133.9413
<i>Nonionellina labradorica</i>	0-1	1401-1402	n	17.46585	1.97505	0.05254	1096.166	1.80934	29.23285
<i>Nonionellina labradorica</i>	0-1	1501-1502	n	12.41374	2.00380	0.20100	1046.454	2.40395	187.4422
<i>Nonionellina labradorica</i>	0-1	1601-1602	n	14.50676	1.52029	0.00443	1085.715	2.17413	199.8429
<i>Nonionellina labradorica</i>	0-1	1701-1702	n	13.56851	1.35130	0.08770	1026.660	2.17048	68.65981
<i>Nonionellina labradorica</i>	0-1	2001	n	10.10421	1.74814	0.01515	1027.758	2.42948	298.1277

Tab. 1 Trace element in the "n chamber" (where "n" is last chamber) of live foraminifera species.

Trace element for *G. auricula* chamber n, Li/Ca, Mg/Ca and Ba/Ca ratios do not show any major difference between individuals. Al/Ca ratio varying from 0.83 mmol/mol at the sample 803 to 0.16 mmol/mol at the sample 1003-1006. Sr/Ca ratio from 1166.695 (sample 1003-1006) to 1091.129 (sample 803), the same trend was observed for the Mn/Ca ratio varying from 133.94 mmol/mol to 65.32 mmol/mol (Tab. 1).

For *N. labradorica*, Li/Ca and Sr/Ca ratios range between 17.46 to 10.10  $\mu\text{mol/mol}$  and 1096.16 to 1027.75  $\mu\text{mol/mol}$  (1401-1402 and 2001 samples), respectively. Mg/Ca ratio shows high value (in the 1401-1402 and 1501-1502 samples) with Mn values of 1.97 and 2.00 mmol/mol, respectively. Al/Ca ratio is higher in the sample 1501-1502 (0.20 mmol/mol) compared to the other individuals, the lowest value was observed in the 1601-1602 sample (0.004 mmol/mol). Mn/Ca ratio shows important difference, varying from 298.12  $\mu\text{mol/mol}$  at the sample 2001 to 29.23  $\mu\text{mol/mol}$  at the 1401-1402 sample (Tab. 1).

Species	Depth interval (cm)	N°sample	Chamber	Li/Ca (µmol/mol)	Mg/Ca (mmol/mol)	Al/Ca (mmol/mol)	Sr/Ca (µmol/mol)	Ba/Ca (µmol/mol)	Mn/Ca (µmol/mol)
<i>Globobulimina auricula</i>	0-1	701-702	n-1	14.96866	2.73488	0.09857	1020.503	2.45502	104.45775
<i>Globobulimina auricula</i>	0-1	801	n-1	13.85720	3.03930	1.60526	1084.497	2.27627	55.21963
<i>Globobulimina auricula</i>	0-1	901-902	n-1	14.43458	2.55810	0.12591	1075.612	1.78746	56.31381
<i>Globobulimina auricula</i>	0-1	1001-1002	n-1	19.55886	3.22260	0.08401	1054.601	3.12258	209.60849
<i>Globobulimina auricula</i>	0-1	1101-1102	n-1	13.85720	3.45266	0.04506	1109.979	3.56033	127.61791
<i>Nonionellina labradorica</i>	0-1	1403-1404	n-1	14.65110	1.96530	0.05237	1104.336	1.71450	88.05416
<i>Nonionellina labradorica</i>	0-1	1503-1504	n-1	14.14589	1.60366	0.00558	1056.333	2.26898	346.92807
<i>Nonionellina labradorica</i>	0-1	1703-1713	n-1	15.63746	1.60358	0.22094	1049.255	3.40955	158.80203
<i>Nonionellina labradorica</i>	0-1	1803-1804	n-1	11.83636	1.37552	0.00525	1114.925	2.56810	388.26986
<i>Nonionellina labradorica</i>	0-1	2003-2004	n-1	25.11618	2.39884	1.46688	1124.261	4.37380	384.92354

Tab. 2 Trace element of "n-1 chamber" (where "n-1" is the penultimate chamber) of live foraminifera species.

Trace element at the n-1 chamber, for *G.auricula* the Mg/Ca, Sr/Ca and Ba/Ca ratios show higher values (3.45, 1108.97 and 3.56 µmol/mol, respectively) compared to the other samples. Li/Ca ratio ranges from 19.55 µmol/mol at the 1001-1002 sample to 13.85 µmol/mol at the samples 801 and 1101-1102. Al/Ca ratio appears higher at the sample 801 (1.6 mmol/mol) compared to the lowest value 0.04 mmol/mol at the sample 1101-1102. Mn/Ca ratio from 209.60 µmol/mol (1001-1002 sample) to 55.21 µmol/mol (sample 801) (Tab. 2).

For *N. labradorica*, the sample 2003-2004 shows higher all element ratios values (25.11, 2.39, 1.46, 1124.26, 4.37 and 384.92 µmol/mol) compared with other samples. In the other samples the values are comparable, except for the Al/Ca ratio that ranges from 0.22 mmol/mol at the 1703-1704 sample to 0.005 mmol/mol at the 1503-1504 and 1803-1804 samples. Also Mn/Ca ratio shows different values, varying from 388.26 µmol/mol (1803-1804 sample) to 88.05 µmol/mol (1403-1404 sample) (Tab. 2).

### 3.2. Macrofauna

A total of 2161 macrofaunal individuals were identified (0-10 cm layers, > 500 µm) belonging to 7 taxa and 5 phyletic groups. The phylum showing the highest abundance is the Nemertea, with 982 individuals, representing the 45% of the total faunal sample. The second largest group is the Annelida (class Polychaeta) with 786 individuals distributed among 13 taxa and representing the 36% of the total faunal sample (Fig. 3). The total macrofaunal biomass is dominated by polychaetes,

representing 0.30 g wet weight (ww) m<sup>-2</sup> and contributing to 83% of total biomass. Nemertea and Mollusca have a weight of 0.03, corresponding to the 8% of the total sample weight (Fig. 2).

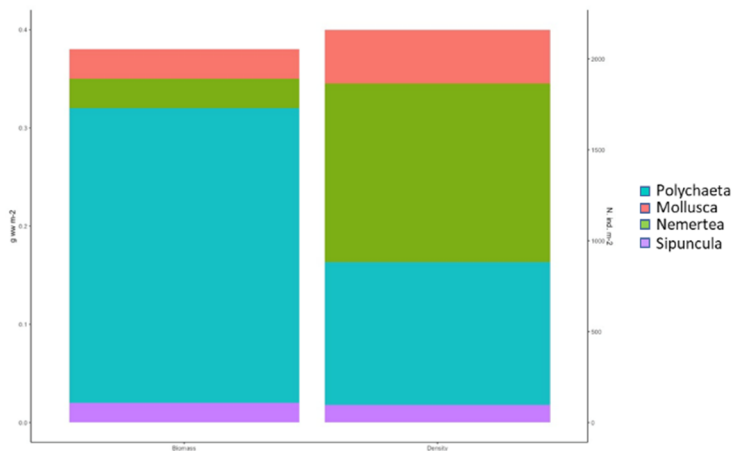


Fig.2 Total Biomass and Abundance of macrofaunal assemblage.

Nemertea are the most abundant faunal group, unfortunately no taxa identification is possible. Polychaetes is the second group and among them, the overall most abundant taxon is polychaeta *Cossura longocirrata* with 393 ind.m<sup>-2</sup>, *Prionospio cirrifera* and *Scoloplos* sp. whit both 193 ind.m<sup>-2</sup>.

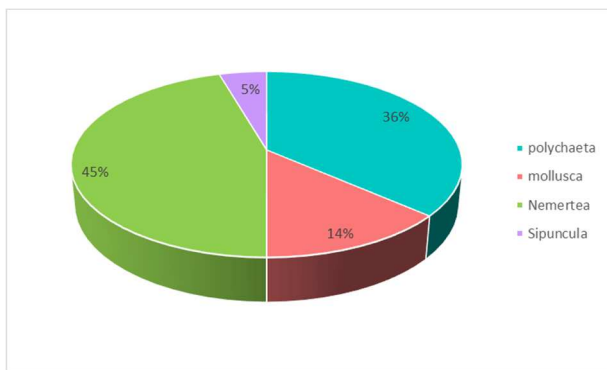


Fig. 3 Taxonomic composition of macrofauna communities

Taxonomic composition shows that Nemertea is the most abundant with a percentage of 45%, followed by polychaetes (36%), Mollusca (14%) and Sipuncula (4.5%) (Fig. 3).

Species richness_S	Dominance_D	Shannon_H	Equitability_J
7	0.26	1.6	0.8

Tab. 3 Diversity index of macrofauna communities

The species richness had a value of 7 and the organism are well distributed between the species (J=0.8). The Shannon index shows that the site was characterized by high diversity (1.6) (Tab. 3).

## 4. Discussion

The site 21 from the shallow Kveithola Trough is located at the northern boundary of the hollow area where the Main Drift developed thanks to strong bottom currents represented by Atlantic Water and Brine-enriched Shallow Water. Moreover, recently collected geochemical and geophysical evidences indicated the occurrence of cold seep events inside the Kveithola, most likely associated to the vertical migration of gas with thermogenic origin (Mau et al., 2017; Weniger et al., 2019). Cold seeps are environments where methane sulphide, or other reduced chemicals emissions occur at the seafloor and contain a variety of geomorphic and biological features that are sources of heterogeneity (Cordes, 2010).

Previous study regarding this area evidence a peculiar environment, where seep activities, high sedimentation rate and strong bottom currents create a stagnant and possibly chemosynthetic environment (Lucchi et al., 2016). As reported in the Chapter 2 of this thesis, foraminiferal assemblage is characterized by low diversity (Tab. 1, Chapter 2) and is dominated by species associated with organic-rich sediment and oxygen-depleted environments as the calcareous species *N.labradorica* and *G.auriculata*. At the same time, a higher percentage of agglutinated and delicate foraminifera monothalamous forms in this part of the Kveithola was also noted. The most abundant species are *Reophax fusiformis*, *Leptohalasis scottii* and *Micrometula* which show an opportunistic behaviour in response to enhanced food conditions and are considered tolerant to hypoxic environment (Ernst and van der Zwaan, 2004; Caille et al. 2015). All these species are well distributed until 4 cm (average ALD<sub>10</sub> = 2.8), therefore suggesting that the high concentration of metabolizable organic matter deeper in the cores could represent an excellent food source for the benthic foraminiferal consumers but probably the population does not benefit totally from this organic stock because despite the food availability the density shows a drastic fall from the first cm. In fact, infaunal species as *N. labradorica* react to these stressful conditions migrating to shallower microhabitats. This suggests that the relative increase of oxygen demand could be at the same time the limiting factor of benthic foraminiferal community health in terms of biodiversity.

