ORIGINAL PAPER

# A deep sea community at the Kebrit brine pool in the Red Sea

Hege Vestheim · Stein Kaartvedt

Received: 13 May 2014 /Revised: 25 September 2014 /Accepted: 12 February 2015 /Published online: 26 February 2015  $\oslash$  Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2015

Abstract Approximately 25 deep sea brine pools occur along the mid axis of the Red Sea. These hypersaline, anoxic, and acidic environments have previously been reported to host diverse microbial communities. We visited the Kebrit brine pool in April 2013 and found macrofauna present just above the brine–seawater interface (~1465 m). In particular, inactive sulfur chimneys had associated epifauna of sea anemones, sabellid type polychaetes, and hydroids, and infauna consisting of capitellid polychaetes, gastropods of the genus Laeviphitus (fam. Elachisinidae), and top snails of the family Cocculinidae. The deep Red Sea generally is regarded as extremely poor in benthos. We hypothesize that the periphery along the Kebrit holds increased biomass and biodiversity that are sustained by prokaryotes associated with the brine pool or co-occurring seeps.

Keywords DHAB · Inactive chimneys · Benthic fauna · Cnidarians . Molluscs . Polychaetes

## Introduction

The Red Sea is a young ocean located on an extrusion zone where the African and Arabian tectonic plates pull apart, a process that started only 40 million years ago (Braile et al. [2006](#page-5-0);

Communicated by P. Martinez Arbizu

H. Vestheim ( $\boxtimes$ ) · S. Kaartvedt King Abdullah University of Science and Technology, Red Sea Research Center, Thuwal 23955-6900, Saudi Arabia e-mail: hege.vestheim@gmail.com

Present Address: S. Kaartvedt Department of Biosciences, University of Oslo, PO Box 1066, Blindern 0316, Oslo, Norway

Coleman [1993](#page-5-0)). Along the mid axis of the Red Sea some 25 deep, sea brine pools occur (Bäcker and Schoell [1972](#page-5-0); Degens and Ross [1969;](#page-5-0) Swallow and Crease [1965\)](#page-6-0). These are topographic depressions consisting of hypersaline with acidic and anoxic water. There is also generally increased temperature compared to the seawater above. On the bottom of the brine pools lay metalliferous sediments (typically several meters thick) of potential high economic value (Anschutz et al. [1999](#page-5-0); Hartmann et al. [1998\)](#page-6-0). At the brine-seawater interfaces, the physical and chemical properties change rapidly over a few meters. How steep these interfaces are, and whether they are gradual or more stepwise differ among and, hence, typify the individual brine pools (Antunes et al. [2011](#page-5-0)).

Methanotrophic (methane oxidising), thiotrophic (sulfur oxidising), and carbon dioxide reducing prokaryotes are found in the brine pools and their interfaces (Antunes et al. [2011\)](#page-5-0). The density gradients at the brine-seawater interface also act as particle traps for inorganic and organic material coming from above (Hartmann et al. [1998](#page-6-0); Henneke and De Lange [1990;](#page-6-0) LaRock et al. [1979](#page-6-0)) that further fuel microbial production (Eder et al. [2002](#page-6-0); Ryan et al. [1969;](#page-6-0) Scholten et al. [2000\)](#page-6-0). RNA/DNA sequencing efforts from Eastern Mediterranean deep hypersaline anoxic basins (DHABs) also indicate the presence of specialized single celled eukaryotes in the brine pool water, especially fungi, ciliates, and stramenopiles (e.g., Edgcomb et al. [2009](#page-6-0); Stock et al. [2012](#page-6-0)). Metazoans seem to be absent from the brine pool itself, though Danovaro et al. [\(2010\)](#page-5-0) reported evidence of a metazoan that can complete its life cycle in a Mediterranean brine basin.

Deep sea brine pools are a special form of cold seeps (defined as an area of the ocean floor where hydrocarbon-rich fluid seepage occurs) and cold seeps are found worldwide in areas with tectonic activity. Cold seeps often have associated macrofauna along the rim where the dominating species tend to be bivalves belonging to the families Vesicomyidae or Mytilidae, vestimentiferan tube worms, frenulates (Siboglinidae), and Cladorhizidae and Hymedesmiidae sponges (e.g., Cordes et al. [2007;](#page-5-0) Levin et al. [2003](#page-6-0); Sibuet and Olu [1998](#page-6-0)). Many of these species are harbouring thiotrophic, methanotropic, or methylotrophic symbiotic bacteria (Dubilier et al. [2008](#page-6-0); Duperron [2010;](#page-6-0) Fisher [1990](#page-6-0)) and are possibly relying on symbiont chemotrophy for their carbon nutrition. Batang et al. [\(2012](#page-5-0)) reported the presence of one shallow (10 m at 840–850 m depths) brine pool at the continental margin of the Red Sea, the Thuwal seep 20 km offshore the Saudi coastline, with associated macrofauna along its rim. However, except for the observations of Oliver et al. ([in](#page-6-0) [press](#page-6-0)) of one species of a bivalve occurring around the Valdivia brine pool, no such fauna is yet documented from any of the other mid axial deep sea brine pools in the Red Sea. We visited the Kebrit brine pool in April 2013 and report here on the presence of macrofauna both associated with inactive chimneys and occurring solitary along the rim just above the brineseawater interface.

