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Diversity and abundances of foraminifera in living sponges of the Norwegian-Greenland Sea

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ABSTRACT

Foraminifera nourishing on fresh organic matter often exhibit an epibiotic or even an epizoic lifestyle. This study investigates the colonization of sponges by foraminifera. For this purpose, 12 siliceous sponges of different genera (*Asconema, Geodia, Lissodendoryx* and *Schaudinnia*) and order *Haplosclerida* were collected in 2018 with a ROV in water depths of 223 to 625 m in the Norwegian-Greenland Sea. Sponges were stained with a Rose Bengal/ethanol mixture to allow a differentiation between foraminifera that had been recently alive and empty tests. Each sponge sample contained 3–42 dead and 1–10 living foraminiferal individuals per cm^3 and summarizing up to 78 different taxa on one single sponge (*Geodia phlegraei*). Even on *Geodia barretti*, which is able to release barrettin (an alkaloid) to avoid colonialization by other organisms, living foraminiferal individuals (1 ind./cm^3) were observed. The highest foraminiferal densities (living and dead individuals) were recorded on *Haplosclerida* sp. (49 ind./cm^3) and *Geodia* sp. (45 ind./cm^3). The lowest densities of foraminifera were found on *G. barretti* (3–14 ind./cm^3) and on *Lissodendoryx complicata* (9 ind./cm^3). The foraminiferal diversity ranges from 7.04 to 17.38 for Fisher α and from 2.40 to 3.33 (Shannon-Wiener *(H)S*). The highest diversity was found on *G. phlegraei* and the lowest one on *L. complicata*. This study is highlighting the ecosystem engineering role of sponges providing niche habitats for a high number of foraminifera.

1. Introduction

1.1. General introduction

Foraminifera are unicellular mainly marine protists that live in a wide variety of habitats all around the world. They inhabit microhabitats (e.g., mud, sand or rocks) in shallow water regions as well as the deep sea (e.g., Corliss, 1985; Gooday, 2019). Their tests are made of calcite, sand particles or organic material and protect the cytoplasm against the surrounding environment (e.g., Marszalek et al., 1969; Pawlowski et al., 2003). A high diversity in shell designs reflects the species adaptation to their lifestyle, the environmental conditions prevailing in their habitat, their nutrition, and eventually protection against predators. Further specialization of the test can be a result of an adaption to special physical or chemical conditions (Sen Gupta, 1999). Therefore, investigations based on foraminifera can be used to draw conclusions about the environmental parameters or the state of the surrounding habitat (Murray, 2001). For example, the interaction of sponges with foraminifera in various reef facies has been confirmed several times in the history of the earth and can give an idea about the past environmental setup (Seibold and Seibold, 1960; Schmalzfriedt, 1991; Munk, 1994).

Sponges are animals with a typically sessile way of life filtering large amounts of sea water to collect algae and smaller animals for their nutrition (Kahn et al., 2015). Besides, they are able to convert dissolved organic matter (DOM) into bioavailable nutrients (Rix et al., 2016), fix nitrogen in shallow waters (Ribes et al., 2015) and thus enrich the outflowing water with dissolved inorganic nitrogen (Southwell et al., 2008; Leys et al., 2018). These processes are heavily dependent on the availability of oxygen. Southwell et al. (2008) assumed that this anaerobic process could strongly influence the role of sponges (from nutrient source to nutrient sink) in the marine ecosystem of the deep sea in the future.

Past research has shown that sponges can shape their environment in many ways (Pomponi et al., 2019). They can dominate ecosystems and provide habitats for diverse invertebrates and economically important

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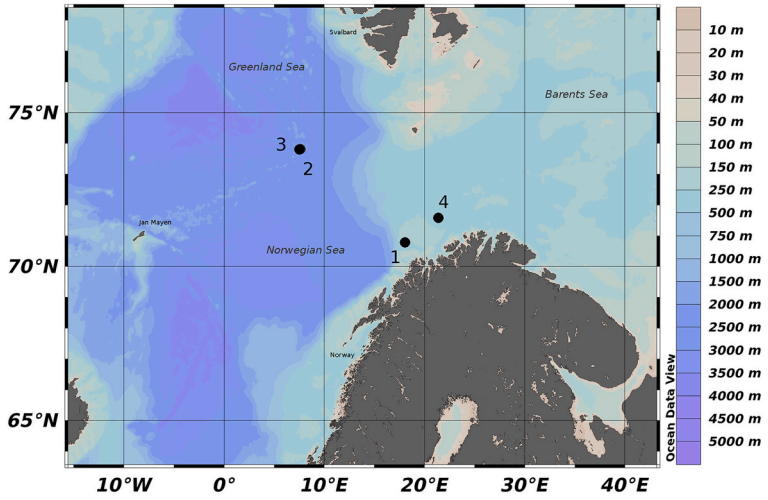

Fig. 1. Location of the study area and sampling sites: 1) Malangsgrunnen, 2) and 3) Schultz summit, 4) Tromsøflaket East (the map was created using Ocean Data View (ODV) software – version 5.2.0, Schlitzer, 2019; http://odv.awi.de).

Table 1
Sampling stations of sponge individuals with sampling device, geographic coordinates, water depths and date.

