Fifteen years investigation of the meiofauna of the Faroe Bank (NE Atlantic)

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Abstract

During the last 13 years five cruises (1989, 90, 92, 98 and 2001) have collected bottom samples on the Faroe Bank for qualitative analysis of meiofauna, i.e. examination of the taxonomic composition and life cycle of small invertebrates (50-500 µm). These meiofaunal animals that live between the sand grains belong to the interstitial fauna and are normally known from shallow water. Samplings were conducted between 90 and 1,040 meters, and the sediments varied from basalt cobble and coarse shell-gravel to fine carbonate silt/mud. For comparison mud samples from 20-80 m were taken in the Kaldbak Fjord. It was discovered already in 1989, that the species diversity of the interstitial fauna of the Faroe Bank is very high, and similar to the meiofauna seen in carbonate sand in the tropics. However, like the macrofauna, only few meiofauna species had a high abundance. Therefore new techniques such as freshwater shocking and bulk trialdehyde fixation of very large sediment samples had to be developed during the first 15 years of investigation. The coarse calcareous sediment on the plateau of the bank (92-150 m depth) is very similar to the *Polygordius*-shell gravel found at much lower water depths at Helgoland (Germany) and Roscoff (France). The key macrofauna animals for the indication of a rich interstitial fauna are the annelid *Polygordius lacteus* and the echinoderm *Echinocyamus pusillus*. The calcareous sediments on the slopes of the Faroe Bank (160-270 m depths) are finer and have a fine fraction of coccoliths from the coccolithophorans *Emiliania huxleyi* and *Coccolithus pelagicus*. The meiofauna is similar to the communities from sea mounts in the Atlantic (400-500 m) and interestingly also the meiofauna found in calcareous *Globigerina* ooze (1,000-4,000 m). Until now only the gastrotrichs (19 species), loriciferans (12 species) and tardigrades (35 species) have been accounted for, however the aberrant families of nematodes, Epsilonematidae and Draconematidae, have been sorted out. New types of life cycles of the loriciferans were discovered in the otherwise well-known genus such as *Rugiloricus* and *Pliciloricus*; furthermore, a new order of Loricifera was discovered on the slopes of the bank. Among the most remarkable results is the high diversity of arthrotardigrades, however only few species are really common.

Introduction

The Faroe Bank is situated southwest of the Faroe Plateau, and the bank rises from the sea floor at 1,042 m until 92 m below sea level. The Faroe Bank, which is only one of the banks in the area, covers an area of approximately 5,000 km^2 (Magnussen, 2002). During the last 13 years the author has participated in five cruises (1989, 90, 92, 98 and 2001), and has collected bottom samples for qualitative analyses of the interstitial fauna of the bank. This meiofauna program was a part of the BIOFAR programme, which investigated the macrobenthic fauna of the Faroe Bank (see Bruntse and Tendal, 2001).

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Coarse sediment, primarily carbonate in origin, is predominant between 100-200 m on the rise of the Faroe Bank (Nørrevang *et al*., 1994), making it a unique habitat since such sediment is usually associated with much more shallow biotopes (5-50 m) at southern latitudes, e.g., the Brittany coast at Roscoff (Kristensen, 1983; Kristensen and Gad, 2004), and the Atlantic coast of Florida and Bermuda.

The areas mentioned are strongly influenced by the North Atlantic Current ("The Gulf Stream") and the sediment consists of mixed coralline/mollusc shell-sand. In the early eighties an American-Danish team investigated the localities and a very rich interstitial fauna was found subtidally for the first time (Kristensen and Higgins, 1989). Most spectacular is a whole new phylum of animals, the loriciferans, described in 1983 from this type of carbonate sediment at Roscoff (Kristensen, 1983). Later the new phylum was also recorded from southeastern U. S. coastal waters (Higgins and Kristensen,1986).

The meiofauna on the Faroe Bank is extremely rich and exhibits a strong taxonomic affinity with the fauna from more southern latitudes, i.e. the Mediterranean Sea (Todaro and Kristensen, 1998; De Zio Grimaldi and D'Addabbo Gallo, 2001; Hansen *et al*., 2003), the southeastern coast of USA and Bermuda (Kristensen and Higgins, 1984a; 1989), and less so to the rich meiofaunal community off the coast of Roscoff, Brittany (Swedmark, 1956; Kristensen, 1978; Kristensen and Renaud-Mornant, 1983). The similarity of the meiofauna, e.g. the loriciferans, from the seamounts (Great Meteor Bank, about 500m, Gad, 2004; Gad and Schminke, 2004) and from the Faroe Bank (100-200m, Heiner and Kristensen, in press) is a new observation. Seamounts may be "the stepping stones" for the southern element of the meiofauna found on the Faroe Bank.

