Polar Biol (2016) 39:851–862
DOI 10.1007/s00300-015-1875-9

ORIGINAL PAPER

Sponge communities of the Antarctic Peninsula: influence of environmental variables on species composition and richness

Daniel Kersken[1] · Barbara Feldmeyer[2] · Dorte Janussen[1]

Received: 14 August 2015 / Revised: 15 December 2015 / Accepted: 16 December 2015 / Published online: 19 January 2016

Abstract Sponge communities on the Antarctic continental shelf currently represent one of the most extensive sponge grounds in the world, and all sponge classes are known to occur in the Southern Ocean. Main objectives of this study conducted at the tip of the Antarctic Peninsula were (1) to identify all sampled sponges and (2) to investigate whether the species composition and species richness of Southern Ocean sponge communities in the area of the Antarctic Peninsula are significantly influenced by environmental variables. The studied material originated from 25 AGT catches and was sampled during the expedition ANT-XXIX/3 of RV *Polarstern*. Samples were collected in three large-scale areas in the vicinity of the Antarctic Peninsula: Bransfield Strait, Drake Passage and Weddell Sea. The following six environmental variables were measured from bottom water samples (except for sea-ice cover): depth (m), light transmission (%), oxygen (μmol/kg), salinity, sea-ice cover (%) and temperature (°C). Two hundred and sixty-three sponge samples were analyzed, and 81 species of 33 genera from all Porifera classes (Calcarea, Demospongiae, Hexactinellida and Homoscleromorpha) were identified. Total numbers of sponge species per sample station ranged from 1 to 29. A detrended correspondence analysis and a backward-stepwise model selection were performed to check whether species composition and richness were significantly influenced by environmental variables. The analyses revealed that none of the measured environmental variables significantly influenced species composition but that species richness was significantly influenced by (1) temperature and (2) the combination of temperature and depth. Results of this study are of crucial importance for development, performance and assessment of future protection strategies in case of ongoing climatic changes at the Antarctic Peninsula.

Keywords Southern Ocean · Climate change · Shelf communities · Antarctic sponges

Introduction

Benthic communities on the Antarctic continental shelves are commonly sponge-dominated in terms of abundance and biomass (Dayton et al. 1974; Barthel and Gutt 1992; Sarà et al. 1992; Gutt and Koltun 1995; Janussen and Tendal 2007; Downey et al. 2012; Fillinger et al. 2013; Gutt et al. 2013), and represent some of the most extensive sponge grounds in the world (Klitgaard and Tendal 2004; Hogg et al. 2010; Kersken et al. 2014). Representatives of all sponge classes are known to occur in the Southern Ocean. In 2014, a total number of 400 species were known from the Antarctic: 293 Demospongiae, 53 Hexactinellida, 51 Calcarea and 3 Homoscleromorpha; many of these are endemic: 112 Demospongiae, 36 Hexactinellida and 27

This article belongs to the special issue on “High environmental variability and steep biological gradients in the waters off the northern Antarctic Peninsula”, coordinated by Julian Gutt, Bruno David and Enrique Isla.

Electronic supplementary material The online version of this article (doi:10.1007/s00300-015-1875-9) contains supplementary material, which is available to authorized users.

✉ Daniel Kersken
daniel.kersken@senckenberg.de

[1] Senckenberg Research Institute and Nature Museum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

[2] Biodiversity and Climate Research Centre by Senckenberg Naturforschende Gesellschaft and Goethe University, Georg-Voigt-Straße 14-16, 60325 Frankfurt am Main, Germany

Calcarea (Janussen and Downey 2014). The high endemism (44 % of Antarctic sponge species) can be explained by the long-lasting isolation of the Antarctic shelf after the breakup of the supercontinent Gondwana during the Mesozoic era (252–66 myr). With the opening of the Drake Passage (49–17 myr), the Antarctic Circumpolar Current (ACC) started to move (Scher and Martin 2006). The ACC functions as a physical and climatic barrier that is believed to have led to allopatric speciation of species on the continental shelves (Dayton et al. 1994; Janussen and Downey 2014). Many species seem to have a circumpolar distribution pattern (Sarà et al. 1992; McClintock et al. 2005; Gutt et al. 2013) which is potentially driven by factors like swimming larvae, free-floating propagules and kelp-rafting. On the other hand, still to be identified cryptic species complexes will result in an over-estimate of circumpolar species (Sarà et al. 1992; Helmuth et al. 1994; McClintock et al. 2005). Antarctic sponges reproduce sexually and asexually through budding and short-lived free-swimming lecithotrophic larvae (McClintock et al. 2005; Teixidó et al. 2006). Approximately 30 % of the sponge species in the Southern Ocean are known to be eurybathic (Janussen and Downey 2014). Still, a depth gradient of sponge community composition based on species occurrence is recorded as relative proportions of sponge classes shift from demosponge-dominated shelf communities to hexactinellid-dominated slope and abyssal communities (Janussen and Tendal 2007; Göcke and Janussen 2011, 2013). Sponges of the genus *Rossella* (Carter, 1872) are the only glass sponges which potentially dominate shelf habitats on a regional scale (Göcke and Janussen 2011).

