

Macro- and micro-fauna from cold seeps in the Palmahim Disturbance (Israeli off-shore), with description of *Waisiuconcha corsellii* n.sp. (Bivalvia, Vesicomysidae)

D. Basso^{a,*}, V. Beccari^b, A. Almogi-Labin^c, O. Hyams-Kaphzan^c, A. Weissman^d, Y. Makovsky^e, A. Rüggeberg^b, S. Spezzaferri^b

^a University of Milano - Bicocca, Department of Earth and Environmental Sciences, CoNISMa, ULR of the University of Milano-Bicocca, Piazza della Scienza 4, 20126, Milano, Italy

^b University of Fribourg, Department of Geosciences, Chemin Du Musée 6, 1700, Fribourg, Switzerland

^c Geological Survey of Israel, Jerusalem, 9371234, Israel

^d Department of Marine Biology, Leon H. Charney School of Marine Sciences (CSMS), University of Haifa, Haifa, 31905, Israel

^e Dr. Moses Strauss Department of Marine Geosciences and Hatter Department of Marine Technology, Leon H. Charney School of Marine Sciences (CSMS), University of Haifa, Haifa, 31905, Israel

ABSTRACT

Chemosymbiotic micro- and macro-fauna related to cold-seep sites were recovered in the Palmahim Disturbance (PD), offshore Israel, during EU EUROFLEETS2 SEMSEEP Cruise, by box-coring and Remotely Operated Vehicle (ROV) dives. No live macrofauna was identified in the collected sediments, with the exception of the seep-related crustacean *Calliax lobata* (de Gaillande and Lagardère, 1966). Numerous *Calliax* claws testify the past colonization of these soft bottoms by several generations of this ghost shrimp. After sediment sieving on 1 mm, we identified gastropods belonging to the families Trochidae, Eucyclidae, unassigned Seguenzioidea (genus *Anekes*), Rissoiidae, Elachisinidae, Raphitomidae, Mangeliidae, Architectonicidae, Orbitestellidae, and Acteonidae. The identified bivalves belong to the families Nuculidae, Yoldiidae, Mytilidae, Lucinidae, Thyasiridae, Semelidae, Kelliellidae, Vesicomysidae, Xylophagidae, and Cuspidariidae. A seep-related group of chemosymbiotic molluscs was detected, including: *Taranis moerchii* (Malm, 1861), *Lurifax vitreus* Warén and Bouchet, 2001, *Idas ghisottii* Warén and Carrozza, 1990, *Lucinoma kazani* Salas and Woodside, 2002, *Thyasira biplicata* (Philippi, 1836), *Isorropodon perplexum* Sturany, 1896, and the newly described Vesicomysid species *Waisiuconcha corsellii* n. sp., that represents also the first record of the genus *Waisiuconcha* in recent Mediterranean sediments.

The ROV dives recorded local patches of several m² of seafloor covered by dead shells of *L. kazani*, with a density of up to about 200 loose shells per square meter. The potential occurrence of seep-related foraminifera, among low-oxygen tolerant species, was explored by comparison with previously sampled adjacent localities, and led to the identification of *Chilostomella oolina*, *Globobulimina affinis* and *G. pseudospinescens* as potential foraminiferal seep indicators in the southeastern Mediterranean Sea. The absence of live, seep-related fauna in surface sediments in the PD, where seepage has been confirmed, suggests intermittent activity and a pause or decline of the investigated seeps.

1. Introduction

Active gas seepage sites were found offshore central Israel on the western edge, the toe region, of the Palmahim Disturbance (PD) at water depths of 1100 to 1300 m. This region is impacted by the history of Nilotic supply of sediments and nutrients (Almogi-Labin et al., 2009; Hennekam et al., 2014). Seepage sites are associated with pockmarks, carbonate buildups and chemohersms.

Benthic deep-sea biota live under conditions of perpetual darkness and relatively low temperature. Since photosynthesis cannot occur, the entire benthic food web is sustained by the planktonic production occurring in the surface waters, or by organic carbon produced in

shallow coastal environments and transferred to depth by sediment transport. For these reasons, the bathyal and abyssal areas of the Mediterranean commonly appear as a muddy desert (Basso et al., 2004). In regions where cold seepage occurs, hydrogen sulfide and/or methane escapes from below the seafloor, and the environment is often toxic to most organisms (Levin et al., 2003). However, like hydrothermal vents, cold seeps may support a huge microbial biomass directly available to consumers. Those prokaryotes are chemoautotrophs, because they oxidize the reducing chemical compounds seeping at the seafloor and use the energy released by the oxidation for the synthesis of organic carbon. Cold seeps also support a unique community of metazoans hosting symbiotic chemosynthetic bacteria. Deep seep infauna exhibit

* Corresponding author.

E-mail address: daniela.basso@unimib.it (D. Basso).

enhanced densities, modified composition and reduced species diversity when compared with surrounding “normal” sediments (e.g. [Levin, 2005](#); [Taviani, 2014](#)).

The most common fauna from these environments consist of bivalves, gastropods, polychaetes and decapods, but also benthic foraminifera (e.g. [Sen Gupta et al., 1997](#); [Robinson et al., 2004](#); [Levin, 2005](#); [Panieri, 2006](#)). The metazoan community is composed of chemosymbiotic species, associated with heterotrophs feeding on the available microbial biomass (primary consumers), and a suite of secondary consumers, predators and scavengers exploiting this opulence oasis. Specialized infaunal communities are associated with different seep habitats and with different vertical zones in the sediment. Hence, cold seeps support an enormous biomass of free-living and symbiotic microbial life that is nourished by the oxidation of methane, higher hydrocarbons and sulfide (e.g. [Joye et al., 2004](#)).

Evidence of chemosymbiosis has been so far described in the deep eastern Mediterranean from mud volcanoes (e.g. [Corseili and Basso, 1996](#); [Olu-LeRoy et al., 2004](#); [Foucher et al., 2009](#); [Mayer et al., 2011](#); [Taviani, 2014](#)) the Nile deep sea fan (e.g. [Bayon et al., 2009](#); [Ritt et al., 2011](#)), the Eratosthenes seamount ([Mayer et al., 2011](#)) and in other localities characterized by cold seeps in the central and western Mediterranean, such as the Gela Basin ([Taviani et al., 2013](#)) and the Alboran Sea ([Blinova et al., 2011](#)).

Among protozoans, a recent strategic survey revealed the occurrence of foraminiferal assemblages characteristic of low oxygen conditions at several sites ([Sen Gupta et al., 1997](#); [Panieri, 2006](#)) suggesting possible relations with seep environments in the PD ([Hyams-Kaphzan et al., 2018](#)).

The aim of this contribution is: 1) to qualitatively document for the first time the composition of the benthic chemosymbiotic macrofauna in the PD, and describe the new vesicomyid species *Waisiiconcha corseilii*; 2) to compare the microfauna with that previously sampled from adjacent localities ([Hyams-Kaphzan et al., 2018](#)); 3) to report on the

distribution of some low-oxygen tolerant benthic foraminifera that can be potentially considered as seep-related species; 4) to test if the co-occurrence of micro- and macrofauna maybe indicative of past seepage.

Study Area A variety of seepage related features were discovered along the base of the Israeli continental slope during the E/V Nautilus 2010, 2011 ROV surveys ([Coleman et al., 2012](#); [Rubin-Blum et al., 2014a, b](#)). The PD ([Fig. 1](#)) is a large-scale (~50x15 km) rotational slide rooted in the Messinian evaporites on the southern Israeli margin ([Garfunkel et al., 1979](#)).

Correlation of the ROV observed seepage sites, carbonates and bioturbated seafloor suggested that the influence of gas seepage extends tens to hundreds of meters away from the seepage focal zones ([Ezra, 2017](#)). Two sediments cores, collected at water depths of ~1100 m in one of the PD seepage sites and in a pockmark field offshore Acre ([Fig. 1](#)), portrayed high concentrations of biogenic methane ([Rubin Blum et al., 2014a](#)). The EUROFLEETS2 Expedition SEMSEEP ([Makovsky et al., 2017](#)), undertaken in September 2016 onboard R/V Aegaeo, revisited the western Palmahim seepage area discovered by the E/V Nautilus cruise (SEMSEEP Working Area 3 = WA3, [Fig. 1](#)) and recorded and investigated additional active gas seepage sites. Also associated with carbonate chimneys and chemosymbiotic fauna, these new gas seepage sites were discovered within the Levant Channel ([Gvirtzman et al., 2015](#)), at the western bound of PD (WA4a, [Fig. 1](#)), and in a major pockmarks system etched within a pressure ridge in Gal-C exploration block, ~40 km to the west (WA2a, [Fig. 1](#)). [Gadol et al. \(2018\)](#) reported the discovery of a 20 km long and 5 to 10 km wide pockmarks field, hosting active seepage, along the base of the continental slope of Israel.

2. Materials and methods

The sets of samples from the PD investigated here include: 1) macrofauna and foraminifera collected in 2016 (SEMSEEP cruise) and 2)

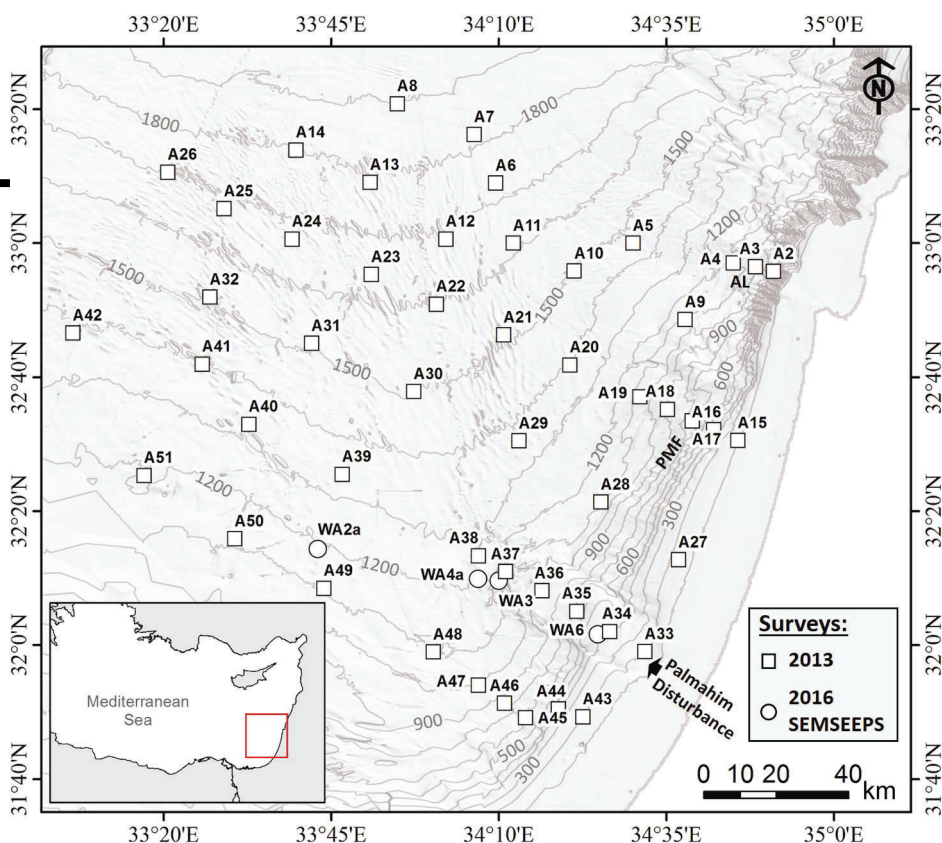


Fig. 1. Seafloor bathymetry of the study area in the southeastern Mediterranean offshore Israel (after [Hall et al. \(2015\)](#) and [Gvirtzman et al. \(2015\)](#)), depicted by contours and shaded relief and overlaid with the 2013 survey stations (squares) and 2016 SEMSEEP (circles) survey working areas (WA). Sites of interest are the Palmahim Disturbance (labeled) extending ~50 km, the Acre pockmarks location (AL) of [Rubin-Blum et al. \(2014a\)](#) and the pervasive pockmarks field (PMF) reported by [Gadol et al. \(2018\)](#). Inset shows the research area in the context of the eastern Mediterranean region (from ESRI OpenStreetMap).

foraminifera collected in 2013 by Lubinevsky et al. (2017) and investigated by Hyams-Kaphzan et al. (2018). In the present study we report only the distribution of 3 species known to be highly tolerant to low-oxygen conditions, being deep sediment dwellers (Jorissen et al., 1995; Spezzaferri et al., 2015) that may be potentially associated with seep environments in the PD (Hyams-Kaphzan et al., 2018). The taxonomy of these species, *Chilostomella oolina* Schwager, 1878, *Globobulimina affinis* (d'Orbigny, 1839) and *Globobulimina pseudospinescens* (Emiliani), follows Hayward et al. (2018).