#### Material and methods

#### Study site

The Kebrit brine pool  $(24^{\circ} 43' 21'' N, 36^{\circ} 16' 37'' E, Fig. 1)$ was visited 15–19 April 2013 during Leg 4 of the 2013 King Abdullah University of Science and Technology (KAUST) Red Sea Expedition. The 1 by 2.5 km Kebrit Deep basin is one of the smallest mid axial brine pools in the Red Sea. Its maximum depth is 1549 m (Pautot et al. [1984;](#page-6-0) Scholten et al. [2000\)](#page-6-0), and it is filled by an 84 m deep layer of brine holding large amounts of  $H_2S$  (125–374  $\mu$ M; Hartmann et al. [1998\)](#page-6-0), high  $CO<sub>2</sub>$  concentrations, small amounts of  $N<sub>2</sub>$ , methane, and ethane (Bäcker and Schoell [1972](#page-5-0); Faber et al. [1998](#page-6-0)). It is the high concentration of  $H_2S$  that has given it its name (*Kebrit* is the Arabic word for sulfur).

The brine seawater interface (around 1465 m) presents a steep gradient where our measurements (using a high range conductivity, temperature, and density (CTD) device) showed that salinity increased from 40.6 to 242, pH drops from 8.00 to 5.17, oxygen levels decreased to zero, and the temperature rose from 21.7 to 23.4 °C (Table [1\)](#page-2-0). This is consistent with what previously has been reported (Bäcker and Schoell [1972](#page-5-0); Eder et al. [1999;](#page-6-0) Hartmann et al. [1998\)](#page-6-0).

Blum and Puchelt [\(1991\)](#page-5-0) reported on the occurrence of porous massive sulfide fragments, some in the shape of smokers  $1-1.5$  m in height and  $15-20$  cm in diameter at Kebrit. They analysed some of these chimneys for chemical composition, but did not report anything on associated fauna.

### Underwater observations and sampling

Underwater observations were conducted using the ROV Max Rover (DSSI, USA) system as described in Batang



Fig. 1 Location of the Kebrit brine pool in the Red Sea

et al. ([2012](#page-5-0)). Video records were made using the SEA MAX Wide Angle & Zoom Color TV universal underwater video camera recording while cruising along the rim of the brine. The ROV was navigated based on the display compass, the depth meter, and sonar with the Tracklink ultrashort baseline transponder system (Linkquest,USA). Two High-Definition Ocean ProHD Undersea cameras (1080×1920 image resolution, 30 frames per second) with pan and tilt (with wide angle and zoom features) were also used at sites of interest. Samples were collected using the ROV's robotic arm fitted with a fabric bag. The samples were then transferred to the surface in the bag and immediately inspected by eye before they were brought back to the laboratory for further analysis; frozen at −20 °C, preserved in ethanol or kept in filtered (GF/F, retaining particles down to 0.7 μm) sea water.

Collected fauna were tentatively identified under a microscope or dissecting microscope. Electron micrographs were taken on a FEI Quanta 200. Shells were examined following cleaning with dilute bleach and coating with 5 nm AuPd. Chimney pieces were cut in slices with a diamond saw and assessed uncoated.

<span id="page-2-0"></span>Table 1 CTD data for a depth range of 1463–1469 m at the Kebrit brine pool indicating rapid and significant changes in salinity, dissolved oxygen, pH, and temperature