Also, macrofaunal benthic communities (Chapter 3) are characterized by low S, H' and biomass. The presence of the Drift and a strong water stratification are responsible for limited dissolved gases vertical exchange leading to oxygen reduction conditions at the sea bottom. In fact, according to Burdige et al., (2007), in the Kveithola Trough the low available organic matter is associated with water stratification and low oxygen penetration in the sediment, which can contribute to organic

matter preservation and accumulation, preventing remineralization. The most important phylum (in term of abundance) is Nemertea that are predators that can exert a significant impact on the populations of their preferred prey organisms (McDermott and Roe, 1985; McDermott, 1988; Nordhausen, 1988; Rowell and Woo, 1990; Thiel and Reise, 1993; Kruse and Buhs, 2000). This group is indicated by previous authors (e.g., Holte and Gulliksen, 1998; Carroll et al., 2008; Cochrane et al., 2009; Riedel et al., 2012; among others) to populate eutrophic benthic ecosystems of the Barents Sea as well as the Mediterranean Sea. Polychaetes is the other abundant group, in fact their density increases in all cold seep sites at the Barents Sea (Astrom et al., 2016; Weslawski et al., 2011). The most representative species are the *Cossura longocirrata*, often reported among dominants in west Spitsbergen glacial bays (Włodarska-Kowalczyk and Pearson, 2004) and chemosynthetic environment characterized by organic matter from chemosynthetic and photosynthetic (phytodetritus) origins (Campanyà-Llovet and Snelgrove, 2018). It is a mobile, burrowing, detritus-feeder (Fauchald and Jumars, 1979) obviously resistant to high sedimentation.

Instead regarding megafauna, the muddy seafloor of this site, as evidenced on OFOS images at chapter 4, appear to be a heterogeneous environment, characterized by carbonate structure, many holes, microbial mats and chemosynthetic worm tufts. Particularly, the carbonate outcrop provided 3D-structure and hard substrate at an otherwise relatively featureless and homogenous soft-bottom seafloor. Seep-associated organisms may rely directly (chemoautotrophic symbionts) or indirectly (trophic relationships) on anaerobic oxidation of methane (AOM). Sulphate reduction can be invoked also as an alternative energy source, instead of, or in addition to, photoautotroph (Boetius and Suess, 2004; Levin, 2005; Thurber et al., 2013). The only obligate chemosynthetic faunal taxa found in the present study are siboglinid worms, which hosts microbial endosymbionts known to utilize methane and sulphur sources (Pleijel et al., 2009). The siboglinid between microbial mat constitute the base of local food chain and motile megafauna are frequently observed in association with them; they are also known to enhance local infaunal diversity and density (Bernardino et al., 2012). Various epifaunal taxa including sponges, hard-bottom anemones, bryozoans and commercial species are distributed on or near the carbonate structures, they provide hard substrate to colonize, protection and high food supply. Furthermore, methane emission creates a biomass and diversity hotspot on the seafloor, that Levin et al., (2016) called “oasi effect”.

The results demonstrate how foraminifera and macrofauna, contrary to megafauna, respond more to quality/quantity and distribution of organic matter as stress driver than methane emissions. To

better understand the site condition, stable isotope and trace element geochemical analysis on foraminiferal shells were attempted.

As for stable isotopes, the microhabitat of benthic foraminifera is recorded in the carbonate chemistry of their test, and this signature can give an indication of their calcification environment or living depth in sediment (Fontanier et al., 2006). With increasing sediment depth and changing redox chemistry, the pore water signature of  $\delta^{13}\text{C}$  becomes increasingly lighter (more negative) as organic matter is remineralized and the  $^{12}\text{C}$  is released into the pore waters (e.g., Schmiedl et al., 2004; Holsten et al., 2004). Foraminiferal taxa calcifying in the pore water of the sediment interval where they preferentially live, should therefore mirror this depletion (Fontanier et al., 2006). The epibenthic species present a heavy  $\delta^{13}\text{C}$  value close to DIC value of the interface water/sediment, while the endobenthic species have a lightest value. In order to quantify the difference between epifauna and endofauna, the  $\Delta \delta^{13}\text{C}$  is considered; this value represent the difference between the  $\delta^{13}\text{C}$  of a species of foraminifera and  $\delta^{13}\text{C}$  DIC of the interface water/sediment ( $\Delta \delta^{13}\text{C} = \delta^{13}\text{C}_{\text{foraminifera}} - \delta^{13}\text{C}_{\text{DIC interface water/sediment}}$ ).

In this study the epibenthic species *Cibicides pseudolobatus* is considered as a proxy of  $\delta^{13}\text{C}$  DIC on the interface water/sediment, in fact his  $\delta^{13}\text{C}$  value (1-1.8‰) corresponds to value expected for epibenthic species. The negative values  $\delta^{13}\text{C}$  (-3.250 – 1.492‰) of the infaunal *G.auriculata* are in agreement with the endobenthic life mode and the  $\Delta \delta^{13}\text{C}$  (obtained as  $\delta^{13}\text{C}_{G.auriculata} - \delta^{13}\text{C}_{C.pseudolobatus}$ , Aydilin unpublished thesis 2017) are comparable to those reported by Fontanier et al.,(2006) (Fig. 4).

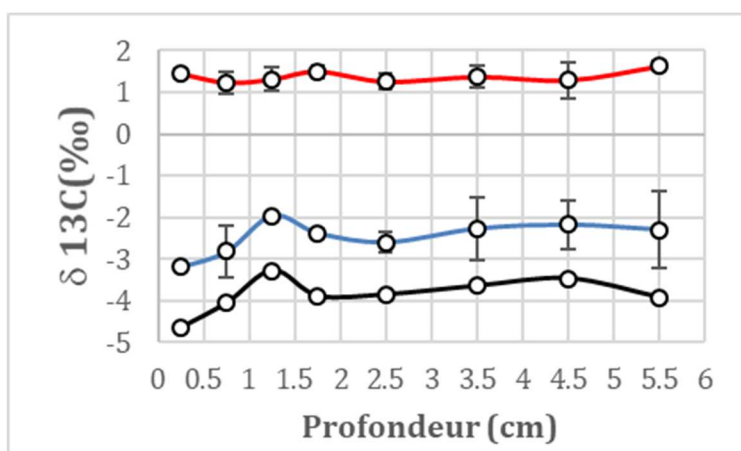


Fig. 4  $\delta^{13}\text{C}$  of *G. auriculata* (blue), of *C. pseudolobatus* (red) and  $\Delta \delta^{13}\text{C}$  of *G.auriculata* (black) in function of sediment depth ( Aydilin unpublished thesis 2017).

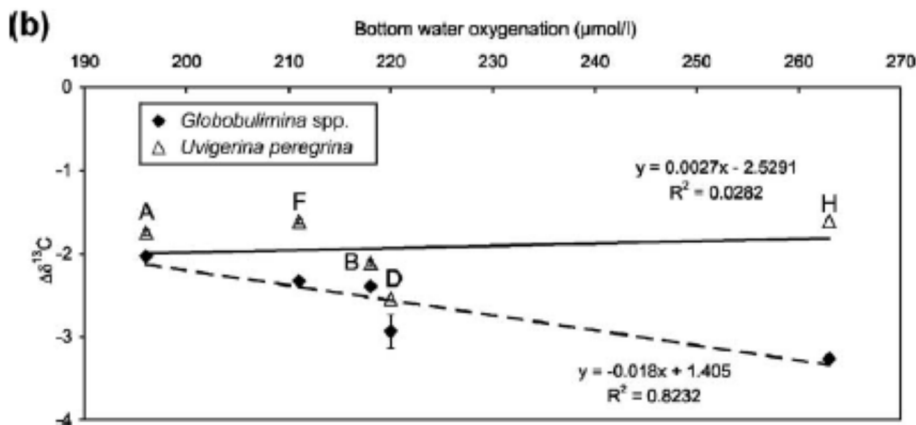


Fig. 5  $\Delta \delta^{13}\text{C}$  of benthic foraminifera in function of bottom water oxygenation (Fontanier et al., 2006).

Fontanier et al., (2006) also shows that the  $\Delta \delta^{13}\text{C}$  of the *Globobulimina* spp. ( $\delta^{13}\text{C}_{G.auriculata} - \delta^{13}\text{C}_{DIC}$  interface water/sediment) is correlated to the bottom oxygenation. *G. auriculata* has a deep infaunal microhabitat and several studies (Risgaard-Petersen et al., 2006; Koho et al., 2011) demonstrated that this species prefers oxygen-depleted environment that corresponds to the sediment redox interface. Light  $\Delta \delta^{13}\text{C}$  identifies a clear separation between the oxygenated water/sediment interface and the oxygenated surface in the sediment, compared to null gradient indicative of anoxic conditions in the bottom water. As Fontanier et al., (2006)(Fig. 5) suggest, the  $\Delta \delta^{13}\text{C}$  value of *G.auriculata* (-3 and -4‰) correlated with the  $\Delta \delta^{13}\text{C}$  distribution of benthic foraminifers in function to the bottom water oxygenation, allow to estimate the amount of dissolved oxygen in the bottom water at more than 270 mol/L (6.05mL/L), which would be consistent with measurements (from 4.52 to 7.43 mL/L along the Kveithola transect) made during BURSTER cruise (water about 6 m from the bottom, ). Therefore,  $\Delta \delta^{13}\text{C}$  value of *G. auriculata* species, occurring in the topmost core centimetres of our samples, suggests a rather oxygenated water/sediment interface. This is consistent with the core sediment description by Lucchi et al., (2016) that show black and organic matter enrich from 3-4 cm top ward of the core. These results are however heavier than those reported from cold seep areas (Panieri et al., al 2016; Rathburn et al., 2000). Particularly, in the continental margin west of Svalbard, Panieri et al., (2016) have recorded intervals characterised by very light  $\delta^{13}\text{C}$  values of the foraminiferal tests, often less than -5 ‰ and falling to -17‰, most likely due to large methane gas venting pulses. This suggests therefore that on  $\delta^{13}\text{C}$  test, the short-life of foraminiferal species and/or the intermittent methane emissions are the principal responsible for the low value recorded.



