



The temporal variability of the macrofauna at the deep-sea observatory HAUSGARTEN (Fram Strait, Arctic Ocean)

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Received: 14 May 2018 / Revised: 27 November 2018 / Accepted: 11 December 2018 / Published online: 2 January 2019
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Abstract

Regular biological observations of the deep sea bottom fauna are very important for understanding the role benthic biota plays in ocean ecosystems. Temporal variability in macrobenthos structure is usually studied in terms of general community characteristics including density, biomass and diversity. In this investigation, we also focused on the species composition and their individual characteristics in terms of temporal dynamics. The deep-sea macrofauna was studied based on the material collected in the Eastern Fram Strait during two expeditions in July–August 2003 and July 2012. Stations were taken at depths of about 2500 m at the deep-sea observatory using the USNEL box corer (0.25 m²). Three stations at varying distances were sampled in 2003 (three cores per station). In 2012, the same stations were resampled with an additional station taken close to the central HAUSGARTEN permanent sampling site (one core per station). No significant changes in the total density and biomass were found between the two sampling events. However, the density of several common species has changed significantly (e.g. densities of *Menicula ockelmanni* and *Chaetozone cf. jubata* have increased). Four species out of total 64 were unique for the 2003 samples, while six species out of 52 were unique for 2012 samples. The absence of several particular species in the samples from the different years is estimated to be not random: the number of samples required to find these species was less than the number of samples collected. The differences in time between the very same stations exceeded the inner spatial heterogeneity of each of the three stations. However, the spatial heterogeneity within the scale of 20–25 km exceeded the temporal differences.

Keywords Arctic · Benthic communities · Fram Strait · Deep Sea · Temporal variability

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00300-018-02442-8>) contains supplementary material, which is available to authorized users.

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Introduction

The benthic biota plays an important role in marine ecosystems and in the global carbon cycle (Vardaro et al. 2009), yet, the dynamics of deep-sea benthic fauna in the vast abyssal and bathyal areas of the world oceans remain poorly understood (Laguionie-Marchais et al. 2013). The assessment of temporal changes in the benthic communities requires long-term observations with regular sampling (Glover et al. 2010; Larkin et al. 2010). For the deep sea below 2000 m water depth, regular biological observations are very scarce and only include a handful of sampling sites in the Mediterranean Sea, the Gulf of Mexico and several areas in the Atlantic and Pacific oceans (summarised in Larkin et al. 2010).

Temporal studies conducted at the Porcupine Abyssal Plane Sustained Observatory (PAP) in the North-East Atlantic (4850 m) since 1989 (Billett and Rice 2001) showed interannual changes in meiobenthos (Gooday and Rathburn

1999), macrobenthos (Galéron et al. 2001; Soto et al. 2010) and megafaunal assemblages (Billett et al. 2001, 2010). In the North-East Pacific (4100 m), the Station M has been sampled regularly since 1991 (Smith and Druffel 1998) exhibiting interannual changes in the density and taxonomical structure of macrofauna (Ruhl et al. 2008; Laguionie-Marchais et al. 2013) and the density of megafaunal echinoderms (Ruhl and Smith 2004). Correlations between the surface primary production, the fluxes of organic matter and metazoan community structure were demonstrated for both PAP and Station M (Galéron et al. 2001; Ruhl et al. 2008). Not only inter-annually but also seasonally varying food supply may affect the benthos as it was shown for the nematodes (Soltwedel et al. 1996) and polychaetes (Soto et al. 2010) in the NE Atlantic and for other benthic groups including arthropods and annelids in Station M (Smith et al. 2009).

In the Arctic, regular studies are conducted mostly in the shallow-water areas, e.g. in the White Sea (Sukhotin and Berger 2013) or in the Bering Strait area (Grebmeier et al. 2015). The Long-Term Ecological Research observatory HAUSGARTEN located in the transition zone between the northern North Atlantic and the Arctic Ocean represents the only time-series study in the Arctic deep sea including regular benthic surveys (Soltwedel et al. 2005, 2015). Interannual variations in meiofaunal abundance were reported during 5 years of investigation (2000–2004 and, separately, 2005–2009) along a bathymetric transect at HAUSGARTEN (Hoste et al. 2007; Gorska et al. 2014). Megafauna studies at HAUSGARTEN showed an overall decrease of megafaunal density during 2002–2007 at 2400–2600 m depth. This observation was correlated with the increase in bottom-water temperatures and decrease in the total organic content and microbial biomass in the surface sediments (Bergmann et al. 2011). Later, differences in megafaunal assemblages at HAUSGARTEN were reported with an overall increase in density for 2015 observations (Müller et al. 2016; Taylor et al. 2017).

Temporal changes in macrofaunal structure are usually assessed by comparing the general community characteristics (i.e. abundance, biomass, diversity), while the detailed species composition is rarely assessed (Soto et al. 2010; Laguionie-Marchais et al. 2013), especially in poorly studied Arctic deep-sea macrofauna with many species remaining undescribed (Bluhm et al. 2015; Oug et al. 2016). Moreover, the identifications of species from different samplings are often (or usually) done by different researchers leading to flawed comparisons of community characteristics because of incorrect taxonomic classifications (Bluhm et al. 2011). Therefore, it is impossible to treat large community data at species level.

Macrofauna investigations at HAUSGARTEN observatory were carried out by Włodarska-Kowalczyk et al. (2004), Budaeva et al. (2008) and Vedenin et al. (2016), providing data from 2000, 2003 and 2012. The latter two studies have

been conducted at comparable water depths (approximately 2500 m) while the study of Włodarska-Kowalczyk et al. (2004) focused on depth-related gradients in community structure (300–3000 m depth range).

In the present study, we aimed to compare the samples taken at the HAUSGARTEN area in 2003 (Budaeva et al. 2008) with those collected in 2012 (Vedenin et al. 2016) since they have been obtained at approximately the same depth and during the same time of the year. This approach removes the depth and season factors from the analysis of temporal variation in the community structure. We carefully re-examined collections of material from both expeditions and revised species identifications by the same taxonomical specialists. Our goal was to reveal the temporal differences in the entire structure of macrobenthos and in the distribution of certain species over spatial scales of ~2 km and ~25 km.

Materials and methods

Sampling

Sediment samples for macrofauna investigations were taken during the RV Polarstern expeditions ARK-XIX/3c in July/August 2003 and ARK-XXVII/2 in July 2012 at the HAUSGARTEN observatory in the eastern part of the Fram Strait. Three stations (S1, S1-a and HGIV-a) were visited in 2003. The sampling was replicated in 2012 with one additional station (HGIV) taken near the northern station. The distances between stations were ~25 km (between HGIV and S1) and ~2 km (between S1 and S1-a and between HGIV and HGIV-a); the exact position of stations is shown in Fig. 1; coordinates and depth are shown in Table 1. All stations were located at water depths around 2500 m. An USNEL box corer (0.25 m²) was used for sampling; three replicated per station were taken in 2003 and only one core per station in 2012 (Table 1). Each sample was washed through a sieve of 0.5-mm in mesh size. In 2003, the entire cores were fixed in 4% formalin; in 2012, subcores of 0.125 m² (one core per station, one subcore per core) were fixed in 10% buffered formalin. For additional information on sampling procedures, see Budaeva et al. (2008) and Vedenin et al. (2016).

Prior to statistical evaluations, the collections of macrofauna organisms from Budaeva et al. (2008) and Vedenin et al. (2016) were re-examined to verify original identifications. A combined species list for two datasets was composed based on the reviewed taxonomical identifications of species from the two collections.