This work attempted to contribute to study the community structures of sponge shelf communities around the tip of the Antarctic Peninsula. The first main objective was an identification of all sampled sponge species, also to expand recent knowledge on species occurrence and distribution patterns in the area of the Antarctic Peninsula. Previous studies were focused on other parts of the Southern Ocean or were pure taxonomic papers giving an inventory of species (e.g., Campos et al. 2007a, b, c), whereas this sponge community analysis follows a mainly ecological approach. Our working hypothesis was that sponge community structures are significantly influenced by the measured environmental variables: we expected to find hexactinellid-dominated communities with lower species numbers at deeper stations, that species richness decreases at stations with sea-ice cover due to lower primary production or comparably species-poor communities with increasing bottom water temperatures. Second main objective of this study was thus to determine which environmental variables significantly influence the sponge community structures. It was also aimed to achieve general insights on patterns and processes of Antarctic sponge communities in a changing environment. Six presumably sponge-limiting environmental variables were included in the statistical analyses, to test for their potential effects on species composition and species richness of Antarctic sponge communities. Results of this study are important for development, performance and assessment of future protection strategies in case of ongoing climate-induced environmental changes, especially the western Antarctic Peninsula is one of the areas showing the most rapid warming worldwide (Meredith and King 2005; Gutt 2013; Kaiser et al. 2013).

Materials and methods

The studied material was sampled during the expedition PS81 ANT-XXIX/3 of RV *Polarstern* (January 22–March 18, 2013). The expedition contributes to the SCAR (Scientific Committee on Antarctic Research) biology program called AnT-ERA (Antarctic Thresholds-Ecosystem Resilience and Adaptation). AnT-ERA is focused on the investigation of changes in biological processes due to the climate effect in Antarctic and subantarctic ecosystems. The ecological study design with thirty benthic sample stations in three regions around the Antarctic Peninsula comprises two approaches to analyze patterns and processes at different spatial scales (1) comparison of large-scale areas: Bransfield Strait (BS), Drake Passage (DP) and the western Weddell Sea (WS); (2) comparison of intermediate-scale areas and environmental gradients: sample stations at different depths and topography located within the three large-scale areas. Sixteen sample stations were located in the Bransfield Strait, eight in the western Weddell Sea and six in the Drake Passage (Fig. 1).

Study site

The sampling area was located in three regions around the tip of the Antarctic Peninsula (Fig. 1). Sample stations in the Bransfield Strait were in the shelf area around the South Shetland Islands and the shelf area around the tip of the Antarctic Peninsula, which are separated by a central basin with a maximum depth of ca. 2000 m and a width of ca. 65 km (Fisk 1990). All stations were located close to the margin of the shelf area west of the Antarctic Peninsula, but some were in deep canyons: stations #196-8, #204-2 and #220-2 were situated in three canyons that extend from the deep central basin of the Bransfield Strait. All six stations in the Drake Passage were located on the margin of the shelf area, which extends to the northwest of the South Shetland Islands. The Weddell Sea is separated from the Bransfield Strait by the landmasses of the Antarctic Peninsula. Shelf areas of both regions are linked via the Antarctic Sound and the Joinville Islands. The stations #159-3 and #160-3 were situated on the shelf, north of the

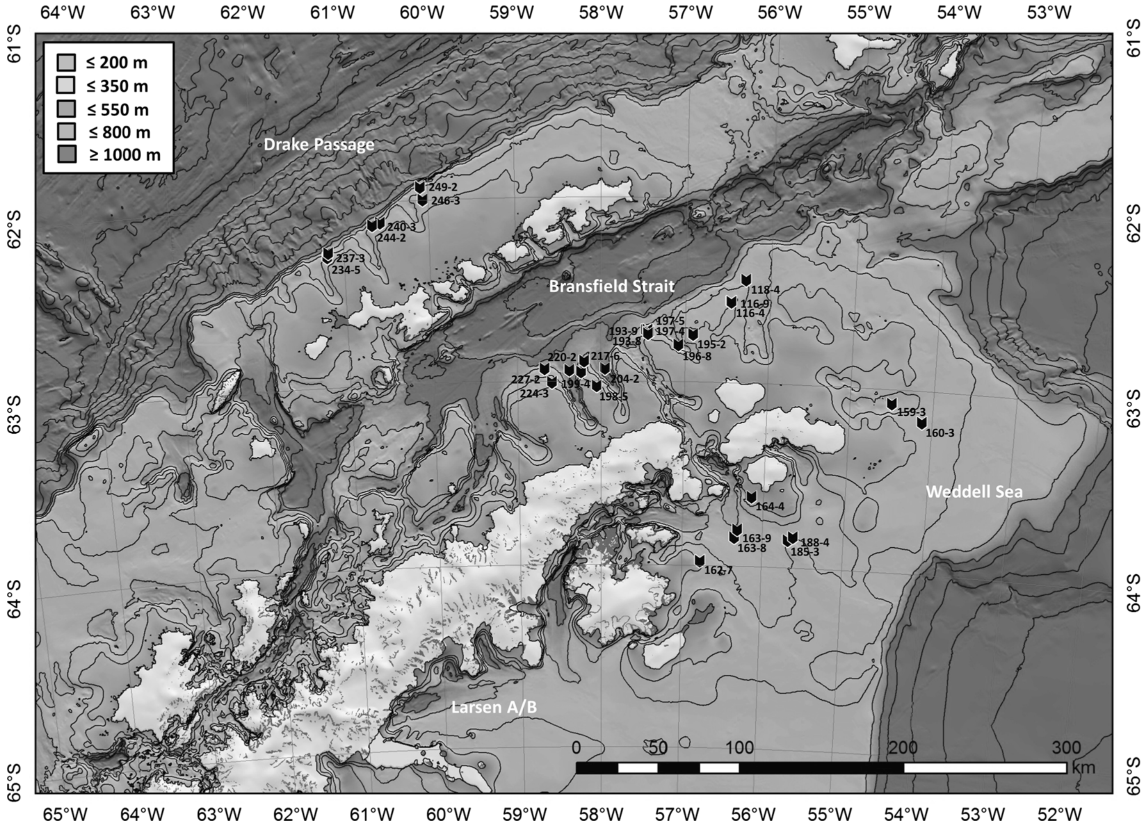

Fig. 1 Map of all stations with deployment of AGT, three large-scale areas and the Larsen Ice Shelf areas Larsen A/B (bathymetric analyses were performed with ArcGIS$^{®}$)

Joinville Island group, while other stations were in the Erebus and Terror Gulf in the west Weddell Sea, with station #164-4 close to the Antarctic Sound.

