



ORIGINAL ARTICLE

A new genus and two new species of Thyasiridae associated with methane seeps off Svalbard, Arctic OceanEmmelie K.L. Åström^a, P. Graham Oliver^b and Michael L. Carroll^{a,c}^aCAGE – Centre for Arctic Gas Hydrate, Environment and Climate, Department of Geosciences, UiT The Arctic University of Norway, Tromsø, Norway; ^bNational Museum of Wales, Cardiff, UK; ^cAkvaplan-niva, Fram – High North Centre for Climate and Environment, Tromsø, Norway**ABSTRACT**

Bivalves have been found in unique benthic assemblages associated with active methane seeps and mounds along the western and southern margins of the Svalbard shelf (75–79°N) at 350–380 m depth. Among the samples collected were a number of shells of Thyasiridae that are distinct from any species previously described. Here we describe one new genus *Rhacothyas* gen. nov. and two new species *Thyasira capitanea* sp. nov. and *Rhacothyas kolgae* sp. nov., including their distinguishing characteristics and the environmental setting where they were found. *Thyasira capitanea* sp. nov. is large compared to many other thyasirids, has an equilateral shell and demarcated zones on the median and anterior areas along with a distinct posterior sulcus. *Rhacothyas kolgae* sp. nov. is unique among other thyasirid genera and species regarding its characteristic outline, sunken lunule, lack of submarginal sulcus and wrinkled surface. Furthermore, we discuss their present occurrence in the context of the glaciomarine history of the Svalbard margin. We posit that these new species, after the deglaciation of the Barents Sea Ice Sheet, may have originated from other chemosynthetic or reducing environments along the Atlantic shelf margin or the southern Barents Sea shelf by following the net transport of the North Atlantic Current rather than having evolved *in situ*.

ARTICLE HISTORYReceived 15 July 2016
Accepted 2 December 2016**RESPONSIBLE EDITOR**

Andrey Gebruk

KEYWORDS

Arctic; chemosymbiosis; cold seep; new species; Thyasiridae

Introduction

Cold seeps and vents are known to host specialized faunal assemblages associated with seafloor emissions of hydrocarbons, sulphide and other reduced compounds, that can be fuelled by microbial chemoautotroph production (Sibuet & Olu 1998; Levin et al. 2000; Thurber et al. 2010). Chemosynthesis can provide an alternative energy source, in addition to photosynthesis, at methane cold seeps through methane oxidation processes (Boetius & Suess 2004). Such activity can support associated macrofauna through trophic interactions or mutualistic relationships with symbionts, such as sulphide-oxidizing bacteria, where the source of sulphide is the anaerobic oxidation of methane (AOM) coupled to sulphate reduction (Lösekan et al. 2007; Vanreusel et al. 2009). The discovery of chemosynthetic communities at cold seeps has been accompanied by the description of a diverse and unique fauna including many Bivalvia, mainly belonging to chemosymbiotic Vesicomidae, Solemyidae, Bathymodiolinae, Lucinidae and Thyasiridae (Taylor & Glover 2010). Within the Atlantic and Arctic Oceans, there is an apparent high degree of

endemism with closely related but distinct species occurring at seep sites as exemplified by the vesicomid genus *Isorropodon* (Krylova et al. 2011; Oliver et al. 2011; Oliver & Drewery 2013). A similar pattern within the Thyasiridae is also becoming apparent, with new species described from the Gulf of Guinea (Oliver 2014), Gulf of Cadiz (Rodrigues et al. 2008) and off Scotland (Oliver & Drewery 2013). Cold seeps and vents are known in polar areas and the North Atlantic but many bivalves recorded from here are often distinct from the larger-bodied taxa (such as Vesicomidae and Bathymodiolinae) seen at seeps in lower latitudes. *Thyasira dunbari* Lubinsky 1976, is a small Arctic species (<7 mm) not confined to chemosynthetic settings (Oliver et al. 2002) but recorded both from shallow fjord and deep water habitats (Soltwedel et al. 2015) including the Håkon Mosby mud volcano 72°N (Gebruk et al. 2003) and at vent sites on the Mohn Ridge 71°N (Schander et al. 2010). The exception where larger-bodied chemosymbiotic bivalves (Vesicomidae) have been found is Storegga 64°N on the west Norwegian shelf (Krylova et al. 2011).

Large thyasirids are present in the fossil seeps from Svalbard dating from the Jurassic/Cretaceous boundary

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through to the Eocene. The earliest is *Cretaxinus hurumi* Hryniewicz et al., 2014, an atypical thyasirid being triangular in form with a relatively small anterior adductor scar (Hryniewicz et al. 2014). *Conchocele conradi* Rosenkrantz, 1942 originally identified as the recent *C. bisecta* (Conrad, 1849) by Hägg (1925) was described from late Cretaceous/Eocene deposits of Svalbard and also from Cretaceous to Paleocene strata in West Greenland (Rosenkrantz 1970; Dam et al. 2009). Living *Conchocele* are now restricted to methane seeps along the Pacific rim (Kamenev et al. 2001). Valentich-Scott et al. (2014) described an Arctic seep-associated thyasirid, *Wallerconcha sarae* Valentich-Scott & Powell, 2014, from the Beaufort Sea, but up to present date, species descriptions exist solely from collected shell material.

Cold seeps in the high Arctic are poorly studied compared with other regions at lower latitudes e.g. the Mediterranean Sea and Gulf of Mexico (Sibuet & Olu 1998; Fisher et al. 2007; Vanreusel et al. 2009). Along the western Svalbard margin, vast gas plumes associated with hydrocarbon seepages and dissociating gas hydrates have been reported (Westbrook et al. 2009; Sahling et al. 2014). These areas are being surveyed to assess the sources and sinks of methane and gas hydrates in the Arctic (Ferré et al. 2012; Plaza-Faverola et al. 2015; Portnov et al. 2016) and their temporal histories (Ambrose et al. 2015). The growing evidence of widespread gas seepages in Svalbard indicates a potent environmental driver affecting local seafloor conditions, including community structure and ecosystem function (Åström et al. 2016). Marine chemosynthetic habitats and seep-associated fauna in high Arctic regions are, however, poorly explored, but through an increasing number of biological studies, a better understanding of the community structure and ecological functioning is emerging in Arctic areas (Schander et al. 2010; Barrie et al. 2011; Sweetman et al. 2013; Åström et al. 2016). Among faunal samples we collected in 2014 and 2015 at active cold seeps along the western and southern Svalbard continental shelf are numerous representatives of bivalve shells belonging to the family of Thyasiridae. Here, we describe one new genus and two new species of Thyasiridae from methane seeps off the west coast of Svalbard (75–79°N) including their distinguishing characteristics and the environmental settings for the sites of record.