Depth $(m)$	Temperature $(^{\circ}C)$	Salinity	Oxygen (mg $L^{-1}$ )	pH
1462.8	21.7	40.6	4.03	8.00
1463.2	21.7	40.6	4.07	8.00
1463.3	21.7	40.7	4.09	8.00
1463.6	21.8	60.3	3.57	7.62
1464.0	21.9	125.5	2.33	6.63
1464.3	21.9	163.7	1.81	6.08
1464.6	22.0	180.1	1.63	5.80
1464.8	22.1	194.6	1.46	5.61
1465.2	22.2	208.3	1.32	5.49
1465.6	22.3	219.0	1.18	5.39
1465.9	22.4	226.4	1.09	5.32
1466.3	22.5	230.9	1.02	5.26
1466.6	22.6	234.2	0.96	5.22
1466.9	22.7	236.8	0.91	5.19
1467.2	22.8	238.0	0.87	5.17
1467.3	22.8	237.7	0.83	5.17
1467.3	22.9	237.4	0.81	5.17
1467.4	22.9	237.3	0.78	5.16
1467.4	22.9	238.0	0.77	5.16
1467.5	23.0	238.0	0.75	5.16
1467.8	23.0	239.7	0.72	5.16
1468.2	23.1	241.1	0.71	5.16
1468.4	23.1	241.4	0.69	5.17
1468.4	23.2	240.8	0.68	5.17
1468.5	23.1	241.0	0.67	5.17
1468.8	23.2	242.0	0.65	5.17
1469.2	23.3	242.2	0.64	5.17

## Molecular methods

Total genomic DNA was extracted from ethanol-preserved specimens using the DNA Easy Blood and Tissue Kit (Qiagen) following the manufacture's protocol for animal tissue. DNA yield of the extractions was quantified on a Qubit 2.0 fluorometer (invitrogen) and partial COI, 28S, 18S, and 16S sequences were generated by PCR using the primer pairs as described in Oliver et al. (in prep). The 25 μL PCR reactions included 5 μL 5X Phusion buffer,  $0.5$  μL 10 mM dNTPs, 1.25 μL each primer (10 μM), 1.25 μL 50 mM MgCl, 0.125 μL Phusion High-Fidelity DNA polymerase, and 1 μL DNA extract  $(\sim 10 \text{ ng/µL}).$ 

Thermal cycling conditions were: 98 °C for 2 min, then 37 cycles of 98 °C for 30 s, 30–40 s at annealing temperature, and 72 °C for 1 min, followed by a final extension of 10 min at 72 °C. A negative (no template DNA) and positive control (template DNA known to amplify) were included in all PCRs. All PCR products were checked on a 1 % agarose gel

and cleaned with illustra ExoStar 1-Step (GE Healthcare) before being sequenced on an ABI 3730xl Capillary Sequencer (Applied Biosystems) using the respectively forward and backward PCR primer.

# Results

## In situ underwater observations

A distinct "shoreline" is present above the Kebrit brine–seawater interface. Two types of fish were seen; one unidentified flatfish was seen on several occasions dwelling on the rim, swimming slowly away when disturbed by the ROV (Fig. [2a\)](#page-3-0). Some individuals of an ophidiform fish were also observed, at times swimming almost into the brine pool (Fig. [2b](#page-3-0)). Also, specimens of caridean shrimps were encountered (Fig. [2a](#page-3-0)).

We observed a number of inactive chimneys at the Kebrit site. Many of the chimneys were located along the rim within a meter from the brine seawater interface, and one chimney was also popping out within the brine pool. A closer inspection of some of the chimneys revealed associated epifauna that included hydroids, sea anemones, and sabellid type polychaetes (Fig. [2c, d](#page-3-0), Table [2](#page-3-0)).

# Collected samples

Two chimneys were retrieved using the robotic arm of the ROV, and some sediment samples were also grabbed together with the chimneys. Remains (periostracum fragments) and one live individual of a solemyid clam (based on sequence data to be a Solemya sp.), along with one corbulid bivalve, and two gastropods (one of the family Marginellidae and one of the genus Putzeysia (fam. Calliotropidae)) followed with the sediment samples. The chimneys were of porous and layered structure (Fig. [3a](#page-4-0)–c), 17 and 28 cm long, around 4 cm wide, and 2–3 cm deep. When crushing part of the chimney, live animals and mollusc shells were frequently retrieved. Four  $\sim$ 2 cm high chimney fragments contained capitellid polychaetes  $(N=5)$ , gastropods of the genus *Laeviphitus* (fam. Elachisinidae)  $(N=21)$ , and top snails based on DNA sequence data found to be one species belonging to the family Cocculinidae ( $N=17$ ), as well as tiny bivalves ( $N=7$ ), which had settled in the empty gastropod and bivalve shells (Table [2](#page-3-0)). The shells were often highly corroded and covered with mineral deposits. Numerous reddish faecal pellets were also found inside the chimney pieces.

Partial COI, 28S, 18S, and 16S DNA sequences were retrieved for nine specimens (though it was not successful for all genes for all individuals; see Table [3](#page-4-0) for details and accession numbers and best BLAST match). There was a lack of available sequences from closely related species, and any phylogenetic analysis beyond blasting was, therefore, not done.