Site	Dive	Sample	Lat (N)	Lat (O)	Depth [m]	Location	Date
1	ROV 1	*Geodia barretti* 1 *Geodia barretti* 2 *Geodia barretti* 3 *Geodia* sp.	70°47.226'	18°03.366'	223	Malangsgrunnen	28.07.2018
2	ROV 5	*Schaudinnia* sp.	73°49.800'	07°33.690'	580	Schultz summit	31.08.2018
3	ROV 15	*Lissodendoryx complicata*	73°49.668'	07°32.706'	625	Schultz summit	03.08.2018
4	ROV 30	*Asconema* sp. *Geodia phlegraei* 1 *Geodia phlegraei* 2 *Geodia phlegraei* 3 *Geodia macandrewii* *Haplosclerida* sp.	71°35.232'	21°22.410'	330	Tromsøflaket East	08.08.2018

fish species (Pomponi et al., 2019; Barnes, 2001). For example, Uriz et al. (1992) postulated, that there is a close relationship between the occurrence of scyphozoan *Nausithoe punctata* and horny sponges. Also, thousands of polychaetes, amphipods, ostracods, isopods, shrimps or ophiuroids can live inside or on top of sponges (Duris et al., 2011; Duarte and Nalesso, 1996; Pearse, 1932). Likewise, Cleary et al. (2013) postulated, that sponges can have a huge amount of microbial communities inhabiting them. These microbes can make up to 50% (in *Geodia barretti* even 90%, Leys et al., 2018) of the total sponge volume (Vacelet, 1975) and differ significantly from the bacterioplankton of the sponge's surrounding (Santavy et al., 1990).

So far only few studies address the benthic foraminifera on and around sponges. Foraminifera can be found lying loosely next to, inside or on top of sponges and even sunken or firmly anchored to the silicate matrix of siliceous sponges (Guilbault et al., 2006; Bukenberger et al., 2020). However, no detailed faunal analysis based on the diversity of foraminifera associated with sponges exists. The aim of this study is to investigate the foraminiferal density on different sponge taxa to get insight into the foraminiferal diversity and abundance on sponges and verify if the foraminiferal diversities vary between the different sponge genera or taxa.

1.2. Study area

The studied sponges were collected from the Greenland Sea and Norwegian Sea (Fig. 1, Table 1).

The Norwegian Sea is located between Norway and Greenland, with a boundary at the south by 62°N (Greenland-Scotland Ridge) and at the north by 80°N (Svalbard) (Creegan, 1976). It is a transit zone from which North Atlantic Water is transported to the Arctic Ocean (Dugstad et al., 2019). The Norwegian Sea has a stratified water body with a mean salinity of 34.9–35.2 g/kg (Worthington, 1970; Merchel and Walczowski, 2020) and a temperature between 8 °C (Shetland-Faroe Strait) und 5 °C (Svalbard) (Mork et al., 2014), with a decade- to century-scale variation of 1–2 °C in the shallow (up to 50 m) water area (Sejrup et al., 2010). The topography of the northern coast of Norway has a special influence on the flow behaviour of the water masses (Sundby, 1984). During the winter months the current is deep and narrow, whereas in summer it is wide and shallow (Sætre and Liøen, 1971). In the area of the sampling sites, the Norwegian Coastal Waters (as part of the Norwegian Coastal Current) and waters of Atlantic origin (AW) are dominating (Skardhamar and Svendsen, 2005). The NCW with an average salinity of 34.5 g/kg comprises the upper 200–250 m and the AW with a salinity >35 g/kg is present below.

The Greenland Sea is located between the 71°N in the south, the 79°30′N in the north, and east and west by the 2000-m isobath (Carmack and Aagaard, 1973). Based on the domains of upper water the Greenland Sea is divided into three sub areas: Norwegian Current (94,300 km^3), Greenland Gyre (91,600 km^3) and the modified Polar area (65,600km^3) (Carmack and Aagaard, 1973). The upper 500 m of the western Greenland Sea is formed by an inflow of the Polar Water (PW) from the Arctic Ocean which is mixed with the Atlantic Water (AW) that is advected from the south. The PW has a temperature close to zero and a salinity of 33–34 g/kg, whereas the AW has a mean temperature of 3 °C and a mean salinity of 34.9 g/kg (Selyuzhenok et al., 2020). In the central Greenland Sea, the mixed PW and AW are further mixed with the

Greenland Sea Intermediate Water which has a temperature of −0.4–0.8 °C and a salinity of about 34.9 g/kg (Selyuzhenok et al., 2020). Below the Greenland Sea Intermediate Water (1000 m downwards), the Greenland Sea Deep Water with a temperature of −0.8 to −1.2 °C and a salinity of 34.9 g/kg can be found (Selyuzhenok et al., 2020).