2.1. The 2016 sampling

In the framework of the EUROFLEETS2 expeditions in September 2016, the SEMSEEP cruise was conducted with the R/V AEGAEON equipped with a ROV Max Rover, in the PD on the continental slope of Israel (Fig. 1). Surface, push-core and box-core samples were collected during the cruise. The 2016 investigation addressed both micro- and macrofauna, exclusively from samples collected in seep areas identified during previous explorations (Coleman et al., 2012; Rubin-Blum et al., 2014a). The seep areas have been confirmed during the SEMSEEP cruise, based on indirect evidence such as occurrence of pockmarks, bacterial mats, carbonate crusts and chimneys: Gal-C pockmarks (WA2a), Palmahim pockmarks (WA3), Palmahim channel (WA4a), and Palmahim chemohierms (WA6), (Table 1).

A box corer with a sampling area of 30 x 30 cm and a maximal penetration of 60 cm was used to obtain undisturbed seafloor samples. It was equipped with a Tracklink 1500 HA USBL transponder mounted 30 m above the gear on the cable to make precise positioning (Makovsky et al., 2017). All visibly living macrofauna was removed from the box-core surface and afterward, surface sediments were collected for living (stained) foraminiferal investigations. Subcores 9 cm in diameter were collected from each box-core, for faunal analyses.

Foraminifera: surface samples from Box cores AG16-22-BC1 (WA6, Fig. 1), AG16-23-BC1 and AG16-23-BC2 (WA3, Fig. 1) were processed by picking 300 specimens and counting only *Chilostomella oolina* Schwager, *Globobulimina affinis* (d'Orbigny) and *Globobulimina pseudospinescens* (Emiliani). Details of the protocol can be found in Schönfeld et al. (2012). Only deviation from the protocol was the use of the 32 µm mesh sieve. Samples from selected subcores (AG16-17-BC3 (WA3), AG16-22-BC1 and AG16-23-BC1) were also washed with the 32 µm mesh sieve. However, in this study we investigated only the >250 µm specimens for comparison with the data of Hyams-Kaphzan et al. (2018).

Sediments of Dive 9 ROV 2-4-6 (WA2a, Fig. 1), Dive 2 PC1 (WA3), Box cores AG16-15-BC1 (WA4a, Fig. 1), AG16-17-BC3, AG16-22-BC1 and AG16-23-BC1 were processed onboard and washed through the 20, 10, 0.5 and 0.25 mm mesh sieves to collect foraminifera and macrofauna.

Macrofauna: After the collection of the subcores, further material for the investigation of the macro-fossils was obtained by sieving the remaining of the box-cores on 1 mm mesh (Kidwell, 2001; Basso and

Corselli, 2007). Supraspecific taxonomy of molluscs follows Mollusca-Base (2018). In addition to the whole mollusc shells, fragmented bivalves preserving the hinge and fragmented gastropods preserving at least two third of the shell including either the aperture or the apex have been extracted from the sediment. Molluscs have been identified under optical microscope. For mollusc descriptions, further observations have been performed under the Scanning Electron Microscope Thermo Fisher FEIXL30SFEG at the Fribourg University laboratories. For bivalves, hinge nomenclature and other descriptive terms follow Cosel and Salas (2001).

2.2. The 2013 sampling

The 2013 sampling was devoted exclusively to a regional survey of benthic foraminifera that were sampled from an area of approximately 23,000 km² in the southeastern Levantine Basin (Fig. 1). Sixteen sites were sampled in the continental shelf margin and the continental slope (100–1000 m water depth = wd) and 34 sites in the bathyal plain (1000–1900 m wd). The live (Rose Bengal stained) and the dead foraminifera were separated from a box corer sample of 0.0602 m² and were normalized to the number of specimens m⁻² (Hyams-Kaphzan et al., 2018).

3. Results

3.1. Benthic foraminiferal assemblages

3.1.1. Results from 2016 sampling

Only one living specimen of *G. pseudospinescens* was detected in AG16-22-BC1 0–1 cm at 420 m (WA6; Fig. 1, Pl. 1). Dead specimens of *G. affinis*, *G. pseudospinescens* and *C. oolina* mostly occur in AG16-17-BC3 at 1038 m (WA3; Fig. 1, Pl. 1), with the highest abundance of *G. pseudospinescens* at 30–45 cm depth in the subcore, and in AG16-23-BC1 at 1037 m (WA3; Fig. 1, Table 2).

At station AG16-17-BC3 (1038 m; WA3; Fig. 1) these 3 foraminiferal species co-occur with the chemosynthetic molluscs *Taranis moerchii* (Malm, 1861), *Myrtea amorpha* (Sturany, 1896), *Lucinoma kazani* Salas and Woodside (2002), *Isorropodon perplexum* Sturany (1896) and *Waisiiconcha corsellii* (n.sp.). At site AG16-23-BC1 (WA3; Fig. 1) they also co-occur with the chemosynthetic bivalve *Thyasira biplicata* (Philippi, 1844). At site AG16-22-BC1 (WA6; Fig. 1) *G. pseudospinescens* co-occurs with the chemosymbiotic gastropod *Lurifax vitreus* Warén and Bouchet (2001), not present in other samples (Table 4).

3.1.2. Results from 2013 sampling

The benthic foraminiferal species *C. oolina*, *G. affinis* and *G. pseudospinescens* show a distinct depth-dependent distribution pattern in the 2013-southeastern Levantine sampling (SE-LB). In the deeper water exceeding ~1000 m they occur only in 6 out of 34 studied sites, mostly in the dead assemblage (except a single occurrence at 1812 m

Table 1

Sample code; site name and working area (WA); geographic coordinates and depth; sampling gear; recovery as cm below seafloor (bsf); sampled interval for the collection of molluscs (moll) and foraminifera (foram).

Sample ID	Site and Working Area (WA)	Lat. N	Long. E	wd (m)	Gear	Recovery (cm bsf)	Sampled interval
AG16-Dive 2-PC1-CC	Palmahim pockmarks (WA 3)	32°09.884'	34°06.887'	1232	ROV push-corer core-catcher	35	35 cm (moll)
AG16-Dive 9-ROV 2-4-6	Gal-C pockmarks (WA2a)	32°14.341'	33°42.974'	1171	ROV manipulator	surface	surface (moll)
AG16-15-BC1	Palmahim channel (WA4a)	32°09.866'	34°06.915'	1241	Box-corer	43	0–43 cm (moll)
AG16-17-BC3	Palmahim pockmarks (WA 3)	32°09.588'	34°10.030'	1038	Box-corer	50	0–15 cm (foram, moll)
AG16-22-BC1	Palmahim chemohierms (WA6)	32°01.628'	34°24.820'	420	Box-corer	60	0–1 cm (foram) 0–15 cm (moll)
AG16-23-BC1	Palmahim pockmarks (WA 3)	32°09.652'	34°10.066'	1037	Box-corer	41	0–1 cm (foram) 0–41 cm (moll)
AG16-23-BC2	Palmahim pockmarks (WA 3)	32°09.652'	34°10.066'	1037	Box-corer	41	0–1 cm (foram)

Table 2
Distribution of *Chilostomella oolina*, *Globobulimina affinis* and *G. pseudospinescens* in bottom samples and sub-cores collected during the EUROFLEETS2 cruise SEMSEEP in 2016.

Site ID	wd (m)	Live (%)				Dead (%)			
		<i>C. oolina</i>	<i>G. affinis</i>	<i>G. pseudo-spinescens</i>	^a Total	<i>C. oolina</i>	<i>G. affinis</i>	<i>G. pseudo-spinescens</i>	^a Total
AG16-17-BC3 0–15 cm	1038					0.33	2.61	2.94	306
AG16-17-BC3 15–30 cm	1038					0.32	0.64	6.71	313
AG16-17-BC3 30–45 cm	1038					0.32	1.91	8.28	314
AG16-22-BC1 0–1 cm	420			1.6	87			0.72	138
AG16-22-BC1 7–8 cm	420							3.13	128
AG16-22-BC1 22–23 cm	420							0.97	103
AG16-22-BC1 40–41 cm	420								
AG16-23-BC1	1037					0.36	0.36	0.71	280
AG16-23-BC2	1037					0.8			250

^a Total refers to the total number of specimens counted in the fraction >250 µm.

Table 3
Distribution of *Chilostomella oolina*, *Globobulimina affinis* and *G. pseudospinescens* in surface samples collected in 2013 (Hyams-Kaphzan et al., 2018). Grey bands indicate the samples where abundant *Thyasira* spp. were found in Lubinevsky et al. (2017).

Site ID	Lat. N	Long. E	wd (m)	Live (%)				Dead (%)			
				<i>C. oolina</i>	<i>G. affinis</i>	<i>G. pseudo-spinescens</i>	^a Total	<i>C. oolina</i>	<i>G. affinis</i>	<i>G. pseudo-spinescens</i>	^a Total
A2	32.9301	34.8503	601			6.7	15	2.6		66.1	937
A3	32.9420	34.8052	994	0.3	1.2	16.6	338		0.3	0.6	3584
A4	32.9513	34.7499	1128				392			0.9	4407
A5	33.0005	34.5012	1453				35			2.5	1483
A6	33.1499	34.1595	1730				2	0.7		0.5	4072
A7	33.2705	34.1053	1822				60	0.1			7627
A8	33.3474	33.9141	1901				192				30677
A9	32.8101	34.6304	1085				22				3378
A10	32.9307	34.3547	1496				8				3112
A11	33.0003	34.2025	1624				56				4126
A12	33.0105	34.0351	1689				96	0.1			7069
A13	33.1517	33.8468	1794				184				7176
A14	33.2321	33.6624	1812			5.3	152		0.1		11312
A15	32.5092	34.7619	105		4.1		148		2.5		3824
A16	32.5358	34.7018	422		58.7		104	5.4	34.2		1139
A17	32.5583	34.6479	752				18		1.4	0.2	5388
A18	32.5868	34.5864	883				212				5848
A19	32.6174	34.5176	1063				95				4017
A20	32.6971	34.3435	1387				71				1448
A21	32.7720	34.1792	1524				42				5748
A22	32.8486	34.0118	1587				68				4168
A23	32.9221	33.8494	1644				64				6456
A24	33.0103	33.6530	1653				336				6416
A25	33.0859	33.4835	1669				224				19296
A26	33.1767	33.3437	1678				352				16432
A27	32.2121	34.6143	158	1.6	57.9		385		13.8		1990
A28	32.3557	34.4210	1122				102				4360
A29	32.5083	34.2169	1367				244				2676
A30	32.6312	33.9555	1504				212				4360
A31	32.7508	33.7013	1526				512				9384
A32	32.8661	33.4479	1529				7				8864
A33	31.9837	34.5299	214	30.5	16.9	1.7	59	8.9	1.1		359
A34	32.0335	34.4431	400	1.7		34.2	480	3.8		19.4	1854
A35	32.0842	34.3611	682				275				8993
A36	32.1351	34.2744	889			19.0	84				6440
A37	32.1827	34.1841	991				21				5774
A38	32.2223	34.1164	1301				7				3255
A39	32.4248	33.7778	1343				452				10156
A40	32.5494	33.5449	1337				144				7987
A41	32.6991	33.4287	1388				472				11552
A42	32.7768	33.1067	1370				74				15242
A43	31.8212	34.3761	198				61	1.8	5.0	0.6	2167
A44	31.8406	34.3151	452	2.6	0.3	65	680	3.0	0.3	17.1	4336
A45	31.8188	34.2334	698				48			0.6	4156
A46	31.8552	34.1813	875				224				23248
A47	31.9000	34.1160	1003				360				3128
A48	31.9825	34.0038	1094				5				4180
A49	32.1410	33.7321	1113				32				8488
A50	32.2645	33.5099	1120				6				6546
A51	32.4220	33.2838	1198				176				18651

^a Total refers to the total number of specimens in the box corer area of 0.0602 m²

Table 4
Distribution of benthic Gastropoda, Bivalvia and ghost shrimp claws (Arthropoda) in samples collected during the EUROLLEETS2 cruise SEMSEEP in 2016. Cold seep-related species are in bold. Asterisk indicates the species occurring also in the cold seeps of the Marmara Sea (Ritt et al., 2010; Taviani et al., 2013).