The trace metal signature of foraminiferal carbonate test can also provide information on their microhabitat. Many trace metals are redox sensitive, at certain thresholds of reduction potential, these elements could be released or precipitated out of solution (Tribovillard et al., 2006). In this study, the proxies of Mg/Ca and Mn/Ca ratios in two different calcareous species, *N. labradorica* and *G. auriculata* is explored. Previous studies on the thermodynamic controls on Mg incorporation into benthic foraminiferal calcite suggested linear or exponential relationship with temperature (e.g., Toyofuku et al., 2000; Lear et al., 2002; Marchitto et al., 2007). Incorporation of magnesium (Mg) into carbonates is an endothermic reaction favoured at warmer temperatures (Lea, 2003). *N. labradorica* in both case (n and n-1 chamber) shows values ranging from 1.3-2.3  $\mu\text{mol/mol}$ , this result agrees with Skirbekk et al., (2016). They demonstrated a correlation between Mg/Ca-ratios and measured bottom water temperatures, indicating interspecies variability and particularly that for example, *N. labradorica* calcified in autumn. Instead, *G. auriculata* shows higher values (average 3.49  $\mu\text{mol/mol}$ ), maybe due to high temperature sensitivity of Mg/Ca in a deep- infaunal *Globobulimina* spp., which provides a robust tool to reconstruct thermal changes in the deep ocean as reported by Weldeab et al., (2016). In addition, as Filipsson et al., (2010) data suggests the excess Mg can be due to the presence of either organic material or an amorphous calcium carbonate phase (Barker et al., 2003). Therefore, Mg/Ca ratio is highly variable within and between species, suggesting an influence of different environmental patterns (oxygen, organic matter, temperature, etc..) on the incorporation of  $\text{Mg}^{2+}$  into the shells.

The Mn/Ca ratio might prove to be a valuable proxy for redox conditions in the bottom and pore waters (Koho et al., 2015,2017; Mckay et al., 2015). The results of Mn/Ca ratios show that both intermediate and deep infaunal species present relatively highest values (Tab. 1 and Tab. 2), according to literature data (Koho et al., 2017; Petersen et al., 2018). These studies infer that Mn/Ca ratios in benthic foraminifera are primarily driven by environmental changes, such as redox conditions, affecting the concentration of Mn in pore waters. The environmental conditions of the site 21, characterized by strong bottom water and high sedimentation rate, support this hypothesis. In fact, Petersen et al., (2018) suggest that when eutrophication and stratification of the water column lead to (seasonally) hypoxic bottom water conditions, the oxygen penetration depth is reduced, causing an upward migration of the Mn redox front and diminishing the possibility that pore water  $\text{Mn}^{2+}$  is oxidized. At the same time, the results of this thesis (Fig. 6) highlight an intra-test variability, suggesting that both environmental change and active or passive vertical foraminiferal migration are the main factor responsible for this large intra-test variability. Moreover,

the ALD value (Tab. 1, Chapter 2) and isotope results (Fig. 4) support the idea that foraminifera respond to a stressful environment migrating to their preferred microhabitat (Gross, 2000; Geslin et al., 2004).

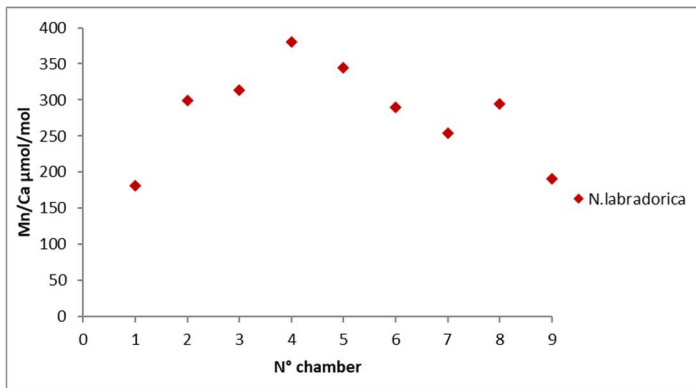


Fig.6 Mn/Ca ( $\mu\text{mol/mol}$ ) variability in *N. labradorica* chambers.

Concluding, the presented data are mainly related to the organic matter and does not support the evidence of methane influence. Moreover, these results support the theory of Dando, (2010), that chemosynthesis is not an advantageous life strategy in shallow cold seeps supported by photosynthetically derived organic matter. At the same time, heterogeneity and few chemosymbiotic foundation species associated with cold seep environments (e.g., bacterial mats, siboglinid tubeworms) not only attract epifauna and vagrant mobile organisms from surrounding habitats, but influence also organisms occupying peripheral habitats (i.e., foraminifera and macrofauna). They benefit from increased productivity close to the seep because advection from seafloor emissions may influence the amount of particulate organic matter in adjacent areas. Increased vertical mixing can enhance water column productivity, supporting nearby benthic communities as suspension feeders and few specialized species (Levin et al., 2016).

## 5. Conclusions

The site 21 from the Main Drift of Kveithola Trough is characterized by strong bottom currents represented by Atlantic Water and Brine-enriched Shallow Water. Moreover, recently collected geochemical and geophysical evidences indicated the occurrence of cold seep events. These peculiar conditions influence the heterogeneity distribution of benthic communities, which reflect a stressful environment. In particular, the results show how foraminifera and macrofauna respond more to quality/quantity and distribution of organic matter as stress driver than methane emissions. In fact, there are few opportunistic species as foraminifera *N. labradorica*, *G.auriculata* and metazoan species as polychaete *C. longicirrata* and Nemertea which inhabit low-oxygen and organic-enriched environments. Also, the geochemical analysis on foraminiferal shells do not support the evidence of methane emission, perhaps due to the short-life of foraminiferal species and/or the intermittent flair. Meanwhile, megafauna results suggest the possibility of the methane emission creating a biomass and diversity hotspot on the seafloor. Various epifaunal taxa including sponges, hard-bottom anemones, bryozoans and commercial species are distributed on or near the carbonate structures, they provide hard substrate to colonize, protection and high food supply.

These chapter results support the theory of Dando, (2010), that chemosynthesis is not an advantageous life strategy in shallow cold seeps supported by photosynthetically derived organic matter.

## References

- Andreassen, K., Hubbard, A., Winsborrow, M., Patton, H., Vadakkepuliambatta, S., Plaza-Faverola, A., Gudlaugsson, E., Serov, P., Deryabin, A., Mattingsdal, R., Mienert, J., and Bünz, S. (2017). Massive blow-out craters formed by hydrate-controlled methane expulsion from the Arctic seafloor, *Science*, 356, 948–953. <https://doi.org/10.1126/science.aal4500>
- Åström, E. K. L., Carroll, M. L., Ambrose, W. G., and Carroll, J. (2016). Arctic cold seeps in marine methane hydrate environments: Impacts on shelf macrobenthic community structure offshore Svalbard. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps11773>
- Åström, E. K. L., Carroll, M. L., Ambrose, W. G., Sen, A., Silyakova, A., and Carroll, J. (2017b). Methane cold seeps as biological oases in the high-Arctic deep sea, *Limnol. Oceanogr.*, 23 pp. <https://doi.org/10.1002/lno.10732>
- Bergh, S. G., and Grogan, P. (2003). Tertiary structure of the Sørkapp-Hornsund Region, South Spitsbergen, and implications for the offshore southern extension of the fold-thrust Belt. *Norsk Geologisk Tidsskrift*.
- Barker, S., Cacho, I., Benway, H., and Tachikawa, K. (2005). Planktonic foraminiferal Mg/Ca as a proxy for past oceanic temperatures: a methodological overview and data compilation for the Last Glacial Maximum. *Quaternary Science Reviews*, 24(7-9), 821-834. <https://doi.org/10.1016/j.quascirev.2004.07.016>
- Bernardino, A. F., Levin, L. A., Thurber, A. R., and Smith, C. R. (2012). Comparative composition, diversity and trophic ecology of sediment macrofauna at vents, seeps and organic falls. *PLoS One* 7: 1–17. <https://doi.org/10.1371/journal.pone.0033515>
- Berndt, C., Feseker, T., Treude, T., Krastel, S., Liebetrau, V., Niemann, H., Bertics, V. J., Dumke, I., Dünnbier, K., Ferré, B., Graves, C., Gross, F., Hissmann, K., Hühnerbach, V., Krause, S., Lieser, K., Schauer, J., and Steinle, L. (2014). Temporal constraints on hydrate-controlled methane seepage off Svalbard. *Science*, 343(6168), 284-287. <https://doi.org/10.1126/science.1246298>
- Bjarnadóttir, L. R., Rùther, D. C., Winsborrow, M. C. M., and Andreassen, K. (2013). Grounding-line dynamics during the last deglaciation of Kveithola, W Barents Sea, as revealed by seabed geomorphology and shallow seismic stratigraphy. *Boreas*. <https://doi.org/10.1111/j.1502-3885.2012.00273>
- Boetius, A., and Suess, E. (2004). Hydrate Ridge: a natural laboratory for the study of microbial life fueled by methane from near-surface gas hydrates. *Chemical Geology*, 205(3-4), 291-310. <https://doi.org/10.1016/j.chemgeo.2003.12.034>

- Bohrmann, G., Greinert, J., Suess, E., and Torres, M. (1998). Authigenic carbonates from the Cascadia subduction zone and their relation to gas hydrate stability. *Geology*, 26(7), 647-650. [https://doi.org/10.1130/0091-7613\(1998\)026<0647:ACFTCS>2.3.CO;2](https://doi.org/10.1130/0091-7613(1998)026<0647:ACFTCS>2.3.CO;2)
- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*. <https://doi.org/10.1021/cr050347q>
- Campanyà-Llovet, N., and Snelgrove, P. V. (2018). Temporal variation in infaunal community structure of chemosynthetic and non-chemosynthetic environments in Barkley Hydrates, British Columbia, Canada. *Deep Sea Research Part I: Oceanographic Research Papers*, 140, 118-127. <https://doi.org/10.1016/j.dsr.2018.06.008>
- Carbonara, K., Mezgec, K., Varagona, G., Musco, M. E., Lucchi, R. G., Villa, G., Melis, R., and Morigi, C. (2016). Late Quaternary deglaciation in the Arctic Ocean: evidences from microfossils. In *PAST Gateways conference* (Vol. 2016, pp. 24-25). Geological Survey of Norway (NGU).
- Caricchi, C., Lucchi, R. G., Sagnotti, L., Macri, P., Morigi, C., Melis, R., Caffau, M., Rebesco, M., and Hanebuth, T. J. J. (2018). Paleomagnetism and rock magnetism from sediments along a continental shelf-to-slope transect in the NW Barents Sea: Implications for geomagnetic and depositional changes during the past 15 thousand years. *Global and Planetary Change*. <https://doi.org/10.1016/j.gloplacha.2017.11.007>
- Carroll, M. L., Denisenko, S. G., Renaud, P. E., and Ambrose, W. G. (2008). Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing. *Deep-Sea Research Part II: Topical Studies in Oceanography*. <https://doi.org/10.1016/j.dsr2.2008.05.022>
- Caulle, C., Mojtahid, M., Gooday, A. J., Jorissen, F. J., and Kitazato, H. (2015). Living (Rose-Bengal-stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea). *Biogeosciences*, 12(16), 5005-5019. <https://doi.org/10.5194/bg-12-5005-2015>
- Cochrane, S. K. J., Denisenko, S. G., Renaud, P. E., Emblow, C. S., Ambrose, W. G., Ellingsen, I. H., and Skardhamar, J. (2009). Benthic macrofauna and productivity regimes in the Barents Sea - Ecological implications in a changing Arctic. *Journal of Sea Research*. <https://doi.org/10.1016/j.seares.2009.01.003>
- Cordes, E. E., Cunha, M. R., Galeron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaeve, S., Vanreusel, A., and Levin, L. A. (2010). The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. *Marine Ecology*, 31(1), 51-65. <https://doi.org/10.1111/j.1439-0485.2009.00334.x>