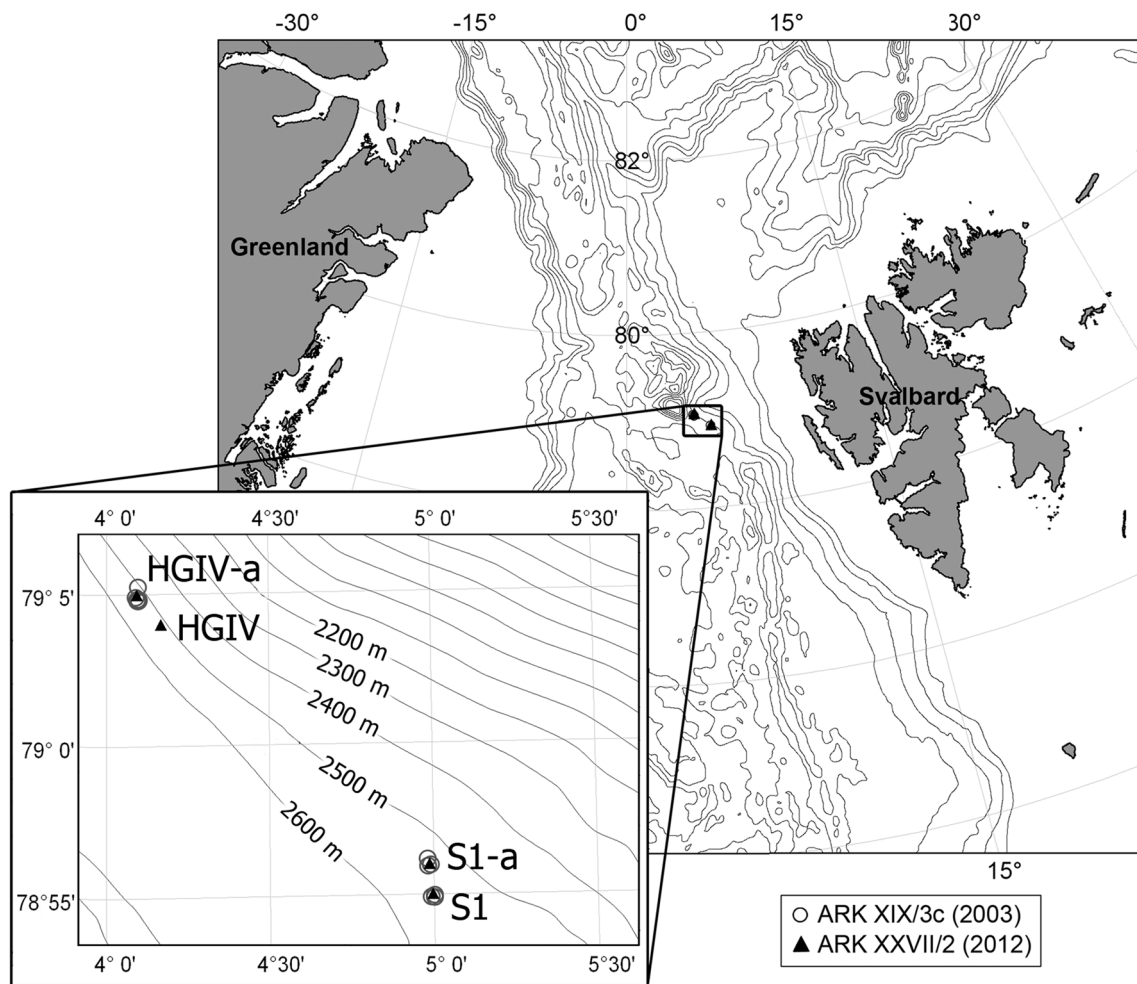


Fig. 1 Sampling area with box-corer stations taken during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

Table 1 Stations where box-corer samples were taken during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

Sampling date	Station	Core	Latitude	Longitude	Depth (m)
27/07/2003	HGIV-a	PS64/440	79°04.79'N	4°06.05'E	2500
27/07/2003	HGIV-a	PS64/441	79°04.89'N	4°05.77'E	2500
27/07/2003	HGIV-a	PS64/442	79°05.22'N	4°06.13'E	2482
31/07/2003	S1	PS64/454	78°55.01'N	5°00.27'E	2637
31/07/2003	S1	PS64/455	78°54.97'N	5°00.24'E	2637
31/07/2003	S1	PS64/456	78°54.97'N	5°00.04'E	2638
01/08/2003	S1-a	PS64/461	78°56.02'N	4°59.60'E	2610
01/08/2003	S1-a	PS64/462	78°56.04'N	4°59.62'E	2610
02/08/2003	S1-a	PS64/463	78°56.21'N	4°59.18'E	2606
16/07/2012	HGIV	PS80/165–9	79°03.91'N	4°10.73'E	2465
27/07/2012	HGIV-a	PS80/195–3	79°04.93'N	4°05.90'E	2458
19/07/2012	S1-a	PS80/174–1	78°56.01'N	4°59.58'E	2609
27/07/2012	S1	PS80/197–1	78°55.08'N	5°00.10'E	2594

Statistics

Densities and biomasses for all species were taken from

original studies by Budaeva et al. (2008) and Vedenin et al. (2016) with adjustments regarding the revised identification of selected species.

We used untransformed data as a measure of species abundance and biomass. The similarity between the samples was estimated by using the Bray–Curtis similarity index. Hierarchical cluster analysis and nonmetric multidimensional scaling analysis (n-MDS) were used for examining the multivariate similarities. The results of the clusterisation were verified by ANOSIM analysis to reveal clusters significance level (Clarke and Warwick 2001). Temporal variability between the 2003 and 2012 samples was estimated by comparing the community characteristics over the different spatial scales: ~25 km (comparison of all samples) and ~2 km (comparison of the station pairs HGIV–HGIV-a and S1–S1-a). We estimated the species richness as the total number of the species in each sample. The species-individuals accumulation curves for the total fauna were plotted to estimate the level of saturation in the samples. Species diversity was measured in each sample using Pielou evenness (Pielou 1966), Hurlbert rarefaction index for 100 individuals (Hurlbert 1971) and Simpson index (Simpson 1949). The similarity percentage routine (SIMPER) was used to reveal species with highest contributions to between-years dissimilarities (Clarke and Warwick 2001). The Kruskal–Wallis test was used to identify the reliability of differences in abundance between the 2003 and 2012 samplings for certain taxa (Kruskal and Wallis 1952).

For the species present in either 2003 or 2012 samples, an algorithm estimating the likelihood of accidental presence or absence of a species in either sampling was applied. If we assume the constancy of the species distribution in two given samplings A and B, the probability of the species absence in every core of the sampling B would be $(1 - P_A)^{N(B)}$, where $N(B)$ is the number of cores in sampling B and P_A is the species occurrence (i.e. the percentage of cores where the species occurred) in sampling A. Using this ratio, we estimated the likelihood of the accidental absence of any species in either of the samplings. The number of cores required for species finding in sampling B was calculated by the equation: $n = [\log(\alpha)] [\log(1 - P_A)]^{-1}$, where α is the likelihood of species finding in sampling B assumed as 0.95 (Azovsky 2018; Mheidze and Mirvis 1975; Kozlov 2014).

Statistical analyses were performed in Primer V6 (Clarke and Warwick 2001) and Past 3 (Hammer et al. 2003) software.