	Dive 9 ROV 2-4-6	Dive 2 PC1-CC	AG16-15-BC1	AG16-17-BC3	AG16-22-BC1	AG16-23-BC1
MOLLUSCA						
Gastropoda						
<i>Clelandella miliaris</i> (Brocchi, 1814)		✓	✓		✓	✓
<i>Putzeysia wiseri</i> (Calcare, 1842)*			✓	✓	✓	✓
<i>Anekes paucistriata</i> Warén, 1992						✓
<i>Alvania subsoluta</i> (Aradas, 1847)				✓		
<i>Benthonella tenella</i> (Jeffreys, 1869)			✓	✓	✓	
<i>Laeviphitus verduini</i> van Aartsen, Bogi & Giusti, 1989*						✓
<i>Pleurotomella eurybrocha</i> (Dautzenberg & Fisher, 1896)				✓		✓
<i>Benthomangelia macra</i> (Watson, 1881)						✓
Taranis moerchii (Malm, 1861)	✓	✓	✓	✓	✓	✓
<i>Heliacus alleryi</i> (Seguenza, 1876)					✓	
Lurifax vitreus Warén and Bouchet (2001)					✓	
<i>Crenilabium exile</i> (Jeffreys, 1870)						✓
Bivalvia						
<i>Ennucula corbuloides</i> (Seguenza, 1877)				✓		
<i>Yoldiella nana</i> (Sars, 1865)			✓	✓		
<i>Yoldiella striolata</i> (Brugnone, 1876)*			✓	✓	✓	
Idas ghisottii Warén & Carrozza, 1990	✓	✓	✓		✓	✓
<i>Bathymodiolinae</i> ind.						✓
Myrtea amorpha (Sturany, 1896)*	✓	✓	✓	✓	✓	✓
Lucinoma kazani Salas and Woodside, 2002*	✓	✓	✓	✓	✓	
<i>Thyasira biplicata</i> (Philippi, 1836)						✓
<i>Abra longicallus</i> (Scacchi, 1835)						✓
<i>Kelliella miliaris</i> (Philippi, 1844)			✓			
Isorropodon perplexum Sturany, 1896*	✓	✓	✓	✓	✓	✓
Waisiuconcha corsellii n. sp.			✓	✓	✓	✓
<i>Xylophaga dorsalis</i> (Turton, 1819)						✓
<i>Cardiomya costellata</i> (Deshayes, 1835)			✓			
ARTHROPODA						
Malacostraca						
Calliax lobata (de Gaillande and Lagardère, 1966)	✓	✓	✓	✓	✓	✓

where both live and dead specimens were found), in low numbers and only in the north-western sites (Figs. 1, 2; Table 3). Along the continental slope (100–1000 m depth) these species occur in 12 out of the 16 studied sites, often in the live and the dead assemblage, and often in high numbers of up to ~30%, ~60% and 65% respectively, out of the entire living assemblage (Figs. 1, 2; Table 3).

Among these species, *G. affinis* is the shallowest, living in higher numbers at 158 m and at 422 m, out of a total depth range between 105–994 m. In the dead assemblages, the highest numbers occur at 422 m (Table 3). The highest numbers of *G. pseudospinescens* occur between 400–452 m with a total depth range between 400–994 m. The maximal abundance of this species in the dead assemblage is at 600 m, comprising 66% of the total dead assemblage (Site A2, Figs. 1, 2; Table 3). *C. oolina* is rarer than the two *Globobulimina* species. Its total depth range is between 158–994 m and at 214 m it comprises ~30% of the living assemblage. In the dead assemblages, it occurs along a depth range between 198–994 m with the highest percentage (9%) at 214 m.

3.2. Invertebrate macrofauna

Live specimens of the ghost shrimp *Calliax lobata* (de Gaillande and Lagardère, 1966) were recovered from box-cores. Its claws are consistently present and volumetrically dominant in the >2 mm fraction of the box-cores (Fig. 3), exhibiting a variety of sizes, which indicate the species goes through a full life cycle with several moulting stages at the locality. Several clusters of living chemosymbiotic tubeworms *Lamellibrachia anaximandri* Southward et al. (2011) have been observed by ROV at seeps upon carbonates at WA2a and WA3 (Fig. 4).

Only dead specimens of molluscs were observed and documented in the SEMSEEP cruise (Table 4, Pls 2–3). The identified gastropods belong to the families Trochidae, Eucyclidae, unassigned Seguenzioidea (genus

Anekes), Rissoidae, Elachisinidae, Raphitomidae, Mangeliidae, Architectonicidae, Orbitestellidae, and Acteonidae. The identified bivalves (articulate and disarticulate valves) belong to the families Nuculidae, Yoldiidae, Mytilidae, Lucinidae, Thyasiridae, Semelidae, Kelliellidae, Vesicomyidae, Xylophagidae, and Cuspidariidae.

In all of the samples the most common bivalve is *Isorropodon perplexum*, in agreement with previous observations in the eastern Mediterranean (Cosel and Salas, 2001). *Isorropodon perplexum* is accompanied by less common, but consistently present *Waisiuconcha corsellii* Basso, Beccari and Spezzaferri n. sp. *T. moerchii*, *M. amorpha* and *L. kazani* are generally common, while other species are uncommon to rare (Table 4).

An annotated systematic summary of the chemosymbiotic species is presented in Appendix I. The new bivalve species is described below:

Family Vesicomyidae Dall & Simpson, 1901

Genus *Waisiuconcha* Beets, 1943

Beets, 1943:315–316, fig. 147–151.

Type species: *Waisiuconcha alberdinae* Beets, 1943.

Waisiuconcha corsellii Basso, Beccari, Spezzaferri, sp. nov.

(Pl. 2, Figs. 9 and 10; Pl. 3)

Type material: holotype deposited in the Natural History Museum Fribourg (NHMF) collected off Israel, Levant Channel, west of PD, R/V AEGAE (HCMR, Greece), SEMSEEP Cruise Stn AG16-15, 2016, leg. D. Basso, in the sediment of box-core BC1, 1 right valve and 1 left valve, dead. Paratypes: same locality, 1 right v., 1 left v., NHMF.

Type locality: off Israel, Levant Channel, west of PD (WA4a; Fig. 1), 32°09.866'N, 34°06.915'E, 1241 m.

Description: Shell very small, 2.1 to 4.8 mm long, 1.8 to 4 mm high, L/H ratio about 1.3. Each valve up to 1.2 mm in width (W/L 0.25). Shell oval to oblong-oval, longer than high, inflated, solid, entirely white. Anterior margin rounded, ventral margin convex, posterior margin

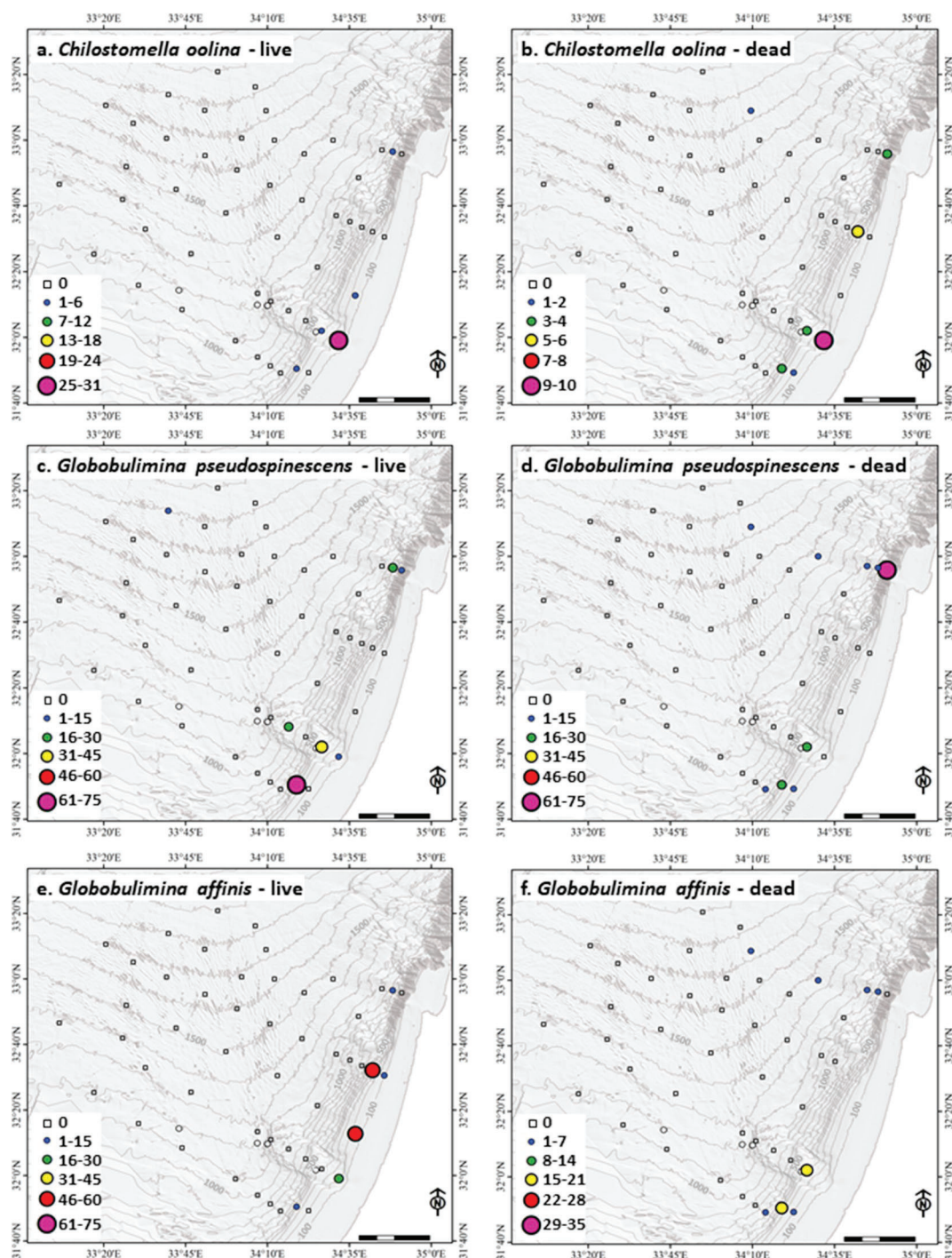


Fig. 2. Relative abundance distribution (shown by the different colored circles) of living and dead *C. oolina*, *G. affinis* and *G. pseudospinescens* in 2013 samples (after Hyams-Kaphzan et al., 2018) overlaid on Fig. 1. More details on species and locations in Table 3.

convex and rounded to somewhat truncate. Beaks prominent, prosogyrous, slightly enroled, situated in front of the vertical midline. Surface with unevenly spaced, commarginal, shallow grooves, less visible toward the umbos. Lunule short, broader than long, not sunken, delimited by a weakly marked lunular incision. Escutcheon long and narrow, stretching over the postero-dorsal part, delimited by a keel.

Hinge line strong, broad, broader just in front of the beaks. Two teeth in each valve, slightly variable in thickness. Cardinal 1 in the right valve strong, short and concave, situated just in front and beneath cardinal 3a. Cardinal 3a strongly curved, running from the anterior end of cardinal 1 backwards to beneath the umbonal end of the ligament. Cardinal 3b

overlapping and fused with 3a. In the left valve, cardinals 2a and 2b are fused and form a deep socket for accommodating cardinal 1. Cardinal 4 is rather thin and well separated from cardinal 2a-b, subparallel or slightly inclined in respect of the hinge margin. Ligament reaching one-third of the way to the posterior margin. Adductor muscle scars impressed. Pallial line distant from the margins, no pallial sinus. Ventral margin broad, with two internal thin incisions running parallel or diagonally to the edges. Protoconch rounded and convex.

Distribution: known only from the Eastern Mediterranean Sea.

Material examined: off Israel (Fig. 1), RV Aegaeo, 2016, WA4a, core AG16-15-BC1 (8 valves); WA3, AG16-17-BC3 (4 valves) and AG16-23-



Fig. 3. Overview of the sediments size fraction >2 mm, containing remains of the chemosymbiotic fauna, including vesicomyid shells (arrow), and claws of *Calliax lobata*.



Fig. 4. Gregarious settlement of the siboglinid *Lamellibrachia anaximandri* on chemohermes in the Palmahim Disturbance (Beccari et al., 2019). The distance between the two laser dots is 10 cm. Photograph taken by the ROV Max Rover.

BC1 (2 valves); WA6, AG16-22-BC1 (10 valves).

Biotope: predominantly in cold seep areas, with muddy sediments and authigenic carbonate crusts, 420 to 1241 m of wd.

Derivatio nominis: the species is named after Prof. Cesare Corselli, the Italian marine geologist who first demonstrated the existence of a chemosymbiotic fauna in the Mediterranean Sea.

Remarks: No live molluscs were recovered. The state of preservation of the shells of *W. corsellii* varies from fresh (preserving white colour and luster), to poorly preserved (brownish, partially corroded, fragmented). Shell size is also variable, as expected in resident populations of benthic species.

Waisiuconcha corsellii occurs mixed with shells of *Isorropodon perplexum*, which is coarsely similar in outline. As no genetic data are available for these closely related species, and because of the absence of

preserved tissues, this description is based on the morphological characters of the shell. A comprehensive revision and a comparative synopsis of the shells distinguishing the eastern Atlantic and Mediterranean genera of Vesicomyidae is provided by Cosel and Salas (2001). *Waisiuconcha corsellii* is easily distinguished from *I. perplexum* on the basis of the much thicker hinge structure and teeth geometry (Cosel and Salas, 2001, Figs. 2 and 3), the distinctive incisions on the internal ventral margin, always absent in *Isorropodon*, and the complete absence of pallial sinus.