Gear deployment

Sponge samples from each station were taken by deployment of a modified AGT (Agassiz trawl). The AGT is a semiquantitative gear and consisted of a non-symmetrical constructed metal frame with a total dimension of 3.0 m in width, 2.5 m in length and 1.0 m in height. The frame was equipped with a net having a total length of 5.0 m. The mesh size was decreasing from net opening, with 20 mm meshes, toward the cod end with a mesh size of 10 mm. Bottom water samples at each AGT station were taken and analyzed by a Rosette + CTD (conductivity–temperature–depth recorder) equipped with an additional C-Star transmissometer with an optical path length of 25 cm (Table 1).

Sample handling

Benthic organisms were cleaned on deck by using running seawater at low pressure. Later on, they were sorted, labeled and preserved in denatured ethanol (96 %). Identified specimens and their metadata were electronically cataloged with SMF-numbers (Online Resource 1), and now they are online available in the SESAM database (SEnckenberg SAMmlungsmanagement - http://www.sesam.senckenberg.de) of the Senckenberg Research Institute and Nature Museum in Frankfurt am Main, Germany. For skeletal preparation, the standard method by Boury-Esnault and Rützler (1997) was applied where fragments of sponge material ($\sim$0.5 cm^3) were dissolved in nitric acid (HNO_3). The deployment of nitric acid was only feasible for sponges with siliceous spicules (Demospongiae, Hexactinellida and Homoscleromorpha). For sponges with calcareous spicules (Calcarea), it was necessary to use a sodium hypochlorite solution (NaClO) to dissolve the cellular material. Species identification was carried out using the standard literature (Boury-Esnault and Rützler 1997; Hooper and Van Soest 2002), the World Porifera Database (WPD: http://www.worldporiferadatabase.com) (Van Soest et al. 2015) as well as relevant taxonomical literature (Online Resource 2).

Biostatistics

All statistical measurements for the community analyses were based on the presence/absence data, and six

Table 1 AGT deployment during ANT-XXIX/3

Area	Station	Date (2013)	Time (UTC)	Position (lat S)	Position (lon W)
WS	116-4	26.01	16:47:00	62°33.80′	56°27.57′
	116-9		21:59:00	62°33.80′	56°27.42′
BS	118-4	27.01	13:46:30	62°26.41′	56°17.33′
WS	159-3	08.02	10:07:00	63°04.76′	54°29.57′
	160-3		21:46:00	63°10.38′	54°07.09′
	162-7	10.02	13:16:00	63°58.69′	56°46.26′
	163-8	11.02	06:45:00	63°50.66′	56°20.75′
	163-9		08:47:00	63°48.18′	56°18.55′
	164-4		18:35:00	63°37.32′	56°08.84′
	185-3	19.02	12:15:00	63°51.14′	55°40.81′
	188-4	20.02	13:57:00	63°49.98′	55°37.11′
BS	193-8	23.02	12:15:00	62°43.55′	57°28.06′
	193-9		14:13:00	62°43.36′	57°26.89′
	195-2	24.02	06:34:00	62°44.59′	56°54.22′
	196-8		19:56:00	62°48.08′	57°04.73′
	197-4	25.02	13:04:00	62°44.28′	57°25.50′
	197-5		14:38:00	62°44.57′	57°26.52′
	198-5	26.02	12:58:00	63°01.65′	58°02.94′
	199-4	27.02	07:54:00	62°57.13′	58°14.17′
	204-2	28.02	11:22:00	62°56.02′	57°57.06′
	217-6	02.03	10:50:00	62°53.48′	58°12.24′
	220-2	03.03	08:33:30	62°56.58′	58°22.65′
	224-3	04.03	07:26:00	63°00.50′	58°35.39′
	227-2	05.03	09:02:30	62°56.07′	58°40.47′
DP	234-5	07.03	16:09:00	62°17.37′	61°11.90′
	237-3	08.03	12:08:00	62°16.10′	61°11.00′
	240-3	09.03	08:50:00	62°06.97′	60°33.92′
	244-2	10.03	13:07:00	62°07.68′	60°39.38′
	246-3	11.03	12:43:00	62°00.03′	60°03.85′
	249-2	12.03	11:06:30	61°55.89′	60°05.21′

WS Weddell Sea, *BS* Bransfield Strait, *DP* Drake Passage

environmental variables were included: depth (m), oxygen (μmol/kg), salinity, temperature (°C), light transmission (%) and mean sea-ice cover (%). Data of depth, light transmission, oxygen, salinity and temperature were obtained from Schröder et al. (2013) and data of sea-ice cover from Bracher and Huntemann (2015); further information on the physical background at the study area is given in Dorschel et al. (in review). All variables except for light transmission and sea-ice cover were measured with CTD water bottle samples taken from the bottom water layer. Light transmission was also measured in the bottom water layer but with a C-Star transmissometer. Mean sea-ice cover (2003–2012) was derived from the archive of the GlobColour project led by the ESA (European Space Agency) and measured daily by satellite systems with a 6.25-km^2 spatial resolution. The following analyses were focused on both species composition and species richness of Antarctic sponge communities. A detrended correspondence analysis (DCA; vegan package in R) was performed to measure whether environmental variables significantly influence the species composition of sponge communities. The effect of environmental variables on species numbers was analyzed using a linear mixed model (lmer function implemented in the lme4 package (Bates et al. 2015)) with log-transformed number of species as dependent variable, the above-mentioned environmental variables as predictors, and sample stations as random factor. We used a backward-stepwise model procedure for model selection ($\alpha = 0.05$). Furthermore, we conducted Pearson's Chi-squared test to determine whether species numbers of single sample stations were significantly different. Statistical analyses were performed with the R statistical package 3.0.2 (R Core Team 2015).