Study area and regional settings

Svalbard is an archipelago located at the northern North Atlantic continental shelf (76–81°N). The

climate in Svalbard is relatively mild compared with other regions in the high Arctic due to the North Atlantic Current system, which transports heat and saline water from the Atlantic along the west coast of Svalbard (Orvik & Niiler 2002; Rudels et al. 2005). Atlantic source water (>35 psu and >3°C) typically dominates the western continental shelf areas west of Svalbard (Svendsen et al. 2002; Nilsen et al. 2008), and limits seasonal sea ice formation in this region (Seager et al. 2002; Serreze et al. 2003; Stroeve et al. 2012). In the Barents Sea, a marginal sea to the Arctic Ocean, cold Arctic water (<34.8 psu and <0°C) encounters the warmer Atlantic water in a mixing zone known as the Polar Front. Dense Arctic water follows the submarine troughs, rounds the southern tip of Spitsbergen, and continues as a coastal current northwards along the west coast (Figure 1) (Johannessen & Foster 1978; Harris et al. 1998).

Materials and methods

Benthic sampling

Sampling activities were carried out during cruises in June and July 2014 and May 2015 onboard the R/V Helmer Hanssen. Three main regions were surveyed: (1) Western Svalbard i.e. Prins Karls Forland shelf (PKF), (2) the western Barents Sea i.e. Storfjordrenna (Storfjord Trough) seep site (SR) and (3) Pingo-like features (PLF), in Storfjordrenna (Figure 1). Areas of active methane seepage were identified by detecting acoustic flares on a keel mounted single beam echo sounder (Simrad EK 60, frequencies 18 KHz and 38 KHz). At Prins Karls Forland, a box corer was used for sampling the sea floor at identified target flare sites. In Storfjordrenna in 2014, a triangular scraper (1 × 1 × 1 m) was trawled over the sea bottom at an extensive field of seepages for ~5 min, bringing up sediments, shell material and carbonate crust. In Storfjordrenna, in 2015, material was collected from quantitative benthic sampling at seep sites with a van Veen grab 0.1 m², and a camera-towed multicorer (equipped with 6 liners with inner diameter = 10 cm). At all locations and with all sampling methods, shells were collected by sieving (1 and 5 mm) of bulk sediments. On board, shell material was sorted and identified as individuals in the Thyasiridae family due to the characteristic furrow on the shell. Following the cruises, bivalves were sent to the National Museum of Wales for identification.

The shells were examined and photographed using a Leica Z6 microscope supported by Helicon Focus stacking software. Direct comparisons were made

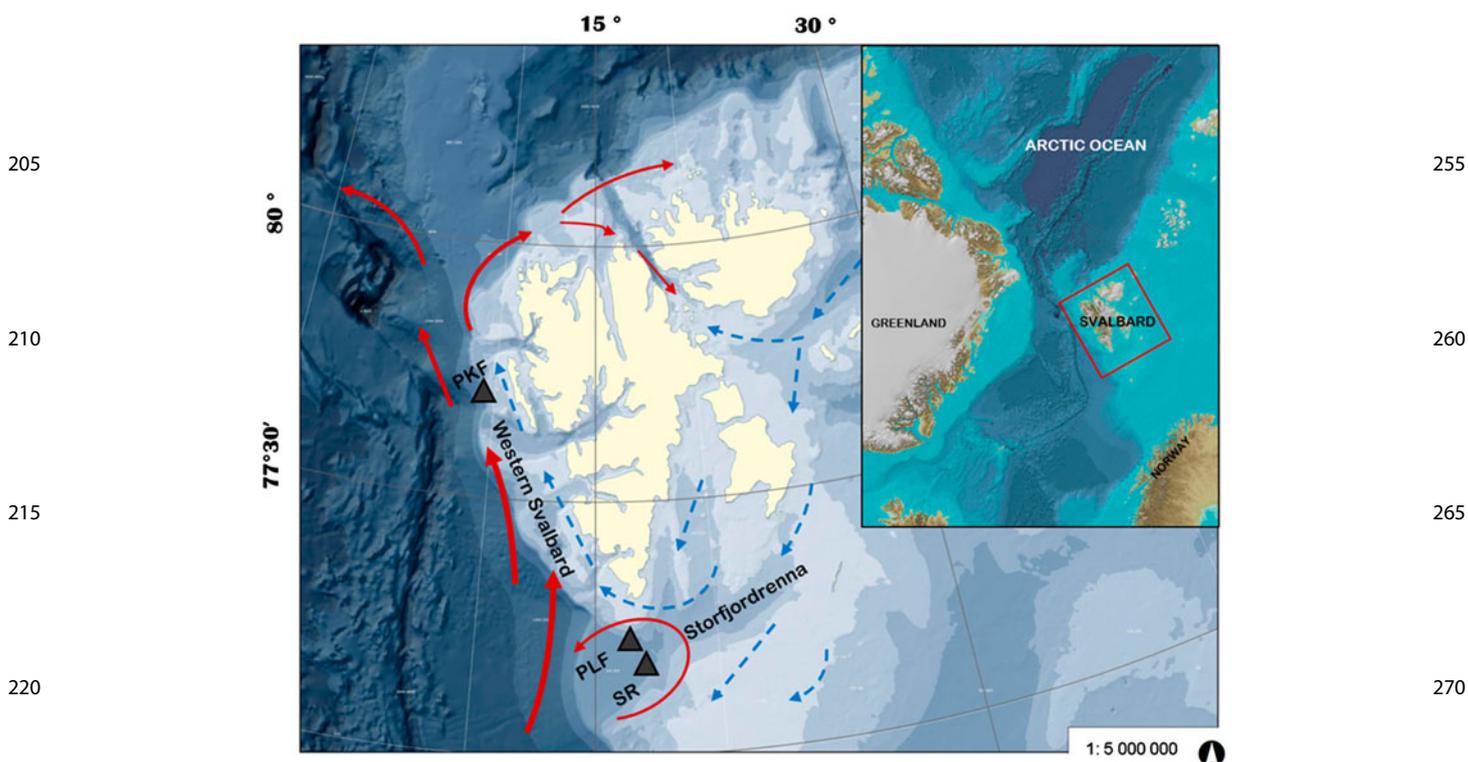


Figure 1. Collection sites (black triangles) and the main surface current patterns around Svalbard. Red solid arrows indicate Atlantic water and blue dashed arrows represent Arctic water. Modified from Norwegian Polar Institute (2016) and Loeng (1991). Inset map from Jakobsson et al. (2012). Site names abbreviations PKF = Prins Karls Forland, SR = Storfjordrenna seep, PLF = Pingo-like features.

with other thysasirids from the North Atlantic and Arctic Oceans held in the collections of the National Museum of Wales.