<span id="page-3-0"></span>Fig. 2 Fauna on the Kebrit rim 24° 43′ 21″ N, 36° 16′ 37″ E,  $\sim$ 1465 m depth. Images are captured from the ROV. The two red laser points are 10 cm apart. a A flatfish. b An ophidiform fish and a shrimp. c and d Inactive chimneys seen populated by sabellid type polychaetes, hydroids, and sea anemones. Chimney (c) was 17 cm long, around 4 cm wide, and 2 cm deep, chimney (d) was 28 cm long, 5.5 to 3.5 cm wide and 2–3 cm deep, thinnest at the bottom



## **Discussion**

Since their initial discovery in the late 1970s, vent and seep macrofauna communities have been described from numerous places around the world (Baker et al. [2010\)](#page-5-0). Yet, any reports from the mid axial brine pools in the Red Sea has so far been missing, with the only proof of benthic macrofaunal life being

Table 2 Sampled fauna at the rim of the Kebrit brine

Species	Location	Number of individuals
Cnidaria		
Actiniaria indet.	СE	4
Hydroida indet.	СE	8
<b>Bivalvia</b>		
Bivalvia juv. indet.	СI	7
Corbulidae gen. et sp. nov	S	
Solemya sp.	S	1
Gastropoda		
Cocculinidae indet.	СI	17 <sup>a</sup>
Laeviphitus sp.	СI	2.1 <sup>a</sup>
Marginellidae indet.	S	1
Putzeysia sp.	S	1
Polychaeta		
Capetellidae indet.	СI	5
Sabellidae indet.	CE	19

CE chimney exterior, CI chimney interior, S sediment

a Number includes empty shells

the documentation of holes in the sediment close to the brine pools indicating burrowing polychaetes (Monin et al. [1982;](#page-6-0) Young and Ross [1974\)](#page-6-0). However, Oliver et al. ([in press](#page-6-0)) recently observed small bivalves associated with one of the brines. We did not bring equipment for quantitative sediment sampling. Our findings are, therefore, only qualitative, but despite that, provide a first glance into a novel, and to the Red Sea, a unique community.

The most conspicuous feature at the Kebrit rim was the inactive chimneys. Several species of macrofauna were associated with the chimneys; hydroids, sabellid type polychaetes, and sea anemones had settled outside and molluscs and capitellids were living inside. With their porous bubble structure and complex mineral composition, the interior of the chimneys probably provide an intricate habitat for microorganisms and a sheltered habitat for the metazoans where they can live inaccessible to predators such as fish.

The species found at Kebrit were typical for a reducing community (Baker et al. [2010;](#page-5-0) Sibuet and Olu [1998](#page-6-0)). All the solemyid remains collected together with the sediments suggest that the group is common in the Kebrit rim sediments. Solemyid bivalves are species with reduced and sometimes totally lacking digestive systems relying on thiotrophic microbial symbionts for their nutrition (Taylor and Glover [2010\)](#page-6-0). Finding this bivalve in the Kebrit sediments is not surprising. The gastropod genus *Laeviphitus* that was found to be numerous inside the chimneys is also frequently reported as a member of vent and seep fauna (e.g. Galkin and Goroslavskaya

<span id="page-4-0"></span>Fig. 3 Cross sections of the chimneys a Photograph showing the layered structure. Variation of blackish, lighter greyish (more silica rich) and red (iron rich) areas. Scale bar is 1 cm b Representative photomicrographs from the cross section of the chimney (electron microscopy) showing the porous bubble structure



[2010;](#page-6-0) Mullineaux et al. [2005;](#page-6-0) Ritt et al. [2010\)](#page-6-0). Cocculiniform limpets that also were abundant inside the chimneys have likewise been reported from sulfide-rich, reducing environments such as whale bones and sunken drift-wood (Baco and Smith [2003;](#page-5-0) McLean [1992\)](#page-6-0). Most vent/seep organisms are endemic to a narrow geographical area (Dover and Trask [2000;](#page-6-0) Sasaki et al. [2010\)](#page-6-0). As this is the first report on this type of fauna from the Red Sea, it is likely that many of the species found are new to science. Some of the species will be described elsewhere.

Cold seep communities in oligotrophic oceans rely to a large extent on chemosynthetic processes (either directly via symbioses or indirectly via heterotrophy) and are not fuelled by carbon sources of phytoplanktic origin (e.g., Carlier et al.