Special Methods

The meiobenthos sampling was modified and developed during the BIOFAR programme. Different sampling gears such as Multiple cores, Reineck box corer and Smith-McIntyre grab were tried, especially during the *Valdivia* cruise (1990). However, none of these classical gear types were working sufficiently well in the coarse and rough bottom sediments of the Faroe Bank. The specially designed Higgins Meiofauna dredge (Fig.1B) was working perfectly, however it took too small samples, so in most cases it was necessary to use a heavy and sturdy triangular dredge, which could take up to 1,000 kg sediment. We supported the dredge with a very fine net made out of old salt sacs. This dredge was working excellently on the plateau of the bank. However, the most interesting localities were located on the slopes (see Fig. 1., Heiner, 2005). Here the topography was very rough with basalt pillars, and after loosing two triangular dredges, we finally decided to use a modified Plymouth anchor dredge (Fig. 1A). In fact, this dredge works as a large grab. We employed it only for a few minutes before it was hauled again, and it could collect more than 1,000 kg sediment in one sample.

In total, 31 samples (1989-2001) were

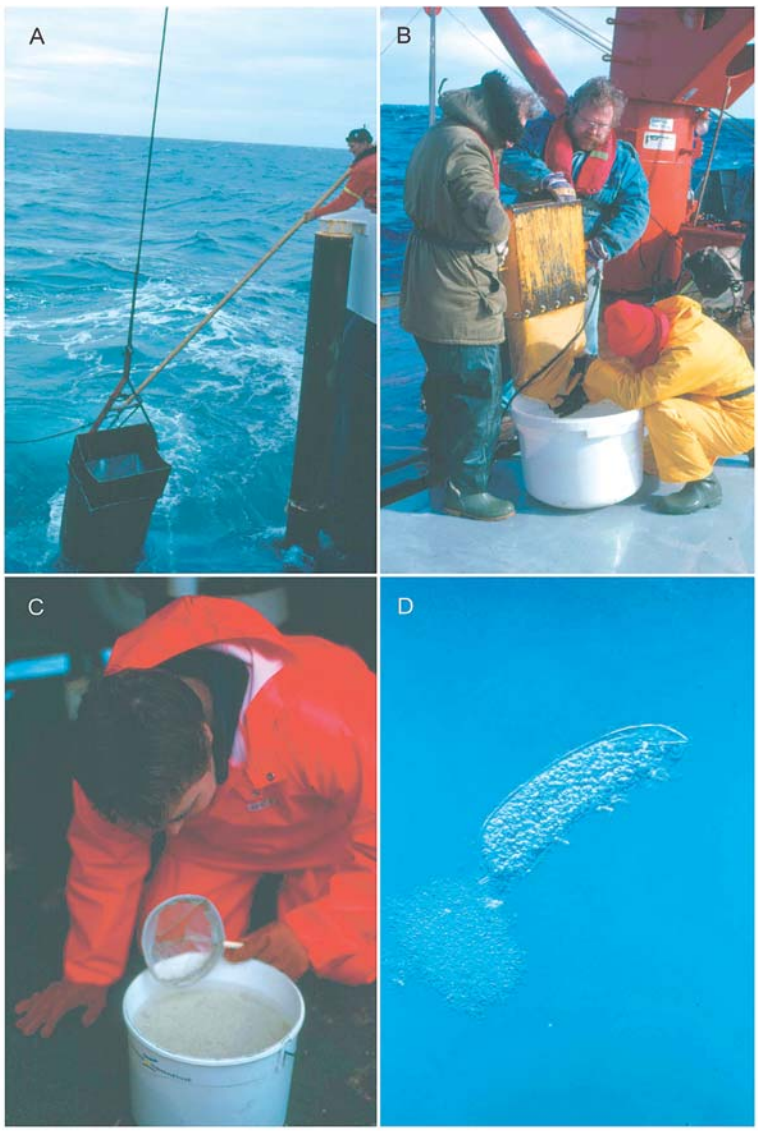

Fig. 1. *Collection methods and techniques for meiofauna in the BIOFAR program. A. The sample from BIOFAR St. 627 is 500 kg clean carbonate sand in a modified Plymouth anchor dredge ('Valdivia' cruise). B. The sample (50 kg) of clean shell hash from BIOFAR St. 626 is emptied in the bucket. Sample gear was a Higgins Meiofauna dredge ('Valdivia' cruise). C. Clean carbonate sand from BIOFAR St. 2013. The sample consists of 250 kg, however it was divided into six subsamples. The subsample shown at the photo was treated with freshwater and the meiofauna was decanted through a 32 μm net (Gwen's mermaid bra). D. The deep-sea tardigrade genus* Coronarctus *from BIOFAR St. 627. Note the bacteria colony on the rear end of the tardigrade. The animal is about 250 μm long.*