Waisiuconcha alberdinae Beets, 1942, the type species, is known from the late Miocene of Buton Island, Indonesia. It differs from *W. corsellii* for its larger size, attaining 23 mm in length, the more inflated shell, and the very marked lunular incision. The eastern Atlantic *W. haeckeli* Cosel and Salas (2001) differs for the different outline, roundish in *W. haeckeli*, oval to oblong-oval in *W. corsellii*, the marked lunular incision, the shape of the cardinal 2, longer in *W. corsellii*, and for the shape of cardinal 3a, that does not extend to cover completely cardinal 1 in *W. corsellii*.

This is the first record of the genus *Waisiuconcha* in recent Mediterranean sediments. Therefore, the geographic distribution of the modern genus *Waisiuconcha* can be extended from the Western Pacific to the Eastern Atlantic, including the Mediterranean Sea. In the Cenozoic of the Mediterranean, three species of the genus *Waisiuconcha* are described (Janssen and Krylova, 2012): the early Pliocene *Waisiuconcha ruggierii* (Ceregato and Tabanelli 2001), the late Miocene *Waisiuconcha borelliana* and the early Miocene *Waisiuconcha* sp. aff. *borelliana* Janssen and Krylova (2012). *Waisiuconcha ruggierii* is very similar to the modern, eastern Atlantic *W. haeckeli*, and a possible synonymy between the two species has been suggested (Janssen and Krylova, 2012). *Waisiuconcha borelliana* and *W. aff. borelliana* differ from *W. corsellii* for the marked lunular incision and the more regular commarginal sculpture, consisting of broad ribs and narrow interstices (Janssen and Krylova, 2012). Based on the shell morphology and especially the hinge structure, *W. borelliana* is probably the closest relative of *W. corsellii*. *Waisiuconcha* species in the Cenozoic of the Mediterranean suggests a predominant Tethyan affinity of the pre-Messinian vesicomyids fauna.

4. Discussion

4.1. Benthic foraminifera

The existing studies on benthic foraminifera from marine cold seeps mostly focus on their $\delta^{13}\text{C}$ signature. These environments are characterized by the presence of methane-derived $\delta^{13}\text{C}$ -depleted dissolved inorganic carbon (DIC). These studies are mostly controversial especially concerning the $\delta^{13}\text{C}$ signature in foraminiferal tests and assemblages composition.

Several authors (Wefer et al., 1994; Kennett and Stott, 1991; Sen Gupta et al., 1997; Stott et al., 2002; Thomas et al., 2002; Panieri, 2003; Mackensen et al., 2006) describe episodic negative shifts in benthic

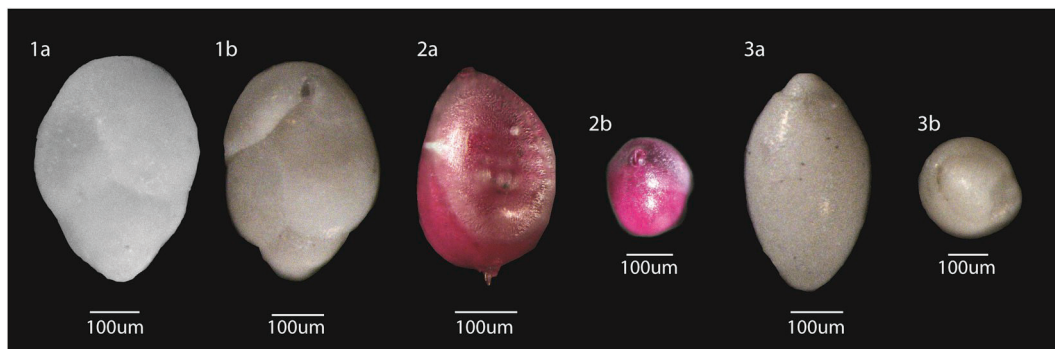


Plate 1. *Chilostomella oolina* and Globobuliminids from the PD. 1a-b. *Globobulimina affinis*; 2a-b. *G. pseudospinescens*, purple colour is due to the rose Bengal stain marking the cytoplasm of living specimens. 3a-b. *Chilostomella oolina*.

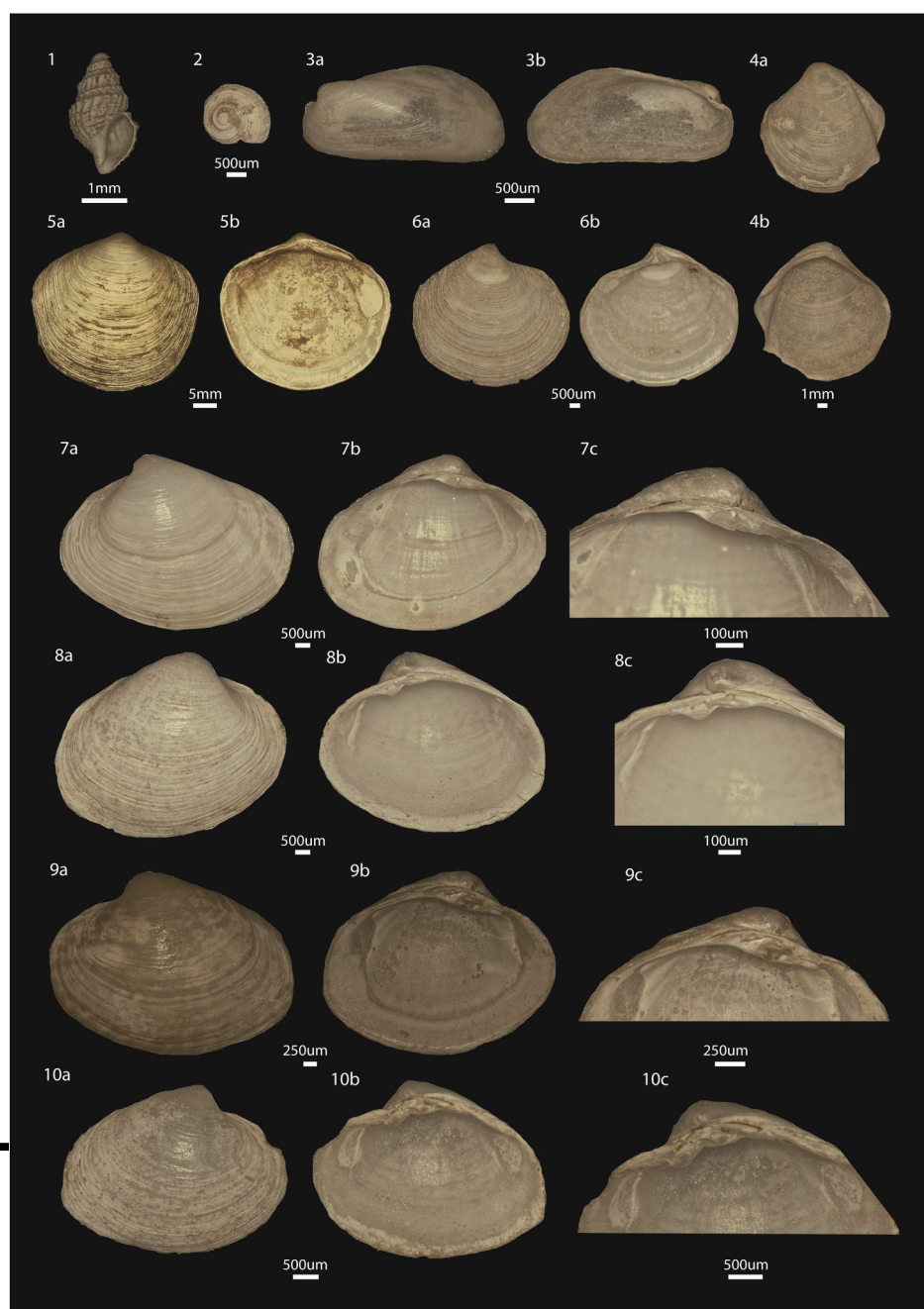


Plate 2. Mollusc fauna from the PD.

1. *Taranis moerchii* (AG16-23-BC1); 2. *Lurifax vitreus* (AG16-22-BC1); 3a-b. *Idas ghisottii*, external and internal view of left valve (AG16-15-BC1); 4a-b. *Thyasira biplicata*, external and internal view of left valve (AG16-23-BC1); 5a-b. *Lucinoma kazani*, external and internal view of right valve (AG16-22-BC1); 6a-b. *Myrtea amorpha*, external and internal view of left valve (AG16-23-BC1); 7-8. *Isorropodon perplexum*, 7a-c. External, internal and hinge view of left valve, 8a-c. External internal and hinge view of right valve (Dive 2 PC1-CC); 9-10. *Waisiuconcha corsellii* (n.sp.), 9a-c External, internal, and hinge view of left valve (AG16-15-BC1), 10a-c. External, internal, and hinge view of right valve (AG16-15-BC1).

foraminiferal test $\delta^{13}\text{C}$. Experimental culturing of *Cibicides wuellerstorfi* (Schwager, 1866) documented the incorporation of methane during biomineralization (Wollenburg et al., 2015).

However, in many cases, living foraminifera sampled from seep locations show slightly negative $\delta^{13}\text{C}$ values (as low as -5.6‰) and extreme negative excursions, as low as -27.8‰ in the Svalbard area, considered mainly due to the methane-derived authigenic carbonate (MDAC) that precipitate on the benthic tests rather than incorporation within the test during biomineralization (Panieri et al., 2017). In foraminiferal tests from the Marmara Sea, Fontanier et al. (2018) do not record geochemical signatures of methane seepage.

A typical and endemic methane seep benthic foraminiferal fauna has not been documented yet. However, all the described assemblages are characterized by the genera *Bolivina*, *Cassidulina*, *Bulimina*, *Uvigerina* and *Lenticulina*, *Fursenkoina*, *Globobulimina*, *Nonionella* and *Chilostomella*, grouping species that are highly tolerant of low-oxygen conditions (e.g.

Bernhard et al., 2001; Levin et al., 2003; Fontanier et al., 2014). Panieri (2003) documented a drastic drop in density and diversity in the Adriatic Sea compared to the baseline site. Severe oxygen depletion, high H_2S toxicity and low-oxygen tolerant benthic foraminifera living under *Beggiatoa* (bacteria) mats were reported from the Gulf of Mexico (Sen Gupta and Aharon, 1994; Sen Gupta et al., 1997; Bernhard et al., 2001).

In this study we focus on globobuliminids and chilostomellids, oxygen-tolerant species that can potentially be considered as seep-related taxa. According to Jorissen (1999), *Chilostomella* and *Globobulimina* occur in deep infaunal habitats and can thrive in completely anoxic conditions. They prefer high amounts of sedimentary organic carbon (De Rijk et al., 1999) and feed on nitrate- or sulphate-reducing bacteria (Jorissen et al., 1998). In case of complete anoxia they can completely replace other less tolerant taxa (Jorissen, 1999).

According to de Rijk et al. (1999, 2000) these 3 species are common dwellers in the deeper-water of the Western Mediterranean. Moving

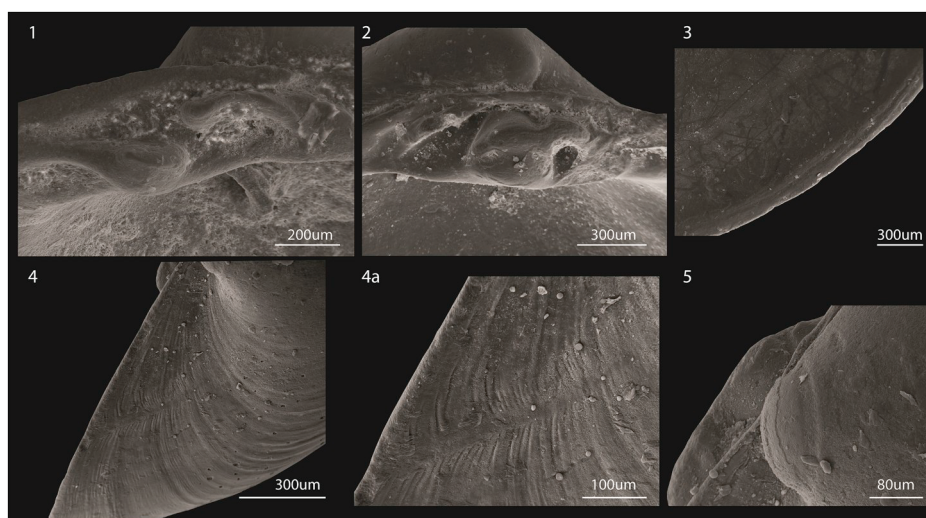


Plate 3. Details of *Waisiuconcha corsellii* (n.sp.). Sample SEMSEEP AG16-15-BC1.

1. Hinge of right valve, 2. Hinge of left valve, 3. Line on margin of left valve, 4. Anterior part of the shell with lunule, 4a. Detail of the lunule, 5. Umbonal part of the shell with prodissococonch.

toward the Eastern Mediterranean they become progressively rarer and appear in shallower water than in the Western Mediterranean as a result of the increasing oligotrophy of this part of the basin (Hyams-Kaphzan et al., 2018). Their occurrence in very shallow water may be related to the shutdown of the Nile discharge to the Levantine basin due to the Aswan Dam, making this area ultra-oligotrophic (Hyams-Kaphzan et al., 2018).