Environmental settings in Storfjordrenna

Storfjordrenna is located to the south of the main archipelago of Svalbard at the western margin of the Barents Sea. The trough was formed by erosion of glacial ice streams from the Barents Sea ice sheet (Patton et al. 2015). Storfjordrenna stretches ~250 km into the Barents Sea in a north-east-south-west direction and is characterized by mega-scale glacial lineations on the seabed originating from the last deglaciation (Andreassen & Winsborrow 2009; Patton et al. 2015). Along the border of the south-west Svalbard margin, several sites with active seepages and plumes have been observed at the depth range of the predicted gas hydrate stability zone <00 m (Westbrook et al. 2009; Portnov et al. 2016). The Storfjordrenna seep site, SR, is located close to a glacial grounding zone wedge and is characterized as a relatively homogeneous and featureless soft bottom environment with predominantly silty sediments, ~350 m deep, where sporadic out-crops of authigenic carbonate crust were seen.

Sediments were black and had a distinct hydrogen sulphur (H_2S) odour.

A few tens of kilometres north in Storfjordrenna and slightly deeper (380 m), the PLF site is characterized by several gas hydrate bearing mounds with high flare activity. Fine silty sediments with records of authigenic carbonates dominated the bottom substrate and recovered sediments had a strong smell of H_2S . This shelf region was influenced by transformed Atlantic water, with salinity over 35 psu and water temperatures of 2.40°C, indicative of Atlantic water.

Environmental settings at Western Svalbard shelf

Prins Karls Forland is an elongated fore island located at the shelf to the west of the main island of Svalbard, Spitsbergen. Along this continental shelf, gas seepage and extensive plumes have been reported in a range of water depths between 80–400 m, along with elevated concentrations of methane in the water column (Westbrook et al. 2009; Sahling et al. 2014; Steinle et al. 2015). A more detailed overview of the oceanographic conditions at the western Svalbard shelf and seepage into the water column is given in Graves et al. (2015) and Steinle et al. (2015). The bottom substrate is heterogeneous with a coarse mix of gravel

and sand with glaciomarine ice rafted debris covering layers of silty hemi-pelagic mud (Åström et al. 2016). The overriding bottom water-mass at the sampling site was Atlantic water (salinity 35.10 psu, temperature 3.40°C).

Scientific collection acronyms

FMNH	Field Museum of Natural History, Chicago
NMWZ	National Museum of Wales, Zoology
NSMT	National Science Museum, Tokyo
RBCM	Royal British Columbia Museum
SBMNH	Santa Barbara Museum of Natural History
USNM	United States National Museum
ZMMU	Zoological Museum of Moscow University
ZMNB	University Museum of Bergen
HT PT	Holotype Paratype

Comparative material examined

Thyasira vulcolutre Rodrigues, Oliver & Cunha, 2008. NMW.Z.2007.003.00001, HT, shell, North-east Atlantic, Gulf of Cadiz, Captain Arutyunov mud volcano, cruise MS Merian 01-03, st. 217 GKG10, 35°39.643'N, 07°20.046''W, 1321 m, 30 Apr. 2006, M.R.

Cunha; NMW.Z.2007.003.00002-3, PT, $n = 2$, shells, same collection data as holotype.

Thyasira southwardae Oliver & Holmes, 2006. ZMMU Ld-29999, HT, 13.4 mm long, Mid-Atlantic Ocean, Logatchev Vent Site, Anyas Garden, DSRV Alvin, st. Dive 3133, 14°45.189''N 4 4 °58.829''W, 3038 m, 27 Jul. 1997; NMWZ. 2006.6.1, PT, same collection data as HT. *Thyasira oleophila* (Clarke, 1989). FMNH 307755, $n = 7$, Gulf of Mexico, Louisiana slope, st. Bush Hill GC-185, 27°46.941'N, 91°30.479'W, 529 m.

Thyasira insignis (Verrill & Bush, 1898). USNM52596, syntype, West Atlantic Ocean, off Nova Scotia, RV Albattross, st. 2499, 44°46''30" N 5 9 °55''45" W, 238 m, from photographs only.

Thyasira sp. Western North Atlantic, Laurentian Fan, RV Hudson, Cruise 87-0003, st. 13, 43°834.46'N, 55°38.35'W to 43°35.32'N, 55°38.23'W, 3718–3720 m, photographs, courtesy of Professor Rose Petrecca, Rutgers University Marine Field Station, NJ, USA.

Thyasira sarsi (Philippi, 1845). NMWZ, $n = 100$, North Sea, Atlantic Ocean, including shells from the Skagerrak methane seep (58°1.3'N, 9°34.6'E) and Norwegian fjords (Bokn).

Thyasira sp. $n = 1$, 32 mm height, damaged shell, North Sea off Norway, Storrega Pockmark, ROV Victor, Campagne Vicking, RV Pourquoi pas?, 64°38.58''N, 04°53.02''E, 745 m, 31 May 2006, photographs, courtesy of Anders Warén, Swedish Natural History Museum. *Thyasira scotiae* Oliver & Drewery, 2014. NMWZ.2012.074.4, HT, 18.6 mm long, North-east

Atlantic, Hatton-Rockall site west of Scotland, FRV Scotia, cruise 0712S, st. S12283a, 57°57'N, 15°33'W, 1187–1200 m, 23 Jun. 2012, 2012.074.5, 3 PT, 13.9–19.8 mm long, same collection data as HT.

Ascetoaxinus quatsinoensis Oliver & Frey, 2014. RBCM 010-00221-005, HT, 31.3 mm long, Canada, British Columbia, Vancouver Island, Quatsino Sound, 50°15.482'N, 128°26.400'W to 50°14.519'N, 128°26.567'W, 1086–1318 m, 2 Sep. 2004, J. Boutillier, Fisheries and Oceans Canada.

Axinus cascadiensis (Oliver & Holmes, 2007). NMWZ, PT, $n = 5$, NE Pacific Ocean, Baby Bare Seamount, Cascadia Basin, DSRV Alvin, Dive 3152, 47°42.65'N, 127°47.15'W, 2591 m, 14 Oct. 1997, originally from same collection as HT, FMNHC 280989 (Oliver & Holmes 2007).

Conchocele bisecta (Conrad, 1849). RBCM, 006-00076-001, PT, $n = 1$, locality unknown, probably Queen Charlotte Sound, British Columbia.