Results

Standardisation of datasets from 2003 and 2012

All the macrofauna taxa named differently in the previous publications are shown in the Table 2. Incorrect identifications were found among 53 taxa from 2003 samples and among 11 taxa from 2012 samples. Several taxa were

excluded from the further statistical analysis: the foraminiferan *Crithionina hispida* (previously identified erroneously as the sponge *Tetractinomorpha* gen.sp. A), the pelagic amphipod *Gammarus wilkitzkii* (previously identified erroneously as *Podoceridae* gen.sp. or nonspecifically as *Amphipoda* gen.sp.), and the echinoid *Pourtalesia jeffreysi* (previously identified nonspecifically as *Echinoidea* gen.sp.) now considered as megafauna (Table 2).

After combining the datasets, several previously identified characteristics including abundance, biomass and species richness changed. The species number increased from 59 to 64 taxa in samples from 2003, and from 51 to 52 taxa in samples from 2012. Abundance and biomass values for the 2003 samples decreased significantly due to the exclusion of several taxa. New values of abundance, biomass, diversity and species number for each macro taxon are shown in Tables 3 and 4. The complete list of species densities from each sample (both 2003 and 2012) is shown in the Electronic Supplementary Material 1 (ESM 1). Most of the taxa identified to only generic or family level (e.g. *Abyssoninoe* sp., *Desmosoma* sp., Bonelliidae gen.sp., Harrimaniidae gen.sp.) are probably new to science.

Comparison of community characteristics in 2003 and 2012

General characteristics of samples

The species-individuals accumulation curves were calculated for four combined sets of samples (northern 2003, northern 2012, southern 2003 and southern 2012 samples separately) (Fig. 2). The curves for 2012 were distinctly steeper than the curves for 2003. However, neither of them reached the saturation point. Most of the species, including the dominants (*Galathowenia fragilis* and *Myriochele heeri*), were present in both 2003 and 2012. In total, 76 macrofaunal species were found. Among the 39 species common for both years, 23 species were present only in the samples from 2003, while 14 species were present only in the samples from 2012 (ESM 1). The mean level of Bray–Curtis similarity was high (about 51 among all samples, 59 among the 2003 samples and 48 among the 2012 samples).

Despite the high taxonomical similarity among all samples, there was a difference in species composition between the northern stations (HGIV and HGIV-a, spatial scale ~2 km) and the southern stations (S1 and S1-a, spatial scale ~2 km). Biomass and abundance data showed same results. The 2003 samples from stations S1 and S1-a were very close to each other in the plot (mean similarity value over 77), the samples from station HGIV-a were equally similar (Fig. 3). In 2012, the stations S1 and S1-a were also closer to each other in the plot than to HGIV and HGIV-a, but the similarity value was lower than in 2003. The dendrogram shows

Table 2 List of reidentified taxa from 2003 and 2012 box-corer samples taken during RV “Polarstern” expeditions ARK-XIX/3c and ARK-XXVII/2. Taxa with previously wrong names are shown

Taxon	Old name from Budaeva et al. (2008), 2003 samples	Old name from Vedenin et al. (2016), 2012 samples	New name
Por	Tetractinomorpha gen.sp. A	-	<i>Crithionina hispida</i> ^a
Por	Tetractinomorpha gen.sp. B	<i>Thenia abyssorum</i>	<i>Thenia abyssorum</i>
Por	Ceractinomorpha gen.sp.	-	<i>Hymedesmia</i> cf. <i>nummulus</i>
Por	<i>Radiella sol</i>	-	<i>Radiella sarsi</i>
Por	<i>Tentorium</i> sp.	<i>Tentorium semisuberites</i>	<i>Tentorium semisuberites</i>
Cni	Actinaria gen.sp.	<i>Bathypheilia margaritacea</i>	<i>Bathypheilia margaritacea</i>
Cni	Actinaria gen.sp.	-	Edwardsiidae gen.sp.
Pol	Polynoidae gen.sp.	-	<i>Bylgides groenlandicus</i>
Pol	Lumbrineridae gen.sp.	<i>Abyssoninoe</i> cf. <i>scopa</i>	<i>Abyssoninoe</i> sp.
Pol	Lumbrineridae gen.sp.	-	<i>Augeneria algida</i>
Pol	Spionidae gen.sp. A	<i>Prionospio</i> sp.	<i>Prionospio</i> sp.
Pol	Spionidae gen.sp. B	<i>Laonice sarsi</i>	<i>Laonice</i> cf. <i>sarsi</i>
Pol	<i>Ophelina</i> sp.	<i>Ophelina opisthobranchiata</i>	<i>Ophelina opisthobranchiata</i>
Pol	<i>Chaetozone</i> group	<i>Chaetozone</i> cf. <i>jubata</i>	<i>Chaetozone</i> cf. <i>jubata</i>
Pol	Oweniidae gen.sp.	<i>Galathowenia oculata</i>	<i>Galathowenia oculata</i>
Pol	-	<i>Laphania boeckii</i>	<i>Polycirrus</i> sp.
Pol	<i>Terebellides stroemi</i>	<i>Terebellides atlantis</i>	<i>Terebellides atlantis</i>
Pol	Sipuncula gen.sp.	<i>Nephasoma diaphanes</i>	<i>Nephasoma diaphanes</i>
Pol	-	<i>Bruunellia</i> sp.	Bonelliidae gen.sp.
Mol	<i>Cryptonatica</i> aff. <i>bathybii</i>	-	<i>Cryptonatica bathybii</i>
Mol	<i>Mohnia mohni</i>	-	<i>Oenopota ovalis</i>
Mol	Rissoiidae gen.sp.	-	<i>Skenea turgida</i>
Mol	Rissoiidae gen.sp.	-	<i>Pseudosetia</i> cf. <i>griegi</i>
Mol	<i>Thyasira</i> sp.	<i>Thyasira ockelmanni</i>	<i>Mendicula ockelmanni</i>
Mol	<i>Thyasira</i> (<i>Mendicula</i>) aff. <i>ferruginea</i>	<i>Thyasira ockelmanni</i>	<i>Mendicula ockelmanni</i>
Mol	<i>Cuspidaria</i> sp.	<i>Cuspidaria centobi</i>	<i>Cuspidaria centobi</i>
Cru	Tanaidacea gen.sp. A	<i>Pseudosphyrapus serratus</i>	<i>Pseudosphyrapus serratus</i>
Cru	Tanaidacea gen.sp. B	<i>Chaulioleona hastata</i>	<i>Chaulioleona hastata</i>
Cru	Isopoda gen.sp.	<i>Caecognathia stygia</i>	<i>Caecognathia stygia</i>
Cru	Isopoda gen.sp.	-	<i>Saduria megalura</i>
Cru	Desmosomatidae gen.sp.	-	<i>Nannoniscus profundus</i>
Cru	Desmosomatidae gen.sp.	-	<i>Eugerdia arctica</i>
Cru	<i>Eugerdia</i> sp. A	-	<i>Eugerdia arctica</i> (females)
Cru	<i>Eugerdia</i> sp. B	-	<i>Eugerdia arctica</i> (males)
Cru	<i>Cryodesma</i> sp.	-	<i>Cryodesma agnari</i>
Cru	<i>Eurycope</i> sp. A	-	<i>Eurycope hanseni</i>
Cru	<i>Eurycope</i> sp. B	-	<i>Eurycope hanseni</i>
Cru	<i>Ilyarachna</i> sp. A	<i>Ilyarachna hirticeps</i>	<i>Ilyarachna hirticeps</i>
Cru	<i>Ilyarachna</i> sp. B	-	<i>Ilyarachna longicornis</i>
Cru	<i>Munna</i> sp.	<i>Munna</i> cf. <i>truncata</i>	<i>Munna acanthifera</i>
Cru	<i>Haplomesus spinosus</i>	<i>Haplomesus quadrispinosus</i>	<i>Haplomesus quadrispinosus</i>
Cru	<i>Haplomesus gorbunovi</i>	<i>Gracilimesus gorbunovi</i>	<i>Gracilimesus gorbunovi</i>
Cru	<i>Haplomesus gorbunovi</i>	<i>Gracilimesus modestus</i>	<i>Gracilimesus modestus</i>
Cru	<i>Haplomesus gorbunovi</i>	<i>Gracilimesus tenuispinis</i>	<i>Gracilimesus insignis</i>
Cru	Amphipoda gen.sp.	-	<i>Gammarus wilkitzkii</i> ¹
Cru	Podoceridae gen.sp.	-	<i>Gammarus wilkitzkii</i> ¹
Cru	<i>Pleustes</i> sp.	<i>Oedicerina ingolfi</i>	<i>Monoculodes</i> cf. <i>coecus</i>
Cru	<i>Paroediceros</i> sp.	<i>Ischyrocerus stephenseni</i>	<i>Ischyrocerus tenuicornis</i>
Cru	<i>Aristias tumidus</i>	-	<i>Tryphosella abyssalis</i>
Cru	<i>Aristias tumidus</i>	<i>Centromedon calcaratus</i>	<i>Centromedon calcaratus</i>
Cru	<i>Aristias tumidus</i>	-	<i>Centromedon typhlops</i>
Cru	<i>Aristias</i> sp.	-	<i>Centromedon typhlops</i>
Cru	<i>Liljeborgia fissicornis</i>	<i>Liljeborgia fissicornis</i>	<i>Liljeborgia caliginis</i>
Ech	<i>Acanthotrochus mirabilis</i>	<i>Prototrochus zenkevichi</i>	<i>Prototrochus zenkevichi</i>
Ech	Echinoidea gen.sp.	-	<i>Pourtalesia jeffreysi</i> (juvenile) ^a