2. Material and methods

The samples were collected during the expedition GS2018108 on board of RV G. O. Sars in July and August 2018. With a remote operated vehicle (ROV Ægir 6000, University of Bergen) 12 sponges were collected at water depths from 223 to 625 m (Table 1). Subsamples of these sponges were transferred into a Kautex bottle, poured with 96%-ethanol for preservation and stored at 4 °C until further processing at the Alfred Wegener Institute in Bremerhaven. The sponge sample collection included 1 *Asconema* sp., 3 *Geodia barretti* (Bowerbank, 1858), 3 *Geodia phlegraei* (Sollas, 1880), 1 *Geodia macandrewii* (Bowerbank, 1858), 1 *Geodia* sp., 1 *Haplosclerida* sp., 1 *Lissodendoryx complicata* (Hansen, 1885) and 1 *Schaudinnia* sp. The sponges *Schaudinnia* sp. and *L. complicata* were collected in the Greenland Sea, all other sponges were collected in the Norwegian Sea. They were taxonomically identified by visual inspection on board.

For the faunal analysis, the volume of each sponge subsample was determined by the Archimedes' principle (see Mohazzabi, 2017). The dry density was obtained by weighting the samples and dividing mass by volume. Besides, each sample was transferred in a Kautex bottle and stained with Rose Bengal (2 g l^{-1}). Rose Bengal stains cytoplasmic proteins and therefore it is possible to differentiate specimens that had been recently alive prior sampling from the dead foraminiferal fauna (Lutze, 1965; Schönfeld et al., 2012). After 24 h, the stained sponge samples were wet-sieved over a 63 and 32 μm sieve. The two fractions (> 63 μm and 63–32 μm) were dried at 50 °C and filled into glass vials. Only the fraction >63 μm was used for this study. This fraction was further subdivided into the sponge itself and the residuum, which includes any material that was detached of the sponge during the transport or washing process.

Each of the 12 investigated sponges were weighted before staining and splitting into half. One half of the sponge was further crushed to find both the foraminifera on the sponge and those inside of the sponge and was completely analyzed for foraminifera. All specimens of benthic foraminifera, dead (empty tests) and living (stained, with a vivid pink color in at least one chamber) were picked under a binocular/stereo microscope (Nikon SMZ18) and determined on taxon level. Light microscopy photos were taken with a Zeiss Axio Zoom V16 microscope with ZEN blues software, using an Axiocam 506 color camera.

For the identification of taxa, the concepts of Loeblich and Tappan (1988, 1994) and the Catalogue of Foraminifera (Ellis and Messina, 1940) were used. A detailed study with the identification of foraminifera on species level is in preparation.

Diversity was evaluated using the free software Past4 (Hammer et al., 2001), which calculated the diversity indices Fisher α, Shannon-Wiener *H(S)* and the evenness index *E* (Fisher et al., 1943; Buzas and Gibson, 1969). The diversity indices were calculated using the total number of individuals (N) and the number of species (S) by following the instruction manual of Past4 software. The micropaleontological slides are deposited as reference at the University of Vienna, Department of Palaeontology.

3. Results

3.1. Species richness

The 12 investigated sponge parts contained 157 different foraminiferal taxa (living and dead), including 103 calcareous and 54 agglutinated taxa. Agglutinated foraminifera (living and dead) accounted for 2.6–14.2% of the total foraminiferal assemblage. Diversity index

Table 2
Evaluated data from the faunal analysis of the sponges. N = number of foraminiferal counts, S = number of species. The abbreviations for the location are M = Malangsgrunnen, SS = Schultz summit and TE = Tromsøflaket East.

sponge	*G. barretti 1*	*G. barretti 2*	*G. barretti 3*	*Geodia* sp.	*Schaudinnia* sp.	*L. complicata*	*Asconema* sp.	*G. phlegraei 1*	*G. phlegraei 2*	*G. phlegraei 3*	*G. macandrewii*	*Haplosclerida* sp.
location	M	M	M	M	SS	SS	TE	TE	TE	TE	TE	TE
mass [g]	9.850	8.998	6.298	1.940	1.615	2.487	0.455	9.824	7.665	11.972	14.103	0.253
volume [cm3]	54.5	44.2	40.0	14.0	30.0	45.0	14.0	35.0	28.0	47.5	67.0	10.0
dry density [g/cm3]	0.18	0.20	0.16	0.14	0.05	0.06	0.03	0.28	0.27	0.25	0.21	0.03
foraminifera	*G. barretti 1*	*G. barretti 2*	*G. barretti 3*	*Geodia* sp.	*Schaudinnia* sp.	*L. complicata*	*Asconema* sp.	*G. phlegraei 1*	*G. phlegraei 2*	*G. phlegraei 3*	*G. macandrewii*	*Haplosclerida* sp.
N (total)	155	175	560	624	436	426	322	480	911	1526	1142	487
N (total living)	1	17	23	38	17	66	63	156	183	121	11	97
N (calcareous)	147	168	515	608	404	417	285	444	782	1343	1105	441
N (agglutinated)	8	7	45	16	32	9	36	36	130	182	38	46
S (total)	26	30	58	49	50	29	41	41	57	78	48	52
S (calcareous)	22	26	39	41	39	27	23	33	40	50	37	33
S (agglutinated)	4	4	19	8	11	2	18	8	17	28	11	19
total ind./g sponge	16	19	89	322	270	171	707	49	119	127	81	1925
living ind./g sponge	0	2	4	20	11	27	138	16	24	10	1	383
total ind./cm^3 sponge	3	4	14	45	15	9	23	14	33	32	17	49
living ind./cm^3 sponge	1	1	1	3	1	1	5	4	7	3	1	10
Diversity indices:	*G. barretti 1*	*G. barretti 2*	*G. barretti 3*	*Geodia* sp.	*Schaudinnia* sp.	*L. complicata*	*Asconema* sp.	*G. phlegraei 1*	*G. phlegraei 2*	*G. phlegraei 3*	*G. macandrewii*	*Haplosclerida* sp.
H(S)	2.65	2.79	3.21	3.04	2.99	2.40	2.56	2.64	2.90	3.33	2.60	2.68
Evenness $E^{H(S)}$	0.54	0.54	0.43	0.43	0.40	0.38	0.32	0.34	0.32	0.36	0.28	0.28
Fisher α	8.94	10.42	16.23	12.45	14.56	7.04	12.46	10.73	13.46	17.38	10.14	14.78