Another observation is that within the Israeli upper continental slope (UCS), two biotopes were identified by Hyams-Kaphzan et al. (2018). One (UCS1) contains the 3 deep infaunal taxa while the other one at the same water depths is dominated by *Gyroidina orbicularis* d'Orbigny (1826). This suggests that even within the same depth range the occurrence/absence of cold seeps dictates the assemblage composition of the foraminifera in this part of the Mediterranean Sea. Sites containing the UCS1 biotope are distributed across the entire Israeli deep offshore (Fig. 1). Other sites (A33, A34, A36) are in the PD, a region rich in cold seeps. Further to the north, they occur at site A16. Sites A2 and A3 are located within a large pockmark area reported by Rubin-Blum et al. (2014a). The recolonization of these 3 species in waters as deep as ~470 m in the PD is documented at ~1700 y in sediment cores (Reiss et al., 1999).

The occurrence of these species in water deeper than 1000 m mostly in the dead assemblage and in low numbers (Tables 2–3) may suggest that they did not live in this region and at this depth in recent times. According to Lubinevsky et al. (2017) the highest abundances of *Globobulimina* spp., and *C. oolina* are documented in correspondence of abundant specimens of the Lucinidae molluscs *Thyasira* (Table 4). The co-occurrence of these three foraminiferal species with a mollusc fauna typical of cold seeps, as observed in other Mediterranean regions, supports the hypothesis that they should also be associated with these environments.

5. Macrofauna

The ghost shrimp *C. lobata*, and the siboglinid *L. anaximandri* tube-worm are bioindicators of chemoautotrophic environments. *Calliax lobata* is consistently found in reducing environments and the abundance of specimens in mud volcanos and seeps indicate chemosynthetic activity in the sediments. *Lamellibrachia anaximandri* is obligated to colonize active seep sites, being highly dependent on the sulfide oxidizing bacteria hosted within the trophosome (Rubin-Blum et al., 2014b).

Chemoautotrophic sulfur or methane-oxidizing bacteria are hosted in vacuolar cells (bacteriocytes) in the gills or gut derivatives of bivalves and of some gastropod taxa that inhabit hydrothermal vents, cold seeps and reducing sediments. Bacterial symbionts have been recorded in all species of Vesicomidae studied so far, therefore the chemosymbiosis in this family is likely obligate (Taylor and Glover, 2010).

Literature data on the microbiological, bio-ecological, and geochemical evidence of chemosymbiosis in macroinvertebrates support the identification of the molluscs *T. moerchii*, *L. vitreus*, *Idas ghisottii* Warén & Carrozza, 1990, *M. amorpha*, *L. kazani*, *T. biplicata*, *I. perplexum*, *W. corsellii* n. sp. and of the ghost shrimp *C. lobata* as members of the chemoautotrophic community of the cold seeps of the Palmahim Disturbance (see Appendix for reference, Table 4, Pls 2–3).

The ROV dives recorded local patches of several m² of seafloor covered by dead shells of *L. kazani*, with a density of up to 180 loose shells per square meter (Beccari et al., 2019). No living mollusc was recovered in the examined samples, down to 43 cm below seafloor (Table 1). The sedimentation rate offshore the PD is rather variable, from 130 cm/ka on the continental slope (Schilman et al., 2001; Hennekam et al., 2014), to much lower sedimentation rates of ~20 to 35 cm/ka in deeper waters (>900 m), beyond the base of the continental slope (Almogi-Labin et al., 2009; Castañeda et al., 2010; Box et al., 2011). On this basis, assuming a constant sedimentation rate, the recovered shells are very recent to some thousands of years old, depending on depth of collection bsf (Table 1). Further analyses are ongoing to clarify this issue.

Gas seeping at the seafloor is known as an intermittent phenomenon at different time scales, with strong spatial variations in the flux of methane and sulfide towards the sediment/water interface (e.g. Tryon et al., 2002; Rodrigues et al., 2012; García Raso et al., 2018). The heterogeneous seepage controls the development, the assemblage composition and the distribution of the chemosymbiotic fauna (e.g. Sibuet and Olu, 1998; Sahling et al., 2002; Levin et al., 2003; Niemann et al., 2009; Lichtschlag et al., 2010; Fischer et al., 2012; Rodrigues et al., 2012). The upward supply of hydrocarbons towards and across the sediment/water interface produces a subsurface geochemical gradient in the pore water, where the anaerobic oxidation of methane (AOM) and other hydrocarbons occurs, accompanied by a release of hydrogen sulfide and bicarbonate into the pore water, at the so-called sulphate/methane transition (SMT: Borowski et al., 1996; Treude et al., 2003). This process supports microbial and chemosymbiotic macrofaunal associations and fosters carbonate authigenesis (e.g. Ritger et al., 1987). In turn, the formation of

authigenic carbonates and chemohalms is the controlling factor for the colonization of the later successional hard-substrate seep-species, like bathymodiolin mussels and siboglinid tubeworms (Bowden et al., 2013).

Evidence of an ecological succession of seep communities, from the onset of fluid flux to senescence, came from several cold seep areas (Pakistan, Fischer et al., 2012; New Zealand, Bowden et al., 2013; Congo, Guillon et al., 2017). There, chemosymbiotic clams and mussels appear able to exploit ephemeral resources through rapid growth and reproduction, and contribute to irrigation of sulphate-rich seawater into sediments, further enhancing AOM (Bowden et al., 2013; Guillon et al., 2017). On the contrary, lamellibrachid tubeworm populations may persist potentially for centuries (Bowden et al., 2013). Within a gradient of decreasing flux intensity, the most intense fluid flux is colonized by mytilid beds, the intermediate methane and sulphide fluxes sustain microbial mats with high macrofaunal densities, and the lower fluxes are exploited by the vesicomyids (Guillon et al., 2017). However, vesicomyids are a large group of several genera, with species-specific vertical and horizontal mobility, and thus bioengineering potential, which characterize a heterogeneous group of habitats. Moreover, they show a complex biogeographic distribution, still incompletely understood, therefore, no generalization can be confidently drawn from different cold seep species associations in far biogeographic provinces.

The biodiversity of the chemosymbiotic macrofaunal assemblage of the Eastern Atlantic cold seep/mud volcanos is very similar at the genus level with that of other regions in the Mediterranean, and numerous endemic species (Oliver et al., 2011) co-occur throughout the central and eastern Mediterranean and into the Marmara Sea (Ritt et al., 2010; Taviani et al., 2013, Table 4). The distinctiveness of the Mediterranean seep fauna is considered to be due to the Messinian Salinity Crisis about 6 Ma (CIESM, 2008), and Mediterranean seeps successive recolonization from the Atlantic Ocean in the Pliocene. However, links between the Mediterranean seep fauna and that in the Gulf of Cadiz (Eastern Atlantic, just outside the Strait of Gibraltar) are not apparent according to a recent biogeographic analysis (Kiel, 2016), while *M. amorphia*, *L. kazani*, and *I. perplexum* are shared with the cold seep communities of the Marmara Sea (Ritt et al., 2010). This suggests that the processes leading to the typical Mediterranean seep fauna are not yet completely understood, and further research is needed, based on field surveys and morpho-genetic analyses of the relationship between separate populations of chemosymbiotic molluscs and their bacterial symbionts. In contrast to the bivalves and the siboglinid *L. anaximandri*, the ghost shrimp *C. lobata* is found both in the Mediterranean and the Gulf of Cadiz (García Raso et al., 2018). *C. lobata* inhabits a wide bathymetric range, found in reducing sedimentary environments as shallow as 2–21 m deep (de Gaillande and Lagardère, 1966; Thessalou-Legaki and Zenetos, 1985; Thessalou-Legaki, 1986; Števcic, 1985, 1990), as well as mud volcanos 455–750 m deep (Rovere et al., 2014; García Raso et al., 2018) enabling a more widespread distribution of the taxa.

6. Conclusions

Our investigation has revealed the occurrence of widespread chemosymbiotic macrofauna including dead bivalves, gastropod, living siboglinid *Lamellibrachia* tubeworms and ghost shrimps *Calliax lobata* in the PD across the Israeli offshore.

A new bivalve species, *Waisiiconcha corsellii*, belonging to the Family Vesicomyidae Dall & Simpson, 1901 has been identified and described. It represents the first record of the genus *Waisiiconcha* in recent Mediterranean sediments.

Although the attribution of the foraminiferal genera *Globobulimina* and *Chilostomella* to seep environments in the Eastern Mediterranean is not straightforward, their co-occurrence with chemosymbiotic molluscs suggests that they can be used as seep-related indicators.

The presence of dead bivalves accompanied with clusters of the siboglinid *L. anaximandri* at seeps in the Palmahim Disturbance, along with the occurrence of *C. lobata* in the bioturbated sediments, indicate a

late successional stage of hydrocarbon seepage; methane at the site is probably depleted and insufficient in sustaining the bivalve populations which are dependent on it as their prime energy source, though sufficient sulfide compounds still sustain the long-lived *L. anaximandri*.

The absence of living chemosymbiotic bivalves and the rare occurrence of seep-related foraminifera in surface sediments and in deep waters in the PD, where seepage has been confirmed, indicate intermittent activity and a pause or decline of the investigated seeps. The occurrence of seep-related micro- and macrofauna in different locations across the Israeli offshore suggests that active and recent cold seeps may be far more abundant in this region than currently known.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

D. Basso: Conceptualization, Investigation, Formal analysis, Writing - original draft. **V. Beccari:** Investigation, Formal analysis, Writing - original draft. **A. Almogi-Labin:** Investigation, Formal analysis, Writing - original draft. **O. Hyams-Kaphzan:** Formal analysis, Writing - original draft. **A. Weissman:** Investigation, Writing - original draft. **Y. Makovsky:** Investigation, Formal analysis, Writing - original draft. **A. Rüggeberg:** Investigation, Resources. **S. Spezzaferri:** Writing - original draft, Resources, Funding acquisition.

Acknowledgements

We warmly thank the crew of the R/V AEGEO and the SEMSEEP onboard team, who helped in the sampling operation. We acknowledge funding for the EUROFLEETS2 SEMSEEP cruise from European Union FP7 Programme under grant agreement n° 312762; the University of Fribourg granted project Fonds de recherche n° 609; the Helmsley Charitable Trust and Charney School of Marine Sciences, University of Haifa, Israel Oceanographic and Limnological Research for additional financial support of the cruise; the Israeli Ministry of Infrastructure, Energy and Water for IOLR support; Yoni Esakow and Coral Group Ltd. for donating their in-port support; Paradigm for geophysical software sponsorship; the State of Israel Ministry of Foreign Affairs, through their Embassy in Cyprus and the Embassy of Switzerland in Cyprus, for their dedicated backing. Thanks to the Swiss National Science Foundation grant Ref. 200021_175587. This article is a contribution to Project MIUR – Dipartimenti di Eccellenza 2018–2022.

APPENDIX I

Taxonomy of the Palmahim chemosymbiotic fauna

Phylum FORAMINIFERA

Order Rotalida Delage & Hérouard, 1896

Family BULIMINIDAE Jones, 1875

Genus *Globobulimina* Cushman, 1927

Globobulimina affinis (d'Orbigny, 1839)

Pl. 1, Fig. 1

Test ovate in outline and circular in section, slightly elongated, composed by 4 whorls, separated by slightly marked sutures. Three slightly convex chambers in each whorl. The last chamber is slightly flat and depressed. The aperture is lop shaped, with double folded tongue joined to one margin of the opening, the free upper part partially fills the opening and forms a fanlike projection lip. The wall is calcareous and finely perforate.

Globobulimina pseudospinescens (Emiliani 1949)

Pl. 1, Fig. 2

Test ovate in outline and circular in section, composed by three whorls and with 3 inflated and strongly overlapping chambers in the last whorl. The last chamber is larger and the aperture is loop-shaped with double folded tongue joined to one margin of the opening, the free upper part partially fills the opening and forms a fanlike projection lip. A few small spines are present on the aboral side. A toothplate is present. The wall is calcareous and finely perforate.

Family CHILOSTOMELLIDAE Brady, 1881

Genus *Chilostomella* Reuss, 1849

Chilostomella oolina Schwager, 1878

Pl. 1, Fig. 3

Test planispiral and involute, ovate in outline, circular in section, and elongate composed by two strongly embracing chambers for each whorl. The aperture is a narrow interiomarginal equatorial slit that may have elevated margins. The wall is calcareous and finely perforate with smooth surface.

Phylum MOLLUSCA

Class Gastropoda Cuvier, 1795

Family RAPHIOMIDAE Bellardi, 1875

Genus *Taranis* Jeffreys, 1870

Taranis moerchii (Malm, 1861)

Pl. 2, Fig. 1

Synonyms: *Trophon moerchii* Malm, 1861; *Taranis alexandrina* Sturany (1896).