Taxa split into several species are marked with grey. Hyphens mark the taxa missing in either of sampling years

Por Porifera, Cni Cnidaria, Pol Polychaeta, Mol Mollusca, Cru Crustacea, Ech Echinodermata

^aThese taxa were excluded from the analysis

Table 3 Number of species and relative proportions of biomass and density of the major taxa in the studied area in 2003 and 2012 box-corer samples taken during RV “Polarstern” expeditions ARK-XIX/3c and ARK-XXVII/2

Taxon	Species number		Biomass, percentage (% ±SD)		Density, percentage (% ±SD)	
	2003	2012	2003	2012	2003	2012
Porifera	6	4	8.2±11.8	5.3±7.9	0.8±0.6	0.9±0.7
Cnidaria	2	2	1.5±4.5	8.9±13.4	0.2±0.8	0.7±0.7
Polychaeta	15	18	25.4±12.3	55.9±23.0	43.9±18.1	68.4±8.7
Mollusca	11	8	21.3±16.6	15.5±16.5	31.6±20.1	14.8±12.5
Crustacea	25	15	19.8±11.2	7.7±3.2	21.0±3.1	9.9±4.4
Echinodermata	2	2	2.5±3.9	5.9±0.5	1.5±1.2	2.2±1.4

Table 4 Species number, density, biomass, Pielou evenness, Hurlbert rarefaction index for 100 individuals and Simpson diversity index calculated for each box-corer sample taken during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

Year	Station	Species number	Density (ind. m ⁻²)	Biomass (g ww m ⁻²)	Pielou evenness	ES (100)	Simpson index
2003	S1 454	29	916	1.96	0.78	21.77	0.88
2003	S1 455	32	900	2.20	0.75	23.28	0.87
2003	S1 456	31	1036	2.58	0.72	22.93	0.82
2003	S1-a 461	31	972	2.37	0.78	22.01	0.90
2003	S1-a 462	25	936	3.49	0.75	18.46	0.86
2003	S1-a 463	23	964	2.18	0.76	18.22	0.84
2003	HGIV-a 440	31	988	3.57	0.67	21.26	0.81
2003	HGIV-a 441	33	1108	4.58	0.72	22.81	0.85
2003	HGIV-a 442	31	1072	3.31	0.69	20.99	0.83
2012	S1	27	896	0.89	0.81	22.32	0.90
2012	S1-a	35	1480	2.40	0.82	25.20	0.92
2012	HGIV	27	980	2.82	0.76	21.76	0.87
2012	HGIV-a	35	968	1.80	0.85	28.46	0.93

the main division of the samples into two groups marking the spatial scale of ~25 km: all samples from the northern stations HGIV and HGIV-a clustered together while all samples from the southern stations S1 and S1-a formed another cluster. Within each of the two main clusters, the samples were separated by the sampling year (Fig. 3). ANOSIM test showed rather low values for comparison between the years ($R=0.384$, $p=0.017$) and high values for comparison between northern and southern stations ($R=0.949$, $p=0.002$). The presence of the two main clusters was caused by slightly different composition of the dominant species: in the two northern stations, the oweniids *Myriochele heeri* and *Galathowenia fragilis* were dominant, while at the southern stations the bivalve *Mendicula ockelmanni* was equally abundant (ESM 1).

Density and biomass values for most of the macrotaxa remained within the 2003 SD-range (Table 3). However, the density of crustaceans in 2012 was significantly lower compared to 2003 (Table 3). Comparisons of the integral community characteristics including total values of biomass, density, species richness, Pielou evenness, Hurlbert rarefaction and Simpson indices showed that most of the parameters remained in the same range (Table 4). However,

Pielou evenness in the samples from 2012 was distinctly higher among all samples, and the Simpson diversity index was higher at the scale of ~2 km, i.e. in the pairs S1 – S1-a and HGIV – HGIV-a, respectively (Fig. 4a, b).

Differences in taxonomical structure

A comparison of the samples using the SIMPER analysis showed significant differences in the species composition between the years 2003 and 2012. The species responsible for these differences are listed in the Table 5. Several species were significantly less abundant in 2012 than in 2003, including the bivalve *Mendicula ockelmanni*, the polychaete *Myriochele heeri* and the crustaceans *Diastylis polaris* and *Pseudosphyrapus serratus*. Most of the polychaetes and the bivalve *Batharca frielei* were more abundant in 2012 than in 2003. The polychaetes *Chaetozone cf. jubata* and *Abyssoninoe* sp. showed the greatest variation in density at the scale of ~25 km. In 2012, their abundance was significantly higher at all stations (p values 0.004) (Fig. 5a, b). The abundance of the cumacean *D. polaris* and the bivalve *Yoldiella annenkovae* in 2012 decreased (less significantly, p values 0.013) at the same scale (Fig. 5c, d). At