- Degen, R., Jørgensen, L. L., Ljubin, P., Ellingsen, I. H., Pehlke, H., and Brey, T. (2016). Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. *Marine Ecology Progress Series*, 546, 1-16. <https://doi.org/10.3354/meps11662>
- Dermott, R. M., and Paterson, C. G. (1974). Determining dry weight and percentage dry matter of chironomid larvae. *Canadian Journal of Zoology*. <https://doi.org/10.1139/z74-165>
- Dickens, G. R. (2011). Methane release from gas hydrate systems during the Paleocene-Eocene thermal maximum and other past hyperthermal events: setting appropriate parameters for discussion. *Climate of the Past Discussions*, 7(2). <https://doi.org/10.5194/cpd-7-1139-2011>
- Dissard, D., Nehrke, G., Reichart, G. J., Nouet, J., and Bijma, J. (2009). Effect of the fluorescent indicator calcein on Mg and Sr incorporation into foraminiferal calcite. *Geochemistry, Geophysics, Geosystems*, 10(11). <https://doi.org/10.1029/2009GC002417>
- Dissard, D., Nehrke, G., Reichart, G. J., and Bijma, J. (2010). The impact of salinity on the Mg/Ca and Sr/Ca ratio in the benthic foraminifera *Ammonia tepida*: Results from culture experiments. *Geochimica et Cosmochimica Acta*, 74(3), 928-940. <https://doi.org/10.1016/j.gca.2009.10.040>
- Elderfield, H., Yu, J., Anand, P., Kiefer, T., and Nyland, B. (2006). Calibrations for benthic foraminiferal Mg/Ca paleothermometry and the carbonate ion hypothesis. *Earth and Planetary Science Letters*, 250(3-4), 633-649. <https://doi.org/10.1016/j.epsl.2006.07.041>
- Ernst, S., and van der Zwaan, B. (2004). Effects of experimentally induced raised levels of organic flux and oxygen depletion on a continental slope benthic foraminiferal community. *Deep Sea Research Part I: Oceanographic Research Papers*, 51(11), 1709-1739. <https://doi.org/10.1016/j.dsr.2004.06.003>
- Fauchald, K., and Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography and marine Biology annual review*.
- Filipsson, H. L., Bernhard, J. M., Lincoln, S. A., and McCorkle, D. C. (2010). A culture-based calibration of benthic foraminiferal paleotemperature proxies: delta O-18 and Mg/Ca results. <http://hdl.handle.net/1721.1/65936>
- Fontanier, C., Mackensen, A., Jorissen, F. J., Anschutz, P., Licari, L., and Griveaud, C. (2006). Stable oxygen and carbon isotopes of live benthic foraminifera from the Bay of Biscay: Microhabitat impact and seasonal variability. *Marine Micropaleontology*, 58(3), 159-183. <https://doi.org/10.1016/j.marmicro.2005.09.004>
- Gaffey, S. J., and Bronnimann, C. E. (1993). Effects of bleaching on organic and mineral phases in biogenic carbonates. *Journal of Sedimentary Research*, 63(4).

- Gabrielsen, R. H., Faerseth, R. B., Jensen, L. N., Kalheim, J. E., and Riis, F. (1990). Structural Elements of the Norwegian Continental Shelf Part I: The Barents Sea Region. *Norwegian Petroleum Directorate Bulletin*.
- Gebruk, A. V., Krylova, E. M., Lein, A. Y., Vinogradov, G. M., Anderson, E., Pimenov, N. V., Cherkashev, G. A., and Crane, K. (2003). Methane seep community of the Håkon Mosby mud volcano (the Norwegian Sea): composition and trophic aspects, *Sarsia*, 88, 394–403.  
<https://doi.org/10.1080/00364820310003190>
- Geslin, E., Heinz, P., Jorissen, F., and Hemleben, C. (2004). Migratory responses of deep-sea benthic foraminifera to variable oxygen conditions: laboratory investigations. *Marine Micropaleontology*, 53(3-4), 227-243. <https://doi.org/10.1016/j.marmicro.2004.05.010>
- Glock, N., Eisenhauer, A., Liebetrau, V., Wiedenbeck, M., Hensen, C., and Nehrke, G. (2012). EMP and SIMS studies on Mn/Ca and Fe/Ca systematics in benthic foraminifera from the Peruvian OMZ: a contribution to the identification of potential redox proxies and the impact of cleaning protocols. *Biogeosciences*, 9(1), 341-359. <https://doi.org/10.5194/bg-9-341-2012>
- Gross, O. (2000). Influence of temperature, oxygen and food availability on the migrational activity of bathyal benthic foraminifera: evidence by microcosm experiments. In *Life at Interfaces and Under Extreme Conditions* (pp. 123-137). Springer, Dordrecht.
- Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallufredsson, E. H., Høines, Å. S., Håkon Hoel, A., Ingvaldsen, R.B., Jørgensen, L. L., Knutsen, T., Loeng, H., Naustvoll, L. J., Røttingen, I. and Sunnanå, K. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fisheries Research*, 188, 38-57.  
<https://doi.org/10.1016/j.fishres.2016.12.002>
- Holsten, J., Stott, L., and Berelson, W. (2004). Reconstructing benthic carbon oxidation rates using  $\delta^{13}\text{C}$  of benthic foraminifers. *Marine Micropaleontology*, 53(1-2), 117-132.  
<https://doi.org/10.1016/j.marmicro.2004.05.006>
- Holte, B., and Gulliksen, B. (1998). Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar Biology*. <https://doi.org/10.1007/s003000050262>
- Koho, K. A., Piña-Ochoa, E., Geslin, E., and Risgaard-Petersen, N. (2011). Vertical migration, nitrate uptake and denitrification: survival mechanisms of foraminifers (*Globobulimina turgida*) under low oxygen conditions. *FEMS microbiology ecology*, 75(2), 273-283. <https://doi.org/10.1111/j.1574-6941.2010.01010.x>
- Koho, K. A., de Nooijer, L. J., and Reichart, G. J. (2015). Combining benthic foraminiferal ecology and shell

Mn/Ca to deconvolve past bottom water oxygenation and paleoproductivity. *Geochimica et Cosmochimica Acta*, 165, 294-306. <https://doi.org/10.1016/j.gca.2015.06.003>

Koho, K. A., de Nooijer, L. J., Fontanier, C., Toyofuku, T., Oguri, K., Kitazato, H., and Reichart, G. J. (2017). Benthic foraminiferal Mn/Ca ratios reflect microhabitat preferences. *Biogeosciences*. <https://doi.org/10.5194/bg-14-3067-2017>

Kruse, I., and Buhs, F. (2000). Preying at the edge of the sea: The nemertine *Tetrastemma melanocephalum* and its amphipod prey on high intertidal sandflats. *Hydrobiologia*. <https://doi.org/10.1023/A:1003955523468>

Lantsch, H., Hanebuth, T. J. J., Horry, J., Grave, M., Rebesco, M., and Schwenk, T. (2017). Deglacial to Holocene history of ice-sheet retreat and bottom current strength on the western Barents Sea shelf. *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2017.08.016>

Lea, D. W. (2003). Elemental and isotopic proxies of marine temperatures. Pp. 365-390 in: *The Oceans and Marine Geochemistry* (H. Elderfield, editor). Treatise on Geochemistry, 6.

Lear, C. H., Rosenthal, Y., and Slowey, N. (2002). Benthic foraminiferal Mg/Ca-paleothermometry: A revised core-top calibration. *Geochimica et Cosmochimica Acta*, 66(19), 3375-3387. [https://doi.org/10.1016/S0016-7037\(02\)00941-9](https://doi.org/10.1016/S0016-7037(02)00941-9)

Levin, L. A. (2005). Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. In *Oceanography and Marine Biology* (pp. 11-56). CRC Press.

Levin, L. A., Baco, A. R., Bowden, D. A., Colaco, A., Cordes, E. E., Cunha, M. R., Demopoulos, A. W. J., Gobin, J., Grupe, B. M., Le, J., Metaxas, A., Netburn, A. N., Rouse, G. W., Thurber, A. R., Tunnicliffe, V., Van Dover, C. L., Vanreusel, A., and Watling, L. (2016). Hydrothermal vents and methane seeps: rethinking the sphere of influence, *Front. Mar. Sci.*, 3, 72. <https://doi.org/10.3389/fmars.2016.00072>

Lösekan, T., Knittel, K., Nadalig, T., Fuchs, B., Niemann, H., Boetius, A., and Amann, R. (2007). Diversity and abundance of aerobic and anaerobic methane oxidizers at the Haakon Mosby Mud Volcano, Barents Sea. *Appl. Environ. Microbiol.*, 73(10), 3348-3362. <https://doi.org/10.1128/AEM.00016-07>

Lösekan, T., Robador, A., Niemann, H., Knittel, K., Boetius, A., and Dubilier, N. (2008): Endosymbioses between bacteria and deep-sea siboglinid tubeworms from an Arctic Cold Seep (Haakon Mosby Mud Volcano, Barents Sea), *Environ. Microbiol.*, 10, 3237-3254. <https://doi.org/10.1111/j.1462-2920.2008.01712>

Lucchi, R. G., Camerlenghi, A., Rebesco, M., Colmenero-Hidalgo, E., Sierro, F. J., Sagnotti, L., Urgeles, R., Melis, R., Morigi, C., Bárcena, M.A., Giorgetti, G., Villa, G., Persico, D., Flores, J.A., Rigual-