Channelaxinus excavatus (Dall, 1901). SBMNH 83964, PT, $n = 1$, Farallon Islands, Gulf of the Farallones, California, USA, st. J-13 (Benthos 9).

Wallerconcha sarae Valentich-Scott & Powell, 2014. SBMNH 235481, HT, 23.9 mm long, Beaufort Sea, Alaska, Canning Seafloor Mound, st. ECS004 137, core IP-1, section 3, 31 cm, 4.65 mbsf, 71.317°N, 143.999°W, 2358 m, Aug. 2010, photographs from Paul Valentich-Scott.

Axinulus hadalis (Okutani, Fujikura & Kojima, 1999). NSMT 71431, HT, Pacific Ocean, Japan Trench, ROV Kaiko, 7326 m, from photographs from Paul Valentich-Scott, 5 Aug. 1998.

Taxonomy

Class BIVALVIA Linnaeus, 1758 **Subclass**

HETERODONTA Neumayr, 1884 **Order**

VENEROIDA H. & A. Adams, 1856

Superfamily THYASIROIDEA Dall, 1900

Family THYASIRIDAE Dall, 1900

Genus *Thyasira* Lamarck, 1818

Type species *Tellina flexuosa* Montagu, 1803

Diagnosis

Fragile shells, subcircular, ovate to ovate-polygonal in outline with a posterior sulcus; escutcheon variably expressed, absent to deep, with or without an auricle producing a submarginal sulcus. Lunule not demarcated. Hinge teeth lacking or as a single 'cardinal' tubercle, ligament sunken. Sculpture weak of commarginal lines and growth stops, periostracum thin. Anterior adductor scar elongate, posterior adductor

scar ovate, pallial line entire. Ctenidium with two demi-branches, lateral body pouches large and multilobed, foot vermiform, heel obsolete, toe developed.

Remarks

The genera of the Thyasiridae are not fully resolved and the limited molecular data available suggest that there is not full congruence between current taxa and molecular based clades (Taylor et al. 2007). Oliver & Frey (2014) illustrated anatomical characters that also challenged current taxonomy, further suggesting that shell based taxonomies are not fully reliable. Here, shells alone are available and consequently their generic placing cannot be made with certainty. The following species is therefore referred to *Thyasira sensu lato*.

***Thyasira capitanea* sp. nov.** Åström & Oliver
(Table I, Figures 2A-I)

Type material

Holotype ZMBN 106013, 1 complete shell, 27.2 mm height, Barents Sea, Svalbard, Storfjordrenna, R/V Helmer Hanssen, CAGE-14-3 cruise, st. SR 1, 75° 50.56'N, 16°37.75'E, 350 m, 9 Jul. 2014.

Paratypes $n = 2$ v, same collection data as HT; ZMNB 106014, $n = 4$ v, Barents Sea, Svalbard, Storfjordrenna, R/V Helmer Hanssen, CAGE-15-2 cruise, st. PLF 2, 76° 06.37'N, 16°02.25'E, 383 m, 23 May 2015.

Diagnosis

Shell to 50 mm in height (holotype 27.2 mm), thin, equivalve, equilateral, moderately inflated, beaks prosogyre. Outline pyriform-polygonal, higher than long, except in shells smaller than 15 mm where height and length are approximately equal. Contour complex, lunule flattened, smooth, set off by a subtle change in angle from the distinct flattened anterior slope itself demarcated from the remainder of the anterior by a weak anterior ridge; the median area is

Table I. *Thyasira capitanea* sp. nov. measurements (mm). Abbreviations: lv = left valve, rv = right valve, pr = paired (articulated) valves.

	Height	Length	Tumidity (paired)
Holotype pr	27.2	25.6	15.3 (7.7)
Paratype rv	33.2	29.6	10.7
Paratype rv	15.9	15.4	4.6
Paratype rv	33.7	31.5	10.6
Paratype lv	19.2	17.7	5.8
Paratype lv	17.0	15.8	5.1
Paratype lv	12.0	12.1	4.0
subfossil pr	18.7	18.1	10.7

divided by a weak change in angulation, posterior sulcus prominent but not deep or sharply angled; submarginal sulcus very narrow, auricle absent. Outline reflecting the contours; posterior long, very steep, submarginal sinus indistinct; posterior sinus shallow; lunule margin slightly concave, upper anterior short, straight; anterior weakly curved; ventral narrower, rounded; posterior ventral straight or slightly concave.

Hinge plate narrow, lacking teeth; ligament very long, almost as long as the submarginal sulcus, set on a shallow resilifer. Muscle scars indistinct, anterior adductor scar elongate, separated from the pallial line for half its length; posterior adductor scar oval about half the size of the anterior scar.

Sculpture weak of low but dense commarginal raised ridges and more prominent growth stops. Shell white in colour, periostracum persistent, thin, adherent, and beige to greyish-green in hue.

Etymology

'*Capitanea*' from the Latin *capitaneus* means 'chief in size' (Brown 1956) and refers to the large size of this species.

Comparisons

Thyasira capitanea sp. nov. is large for the majority of thyasirids compared only with species in *Conchocele*, *Ascetoaxinus* and *Channelaxinus*. These latter taxa have obliquely skewed shells quite unlike the equilateral shell of *T. capitanea* sp. nov. Other moderately large thyasirids have been found at cold seeps, most recently *T. scotiae* Oliver & Drewery, 2013 from the Hatton-Rockall site west of Scotland, and this species and other similar Atlantic forms are compared and illustrated in Oliver & Drewery (2013). *Thyasira capitanea* sp. nov. has demarcated zones on the median and anterior areas as well as a distinct posterior sulcus. Such demarcation over the whole genus is not seen in other Atlantic species associated with seep settings: *T. scotiae*; *T. vulcolutre* Rodrigues et al., 2008; *T. sarsi*, (Philippi, 1845); *T. insignis* (Verrill & Bush, 1898); *T. southwardae* Oliver & Holmes, 2006; or *T. oleophila* Clarke, 1989. A faint anterior angulation is present in *T. oleophila* but not on the median area, this species is atypical in having a pustulose surface. The pyriform-polygonal outline is not shared with any of these species but is reminiscent of species assigned to *Channelaxinus* although here the angulation is much stronger, the lunule is excavated and the posterior sulcus and submarginal sulcus are steeply and sharply defined (Oliver & Frey 2014; Oliver 2015). *Channelaxinus* is

represented in the deep Atlantic only by the rarely collected and much smaller *C. perplicata* (Salas, 1996) and to date has not been associated with any chemosynthetic setting.