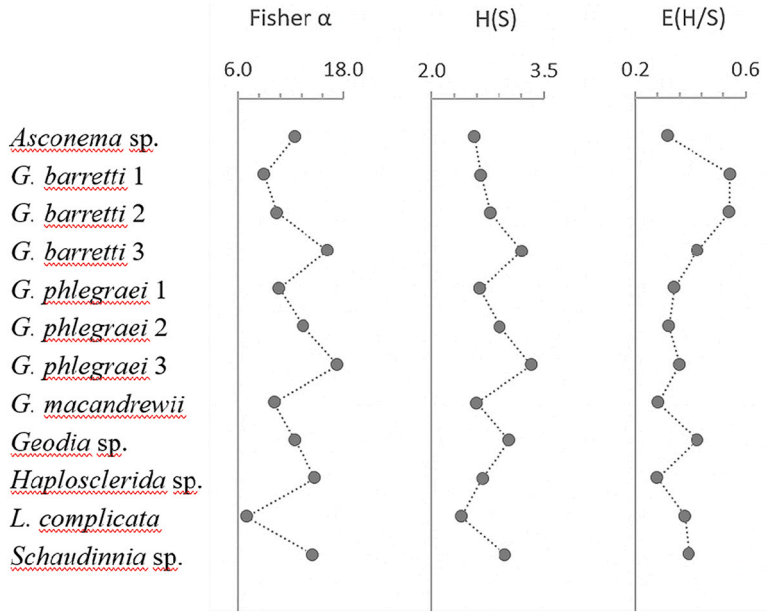

Fig. 2. Graphical representation of the diversity indices.

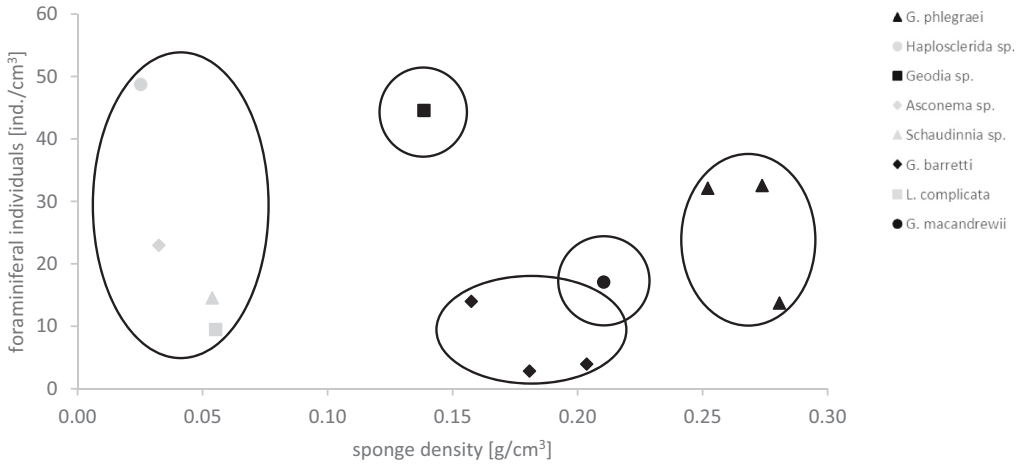

Fig. 3. Correlation between the number of foraminifera on the sponge and the density of the sponge.

Shannon-Wiener *H(S)* varied from 2.40 to 3.33 and the Fisher α values range between 7.04 and 17.38. *Geodia phlegraei* showed the highest *H(S)* (3.33) and Fisher α (17.38) values, but the highest evenness (0.54) was found in *Geodia barretti*. All results are listed in detail in Table 2 and Fig. 2.

Geodia phlegraei contained the highest number of living individuals (3–7 ind./cm^3 sponge) from all *Geodia* sponges, followed by *Geodia* sp. (3 ind./cm^3 sponge), *G. macandrewii* (1 ind./cm^3 sponge) and *G. barretti* (1 ind./cm^3 sponge). The living foraminiferal assemblage from the other sponges was highest at *Haplosclerida* sp. (10 ind./cm^3 sponge) followed by *Asconema* sp. (5 ind./cm^3 sponge), *L. complicata* (1 ind./cm^3 sponge) and *Schaudinnia* sp. (1 ind./cm^3 sponge).