- Hernández, A.S., Pedrosa, M.T., Macri, P., and Caburlotto, A. (2013). Postglacial sedimentary processes on the Storfjorden and Kveithola trough mouth fans: Significance of extreme glacial marine sedimentation. *Global and planetary change*, 111, 309-326.  
<https://doi.org/10.1016/j.gloplacha.2013.10.008>
- Lucchi, R. G., Bazzaro, M., Biebow, N., Carbonara, K., Caridi, F., De Vittor, C., ... and Krueger, M. (2016). BURSTER-Bottom Currents in a Stagnant Environment. EUROFLEETS-2 Cruise Summary Report.
- Marchitto, T. M., Bryan, S. P., Curry, W. B., and McCorkle, D. C. (2007). Mg/Ca temperature calibration for the benthic foraminifer *Cibicides pachyderma*. *Paleoceanography*, 22(1).  
<https://doi.org/10.1029/2006PA001287>
- Mau, S., Römer, M., Torres, M. E., Bussmann, I., Pape, T., Damm, E., Geprägs, P., Wintersteller, P., Hsu, C.W., Loher, M. and Bohrmann, G. (2017). Widespread methane seepage along the continental margin off Svalbard—from Bjørnøya to Kongsfjorden. *Scientific Reports*.  
<https://doi.org/10.1038/srep42997>
- McDermott, J J, and Roe, P. (1985). Food, Feeding Behavior and Feeding Ecology of Nemertean. *American Zoologist*. <https://doi.org/10.1093/icb/25.1.113>
- McDermott, John J. (1988). The role of hoplonemertean in the ecology of seagrass communities. *Hydrobiologia*. <https://doi.org/10.1007/BF00027972>
- McKay, C. L., Groeneveld, J., Filipsson, H. L., Gallego-Torres, D., Whitehouse, M. J., Toyofuku, T., and Romero, O. E. (2015). A comparison of benthic foraminiferal Mn/Ca and sedimentary Mn/Al as proxies of relative bottom-water oxygenation in the low-latitude NE Atlantic upwelling system. *Biogeosciences*, 12, 5415-5428. <https://doi.org/10.5194/bg-12-5415-2015>
- Nordhausen, W. (1988). Impact of the nemertean *Lineus viridis* on its polychaete prey on an intertidal sandflat. *Hydrobiologia*. <https://doi.org/10.1007/BF00027976>
- Onarheim, I. H., and Årthun, M. (2017). Toward an ice-free Barents Sea. *Geophysical Research Letters*, 44(16), 8387-8395. <https://doi.org/10.1002/2017GL074304>
- Panieri, G. (2006). Foraminiferal response to an active methane seep environment: a case study from the Adriatic Sea. *Marine Micropaleontology*, 61(1-3), 116-130.  
<https://doi.org/10.1016/j.marmicro.2006.05.008>
- Panieri, G., Graves, C. A., and James, R. H. (2016). Paleo-methane emissions recorded in foraminifera near the landward limit of the gas hydrate stability zone offshore western Svalbard. *Geochemistry, Geophysics, Geosystems*, 17(2), 521-537. <https://doi.org/10.1002/2015GC006153>

- Pedrosa, M. T., Camerlenghi, A., De Mol, B., Urgeles, R., Rebesco, M., and Lucchi, R. G. (2011). Seabed morphology and shallow sedimentary structure of the Storfjorden and Kveithola trough-mouth fans (North West Barents Sea). *Marine Geology*, 286(1-4), 65-81.  
<https://doi.org/10.1016/j.margeo.2011.05.009>
- Petersen, J., Barras, C., Bézos, A., La, C., de Nooijer, L. J., Meysman, F. J., Filip, F.R., Mouret, A., Slomp, C. P. and Jorissen, F. J. (2018). Mn/Ca intra-and inter-test variability in the benthic foraminifer *Ammonia tepida*. *Biogeosciences*, 15(1), 331-348. <https://doi.org/10.5194/bg-15-331-2018>
- Pinero, E., Marquardt, M., Hensen, C., Haeckel, M., and Wallmann, K. (2013). Estimation of the global inventory of methane hydrates in marine sediments using transfer functions. *Biogeosciences (BG)*, 10(2), 959-975. <http://dx.doi.org/10.5194/bg-10-959-2013>
- Pleijel, F., Dahlgren, T. G., and Rouse, G. W. (2009). Progress in systematics: From Siboglinidae to Pogonophora and Vestimentifera and back to Siboglinidae. *C. R. Biol.* 332:140–148.  
<https://doi.org/10.1016/j.crvi.2008.10.007>
- Pucci, F., Geslin, E., Barras, C., Morigi, C., Sabbatini, A., Negri, A., and Jorissen, F. J. (2009). Survival of benthic foraminifera under hypoxic conditions: Results of an experimental study using the CellTracker Green method. *Marine Pollution Bulletin*, 59(8-12), 336-351.  
<https://doi.org/10.1016/j.marpolbul.2009.08.015>
- Rathburn, A. E., Pérez, M. E., Martin, J. B., Day, S. A., Mahn, C., Gieskes, J., Ziebis, W., Williams, D., and Bahls, A. (2003). Relationships between the distribution and stable isotopic composition of living benthic foraminifera and cold methane seep biogeochemistry in Monterey Bay, California. *Geochemistry, Geophysics, Geosystems*, 4(12). <https://doi.org/10.1029/2003GC000595>
- Ravelo, A. C., and Hillaire-Marcel, C. (2007). Chapter eighteen the use of oxygen and carbon isotopes of foraminifera in paleoceanography. *Developments in marine geology*, 1, 735-764.  
[https://doi.org/10.1016/S1572-5480\(07\)01023-8](https://doi.org/10.1016/S1572-5480(07)01023-8)
- Rebesco, M., Özmaral, A., Urgeles, R., Accettella, D., Lucchi, R. G., Rütther, D., Winsborrow, M., Liopart, J., Caburlotto, A., Lantzsch, H., and Hanebuth, T. J. J. (2016). Evolution of a high-latitude sediment drift inside a glacially-carved trough based on high-resolution seismic stratigraphy (Kveithola, NW Barents Sea). *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2016.02.007>
- Riedel, B., Zuschin, M., and Stachowitsch, M. (2012). Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: A realistic scenario. *Marine Ecology Progress Series*.  
<https://doi.org/10.3354/meps09724>

- Risgaard-Petersen, N., Langezaal, A. M., Ingvarlsen, S., Schmid, M. C., Jetten, M. S., den Camp, H. J. O., Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Nielsen, L.P., Revsbech, N.P., Cedhagen, T., and Revsbech, N. P. (2006). Evidence for complete denitrification in a benthic foraminifer. *Nature*, *443*(7107), 93. <https://doi.org/10.1038/nature05070>
- Rowell, T. W., and Woo, P. (1990). Predation by the Nemertean Worm *Cerebratulus-Lacteus* Verrill on the Soft-Shell Clam *Mya-Arenaria* Linnaeus 1758 and Its Apparent Role in the Destruction of a Clam Flat. *Journal of Shellfish Research*.
- Sahling, H., Römer, M., Pape, T., Bergès, B., dos Santos Fereirra, C., Boelmann, J., Geprägs, P., Tomczyk, M., Nowald, N., Dimmler, W., Schroedter, L., Glockzin, M., and Bohrmann, G. (2014). Gas emissions at the continental margin west of Svalbard: mapping, sampling, and quantification. *Biogeosciences*, *11*(21), 6029-6046. <https://doi.org/10.5194/bg-11-6029-2014>
- Schmiedl, G., Pfeilsticker, M., Hemleben, C., and Mackensen, A. (2004). Environmental and biological effects on the stable isotope composition of recent deep-sea benthic foraminifera from the western Mediterranean Sea. *Marine Micropaleontology*, *51*(1-2), 129-152. <https://doi.org/10.1016/j.marmicro.2003.10.001>
- Skirbekk, K., Hald, M., Marchitto, T. M., Junttila, J., Klitgaard Kristensen, D., and Aagaard Sørensen, S. (2016). Benthic foraminiferal growth seasons implied from Mg/Ca-temperature correlations for three Arctic species. *Geochemistry, Geophysics, Geosystems*, *17*(11), 4684-4704.
- Tameler, T., Renaud, P. E., Hop, H., Carroll, M. L., Ambrose Jr, W. G., and Hobson, K. A. (2006). Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. *Marine Ecology Progress Series*, *310*, 33-46. <https://doi.org/10.3354/meps310033>
- Thiel, M., and Reise, K. (1993). Interaction of nemertines and their prey on tidal flats. *Netherlands Journal of Sea Research*. [https://doi.org/10.1016/0077-7579\(93\)90006-E](https://doi.org/10.1016/0077-7579(93)90006-E)
- Thurber, A. R., Levin, L. A., Rowden, A. A., Sommer, S., Linke, P., and Kröger, K. (2013). Microbes, macrofauna, and methane: a novel seep community fueled by aerobic methanotrophy. *Limnology and Oceanography*, *58*(5), 1640-1656. <https://doi.org/10.4319/lo.2013.58.5.1640>
- Toyofuku, T., Kitazato, H., Kawahata, H., Tsuchiya, M., and Nohara, M. (2000). Evaluation of Mg/Ca thermometry in foraminifera: Comparison of experimental results and measurements in nature. *Paleoceanography*, *15*(4), 456-464. <https://doi.org/10.1029/1999PA000460>
- Tribouillard, N., Algeo, T. J., Lyons, T., and Riboulleau, A. (2006). Trace metals as paleoredox and paleoproductivity proxies: an update. *Chemical geology*, *232*(1-2), 12-32.

<https://doi.org/10.1016/j.chemgeo.2006.02.012>

- Van Dover, C. (2000). *The ecology of deep-sea hydrothermal vents*. Princeton University Press.
- Weldeab, S., Arce, A., and Kasten, S. (2016). Mg/Ca- $\Delta$ CO<sub>3</sub>porewater<sup>2</sup>—temperature calibration for Globobulimina spp.: A sensitive paleothermometer for deep-sea temperature reconstruction. *Earth and Planetary Science Letters*, 438, 95-102. <https://doi.org/10.1016/j.epsl.2016.01.009>
- Weniger, P., Blumenberg, M., Berglar, K., Ehrhardt, A., Klitzke, P., Krüger, M., and Lutz, R. (2019). Origin of near-surface hydrocarbon gases bound in northern Barents Sea sediments. *Marine and Petroleum Geology*, 102, 455-476. <https://doi.org/10.1016/j.marpetgeo.2018.12.036>
- Węśławski, J. M., Kendall, M. A., Włodarska-Kowalczyk, M., Iken, K., Kędra, M., Legezynska, J., and Sejr, M. K. (2011). Climate change effects on Arctic fjord and coastal macrobenthic diversity—observations and predictions. *Marine Biodiversity*, 41(1), 71-85. <https://doi.org/10.1007/s12526-010-0073-9>
- Włodarska-Kowalczyk, M., and Pearson, T. H. (2004). Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biology*. <https://doi.org/10.1007/s00300-003-0568-y>
- Zapata-Hernández, G., Sellanes, J., Thurber, A. R., Levin, L. A., Chazalon, F., and Linke, P. (2014). New insights on the trophic ecology of bathyal communities from the methane seep area off Concepción, Chile (~ 36 S). *Marine ecology*, 35(1), 1-21. <https://doi.org/10.1111/maec.12051>

## Chapter 6

### 1. General Conclusions

#### 1.1. Environmental patterns of Kveithola Trough

For the first time, we have documented the Arctic benthic micro, macro and megafaunal communities in Kveithola Trough located in the NW Barents Sea, to improve knowledge gaps existing in this area. The Kveithola is characterized by peculiar morpho-depositional and hydrographic conditions, which allow to distinguish three main areas (the outer, the inner area and the shallowest 07).