taken for meiofauna, and several others for sediment analyses and foraminifers. The large samples were immediately subdivided into several subsamples. About half were treated with freshwater on board the ship and the detritus with meiofauna was decanted through a 32-63 µm net (Gwen's mermaid bra, Fig. 1C). After the freshwater treatment the samples were again subdivided. For transmission electron microscopy the meiofauna was bulk fixated in a trialdehyde fixation mixture (Neuhaus *et al*., 1997; Kristensen and Neuhaus, 1999). For light and scanning electron microscopy it was fixated in 4% formaldehyde buffered with Borax (Jørgensen and Kristensen, 2001). Finally, the meiofauna was fixated in 80% ethanol or dimethyl sulphoxide (DMSO) for molecular studies. All animals were later sorted out in the laboratory and in many cases the decanted material with meiofauna was stained with Rose Bengal. The soft body meiofauna (Turbellaria, Gastrotricha, Annelida and Mollusca) do not tolerate the freshwater treatment; therefore these animals were treated with isotonic magnesium chloride (Mg_2Cl) and observed alive before they were preserved in glycerol.

Main results

The tardigrades (Hansen *et al*., 2001; 2003; Jørgensen and Kristensen, 2001), loriciferans (Heiner, 2003; Heiner, 2005, b; Heiner and Kristensen, 2004) and gastrotrichs (Clausen, 2004) at the Faroe Bank have been extensively studied and several species new to science have been described. However, the processing of the material requires thousands of man-hours before final results can be published. The sorting and preparations for light microscopy and scanning and transmission electron microscopy are very time consuming as is thorough descriptions of the many new species. The papers that have been published on the material have treated tardigrades (Hansen *et al.,* 2001; 2003; Jørgensen and Kristensen, 2001) and the crustacean class Tantulocarida (Huys *et al.*, 1992). Furthermore, loriciferans (BIOFAR st. 785) and tardigrades (BIOFAR st. 785, st. 787) from the Faroe Bank have been used for ultrastructural research and demonstration of chitin in the cuticle (Neuhaus *et al.*, 1997; Kristensen and Neuhaus, 1999).

The nematodes are usually the most dominant phylum of meiofauna animals, however in coarse sediments the typical worm-shaped nematodes are often rare. Instead, the aberrant families Epsilonematidae and Draconematidae are very common. These animals have a very specialised external morphology, and they move around on the sand grains as an inch worm. The species from the Faroe Bank have been sorted out, and a species list is under preparation (Gad, in prep).

The high diversity (19 species) of gastrotrichs from six stations (BIOFAR sts. 570, 571, 572, 586, 625 and 626) is unusual (Clausen, 2004). Especially interesting are the new records of *Chordodasys antennatus* from the plateau of the Bank (BIOFAR sts, 786, 1991). This very modified gastrotrich was described from North Carolina (Rieger *et al.*, 1974), the holotype be-

ing collected at 97 m depth in sandy shell off Beaufort. The two genera *Xenodasys* and *Chordodasys* are closely related and both have developed a chordoid organ in the back. *Xenodasys sanctigoulveni* was taken at several BIOFAR stations, while *Chordodasys antennatus* only occurred in very clean coarse sediment. With the long antennae-like sense organs this gastrotrich looks more like an arthropod, and it may have been overlooked by us in the first years' samplings of BIOFAR.

One of the highlights was to discover a tardigrade, *Tanarctus bubulubus* Jørgensen and Kristensen, 2001 with 18 buoyant bodies (see Fig. 2). One specimen was observed alive drifting in the water column with the head downwards (Jørgensen and Kristensen, 2001); this may be the first observation of true dispersal organs in an interstitial animal. Otherwise the dispersal of interstitial species has been called the "meiofauna paradox" (Giere, 1993; Gad and Schminke, 2004). Nearly all groups of interstitial animals are strongly attached to the sediment grain, and they lack planktonic larvae for dispersal; however there is a high percentage of cosmopolitan species in all described phyla from coarse marine sands. The cosmopolitan tardigrade, *Tholoarctus natans* was found at several stations on the Faroe Bank (see figs. 22-29, Kristensen and Neuhaus, 1999). This animal may be semi-planktonic and it seems to be widely distributed chiefly in tropical coralline sand (Kristensen and Renaud-Mornant, 1983). The dispersal organ may be the enlarged bell-shaped epicuticle. It was suggested in the description that the bell was used for swimming just above the sediment, but it could also be used for passive dispersal.