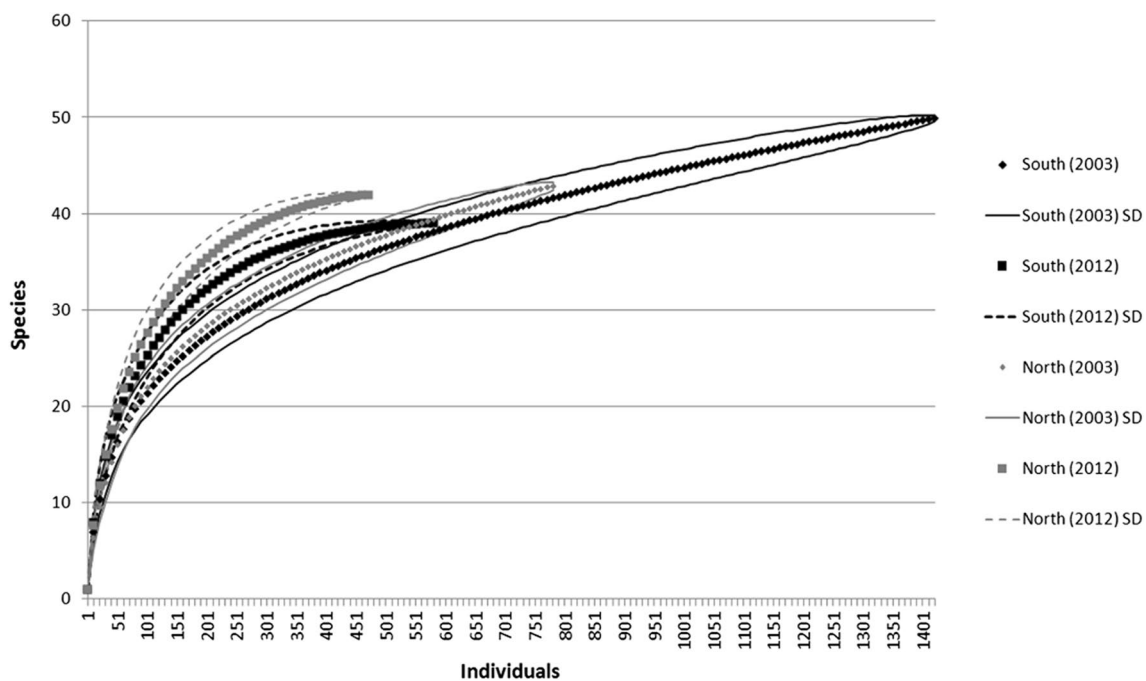


Fig. 2 The species–individuals accumulation curves for the northern (HGIV and HGIV-a) and southern (S1 and S1-a) stations built separately for 2003 and 2012 samplings. Samples were taken by box-corer

during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

the scale of ~2 km the density of the bivalve *M. ockelmanni* decreased: in S1–S1-a pair (from 75 to 33 ind. 0.25 m⁻²) and in HGIV–HGIV-a pair (from 4 to 0 ind. 0.25 m⁻²) (Fig. 6a). The results of the Kruskal–Wallis test confirmed the significant difference in density of these five species between 2003 and 2012. Chi-square and *p* values are shown in the Table 6. The abundance of other taxa shown in the Table 5 did not change significantly.

At least two species (the gastropod *Pseudosetia* cf. *griegi* and the isopod *Eugerda arctica*) were found only in 2003 and six species (polychaetes *Jasmineira schaudinni*, *Polycirrus* sp. and *Spiochaetopterus typicus*, echiurans Bonelliidae gen.sp., nemerteans and enteropneusts Harrimaniidae gen.sp.) were found only in 2012 not randomly. The number of samples required to find these species is less than the number of samples collected for both groups (Table 7). Thus their presence/absence should unequivocally be interpreted as a result of temporal changes in the community composition.

Discussion

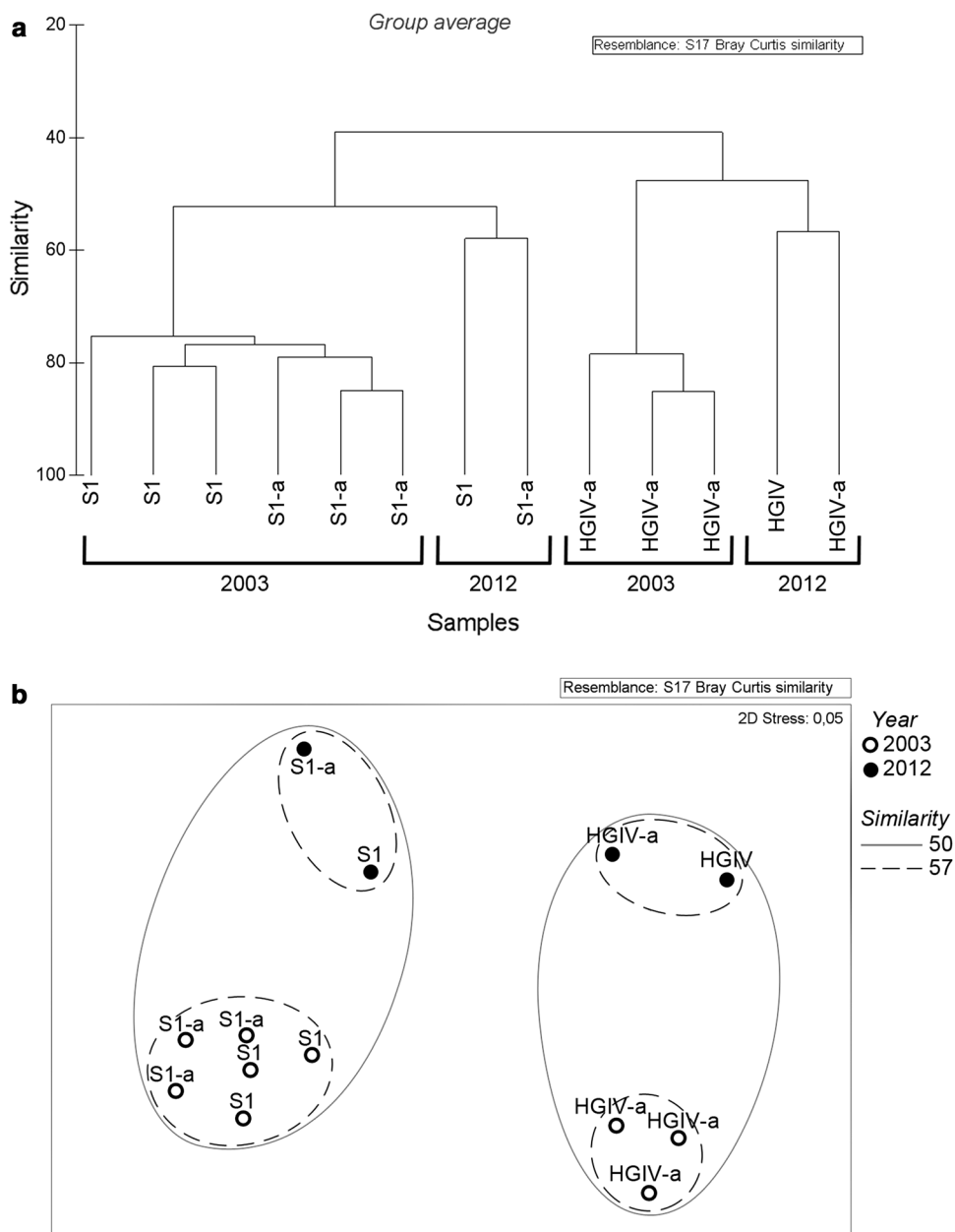
Temporal changes in general community characteristics

Temporal changes in the macrofaunal abundance, biomass and diversity were previously reported from the PAP and

Station M observatories (Smith et al. 2009; Soto et al. 2010). The density and biomass, including the total values and the values determined for selected taxa (Polychaeta, Bivalvia, Arthropoda, etc.) varied significantly in relation to the flux of particulate organic carbon to the seafloor (Galéron et al. 2001; Ruhl et al. 2008). Specifically, seasonal increases in macrofaunal abundance and changes over a longer 10-year period in response to the altering food supply were demonstrated for Station M. At the same time, no changes were recorded across the two-year span (Smith et al. 2008, 2009). In our study, the total density and biomass as well as the abundance and biomass of macrofaunal taxa (e.g. Polychaeta, Mollusca, Echinodermata) showed no significant differences over the nine-year period. The only exception was Crustacea—their density decreased significantly.