Table 3 Overview of individuals sequenced in this study and their associated accession numbers

Specimen (Number of individuals sequenced)	Location	Successful target	<b>EMBL</b> accession numbers	Best NCBI BLASTN match (species, accession number and $(\%$ identity)
Solemyid clam (1)	Sediment	18S	HG942544	<i>Solemya</i> sp., AM293666 (95 %)
		16S	HG942545	Solemya velesiana, KC984674 (87 %)
		<b>COI</b>	HG942539	Solemya velesiana, KC984744.1 (84 %)
Capitellid polychaete (2)	Chimney, interior	18S	HG942552	<i>Notomastus latericeus, AY040697 (96 %)</i>
		16S	HG942553	No match
		$28S$ v1: 28S v2	HG942554; HG942555	<i>Dasybranchus</i> sp., AB771480.1 $(88\%)$
Cocculoid limpet (5)	Chimney, interior	18S	HG942546	Cocculina messingi, AF120508.1 (96 %)
		16S	HG942547	Cocculina sp., GQ160670.1 (90 %)
		28S	HG942548	Cocculina sp., AB282796.1 (91 %)
		<b>COI</b>	HG942540	<i>Cocculina</i> sp., AB238591 (88 %)
<i>Laeviphitus</i> sp. (1)	Chimney, interior	18S 16S	HG942549 HG942550	18S/16S/28S/COI: None available for comparison.
		28S	HG942551	
		<b>COI</b>	HG942538	

<span id="page-5-0"></span>2010). This is also to be expected for the Kebrit benthic community. Vent/seep gastropods typically feed by grazing on bacterial and detritus films though some also have bacteria symbionts (Dubilier et al. [2008;](#page-6-0) Sasaki et al. [2010\)](#page-6-0). Capitellids are regarded as opportunistic deposit feeders that also would exploit brine-derived carbon via heterotrophy (Carlier et al. 2010; Tsutsumi et al. [2001](#page-6-0)). Symbiotic bacteria are not known for this group (Cuomo 1985; Felbeck et al. [1981\)](#page-6-0). Sabellid type polychaetes, sea anemones, and hydroids could probably settle on any suitable hard substrate in the vicinity of the brine pools. Hence, it is unclear if the chimney epifauna took advantage of the chimneys only as a hard substrate to settle on, or if they depended on them for other reasons. But, given the extreme oligotrophic character of the deep Red Sea (Wishner [1980\)](#page-6-0), it would be likely that the fauna relied on carbon derived directly or indirectly from the brine pools or associated seeps at the rim.

Shrimps and two species of fish were recorded by the brine pool. To what extent these motile animals were associated with the brine pools, as, e.g., shown for shrimps living near brines elsewhere (Copley and Young 2006), or just incidental visitors, await further studies. We were unable to collect any of the shrimps and fishes and can, therefore, not say anything about their feeding preferences.

No empty benthic mollusc shells were found with the sediments and most of the shells retrieved from the chimneys were damaged. The damage was probably caused partly by corrosion and partly because other gastropods had been grazing on them. Vent/seep molluscs commonly have thin shells as calcium carbonate is more energetically costly to produce in high pressure environments and also more easily corroded (Sasaki et al. [2010](#page-6-0); Vermeij [1993\)](#page-6-0). The calcium layer disappears before the periostracum (the organic coating around the shells) (Sasaki et al. [2010\)](#page-6-0), and this could explain the high amounts of solemyid periostracum remains that were found. All the shells retrieved from within the chimneys were covered with mineral deposits that for some were not possible to remove with bleach in order to help identification. Mineral deposits are common on shell surfaces of vent/seep molluscs and are precipitated by bacterial activity (Warén and Bouchet [1989\)](#page-6-0).

The Red Sea is a highly oligotrophic ocean and unique compared to other oceanic regions in that its water temperature remains higher than 21  $\degree$ C all the way to the bottom (Wishner [1980\)](#page-6-0). Such high bottom temperatures lead to faster mineralisation of organic material and a higher metabolic demand of deep sea organisms compared to other deep sea ecosystems. This likely is part of the explanation why the deep areas of Red Sea are extremely poor in benthos with only  $0.05$  g C/m<sup>2</sup> (Monin et al. [1982](#page-6-0); Pfannkuche [1993\)](#page-6-0). With that background, the Kebrit rim apparently is an ecosystem with increased biomass and biodiversity compared to the surroundings.