Nearly all metazoan meiofauna phyla were found at the Faroe Bank, but one, Priapulida, was missing. This is very interesting because interstitial priapulids are elsewhere very common in carbonate sediments, especially the genus *Tubiluchus* in coralline sand, which has been found as far north as Tjärnö, Sweden, in dirty shell-sand (Erséus, pers. com.). The kinorhynchs were also rare on the bank compared to the very rich kinorhynch fauna we found in the mud of the fjords (BIOFAR sts. 628-634).

The overall impression is that there is a greater meiofauna diversity on the bank than in the mud. The interstitial Turbellaria, Nematoda, Gastrotricha, Polychaeta, Tardigrada, harpacticoid Copepoda, Ostracoda, and Halacaridae (Acarina) were the most abundant taxa present. Less abundant taxa were Cnidaria, Kinorhyncha, Loricifera and Mollusca (Aplacophora and Gastropoda). A total overview of the meiofauna of the Faroe Bank is under preparation.

The mysterious "Ghost larva".

Jeanne Renaud-Mornant found the first ghost larva (Kristensen *et al*., 2003) at 3,660 m depth in calcareous *Globigerina* ooze, which was collected the 27 August 1986 by CENTOB (Brest) from the station KG 228 (Bay of Biscay)**.** The ovoid larva does not have any external sensory structures, but a few internal scalid-like structures in the anterior part of the body and an ovary with a large oocyte in the abdomen. It was not until 1992 that the mystery of what