A relatively large (32 mm) thyasirid has been collected from the Storegga Pockmark off the coast of Norway at ~64°N. It is known only from a single damaged shell (illustrated in Oliver & Drewery 2013) and has not been described. It differs from *T. capitanea* in having a very long anterior slope continuous with the lunule margin such that there are no anterior angles or ridges.

***Rhacothyas* gen. nov.** Åström & Oliver

Type species. *Rhacothyas kolgae* sp. nov. (this paper)

Diagnosis

Moderate sized shell to 28 mm, thin, equivalve, sub-equilateral, prosogyrous beaks slightly in front of midline, somewhat compressed. Outline subovate, distinctly longer than high, lunule sunken, posterior sulcus shallow, submarginal sulcus obsolete. Ligament deeply sunken, in a rather wide resilifer. Hinge edentulous. Sculpture of dense, but variably expressed, raised lines and weak ridges covered by an adherent wrinkled periostracum.

Etymology

'*Rhaco*' from the Greek *rhakodes* meaning wrinkled (Brown 1956) and '*thyas*' a contraction of *Thyasira*.

Differential diagnosis and remarks

While it is not normal protocol to create novel taxa based on such limited material, these shells are so distinctive that it is not logical to assign them to any current genus. The majority of thyasirids have shells that are oval, polygonal or obliquely oval in outline, that is, generally slightly higher than long. The combination here of the characters of the outline, sunken lunule, lack of a submarginal sulcus and wrinkled surface are not seen in any other genus.

Only two other shells bear any similarity, *Axinulus hadalis* (Okutani, Fujikura & Kojima, 1999) (Figure 3E–F) from 7000 m in the Japan Trench and *Wallerconcha sarae* Valentich-Scott & C.L. Powell, 2014 (Figure 3C–D) from 2385 m in the Beaufort Sea. Both have a similar wrinkled surface but both lack a defined lunule and the posterior sulcus is by comparison poorly developed. *Axinulus hadalis* has a short ligament on a shallow resilifer while that of *Wallerconcha* is

more like that of *Rhacothyas* (Figure 3A–B). While there are similarities with *A. hadalis*, the type of the genus *Maorithyas marama* Fleming, 1950 is radically different and doubtfully distinguishable from *Thyasira sensu stricto* (see Oliver 2014 p. 127). *Wallerconcha* further differs in the long anterior slope such that the anterior is much narrower than the posterior whereas in *Rhacothyas* the outline is almost symmetrical.

***Rhacothyas kolgae* sp. nov.** Åström & Oliver
(Figures 4A–F)

Type material

Holotype ZMNB 106015, 1 v, 24.5 mm long, Arctic Ocean, West Svalbard, Prins Karls Forland, R/V Helmer Hansen, CAGE-14-1 cruise, st. PKF 2, 78° 37.59'N, 09°24.29'E, 350 m, 22 Jun. 2014 (Figure 4D).

Paratypes 1 complete v and 3 broken v, same collection data as HT.

Other material examined

A third complete right valve (Figures 4E–F), 27.7 mm long, same collection data as HT, used for chemical assay.

Diagnosis

See generic account

Description

Holotype (Figures 4A–C) of a single right valve, 24.5 mm length, 21.0 mm height, 6.4 mm width. Thin, equivalve, sub-equilateral, prosogyrous beaks slightly in front of midline, somewhat compressed. Outline subovate, distinctly longer than high, lunule sunken demarcated by a weak ridge, rugose; posterior sulcus shallow, submarginal sulcus obsolete. Ligament deeply sunken, in a rather wide resilifer about 2/3 the length of the posterior slope. Hinge edentulous. Sculpture of dense, but variably expressed, raised lines and weak ridges covered by an adherent wrinkled periostracum. Shell white in colour, periostracum a pale olive drab in hue. Anterior adductor scar elongate and relatively wide, the ventral third separated from the pallial line; posterior adductor scar ovate about half the size of the anterior scar.

Etymology

'*Kolgae*' after Kolga, the Norse goddess of the Arctic Ocean.

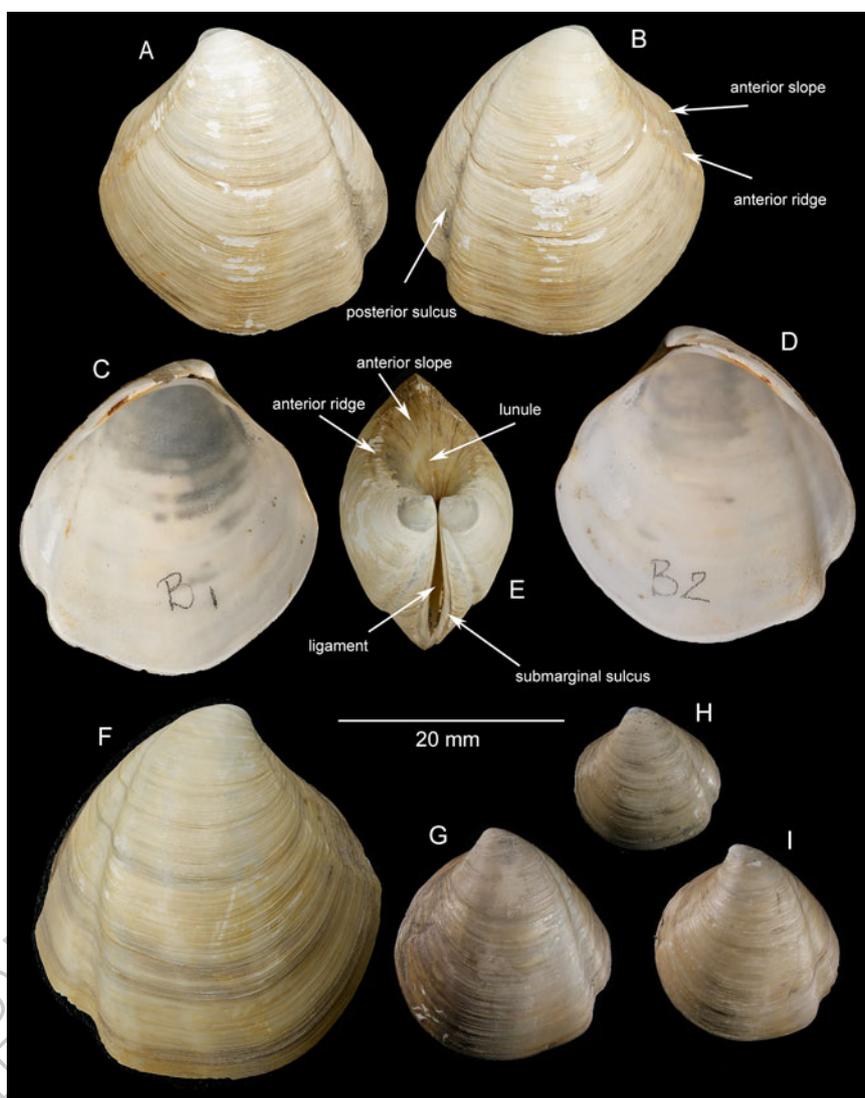


Figure 2. A–I. *Thysira capitanea* sp. nov. A–D, external and internal views of the holotype. E, dorsal view of the holotype. F–I, external views of shells from CAGE-15-2.