Results

Environmental data

Environmental data of the bottom water layer (except for sea-ice cover) include depth (m), light transmission (%), salinity, oxygen (µmol/kg), mean sea-ice cover (%) and temperature (°C) as shown in Table 2. The total depth range is between 170 and 739 m with deepest stations in the Bransfield Strait. Light transmission is between ~93 and 97 % and is used as a proxy for sedimentation and resuspension processes in the bottom water layer. Salinity is showing an overall difference of 0.2 with values from ~34.38 to 34.56. Oxygen values range from ~233 to 324 µmol/kg. Mean sea-ice cover for the years 2003–2012 corresponds to the percentage cover of the water surface in a cell of 6.25 km^2 and ranges from ~6 to 57 % showing that the Drake Passage has less ice cover than Bransfield Strait and Weddell Sea. The measured bottom water temperature is between ~0.4 and 1.9 °C showing also higher bottom water temperatures in the Drake Passage.

Sponge taxonomy

The study material includes a number of 270 sponge specimens, of which 263 (97 %) are identified to species or genus level (Table 3). The remaining seven sponges are excluded from the community analyses. The analyzed material comprises 81 species belonging to 33 genera. Representatives of all sponge classes were identified: Homoscleromorpha (1 species), Demospongiae (71 species), Hexactinellida (7 species) and Calcarea (4 species). Four specimens, obviously belonging to different species, represent calcareous sponges, but none of them could be identified to species level due to the complicated taxonomy of this group. One specimen of the genus *Plakina* sp. (Schulze, 1880) represents the class Homoscleromorpha. The class Demospongiae is the most species rich compared to the other classes, 71 species belonging to 30 genera, 20 families and 5 orders are identified. The order Poecilosclerida is the biggest demosponge group within this study, as it comprises 55 species (corresponding to approximately one quarter of the total number of recent

Table 2 Environmental data from CTD water bottle samples from bottom water layer at all related AGT stations during ANT-XXIX/3

Station	Depth (m)	Light transmission (%)	Oxygen (µmol/kg)	Salinity	Sea-ice cover (%)	Temperature (°C)
116-4	183	97.093	295.75	34.4856	29.5708	−1.5447
116-9	183	97.093	295.75	34.4856	29.5708	−1.5447
118-4	421	96.931	273.46	34.5433	29.9714	−1.1456
160-3	236	93.236	294.48	34.4312	39.9975	−1.7456
162-7	208	94.323	299.94	34.4647	49.2700	−1.8654
164-4	185	94.287	323.81	34.3753	57.4400	−1.3353
185-3	391	94.117	285.06	34.5201	54.9136	−1.4564
188-4	391	94.117	285.06	34.5201	55.0700	−1.4564
193-8	442	97.055	269.02	34.5342	26.2623	−0.9957
193-9	442	97.055	269.02	34.5342	26.2623	−0.9957
196-8	544	96.919	281.76	34.4980	25.8707	−1.3096
197-4	226	96.955	289.91	34.4722	26.2179	−1.4659
197-5	226	96.955	289.91	34.4722	26.2179	−1.4659
198-5	170	95.934	306.65	34.4144	25.6200	−1.2883
199-4	239	96.950	286.88	34.4776	25.8869	−1.3310
204-2	739	97.459	257.48	34.5628	25.8540	−0.7214
217-6	521	97.315	266.83	34.5370	25.7421	−0.9491
220-2	672	97.364	259.78	34.5584	25.5023	−0.8011
224-3	252	96.658	288.22	34.4665	25.2475	−1.1987
227-2	526	97.428	262.17	34.5512	24.4079	−0.8534
234-5	229	95.665	261.14	34.4150	7.8121	0.0317
237-3	373	96.686	232.78	34.5138	7.7643	0.4226
240-3	274	96.397	265.82	34.3986	7.0000	0.0376
246-3	295	95.964	258.07	34.4448	6.4386	−0.1569
249-2	396	96.824	238.63	34.5348	6.4907	0.1185

Table 3 List of identified sponge species and taxa, subdivided by classes and occurrence in large-scale areas, gray boxes indicate occurrence of species (WS = Weddell Sea, BS = Bransfield Strait and DP = Drake Passage)