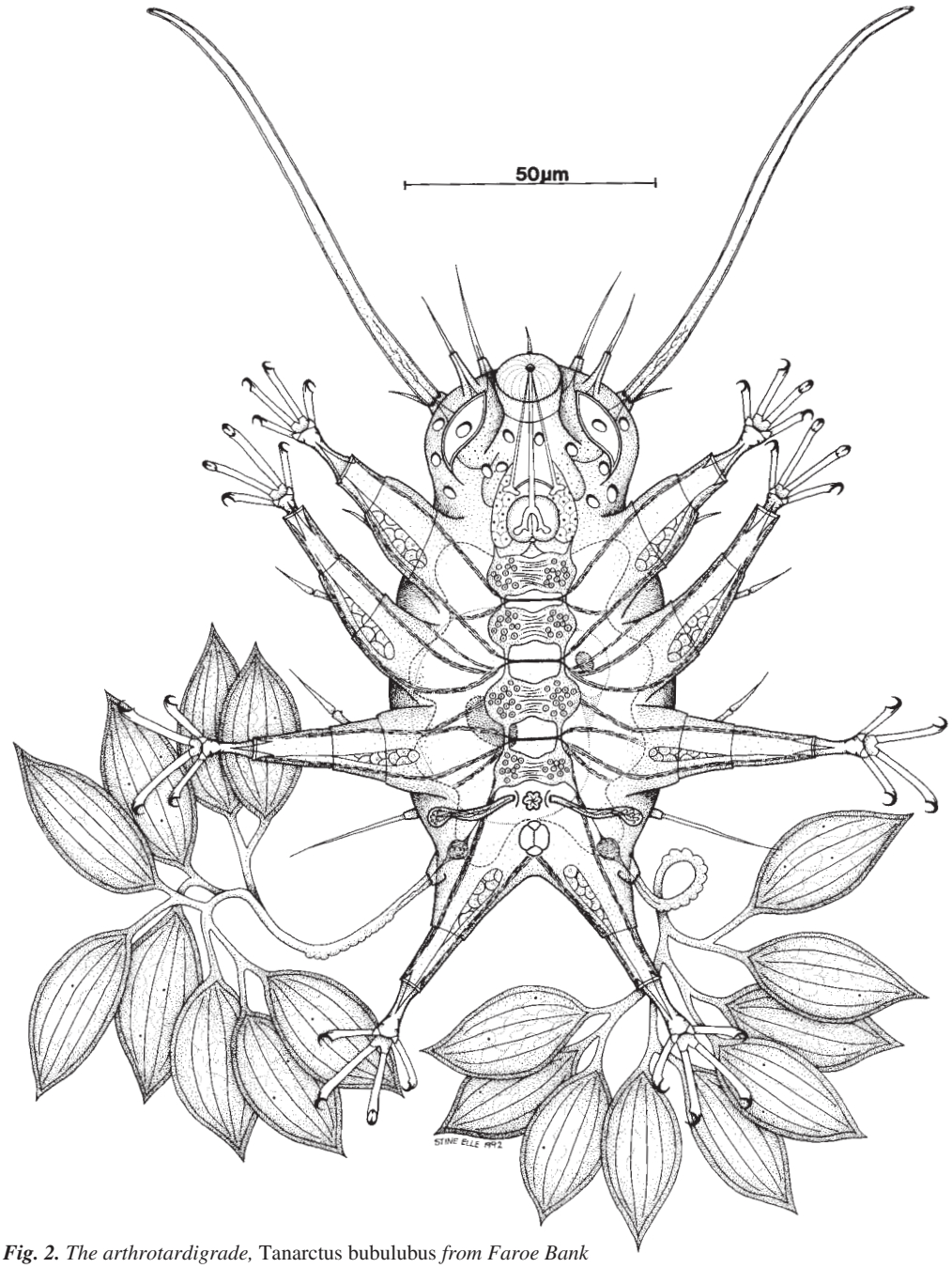

Fig. 2. *The arthrotardigrade,* Tanarctus bubulubus *from Faroe Bank (BIOFAR St. 573). The 18 balloons are modified sense organs. They may function as buoyant bodies (Drawn by Stine Elle).*

kind of animal the ghost larva belonged to was solved. A large material of Higgins larvae of the loriciferan genus *Rugiloricus* was found on the Faroe Bank. Inside several exuvia of larvae with toes a single strongly modified ghost larva was discovered. In some exuvia the ghost larvae had laid eggs, otherwise they looked exactly like the first discovered free-living larva from 1986. Several eggs were embryonated, and in two eggs a fully developed Higgins larva with toes could be observed. After a search for free-living ghost larvae in sediment from the Faroe Bank no less than three types of larvae were found, all containing oocytes or eggs. These ghost larvae do not resemble any other kind of larvae seen in the loriciferans, and this makes the life cycles of the genus *Rugiloricus* much more complicated than first assumed. Three types of life cycles have now been discovered in this genus. In *R. cauliculus* the Higgins larva moults into a postlarva without toes and gonads. The postlarva becomes cyst-like and perhaps after months it moults into the adult. In *R. carolinensis* and the genus *Pliciloricus* the Higgins larva moults directly into the adult. Interestingly, during metamorphosis the larva forms a very thin extra cuticle before the adult cuticle. This could indicate that the postlarva has been reduced inside the Higgins larva. The three new species of *Rugiloricus* from the Faroe Bank seem to have both a normal sexual reproduction with males and females, and a parthenogenetic reproduction (neoteny) with ghost larvae. In these species the Higgins larva grows bigger than the adult and develops a large single ovary: This larva forms a cyst-like stage inside which a moult occurs. The new larva, the ghost larva, may be retained in the old exuvium of the Higgins larva; after forming several eggs from the ovary the ghost larva disintegrates. The eggs mature to new neotenous larvae, each of which develop an ovary. Unknown factors may cause the ghost larva to hatch from the exuvium of the Higgins larva, which results in the mysterious ghost larva - first found in 1986.

BIOFAR St. 627

The BIOFAR station 627 (taken during the Valdivia-cruise 1990, 18 April) differs from all other stations with coarse sediments. The sampling site (61º17.66'N, 08º32.25'W, depth 260 m) is located near an area of a natural gas discharge on the northern slope of the Faroe Bank. A more than 500 kg sample was taken with a Plymouth anchor dredge (Fig. 1A). The sediment consists of a mixture of fine carbonate shell-sand and basalt-sand. The calcareous part of the sediment had a fine fraction of coccoliths from the coccolithophorans *Emiliania huxleyi* and *Coccolithus pelagicus*. The very clean sediment contained a negligible amount of detritus, but high numbers of bacteria were present (own observation). The bacteria were found free in the sediments or attached to meiofauna animals (fig. 1D). The bacteria may have been methano-bacteria associated with the gaseous emissions, however no analysis was made.

The interstitial fauna in the sample was unique! The dominant groups were interstitial nematodes (several species of the aber-

rant genera *Desmoscolex*, *Draconema* and *Epsilonema*) and harpacticoid copepods; however the meiofauna also included 6 genera of gastrotrichs, 15 species of tardigrades (one species belonging to the deep-sea family Coronarctidae (fig. 1D), and another species, belonging to the tidal genus *Batillipes*), and seven species of Loricifera, one of which belongs to a new order with pedogenesis (Heiner, 2003; 2004). Later this type of Loricifera was also found in the deep-sea (Gad, 2003). One stage of the new loriciferan order was totally covered with coccoliths, and the loriciferan was first discovered after squeezing the species on the slide. Seven species of loriciferans gives this station the highest diversity of loriciferans in the world.