Comparisons

See generic account.

Discussion

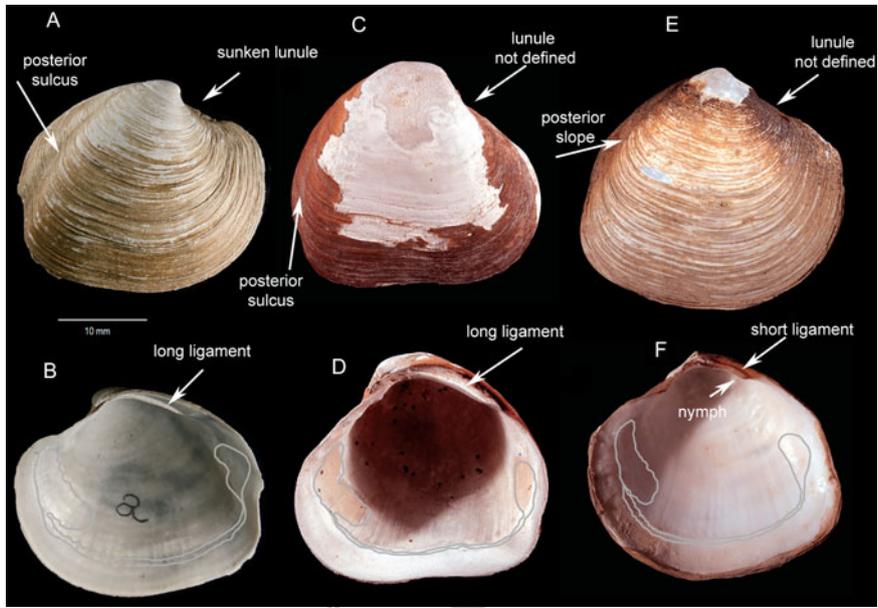
We have described one new genus and two new species of Thysiridae from methane seeps off the western and southern shelf of Svalbard and Barents Sea (75–79°N). These Svalbard shells are quite distinct from other larger-bodied seep-associated species known from the north-east Atlantic. Since the benthic habitats where these thysirids were found are geologically relatively young (<15,000 years) (Patton et al. 2015), it is likely that the bivalves have evolved elsewhere and spread into this region from adjacent chemosynthetic environments, and possibly from the north-west Atlantic (Skarke et al. 2014).

The discovery of chemosymbiotic bivalves at active cold seeps in the Arctic is not surprising in light of chemosynthetic faunas in the geological record dating back to the Early Cretaceous and Late Jurassic and the reporting that methane seepage west of Svalbard has been active for the past 2.7 million years (Plaza-Faverola et al. 2015). However, the fauna at Storfjordrenna and Prins Karls Forland seeps contains two species of large thysirid that are not known elsewhere in the Arctic or Atlantic Oceans. The genus *Rhacothyas* is so far only known from the PKF seep and *Thysira capitanea* sp. nov. is quite distinct from the other larger thysirids associated with seeps in the Atlantic Ocean. Krylova et al. (2011), in the discussion on the vesicomid *Isorropodon*, suggested that this genus had penetrated the Norwegian Sea from the Atlantic along the African-European continental margin.

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Figure 3. A–F. Comparative figures of (A–B) *Rhacothyas kolgae* gen. et sp. nov., (C–D) *Wallerconcha sarae*, (E–F) *Axinulus hadalis*.

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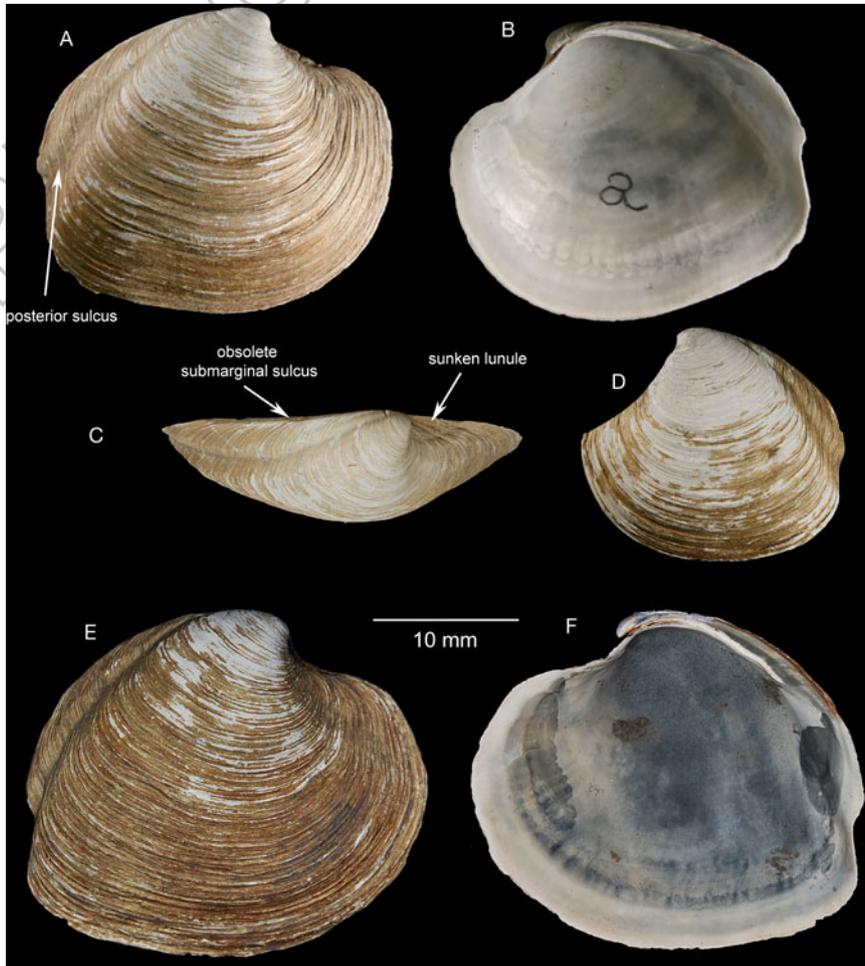
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Figure 4. A–F. *Rhacothyas kolgae* gen. et sp. nov. A–B, external and internal of holotype. C, dorsal of holotype. D, external of paratype, lunule broken. E–F, external and internal of assayed valve.