Class Homoscleromorpha

Species	WS	BS	DP
Plakina sp.	–	+	–

Class Demospongiae

Species	WS	BS	DP
Acanthorhabdus fragilis Burton, 1929	–	+	–
Asbestopluma sp.	–	+	–
Biemna strongylota Rios & Cristobo, 2006	–	+	–
Calyx arcuarius (Topsent, 1913)	–	+	–
Cinachyra antarctica (Carter, 1872)	+	–	+
Cinachyra barbata Sollas, 1886	–	+	–
Clathria (Axosuberites) flabellata (Topsent, 1916)	+	–	–
Clathria (Axosuberites) nidificata (Kirkpatrick, 1907)	–	+	–
Clathria (Axosuberites) sp.	–	+	–
Clathria (Clathria) inanchorata Ridley & Dendy, 1886	–	+	–
Clathria (Clathria) pauper Brøndsted, 1927	+	+	–
Clathria sp. 1	–	+	–
Clathria sp. 2	+	–	–
Clathria sp. 3	–	+	–
Clathria sp. 4	–	+	–
Guitarra sigmatifera Topsent, 1916	+	+	–
Halichondria sp. 1	–	+	–
Halichondria sp. 2	–	+	–
Haliclona sp.	+	+	+
Hemigellius bidens (Topsent, 1901)	+	–	–
Hemigellius fimbriatus (Kirkpatrick, 1907)	–	+	–
Homaxinella balfourensis (Ridley & Dendy, 1886)	+	+	–
Hymedesmia sp.	–	+	–
Inflatella belli (Kirkpatrick, 1907)	+	–	–
Iophon gaussi Hentschel, 1914	–	+	–
Iophon terranovae Calcinai & Pansins, 2000	+	+	–
Iophon unicorne Topsent, 1907	+	+	–
Iophon sp.	–	+	–
Isodictya bentarti Rios, Cristobo & Urgorri, 2004	+	–	–
Isodictya cavicornuta Dendy, 1924	–	+	–
Isodictya erinacea (Topsent, 1916)	+	+	+
Isodictya kerguelenensis (Ridley & Dendy, 1886)	–	+	–
Isodictya lankesteri (Kirkpatrick, 1907)	+	–	–
Isodictya setifera (Topsent, 1901)	+	–	–
Isodictya toxophila Burton, 1932	–	+	–
Isodictya verrucosa (Topsent, 1913)	+	+	–
Isodictya sp.	+	–	–
Kirkpatrickia coulmani (Kirkpatrick, 1907)	–	+	–
Kirkpatrickia variolosa (Kirkpatrick, 1907)	–	+	–
Latrunculia (Latrunculia) biformis Kirkpatrick, 1907	–	+	–
Latrunculia (Latrunculia) bocagei Ridley & Dendy, 1886	–	+	–
Lissodendoryx (Ectyodoryx) ramilobosa (Topsent, 1916)	–	+	–
Lissodendoryx (Lissodendoryx) flabellata Burton, 1929	–	+	–

Table 3 continued

Class Demospongiae

Species	WS	BS	DP
Lissodendoryx sp.	–	+	–
Microxina benedeni (Topsent, 1901)	–	+	–
Microxina phakelloides (Kirkpatrick, 1907)	–	+	–
Microxina sp.	–	+	–
Mycale tylotornota Koltun, 1964	+	+	–
Mycale fibrosa Boury-Esnault & van Beveren, 1982	–	+	–
Mycale (Carmia) gaussiana Hentschel, 1914	–	+	–
Mycale (Mycale) tridens Hentschel, 1914	–	+	–
Mycale (Oxymycale) acerata Kirkpatrick, 1907	+	+	+
Mycale sp.	–	+	–
Myxilla (Ectomyxilla) hentscheli Burton, 1929	+	+	–
Myxilla (Myxilla) elongata Topsent, 1917	+	+	–
Myxilla (Myxilla) mollis Ridley & Dendy, 1886	+	+	–
Myxodoryx hanitschi (Kirkpatrick, 1907)	+	+	–
Phorbas glaberrimus (Topsent, 1917)	+	+	–
Phorbas megasigma Rios & Cristobo, 2007	–	+	–
Plocamionida gaussiana (Hentschel, 1914)	–	+	–
Polymastia invaginata Kirkpatrick, 1907	–	+	–
Pseudosuberites sp.	–	+	–
Stylocordyla chupachups Uriz, Gili, Orejas & Perez-Porro, 2011	+	+	–
Tedania (Tedaniopsis) charcoti Topsent, 1907	+	+	–
Tedania (Tedaniopsis) massa Ridley & Dendy, 1886	–	+	–
Tedania (Tedaniopsis) oxeata Topsent, 1916	–	+	–
Tedania (Tedaniopsis) tantula (Kirkpatrick, 1907)	+	+	–
Tentorium papillatum (Kirkpatrick, 1908)	+	+	–
Tetilla leptoderma Sollas, 1886	+	+	+

Class Calcarea

Species	WS	BS	DP
Calcarea gen. sp. 1	–	+	–
Calcarea gen. sp. 2	–	+	–
Calcarea gen. sp. 3	+	–	–
Calcarea gen. sp. 4	–	+	–

Class Hexactinellida

Species	WS	BS	DP
Anoxycalyx (Anoxycalyx) ijimai Kirkpatrick, 1907	–	–	+
Anoxycalyx (Scolymastra) joubini (Topsent, 1916)	+	–	–
Rossella cf. *antarctica* Carter, 1872	+	+	–
Rossella cf. *fibulata* Schulze & Kirkpatrick, 1910	–	+	–
Rossella cf. *racovitzae* Topsent, 1901	+	+	+
Rossella cf. *vanhoeffeni* (Schulze & Kirkpatrick, 1910)	–	+	+
Rossella sp.	+	+	–

Antarctic demosponge species (Janussen and Downey 2014)). The hexactinellid sponges are represented by seven species: two species belong to the genus *Anoxycalyx* (Kirkpatrick, 1907) and five to the genus *Rossella*, both genera being part of the subclass Hexasterophora.