The outer part of the trough is the deepest studied area along the Kveithola Trough (400–450 m bsl) and is directly influenced by the North Atlantic Current (NAC, warm and saline ,Slubowska-Woldengen et al., 2008); the NAC sweeps the outer seafloor and remove the fine sediment fraction leaving a coarse lag of pebbly sands (Caricchi et al., 2018). Instead, the inner part which comprises the Main Drift and the Minor Drift, located between the Hornsund and Knølegga fracture zones (mean depth around 300 m bsl), is subject to continuous fine-grained sediment deposition due to cold and less saline Arctic Water (AW) and dense cold Brine-enriched Shelf Water (BSW) flow. These dense brine waters generate bottom currents that shape the Kveithola Drift moat (Rebesco et al., 2016; Lantzsch et al., 2017). Moreover, recently geophysical and geochemical evidence collected in occasion of two surveys conducted along the north-western Barents Sea margin by Lucchi et al., (2016) and Mau et al., (2017), indicated the presence of a few single methane flares along the northern edge of the Trough. Furthermore, these emitted gases were associated to the vertical migration of thermogenic gas, as reported by Weniger et al., (2019). A third area is represented by site 07 (the shallowest site) located in the Northern channel (namely the Knølegga fracture zones).

Furthermore, the Kveithola is characterized by high primary production and high nutrient rates that reach the benthic community, suggesting a close relationship between the pelagic and benthic compartments. The water circulation and the hydrodynamic regime, other than sediment and its granulometry, still influence composition and accumulation of organic matter content (Martins et al., 2016). This thesis results show that high hydro-dynamism, that characterized the outer part of Kveithola trough, does not favour the accumulation of the organic matter, the presence of which is mainly related to the settlement of organic rich fine-grained sediments (Gremare et al., 2002). In fact, organic matter content in this area are lower compare those measured in the sediment

collected in the inner trough area (the Drift and Northern channel of the Kveithola Trough), where the organic C load, considered as BPC concentration, is comparable to values typically encountered in eutrophic systems varying from 4.5 mg/g to 6.9 mg/g (Dell'Anno et al., 2002). Meanwhile, strong water stratification and high supplies of organic matter are responsible for limited vertical exchange of dissolved gases leading to oxygen reduction conditions at the sea bottom; at the same time, it can contribute to organic matter preservation and accumulation, often associated with the absence of remineralization (Burdige, 2007).

Finally, separate considerations must be made for the site 21, located at the northern boundary of the hollow area where the Main Drift developed thanks to strong bottom currents represented by Atlantic Water and Brine-enriched Shallow Water. Moreover, recently collected geochemical and geophysical evidences indicated the occurrence of cold seep activity. Cold seeps are environments where methane sulphide, or other reduced chemicals emissions occur at the seafloor and contain a variety of geomorphic and biological features that are sources of heterogeneity (Cordes, 2010). In fact, the muddy seafloor of this site, as evidenced by OFOS video, appear to be a heterogeneous environment, characterized by carbonate structure many holes, microbial mats and chemosynthetic worm tufts. Particularly, the carbonate outcrop provided 3D-structure and hard substrate at an otherwise relatively featureless and homogenous soft-bottom seafloor.

## **1.2. Faunal response**

These distinct geomorphological and environmental feature between high productivity and seep activity of Kveithola trough, are key drivers of benthic communities structure and their heterogeneity distribution.

One of the main determining factors of spatial distribution, density and species composition of benthic foraminifera and macrofaunal communities is the supply of organic matter and its quality and the results evidence a difference between the outer and inner trough. In the outer sites, a low bioavailability of sediment organic carbon supports a poorly sediment community oxygen consumption and high hydrodynamic does not favour the accumulation of the organic matter and can enhance sediment resuspension injecting in the bottom water column organic matter pools more refractory in nature (e.g., carbohydrates). The inner trough represents an eutrophic high metabolizable organic matter area, dominated by a detritivorous community (small subsurface-feeding polychaeta *M. sarsi*, the surface-feeding polychaeta *L. gracilis*, the subsurface lamellibranch

bivalve *M. cf. pigmea*, the subsurface protobranch bivalve genus *Yoldiella*), predators belonging to Nemertea and foraminifera as calcareous *Nonionellina labradorica* *Globobulimina auriculata*, agglutinated *L. difflugiformis*. These taxa indicate the presence of an organic-rich sediment and oxygen-depleted environment possibly linked to a cold seep system; they are also responsible for the organic matter mineralization due to bioturbation activity. Interestingly, delicate foraminifera monothalamous taxa (organic-walled allogromiids, agglutinated saccamminids, psammosphaerids and tubular forms) were reported from all sites with high percentage, the results show a dominance of *Micrometula* and *Cylindrogullmia* morphotypes inhabiting typically the detritus layer of Arctic fjords and live in an extremely oxygen-deficient environment (Gooday, 2002).

Meanwhile, megafauna results suggest the possibility of the methane emission creating a biomass and diversity hotspot on the seafloor. In fact, a difference between the site 21 (cold seep) and the outside are demonstrated. The principal driver is the bottom substrate that in the outside is relatively homogeneous, dominated by soft bottom substrate and organisms, while the site 21 is characterized by carbonate formation, suggestive of long-term seepage, bacterial mats and seep-obligate siboglinid between with habitat complexity are all believed to be important factors in attracting organisms to such structures. Various epifaunal taxa including sponges, hard-bottom anemones, bryozoans and commercial species are distributed on or near the carbonate structures, they provide hard substrate to colonize, protection and high food supply.

To conclude, the distinct geomorphological and environmental features (e.g. currents, temperature, oxygenation, grain size, and cold seep) which characterize the Kveithola Trough, seems to exert an important role on the distribution, quality and quantity of the organic matter, which allow to describe the trough as a eutrophic hot-spot in an oligotrophic Arctic ocean. In turn, this scenario influences the abundance and diversity of benthic assemblage, which seems to respond in different way to environmental drivers. In fact, foraminifera and macrofauna respond more to quality/quantity and distribution of organic matter as stress driver than methane emissions, which in turn creates a biological "oasis" for megafaunal community at the site 21.

## References

- Burdige, D. J. (2007). Preservation of Organic Matter in Marine Sediments: Controls, Mechanisms, and an Imbalance in Sediment Organic Carbon Budgets? *Chemical Reviews*.  
<https://doi.org/10.1021/cr050347q>
- Caricchi, C., Lucchi, R. G., Sagnotti, L., Macrì, P., Morigi, C., Melis, R., Caffau, M., Rebesco, M., and Hanebuth, T. J. J. (2018). Paleomagnetism and rock magnetism from sediments along a continental shelf-to-slope transect in the NW Barents Sea: Implications for geomagnetic and depositional changes during the past 15 thousand years. *Global and Planetary Change*.  
<https://doi.org/10.1016/j.gloplacha.2017.11.007>
- Cordes, E. E., Cunha, M. R., Galéron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A., and Levin, L.A. (2010). The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity: Seep habitat heterogeneity, *Mar. Ecol.*, 31, 51–65,  
<https://doi.org/10.1111/j.1439-0485.2009.00334>
- Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R. (2002). Assessing the trophic state and eutrophication of coastal marine systems: A new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin*. [https://doi.org/10.1016/S0025-326X\(01\)00302-2](https://doi.org/10.1016/S0025-326X(01)00302-2)
- Gooday, A. J. (2002). Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography*, 58(2), 305-332. <https://doi.org/10.1023/A:1015865826379>
- Grémare, A., Medernach, L., DeBovee, F., Amouroux, J. M., Vétion, G., and Albert, P. (2002). Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Marine Ecology Progress Series*, 234, 85-94.  
<https://doi.org/10.3354/meps234085>
- Lantzsch, H., Hanebuth, T. J. J., Horry, J., Grave, M., Rebesco, M., and Schwenk, T. (2017). Deglacial to Holocene history of ice-sheet retreat and bottom current strength on the western Barents Sea shelf. *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2017.08.016>
- Lucchi, R. G., Bazzaro, M., Biebow, N., Carbonara, K., Caridi, F., De Vittor, C., ... and Krueger, M. (2016). BURSTER-Bottom Currents in a Stagnant Environment. EUROFLEETS-2 Cruise Summary Report.
- Martins, M. V. A., Pinto, A. F. S., Frontalini, F., da Fonseca, M. C. M., Terroso, D. L., Laut, L. L. M., Zaaboub, N., Rodriguez, M.A.C., and Rocha, F. (2016). Can benthic foraminifera be used as bio-indicators of pollution in areas with a wide range of physicochemical variability?. *Estuarine, Coastal and Shelf Science*, 182, 211-225. <https://doi.org/10.1016/j.ecss.2016.10.011>



- Mau, S., Römer, M., Torres, M. E., Bussmann, I., Pape, T., Damm, E., Geprägs, P., Wintersteller, P., Hsu, C.W., Loher, M. and Bohrmann, G. (2017). Widespread methane seepage along the continental margin off Svalbard-from Bjørnøya to Kongsfjorden. *Scientific Reports*.  
<https://doi.org/10.1038/srep42997>
- Rebesco, M., Özmaral, A., Urgeles, R., Accettella, D., Lucchi, R. G., Rüter, D., Winsborrow, M., Liopart, J., Caburlotto, A., Lantsch, H., and Hanebuth, T. J. J. (2016). Evolution of a high-latitude sediment drift inside a glacially-carved trough based on high-resolution seismic stratigraphy (Kveithola, NW Barents Sea). *Quaternary Science Reviews*. <https://doi.org/10.1016/j.quascirev.2016.02.007>
- Ślubowska-Woldengen, M., Koç, N., Rasmussen, T. L., Klitgaard-Kristensen, D., Hald, M., and Jennings, A. E., (2008). Time-slice reconstructions of ocean circulation changes on the continental shelf in the Nordic and Barents Seas during the last 16,000 cal yr BP. *Quaternary Science Reviews*, 27(15-16), 1476-1492.  
<https://doi.org/10.1016/j.quascirev.2008.04.015>
- Weniger, P., Blumenberg, M., Berglar, K., Ehrhardt, A., Klitzke, P., Krüger, M., and Lutz, R. (2019). Origin of near-surface hydrocarbon gases bound in northern Barents Sea sediments. *Marine and Petroleum Geology*, 102, 455-476. <https://doi.org/10.1016/j.marpetgeo.2018.12.036>

## Plate I

## Plate I

1. *Micrometula* sp.
2. *Allogromiid* sp. 35
3. *Allogromiid* sp. 9
4. *Cylindrogullmia* like
5. *Vellaria*-like
6. *Psammophaga* sp. 1
7. *Saccamminid* sp. 27
8. *Gromia ovale*