3.2. Foraminiferal density and number of empty tests

The investigated sponges have different morphologies, masses and volumes. To compare the number of foraminifera that colonized the different sponges, the living foraminiferal density and number of empty tests was standardized to 1 g dry mass, and 1 cm^3 sponge, respectively (Table 1; Fig. 5).

The number of foraminifera found on a sponge was plotted against the density of the sponge (Fig. 3). This plot shows a separation of the sponges in two morphological groups: with a meshlike structure (soft consistence), consisting of *Haplosclerida, Asconema, Schaudinnia* and *Lissodendoryx*, and with compact structure (hard consistence), including all investigated *Geodia*. The group of *Geodia* can be further divided into several sub classes. The highest sponge-tissue density was found at *G. phlegraei*, followed by *G. macandrewii* and *G. barretti*. Based on that method it would be possible to determine undefined sponge taxa like *Geodia* sp. in our case, by plotting the number in foraminifera on a sponge against the sponge-tissue density (Fig. 3), but further studies are needed to underline this statement.

The highest number of individuals (living and dead) per g sponge was found in *Haplosclerida* sp. (a total of 1925 individuals), followed by *Asconema* sp. (707 ind.), *Geodia* sp. (322 ind.), *Schaudinnia* sp. (270 ind.) and L. *complicata* (171 ind., Fig. 5A). The lowest number was found in *G. barretti* 1 (16 ind.), *G. barretti* 2 (19 ind.) and *G. phlegraei* 1 (49 ind.).

Considering the volume of the sponge instead of the mass, the results of foraminiferal density change (Fig. 5B). *Haplosclerida* sp. still shows the highest number with 49 individuals per cm^3 sponge, but then follows

Table 3
Calculated ratios of living (l) and dead (d) foraminifera in the sponges and calculated ratio of the distribution of foraminifera. s:r ratio describes the locality of foraminifera (sponge attached (s) and residuum accumulated (r)).

Species	l:d sponge	l:d residuum	s:r ratio
Asconema sp.	0.33	0.22	0.60
G. barretti 1	0.00	0.01	0.03
G. barretti 2	0.00	0.13	0.22
G. barretti 3	0.00	0.05	0.11
G. phlegraei 1	0.50	0.46	1.32
G. phlegraei 2	0.05	0.33	0.31
G. phlegraei 3	0.02	0.13	0.64
G. macandrewii	0.00	0.06	5.14
Geodia sp.	0.08	0.06	0.31
Haplosclerida sp.	0.32	0.23	0.26
L. complicata	0.11	0.22	0.48
Schaudinnia sp.	0.02	0.05	0.34

Geodia sp. with 45 individuals per cm^3 sponge. The lowest number of individuals per cm^3 sponge was found on *G. barretti* 1 (3 ind.), followed by *G. barretti* 2 (4 ind.) and *L. complicata* (9 ind.).

Based on the distribution of living and dead foraminifera, a live:dead ratio (l:d) was calculated for every sponge (Table 3, Fig. 6). This ratio was calculated once for the foraminifera which were firmly attached to the sponge (s) and for the foraminifera in the residuum (r) (see chapter 3.3.). For that purpose, the number of all living foraminifera (on the sponge or in the residuum) was divided by the number of all dead foraminifera (from the same sponge or residuum). Generally, the higher the ratio, the more living (stained) foraminiferal individuals were observed. The live to dead ratios (l:d) are shown in Table 3. It should be noted, that a l:d ratio of 0 does not indicate, that there were no living foraminifera on a sponge. In table 3, the results were rounded to 2 decimal digits, which results in an arithmetical value of 0.

The highest l:d ratio was observed in *G. phlegraei* 1 and *Asconema* sp. For *G. phlegraei* 1 the ratios in the sponge and in the residuum were similar. In contrast, *Asconema* sp. showed a higher number of living foraminifera in the sponge (l:d ratio = 0.33) than in the residuum (l:d ratio = 0.22). The same pattern was also observed in *Haploslcerida* sp., with a higher l:d ratio in the sponge than in the residuum. For L. *complicata* the opposite was observed, here the ratio was twice as high in the residuum than in the sponge. A similar l:d ratio from the sponge and the residuum was calculated for *Geodia* sp., but the values (l:d ratio = 0.08 in sponge, l:d ratio = 0.06 in residuum) indicated that the number of living foraminifera is in both cases low. The lowest ratios were observed in *G. barretti* 1–3, *G. phlegraei* 2 and 3, *G. macandrewii* and *Schaudinnia* sp.