Bergmann et al. (2011) reported an almost two-fold decrease in megafaunal density during the period of five years (2002–2007) at the HAUSGARTEN area. After 2007, the total megafaunal density increased again approaching 2002-level in 2011 (Müller et al. 2016). This decrease concurred with an overall increase of the surface and near-bottom-water temperatures during 2002–2007 (Beszczynska-Möller et al. 2012), significant changes in plankton communities (e.g. the overall rise in pteropods numbers accompanied by a switch in dominance of species from *Limacina helicina* toward *Limacina retroversa* in 2004–2005) and subsequent changes in organic matter

Fig. 3 Dendrogram of Bray–Curtis similarity (**a**) and n-MDS plot (**b**) for the cores from 2003 and 2012 samplings. Samples were taken by box-corer during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)



availability (potential food) at the seafloor (Soltwedel et al. 2015). In a study with similar two-point dataset but on megafauna, Taylor et al. (2017) reported that the overall increase of megafaunal densities coincided with the sediment-bound phytodetrital matter during 2004–2015. In our study, no overall increase in density was observed. The absence of complete 2003 and 2012 environmental data as well as lack of macrofaunal data between 2003 and 2012 does not allow to trace possible temporal changes similar to those found for megafaunal communities in the same area, and underlines the importance of time-series studies at higher temporal resolution. The slight increase in diversity in all 2012 samples (shown in Figs. 2, 4) could probably be explained

by an overall increased organic matter availability at the seafloor in more recent years (Soltwedel et al. 2015). However, another possible explanation might be that certain taxa (e.g. polychaetes *Polycirrus* sp. or echiurans *Bonelliidae* gen.sp., see ESM 1) were overlooked in 2003 (see explanation in Table 5).

Temporal changes in taxonomical structure

Temporal versus spatial heterogeneity

Budaeva et al. (2008) reported a two-levelled horizontal heterogeneity in the 2003 samples. The first level represented

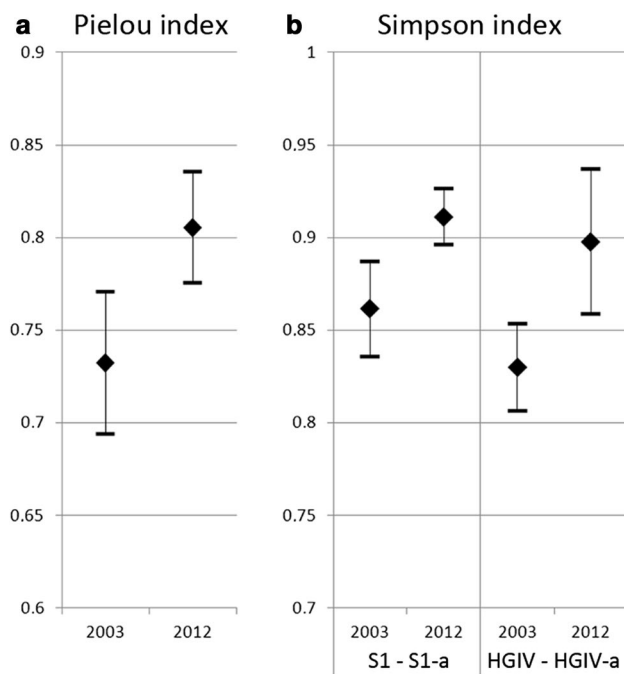


Fig. 4 Mean values with standard deviation for the community integral parameters from 2003 and 2012 samples. **a** Pielou evenness for the scale of ~ 25 km; **b** Simpson diversity index for the scale of ~ 2 km. Samples were taken by box-corer during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

by species assemblages occupied an area of several kilometres, the second was represented by certain species patches about 150 cm² size. It was also shown that there is no spatial variability between the samples taken at the distance less than ~ 400 m from each other (Budaeva et al. 2008). Thus, all the significant differences between 2003 and 2012 samplings should be interpreted as temporal. The structure of the dendrogram and MDS plot (Fig. 3) suggests that the differences between the same stations in time exceed the inner spatial heterogeneity of each of the three stations. However, the temporal differences do not exceed the spatial variability in the scale of ~ 25 km (the distance between the northern and the southern sampling sites).

Temporal changes in selected species

Compared to the data provided by Włodarska-Kowalczyk et al. (Włodarska-Kowalczyk et al. 2004) the composition of the dominant species (i.e. *Myriochele* (= *Galathowenia*) *fragilis*, and *M. heeri*) as well as their density and biomass (and that for entire macrofauna) remained within the same range over the 12-year period. Macrofauna densities found between 2000 and 3000 m water depth on the slopes of the Yermak Plateau (~ 100 km north from our study area) and off North-East Greenland in 1997 revealed similar abundance and biomass values for the dominant species (e.g. *G.*

fragilis) at the HAUSGARTEN sites (summarised by Degen et al. 2015). Unlike *G. fragilis* and other oweniid polychaetes, other dominant species like the bivalve *Mendicula ockelmanni* showed much lower densities in 2012 compared to 2003. In fact, this species is completely absent in the species list published by Włodarska-Kowalczyk et al. (2004).

Comparing macrofauna data at HAUSGARTEN between 2003 and 2013, the most severe changes in density occurred among the cirratulid polychaete *Chaetozone* cf. *jubata*. A similar high temporal variability in the abundance of cirratulid polychaetes (i.e. *Chaetozone* spp. and/or *Tharyx* spp.) was previously shown for the PAP site (Soto et al. 2010). The increase of *Chaetozone* spp. is commonly associated with increased organic matter input. However, the cirratulids (especially the deep-sea species) are poorly studied in terms of taxonomy and biology, and any conclusions based on the changes in cirratulid density should be done with caution (Chambers and Woodham 2003).

At HAUSGARTEN, about half of the total number of species was unique for either 2003 or 2012 samples. Among ten species unique for 2012, at least six were absent in 2003. However, it must be admitted that some of those taxa become almost unidentifiable after fixation, and therefore some specimens had a good chance to be overlooked or classified as undeterminable fragments while sorting the sediments. These specimens include the polychaetes *Polycirrus* sp., echiurans Bonelliidae gen. sp., nemertean and harrimaniid enteropneusts (Table 7). With the exception of these species, only two species are left to be unique for 2012. Overlooking of these species may also explain the different shapes of the species-individuals accumulation curves with the steeper 2012-curves (Fig. 2). The poor state of preservation after fixation is a common problem for some taxa. It has been noted for different fragile species of Polychaeta (Zhirkov 2001), Nemertea (Buzhinskaja 2010), Echiura (Zenkevitch 1966), Enteropneusta (Osborn et al. 2011) and other groups. Their identification in the samples fixed together with the sediment is therefore often complicated or even impossible. The only way to avoid this problem is treating the samples onboard before fixation, which is rarely possible.