The species *T. alexandrina* Sturany (1896) is a younger heterotypic synonym of *T. moerchii*, the latter having priority. The holotype of *T. alexandrina* was collected by Sturany in the "Pola" expedition station 82, N of Alexandria (Egypt), at 2420 m of water depth (Albano et al., 2018).

Taranis moerchii is a deep infaunal burrower, with a wide depth-distribution, amphi-Atlantic and Mediterranean (Bouchet and Warén, 1980). It is uncommonly recorded in the Mediterranean outside the cold seep areas. For this reason, it is considered a putative chemosymbiotic species (Taviani et al., 2013; García Raso et al., 2018).

Family ORBISTELLIDAE Iredale, 1917.

Genus *Lurifax* Warén and Bouchet, 2001.

Lurifax vitreus Warén and Bouchet (2001)

Pl. 2, Fig. 2

Since its first description, the species was recorded as a component of the hydrothermal vents and cold seeps (Warén and Bouchet, 2001). It is an epifaunal species, poorly known in the Mediterranean (Smriglio and Mariottini, 2002; Warén et al., 2006). For the first time among heterobranch gastropods, Hawe et al. (2014) have identified symbiotic chemoautotrophic bacteria in bacteriocytes of the mantle cavity of *L. vitreus*.

Class Bivalvia Linnaeus, 1758

Family MYTILIDAE Rafinesque, 1815

Genus *Idas* Jeffreys, 1876

Idas ghisottii Warén & Carrozza, 1990

Pl. 2, Fig. 3

A valid species placed in genus *Idas*, recently described from sunken woods. Shell-based species identification within the genus *Idas* is ambiguous, because morphological descriptions based on few specimens cannot consider allometric growth, environmental plasticity and crypticism, and the group needs a systematic revision based on integrated taxonomy (Lorion et al., 2012; Ritt et al., 2012). *Idas* spp. from the eastern Mediterranean harbour both methanotrophs and sulfur-oxidizing bacteria (Duperron et al., 2008; Lorion et al., 2012). Although not all *Idas* species are chemosymbiotic (Taylor and Glover, 2010), the genus is commonly recorded in cold seep communities and reducing sediments worldwide, including the deep eastern Mediterranean Sea and the Marmara Sea (Sturany, 1896 as *Myrina modiolaeformis*; Olu-Le Roy et al., 2004; Giusti et al., 2012; Ritt et al., 2012; Taviani,

2014). Eastern Mediterranean live specimens were found attached to authigenic carbonate crusts, tubes of Siboglinid tubeworm and wood chips (Lorion et al., 2012).

Family THYASIRIDAE Dall, 1900

Genus *Thyasira* Lamarck, 1818

Thyasira biplicata (Philippi, 1836)

Pl. 2, Fig. 4

Synonym: *Ptychina biplicata* Philippi, 1836.

The dominant bivalves at cold seeps are large chemosymbiotic species belonging to the families Vesicomidae and Mytilidae with Thyasiroidea, Solemyoidea and Lucinoidea sometimes also abundant. Thyasirids have a much wider distribution than other chemosymbiotic bivalve families; they are found from coastal to hadal depths, in different types of sediments, and from both the poles to the equator. They may show a wide variation in their anatomical characters and in the extent of their nutritional reliance upon symbionts (Dufour and Felbeck, 2006). The generic definitions within the Thyasiroidea have been recognized to be problematic (Payne and Allen, 1991; Oliver and Sellanes, 2005). Thyasiridae are infaunal chemo-symbiotic bivalves although only the species with large, dorso-ventrally extended shells, like *T. biplicata* harbour bacterial symbionts (Payne and Allen, 1991; Rodrigues et al., 2008).

Family LUCINIDAE Fleming, 1828

Genus *Myrtea* Turton, 1822

Myrtea amorphia (Sturany, 1896)

Pl. 2, Fig. 5

Synonyms: *Lucina amorphia* Sturany (1896): 16, pl. I, fig. 22; *Myrtea* sp. Corselli and Basso (1996); Brissac et al. (2011); *Myrtea amorphia* - Olu-Le Roy et al. (2004); Taviani et al. (2013)

The type locality of *M. amorphia* Sturany is the Pola Expedition Station 82, north of Alexandria, Egypt, (32°30'N, 29°8'E), at 2420 m of water depth. Recently, the species has been recorded from cold seep communities in the deep eastern and central Mediterranean Sea (Olu-Le Roy et al., 2004; Taviani et al., 2013).

Although the holotype of *M. amorphia* is a single abnormal right valve (Sturany, 1896; Albano et al., 2018), the species is considered valid (MolluscaBase, 2018). Excluding the character of the teratological sulcus in the holotype of *M. amorphia*, the species would differ from *M. spinifera* (Montagu, 1803) for the higher number of finer concentric ridges (Sturany, 1896; Brissac et al., 2011), the deeper lunule, and the inconspicuous posterior lateral tooth in the left valve (Corselli and Basso, 1996, as *Myrtea* sp.). However, recent molecular analysis revealed that specimens from the Eastern Mediterranean cold seeps, morphologically corresponding to *M. amorphia* (sensu Olu-Le Roy et al., 2004; Taviani et al., 2013), are genetically closely related to *Myrtea spinifera* (Montagu, 1803) (Brissac et al., 2011). Further analyses based on molecular genetics are needed to clarify the species boundaries within the genus *Myrtea* (Taylor et al., 2011; Brissac et al., 2011). The chemosymbiosis between the infaunal bivalves Lucinidae and sulphide- and methane-oxidizing bacteria has been identified in all species, and is likely obligate (Taylor and Glover, 2010).

Genus *Lucinoma* Dall, 1901

Lucinoma kazani Salas and Woodside (2002).

Pl. 2, Fig. 6

The species was originally discovered in gas-saturated sediments from cold seeps on the eastern Mediterranean mud volcanoes, at 1700 m of water depth. As known for the other lucinids, *L. kazani* holds chemoautotrophic bacterial symbionts in the ctenidia, and live in reducing sediments (Salas and Woodside, 2002). It is considered a thiotroph-associated lucinid (Duperron et al., 2007).

L. kazani has the largest shells among the molluscs collected in the sediments of the Palmahim disturbance, reaching a length of 37 mm in the examined material.

Family VESICOMYIDAE Dall & Simpson, 1901

Genus *Isorropodon* Sturany, 1896.

Isorropodon perplexum Sturany (1896).

Pl. 2, Figs. 7-8

Synonym: *Vesicomya* sp. Corselli and Basso (1996).

The type material was collected by Sturany (1896:17, pl. I, Figs. 24–27) at the “Pola” expedition station no. 82, north of Alexandria, Egypt (same as for *M. amorphia*). The species has a unique phylotype of bacterial chemoautotrophic (thiotrophic) symbionts (Olu-Le Roy et al., 2004; Rodrigues et al., 2012), although Vesicomidae may acquire their symbionts from the sediment (Taylor et al., 2011). *I. perplexum* harbours sulfur-oxidizing bacteria (Salas and Woodside, 2002). It is an infaunal species of the muddy sediments from cold seeps of the eastern and central Mediterranean Sea, from 1950 to 2500 m of water depth (Cosel and Salas, 2001; Werne et al., 2004; Taviani, 2014).

Phylum ANNELIDA

Class Polychaeta Grube, 1850

Order Sabellida

Family Siboglinidae Caullery, 1914

Genus *Lamellibrachia* Webb, 1969

Lamellibrachia anaximandri Southward et al. (2011).

The species was first described from the Anaximander Mountains off the southwest shore off Turkey (Southward et al., 2011) and found to be closely related to *Lamellibrachia luyesi* from the Gulf of Mexico. Tube worms belonging to the genus *Lamellibrachia* were located in various mud volcanos and cold seeps in the Mediterranean sea typically 1100–2800 m deep (Olu-Le Roy et al., 2004; Duperron et al., 2009; Hilário et al., 2011; Carey et al., 2012; Thiel et al., 2012). Siblogid tubeworms lack a gut and digestive system and rely on chemoautotrophic bacteria, specifically sulfide oxidizing bacteria which live as endosymbionts the worms’ tissue trophosome and are therefore they may live only in the vicinity of reducing environments containing sulfur compounds (Stewart and Cavanaugh, 2006). The endosymbiotic bacterial community within the trophosome of *Lamellibrachia anaximandri* has been described from specimens collected at the cold seeps of the Palmahim Disturbance and compared with the endosymbiotic bacterial community of specimen collected from the Eratosthenes seamount and the Palinuro volcanic complex in Tyrrhenian Sea, which exhibited several phylotypes depending on their geographic locality (Rubin-Blum et al., 2014b).

Phylum ARTHROPODA

Subphylum Crustacea Brünnich, 1772

Class Malacostraca Latreille, 1802

Order Decapoda Latreille, 1802

Family Eucalliidae Manning & Felder, 1991

Genus *Calliax* de Saint Laurent, 1973

Calliax lobata (de Gaillande and Lagardère, 1966)

The holotype was described from Port Miou, Toulon, France at a depth of 2–8 m (de Gaillande and Lagardère, 1966), and since then found in reducing sedimentary environments covering a wide bathymetric range, from both shallow water 2–21 m deep in the Mediterranean (de Gaillande and Lagardère, 1966; Thessalou-Legaki and Zenetos, 1985; Thessalou-Legaki, 1986; Števcic, 1985, 1990), as well as mud volcanos 653–750 m deep in the southern Tyrrhenian Sea (Rovere et al., 2014) and the Gulf of Cadiz in the Atlantic ocean 455–501 m deep (García Raso et al., 2018). In recent papers (Rovere et al., 2014; García Raso et al., 2018), as well as the current study, the axiidean *Calliax lobata* was the only decapod crustacean to be found burrowing in the reducing sediments it inhabits, highlighting its unique adaptations to survive in an environment inhospitable to other decapod species.