3.3. Attachment of foraminifera to sponges

The analyzed foraminiferal assemblage (Fig. 5) can be divided into two groups: 1) foraminifera that were found living firmly attached to the exterior or interior of the sponges and 2) foraminifera that detached from the sponge during the transport and processing of the samples. Since ethanol has a strong dehydrating effect, foraminifera with a weak adhesion fall off with this preparation method. Therefore, some foraminifera which were weakly attached to the sponge settled to the ground of the transport box. For further discussion, we called the first group sponge attached foraminifera (s) and the second group residuum accumulated foraminifera (r). Based on that, a s:r ratio can be calculated (Table 3, Fig. 6), that shows the distribution of foraminifera between the sponge and the residuum. Due to the low number of living foraminifera in the samples, the s:r ratio was calculated for the whole amount of counted foraminifera (stained/living and unstained/dead). The ratio showed, that *G. macandrewii* had the highest amount of sponge-attached foraminifera (s:r = 5.14) in contrast to all other tested sponges. Also, some *G. phlegraei* (1.32; 0.64; 0.31) had a high s:r ratio, followed by *Asconema* sp. (0.60) and L. *complicata* (0.48). *Schaudinnia* sp. (0.34) and *Haplosclerida* sp. (0.26) showed a lower s:r ratio. The smallest s:r ratio was found at *G. barretti* (0.22; 0.11; 0.03), due to lower abundances of foraminiferal individuals on or inside of the sponge.

4. Discussion

The investigated sponge material contained up to 78 different foraminiferal taxa and up to 1500 foraminiferal individuals on a single sponge. The foraminiferal density on different sponges was investigated and calculated for a certain volume and a certain dry mass. The data representation using dry mass is not really accurate, due to different densities and the diversity in constructions plans of the different sponge tissues (see Fig. 4). For example, *G. phlegraei* consist out of a very dense inner part, where no foraminifera were observed, and an outer part with long protruding spicules where foraminiferal individuals were found. The dense part makes up a high amount of the total mass of the sponge,

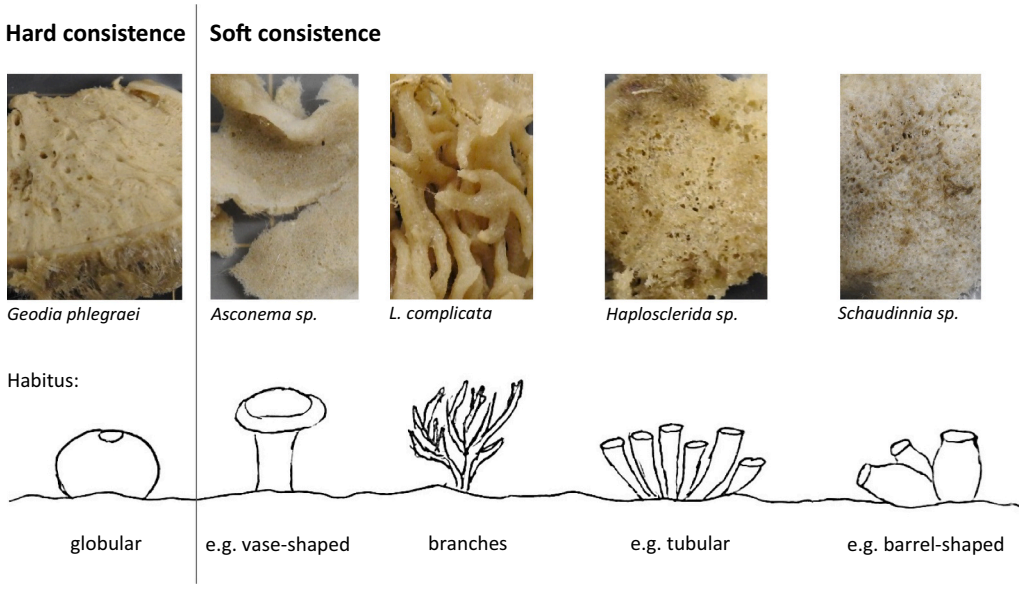

Fig. 4. Macroscopic images of the hard/dense matrix of *G. phlegraei* (left) and soft/meshlike structure of *Asconema* sp., *L. complicata, Haplosclerida* sp. *and Schaudinnia* sp. (right).