Acknowledgments We are grateful to all help from the other Leg 4 Red Sea Expedition 2013 KAUST participants; André Antunes, Ioannis Georgakakis, Thor A. Klevjer, Perdana Karim Prihartato, Anders Røstad, and Ingrid Solberg. The Red Sea Expedition 2013 was sponsored by KAUST. Leonidas Manousakis and Manolis Kalergis from Hellenic Centre for Marine Research (HCMR) assisted in ROVoperations. The captain and crew of the R/V Aegaeo provided support during the entire cruise. Ohoud Mohammed Eid Alharbi assisted with the electron microscopy. We solicited taxonomic opinions from Anders Warén and Yasunori Kano on gatropods, Graham Oliver on bivalves, and Fran Saborido-rey on fish.

## References

- Anschutz P, Blanc G, Chatin F et al (1999) Hydrographic changes during 20 years in the brine-filled basins of the Red Sea. Deep Sea Res Part Oceanogr Res Pap 46:1779–1792. doi:[10.1016/S0967-0637\(99\)](http://dx.doi.org/10.1016/S0967-0637(99)00019-9) [00019-9](http://dx.doi.org/10.1016/S0967-0637(99)00019-9)
- Antunes A, Ngugi DK, Stingl U (2011) Microbiology of the Red Sea (and other) deep-sea anoxic brine lakes. Environ Microbiol Rep 3:416– 433. doi[:10.1111/j.1758-2229.2011.00264.x](http://dx.doi.org/10.1111/j.1758-2229.2011.00264.x)
- Bäcker H, Schoell M (1972) New deeps with brines and metalliferous sediments in the Red Sea. Nat Phys Sci 240:153–158. doi[:10.1038/](http://dx.doi.org/10.1038/physci240153a0) [physci240153a0](http://dx.doi.org/10.1038/physci240153a0)
- Baco AR, Smith CR (2003) High species richness in deep-sea chemoautotrophic whale skeleton communities. Mar Ecol Prog Ser 260:109– 114
- Baker MC, Ramirez-Llodra EZ, Tyler PA et al (2010) Biogeography, ecology, and vulnerability of chemosynthetic ecosystems in the deep sea. In: McIntyre AD (ed) Life worlds oceans. Wiley-Blackwell, pp 161–182
- Batang ZB, Papathanassiou E, Al-Suwailem A et al (2012) First discovery of a cold seep on the continental margin of the central Red Sea. J Mar Syst 94:247–253. doi:[10.1016/j.jmarsys.2011.12.004](http://dx.doi.org/10.1016/j.jmarsys.2011.12.004)
- Blum N, Puchelt H (1991) Sedimentary-hosted polymetallic massive sulfide deposits of the Kebrit and Shaban Deeps, Red Sea. Mineral Deposita 26:217–227. doi:[10.1007/BF00209261](http://dx.doi.org/10.1007/BF00209261)
- Braile LW, Keller GR, Wendlandt RF et al (2006) Chapter 5 The east african rift system. In: Olsen KH (ed) Dev Geotecton. Elsevier, pp 213–231, I–III
- Carlier A, Ritt B, Rodrigues CF et al (2010) Heterogeneous energetic pathways and carbon sources on deep eastern Mediterranean cold seep communities. Mar Biol 157:2545–2565. doi:[10.1007/s00227-](http://dx.doi.org/10.1007/s00227-010-1518-1) [010-1518-1](http://dx.doi.org/10.1007/s00227-010-1518-1)
- Coleman RG (1993) Geological evolution of the Red Sea. Oxford monographs on geology and geophysics. Oxford University Press, New York, 186 pp
- Copley JTP, Young CM (2006) Seasonality and zonation in the reproductive biology and population structure of the shrimp Alvinocaris stactophila (Caridea: Alvinocarididae) at a Louisiana Slope cold seep. Mar Ecol Prog Ser 315:199–209. doi[:10.3354/meps315199](http://dx.doi.org/10.3354/meps315199)
- Cordes EE, Carney SL, Hourdez S et al (2007) Cold seeps of the deep Gulf of Mexico: community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. Deep Sea Res Part Oceanogr Res Pap 54:637–653. doi[:10.1016/j.dsr.2007.01.001](http://dx.doi.org/10.1016/j.dsr.2007.01.001)
- Cuomo MC (1985) Sulphide as a larval settlement cue for Capitella sp I. Biogeochemistry 1:169–181. doi[:10.1007/BF02185040](http://dx.doi.org/10.1007/BF02185040)
- Danovaro R, Dell'Anno A, Pusceddu A, Gambi C, Heiner I, Kristensen RM (2010) The first metazoa living in permanently anoxic conditions. BMC Biol 8:30