References

- Albano, P.G., Schnedl, S.M., Eschner, A., 2018. An illustrated catalogue of Rudolf Sturany’s type specimens in the Naturhistorisches Museum Wien, Austria (NHMW): deep-sea Eastern Mediterranean molluscs. *Zoosystematics Evol.* 94, 29.
- Almogi-Labin, A., Bar-Matthews, M., Shriki, D., Kolosovsky, E., Paterne, M., Schilman, B., Ayalon, A., Aizenshtat, Z., Matthews, A., 2009. Climatic variability during the last ~90 ka of the southern and northern Levantine Basin as evident from marine records and speleothems. *Quat. Sci. Rev.* 28, 2882–2896.
- Basso, D., Corselli, C., 2007. Molluscan paleoecology in the reconstruction of coastal changes. In: Yanko-Hombach, V., Gilbert, A.S., Panin, N., Dolukhanov, P.M. (Eds.), *The Black Sea Flood Question: Changes in Coastline, Climate and Human Settlement*. Springer, pp. 23–46.
- Basso, D., Thomson, J., Corselli, C., 2004. Indications of low macrobenthic activity in the deep sediments of the eastern Mediterranean sea. In: Sardà, F., D’Onghia, G., Politou, C.-Y., Tselepidis, A. (Eds.), *Mediterranean Deep-Sea Biology*, vol 68. Scientia Marina, pp. 53–62 suppl. 3.
- Bayon, G., Loncke, L., Dupré, S., Caprais, J.-C., Ducassou, E., Duperron, S., Etoubleau, J., Foucher, J.-P., Fouquet, Y., Gontharet, S., Henderson, G.M., Huguen, C., Klauke, I., Mascle, J., Migeon, S., Olu-Le Roy, K., Ondreas, H., Pierre, C., Sibuet, M., Stadnitskaia, A., Woodside, J., 2009. Multi-disciplinary investigation of fluid seepage on an unstable margin: the case of the Central Nile deep sea fan. *Mar. Geol.* 261, 92–104.
- Beccari, V., Basso, D., Spezzaferri, S., Rüggeberg, A., Neuman, A., Makovsky, Y., 2019. Preliminary Video-Spatial Analysis of Cold Seep Bivalve Beds at the Base of the Continental Slope of Israel (Palmahim Disturbance). *Deep Sea Research Part II: Tropical Studies in Oceanography*, p. 104664.
- Bernhard, J.M., Buck, K.R., Barry, J.P., 2001. Monterey Bay cold-seep biota: assemblages, abundance, and ultrastructure of living foraminifera. *Deep Sea Res. Oceanogr. Res. Pap.* 48, 2233–2249.
- Blinova, V.N., Comas, M.C., Ivanov, M.K., Poludetkina, E.N., Matveeva, T.V., 2011. Active mud volcanism in the West Alboran Basin: geochemical evidence of hydrocarbon seepage. *Mar. Pet. Geol.* 28, 1483–1504.
- Borowski, W.S., Paull, C.K., Ussler III, W., 1996. Marine pore-water sulfate profiles indicate in situ methane flux from underlying gas hydrate. *Geology* 24, 655–658.
- Bouchet, P., Warén, A., 1980. Revision of the Northeast Atlantic bathyal and abyssal turridae (Mollusca, gastropoda). *J. Molluscan Stud.* 46 (Suppl. 8), 1–119.
- Bowden, D.A., Rowden, A.A., Thurber, A.R., Baco, A.R., Levin, L.A., Craig, R., Smith, C. R., 2013. Cold seep epifaunal communities on the Hikurangi Margin, New Zealand: composition, succession, and vulnerability to human activities. *PLoS One* 8, e76869.
- Box, M.R., Krom, M.D., Cliff, R.A., Bar-Matthews, M., Almogi-Labin, A., Ayalon, A., Paterne, M., 2011. Response of the Nile and its catchment to millennial-scale climatic change since the LGM from Sr isotopes and major elements of East Mediterranean sediments. *Quat. Sci. Rev.* 30, 431–442.
- Brissac, T., Rodrigues, C.F., Gros, O., Duperron, S., 2011. Characterization of bacterial symbioses in *Myrtea* sp. (Bivalvia: Lucinidae) and *Thyasira* sp. (Bivalvia: Thyasiridae) from a cold seep in the eastern Mediterranean. *Mar. Ecol. Prog. Ser.* 32, 198–210.
- Carey, S.N., Croff, B.L., Rosi, M., Marani, M., Nomikou, P., Walker, S.L., Faure, K., Kelly, J., 2012. Submarine volcanoes of the Aeolian arc, Tyrrhenian Sea. *Oceanography* 25, 32–33.
- Castañeda, I.S., Schefuß, E., Pätzold, J., Sinninghe Damsté, J.S., Weldeab, S., Schouten, S., 2010. Millennial-scale sea surface temperature changes in the eastern Mediterranean (Nile River Delta region) over the last 27,000 years. *Paleoceanography* 25 (1).
- CIESM, 2008. The Messinian Salinity Crisis from Mega-Deposits to Microbiology - A Consensus Report. N, vol 33. CIESM Workshop Monographs, pp. 7–10.
- Coleman, D.F., Austin Jr., J.A., Ben-Avraham, Z., Makovsky, Y., Tchernov, D., 2012. Seafloor pockmarks, deepwater corals, and cold seeps along the continental margin of Israel. *Oceanography* 25 (Suppl. 1), 40–41.
- Corselli, C., Basso, D., 1996. First evidence of benthic communities based on chemosynthesis on the Napoli mud volcano (Eastern Mediterranean). *Mar. Geol.* 132, 227–239.
- Cosel, R. von, Salas, C., 2001. Vesicomidae (Mollusca: Bivalvia) of the genera *Vesicomya*, *Waisiiconcha*, *Isorropodon* and *Callogonia* in the eastern Atlantic and the Mediterranean. *Sarsia* 86, 333–366.
- de Gaillande, D., Lagardère, J.P., 1966. Description de *Callianassa (Callichirus) lobata* nov. sp. (Crustacea Decapoda Callianassidae). *Recueil des travaux de la Station marine d’Endoume* 40, 259–265.
- De Rijk, S., Troelstra, S.R., Rohling, E.J., 1999. Benthic foraminiferal distribution in the Mediterranean sea. *J. Foraminif. Res.* 29, 93–103.
- De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on bathymetric zonation of Mediterranean benthic foraminifera. *Mar. Micropaleontol.* 40, 151–166.
- Dufour, S.C., Felbeck, H., 2006. Symbiont abundance in thyasirids (Bivalvia) is related to particulate food and sulphide availability. *Mar. Ecol. Prog. Ser.* 320, 185–194.
- Duperron, S., Fiala-Medioni, A., Caprais, J.C., Olu, K., Sibuet, M., 2007. Evidence for chemoautotrophic symbiosis in a Mediterranean cold seep clam (Bivalvia: Lucinidae): comparative sequence analysis of bacterial 16S rRNA, APS reductase and RubisCO genes. *FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol.* 59, 64–70.
- Duperron, S., Halary, S., Lorion, J., Sibuet, M., Gaill, F., 2008. Unexpected co-occurrence of six bacterial symbionts in the gills of the cold seep mussel *Idas* sp. (Bivalvia: Mytilidae). *Environ. Microbiol.* 10, 433–445.
- Duperron, S., De Beer, D., Zbinden, M., Boetius, A., Schipani, V., Kahil, N., Gaill, F., 2009. Molecular characterization of bacteria associated with the trophosome and the tube of *Lamellibrachia* sp., a siboglinid annelid from cold seeps in the eastern Mediterranean. *FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol.* 69, 395–409.

- Ezra, O., 2017. Topology and Formation Settings of Deep-Water Carbonates at the Boundaries of the Palmahim Disturbance, Offshore Israel. M.Sc. thesis. The Moses Strauss Department of Marine Geosciences, University of Haifa, Haifa, Israel.
- Fischer, D., Sahling, H., Nöthen, K., Bohrmann, G., Zabel, M., Kasten, S., 2012. Interaction between hydrocarbon seepage, chemosynthetic communities, and bottom water redox at cold seeps of the Makran accretionary prism: insights from habitat-specific pore water sampling and modeling. *Biogeosciences* 9, 2013–2031.
- Fontanier, C., Koho, K.A., Goni-Urriza, M.S., Deflandre, B., Galaup, S., Ivanovsky, A., Gayet, N., Dennielou, B., Gremare, A., Bichon, S., Gassie, C., Anschütz, P., Duran, R., Reichart, G.J., 2014. Benthic foraminifera from the deep-water Niger delta (Gulf of Guinea): assessing present-day and past activity of hydrate pockmarks. *Deep Sea Res. Oceanogr. Res. Pap.* 91, 120–133.
- Fontanier, C., Dissard, D., Ruffine, L., Mamo, B., Ponzevera, E., Pelleter, E., Baudin, F., Roubi, A., Boissier, A., Chéron, S., Gayet, N., Bermell-Fleury, S., Guyader, V., Lesongeur, F., Savignac, F., 2018. Living (stained) deep-sea foraminifera from the Sea of Marmara: a preliminary study. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 153, 61–78.
- Foucher, J.-P., Westbrook, G.K., Boetius, A., Ceramicola, S., Dupré, S., Mascle, J., Mienert, J., Pfannkuche, O., Pierre, C., Praeg, D., 2009. Structures and drivers of cold seep ecosystems. *Oceanography* 22, 58–74.
- Gadol, O., Lifshitz, I., Bialik, O., Zeidner, G., Makovsky, Y., 2018. Multi-scale geophysical observation of seafloor pockmarks along the base of the southeastern margin of the Levant. In: 14th International Conference on Gas in Marine Sediments GIMS, vol 14. Israel, Haifa.
- García Raso, J.E., García –Munoz, J.E., Mateo-Ramirez, A., Lopez Gonzalez, N., Fernandez-Salas, L.M., Rueda, J.L., 2018. Decapod crustaceans Eucalliidae in chemosynthetic bathyal bottoms of the Gulf of Cadiz (Atlantic Ocean), environmental characteristics and associated communities. *J. Mar. Biol. Assoc. U. K.* <https://doi.org/10.1017/S0025315418000280>.
- Garfunkel, Z., Arad, A., Almagor, G., 1979. The Palmahim Disturbance and its regional settings. *Geol. Surv. Isr. Bull.* 72, 56.
- Giusti, F., Mietto, P., Sbrana, C., 2012. Il genere *Idas* (Mytilidae, Bathymodiolinae) in Mediterraneo, con la descrizione di quattro nuove specie. *Bollettino Malacologico* 48, 122–135.
- Guillon, E., Menot, L., Decker, C., Krylova, E., Olu, K., 2017. The vesicomyid bivalve habitat at cold seeps supports heterogeneous and dynamic macrofaunal assemblages. *Deep Sea Res. Oceanogr. Res. Pap.* 120, 1–13.
- Gvrtzman, Z., Reshef, M., Buch-Leviatan, O., Groves-Gidney, G., Karcz, Z., Makovsky, Y., Ben-Avraham, Z., 2015. Bathymetry of the Levant basin: interaction of salt-tectonics and surficial mass movements. *Mar. Geol.* 360, 25–39.
- Hall, J.K., Lippman, S., Gardosh, M., Tibor, G., Sade, A.R., Sade, H., 2015. A New Bathymetric Map for the Israeli EEEZ : Preliminary Results, vol 11. Ministry of National Infrastructures, Energy and Water Resources and the Survey of Israel Report, Jerusalem.
- Hawe, A., Gensler, H., Haszprunar, G., 2014. Bacteriocytes in the mantle cavity of *Lurifax vitreus* Warén & Bouchet, 2001 (Orbistellidae): the first case among heterobranch gastropoda. *J. Molluscan Stud.* 80, 337–340.
- Hayward, B.W., Le Coze, F., Gross, O., 2018. World foraminifera database. Foraminifera. <http://www.marinespecies.org/foraminifera/> on Jan 6, 2019.
- Hennekam, R., Jilbert, T., Schnetger, B., de Lange, G.J., 2014. Solar forcing of Nile discharge and sapropel S1 formation in the early to middle Holocene eastern Mediterranean. *Paleoceanography* 343–356.
- Hilário, A., Capa, M., Dahlgren, T.G., Kenneth, M., Halanich, K.H., Crispin, T.S., Little, C. T.S., Thornhill, D.J., Verna, C., Glover, A.G., 2011. New perspectives on the ecology and evolution of siboglinid tubeworms. *PLoS One* 6, 1–14.
- Hyams-Kaphzan, O., Lubinevsky, H., Crouvi, O., Harlavan, Y., Herut, B., Kanari, M., Moshe, T., Almogi-Labin, A., 2018. Live and dead deep-sea benthic foraminiferal macrofauna of the Levantine basin (SE Mediterranean) and their ecological characteristics. *Deep Sea Res. Oceanogr. Res. Pap.* 136, 72–83.
- Janssen, R., Krylova, E.M., 2012. Bivalves of the family Vesicomidae from the neogene Mediterranean basin (Bivalvia: Vesicomidae). *Archiv für Molluskenkunde: International Journal of Malacology* 141, 87–113.
- Jorissen, F.J., 1999. Benthic foraminiferal successions across late quaternary Mediterranean sapropels. *Mar. Geol.* 153, 91–101.
- Jorissen, F.J., de Stigter, H.C., Widmark, J.G., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Mar. Micropaleontol.* 26, 3–15.
- Jorissen, F.J., Witting, I., Peyrouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cape Blanc, NW-Africa: community structure and microhabitats. *Deep Sea Res. Oceanogr. Res. Pap.* 45, 2157–2188.
- Joye, S.B., Boetius, A., Orcutt, B.N., Montoya, J.P., Schulz, H.N., Erickson, M.J., Lugo, S. K., 2004. The anaerobic oxidation of methane and sulfate reduction in sediments from Gulf of Mexico cold seeps. *Chem. Geol.* 205, 219–238.
- Kennett, J.P., Stott, L.D., 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* 353, 225.
- Kidwell, S., 2001. Preservation of species abundance in marine death assemblages. *Science* 294, 1091–1094.
- Kiel, S., 2016. A biogeographic network reveals evolutionary links between deep-sea hydrothermal vent and methane seep faunas. *Proc. R. Soc. Biol. Sci.* 283, 20162337.
- Levin, L.A., 2005. Ecology of Cold Seep Sediments: Interactions of Fauna with Flow, Chemistry and Microbes. *Oceanography and Marine Biology*. CRC Press, pp. 11–56, 2005.
- Levin, L.A., Ziebis, W., Mendoza, G.F., Growney, V.A., Tryon, M.D., Brown, K.M., Mahn, C., Gieskes, J.M., Rathburn, A.E., 2003. Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. *Mar. Ecol. Prog. Ser.* 265, 123–139.
- Lichtschlag, A., Felden, J., Brüchert, V., Boetius, A., de Beer, D., 2010. Geochemical processes and chemosynthetic primary production in different thiotrophic mats of the Håkon Mosby Mud Volcano (Barents Sea). *Limnol. Oceanogr.* 55, 931–949.
- Lorion, J., Halary, S., do Nascimento, J., Samadi, S., Couloux, A., Duperron, S., 2012. Evolutionary history of *Idas* sp. (Bivalvia: Mytilidae), a cold seep mussel bearing multiple symbionts. *Cah. Biol. Mar.* 53, 77–87.
- Lubinevsky, H., Hyams-Kaphzan, O., Almogi-Labin, A., Silverman, J., Harlavan, Y., Crouvi, O., Herut, B., Kanari, M., Tom, M., 2017. Deep-sea soft bottom infaunal communities of the Levantine Basin (SE Mediterranean) and their shaping factors. *Mar. Biol.* 164, 36.
- Mackensen, A., Wollenburg, J., Licari, L., 2006. Low $\delta^{13}\text{C}$ in tests of live epibenthic and endobenthic foraminifera at a site of active methane seepage. *Paleoceanography* 21 (2).
- Makovsky, Y., Rüggeberg, A., Bialik, O., Foubert, A., Almogi-Labin, A., Alter, Y., Bampas, V., Basso, D., Feenstra, E., Fentimen, R., Friedheim, O., Hall, E., Hazan, O., Herut, B., Kallergis, E., Karageorgis, A., Kolountzakis, A., Manousakis, L., Nikolaidis, M., Pantazoglou, F., Rahav, E., Renieris, P., Schleinkofer, N., Sisma Ventura, G., Stasios, V., Weissman, A., the EuroFLEETS2 SEMSEEP Participants, 2017. South East Mediterranean SEEP Carbonate. R/V Aegaeo Cruise EuroFLEETS2 SEMSEEP, pp. 1–38.
- Mayer, L., Croff Bell, K.L., Ballard, R., Nicolaides, S., Konnaris, K., Hall, J., Tibor, G., Austin jr., J.A., Shank, T., 2011. Discovery of sinkholes and seeps on Eratosthenes seamount. *Oceanography* 24 (Suppl. I), 28–29.
- MolluscaBase, 2018. Accessed at <http://www.molluscabase.org> on 18 August 2018.
- Niemann, H., Fischer, D., Graffe, D., Knittel, K., Montiel, A., Heilmayer, O., Nöthen, K., Pape, T., Kasten, S., Bohrmann, G., Boetius, A., Gutt, J., 2009. Biogeochemistry of a low-activity cold seep in the Larsen B area, western Weddell Sea, Antarctica. *Biogeosciences* 6, 2383–2395.
- Oliver, G., Rodrigues, C.F., Cunha, M.R., 2011. Chemosymbiotic bivalves from the mud volcanoes of the Gulf of Cadiz, NE Atlantic, with descriptions of new species of solemyidae, Lucinidae and Vesicomidae. *ZooKeys* 113, 1–38.
- Oliver, P.G., Sellanes, J., 2005. New species of Thyasiridae from a methane seepage area off Concepción, Chile. *Zootaxa* (1092), 1–20.
- Olu-Le Roy, K., Sibuet, M., Fiala-Médioni, A., Gofas, S., Salas, C., Mariotti, A., Foucher, J.-P., Woodside, J., 2004. Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial distribution on mud volcanoes. *Deep Sea Res. Oceanogr. Res. Pap.* 51, 1915–1936.
- Panieri, G., 2003. Benthic foraminifera response to methane release in an Adriatic Sea pockmark. *Rev. Ital. Paleontol. Stratigr.* 109, 549–562.
- Panieri, G., 2006. Foraminiferal response to an active methane seep environment: a case study from the Adriatic Sea. *Mar. Micropaleontol.* 61, 116–130.
- Panieri, G., Lepand, A., Whitehouse, M.J., Wirth, R., Raanes, M.P., James, R.H., Graves, C.A., Crémère, A., Schneider, A., 2017. Diagenetic Mg-calcite overgrowths on foraminiferal tests in the vicinity of methane seeps. *Earth Planet. Sci. Lett.* 458, 203–212.
- Payne, C.M., Allen, J.A., 1991. The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic ocean. *Phil. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 334, 481–566.
- Reiss, Z., Halicz, E., Luz, B., 1999. Late-holocene foraminifera from the SE Levantine basin. *Isr. J. Earth Sci.* 48, 1–27.
- Ritger, S., Carson, B., Suess, E., 1987. Methane-derived authigenic carbonates formed by subduction-induced pore-water expulsion along the Oregon/Washington Margin. *Geol. Soc. Am. Bull.* 98, 147–156.
- Ritt, B., Sarrazin, J., Caprais, J.-C., Noël, P., Gauthier, O., Pierre, C., Henry, P., Desbruyères, D., 2010. First insight into the structure and environmental setting of cold-seep communities in the Marmara Sea. *Deep Sea Res. Oceanogr. Res. Pap.* 57, 1120–1136.
- Ritt, B., Pierre, C., Gauthier, O., Wenzhöfer, F., Boetius, A., Sarrazin, J., 2011. Diversity and distribution of cold-seep fauna associated with different geological and environmental settings at mud volcanoes and pockmarks of the Nile Deep-Sea Fan. *Mar. Biol.* 158, 1187–1210.
- Ritt, B., Duperron, S., Lorion, J., Lazar, C.S., Sarrazin, J., 2012. Integrative study of a new cold-seep mussel (Mollusca: Bivalvia) associated with chemosynthetic symbionts in the Marmara Sea. *Deep Sea Res. Oceanogr. Res. Pap.* 67, 121–132.
- Robinson, C.A., Bernard, J.M., Levin, L.A., Mendoza, G.F., Blanks, J.K., 2004. Surficial hydrocarbon seep infauna from the Blake ridge (Atlantic ocean, 2150 m) and the Gulf of Mexico (690–2240 m). *Mar. Ecol.* 25, 313–336.
- Rodrigues, C.F., Oliver, P.G., Cunha, M.R., 2008. Thyasiroidea (Mollusca: Bivalvia) from the mud volcanoes of the Gulf of Cadiz (NE Atlantic). *Zootaxa* 1752, 41–56.
- Rodrigues, C., Cunha, M., Olu, K., Duperron, S., 2012. The smaller vesicomyid bivalves in the genus *Isorropodon* (Bivalvia, Vesicomidae, Pliocardiinae) also harbour chemoautotrophic symbionts. *Symbiosis* 56, 129–137.
- Rovere, M., Gamberi, F., Mercorella, A., Rashed, H., Gallerani, A., Leidi, E., Marani, M., Funari, V., Pini, G.A., 2014. Venting and seepage systems associated with mud volcanoes and mud diapirs in the southern Tyrrhenian Sea. *Mar. Geol.* 347, 153–171.
- Rubin-Blum, M., Antler, G., Turchyn, A.V., Tsadok, R., Goodman-Tchernov, B.N., Shemesh, E., Austin Jr., J.A., Coleman, D.F., Makovsky, Y., Sivan, O., Tchernov, D., 2014a. Hydrocarbon-related microbial processes in the deep sediments of the eastern Mediterranean Levantine basin. *FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol.* 87, 780–796.
- Rubin-Blum, M., Tsadok, R., Shemesh, E., Goodman-Tchernov, B.N., Austin, J.A., Coleman, D.F., Ben-Avraham, Z., Gruber, D.F., Tchernov, D., 2014b. Distribution of the *Lamellibrachia* spp. (Siboglinidae, Annelida) and their trophosome endosymbiont phylotypes in the Mediterranean sea. *Mar. Biol.* 161, 1229–1239.