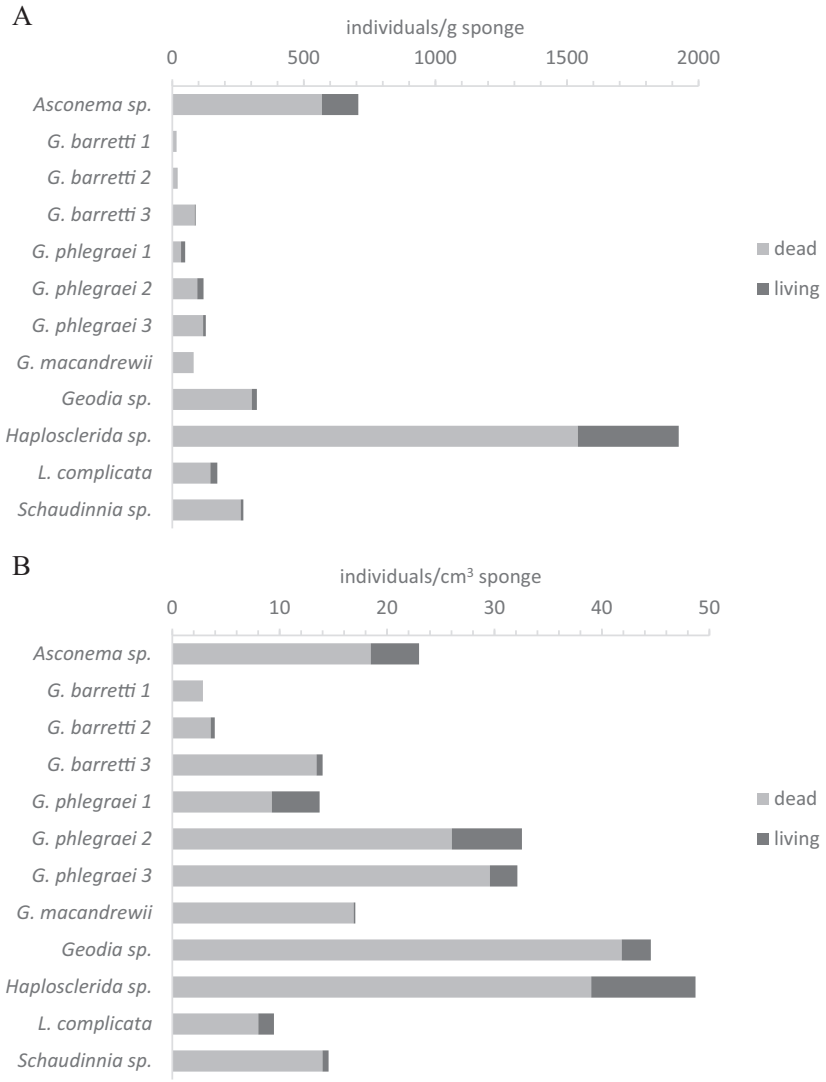

Fig. 5. Abundances of foraminifera standardized by (A) dry mass and (B) volume of sponge.

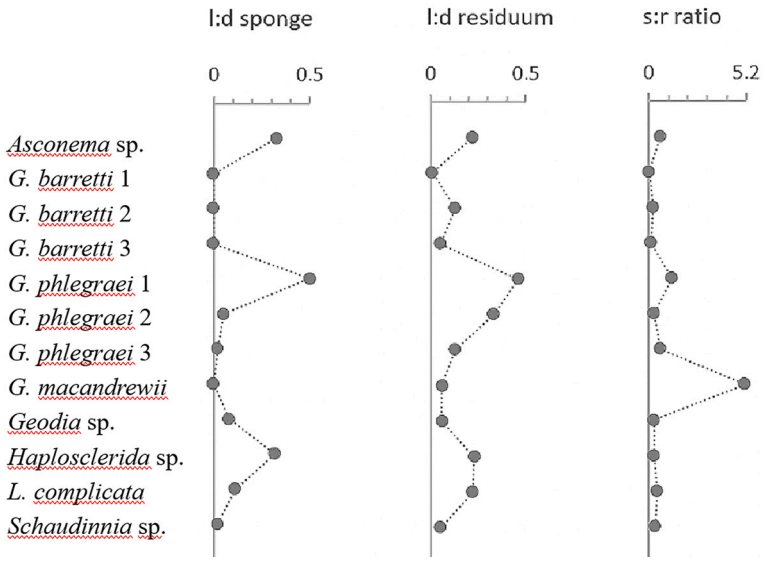

Fig. 6. Graphical representation of the calculated ratios l:d sponge, l:d residuum and s:r.

which results in a very low number of foraminifera per g dry mass (see Fig. 5). In contrast *Haplosclerida* sp. is just made of a very porous matrix and does not contain denser parts like *Geodia* spp. Therefore, a hundred-fold higher number of foraminifera in *Haplosclerida* sp. can be explained by a soft and porous sponge matrix and therefore a more attractive habitat for foraminifera (Fig. 4). This problem does not arise, if the number of foraminifera is calculated on the basis of the volume. The foraminifera are mainly found on the surface of the sponges and only a few were embedded in the sponge matrix. This observation further supports the method of calculating the density of foraminifera on a sponge over the volume. It is also possible to carry out the calculation using the surface of the sponge. However, this method has several disadvantages. On the one hand, the surface of the sponge must be measured immediately after taking the sample, as preservation in ethanol leads to a dehydration of the sponge and thus incorrect results. On the other hand, it would lead to underestimation, as some foraminifera live in the sponge and therefore cannot be found on the surface. Summarizing, the data representation using the volume as common thread is more precise than per dry mass or surface area, and we would recommend it for similar studies.

The highest diversity of foraminifera was found in *G. phlegraei* 3 (Fisher α (17.38), *H(S)* = 3.33) at 330 m near Tromsoflaket East. Generally, the highest amount of living foraminifera was also observed in *G. phlegraei* 1–3. In contrast, the lowest diversity (Fisher α = 7.04), *H(S)* = 2.40) was found on L. *complicata* at 625 m near the Schultz summit. Eight from twelve tested sponges belonged to the genus *Geodia*. Within this genus we differ between four species: *G. phlegraei, G. barretti, G. macandrewii* and *Geodia* sp. Based on the foraminiferal diversity no differences between the sponges of the genus *Geodia* were found, but generally they were more preferred as a habitat compared to the four other sponges investigated. In contrast, living foraminiferal assemblages (composition and total number) varied between *Geodia* sponges. All foraminifera which occurred on *Geodia* were found on top (outside the inner sponge-tissue) of the sponge. Considering the compact inner structure of *Geodia*, it is not surprising that no foraminifera were found inside the sponge, as they were not able to enter the hard and dense matrix of the sponge. Regarding the variations within sponge species, it should be mentioned that *G. barretti* 1 and 2 show very low total numbers of foraminifera. Likewise, few living foraminifera (attached sponge-tissue connected and those in the residuum) could be found on these sponges. No living agglutinated foraminifera were observed at all sponges from this taxon and the amount of living calcareous specimens was small (1 ind./cm^3 sponge). *Geodia barretti* 3, on the other hand has a significantly higher number of living foraminifera (Fig. 5). One possible explanation could be, that *G. barretti* 3 itself was less vital and thus secreted less of the antimicrobial substance barrettin. These sponges are able to produce and secrete the indole alkaloid (brominated cyclopeptide), called barrettin (Lidgren and Bohlin, 1986), into the surrounding seawater. Barrettin is a strongly bioactive substance and can inhibit the settlement of different larvae on substances (Sjögren et al., 2006). Based on that, it can be assumed, that this substance can also inhibit the accretion of foraminifera, and therefore *G. barretti* may not be a preferred habitat for foraminifera.