Data quantity and quality

Unlike the HAUSGARTEN area, other deep-sea observatories (e.g. PAP or St. M) have been regularly sampled for macrofauna for more than 20 years. Numerous replicates of macrofaunal samples are taken at PAP and St. M since 1989, in some years even seasonally, allowing to reveal correlation between different environmental factors, organic input and macrofaunal density and biomass (Galéron et al. 2001; Ruhl et al. 2008; Smith et al. 2009; Soto et al. 2010). Unfortunately, due to lack of taxonomical expertise, deep-sea macrofauna is usually identified only to family or even

Table 5 Results of the SIMPER analysis of box-corer samples taken during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012). Comparison between the cores taken in 2003 and 2012

Group	Species	Average abundance		Average dissimilarity	Dissimilarity SD
		2003	2012		
Bivalvia	<i>Mendicula ockelmanni</i>	51.11	16.50	8.75	1.51
Polychaeta	<i>Galathowenia fragilis</i>	19.22	33.00	5.23	1.19
Polychaeta	<i>Myriochele heeri</i>	52.11	39.50	5.13	1.22
Polychaeta	<i>Chaetozone cf. jubata</i>	0.44	26.00	4.77	2.99
Polychaeta	<i>Prionospio</i> sp.	6.89	18.00	2.73	0.78
Bivalvia	<i>Bathyarca frielei</i>	11.67	13.50	2.33	1.52
Cumacea	<i>Diastylis polaris</i>	17.11	7.00	2.04	1.26
Tanaidacea	<i>Pseudosphyrapus serratus</i>	12.11	3.50	1.86	1.61
Polychaeta	<i>Tharyx</i> sp.	7.33	13.50	1.75	1.47
Polychaeta	<i>Aricidea abranchiata</i>	2.56	11.00	1.56	1.85
Polychaeta	<i>Ophelina opisthobranchiata</i>	11.89	13.50	1.51	1.26
Polychaeta	<i>Abyssoninoe</i> sp.	0.56	7.00	1.25	2.67
Polychaeta	<i>Galathowenia oculata</i>	2.56	7.50	1.25	0.77
Bivalvia	<i>Yoldiella annenkovae</i>	6.00	1.50	0.93	1.33
Isopoda	<i>Eugerdia arctica</i>	4.56	0.00	0.90	1.06
Polychaeta	<i>Polycirrus</i> sp. ^a	0.00	4.50	0.84	1.26
Nemertea	Nemertea gen.sp. ^a	0.00	4.00	0.80	1.52
Bivalvia	<i>Cuspidaria centobi</i>	2.44	4.00	0.77	1.31
Bivalvia	<i>Tindaria derjugini</i>	4.00	1.00	0.76	1.08
Amphipoda	<i>Ischyrocerus tenuicornis</i>	2.89	1.50	0.72	0.76
Amphipoda	<i>Harpinia plumosa</i>	6.56	4.00	0.67	1.20
Polychaeta	<i>Notomastus</i> sp.	2.89	2.00	0.65	1.27
Isopoda	<i>Ilyarachna hirticeps</i>	2.00	5.00	0.59	0.72
Holothuroidea	<i>Prototrochus zenkevichi</i>	0.22	3.00	0.55	1.30
Polychaeta	<i>Spiochaetopterus typicus</i>	0.00	2.50	0.51	0.95
Enteropneusta	Harrimaniidae gen.sp. ^a	0.00	2.50	0.49	1.39
Bivalvia	<i>Hyalopecten frigidus</i>	0.67	2.50	0.43	1.05
Sipuncula	<i>Nephasoma diaphanes</i>	2.00	1.00	0.43	0.95
Holothuroidea	<i>Acanthotrochus mirabilis</i>	3.56	3.00	0.39	1.02

^aThese species could be overlooked in 2003 samples because of the bad shape of preservation

class level (Galéron et al. 2001; Smith et al. 2009; Soto et al. 2010). Bluhm et al. (2011) reported that the differences in species identification by different investigators may often coincide with regional differences when studying the spatial structure of macrobenthos. The number of renamed taxa shown in Table 2 is a good example illustrating the importance of careful re-identification to the species level by the same specialist, when looking for temporal variations in the community structure.

As a conclusion, this study provides first data on temporal dynamics of macrobenthos in the Arctic deep sea. Only a two-point dataset on HAUSGARTEN macrobenthos is available which allows only a first glimpse into temporal variability. Another limitation in the interpretation of results from macrofauna studies at HAUSGARTEN is the lack of background data for more than half of the stations. Previously Vedenin et al. (2016) showed correlation in certain species abundance with latitude (and, possibly, with the food availability). However,

in our case, environmental data are only available for stations HGIV and S1, i.e. for 5 out of 13 samples (Klages et al. 2004; Soltwedel 2013), which impedes correlating the macrofaunal variations with the environmental parameters over the different spatial scales (~2 km and ~25 km) investigated.

Conclusions

Investigations on temporal dynamics in benthic communities generally focus on changes in main community characteristics and/or the changes in certain taxa. In this study, we focused on the complete species lists which allowed us tracing changes in density of certain species between two sampling events in 2003 and 2012. Over the nine-year period no variability in total density, biomass and diversity were found. However, while significant differences in abundance were detected for several common species (e.g.