A new genus of the parasitic crustacean class, Tantulocarida (Huys *et al.*, 1992) was also present at this unique station. The class was first described in 1983 (Boxshall and Lincoln, 1983) and there are still only few records of the free-living larva. The rare free larva (tantulus) of the new species *Tantulacus hoegi* was found in the sediment. The adults were not found, however they may parasize the harpacticoid copepods present.

BIOFAR St. 785

The station BIOFAR St. 785 was sampled with a Plymouth anchor dredge at the 1 April 1992 ('Ólavur Halgi' cruise). The sampling site (61º17.78'N, 08º32.25'W, depth 249 m) is close to the BIOFAR 627 with the natural gas discharge on the northern slope of Faroe Bank. However, there were few bacteria in the sediment. The sample was relative small (20 kg) consisting of fine carbonate sand with a small fraction of basalt pebbles. The meiofauna was totally dominated by loriciferans, more than 200 specimens. Three types of the free ghost larvae and the postlarva of *Rugiloricus* were found. Furthermore, the larva and the cyst-like ghost larva of the new order were present in the same sample. However, 85% of all specimens are *Rugiloricus* larvae, only very few adults were found. Several of the larvae had an ovary (neoteny) and a few had moulted to the ghost larva, which had already laid eggs. Without BIOFAR St. 785 we would never have figured out the riddle about the ghost larva in the deep-sea (Kristensen *et al.,* 2003).

The sample also contains a high diversity of tardigrades. More than 150 specimens were sorted out from this sample and until now 19 species belonging to 11 genera have been identified. The most dominating species were *Actinarctus* cf. *physophorus* and *Raiarctus aureolatus*. (see Hansen *et al.,* 2001). The association between the mini sand dollar *Echinocyamus pusillus* and the tardigrade *Actinarctus* cf. *physophorus* was refound, this association was already mentioned from *Polygordius*-sand (Helgoland), when the genus *Actinarctus* was described (Schulz, 1935/37). A new species of *Pseudostygarctus* was also common at this station. This is the most northern record of the family Stygarctidae. The new species has only two claws on each leg (larval character = progenesis); however, the females have seminal receptacles and a well-developed ovary.

Discussion

The calcareous sediment and the hydrography of the area are probably the key factors responsible for the high biodiversity, and for making the diversity of meiofauna at the Faroe Bank comparable to the rich calcareous sediments found at tropical coral reefs. Due to the influence of the North Atlantic Current the plateau of the Bank is warm (9-11 °C) even during winter (Westerberg, 1990). Furthermore, the strong current, so-called anti-gyro give the reason for the coarse sediments on the Faroe Bank

The high temperature may explain the composition of species, which exhibits a strong taxonomic affinity with the fauna from more southern latitudes, i.e. the Mediterranean Sea and the southeastern coast of USA (Kristensen and Higgins, 1989). However, the physical-chemical characteristics of the sediment may be more influential in the distribution of meiofauna than depth or water temperature. This theory is supported by the fact that the meiofauna in the mud both from shallow water (Kaldbak Fjørður, 20-80 m) and deeper water (Faroe Bank Channel, 1,040 m) has a northern origin. This so-called "carbonate sediment theory" may also explain why deep-sea tardigrade genera (*Coronarctus* and *Parmursa*) elsewhere found in calcareous *Globigerina* ooze (1,000-4,000 m) are found on the slopes of the Faroe Bank (Hansen *et al.,* 2003; Hansen, 2005). The type species of *Rhomboarctus* (*R. thomassini* Renaud-Mornant, 1984) was found at 770 m in the Mozambique Channel, and the new species from the Faroe Bank, *R. aslaki* Hansen, Gallo D'Addabbo and De Zio Grimaldi, 2003 was found at water depths from 139 to 260 m.

The carbonate sediment theory cannot explain why the arthrotardigrade genus *Batillipes* has been found at several BIOFAR stations. The deepest record in the world is BIOFAR St. 627 (260 m). The genus *Batillipes* is usually found in tidal sandy beaches. These findings may support the theory that the Faroe Bank has partly been dry during the Ice Age (Heinesen, 1993) and that several low-water species have survived after the sea level has risen with about 100 m. This "sunken Atlantis theory" was first suggested by Kristensen (1999) based on low-water tardigrades. A component of arctic low-water meiofauna could have survived since the Ice Age on the Bank. Two Arctic species of arthrotardigrade genus *Styraconyx* are recorded from the Bank, *S. qivitoq* and *S. nanoqsunguak* which were originally described from Disko Bay, West Greenland (Kristensen and Higgins, 1984b). Recently (own observation) we also found the kinorhynch *Echinoderes peterseni*, which was described by Higgins and Kristensen (1988) from the Disko Fjord. However, the two species of tardigrades and the kinorhynch have been found inside nodules of the $CaCO_3$-encrusted red alga *Lithothamnion glaciale*, so these findings rather show that these low-water species prefer carbonate substrate. During the symposium in Tórshavn (2003) we discussed "the sunken Atlantis theory". At stations with coarser shell-sand and shell-gravel (100-200 m), a varying number of live specimens of the

large shallow water bivalve *Gari fervensis* (Gmelin, 1791) can be observed. This macrofauna species may support the "the sunken Atlantis theory".