# Plate I

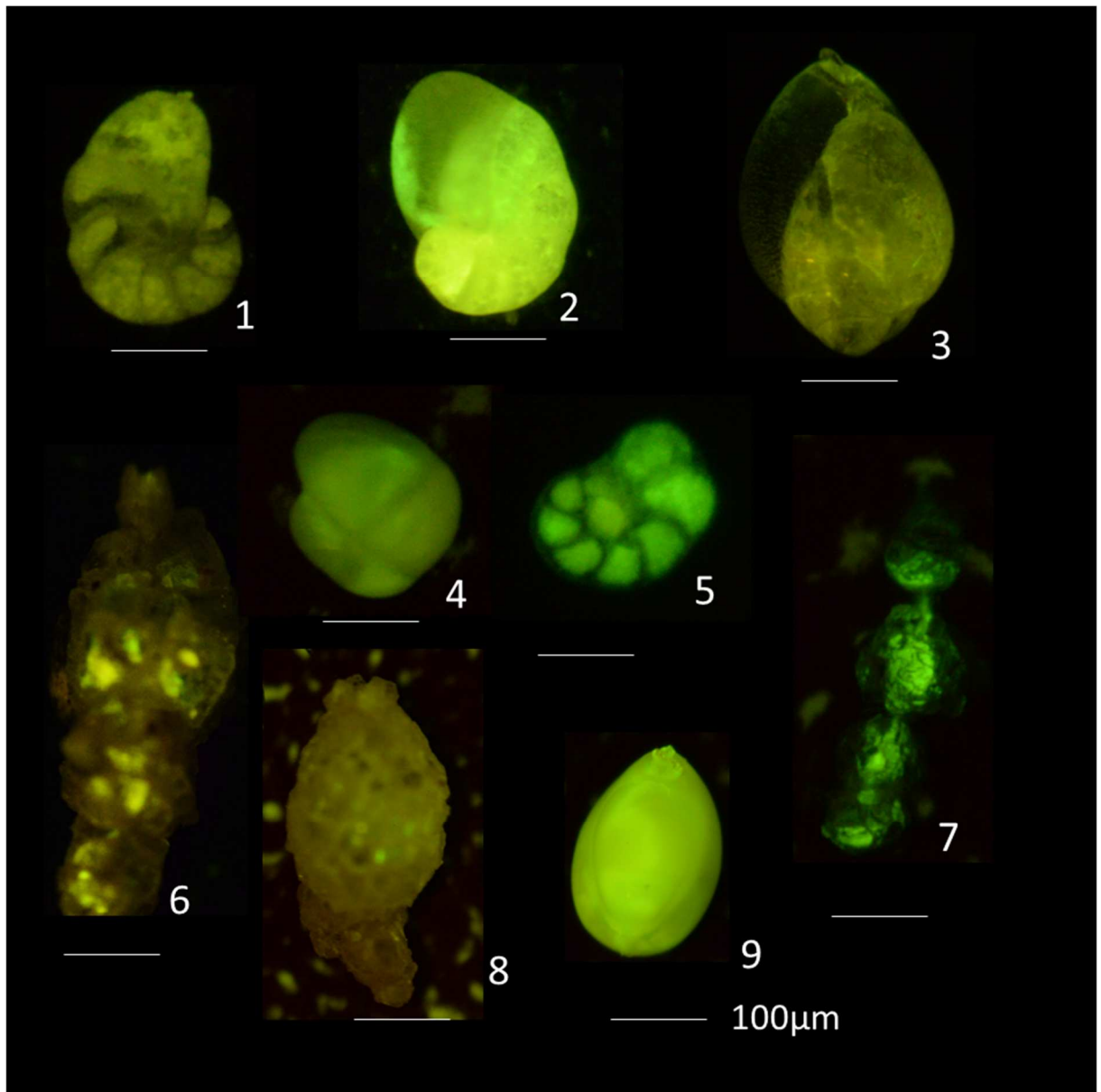


## Plate II

## Plate II

1. *Astrononion galloway*
2. *Nonionellina labradorica*
3. *Globobulimina auriculate*
4. *Pullenia bulloides*
5. *Islandiella norcrossi*
6. *Reophax scorpiurus*
7. *Hormosinelloides guttifer*
8. *Reophax subfusiformis*
9. *Pyrgo oblonga*

# Plate II



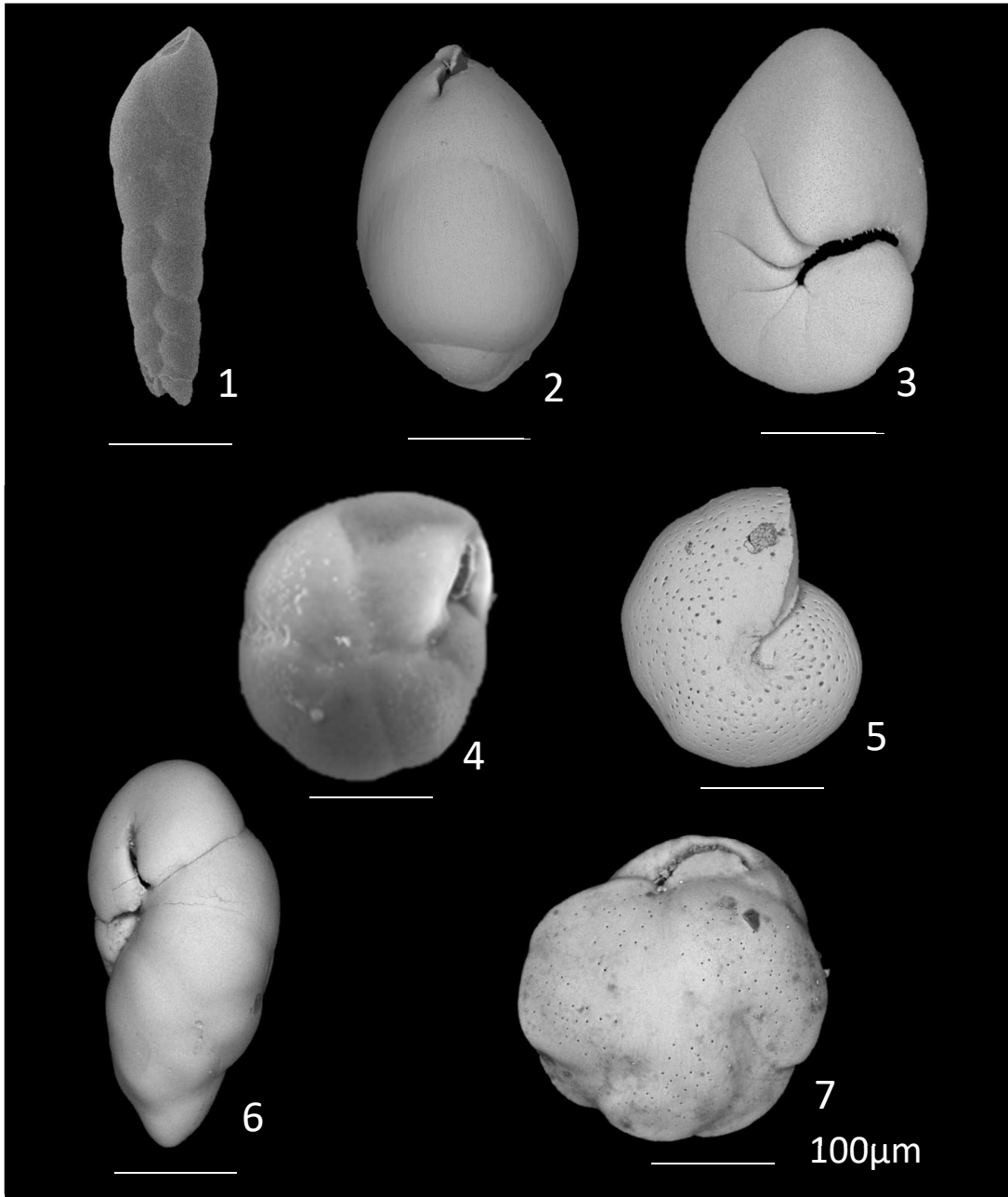
## Plate III



## Plate III

1. *Bolivinellina pseudopunctata*
2. *Globobulimina auriculate*
3. *Nonionellina labradorica*
4. *Islandiella norcrossi*
5. *Melonis barleanus*
6. *Robertinoides charlottensis*
7. *Cassidulina carinata*