- Degens ET, Ross DA (1969) Hot brines and recent heavy metal deposits in the Red Sea—geochemical and geophysical account. Springer, New York, 600 pp
- <span id="page-6-0"></span>Dover CLV, Trask JL (2000) Diversity at deep-sea hydrothermal vent and intertidal mussel beds. Mar Ecol Prog Ser 195:169–178. doi:[10.](http://dx.doi.org/10.3354/meps195169) [3354/meps195169](http://dx.doi.org/10.3354/meps195169)
- Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. Nat Rev Microbiol 6: 725–740. doi[:10.1038/nrmicro1992](http://dx.doi.org/10.1038/nrmicro1992)
- Duperron S (2010) The diversity of deep-sea mussels and their bacterial symbioses. In: Kiel S (ed) Vent Seep Biota. Springer, Dordrecht, pp 137–167
- Eder W, Ludwig W, Huber R (1999) Novel 16S rRNA gene sequences retrieved from highly saline brine sediments of Kebrit Deep, Red Sea. Arch Microbiol 172:213–218. doi[:10.1007/s002030050762](http://dx.doi.org/10.1007/s002030050762)
- Eder W, Schmidt M, Koch M et al (2002) Prokaryotic phylogenetic diversity and corresponding geochemical data of the brine–seawater interface of the Shaban Deep, Red Sea. Environ Microbiol 4:758– 763. doi[:10.1046/j.1462-2920.2002.00351.x](http://dx.doi.org/10.1046/j.1462-2920.2002.00351.x)
- Edgcomb V, Orsi W, Leslin C et al (2009) Protistan community patterns within the brine and halocline of deep hypersaline anoxic basins in the eastern Mediterranean Sea. Extremophiles 13:151–167. doi:[10.](http://dx.doi.org/10.1007/s00792-008-0206-2) [1007/s00792-008-0206-2](http://dx.doi.org/10.1007/s00792-008-0206-2)
- Faber E, Botz R, Poggenburg J, Schmidt M, Stoffers P, Hartmann M (1998) Methane in Red Sea brines. Org Geochem 29:363–379
- Felbeck H, Childress JJ, Somero GN (1981) Calvin-Benson cycle and sulphide oxidation enzymes in animals from sulphide-rich habitats. Nature 293:291–293. doi[:10.1038/293291a0](http://dx.doi.org/10.1038/293291a0)
- Fisher CR (1990) Chemoautotrophic and methanotrophic symbioses in marine-invertebrates. Rev Aquat Sci 2:399–436
- Galkin SV, Goroslavskaya EI (2010) Bottom fauna associated with Bathymodiolus azoricus (Mytilidae) mussel beds in the hydrothermal fields of the Mid-Atlantic Ridge. Oceanology 50:51–60. doi:[10.](http://dx.doi.org/10.1134/S0001437010010066) [1134/S0001437010010066](http://dx.doi.org/10.1134/S0001437010010066)
- Hartmann M, Scholten JC, Stoffers P, Wehner F (1998) Hydrographic structure of brine-filled deeps in the Red Sea—new results from the Shaban, Kebrit, Atlantis II, and Discovery Deep. Mar Geol 144: 311–330. doi:[10.1016/S0025-3227\(97\)00055-8](http://dx.doi.org/10.1016/S0025-3227(97)00055-8)
- Henneke E, De Lange GJ (1990) The distribution of DOC and POC in the water column and brines of the Tyro and Bannock Basins. Mar Chem 31:113–122. doi[:10.1016/0304-4203\(90\)90033-9](http://dx.doi.org/10.1016/0304-4203(90)90033-9)
- LaRock PA, Lauer RD, Schwarz JR et al (1979) Microbial biomass and activity distribution in an anoxic, hypersaline basin. Appl Environ Microbiol 37:466–470
- Levin LA, Ziebis W, Mendoza GF et al (2003) Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. Mar Ecol Prog Ser 265:123–139. doi:[10.3354/meps265123](http://dx.doi.org/10.3354/meps265123)
- McLean JH (1992) Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. J Molluscan Stud 58:401–414. doi[:10.1093/mollus/58.4.401](http://dx.doi.org/10.1093/mollus/58.4.401)
- Monin AS, Litvin VM, Podrazhansky AM et al (1982) Red sea submersible research expedition. Deep Sea Res Part Oceanogr Res Pap 29: 361–373. doi[:10.1016/0198-0149\(82\)90100-5](http://dx.doi.org/10.1016/0198-0149(82)90100-5)