- Sahling, H., Rickert, D., Lee, R.W., Linke, P., Suess, E., 2002. Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Mar. Ecol. Prog. Ser.* 231, 121–138.
- Salas, C., Woodside, J., 2002. *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the Eastern Mediterranean Sea. *Deep Sea Res. Oceanogr. Res. Pap.* 49, 991–1005.
- Schilman, B., Bar-Matthews, M., Almogi-Labin, A., Luz, B., 2001. Global climate instability reflected by Eastern Mediterranean marine records during the late Holocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 176, 157–176.
- Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Members of the FOBIMO Group, 2012. The FOBIMO (Foraminiferal Blo-MOnitoring) initiative – towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. *Mar. Micropaleontol.* 94–95, 1–13.
- Sen Gupta, B.K., Aharon, P., 1994. Benthic foraminifera of bathyal hydrocarbon vents of the Gulf of Mexico: initial report on communities and stable isotopes. *Geo Mar. Lett.* 14, 88–96.
- Sen Gupta, B.K., Platon, E., Bernhard, J.M., Aharon, P., 1997. Foraminiferal colonization of hydrocarbon-seep bacterial mats and underlying sediment, Gulf of Mexico slope. *J. Foraminif. Res.* 27, 292–300.
- Sibuet, M., Olu, K., 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 45, 517–567.
- Smriglio, C., Mariottini, P., 2002. *Lurifax vitreus* Warén & Bouchet, 2001 first report from western Mediterranean sea. (Gastropoda, Orbitellidae). *Bollettino Malacologico* 38, 45–47.
- Southward, E.C., Andersen, A.C., Hourdez, S., 2011. *Lamellibrachia anaximandri* n. sp., a new vestimentiferan tubeworm (Annelida) from the Mediterranean, with notes on frenulate tubeworms from the same habitat. *Zoosystema* 33, 245–279.
- Spezzaferri, S., Rüggeberg, A., Stalder, C., 2015. Atlas of Benthic Foraminifera from Cold-Water Coral Reefs. Cushman Foundation for Foraminiferal Research.
- Števcic, Z., 1985. New and rarely reported species of decapod Crustacea from the Adriatic Sea. *Rapports Comm. International Mer Méditer.* 29, 313–314.
- Števcic, Z., 1990. Check-list of the adriatic decapod Crustacea. *Acta Adriat.* 31, 183–274.
- Stewart, F.J., Cavanaugh, C.M., 2006. Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia) – model systems for studies of symbiont-host adaptation. *Antonie Leeuwenhoek* 90, 343–360.
- Stott, L.D., Bunn, T., Prokopenko, M., Mahn, C., Gieskes, J., Bernhard, J.M., 2002. Does the oxidation of methane leave an isotopic fingerprint in the geologic record? *Geochem. Geophys. Geosyst.* 3 (2).
- Sturany, R., 1896. Zoologische Ergebnisse VII. Mollusken I (Prosobranchier und Opisthobranchier; Scaphopoden; Lamellibranchier) gesammelt von S.M. Schiff “Pola” 1890–1894. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematische-Naturwissenschaftliche Classe* 63, 1–36.
- Taviani, M., 2014. Marine Chemosynthesis in the Mediterranean Sea. Springer, Dordrecht, pp. 69–83, 2014.
- Taviani, M., Angeletti, L., Ceregato, A., Fogliani, F., Frogliani, C., Trincardi, F., 2013. The Gela Basin pockmark field in the strait of Sicily (Mediterranean Sea): chemosymbiotic faunal and carbonate signatures of postglacial to modern cold seepage. *Biogeosciences* 10, 4653–4671.
- Taylor, J.D., Glover, E.A., 2010. Chemosymbiotic Bivalves. Springer, Dordrecht, pp. 107–135, 2010.
- Taylor, J.D., Glover, E.A., Smith, L., Dyal, P., Williams, S.T., 2011. Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zool. J. Linn. Soc.* 63, 15–49.
- Thessalou-Legaki, M., 1986. Preliminary data on the occurrence of Thalassinidea (Crustacea, Decapoda) in the Greek seas. *Biol. Gallo-Hellenica* 12, 181–187.
- Thessalou-Legaki, M., Zenetos, A., 1985. Autoecological studies on the thalassinidea (Crustacea, Decapoda) of the Patras Gulf and ionian sea (Greece). *Rapports et Procès-Verbaux des Réunions Commission internationale pour l'Exploration scientifique de la Mer Méditerranée* 29, 309–312.
- Thiel, V., Hügl, M., Blümel, M., et al., 2012. Widespread occurrence of two carbon fixation pathways in tubeworm endosymbionts: lessons from hydrothermal vent associated tubeworms from the Mediterranean Sea. *Front. Microbiol.* 3, 423.
- Thomas, D.J., Zachos, J.C., Bralower, T.J., Thomas, E., Bohaty, S., 2002. Warming the fuel for the fire: evidence for the thermal dissociation of methane hydrate during the Paleocene-Eocene thermal maximum. *Geology* 30, 1067–1070.
- Treude, T., Boetius, A., Knittel, K., Wallmann, K., Jørgensen, B.B., 2003. Anaerobic oxidation of methane above gas hydrates at hydrate ridge, NE Pacific ocean. *Mar. Ecol. Prog. Ser.* 264, 1–14.
- Tryon, M.D., Brown, K.M., Torres, M.E., 2002. Fluid and chemical flux in and out of sediments hosting methane hydrate deposits on Hydrate Ridge, OR, II: hydrological processes. *Earth Planet. Sci. Lett.* 201, 541–557.
- Warén, A., Bouchet, P., 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps, new taxa and records. *Veliger* 44, 116–231.
- Warén, A., Bouchet, P., Cosel, von R., 2006. Mollusca, gastropoda, heterobranchia, Orbitellidae. In: Desbruyères, D., Segonzac, M., Bright, M. (Eds.), *Handbook of Deep-Sea Hydrothermal Vent Fauna*, vol 18. Denisia, p. 136.
- Wefer, G., Heinze, P.M., Berger, W.H., 1994. Clues to ancient methane release. *Nature* 369, 282.
- Werne, J.P., Haese, R.R., Zitter, T., Aloisi, G., Bouloubassi, I., Heijfs, S., Fiala-Medioni, A., Pancost, R.D., Sinninghe Damsté, J.S., de Lange, G., Forney, L.J., Gottschal, J.C., Foucher, J.P., Mascle, J., Woodside, J., 2004. Life at cold seeps: a synthesis of biogeochemical and ecological data from Kazan mud volcano, eastern Mediterranean Sea. *Chem. Geol.* 205, 367–390.
- Wollenburg, J.E., Raitzsch, M., Tiedemann, R., 2015. Novel high-pressure culture experiments on deep-sea benthic foraminifera — evidence for methane seepage-related $\delta^{13}\text{C}$ of *Cibicides wuellerstorfi*. *Mar. Micropaleontol.* 117, 47–64.