Plate III

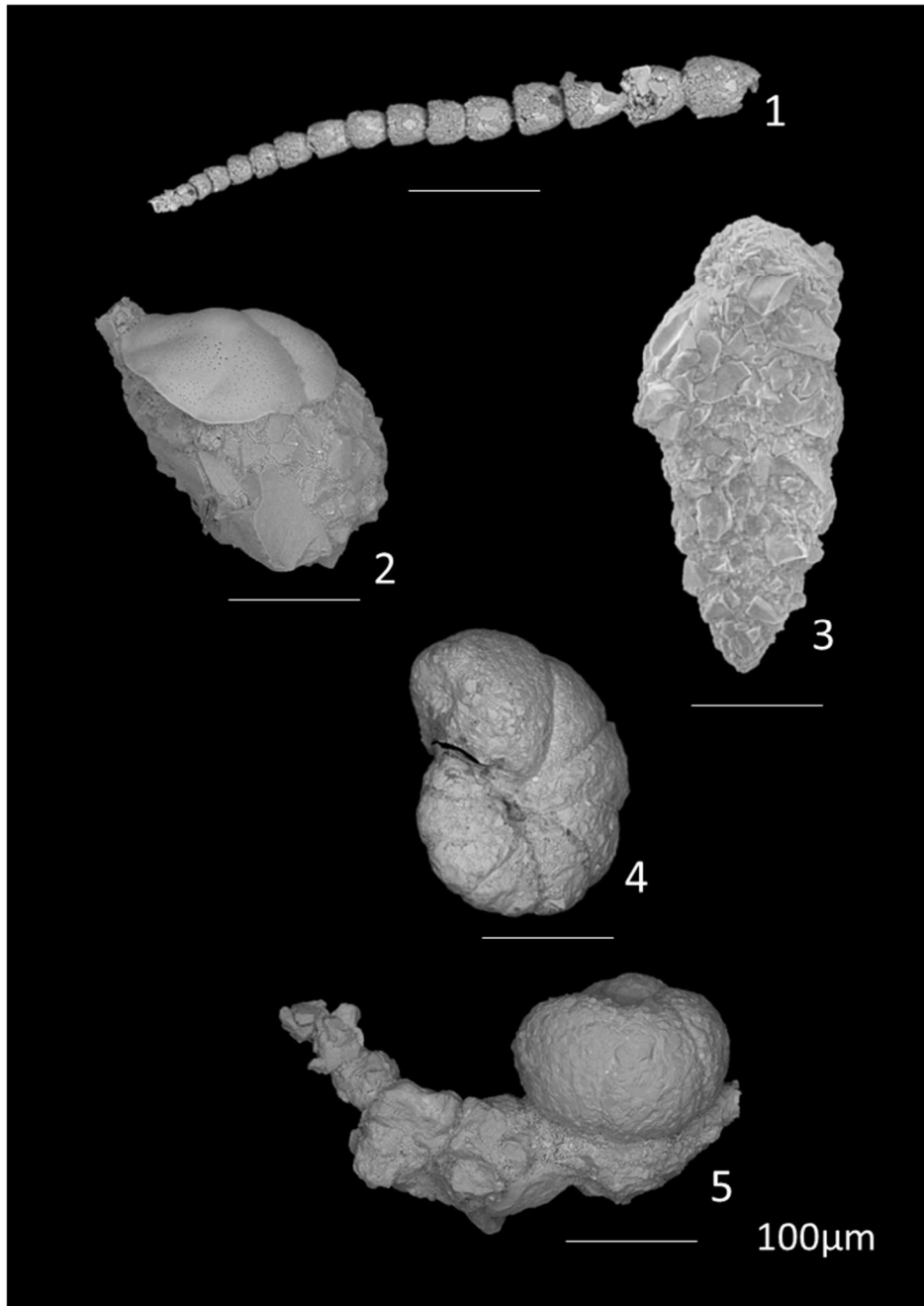


## Plate IV

## Plate IV

1. *Leptohalysis scottii*
2. *Lagenammina difflugiformis*
3. *Textularia earlandi*
4. *Labrospira crassimargo*
5. *Reophax scorpiurus*

Plate IV



## Plate V

## Plate V

1. *Allogromiid* sp. 35
2. *Allogromiid* sp. 7
3. *Allogromiid* sp. 9
4. *Vellaria*-like
5. *Gloiogullmia*-like

# Plate V





## Plate VI

## Plate VI

1. Saccamminiid sp. 7
2. Saccamminiid sp. 4
3. Saccamminiid sp. 7 (Sabbatini et al., 2013)
4. Saccamminiid sp. 27
5. Saccamminiid sp. 27
6. Psammophaga sp. 1

Plate VI

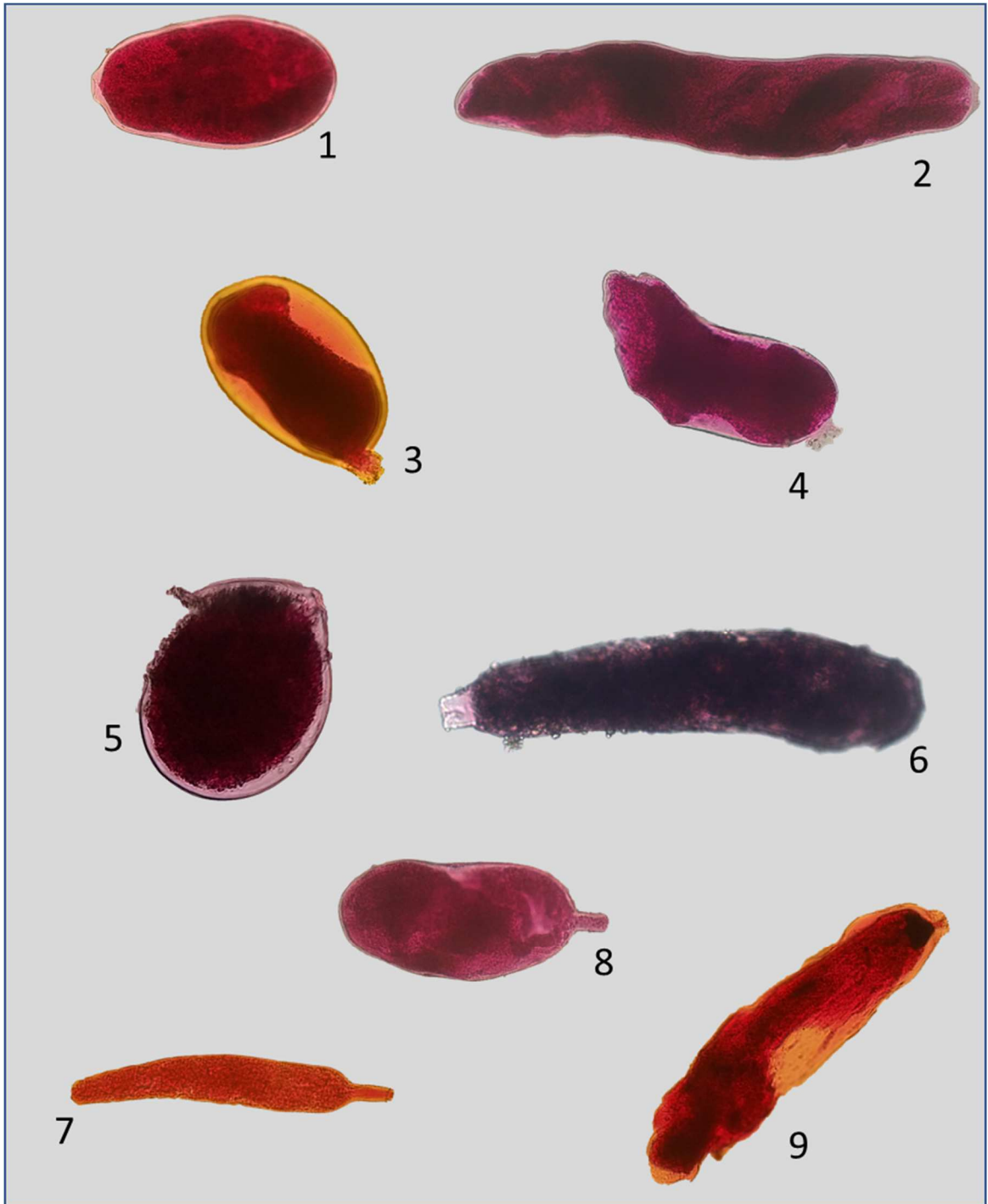


## Plate VII

## Plate VII

1. Allogromiid cf. sp. 3
2. Allogromiid sp. 35
3. Allogromiid sp. E
4. Allogromiid sp. F
5. Allogromiid sp. G
6. Allogromiid sp. F1
7. Allogromiid sp. F2
8. Allogromiid sp. F3
9. Allogromiid sp. F4

# Plate VII



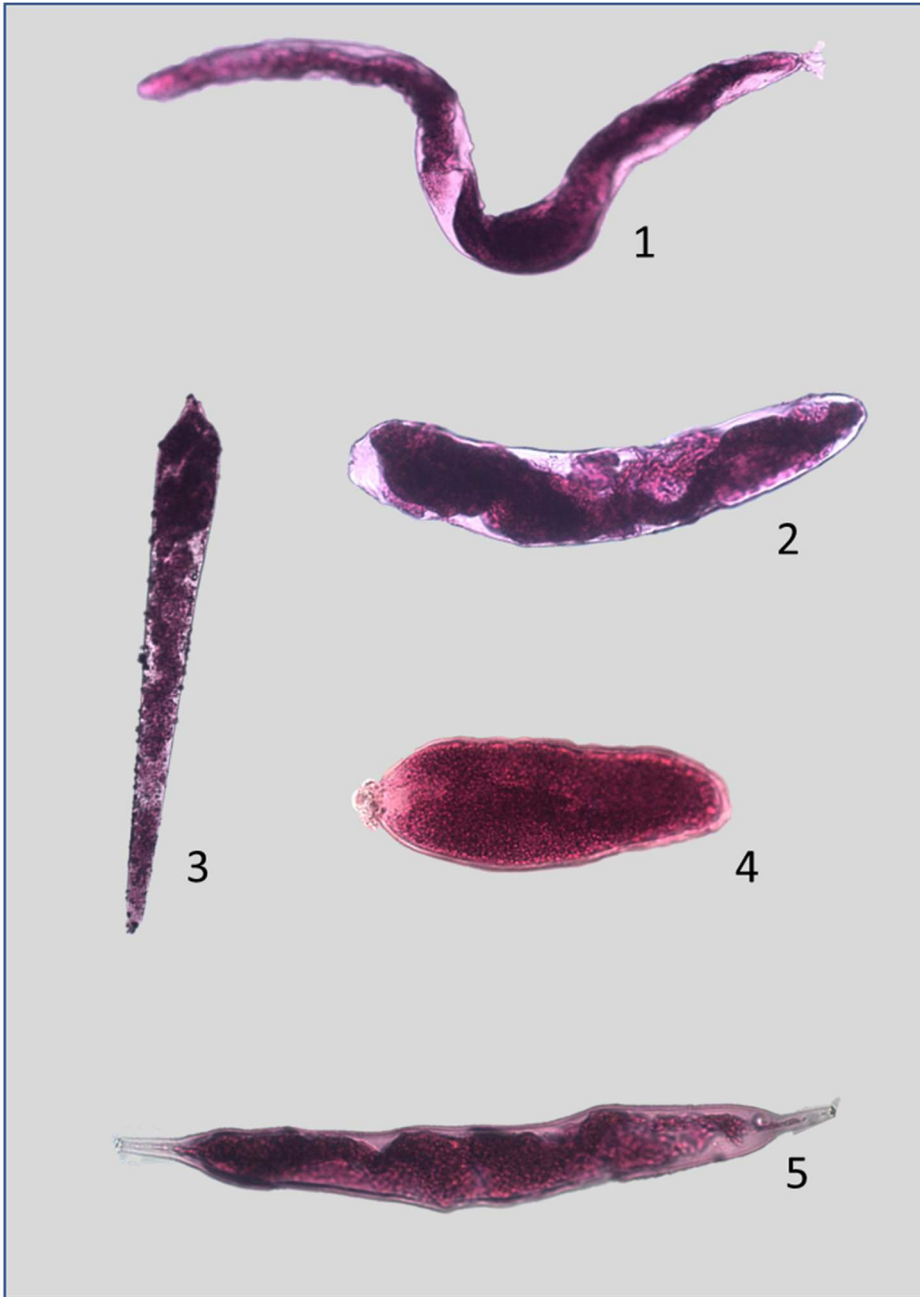
## Plate VIII

## Plate VIII

1. *Cylindrogullmia*-like
2. *Bowseria arctowiskii*
3. *Micrometula* sp.
4. *Gloiogullmia*-like
5. *Tinogullmia*-like



Plate VIII



## Plate IX

## Plate IX

1. Nodellum-like
2. Psammospheride sp. 5
3. Psammophaga arctica
4. Saccamminiid sp. 2
5. Saccamminiid sp. 4
6. Saccamminiid sp. 10
7. Saccamminiid sp. 11
8. Saccamminiid sp. F1

# Plate IX