- Mullineaux L, Mills S, Sweetman A et al (2005) Vertical, lateral and temporal structure in larval distributions at hydrothermal vents. Mar Ecol Prog Ser 293:1–16. doi[:10.3354/meps293001](http://dx.doi.org/10.3354/meps293001)
- Oliver PG, Vestheim H, Antunes A, Kaartvedt S (in press) Systematics, functional morphology and distribution of a bivalve (Apachecorbula muriatica gen. et sp. nov.) from the rim of the "Valdivia Deep" brine pool in the Red Sea. J Mar Biol UK. doi: [10.1017/](http://dx.doi.org/10.1017/S0025315414001234) [S0025315414001234](http://dx.doi.org/10.1017/S0025315414001234)
- Pautot G, Guennoc P, Coutelle A, Lyberis N (1984) Discovery of a large brine deep in the northern Red Sea. Nature 310:133–136. doi[:10.](http://dx.doi.org/10.1038/310133a0) [1038/310133a0](http://dx.doi.org/10.1038/310133a0)
- Pfannkuche O (1993) Benthic standing stock and metabolic activity in the bathyal Red Sea from 17°N to 27°N. Mar Ecol 14:67–79. doi[:10.](http://dx.doi.org/10.1111/j.1439-0485.1993.tb00365.x) [1111/j.1439-0485.1993.tb00365.x](http://dx.doi.org/10.1111/j.1439-0485.1993.tb00365.x)
- Ritt B, Sarrazin J, Caprais J-C et al (2010) First insights into the structure and environmental setting of cold-seep communities in the Marmara Sea. Deep Sea Res Part Oceanogr Res Pap 57:1120–1136. doi[:10.](http://dx.doi.org/10.1016/j.dsr.2010.05.011) [1016/j.dsr.2010.05.011](http://dx.doi.org/10.1016/j.dsr.2010.05.011)
- Ryan WBF, Thorndike EM, Ewing M, Ross DA (1969) Suspended matter in the Red Sea brines and its detection by light scattering. In: Degens ET, Ross DA (eds) Hot brines recent heavy met. Depos Red Sea. Springer, Berlin, pp 153–157
- Sasaki T, Warén A, Kano Y et al (2010) Gastropods from recent hot vents and cold seeps: systematics, diversity and life strategies. In: Kiel S (ed) Vent Seep Biota. Springer, Netherlands, pp 169–254
- Scholten JC, Stoffers P, Garbe-Schönberg D, Moammar M (2000) Hydrothermal mineralization in the Red Sea. CRC Mar Sci Ser 17
- Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep Sea Res II Top Stud Oceanogr 45:517–567. doi[:10.1016/](http://dx.doi.org/10.1016/S0967-0645(97)00074-X) [S0967-0645\(97\)00074-X](http://dx.doi.org/10.1016/S0967-0645(97)00074-X)
- Stock A, Breiner H-W, Pachiadaki M et al (2012) Microbial eukaryote life in the new hypersaline deep-sea basin Thetis. Extremophiles 16: 21–34. doi:[10.1007/s00792-011-0401-4](http://dx.doi.org/10.1007/s00792-011-0401-4)
- Swallow JC, Crease J (1965) Hot salty water at the bottom of the Red Sea. Nature 205:165–166. doi[:10.1038/205165a0](http://dx.doi.org/10.1038/205165a0)
- Taylor JD, Glover EA (2010) Chemosymbiotic bivalves. In: Kiel S (ed) Vent Seep Biota. Springer, Netherlands, pp 107–135
- Tsutsumi H, Wainright S, Montani S et al (2001) Exploitation of a chemosynthetic food resource by the polychaete Capitella sp. I. Mar Ecol Prog Ser 216:119–127. doi[:10.3354/meps216119](http://dx.doi.org/10.3354/meps216119)
- Vermeij GJ (1993) A natural history of shells. Princeton University Press, Princeton, 207 pp
- Warén A, Bouchet P (1989) New gastropods from East Pacific hydrothermal vents. Zool Scr 18:67–102. doi:[10.1111/j.1463-6409.1989.](http://dx.doi.org/10.1111/j.1463-6409.1989.tb00124.x) [tb00124.x](http://dx.doi.org/10.1111/j.1463-6409.1989.tb00124.x)
- Wishner KF (1980) The biomass of the deep-sea benthopelagic plankton. Deep Sea Res Part Oceanogr Res Pap 27:203–216. doi[:10.1016/](http://dx.doi.org/10.1016/0198-0149(80)90012-6) [0198-0149\(80\)90012-6](http://dx.doi.org/10.1016/0198-0149(80)90012-6)
- Young RA, Ross DA (1974) Volcanic and sedimentary processes in the Red Sea axial trough. Deep Sea Res Oceanogr Abstr 21:289–297. doi:[10.1016/0011-7471\(74\)90100-4](http://dx.doi.org/10.1016/0011-7471(74)90100-4)