Acknowledgements

The BIOFAR Steering Committee is thanked for their invitation to the BIOFAR symposium 2003. The following persons are warmly thanked for their support to the present study: Arne Nørrevang, Jan Sørensen, Hjalmar Thiel, Ole S. Tendal and the staff of the Kaldbak Marine Laboratory (BIOFAR). Special thanks to Eyðfinnur Magnussen and Hjalti í Jákupsstovu (Faroese Fisheries Laboratory) who invited all my students and me to participate in the 1998 and 2001 cruises. Especially my students, Iben Heiner and Jesper G. Hansen, are gratefully acknowledged for sharing their results with me, and Aslak Jørgensen for leading the sorting of the tardigrades and loriciferans. I also acknowledge the crew on all the Faroe Bank expeditions, 'Ólavur Halgi' (1989, 1992), R/V 'Valdivia' (1990) and R/V 'Magnus Heinason' (1998, 2001). Financial assistance came from the Danish Research Agency and the Carlsberg Foundation.

References

Bruntse, G. and Tendal, O. S. 2001. *Marine biological investigations and assemblages of benthic invertebrates from the Faroe Islands (with contributions from G. Bruntse, G. Dinesen, A.B. Josefson, A.B. Klitgaard and O.S. Tendal)*. Kaldbak Marine Biological Laboratory, The Faroe Islands. 80 pp.

Boxshall, G.A. and Lincoln, J. 1983. Tantulocarida, a new class of Crustacea ectoparasitic on other crustaceans. *Journal of Crustacean Biology* 3: 1-16.

Clausen, C. 2004. Gastrotricha of the Faroe Bank. *Sarsia* 89: 423-458.

De Zio Grimaldi, S. and D'Addabbo Gallo, M. 2001. Further data on the Mediterranean Sea tardigrade fauna. *Zoologischer Anzeiger* 240: 354-360.

Gad, G. 2003. New light on deep-sea Loricifera. *Deep-sea Newsletter* 32: 4-5

Gad, G. 2004. The Loricifera fauna of the plateau of the Great Meteor Seamount. *Archives of fishery and marine research*: 51: 9-29

Gad, G. and Schminke, H. K. in press. How important are seamounts for the dispersal of meiofauna? *Archives of fishery and marine research*: 51: 43-54

Giere, O. 1993. Meiobenthology – the microscopic fauna in aquatic sediments. Springer Verlag, Berlin, 329 pp.

Hansen, J.G. 2005. The ongoing investigation of the Faroe Bank tardigrade fauna. *BIOFAR Proceedings 2005*: 220-223.

Hansen, J.G., Jørgensen, A. and Kristensen, R.M. 2001. Preliminary studies of the tardigrade fauna of the Faroe Bank. *Zoologischer Anzeiger* 240: 385-393.

Hansen, J.G., Gallo D'Addabbo, M. and De Zio Grimaldi, S. 2003. A comparison of morphological characters within the genus *Rhomboarctus* (Tardigrada: Heterotardigrada) with the description of two new species. *Zoologischer Anzeiger* 242: 83-96.

Heiner, I. 2003. The loriciferan fauna of the Faroe Bank, North Atlantic with emphasis on the different types of life cycles. University of Copenhagen. *Unpublished M. Sc. Thesis.*

Heiner, I. 2004. *Armorloricus kristenseni* (Nanaloricidae, Loricifera) a new species from the Faroe Bank (North Atlantic). *Helgoland Marine Research* 58: 192-205

Heiner, I. 2005. Preliminary account of the Loriciferan fauna of the Faroe Bank. *BIOFAR Proceedings 2005*: 213-219.

Heiner, I. and Kristensen, R.M. in press. Two new species of the genus *Pliciloricus* (Loricifera, Nanaloricida, Pliciloricidae) from the Faroe Bank, North Atlantic. *Zoologischer Anzeiger*:

Heinesen, M.V. 1993. Færø Banke-områdets geologi. *In*: Gaard, E. and Poulsen, M. (eds). *Færøbanke projektet, Seminar om Færøbanken, Torshavn, 12.-13. Nov.,1992*: 113-115.