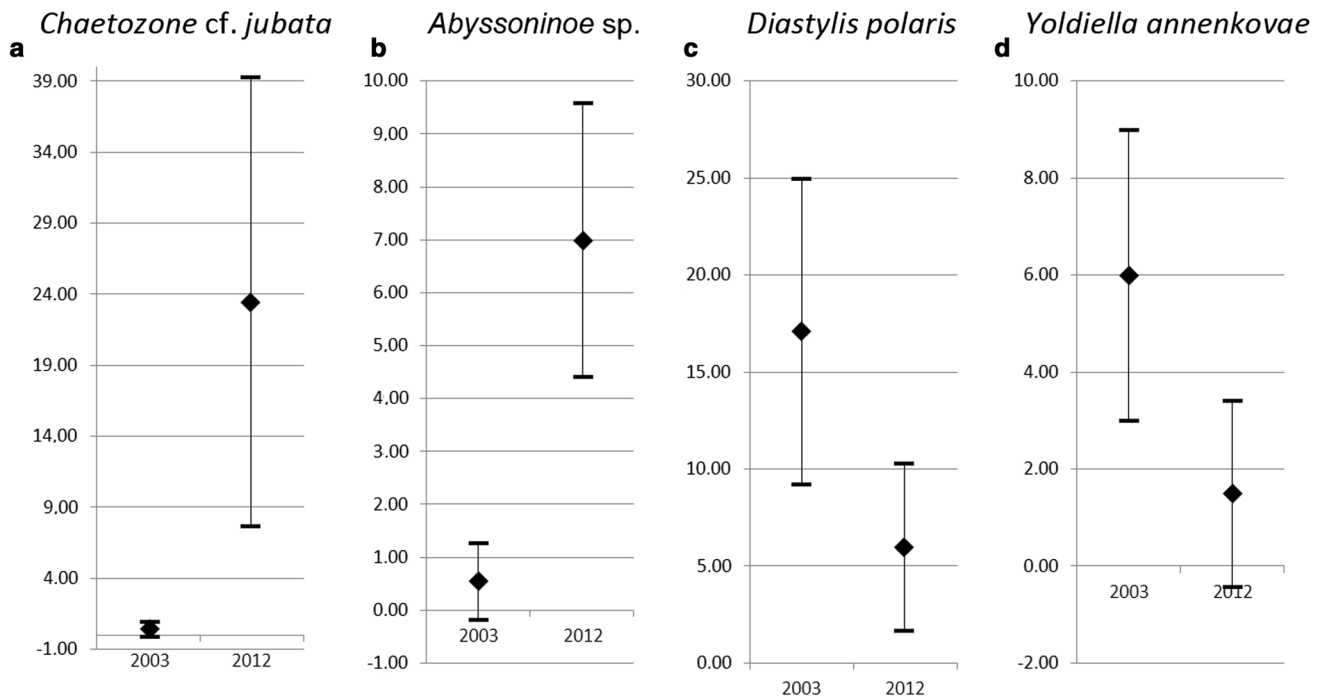
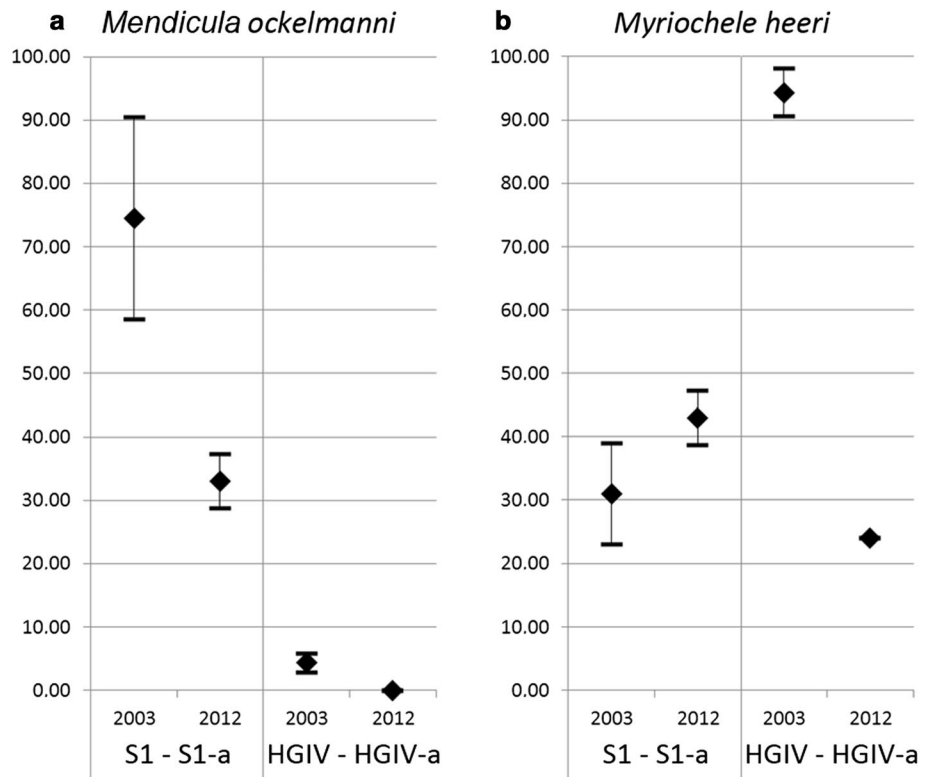


Fig. 5 Mean values with standard deviation of species density (ind 0.25 m⁻²) from 2003 and 2012 samples for the scale of ~25 km. Samples were taken by box-corer during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

Fig. 6 Mean values with standard deviation of species density (ind 0.25 m⁻²) from 2003 and 2012 samples for the scale of ~2 km. Samples were taken by box-corer during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)



the bivalves *Mendicula ockelmanni* and polychaetes *Chaetozone cf. jubata*, other macrofaunal taxa (e.g. Bivalvia and Polychaeta) showed no such differences. Besides these

discrepancies, at least two species (*Pseudosetia cf. griegi* and *Eugerdia arctica*) were unique for 2003 samples and two species (*Jasmineira schaudinni* and *Spiochaetopterus*

Table 6 Results of the Kruskal–Wallis test for the taxa with the different density values between the years 2003 and 2012 from box-corer samples taken during RV “Polarstern” expeditions ARK-XIX/3c and ARK-XXVII/2

Species	H (χ^2)	H_C (tie corrected)	p (same)
<i>Chaetozone cf. jubata</i> ^a	7.714	8.407	0.004
<i>Abyssoninoe</i> sp. ^a	7.714	8.259	0.004
<i>Diastylis polaris</i> ^a	6.095	6.146	0.013
<i>Yoldiella annenkovae</i> ^a	6.095	6.215	0.013
<i>Mendicula ockelmanni</i> ^b	4.000	4.048	0.044

^aComparison of all the stations from 2003 and 2012

^bComparison from only S1 and S1-a stations

typicus) were exclusive for the 2012 samples. We interpret both density changes and presence/absence of certain species as temporal changes in the community structure.

The comparison of the complete species lists from stations using cluster analysis and multidimensional scaling revealed significant temporal variations at the scale of ~2 km (i.e. in the station pairs S1–S1-a and, separately, HGI–HGIV-a). However, the differences in time did not exceed the variability in the scale of ~25 km, i.e. the distance between the northern and the southern station pairs.

Our study confirmed the importance of a reliable identification of species. A careful re-identification of every single specimen from previous samplings is needed before comparing the whole species lists from different sampling events. In this study, only two datasets were compared which allowed a first brief look into the long-term temporal variability of macrofauna. Continued sampling at HAUSGARTEN and simultaneously collected environmental data will allow

assessing the long-term dynamics of macrobenthos and the driving factors for changes.

Acknowledgements The authors wish to thank the crew and the participants of the RV Polarstern expeditions ARK-XIX/3c and ARK-XXVII/2 for their help onboard with sampling and processing of samples. We would like to thank the following specialists for their help in identification of benthic macrofauna: Dr. Caroline Pantke (Porifera), Dr. Elena Krylova (Bivalvia), Dr. Marina Malutina (Isopoda) and Dr. Alexander Mironov (Echinodermata). Our special thanks are to Dr. Andrey Azovsky and Dr. Christiane Hasemann for help in statistical analysis. This work was partly funded by the RSF Grant 14-50-00095 and by RFBR Grants 15-04-01870, 18-05-60053, 18-05-60228 and 17-05-00787 and the State assignment of IORAS (theme N^o 0149-2019-0009). The manuscript has the Eprint ID 41439 of the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Germany.

Compliance of ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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Table 7 Species occurrence, likelihood of not finding a species, number of cores taken and number of cores required for finding a species calculated for the species present only in 2003 and only in 2012 samples

Species	Species occurrence	Likelihood of not finding	Number of cores	
			Required for finding	Taken
Species present in 2003 and absent in 2012				
<i>Pseudosetia cf. griegi</i>	0.50	0.04	3.7	4
<i>Eugerdia arctica</i>	0.78	0.00	1.4	4
Species absent in 2003 and present in 2012				
<i>Jasmineira schaudinni</i>	0.50	0.06	4.3	9
<i>Polycirrus</i> sp. ^a	0.75	0.00	2.2	9
<i>Spiochaetopterus typicus</i>	0.50	0.06	4.3	9
Bonelliidae gen.sp. ^a	0.50	0.06	4.3	9
Nemertea gen.sp. ^a	1.00	0.00	1.0	9
Harrimaniidae gen.sp0.1	0.75	0.00	2.2	9

All samples were taken by box-corer during RV “Polarstern” expeditions ARK-XIX/3c (2003) and ARK-XXVII/2 (2012)

^aThese species could be overlooked in 2003 samples because of the bad shape of preservation

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