While this may also be true for the thyasirids as evidenced by the morphological similarities between *T. southwardae*, *T. vulcolutrae*, *T. scotiae* and *T. sarsi* that form a series along the eastern Atlantic margin (Oliver & Drewery 2013), the Svalbard thyasirids do not fit into this series. The recent discovery of numerous methane seeps along the north-western US Atlantic margin (Skarke et al. 2014) could potentially provide many novel taxa that may or may not have affinity with the taxa found around Svalbard.

Deglaciation of the Barents Sea Ice Sheet

The geological setting for our bivalve records is relatively young. During the Last Glacial Maximum (Late Weichselian interstadial period), the Barents Sea and Svalbard were covered by an extensive marine-based ice sheet, with average global sea level ~126 m lower than today (Peltier & Fairbanks 2006; Patton et al. 2015). Deglaciation of this Barents Sea Ice Sheet (BSIS) from the shelf break started around 20,000 years ago (Jessen et al. 2010) and seawater began to penetrate outer troughs in the Barents Sea by 16,000 ka BP and later on also into the fjords of Svalbard (Jessen et al. 2010; Łącka et al. 2015). Palaeontological records from sediment cores sampled in Storfjordrenna show that communities of foraminifera followed the different water masses (Arctic, Atlantic, fresh or saline), entering Storfjordrenna throughout the deglaciation of the BSIS (Rasmussen et al. 2007; Rütther et al. 2011; Łącka et al. 2015). The physical conditions at the seabed close to a glacier front are an extreme environment for many benthic and sessile organisms (Włodarska-Kowalczyk & Pearson 2004; Włodarska-Kowalczyk et al. 2005). Outflow of fresh water decreases the salinity close to a tidal glacier front, glacio-marine sedimentation is heavy and the turbidity in the water column is high (Szczucinski & Zajackowski 2012), leading to a low diversity benthic community dominated by a few motile opportunists, mostly polychaetes (Włodarska-Kowalczyk et al. 2005, 2007). As the ice sheet and its associated glaciers retreated, it is likely that a more diverse benthic macrofaunal community was established on the newly exposed sea floor.

Along the western shelf of Svalbard, several sites with gas hydrate reservoirs and seabed methane emissions have been identified (Westbrook et al. 2009; Sahling et al. 2014). Gas hydrates are ice crystals enclosing natural gas, and their stability is greatest at high pressure and low temperature (Koh & Sloan 2007). Under the Barents Sea ice sheet, gas hydrates in the sub seabed were stable (Winsborrow et al. 2016). As the thickness of the ice diminished due to deglaciation,

pressures decreased and temperatures rose. This initiated gas hydrate disassociation, and allowed migration of gas in the sediments and venting of gas at the sea floor (Crémière et al. 2016; Portnov et al. 2016). The favourable circumstances of a steady supply of methane or sulphur and a suitable substrate created the basic conditions for specialized seep fauna (Schulze & Halanynch 2003; Dubilier et al. 2008), allowing colonization of a new seep environment. Cold seep communities may establish in timescales from decades to centuries and can persist over thousands of years if there is sufficient seepage to sustain chemolithoautotroph production (Bowden et al. 2013; Ambrose et al. 2015). We propose that the early macro benthic seep communities in this region have been generated as a result of gas hydrate dissociation after deglaciation, and formed ~12,000–14,000 years ago (Rasmussen et al. 2007; Ingólfsson & Landvik 2013; Pau et al. 2014; Patton et al. 2015; Rise et al. 2015; Portnov et al. 2016).

Dispersal of chemosynthetic fauna

Sub seabed hydrocarbon reservoirs occur all along the North Atlantic continental margin and the coast of Norway (Ziegler 1977; Andreassen et al. 1990; Vogt et al. 1997; Mienert et al. 2005; Vadakkepuliambatta et al. 2013; Portnov et al. 2016). The Håkon Mosby mud volcano (HMMV) was discovered in 1989 at the southern border of the Barents Sea (72°N) and has been the focus of extensive biogeochemical and biological studies (Gebruk et al. 2003; Niemann et al. 2006; Lösekann et al. 2007; Decker & Olu 2012; Rybakova et al. 2013). Seafloor emissions of methane at HMMV occur from gas hydrates in the sub seabed (Vogt et al. 1997; Lein et al. 1999) and support chemo-associated faunal populations. The macrofauna at HMMV caldera is represented by known chemosymbiotic organisms including siboglinid worms mixed with bivalves e.g. *Thyasira dunbari* and other conventional, heterotrophic fauna such as amphinomid polychaetes, and caprellids (Gebruk et al. 2003; Decker & Olu 2012; Rybakova et al. 2013). Tissue from thyasirids at HMMV, both from the caldera and in background environments, outside the volcano, showed depleted $\delta^{13}\text{C}$ signals, indicating nutrition from methane carbon sources (Decker & Olu 2012). Globally, there are around 100 species of Thyasiridae recognized from a wide range of habitats including hydrocarbon seeps, vents, oxygen minimum zones and organic enriched sediments, where a few of them are chemo-symbiotic (Taylor & Glover 2010; Duperron et al. 2013). Several degrees of microbial symbiosis have