Distribution patterns

The study area was subdivided into three adjacent large-scale areas to investigate patterns of species distribution. Table 3 gives an overview of species occurrences per area indicated by gray boxes. Five of 81 (6.17 %) species are found to be widely distributed within all three regions: *Haliclona* sp. (Grant, 1836), *Isodictya erinacea* (Topsent, 1916), *Mycale (Oxymycale) acerata* (Kirkpatrick, 1907), *Tetilla leptoderma* (Sollas, 1886) and *Rossella* cf. *racovitzae* (Topsent, 1901). Twenty of 81 (24.69 %) species occur in two of three areas, mainly in Weddell Sea and Bransfield Strait. The majority, 58 of 81 (71.60 %) species, occur in only one of three large-scale areas which is mainly the Bransfield Strait as 50 of 58 species occur solely there. Total numbers of sponge species richness per sample station are shown in Fig. 2. Stations with highest species numbers are located in the Bransfield Strait (#196-8, #217-6 and #116-9). In contrast, stations with lowest species numbers are located in the Drake Passage (#240-3, #249-2 and #237-3). Stations on the recently discovered seamount Nachtigaller Hill located in the Weddell Sea (Dorschel et al. 2014) show moderate to high values with 17 species at station #185-3 (situated at slope) and 8 species at #188-4 (situated at foot). Frequently sampled species are *R.* cf. *racovitzae* (12 stations), *Iophon unicorne* (Topsent, 1907) (11 stations), *T. leptoderma* (10 stations), *M. (O.) acerata* (9 stations) and *Tedania (Tedaniopsis) tantula* (Kirkpatrick, 1907) (8 stations). Genera occurring with exceptionally high species numbers are *Isodictya* (Bowerbank, 1864) (9 species), *Mycale* (Gray, 1867) (6 species), *Iophon* (Gray, 1867) (6 species) and *Rossella* (5 species).

Community structure

The detrended correspondence analysis (DCA) indicates that none of the tested environmental variables are significantly influencing the species composition of the sponge communities (as indicated by probabilities (Pr) in Table 4). The model selection shows that species richness is significantly influenced by water temperature and increases with decreasing temperature levels in the bottom water layer (Table 5; Fig. 4). Furthermore, there is a marginally significant influence on species richness by the interaction of temperature and depth, whereas depth alone is not significant, but indicates that species richness slightly increases with depth. The conducted Pearson's Chi-square test reveals that species numbers of single sample stations are significantly different ($X^2 = 127.63$; $p < 0.001$).

Discussion

Sponge class composition per sample station

Species of all sponge classes were sampled at 25 AGT stations. The classes Calcarea and Homoscleromorpha were rare as Calcarea were present at four stations and Homoscleromorpha at one station. Demospongiae and Hexactinellida, on the contrary, were found at almost every

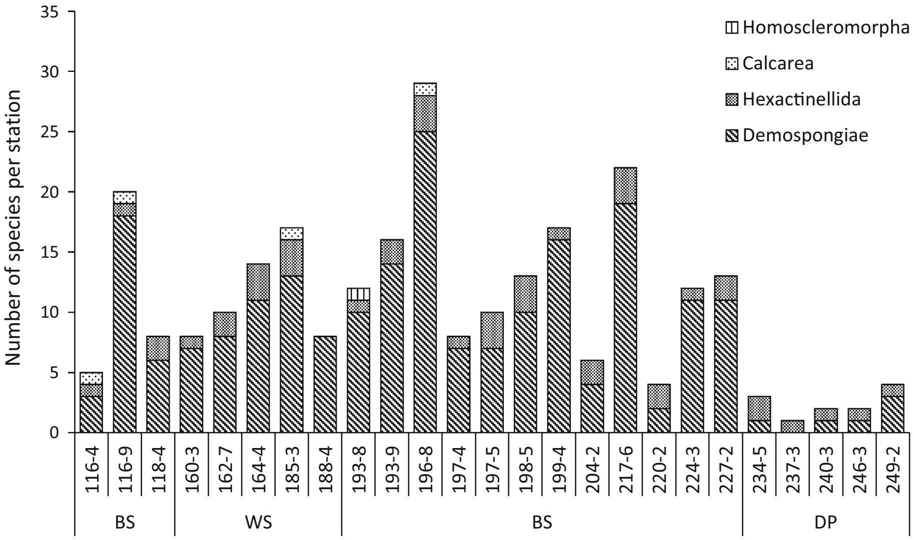

Fig. 2 Total number of sponge species per sampling station subdivided into classes. *WS* Weddell Sea, *BS* Bransfield Strait, *DP* Drake Passage

Table 4 Results of the DCA (Detrended correspondence analysis)

	DCA1	*DCA2*	r^2	*Pr (>r)*
Depth (m)	−0.33958	−0.94058	0.0318	0.8445
Light transmission (%)	−0.93611	0.35171	0.1314	0.4113
Oxygen (μmol/kg)	−0.57569	0.81767	0.0129	0.8523
Salinity	−0.94530	−0.32619	0.0129	0.9174
Sea-ice cover (%)	0.91496	0.40354	0.0191	0.6865
Temperature (°C)	0.99905	0.04353	0.0025	0.9097

None of the retrieved values is significant

Table 5 Results of the stepwise-backward model reduction

	Chi^2	Df	Pr (> Chi^2)	Significance
Depth	1.2766	1	0.2585	
Temperature	12.4633	1	0.0004	***
Temperature + depth	3.6750	1	0.0552	.