Higgins, R.P. and Kristensen, R.M. 1986. New Loricifera from Southeastern United States Coastal Waters. *Smithsonian Contributions to Zoology* 438: 1-70.

Higgins, R.P. and Kristensen, R.M. 1988. Kinorhyncha from Disko Island, West Greenland. *Smithsonian Contributions to Zoology*. 458: 1-56.

Huys, R. Andersen, P.F. and Kristensen, R.M. 1992. *Tantulacus hoegi* gen. et sp. nov. (Tantulocarida: Deoterthridae) from the meiobenthos of the Faroe Bank, North Atlantic. *Sarsia* 76: 287-297.

Jørgensen, A. and Kristensen, R.M. 2001. A new tanarctid arthrotardigrade with buoyant bodies. *Zoologischer Anzeiger* 240: 425-439.

Kristensen, R.M. 1978. Notes on marine heterotardigrades. 1. Description of two *Batillipes* species, using the electron microscope. *Zoologischer Anzeiger* 200: 1-17.

Kristensen, R.M. 1983. Loricifera, a new phylum with aschelminth characters from the meiobenthos. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 21: 163-180.

Kristensen, R.M. 1999. Ten years investigation of a sunken Atlantis: the meiofauna of Faroe Bank. *Danish national council for Oceanology, Norske havforskeres forening, Svenska havforskningsforeningen. 2nd Nordic marine science meeting, 2-4 march, 1999, Abstract book*: pp. 58-59

Kristensen, R.M. and Gad, G. 2004. *Armorloricus* a new genus of Loricifera (Nanaloricidae) from Trezen ar Skoden (Roscoff, France). *Cahiers de biologie marine* 45: 121-156

Kristensen, R.M. and Higgins, R.P. 1984a. A new family of Arthrotardigrada (Tardigrada: Heterotardigrada), from the Atlantic Coast of Florida, USA. *Transactions of the American Microscopical Society* 103: 295-311.

Kristensen, R.M. and Higgins, R.P. 1984b. Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with descriptions of two new species from Disko Bay, West Greenland. *Smithsonian Contributions to Zoology* 391: 1-39.

Kristensen, R.M. and Higgins, R.P. 1989. Marine tardigrades from the Southeastern United States coastal waters. 1. *Paradoxipus orzeliscoides* nov. gen., nov. sp. (Tardigrada: Halechiscidae). *Transactions of the American Microscopical Society* 108: 262-282.

Kristensen, R.M. and Neuhaus, B. 1999. The ultrastructure of the tardigrade cuticle with special attention to marine species. *Zoologischer Anzeiger* 238: 261-281.

Kristensen R.M., and Renaud-Mornant J. 1983. Existence d'arthrotardigrades semi-benthiques de genres nouveaux de la sous-famille des Styraconyxinae subfam. nov. *Cahiers de Biologie Marine* 24: 337-353.

Kristensen, R. M., Heiner, I. and Jørgensen, A. 2003. The mysterious „Ghostlarva" from the deep sea is a loriciferan larva. *First International DIVA Workshop, Wilhelmshaven, pp. 30-31.* (abstract)

Magnussen, E. 2002. Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. *Marine Ecology Progress series* 238: 211-225.

Neuhaus, B., Kristensen, R.M. and Peters, W. 1997. Ultrastructure of the cuticle of Loricifera and demonstration of chitin using Gold-Labelled Wheat Germ Agglutinin. *Acta Zoologica* (Stockholm) 78: 215-225.

Nørrevang, A., Brattegard, T., Josefson, A.B., Sneli, J-A. and Tendal, O.S. 1994. List of BIOFAR stations. *Sarsia* 79:165-180.

Rieger, R.M., Ruppert, E.E., and Schoepfer-Sterrer, C. 1974. On the fine structure of gastrotrichs with description of *Chordodasys antennatus* sp. n. *Zoologica Scripta* 3 : 219-237.

Schultz, E. 1935/37. *Actinarctus doryphorus* nov. gen., nov. spec. ein merkwürdiger Tardigrad aus der Nordsee. *Zoologischer Anzeiger* 111: 285-288.

Swedmark, B. 1956. Nouveaux Gastrotriches Macrodasyoides de la région de Roscoff. *Archives de Zoologie Expérimentale et Générale* 94: 43-57.

Todaro, M.A. and Kristensen, R.M. 1998. A new species and first report of the genus *Nanaloricus* (Loricifera, Nanaloricida, Nanaloricidae) from the Mediterranean Sea, *Italian Journal of Zoology* 65: 219-226

Westerberg, H. 1990. Bentic temperature in the Faroe area. *Department of Oceanography, University of Gothenburg, Sweden. Report no.* 51: 1-19