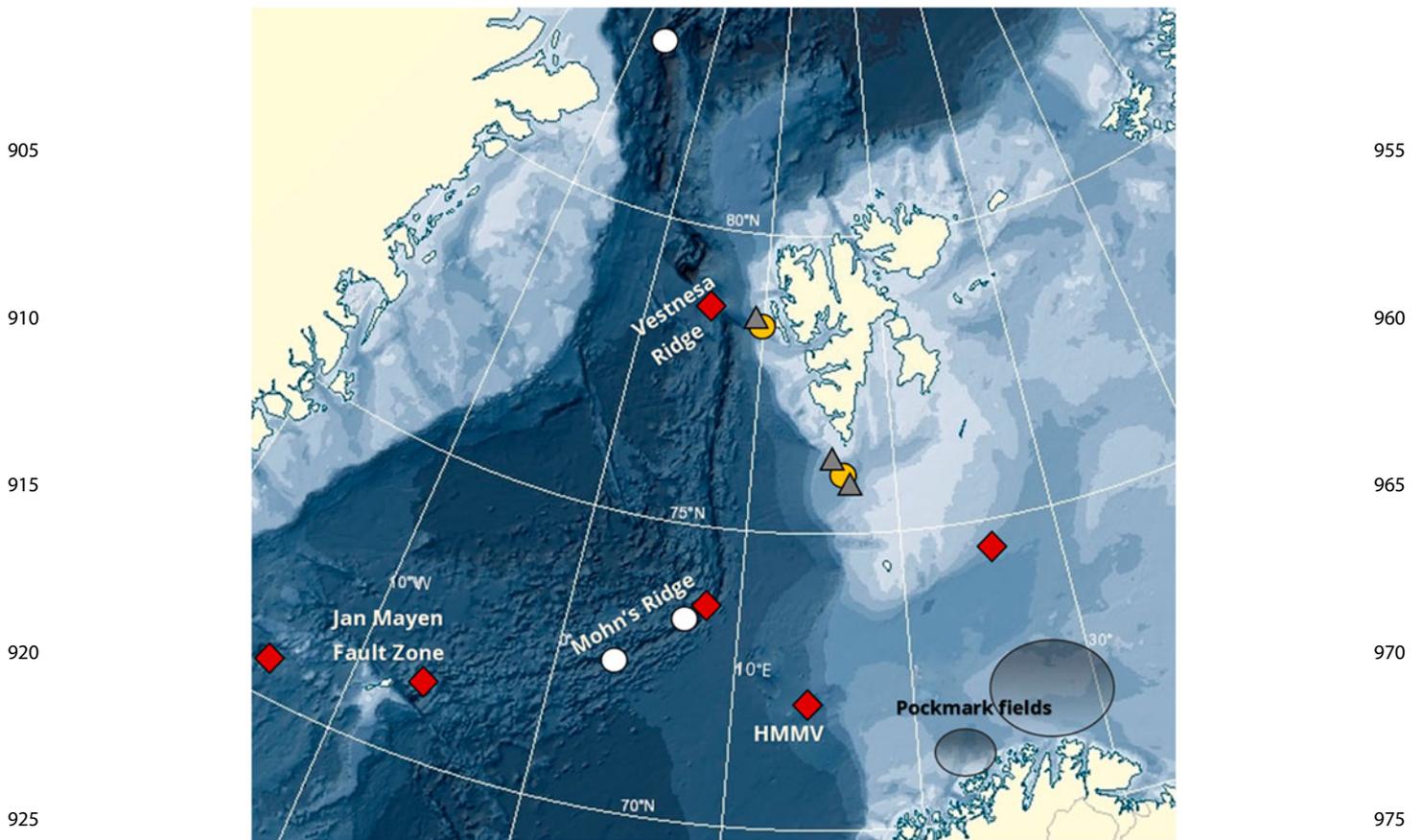


Figure 5. Potential pathways of dispersal of seep-associated fauna from nearby vent and seep localities in the North Sea and Fram Strait to seeping areas at western Svalbard shelf and Storfjordrenna. Samples from this study are indicated by grey triangles. Red diamonds represent known vent and seep areas, light grey circles show sulphide deposits and yellow circles show acoustic methane plumes during sampling of Svalbard bivalves (this study). Map modified from Pedersen et al. (2010) and Norwegian Polar Institute (2016).

been described within this family (Dufour 2005), demonstrating a varying nutritional dependence on symbiosis amongst the chemosynthesizing thyasirids (Dando & Spiro 1993).

Given the young age of the habitats where we found the two new species, there has been insufficient time for evolution of such distinct shell sizes and features in the described taxa. We presume instead that dispersal and colonization of seep-associated bivalves from western Svalbard is likely to have originated from nearby chemosynthetic systems such as the HMMV or others areas known for seepage in this region (Figure 5). In addition to HMMV and known vents and seeps at the Mid-Atlantic Ridge (Pedersen et al. 2010; Schander et al. 2010; Sweetman et al. 2013), there are areas of gas seepage associated with widespread pockmark fields in the southern Barents Sea (Chand et al. 2009; Rise et al. 2015) and along the north-west coast of Norway (Sauer et al. 2015; Crémière et al. 2016). The modern, overriding current regime, driven mainly by the North Atlantic Current and West Spitsbergen

Current system, drives northward transport of planktonic forms, reaching Western Svalbard and the locations of our records (Loeng 1991; Seager et al. 2002; Blindheim & Rey 2004; Berge et al. 2005; Cottier et al. 2010). The connectivity among chemosynthetic habitats and dispersal between chemosynthetic and conventional systems, is poorly known (Duperron et al. 2013; Levin et al. 2016), however, it is believed that whale falls, in addition to vents and seeps can serve as temporary reducing or chemosynthetic 'stepping-stone' environments, allowing dispersal of chemo-associated organisms, over even greater distances (Smith et al. 1989; Dahlgren et al. 2006). Whale falls can support chemo-ecosystems over decades (Smith et al. 1989; Baco & Smith 2003) and have been shown to host unique faunal communities with highly specialized forms (Glover et al. 2005, 2013; Danise et al. 2014). A minke whale fall in the North Sea (Kosterfjord, Sweden) supported high densities of *Thyasira sarsi*, in particular during the final 'sulphidic' stage of the whale decay (Danise et al. 2014). *Thyasira sarsi* is seen

as a mixotroph species, demonstrating a varying nutritional dependence on sulphur oxidizing endosymbionts. In sulphide rich environments, tissues of *T. sarsi* can have highly depleted values of $\delta^{13}\text{C}$ (Dando et al. 1991; Dando & Spiro 1993) and it is suggested that high densities of *T. sarsi* are controlled by the degree of sulphate reduction rates in the sediment (Danise et al. 2014).

Conclusions

Thyasira capitanea sp. nov. and *Rhacothyas kolgae* sp. nov. were found in two separate regions along the western Svalbard shelf margin at ~350–380 m depth associated with methane cold seeps. These two new species have a relatively large size and have morphological features that are very distinct from other known thyasirids and from each other. Colonization has most likely occurred from other nearby seep and vent areas if we consider the age of the present stage of this region and the time frame for initiating seafloor emission in relation to deglaciation. It is plausible that the seep-bivalves at Svalbard have spread into Svalbard shelf waters from adjacent vent and seep systems with the possible assistance of whale falls and evolved *in situ* to their present form.

Acknowledgements

Thanks to captain and crew on board R/V Helmer Hanssen and the cruise leaders Stefan Bünz, Karin Andreassen and Giuliana Panieri. We are grateful to Henry Patton for valuable input and comments on the glaciological history of the Barents Sea. Thanks also to David Hammenstig for comments and discussions on earlier drafts of the manuscript and to three anonymous reviewers for perceptive comments that helped refine the final manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was funded through Norges Forskningsråd through its Centre's of Excellence funding scheme, project number 223259.

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