Significance codes: 0 = '***', 0.001 = '**', 0.01 = '*', 0.005 = '.' and 0.1–1 = ' '

station. Most of the identified species were Demospongiae (71 species, 29 genera), followed by Hexactinellida (7 species, 2 genera), Calcarea (probably 4 species, min. 1 genus) and Homoscleromorpha (1 species, 1 genus). Species numbers at stations were extremely variable and ranged from 1 (#237-3) to 29 (#196-8). Fifteen or more species were found at six sample stations (#116-9, #185-3, #196-8, #199-4 and #217-6), and five or less species were found at seven stations (#116-4, #220-2, #234-5, #237-3, #240-3, #246-3 and #249-2). Species-rich stations were mainly located in the Bransfield Strait, while most species-poor stations were situated in the Drake Passage. Stations in the Weddell Sea yielded moderate to high species numbers. In terms of species richness, it can be stated that sponge communities around the Antarctic Peninsula are dominated by demosponges. The sponges collected in the Drake Passage were generally much smaller than sponges from the Bransfield Strait and Weddell Sea. Based on personal observation, this was especially prominent in abundant species with a well-defined shape, such as *R.* cf. *racovitzae* and *T. leptoderma*.

Influence of environmental variables

Depth is known to influence the distribution of sponge species as several studies have shown that species composition changes along depth gradients, e.g., *T. leptoderma* displays a narrow stenobathic depth distribution (Barthel and Gutt 1992; Sarà et al. 1992; Göcke and Janussen 2013). Göcke and Janussen (2013) reported different types of sponge communities along depth gradients in the deep Weddell Sea but on larger depth scales (500–5500 m). In this study, topography of the seafloor was variable in all three large-scale areas, particularly the shelf regions within the Bransfield Strait, which were segregated by many deep canyons with depths of 1000 m and more, but the depth range is smaller (170–739 m). Light transmission was used as proxy for sedimentation and resuspension processes in the bottom water layer. Gerrodette and Flechsig (1979) showed in a study focused on the tropical sponge species *Aplysina lacunosa* (Lamarck, 1814) that high sedimentation rates significantly reduced pumping rates illustrating the importance of such processes in the bottom water layer, while light transmission ranged from 93.2 to 97.5 %. Oxygen uptake in sponges is realized by choanocytes which are arranged in flagellate chambers. In addition, it is known that sponges can reduce or stop the pumping for several hours or days, e.g., the Mediterranean sponge *Aplysina aerophoba* (Nardo, 1833) that is actively switching its metabolism from aerobic to anaerobic and is thus influencing the inner microbial community (Hoffmann et al. 2008). Oxygen from bottom water samples varied between 233 and 324 μmol/kg. Investigations of salinity-induced effects on sponges are scarce. Only a few studies have been published, and these are mainly focused on tropical reef and mangrove sponges in salinity extreme environments, e.g., encrusting forms of *Haliclona* that occur on trees in mangrove swamps (Barnes 1999). Expectations of this study were that salinity would vary due to sea-ice formation and disintegration processes, formation of the AABW (Antarctic bottom water), complex seafloor topography and current regimes. The values measured for salinity ranged from 34.38 to 34.56 and such differences are of minor importance for sponge communities. Mean sea-ice cover (2003–2012) was included, as it is known to be one of the most important physical drivers affecting Antarctic benthic communities (Cummings et al. 2010; Dorschel et al. 2014). Sea-ice cover is highly variable, especially in the summer months, and can change its state within hours (Cummings et al. 2010). Sea-ice cover ranged from 6.4 to 57.4 %, and we expected that sponge community structures would be indirectly influenced as sea-ice cover reduces primary production (e.g., Arrigo et al. 1997) and thus influences pelagic-benthic coupling processes. In correlation with sea-ice cover, bottom water temperature is increasing from sample stations in the Weddell Sea toward stations in the Drake Passage and varied from −1.87 to 0.42 °C. As stated by Gordon and Mensch (2000), the bottom topography of the Bransfield Strait shows two main basins: (1) the eastern basin near Joinville Island and (2) the central basin between the South Shetland Islands and the western Antarctic Peninsula. The bottom water masses in both basins originate from the Weddell Sea as overflow events which cause the ventilation of the eastern basin, while the same happens in turn between the eastern and central basin (Gordon and Mensch 2000). Bottom water temperatures in the Drake Passage are higher than in other areas caused by relatively warm (>0 °C) circumpolar deep water (CDW) being transported onto shelves of the western Antarctic Peninsula and its offshore islands, e.g., South Shetland Islands (Dinniman et al. 2011).

The conducted DCA revealed that none of the tested environmental variables is significantly influencing the species composition (Fig. 3; Table 4) although we expected that depth and sea-ice cover would have significant influence. It is known that shelf communities are dominated by demosponge species with a shift to deeper community types which are dominated by hexactinellid species (Göcke and Janussen 2013), but it is possible that differences in depth are too small in our study. However, bottom water temperature and marginally the combination of both temperature and depth show an effect on species richness in sponge communities around the tip of the Antarctic Peninsula, with the number of species decreasing with higher temperatures (Table 5; Fig. 4). Implementation of data describing bottom water currents would be interesting for future studies as current regimes are probably one of the physical main drivers shaping the structure of macrobenthic communities. It is important to consider that most measurements (except for mean sea-ice cover) are only snapshots and represent one certain point in time, while data from longtime measurements would be more interesting for future studies. One confounding factor could be that only the presence/absence data were available for the analysis. The information on abundances, if certain sponge species coped better with environmental variables than other species, is thus lacking. Also the sampling method, trawling with an AGT, can bear some problems when sampling sponges as already described in Kersken et al. (2014). The AGT can lose the permanent contact to the seafloor due to rocks or other material and jump or roll. As the temporary loss of contact to the seafloor cannot be recorded nor controlled from the ship, sampling distances might vary from sight to sight and add some variation to the obtained number of species.