Guilbault et al. (2006) found on modern and Jurassic reefal sponges (*Vinelloidea, Thurammina, Tolypammina, Tritaxis, Subbdelloidina* and *Bullopora*) from the Goose Island Trough 40 agglutinated and 53 calcareous foraminiferal species. In this study 54 different agglutinated foraminifera and 103 calcareous species were found. This indicates a general high diversity of foraminifera which can be found in or on sponges. A separation of the fauna into agglutinated and calcareous species led to a different pattern of diversity. The sponge L. *complicata* had the lowest diversity of agglutinated species (*H(S)* = 0.53) and no living agglutinated individual was observed. No physical parameters of the water masses were measured during the sampling and no surrounding sediment was collected either, so no conclusions can be drawn about the origin of the foraminifera from the surrounding area of the sponge. But the presence of agglutinated foraminifera on sponges could be explained, by checking the morphology of the sponge. *Lissodendoryx* is described as bush-like form with anastomosing branches (Tompkins et al., 2017, see Fig. 4). These branches have 2 or 3 mm in diameter and are more or less smooth. Guilbault et al. (2006) mentioned, agglutinated foraminifera which were found on sponges are probably snapshots while they are crossing over the surface of a sponge and may have no further interaction with them. Based on that it can be assumed that no agglutinated foraminifera may climb on the branches of L. *complicata* as they are averted from the seafloor. This may also explain why the diversity of agglutinated foraminifera on nodular sponges like *G. phlegraei* is higher (*H(S)*: 2.60) than those of L. *complicata*. For the calcareous species diversity ranges from *H(S)*: 2.18 to 3.02, but no clear trend between the sponge taxa was recognized. This indicates, that all examined sponges show similar pattern of diversity and calcareous species may benefit from this lifestyle.

So far, there is not much known about this sponge-foraminifera associations and the inhabiting benthic foraminiferal fauna, which makes this topic of particular interest. However, it is possible to make comparisons with similar habitats. Cold-water coral ecosystems are particularly of interest in this area, as they are very popular and can often be found in the Norwegian Sea (e.g., Spezzaferri et al., 2013). These ecosystems contain a variety of benthic organisms that specialize in suspension feeding (Mortensen, 2001). Both sponges and foraminifera are common members of cold-water coral ecosystems (Mortensen, 2001; Spezzaferri et al., 2013). Past studies have shown that the foraminiferal assemblages on corals ("on-reef") differed significantly from those areas where no corals ("off-reef") were found (Spezzaferri et al., 2013). In the study by Spezzaferri et al. (2013), it should be mentioned that the "on-reef" samples were taken at a water depth of 110–600 m water depth and the "off-reef" (mentioned as shallow and deep mud facies) were taken at 287–326 m (Oslofjord) and at 889 to 2098 m (across the continental slope off Røst Reef). As a result, the difference in diversity of the foraminiferal community could be attributed to several factors, not just the presence of corals. However, similar foraminiferal associations could be found on the exposed "on-reef" areas as on the sponges examined here. For the samples from the cold-water coral ecosystem from Norway, the diversity differences between agglutinated and calcareous species were not investigated.

Further, is not yet clarified whether foraminifera specifically colonize sponges or are accidentally sucked in during the pelagic stage (reproduction). One aspect is currently known: foraminifera can use sponges as a habitat and as a food source. Besides, it is known, that for example currents can influence foraminiferal assemblages (Patarroyo and Martinez, 2013; Debenay et al., 2005) and further investigations are needed to clarify their potential impact on the diversity and abundance of foraminifera on sponges.

5. Conclusion

This study shows how many foraminifera can be found in or on sponges and how strong these protists are linked to the animal. Due to the fact, that several thousands of foraminifera can be found on one sponge, this should not be ignored when studying sponges. In summary, this study showed that not only invertebrates (e.g., Duris et al., 2011) or bacteria (e.g., Imhoff and Stöhr, 2003) can inhabit sponges in a high number, also foraminifera can use sponge as a habitat and have different associations with them. The high abundance of foraminifera on deep-sea sponges can have different impacts on the sponge driven organic and inorganic matter turnover and further studies are necessary to investigate these interactions in detail.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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