Conclusions

In this study, sponge communities of the Antarctic shelf were investigated for their species composition and species richness in relation to recorded environmental variables. It turned out that species richness of sponge communities is significantly influenced by temperature and the interaction of temperature and depth. Cold-water temperatures in the bottom water layer support the occurrence of species-rich sponge communities. Species numbers are also higher at comparably cold and deep spots in Antarctic shelf habitats while regions deeper than 740 m stay unconsidered in this study. Any other of the measured environmental variables did not influence species composition of Antarctic sponge communities. One reason could be that biological data were limited to the presence/absence data due to the semiquantitative sampling characteristics of the deployed AGT. A more complex study design with abundance and/or biomass data would possibly throw some light on other effects which remain undetected. Further investigation is needed to understand how sponge communities are

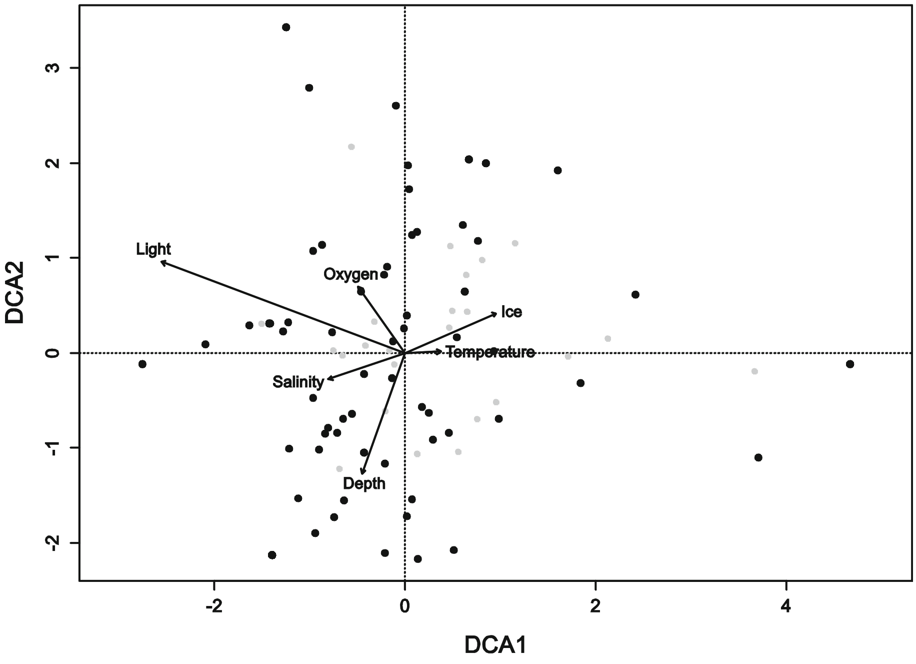

Fig. 3 DCA with sample stations = *gray dots*, sponge species = *black dots* and environmental parameters = *black arrows* in a two-dimensional NMDS plot

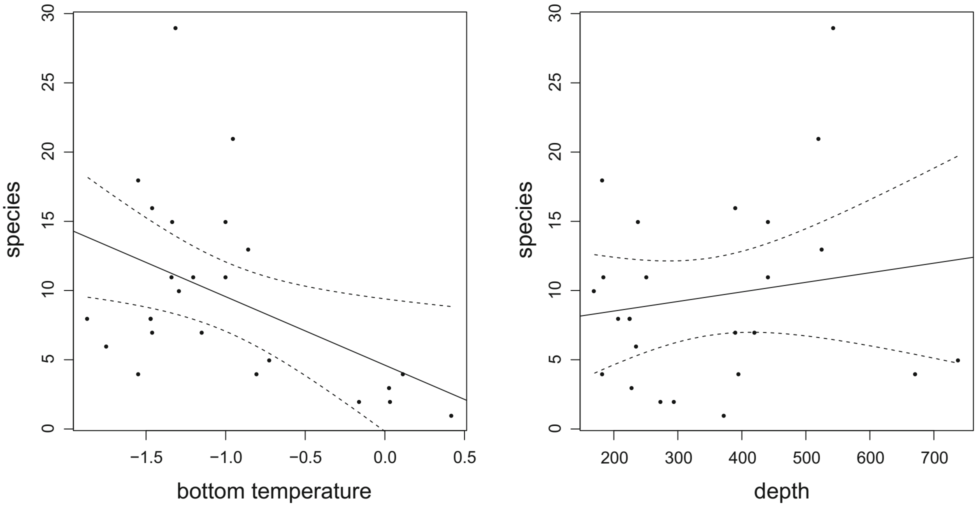

Fig. 4 Effects of bottom temperature and depth on species richness of sponge communities, dashed lines indicate 95 % confidence intervals

influenced by environmental variables. Continuing research will generate a better understanding for patterns and processes within benthic communities in a changing environment. The revealed information is important for development, performance and assessment of protection strategies in the future. We demonstrated that species richness of Antarctic sponge communities significantly decreases with increasing temperature and would expect a decline of such heterogeneous and sponge-dominated macroepibenthic communities in case of ongoing climatic changes at the Antarctic Peninsula.

Acknowledgments The authors want to thank the Fahrtleiter Prof. Dr. Julian Gutt and Dr. Boris Dorschel for bathymetrical data and the other colleagues on board during the expedition ANT-XXIX/3, as well as captain and crew of RV *Polarstern*. We further acknowledge the Deutsche Forschungsgemeinschaft (DFG) for financial support to our Antarctic Porifera project, JA-1168/17-1.

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